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STUDIES ON THE BIOLOGY OF SOME SPECIES OF BRITISH CORIXIDAE.

BY

D.T. CRISP.

- being a thesis presented in candidature for the Degree of
Doctor of Philosophy in the University of Durham, 1959.



ABSTRACT.

The life history of the water-bug, Corixa germari (Fieb.) was studied quantitatively in a Derbyshire reservoir and observations on the biology of the species were also made.

The eggs of C.germari are firmly attached to stones and are laid chiefly on the undersides or in crevices. The oviposition rate and egg mortality during 1958 were estimated by direct counts of eggs in the field, the abundance of the adults and nymphs was measured in terms of a Standard Net Sweep and the number of eggs laid per female per season was calculated from these data.

By means of these methods, it was found that in 1958 the breeding adults gave mean catches of 10 per Standard Net Sweep (43% of the adults were females) and that these adults produced 916 eggs. About 530 hatched and, of the nymphs produced, about 80 survived to become adults in the autumn. About 20 of these survived to breed in 1959. Estimates of the density of eggs laid per m^2 of substratum in 1958 show that the catch per Standard Net Sweep represents about 1/38 of the number of C.germari per m^2 of substratum.

By weighing the various stages in the life history it was shown that the standing crop of C.germari gives a biomass value of about 20 g. dry weight per m^2 of substratum in the autumn. This is the highest value reached in the course of the season.

C.germari has been shown to live at greater depths than most other British species and this may be a means of avoiding the

the effects of wave action. Its ability to exploit deep water is coupled with the fact that it visits the surface less often and swims more rapidly than certain shallow water species.

ACKNOWLEDGEMENTS.

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SECTION A.

INTRODUCTION AND GENERAL.

I. INTRODUCTION.

Of our present knowledge of the Corixidae the parts of most direct interest to the ecologist can be grouped under four main headings :-

(i) The building up of systems of county or vice-county records for the British species. A county distribution of Corixidae in England together with lists for the whole of Scotland and the whole of Ireland are given by Bedwell and Masee (1945), Masee (1946) and Masee (1955). Leston (1958) has produced vice-county lists for Ireland. This work provides a picture of the geographical distribution of some of the species, but does not necessarily give much insight into the ecological factors influencing the distribution of the species. It is possible for such lists to be misleading, for, as Macan and Worthington (1951) point out, differences in the intensity of collecting in different parts of the country may distort the picture given by the records. Macan (1954)^a makes the further point that in compiling distribution maps a single specimen of ~~a single specimen of~~ a species from a particular vice-county carries just as much weight as a large number of individuals of some other species. Thus in a well-worked area a species may be regarded as present on the basis of a single stray specimen whilst being regarded as absent from a little-studied area where it is, in fact, quite common if looked for in the right places.

Another difficulty in compiling or interpreting such distribution lists is that, if the records of only a few collectors are used, then the available data are likely to be too scanty to give



an adequate picture of the distribution of the species concerned. The alternative method of using the results of as many collectors as possible gives rise to the danger of including in such lists data based on material that has not been determined by a competent taxonomist (Macan and Worthington 1951).

(ii) Detailed work on particular aspects of the biology of the Corixidae. These studies are usually based on one or more of the commoner lowland species. Examples are the work of Larsen (1938) on reproduction, Sutton (1951-52) on food and feeding and of Popham (1941 - 1958) on a variety of subjects including background selection and dispersion by flight. A background of general information on the distribution and biology of a species is usually necessary before it is possible to see the relevance of any particular biological peculiarities of that species to its life and habitat. Hence it is difficult to see the ecological implications of information on particular aspects of Corixid biology because it is not possible to synthesise the results of a number of different workers on various species in such a way as to obtain a reasonably complete picture of the biology and ecology of any particular species.

(iii) Classification of the types of habitats occupied by each species and study of the association of species. This approach has been used by a number of workers, but most extensively by Macan. His work in this field is largely summarised by Macan (1954^a) where a large number of samples from all parts of

Britain are analysed and the general habitat types occupied by most of the species are described. He has also obtained a measure of the tendency for certain species to be associated together in similar habitats. According to Macan, one of the major factors influencing the distribution of the various species appears to be the proportion of organic matter in the substratum. Complementary to these investigations is the work of Popham (1941, 1943) who showed that each corixid species tends to have a characteristic colour range and that Corixidae tend to select a background matching their own colour shade. He points out that, in general, the colour shade of the substratum is determined by its content of organic material.

Thus, from the work of Macan and Popham, we have a general description of the distribution of the corixid species on an ecological level and a possible mechanism whereby this distribution is maintained. It is, however, necessary to make more detailed study of this subject in order to obtain further information about the rôle of each species in its habitats and the adaptations shown by each species to its own particular type of environment.

(iv) Detailed investigations of the life histories and distributions of individual species. The most thorough study of this type is Griffith (1945) on the American species, Rhamphocorixa acuminata Uhler, although it gives little information about abundance or fluctuations in abundance. Nevertheless it seems likely that surveys of this type will lead to a much clearer understanding of the ecology of particular species of Corixidae than will be given by studies of a more general nature.

To understand the reasons for the distribution and abundance

of corixid species and the importance of each species in the habitats it occupies, quantitative studies of the life histories of individual species under field conditions should be made. These field observations and conclusions should be backed, wherever possible, by laboratory and field experiments. Thus it should be ultimately possible to obtain a quantitative picture of the relationships of each species to its physical and biotic environments. As far as possible, this approach has been followed in the present work, but only for a single species.

The aims of the present study have been twofold. First to obtain information on the distribution and abundance of a single species, Corixa germari (Fieb), within a single water body and to relate this to the conditions in the different parts of the water body. At the same time information has been accumulated about the biology and behaviour of the species. Secondly, to obtain estimates of the abundance of the various stages of C.germari throughout the year in one fairly uniform part of the water body and hence to find the mortality of each stage and, as far as possible, to list the agencies responsible for the mortality. By weighing samples of each stage the abundance data can then be converted into biomasses which give a rough idea of the quantities of energy involved. It is also important to know the nature and quantities of food taken by Corixidae, but this is an extremely time-consuming study and beyond the scope of the present investigation.

A series of corixid samples from Pennine water bodies has been analysed and the ecological distributions of C.germari and the other species collected have been compared and contrasted. Finally,

an attempt has been made to relate certain biological peculiarities of C.germari to the type of environment which it occupies.

II. THE STUDY AREA.

Most of the field work was done at the Barbrook, Little Barbrook and Ramsley reservoirs and at a small peat pool, which are owned by the North East Derbyshire Joint Water Committee and situated about 8 miles (12.8 Km.) South West of Sheffield (Nat. grid referencess 111/278771, 111/276762, 111/286747 and 111/267775 respectively). The catchment area consists of 1,032 acres (413 ha.) of mixed heather moor and Eriophorum bog overlying alternate bands of sandstone and shale. The mean annual rainfall on the area, based on 44 years readings, is 35.6 in. (904 mm). The system of water flow between the reservoirs and the treatment given to the water are shown in Figure 1. Monthly chemical analyses of the water in Barbrook reservoir have been taken from the records of the Water Committee and are shown in Table 1. These analyses show the very low base status of the water and also the very low pH values which reflect the low base status and the presence of sulphuric acid as a result of atmospheric pollution.

THE SYSTEM OF WATER FLOW AND TREATMENT IN
THE STUDY AREA.

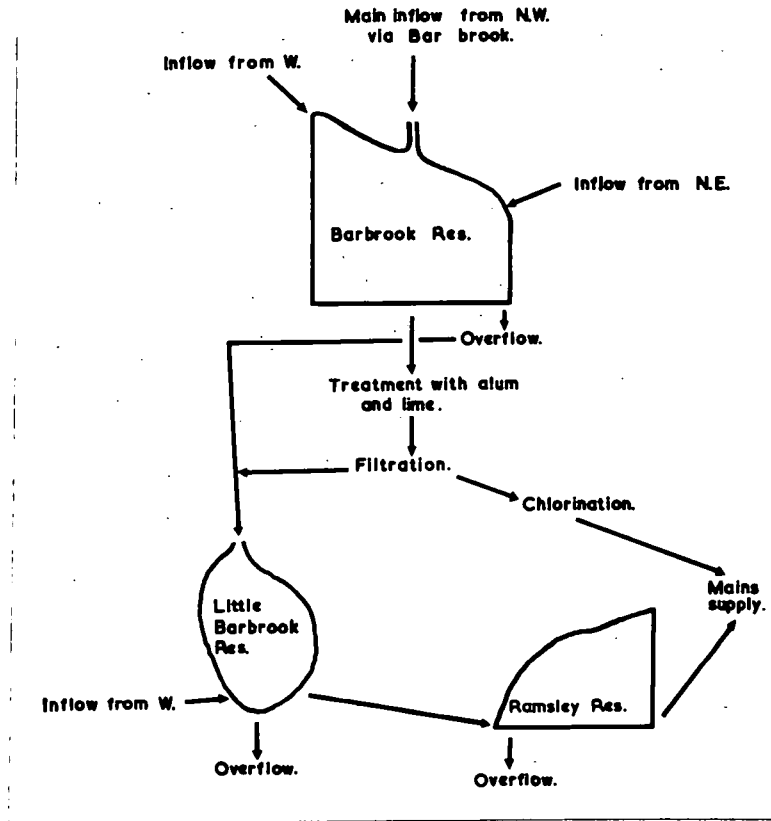


Figure.1.

Date.	pH.	Total solids, dried at 180 deg. C.	Free and saline ammonia.	Albuminoid ammonia.	Nitrogen as nitrite.	Nitrogen as nitrate.	Chloride.	Oxygen absorbed in 4 hours.	Temporary hardness.	Permanent hardness.	Total hardness.	Iron.
2.1.57.	3.85	70	.21	.06	0	0	7	2.1	0	25	25	1.00
30.1.57.	3.90	70	.14	.10	0	0	10	1.8	0	20	20	.74
27.2.57.	3.85	70	.10	.09	0	0	10	1.6	0	25	25	.95
27.3.57.	3.85	75	.09	.09	0	0	11	.9	0	25	25	.92
1.5.57.	3.85	70	.07	.07	0	0	12	.4	0	25	25	.92
5.6.57.	4.10	85	.14	.06	0	0	11	.2	0	20	20	.89
3.7.57.	3.80	73	.42	.07	0	0	12	.4	0	25	25	.87
31.7.57.	3.85	70	.75	.05	0	0	12	.2	0	25	25	.96
28.8.57.	3.85	65	.31	.16	0	0	11	1.3	0	30	30	1.39
25.9.57.	3.80	65	.22	.10	0	0	11	1.3	0	25	25	1.15
20.11.57.	3.75	75	.02	.11	0	0	10	1.5	0	25	25	.78

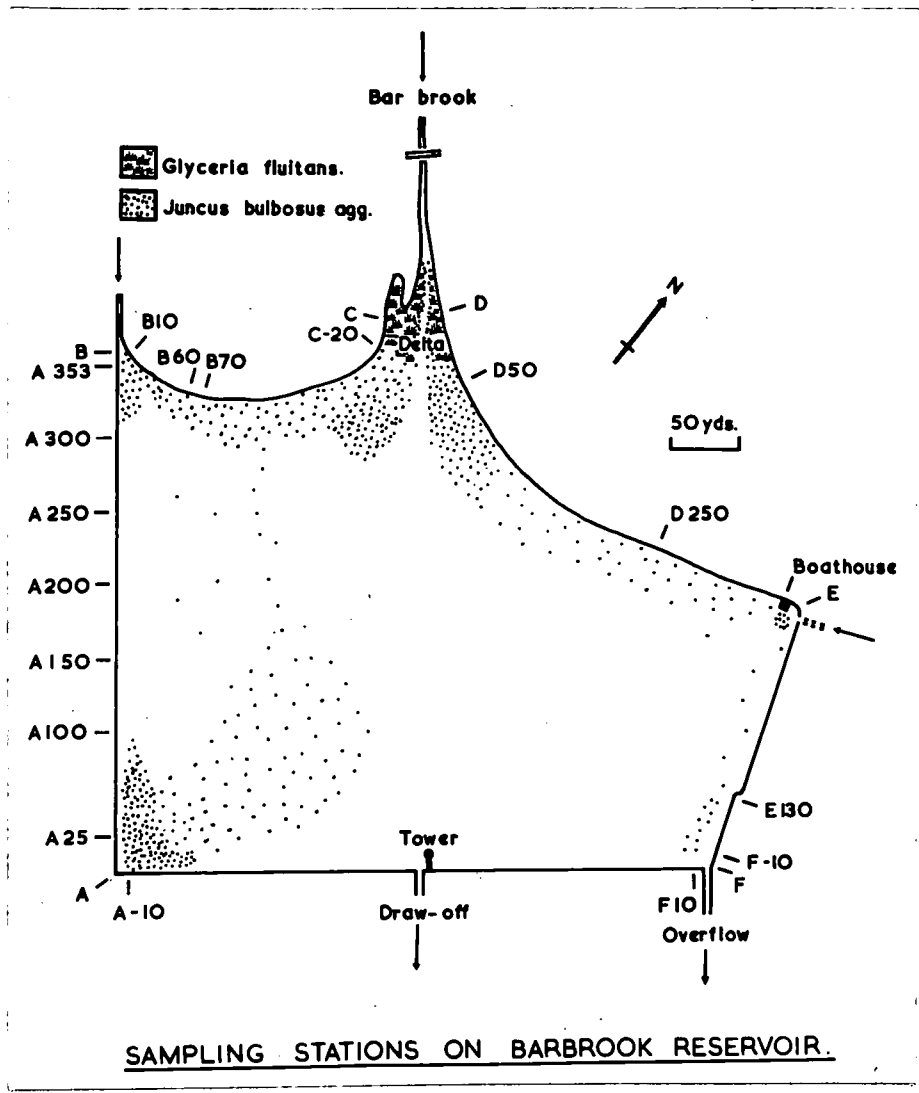
TABLE.1. Chemical analyses of water samples from Barbrook reservoir, showing concentrations in parts per million.

III. BARBROOK RESERVOIR - GENERAL DESCRIPTION, CLIMATE, SAMPLING STATIONS, AND SEASONAL CHANGES IN VEGETATION.

Barbrook reservoir has an area of 32 acres (12.9 ha) and a maximum depth of 27 ft. (8.2 m.). The top water level is 1,072 ft. (326.8 m.) above sea level and water is drawn off at the 1,065 ft. (324.6 m.), 1,058 ft. (322.6 m.) and 1,051 ft. (320.3 m.) levels. The reservoir is in a very exposed position and its shores are subject to considerable wave action on windy days.

Where they do not correspond to a definite landmark on the reservoir margin the sampling stations are each defined in terms of their distance, measured in a clockwise direction round the reservoir margin, from one of six fixed points A, B, C, D, E and F. Thus any point on the reservoir margin can be defined by quoting a prefix letter denoting an adjacent fixed point and a number showing its distance, in yards, from that fixed point. Where the number is positive the distance is measured in a clockwise direction round the reservoir edge and where the number is negative the measurement is made in an anti-clockwise direction. The fixed points and the regular sampling stations are shown on Figure 2.

The aquatic macroflora consists of two species, Glyceria fluitans (L) and Juncus bulbosus L. aggregate. The distribution of these two plants is shown in Figure 2 and the density of the symbols representing each species gives a rough idea of the relative densities of the two species in different parts of the reservoir.



SAMPLING STATIONS ON BARBROOK RESERVOIR.

Figure 2.

On each visit to Barbrook reservoir during 1958 and on a few occasions during 1957 the temperature of the water was measured at station A200 with a mercury thermometer held just below the water surface. The results are shown in Figure 3. Occasional measurements of the temperature of water samples from 1.0 and 2.0 depths showed that the water temperature at those depths was the same as that at the surface, except when the water temperature was only a few degrees above freezing point. At such times the temperatures at 1.0 m. (3 ft.) to 2.0 m. (6 ft.) depths were a little higher than the surface temperature.

Daily records of the water level in the reservoir are kept by the North East Derbyshire Joint Water Committee and the water level data used in this work have been abstracted from these records. Figure 4 A shows the mean water levels for seven-day periods during 1957 expressed in terms of the distance of the water level above (positive values) and below (negative values) the "top water level". Similar data for 1958 are shown in Figure 4 B. For comparison, the mean values for the ten years 1949 to 1958 are shown in Figure 4 C. The latter data show that the general tendency is for the water level to be close to top water level during the first six months of the year and then to fall about 1.0 m. by September or October after which it begins to rise again.

It must be noted that these conclusions are based on mean values and that, in fact, there is considerable variation in water level patterns between years. It is nevertheless true to say that the extremely low levels recorded between May and mid-September 1957 were exceptional and that the absence of any marked fall-off

WATER TEMPERATURES IN BARBROOK RESERVOIR.

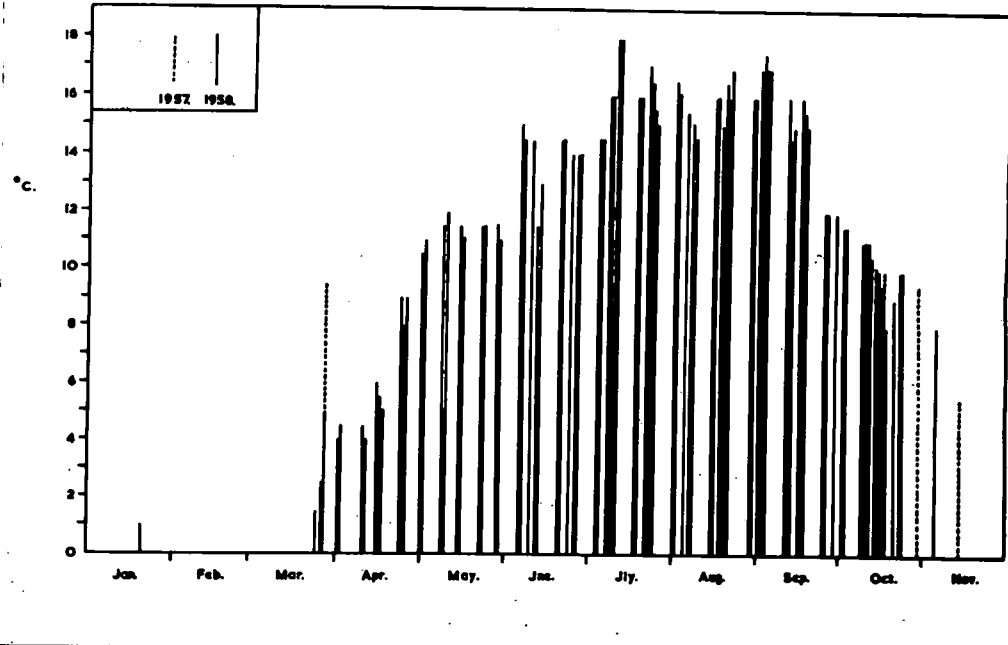


Figure.3.

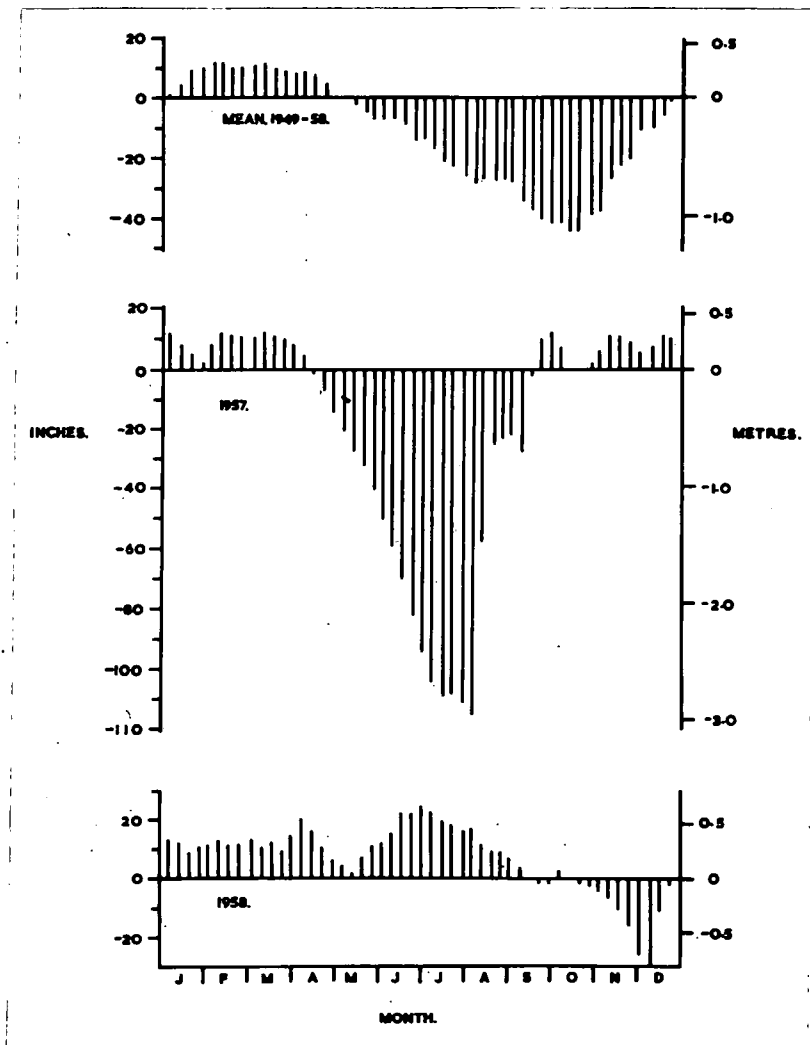


Figure.4. Water levels in Barbhook reservoir.

Top water level is taken as zero.

in level during the summer and early autumn of 1958 was rather unusual.

During 1958 the wind direction was noted each time the reservoir was visited and the wind speed was estimated by reference to the Beaufort wind scale. The results are shown in Table 2. These data are particularly important because the wind can cause considerable wave action on Barbrook reservoir and this, as will be seen later, has marked effects on the Corixidae. Photographs 1 and 2 show the wave action on shore section A100 to A200 on 22. 5. 59 when the wind was blowing from the N.E. at about 20 m.p.h. (32 Km.p.h.) and photograph 3 shows similar conditions in April 1958. On some occasions waves of up to 0.5 m. (1.5 ft.) in height from trough to crest have been observed on Barbrook reservoir.

The mode of construction of the walls at various points on the reservoir margin is shown in Figure 5. The values at each station of the dimensions shown as "a" and "b" in Figure 5 are given in Table 3, together with the distances from the water's edge at which the water depth reaches 1.0 m. (3 ft.), 2.0 m. (6 ft.) and 3.0 m. (9 ft.) (or in some cases 0.5 m. and 0.75 m.) at each station. The nature of the substratum at the various stations is illustrated in a series of photographs taken on 5.5.57 and 12.6.57 when the water level was 17.5 in. (44 cm.) and 62.5 in. (150 cm) respectively, below top water level, thus exposing those parts of the substratum from which samples were normally taken. Other photographs, taken at times when the water level was near to top water level show some of the stations as they are more usually seen.

Date.	Direction.	Speed. (m.p.h.)	Date.	Direction.	Speed. (m.p.h.)
20.1.58	WNW	2	22.5.58	SSW	2-5
5.3.58	WSW	21-35	23.5.58	SSW	2-10
25.3.58	NW	?	X 28.5.58	SE-NW	0-10
27.3.58	NNW	?	29.5.58	S	2-5
28.3.58	S	10	X 5.6.58	S-SE	2-5
X 1.4.58	E	15-20	X 6.6.58	E	5-15
X 2.4.58	SE	5-10	9.6.58	NW	0-2
X 10.4.58	NE	15-27	X 11.6.58	E	2-5
X 11.4.58	NE	15-27	12.6.58	NW	0-2
15.4.58	WNW	10-27	19.6.58	SSW	5-10
16.4.58	WNW	10-21	X 20.6.58	N	2-10
17.4.58	WSW	5-10	X 23.6.58	W-NW	0-5
23.4.58	S	5-10	X 25.6.58	S-SE	2-10
24.4.58	SSW	5-10	26.6.58	S	2-5
25.4.58	SW	10-21	X 3.7.58	NE	2-5
30.4.58	WNW	0-2	X 4.7.58	N	2
1.5.58	SW	0-2	8.7.58	S-NW	0-2
8.5.58	SW	10-21	9.7.58	SW	2-5
9.5.58	SW	2-15	10.7.58	W	2-5
14.5.58	SW	2-10	17.7.58	W	2-10
15.5.58	S	0-2	18.7.58	SW	2-5

TABLE.2. (Part.1.).

Date.	Direction.	Speed. (m.p.h.)	Date.	Direction.	Speed. (m.p.h.)
22.7.58	SW	2-5	X 13.9.58	SE	0-5
24.7.58	W	2-5	X 16.9.58	NE	5-10
31.7.58	W	2-10	17.9.58	S	5-10
1.8.58	W	5-15	18.9.58	S	2-5
4.8.58	W	10-21	25.9.58	WNW	27
6.8.58	W	5-10	26.9.58	WNW	0-2
7.8.58	WSW	2-5	29.9.58	SSW	10-21
14.8.58	WNW	5-10	X 1.10.58	S-SE	5-15
15.8.58	SW	5-15	2.10.58	SW	5-10
18.8.58	NE	5-15	8.10.58	SW	10-15
19.8.58	SW	2-5	9.10.58	WSW	10
20.8.58	SW	0-2	10.10.58	SW	10-15
21.8.58	SW	0-2	11.10.58	SW	5-10
28.8.58	S	0-2	13.10.58	W	15-21
29.8.58	S	2-5	14.10.58	W	15-21
X 1.9.58	SE	2-10	X 15.10.58	WNW	27-35
X 2.9.58	E	0-5	X 16.10.58	WNW	27-35
X 3.9.58	E	5-10	X 17.10.58	NW	27-35
X 4.9.58	ENE	2-10	20.10.58	WNW	15-21
X 11.9.58	NE	2-5	23.10.58	SW	0-5
12.9.58	SE	0-2	4.11.58	-	0

TABLE.2. Wind speed and direction at Barbrook reservoir during 1958.

X denotes dates on which appreciable wave action was observed on section A100 to A300.



Photograph.1. Wave action at section A100 to A300
of Barbrook reservoir, 22.5.59.



Photograph.2. Wave action at section A100
to A300, 22.5.59.



Photograph.3. Wave action at A200,24.3.58.

Shore profiles for Barbrook Reservoir.

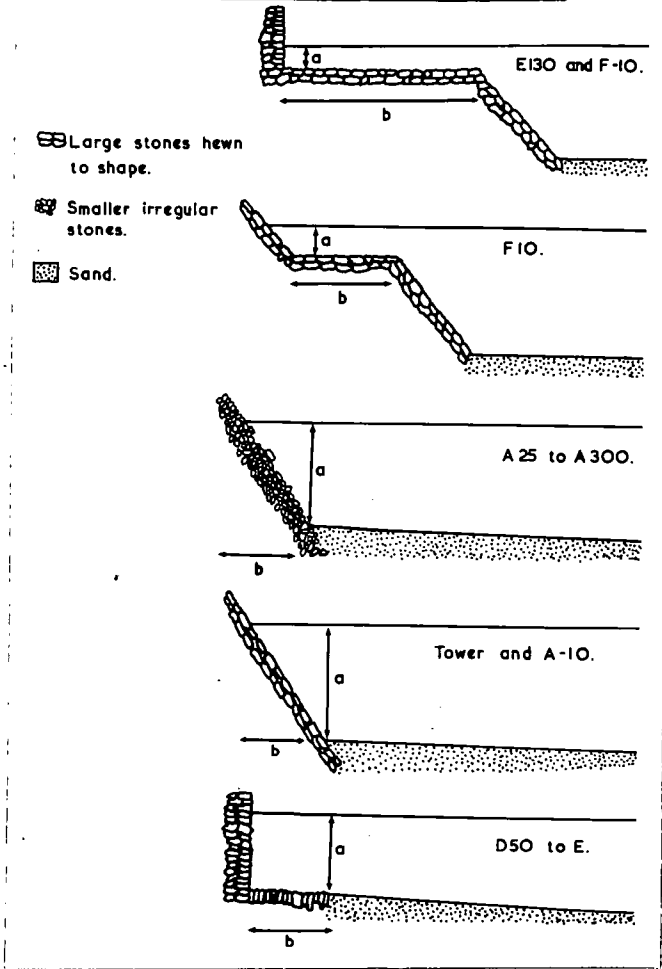


Figure.5.

Station.	"a" (metres)	"b" (metres)	0.5m.	0.75m.	1.0m.	2.0m.	3.0m.
E150	.25	3.85			5.4	6.9	17.0
F-10	.20	7.25			9.3	12.7	21.5
F10	.15	1.80			3.8	6.8	23.6
Tower	3.20	10.70			3.3	6.7	10.0
A-10	.70	2.35	3.4	14.7	24+		
A25	.30	1.70	1.8	2.7	24+		
A100	1.80	5.00			3.1	15.1	24.0
A150	2.50	6.50			2.8	4.9	12.7
A200	2.60	6.70			2.5	4.8	6.5
A250	2.80	6.30			2.4	4.1	5.3
A300	1.70	5.00			2.6	7.6	10.0
A350	0	0			24+		
B60			9.7	15.2			
B70			4.3	9.4			
C-20			6.7	12.1			
Delta			5.8	14.6			

TABLE.3. Values of dimensions "a" and "b" for Figure.4. and distances from the water's edge of the 0.5m., 0.75m., 1.0m., 2.0m., and 3.0m., depth contours in Barbrook reservoir. Measurements made on August 18th. and 19th. 1958 when the water was 0.2m. above top water level.

The shoreline of the reservoir can be conveniently divided into five fairly uniform sections, each of which contains one or more regular sampling stations. Each of these sections is described below and at the same time any marked differences between individual stations within the same section are indicated.

(i) E 130 to A - 10

The shore profiles for this region of the reservoir are represented on Figure 5 and Photographs 4, 5 and 6 illustrate the construction of the walls from large blocks of sandstone hewn to a cuboidal shape. Below the stone wall there is a gently sloping bottom of sand with occasional tufts of J. bulbosus agg. in the region between E 130 and F and a dense growth of the same species at A -10.

(ii) A 100 to A 300

These stations are situated on a bank of irregular loose stones which slopes steeply down into water of 2.0 to 3.0 m. (6 to 9 ft.) depth (Photographs 7 and 8), below which there is a gently sloping sandy bottom. All these stations are sheltered from the prevailing south and west winds by an embankment of clay, stone and peat which extends two or three metres above the top water level.

(iii) B 10 to C -20

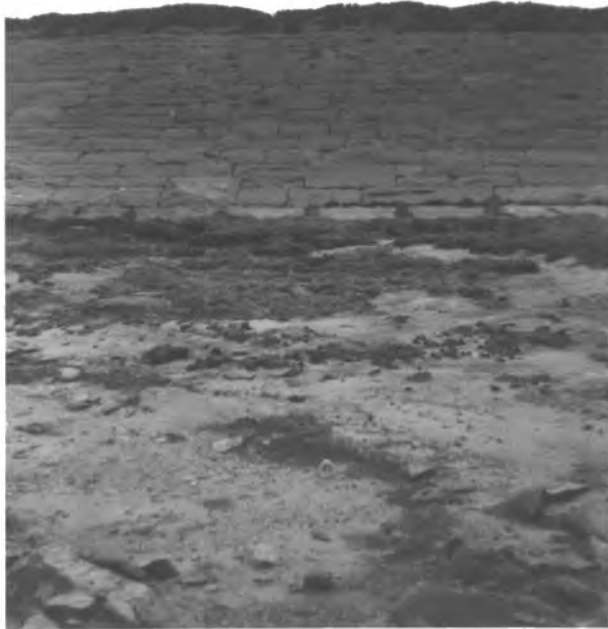
Stations on a gently sloping sandy shore with a few stones and a relatively thick growth of J. bulbosus agg. amongst which peaty debris accumulates to a depth of about 1 cm. (.25 in.) in some places (Photograph 9). When the water is up to top water level the water's edge is fringed by tussocks of Juncus effusus.L.



Photograph.4. View from F-10 towards E130,2.5.57.



Photograph.5. Tower on 12.6.57. Top water level is just below the flange on the base of the tower. Distance from flange to water level shown is about 5 ft. (1.5 m.).



Photograph.6. Station A-10,2.5.57.Note stone
bank and sandy bottom with darker
patches of J.bulbosus sgg.



Photograph.7. Stony bank on section A100 to A300,12.6.57.



Photograph.8. Stony bank and bottom of sand at A350,2.5.57.



Photograph.9. Station B70 on 2.5.57. Note sandy shore with darker patches of J.bulbosus agg.The water level normally reaches to the Juncus effusus in the background.

which can be seen in the background of photograph 9.

(iv) "Delta".

This station comprises the region at which Bar brook enters the reservoir. It is an area of still water up to 1.0 m. (3 ft.) deep with a dense growth of Glyceria fluitans fringed by J. effusus (Photograph 10). Mud and plant fragments cover the bottom to a depth of up to 20 cm. (8 in.).

(v) D 50 to E.

The shore profile of these stations is shown in Figure 5. There is a vertical wall of stones built in the manner of a dry stone wall and at the base of this there is a horizontal flange of similar construction. Beyond this flange there is a gently ~~sloping~~ sandy bottom with occasional stones and a sparse growth of J. bulbosus agg. (Photographs 11 and 12).

The Glyceria at station "Delta" forms a fairly dense stand of vegetation throughout the year but is particularly dense during the summer months and tends to die back during the winter. When growing below the water, the J. bulbosus agg. forms slender pale-green leaves up to 0.5 m. (1.5 ft.) long and is thinned out each autumn and winter when severe wave action causes some of the leaves and, in some cases, whole portions of the rootstock of the plant to be torn up and washed ashore. If at any time the J. bulbosus agg. is exposed above the water level, as during the drought of 1957, the long thin leaves die back and are replaced by shorter, stouter leaves of a darker colour. The plant may then flower. When resubmerged the short leaves are replaced by long



Photograph.10. Glyceria bed at Delta on 22.5.59.

The net pole is at the water's edge
and is 5*5 ft. long.



Photograph.11. Station E on 12.6.57. Note sandy
bottom and horizontal flange at
base of wall.



Photograph.12. Station E10 on 2.5.57. Note sandy bottom
with some stones.

pale ones. During the May to October period the filamentous green alga Microspora sp. forms loose mats amongst the vegetation at "Delta" and B to C -20 and/a ^{to} lesser extent amongst the stones at stations A 25 to A 350.

IV LITTLE BARBROOK RESERVOIR

Little Barbrook reservoir occupies about 3 acres (1.2 ha.) and has a maximum depth of about 12 ft. (4.0 m.). The reservoir is bounded on three sides by steeply sloping stone walls but these are mainly covered by from 1 to 5 cm. (.25 to 2.0 in.) of mud and the bottom is of mud with occasional patches of sand. Most of the margin is covered by a dense growth of G.fluitans with occasional patches of J.bulbosus agg.

V. RAMSLEY RESERVOIR.

The Ramsley reservoir has an area of 9 acres (3.6 ha). It is bounded on all sides by stone walls sloping steeply down into 1.0 (3 ft.) to 1.5 m. (4.5 ft.) of water. The bottom is of sand with no noticeable accumulation of mud. The only plant fragments present are the leaves which fall into the water from a few Salix atrocinerea Brot. bushes which grow near the reservoir margin. At the north east corner of the reservoir there is a drainage channel about 3 m. (9 ft.) wide and up to 0.75 m. (2 ft.) deep through which a little water drains into the reservoir from the surrounding moorland. In this channel there is an accumulation of mud, peat and plant debris and a dense growth of Potamogeton natans.L., G.fluitans, and Callitriche L. sp.

VI. THE DUCKPOOL ON BIG MOOR.

The Duckpool is a typical peat pool, about 15 m. in diameter and up to ~~0.75~~¹m. (2 ft.) deep. It is situated on an Eriophorum bog about ¹/₂ mile (0.8 Km.) north west of Barbrook reservoir. The pool is surrounded by a fringe of J.effusus (Photograph 13). The bottom is of peat littered with dead J.effusus fragments, and the water is heavily peat stained.



Photograph.13. The duckpool on Big Moor. The pole of the net (extreme left) is 5*5 ft. long.

VII. SAMPLING METHODS.

(1) Selection of a suitable sampling locality.

The choice of a suitable water body from which to take samples is of critical importance in a study of this type. A number of criteria must be considered in making the selection. These are outlined below and they are also applied to Barbrook reservoir, which, in the present work, was considered to be a suitable sampling locality for a quantitative survey of the life history of Corixa germari (Fieb.)

(a) The water body should be sufficiently large for a suitable number of samples to be taken from it at regular intervals without serious depletion of the animals as a result of sampling. At the same time it should not be so large that difficulty is experienced in sampling all the sampling stations within a single day. Barbrook reservoir was found to fulfil these requirements.

(b) The water body studied should be readily divisible into a few apparently uniform sampling sections so that it will be statistically valid to combine sample data from within each section. As seen in the description of the sampling stations, the shoreline of Barbrook reservoir can be divided into four long and comparatively uniform sections (E 130 to A -10, A 100 to A 300, B 10 to C -20 and D 50 to E) together with a few small miscellaneous regions exemplified by stations Delta, B -1 and A 25.

(c) Corixidae should be abundant in the sampling locality, so that a relatively large catch per sample unit can be obtained for a relatively small expenditure of time and effort. Preliminary

netting at Barbrook reservoir during the summer and early autumn of 1954 showed that corixids were abundant in the reservoir and were very abundant on section A 100 to A 300.

(d) The eggs and nymphs of the Corixidae are not readily identifiable. It is therefore desirable that the samples of adults should consist almost entirely of a single species, so that only a small inaccuracy is involved in assuming that all the nymphs and eggs taken belong to that species. About 95% of the adult Corixidae taken by random netting in all parts of Barbrook reservoir during 1954 were C.germari and this suggested that it would be reasonable to assume that almost all the eggs and nymphs collected from the reservoir would belong to this species.

(e) Seasonal changes in the density of submerged vegetation can be considerable in some water bodies and such changes may cause variation in the efficiency of the net sampling as a result ~~in the~~ ^{of} changes in the ease with which the net can be moved through the vegetation and variation in the amount of net clogging caused by pieces of plant material. This effect is minimised on sections A 100 to A 300, E 130 to A -10 and D50 to E of Barbrook reservoir because of the negligible quantities of vegetation found there.

(f) The water body studied should have as stable a water level as possible and should suffer a minimum of human interference, so that the interpretation of the data obtained will not be unnecessarily complicated by large but short-term disturbances

of the environment. Barbrook reservoir is situated on private land and is therefore fairly safe from interference by the general public. The water is not treated in any way until after it has left the reservoir, so that the chemical composition of the water does not suffer any unnatural variation. In general the water level does not rise more than about 0.7 m (2 ft.) above top water level and it rarely falls more than about 2.0 m (6 ft.) below that level.

Thus it can be seen that Barbrook reservoir meets most of the conditions required for efficient and meaningful sampling. It has the added advantages of having a relatively simple fauna and flora and of having as its commonest corixid species C.germari, a species about whose life-history and ecology very little is known.

(2) Net Sampling.

Two main methods of measuring the abundance of corixids with a net have been used by previous workers. Popham (1949) mentions the method used by E.S. Brown in which the number of individuals taken after 30 minutes' collecting is recorded. The value of any method of estimating corixid abundance, however, depends on its usefulness in the comparison of abundance between different water bodies, between different parts of the same water body or at the same place on different dates. It is therefore essential that the results obtained shall be amenable to statistical analysis. In order to use Brown's catch/time method in this way it is essential that an adequate number of samples be taken and this means that the time interval used as a sampling unit must be fairly short. This gives rise to difficulties in accurate

measurement of the time interval used. In addition, this method does not allow for changes in the working efficiency of the biologist as a result of various climatic effects. Thus, though this method may be adequate for the purpose for which it has so far been used (i.e. rough comparisons of the relative abundances of a number of species between fairly large numbers of water bodies), it is not suitable for work of a more exact nature.

Popham (1943a) estimated the abundance of Corixidae in different depths of water by making 20 standard net sweeps at each depth and counting the total number of individuals at each depth. This technique, because it measures the abundance in terms of the "catch per unit of work done" rather than the "catch per unit of time taken", cuts down the error due to variation in working efficiency of the biologist. Also, if the catches from the single net sweeps are counted separately, the data can be treated statistically. This method has therefore been used in the present work.

In defining the Standard Net Sweep used, reference must be made to Figure 6 which represents a vertical section through the water in a plane parallel to the water's edge. An ordinary hand pond net was used. The net entered the water at A with its mouth pointing towards D. It was lowered gently until it just touched the bottom at B. From this position the actual net sweep began and the net traced the path B, C, D, B, A, C, D, B, A with the net mouth facing towards the direction of travel. On reaching A for the last time, the net was lifted from the water. As far as possible, the speed at which the net travelled was kept constant for all the

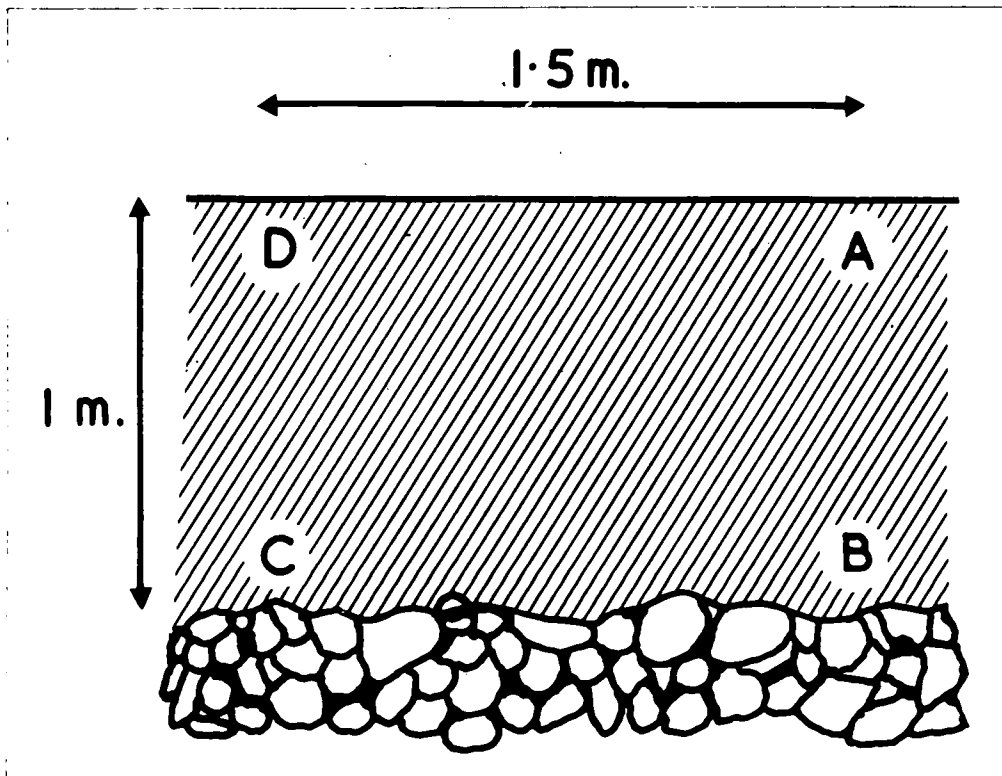


Figure.6.7

Standard Net Sweeps. Unless it is otherwise stated, all subsequent references to a Standard Net Sweep (or S.N.S.) in this work will refer to a standard net sweep as just defined.

For sampling the adults a circular-mouthed net with a mouth of 14 in. (35.5 cm.) diameter and nylon netting with 15 meshes per in. (6 meshes per cm.) on a pole 5.5 ft. (1.8 m.) long was found the most satisfactory and the S.N.S. made with such a net has been used as a standard unit in which to express the results obtained by sampling with other types of net and by direct counting of the eggs. Thus the relative abundance of all stages in the life history can be compared.

In order to select a suitable mesh size for sampling the nymphs of C.germari it was necessary to obtain some idea of the ability of each nymphal instar to escape through netting of different mesh sizes. The need for this is clearly illustrated by Macan's (1958) comparison of the catches of Ephemeroptera nymphs in fine and coarse meshed nets, which will be referred to below. Three types of netting were therefore used in a laboratory experiment and, for convenience, these have been referred to as "coarse mesh", "trap mesh" and "fine mesh". The holes in the trap mesh and the coarse mesh netting were roughly elliptical and the largest and smallest dimensions of each of thirty such holes were measured for each of these two types of netting. The fine mesh netting was woven nylon bolting cloth, the holes in it were rectangular, and the longest and shortest sides of thirty of these holes were measured. All the measurements were made under a microscope with a micrometer eyepiece and for each type of netting the mean values for thirty holes, together with their confidence

limits are shown in Table 4. The relative abilities of each of the five nymphal instars to escape through each of the three types of netting were then measured under standard conditions in the laboratory. For each combination of an instar and a mesh size twenty individuals of the appropriate instar were placed in each of five 2x1 inch glass specimen tubes. A piece of the relevant netting was then tied across the mouth of each tube and the tubes were then laid on their sides in jars full of water at 17°C. Care was taken to ensure that no air bubbles were present in the tubes or on the netting. The number of escapes from each tube was counted each hour throughout ~~the~~ a four hour period and a summary of the results is given in Table 5. The same results are shown in Figure 7, where the total number of escapes out of the initial 100 animals used in each combination of instar and mesh size are plotted against time. These experimental conditions are clearly very different from those experienced by nymphs caught in a net in the field. Nevertheless the following conclusions can be drawn :-

(i) Macfadyen (1957) draws attention to the fact that some freshwater nymphs and larvae can escape from smaller net meshes than might be expected and Macan (1958) showed the enormous discrepancy between catches of Ephemeroptera nymphs in fine and coarse nets that can be caused by escape of the smaller-sized nymphs from coarse meshed nets. Working on chironomid larvae, Jonasson (1955) showed that, though the width of the thoracic segments may exceed the width of the head capsule of these animals, it is the width of the head capsule which decides whether or not the larva can escape through mesh of a particular size.

Netting type.	Meshes/cm.	Mean maximum and minimum dimensions in mm. of 30 holes \pm 5% confidence limits of the mean.	
		Maximum.	Minimum.
Coarse mesh.	6	1.8 \pm .02	1.3 \pm .02
Trap mesh.	7	1.2 \pm .08	1.0 \pm .07
Fine mesh.	24	0.34 \pm .008	0.26 \pm .007

Table 4. Measurements of three types of net material.

Instar.	Hours from start of experiment.	Cumulative totals of escapes out of the initial 100 specimens.	
		Trap mesh.	Coarse mesh
1	1	12	84
	2	17	92
	3	24	93
	4	26	95
2	1		81
	2		90
	3		92
	4		93
3	1		24
	2		33
	3		43
	4		51

Table 5. Rate of escape of the different nymphal instars of C.germari through netting of different mesh sizes. Only those combinations of netting and instar for which escapes were recorded are shown.

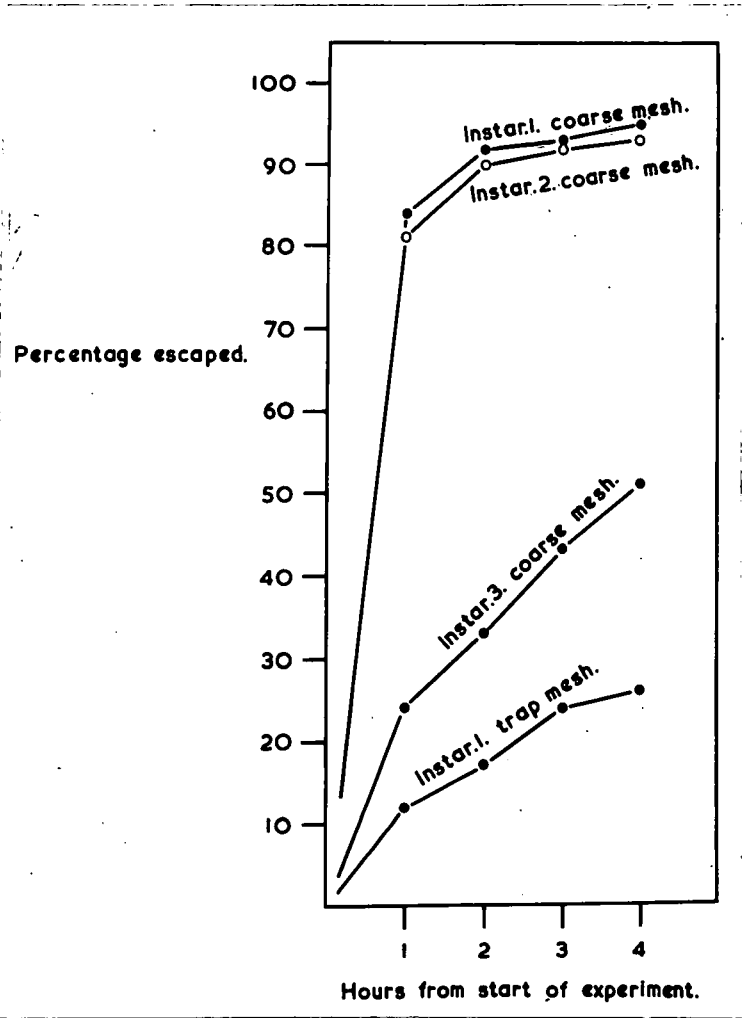


Figure.7. Cumulative totals of escapes out of the initial 100 specimens for each combination of instar and mesh size.

The largest transverse dimension of C.germari nymphs is the width of the widest part of the abdomen. This dimension has been measured in 32 individuals of each nymphal instar and the results are shown in Table 6 together with the mean maximum dimension of the holes in the smallest meshed netting that each instar has been shown to escape through. The data show that under the conditions of the experiment the nymphs of C.germari do not escape through holes narrower than their own width.

(ii) The fine mesh netting will retain all instars.

(iii) The trap mesh netting will retain all nymphal instars of C.germari except instar 1, and even this stage appears to find escape difficult.

(iv) The coarse mesh netting will retain instars 4 and 5, but instars 1 and 2 pass through it quite readily. Instar 3 is capable of escaping through the coarse mesh but, under the conditions of the experiment, it does so much more slowly than instars 1 and 2. It is possible that instar 3 might perform better under more natural conditions, but it must also be remembered that during the course of a single S.N.S. the insects are only in the net for a few seconds, whereas in the laboratory experiment the time was measured in hours. Nevertheless, field evidence is needed to show whether or not the escape of instar 3 through the coarse net is an important factor to consider in selecting a suitable net for sampling this stage. On several occasions during the summer of 1958 20 S.N.S.s with a coarse net and 20 with a fine net were made along the shore section A 100 to A 300. The proportion of instar 3 nymphs in each of the two sets of samples was then found by expressing ^{the number of instar 3 nymphs as a percentage of} the total

Instar	Width of abdomen at its widest point. Mean of 32 measurements in mm. \pm 5% confidence limits.	Largest dimension of net holes through which escape occurred. Mean of 30 measurements \pm 5% confidence limits.
1	1.2 \pm .01	1.2 \pm .08
2	1.4 \pm .02	1.8 \pm .02
3	1.7 \pm .08	1.8 \pm .02
4	2.2 \pm .04	>1.8 \pm .02
5	2.4 \pm .04	>1.8 \pm .02

Table 6.

catch of instars 3, 4 and 5 in the same set of samples. The proportions of instars 4 and instar 5 were calculated in the same way. The results are shown in Table 7 and it can be seen that the different instars are caught in roughly the same proportions in both nets. Thus the escape of instar 3 nymphs through the coarse net is negligible and a coarse meshed net can therefore be used to estimate the abundance of this stage.

The adults were sampled with the coarse meshed net described on page 20. During the period April to November 1957 fortnightly samples were taken from Barbrook reservoir. ~~On each sampling date~~ On each sampling date 3 S.N.Ss. were made at each station (apart from stations A -10 and B -1, at each of which 2 S.N.Ss. were made) the three S.N.Ss. at each station being made at points about 4 m. (12 ft.) apart. During the 1958 season the same procedure was repeated, except that on section A 100 to A 300 4 S.N.Ss. were made at each station and sampling was carried out at weekly intervals. At Ramsley and Little Barbrook reservoirs and at the Duckpool, random net sweeping was carried out round the whole margin of each water body at fortnightly intervals during 1957 so that the data obtained do not give any indication of the abundance of the Corixidae in these places. During 1958, monthly sampling was carried out at each of these water bodies and at Ramsley and Little Barbrook reservoirs 20 S.N.Ss. were made at definite points evenly spaced around the margin of each reservoir. Two additional sweeps were made at Ramsley, on each occasion, in the drainage channel at the north-east corner of the reservoir.

Date.	Instar 3 as % of total catch.		Instar 4 as % of total catch.		Instar 5 as % of total catch.		Total catch of all three instars.	
	Fine.	Coarse.	Fine.	Coarse.	Fine.	Coarse.	Fine.	Coarse.
26.6.58.	100	100					6	4
4.7.58.	100	100					971	2126
10.7.58.	96±1.8	97±1.3	4±1.8	3±1.3			473	728
18.7.58.	74±2.6	70±2.2	26±2.6	30±2.2			1109	1756
24.7.58.	76±2.7	75±2.2	24±2.7	25±2.2			974	1550
1.8.58.	58±3.4	54±1.8	32±1.5	36±1.7	10±1.6	10±1.1	1436	3029
7.8.58.	61±2.1	53±1.6	26±2.0	31±1.5	13±1.5	16±1.2	2066	3679
15.8.58.	43±2.1	49±2.2	34±2.0	34±2.1	23±1.8	16±1.6	2307	2116
21.8.58.	22±2.6	20±1.7	37±3.0	39±2.1	40±3.1	41±2.1	1014	2220
29.8.58.	17±2.6	14±1.7	38±3.4	38±2.4	45±3.5	49±2.4	825	1694
12.9.58.	15±3.0	10±1.5	21±3.4	23±2.1	64±4.0	67±2.4	569	1690
18.9.58.	7±2.3	4±1.4	18±3.5	14±2.5	74±4.0	63±3.4	463	791

TABLE.7. Comparison of the proportions of instars 3,4 and 5 in coarse and fine net samples. The results are expressed as the percentage of the total catch of all three instars formed by each instar and the five percent confidence limits are shown in each case.

The abundance of the nymphs on section A 100 to A 300 of Barbrook reservoir was estimated on the same dates as the samples of adults were taken. All specimens of instars 3, 4 and 5 taken in the coarse net were counted. In addition, a net which had 60 meshes per in. ($2\frac{4}{cm.}$) and a mouth of 8 in. (20 cm.) diameter was used during the period when instars 1 and 2 were present. About an hour after the coarse net sampling, 4 S.N.Ss. of the fine net were made at each station and all the nymphs caught were counted. Ideally it would be expected that, if the two nets had differed only in mouth diameter, the total coarse net catch (=C) of instars 3, 4 and 5 and the total fine net catch (=F) of those stages would be in the same ratio as the areas of the mouth apertures of the two nets. The mouth apertures of the coarse and fine nets respectively are in the ratio 3:1 so that the relationship between the total catches on each sampling occasion should be :- $C = 3 F$.

But, in fact, the smaller net also has a smaller mesh size than the larger one and might therefore be expected to cause a proportionately greater amount of water resistance than the larger one, hence giving:-

$$C > 3F$$

In practice, however, as Table 8 shows, the relationship between the catches is :-

$$C = 2 F$$

This suggests that some other factor must be considered and it seems likely that this factor is the relative abilities of the two nets to stir up the water, so raising animals from amongst the stones on the bottom and bringing them into such a position that they can be caught in the net. Thus the fine net, with its finer mesh size and therefore

Date	Coarse net catch/Fine net catch
4.7.58	2.2
10.7.58	1.5
18.7.58	1.6
24.7.58	1.6
1.8.58	2.1
7.8.58	1.8
15.8.58	0.9
21.8.58	2.2
29.8.58	2.0
12.9.58	2.0
18.9.58	3.3

Table 8. Total coarse net catches of instars 3, 4 and 5 from
20 S.N.Ss. /total fine net catches of the same stages
from 20 S.N.Ss.

proportionately greater water resistance, may catch proportionately less of the animals in its path than does the coarse net, but this may be more than compensated for by ^{its} bringing proportionately more animals into its path than the coarse one does.

Having obtained the nymph sample data with the two types of net it is then necessary to convert them into a form which makes them comparable with the data obtained by sampling the adults with the coarse net. This has been done in two ways :-

(i) By comparing the total catches of nymphs 3, 4 and 5 in each of the two nets on those dates when samples were taken with both nets. It is assumed that there is a linear relationship between the catches of the two nets ($r = .946$ and $P < .001$) and the line of best fit is found. This line is the regression line of the coarse net catches (C) upon the fine net catches (F) and has the equation :-

$C - \bar{C} = b (F - \bar{F})$, where C and F are the total catches of instars 3, 4 and 5 from 20 S.N.Ss. and \bar{C} and \bar{F} are mean values for the period 4. 7. 58 to 18. 9. 58. The constant b is then calculated from the equation :- $b = \sum CF / \sum F^2$. Thus the coarse net equivalent C' of a fine net catch F' is given by :-

$$C' = \bar{C} + \sum CF / \sum F^2 (F' - \bar{F}).$$

The data used and the line of best fit are shown in Figure 8.

If it is then assumed that the numbers of each of the five instars in each set of nymph samples are proportional to the numbers of the different instars in the population sampled, it is possible to convert the fine net catch of all instars on each date into its coarse net equivalent.

Total catches of nymphs 1,2 and 3 in fine and coarse nets with regression line of coarse catches upon fine.

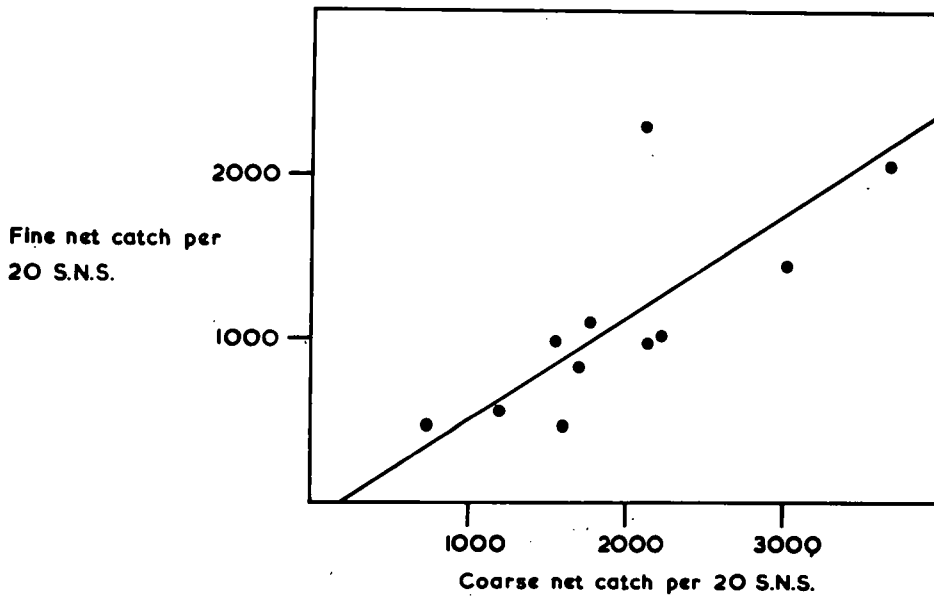


Figure.8.

(ii) The percentage of the fine net catch formed by instars 1 and 2 is known for each sampling date and it is therefore possible to use this and the total catches of instars 3, 4 and 5 in the coarse net on each date to calculate roughly how many instar 1 and 2 nymphs have passed through the coarse net on each occasion. This correction factor ^{for} ~~is~~ instars 1 and 2 can then be added on to the coarse net catch of instars 3, 4 and 5.

The figures obtained by these two methods are shown in Table 9 and are expressed as mean catches per S.N.Ss. in Figure 9. It is clear that there is sufficient agreement between the two sets of figures to justify the assumption that these results give an ^{approximate} ~~appropriate~~ measure of the abundance of the nymphs throughout the season.

(3) Trap Sampling.

The traps used were a modified version of the type described by Kellen (1953). They consisted essentially of a box-shaped wire frame 10 in. (25.4 cm.) long with a square cross-section of 5 in. (12.7 cm.) side. This framework was covered with cotton mosquito netting, previously described as "trap mesh" netting, which had 17 meshes per in. (7 per cm.). Each end of the trap formed a funnel-shaped entrance and in the base of the trap there was a sleeve of netting. The general form of the framework is shown in Photograph 14, and the complete trap is shown in Photograph 15. The traps illustrated had slightly different dimensions from those used at Barbrook reservoir and the dimensions of the latter are shown in Figure 10. The traps were painted with diluted bituminous

Date.	Coarse net catch correction. (20 S.N.S.s)	Fine net catch as coarse net equivalent. (20 S.N.S.s)	Mean coarse net catch/S.N.S.	Mean fine net catch/S.N.S.
6.6.58		312		16
9.6.58		458		23
12.6.58		851		43
20.6.58		2459		123
23.6.58		3882		194
26.6.58		2952		148
4.7.58	5127	4260	256	213
10.7.58	1548	2004	78	100
18.7.58	2876	3159	144	158
24.7.58	4080	4597	204	230
1.8.58	8029	6604	401	330
7.8.58	4655	4433	233	222
15.8.58	2116	3890	106	195
21.8.58	2220	1811	111	91
29.8.58	1694	1507	85	75
4.9.58	1170	-	59	-
12.9.58	1600	1096	80	55
18.9.58	791	958	40	48
26.9.58	638		32	
2.10.58	276		14	
8.10.58	123		6	
9.10.58	172		9	
10.10.58	141		7	
11.10.58	133		7	
13.10.58	54		3	
14.10.58	63		3	
15.10.58	42		2	
16.10.58	25		1	
20.10.58	22		1	
21.10.58	18		1	

TABLE.9.

Mean catches of nymphs per S.N.S. during 1958.

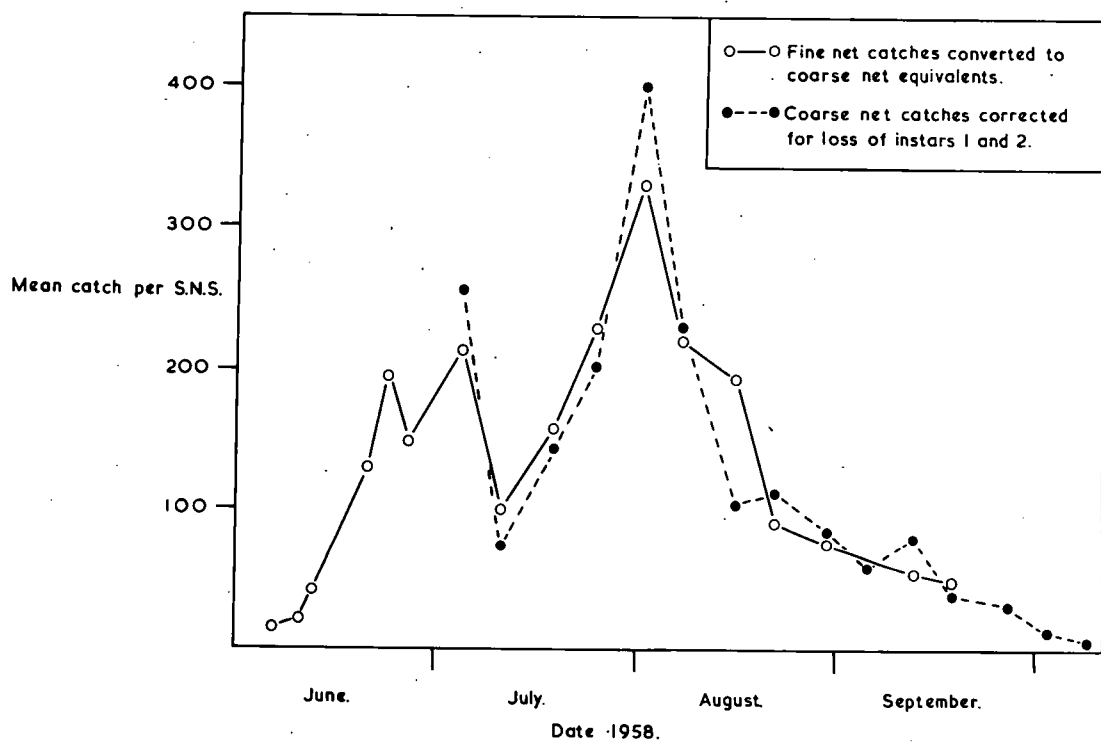
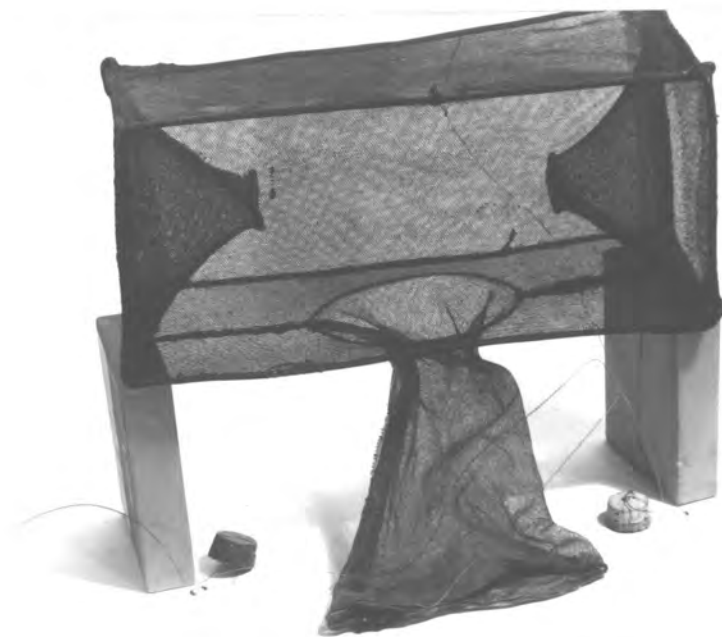


Figure.9.



Photograph.14. Trap frame.



Photograph.15. Completed trap.

MEDIAN LONGITUDINAL SECTION OF TRAP.

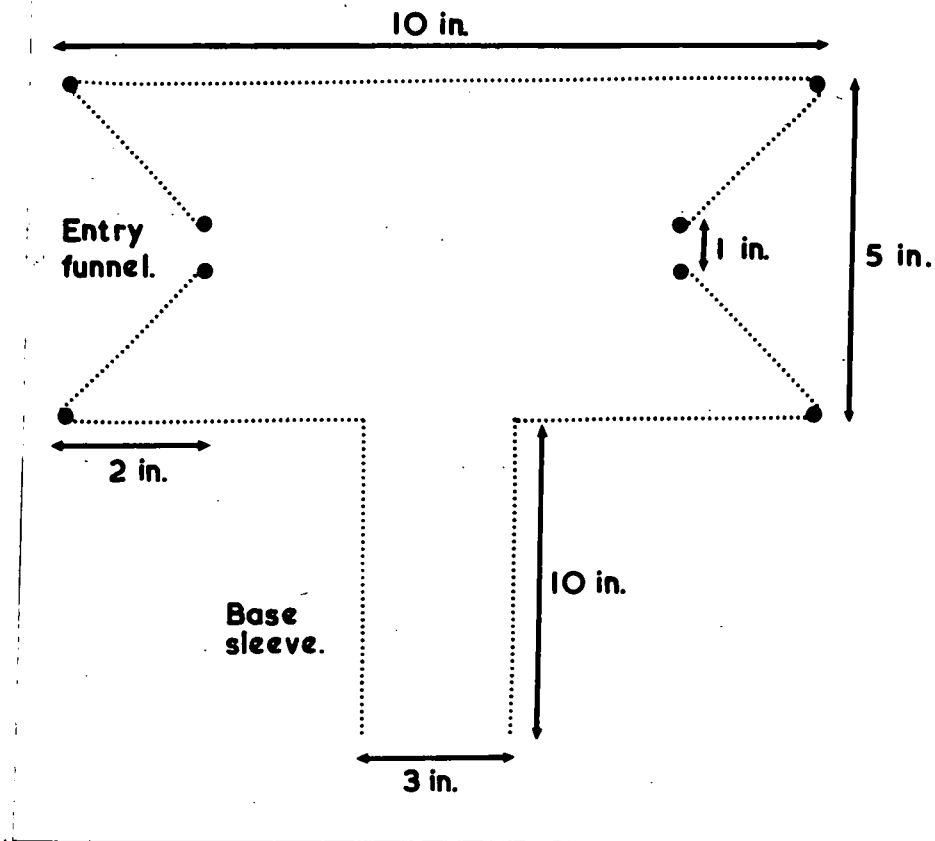


Figure.10.7

paint to give a brownish-black colouration and to provide protection against corrosion. The base sleeve served as a means of removing the catch from the trap and, during operation, the trap was weighted by placing a stone in the sleeve and then tying pieces of string tightly round the sleeve above and below the stone.

The method of positioning the traps is shown in Figure 11. The trap (c) rests on the substratum with its long axis parallel to the water's edge. A piece of nylon fishing line connects the top of the trap to a small cork float (a). The length of the line between the trap and this float is such that when the depth float (a) just reaches the water surface the trap is operating at the required depth. A marker float (b) is attached to the depth float (a) by about 1.5 (4.5 ft.) of line so that the trap can be located even when a rise in water level causes float (a) to be submerged.

When placing the traps in position, the marker float (b) was attached to ^awire hook on the end of a long bamboo pole. The pole was used to swing the trap so as to enter the water at a point beyond the depth at which it was intended to operate it. The trap was then hauled slowly towards the shore until it reached a point where the depth float (a) just broke the water surface if the line between floats (a) and (b) was allowed to go slack. The hook was then disengaged from float (b). During this hauling-in process the water resistance forces operating on the trap were such as to cause the trap to orientate itself with its long axis parallel to the water's edge.

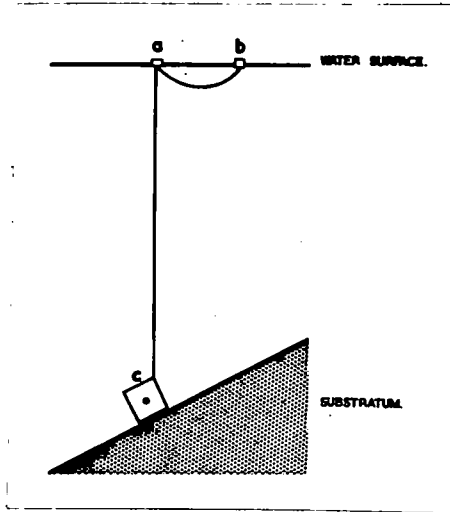


Figure.11.

During 1958 fourteen traps were operated at a depth of 1.0 m. on section A 100 to A 300 of Barbrook reservoir, the traps being evenly spaced along the portions of shore line between the net sampling stations. Between stations A 200 and A 250 this line of traps was intersected by two other lines of seven traps each. These latter two lines extended down the stony bank from 0.33 m. (1 ft.) to 2.33 m. (7 ft.), the traps being placed at depth intervals of 0.33 m. (1 ft.).

The time interval between successive occasions of emptying the traps alternated between six and eight days and on each occasion the catch in the traps at one metre depth was expressed by finding the mean catch per day in each trap and then combining the results for the individual traps by calculating the mean catch per trap per day.

In spite of severe wave action on some occasions during 1958 it was found that these traps held their positions very well. The traps at 0.33 m. (1 ft.) suffered serious tearing and abrasion of the netting under such conditions but the other traps suffered very little damage of this type.

The results obtained with the fourteen traps at 1.0 m. (3 ft.) depth are shown in Table 10 and the data obtained from the other traps will be considered later. Table 10 shows that there was considerable variation in the trap catches during the spring and early summer, a period when the net catches from section A 100 to A 300 were fairly constant from one week to the next (See Table 51). It also shows that the catch per trap per day of adults during a single trapping period in the autumn was smaller than the values given

Date emptied.	Days trapping.	Mean catch/trap/day ± 5% confidence limits.	Water temperature on day of emptying. (°C)
2.4.58	6	6.7 ± 2.43	4.5
11.4.58	8	2.3 ± 1.41	4.5
17.4.58	6	9.6 ± 3.93	5.5
25.4.58	8	27.2 ± 4.44	8.0
1.5.58	6	25.6 ± 6.90	10.5
9.5.58	8	39.4 ± 5.43	11.5
15.5.58	6	25.6 ± 7.12	11.5
23.4.58	8	9.0 ± 2.55	11.5
29.5.58	6	14.4 ± 5.13	11.5
6.6.58	8	20.6 ± 5.23	15.0
12.6.58	6	15.3 ± 3.05	11.5
20.6.58	8	38.8 ± 6.44	14.5
26.6.58	6	16.0 ± 3.22	14.0
23.10.58	7	16.7 ± 2.65	10.0

Table 10. Trap catches at 1.0 m. (3 ft.) depth, 1958.

during several of the spring - summer trapping periods, whereas the net catches in autumn were considerably larger than those taken in the spring and early summer. It is likely that these major discrepancies between the results obtained by trapping and netting are a result of the fact that the trap catches are biased by the activity of the insects to a much greater extent than the net catches are. The factors likely to influence the trap catches are :-

(i) the abundance of the Corixidae.

(ii) Variation in death rate within the traps:- It was noted that on most occasions almost all the Corixidae removed from the traps were still alive and active. It was only on 5.6.58, 19.6.58 and 25.6.58 when the water temperature was above 13°C that most of the animals removed from the traps were dead. Differences in death rate within the traps as a result of temperature fluctuation may be a fruitful source of variation in trap catch, since the sooner an animal dies in the trap the smaller are its chances of escaping again.

(iii) Short term changes in the environment:- Changes in temperature will cause changes in metabolic rate and wave action probably causes changes in the activity and microdistribution of the Corixidae. Phenomena of this type would cause irregularities in the trap catches.

(iv) Seasonal changes in the type of amount of activity shown by the Corixidae:- The catches obtained by most activity samplers (e.g. Pitfall traps for terrestrial Coleoptera - Gilbert 1958) are greatly influenced by the general and in particular the sexual

behaviour of the animals. Table 11 shows the percentage of males in the trap and net samples for comparable dates in 1958. This shows that most of the net samples contained 40 to 60% of males except on those occasions when there was severe wave action on section A 100 to A 300. The trap samples, however, contained 70 to 85% of males on almost all occasions during the spring and early summer but only 45% in the autumn sample. The very high percentage of males in the trap catches during the copulation and oviposition period are probably due to the females spending more time amongst the stones of the substratum in order to oviposit and hence being less likely to find their way into the traps than the males. It is also possible that behavioural peculiarities of the males during the copulation period make them more prone to being caught in traps during that period than at other times of the year. In any case, the results obtained by the traps appear to be greatly biased by the intense reproductive activity which occurs during the spring and early summer.

With such a variety of factors influencing them it is not surprising that the trap catches do not bear much relation to the abundance of the animals as determined by net sampling.

Kellen (1953) used these traps in sewage oxidation ponds in California and claimed that if they were kept clean of mud and alga and were totally submerged during operation they could be used to estimate qualitative and quantitative changes in population density. The results shown above indicate that this was not the case in Barbrook reservoir. This may be a result of differences between the sampling conditions at Barbrook^{and} in Kellen's ponds.

Date of emptying.	% males in trap catches ± 5% confidence limits.	% males in net catches ± 5% confidence limits.
* 2.4.58	72 ± 3.8	61 ± 18.8
*11.4.58	64 ± 6.0	69 ± 12.0
17.4.58	74 ± 3.2	52 ± 7.8
25.4.58	84 ± 1.4	46 ± 7.2
1.5.58	83 ± 1.6	63 ± 6.4
9.5.58	84 ± 1.1	54 ± 6.8
15.5.58	82 ± 1.7	58 ± 6.4
23.5.58	77 ± 2.7	57 ± 7.0
29.5.58	83 ± 2.2	60 ± 6.6
* 6.6.58	83 ± 1.5	68 ± 12.8
12.6.58	73 ± 2.5	44 ± 7.0
20.6.58	71 ± 1.4	56 ± 9.6
26.6.58	67 ± 2.6	72 ± 9.2
23.10.58	44 ± 2.5	52 ± 1.4

* Denotes dates when there was severe wave action on section A 100 to A 300.

Table 11. Percentages of males in trap and net samples during 1958.

The most obvious differences that may be relevant are:-

a) Kellen's pools probably had a lower oxygen tension and higher temperatures than Barbrook reservoir. This would explain why Kellen found that his animals were "quickly drowned" in the traps, whereas at Barbrook the Corixidae were generally able to survive in the traps for several days.

(b) Different species of Corixidae were concerned in the two studies and it is possible that there is specific variation in amenability to trap sampling.

(c) Dr. Kellen states (personal communication) that, in his pools, the free swimming insects were confined to a narrow zone of submerged grass around the pool margins. This suggests that his pools suffered very little severe wave action and this too would help to explain why his traps gave less variable results than the ones at Barbrook.

The work of Popham (1941, 1943_a) on background selection by Corixidae suggests that the colour of the traps might affect their efficiency. This possibility has been investigated on a small scale by carrying out parallel trapping with two pairs of traps, one pair painted white and the other pair black. These traps were operated over six periods ^{of} from 5 to 9 days on section A 100 to A 300, different parts of this section of shore being used on each occasion. The results (Table 12) show that, with the exception of a single occasion when there was no significant difference between the total catches in black and white pairs of traps, the combined catch of the black traps was significantly higher than the combined catch of the white traps. It would therefore appear that the

Date of emptying traps.	Days trapping.	Trap catches.		Probability
		Black.	White.	
2.4.58	6	76	77	$> .90$
16.4.58	6	200	39	$< .001$
16.9.58	5	109	7	$< .001$
25.9.58	9	468	164	$< .001$
1.10.58	6	257	92	$< .001$
9.10.58	8	229	105	$< .001$

Table 12. Comparison of catches between black and white traps. The total catch for each pair of traps during each trapping period is shown. These totals have then been compared by a Chi-squared method and the corresponding probabilities are shown above.

colour of the trap does affect its efficiency and, if this is due to the background selection behaviour described by Popham, it seems likely that the colour of the traps will also influence the species composition of trap catches from mixed populations.

(4) Direct counting.

Oviposition site preferences and the abundance and mortality of the eggs were studied during 1958 by direct counting of the eggs on sites selected at random from the shore and on "artificial" sites placed in the reservoir and examined at intervals of seven days. The techniques employed and the methods used to relate the data obtained to the net sweep data for nymphs and adults will be described in later sections of this account.

VIII. CORIXID SPECIES FOUND IN THE WATER BODIES.

Corixid species lists for the four water bodies are shown in Table 13, which also shows the total number of individuals of each species taken from each water body during net sampling in 1957 and 1958. C.concinna and C. panzéri are additions to the list for Derbyshire given by Masee (1955).

Tables 14 and 15 show the species analyses of the net samples from the whole of Barbrook reservoir during 1957 and 1958 respectively. The identifications are according to Macan (1956). These tables show that, during both years, only a very small percentage of the Corixidae present belonged to species other than C.germari. Comparison of the species totals for the reservoir as a whole and for station "Delta" shows that the majority of the specimens belonging to species other than C.germari were collected at station "Delta". It will also be noted that Glaenocorisa propinqua was never found at "Delta".

Apart from C.germari, only four species, ^{G.}propinqua, C.wollastoni, C.punctata and C.praeusta were represented by more than nine specimens during a single year. The nymphs of C.punctata can be distinguished on size characters and those of G.propinqua are easily picked-out on account of their large protruberant eyes and various other characters (Walton 1943). Nymphs of both these species have been found in Barbrook reservoir. During the autumn of 1958 teneral adults of C. wollastoni were found at station "Delta" and as these pale, soft specimens could hardly have flown there it is reasonable to conclude that they had developed from eggs laid in the reservoir.

<u>Species.</u>	<u>Barbrook.</u>	<u>Ramsley.</u>	<u>Little Barbrook.</u>	<u>Duckpool.</u>
<u>C.germari</u> (Fieb.)	30889	360	523	
<u>G.propinqua</u> (Fieb.)	184	48	2	
<u>C.wollastoni</u> (D & S)	59	14	26	421
<u>C.praeusta</u> (Fieb.)	82	12	56	13
<u>C.dorsalis</u> Leach.	3	6	27	1
<u>C.punctata</u> (Illig.)	20	24	43	13
<u>C.concinna</u> (Fieb.)	2		1	1
<u>C.lateralis</u> (Leach.)	2	8	15	3
<u>C.sahlbergi</u> (Fieb.)	5	1	8	2
<u>C.nigrolineata</u> (Fieb.)	6	3	44	33
<u>C.venusta</u> (D & S)		6	61	1
<u>C.distincta</u> (Fieb.)		2	6	2
<u>C.panzeri</u> (Fieb.)	1	1		
<u>C.linnei</u> (Fieb.)			6	1
<u>C.castanea</u> (Thoms.)			1	2
<u>C.limitata</u> (Fieb.)			2	
<u>C.fossarum</u> (Leach.)		2	1	
<u>C.falleni</u> (Fieb.)		1		
<u>Cy.bonsdorffi</u> (C.Sahlb.)	1	1		
<u>C.dentipes</u> (Thoms.)			2	
<u>C.scotti</u> (D & S)			1	
<u>Total individuals.</u>	31254	489	625	493
<u>Total species.</u>	12	15	17	12

TABLE.13. Species lists for the four water bodies, together with the total number of each species caught in the net samples at each water body during 1957 and 1958.

Date.	<u>C.germari.</u>	<u>G.propinqua.</u>	<u>C.wollastoni.</u>	<u>C.punctata.</u>	<u>C.praeusta.</u>	<u>C.dorsalis.</u>	<u>C.concinna.</u>	<u>C.lateralis.</u>	<u>C.sahlbergi.</u>	<u>C.nigrolineata.</u>	% not <u>C.germari.</u>
3.4.57.	147		2		18		1				12.6
17.4.57.	171		1		6				1		4.5
1.5.57.	198	1	2	1	4				1		4.4
15.5.57.	189	1	2		14	1			1		9.1
29.5.57.	103	1	2	1	4	1			1		9.7
12.6.57.	228	2	4	1	9						6.5
26.6.57.	72	2	4	1	4						13.3
10.7.57.	7	1						1			22.0
24.7.57.	27	1									3.7
7.8.57.	133	17						1			12.0
21.8.57.	529	4									0.7
4.9.57.	521				2						0.4
18.9.57.	734										0
2.10.57.	1319										0
16.10.57.	1500	2									0.1
30.10.57.	1439									1	0.1
13.11.57.	115									1	0.1
24.12.57.	571										0
Totals.	8002	33	17	4	61	2	1	2	4	2	1.3
Totals from St.Delta.	435	0	10	2	32	1	0	0	1	0	9.6

TABLE.14. Species analyses of the 1957 net samples from Barbrook reservoir, together with totals of each species taken from the whole reservoir and from station Delta.

Date.	<u>C.germari.</u>	<u>G.propinqua.</u>	<u>C.wollastoni.</u>	<u>C.punctata.</u>	<u>C.praeusta.</u>	<u>C.dorsalis.</u>	<u>C.concinna.</u>	<u>C.sahlbergi.</u>	<u>C.nigrolineata.</u>	<u>Cy.bonsdorffi.</u>	% not <u>C.germari.</u>
20.1.58.	192										0
28.3.58.	277	2									0.1
11.4.58.	164										0
25.4.58.	304			1	6						2.2
9.5.58.	359	2			3				2		2.0
23.5.58.	415				1						0.2
6.6.58.	283	1	3		6						3.5
4.7.58.	581	2			2	1				1	1.0
18.7.58.	212	5		1							3.0
1.8.58.	117				1		1				2.0
15.8.58.	80		7		1						9.0
29.8.58.	272	1	7								3.0
12.9.58.	419	1	2	3				1			1.5
26.9.58.	1506	4	14	7	1						1.7
10.10.58.	1725	22	16	2				1			1.0
Totals.	6906	40	49	14	21	1	1	1	3	1	2.0
Totals from St.Delta.	360	0	40	11	9	0	0	1	0	0	14.5

TABLE.15. Species analyses of the 1958 net samples from Barbrook reservoir on those dates when samples were taken from all stations, together with totals of each species taken from the whole reservoir and from station Delta.

During both 1957 and 1958, teneral adults of G. propinqua were found in Barbrook reservoir. Thus it would appear that C. wollastoni and G. propinqua are able to complete their life cycle in Barbrook reservoir and that C. punctata breeds there, though it is not clear whether the nymphs produced reach maturity or whether the adults taken in the autumn have flown in from elsewhere. C. praeusta was represented by 61 specimens in 1957 and by 21 in 1958 but no teneral adults were found in either year, so the status of this species in the reservoir must remain obscure. The rest of the species found in Barbrook reservoir were almost certainly extraneous species that had flown in from other habitats.

In general, Barbrook reservoir represents a much more uniform habitat and one with a much poorer substratum than most natural water bodies. It is not therefore surprising that, so far as the Corixidae are concerned, it should approximate to a monospecific culture - having a very marked numerical predominance of C. germari in all parts, together with a relatively small number of G. propinqua living and breeding in the open water regions and a few other species managing to live and complete their life cycles in the restricted area around station "Delta" which has much denser vegetation, a substratum richer in organic material and considerably less wave action than the rest of the reservoir.

Similar species analyses are shown for Ramsley reservoir in Tables 16 and 17. Table 17 shows that G. propinqua was found in the open water areas and never in the stiller, densely vegetated north east inflow channel characterised by stations "a" and "b". This table

Date.	<u>C.germari.</u>	<u>C.propinqua.</u>	<u>C.wollastoni.</u>	<u>C.praeusta.</u>	<u>C.punctata.</u>	<u>C.venusta.</u>	<u>C.lateralis.</u>	<u>C.dorsalis.</u>	<u>C.nigrolineata.</u>	<u>C.distincta.</u>	<u>C.panseri.</u>	<u>% not C.germari.</u>
2.4.57.	33		2	1	1	1	1					18
16.4.57.	24		6	5	1	2	2		1			36
30.4.57.	21		4	3	3	1		1	2	2	1	45
14.5.57.	30		1			2						9
28.5.57.	42						1					2
11.6.57.	42											0
25.6.57.	31											0
9.7.57.	3											0
23.7.57.	3											0
6.8.57.	1							1				50
20.8.57.	4											0
3.9.57.	5	1										17
17.9.57.	4											0
15.10.57.	4	1			2			1				50
31.10.57.	2	1			1							50
Totals.	249	3	13	9	8	66	4	3	3	2	1	21

TABLE.16. Species analyses of 1957 net samples from Ramsley reservoir.

Date.	<u>C.germari.</u>	<u>G.propinqua.</u>	<u>C.praeusta.</u>	<u>G.lateralis.</u>	<u>C.punctata.</u>	<u>C.dorsalis.</u>	<u>C.falleni.</u>	<u>Cy.bonsdorffi.</u>	<u>C.fossarum.</u>	<u>C.wollastoni.</u>	<u>C.sahlbergi.</u>	% not <u>C.germari.</u>
14.4.58.	21	3	4	1	1	1						55
12.5.58.	12		2		1		1					28
7.6.58.	10				1	1						16
7.7.58.	12				1			1				13
5.8.58.					1				1			100
30.8.58.	6			1	4	1				1		54
30.9.58.	14	9		1	3						1	53
21.10.58.	36	33		1	3				1			51
Totals.	111	45	6	4	16	3	1	1	2	1	1	42
Totals for Sts.a & b.	30	0	3	0	14	3	0	1	1	1	1	44

TABLE.17. Species analyses of the 1958 net samples from Ramsley reservoir (including stations a & b.), together with totals of each species from the whole reservoir (including stations a & b.) and from stations a & b.

also shows that the majority of the specimens other than C.germari and G.propinqua were taken from this channel. Nymphs and teneral adults of C.germari, G.propinqua and C.punctata have been found in this reservoir, the nymphs of G.propinqua being fairly abundant in 1958. The other species can probably be regarded as extraneous. The most obvious difference between the corixid faunas of Barbrook and Ramsley reservoirs is the fact that in the Ramsley samples a much smaller proportion of the specimens belonged to the species C.germari.

The net samples from Little Barbrook reservoir are analysed in Tables 18 and 19. The main features of the 1957 data are the relatively large number of species found and the relatively small proportion of the total catch formed by C.germari. The main reason for this is probably the fact that during the drought of 1957 the reservoir was reduced to a very small, shallow pool between 28.5.57 and 11.6.57, after which the water level rose a little, only to fall again so that the reservoir almost dried up completely between 23.7.57 and 6.8.57. After this the reservoir filled up again. Thus, on two occasions during 1957, the reservoir virtually ceased to exist, most of the adults and nymphs present disappeared and subsequent repopulation presumably took place as a result of Corixidae flying in.

The very small numbers of G.propinqua taken from Little Barbrook reservoir during both years further emphasises the fact that this species does not often appear in places where there is a muddy substratum and fairly dense vegetation.

Date.	<i>C.germari.</i>	<i>C.venusta.</i>	<i>C.nigropollinosa.</i>	<i>C.praeusta.</i>	<i>C.dorsalis.</i>	<i>C.punctata.</i>	<i>C.wollastoni.</i>	<i>C.lateralis.</i>	<i>C.linnei.</i>	<i>C.distincta.</i>	<i>C.limitata.</i>	<i>C.fossarum.</i>	<i>C.scotti.</i>	<i>C.castanea.</i>	<i>C.conclina.</i>	<i>O.propinqua.</i>	<i>C.sahlbergi.</i>	Not <i>C.germari.</i>
2.4.57.	22	6		6	1	1		2									2	45
16.4.57.	8	18	2	1		1											2	73
30.4.57.	11	6		13	1		4		3	1								72
14.5.57.	5	11		3	1	1	3		1									80
28.5.57.	2	13	6	5	9		3		5	3	1			1		1		96
11.6.57.							2											100
25.6.57.	3	2	3		1	2												73
9.7.57.		1	20					7		1								100
23.7.57.		3	3	6	1			1		1								100
6.8.57.				1														100
20.8.57.		1			1		1											200
3.9.57.	1		4			1	2	1		1								90
17.8.57.			1	2	5	1		1		1								100
15.10.57.	14		1	1	4	1	1	1				1	1					46
29.10.57.	13		1	1	1	7	1											46
12.11.57	11		2		2	6								1				50
Totals.	80	61	43	39	27	21	17	13	9	6	2	1	1	1	1	1	5	73

TABLE.18. Species analyses of the 1957 net samples from Little Barbrook reservoir.

Date.	<u>C.germari.</u>	<u>C.punctata.</u>	<u>C.praeusta.</u>	<u>C.wollastoni.</u>	<u>C.sahlbergi.</u>	<u>C.nigrolineata.</u> ^Δ	<u>C.dentipes.</u>	<u>C.lateralis.</u>	<u>G.propinqua.</u>	% not <u>C.germari.</u>
14.4.58.	17	1	9	1	2	1				45
12.5.58.	12		1	1	1					20
7.6.58.	14	1		1						12
7.7.58.	136		2				1			2
5.8.58.	4									0
30.8.58.	133	1	1	1				1		3
30.9.58.	86	5	1	1						8
21.10.58.	31	14	3	4			1		1	42
Totals.	433	22	17	9	3	1	2	1	1	12

TABLE.19. Species analyses of the 1958 net samples from Little Barbrook reservoir.

During 1958 fewer specimens were taken and C.germari formed a larger proportion of the catch. Nymphs and teneral adults of C.germari, C.punctata and C.dentipes were taken from this reservoir, showing that these three species are able to complete their life cycles there.

C.venusta was found in Little Barbrook reservoir during July, August and September 1954 and formed about 20% of the Corixidae in the 1957 samples. The nymphs of this species can be distinguished from those of most other species, except C.scotti and C.fossarum by their small size and the fact that the dorsal surface of the abdomen bears a pattern of five longitudinal bands of brown on a paler background. Such nymphs were found in the reservoir during the spring of 1957 but disappeared during the drought of that year. No adults were found during the autumn of 1957 or during the 1958 season. It would therefore seem likely that this species is capable of completing its life cycle in Little Barbrook reservoir, but that it was eliminated during the 1957 drought and had not recolonised the reservoir by the end of the 1958 season.

The filters below Barbrook reservoir are washed out each morning and, during the summer months, in the evenings as well. The filter washings pass into two small settling tanks and the water from these tanks then passes into Bar brook and hence to little Barbrook reservoir. On each of eleven evenings during 1957 a net of 20 meshes per inch (8 meshes per cm.) was fixed in a standard position in the concrete channel which carries the washings into

the settling tanks and was left there until after the filter washing of the following morning. The numbers of C.germari taken in this net are shown in Table 20. Many of these insects were alive and active when removed from the net and it seems likely that these net catches represent only a small proportion of the Corixidae in the filter washings. Thus the numbers of C.germari in Little Barbrook reservoir are probably augmented by a fairly steady flow of specimens coming from Barbrook reservoir via the filters, though it is not possible to assess the importance of this in maintaining the abundance of C.germari in Little Barbrook reservoir.

Tables 21 and 22 show the species composition of the net samples from the Duckpool on Big Moor in 1957 and 1958. The samples are fairly typical of small peat pools on the south eastern Pennines at altitudes of about 1,000 ft. (305 m.), in that the commonest species is C.wollastoni with C.nigrolineata and C.punctata present in smaller numbers and with a number of other species turning up occasionally, probably having flown in from elsewhere.

Date	Nymph 3.	Nymph 4.	Nymph 5.	Adults. Y	Totals.
27.6.57	13			7	20
11.7.57	38	15	1	1	55
25.7.57	7	25	23	4	64
8.8.57	13	13	32	57	119
22.8.57		6	30	123	159
5.9.57			1	8	9
19.9.57			1	2	3
3.10.57				2	2
17.10.57				32	32
31.10.57				13	13
14.11.57				100	100

Table 20. Samples taken from the filter washings in 1957.

Date.	<u>C.wollastoni.</u>	<u>C.nigrolineata.</u>	<u>C.praeusta.</u>	<u>C.punctata.</u>	<u>C.lateralis.</u>	<u>C.castanea.</u>	<u>C.sahlbergi.</u>	<u>C.linnei.</u>	<u>C.venusta.</u>	<u>C.dorsalis.</u>	% not <u>C.wollastoni.</u>
28.3.57.	19	1	1								10
4.4.57.	26	1	3								13
18.4.57.	12		1	1	1						20
2.5.57.	21	1	2								12
16.5.57.	16	1									6
30.5.57.	12	4			1						29
13.6.57.	14	4				1		1	1	1	33
27.6.57.	7	7									50
11.7.57.	2										0
25.7.57.	20										0
8.8.57.	7										0
22.8.57.	5		1								17
5.9.57.	28										0
17.9.57.	15	2									11
3.10.57.	18	2									10
15.10.57.	28	2		1							10
29.10.57.	24	2	1	1		1					17
12.11.57	10	1		1			2				33
Totals.	284	28	9	4	3	2	2	1	1	1	16

TABLE.21. Species analyses of the 1957 net samples from the Duckpool on Big Moor.

Date.	<u>C.wollastoni.</u>	<u>C.nigrolineata.</u>	<u>C.praeusta.</u>	<u>C.punctata.</u>	<u>C.distincta.</u>	<u>C.comcinna.</u>	<u>% not C.wollastoni.</u>
15.4.58.	20	3	1	2			23
13.5.58.	4	1		1			33
3.7.58.	5		3	2	2	1	62
4.8.58.	2						0
1.9.58.	34			3			8
29.9.58.	47	1		1			4
20.10.58.	27						0
Totals.	137	5	4	9	2	1	13

TABLE.22. Species analyses of the 1958 net samples from the Duckpool on Big Moor.

IX. OTHER ANIMALS FOUND IN THE RESERVOIRS.

The animals other than Corixidae that have been identified from each of the reservoirs are listed in Table 23. Those species or groups which were considered, on subjective grounds, to form numerically important components of the fauna are indicated. It must, however, be noted that the numerical abundance attained by a beetle species so indicated will not be comparable to that of a small animal such as a copepod that has been similarly indicated. It must also be noted that the species lists are not strictly comparable between reservoirs because considerably more collecting was done at Barbrook reservoir than at the other two and no attempt was made to obtain adequate lists of such small organisms as Cladocera and Copepoda for the Ramsley and Little Barbrook reservoirs.

Table 24 shows the total numbers of the various larger animals collected from Ramsley and Little Barbrook reservoirs during net sampling in 1958. Most of the species recorded from Ramsley reservoir were found in the north east drainage channel (stations "a" and "b") and in the samples from the rest of the reservoir only the beetle Deronectes 12-pustulatus and the caddis larvae can be considered relatively common. In Little Barbrook reservoir the various aquatic larvae appear to be the most abundant of the larger animals.

The numbers of larger animals taken in the coarse net from Barbrook reservoir on all those occasions during 1957 and 1958 when samples were taken from all stations are shown in Table 25. Water

BARBROOK. LITTLE BARBROOK. RAMSLEY.

O. COLEOPTERA.			
<u>Agabus nebulosus</u> . Forst.	* X	X	X
<u>A. bipustulatus</u> . Linnaeus.	X	X	X
<u>A. sturmi</u> . Gyll.	X		
<u>A. chalconatus</u> . Panz.	X		
<u>A. guttatus</u> . Payk.		X	
<u>Colymbetes fuscus</u> . Linnaeus.	X		
<u>Deronectes 12-pustulatus</u> . Fab.	* X	X	* X
<u>D. elegans</u> . Panz.	X		
<u>Oreodytes rivalis</u> . Gyll.	X		
<u>Hydroporus palustris</u> . Linnaeus.	X	X	X
<u>Platambus maculatus</u> . Linnaeus.	X		
<u>Haliphus immaculatus</u> . Gerh.		X	
<u>Gyrinus natator</u> . Linnaeus.	X	X	X
<u>Dytiscus marginalis</u> . Linnaeus.		X	(X)
<u>Helophorus aquaticus</u> . Linnaeus.	(X)		
<u>H. flavipes</u> . Fab.	(X)	X	
<u>H. brevipalpis</u> . Red.		X	
<u>Anacaena globulus</u> . Payk.		X	
<u>Hydrobius fuscipes</u> . Linnaeus.			X
<u>Hydradephaga</u> larvae.	* X	* X	X
<u>Dytiscus</u> sp. larvae.		X	(X)
O. HEMIPTERA.			
<u>Notonecta obliqua</u> . Gall.	X	X	X
<u>Notonecta</u> sp. nymphs.	X	X	X
OTHER INSECTS.			
<u>Nemoura cinerea</u> (Retz.) nymphs.	X	X	X
<u>Phryganea grandis</u> (?) L. larvae.	X	X	X
<u>P. varia</u> . Fab. larvae.	X	X	X
<u>Plectrocnemia conspersa</u> . Curtis. larvae.	X	X	X
<u>Sialis lutaria</u> L. larvae.	X	X	X
<u>Coenagrion puella</u> . (L.) nymphs.		X	(X)
<u>Pyrrhosoma nymphula</u> (Sulzer) nymphs.		X	
<u>Aeschna juncea</u> (L.) nymphs.		X	
<u>Chironomus anthracinus</u> . Zett. larvae.	* X	* X	* X
PH. ROTIFERA.			
<u>Brachionus urceolaris</u> . O.F. Müller.	* X		
S. PH. CRUSTACEA.			
<u>Chydorus sphaericus</u> . (O.F. Müller.)	* X		
<u>Cyclops vernalis</u> . Fischer.	* X		
CL. ARACHNIDA.			
<u>Hydrozetes lacustris</u> . (Michael).	X		
PH. ANNELIDA.			
<u>Lumbriculus variegatus</u> . (Müller).	* X		
S. PH. VERTEBRATA.			
Larvae of <u>Rana</u> and <u>Bufo</u> .			X
<u>Triturus</u> sp. and larvae.			X

X Denotes presence.

(X) Shows that the species concerned was found only at station Delta in the case of Barbrook reservoir or at stations "a" and "b" in the case of Ramsley reservoir.

Species considered to form a numerically important component of the fauna of each reservoir are indicated by an asterisk.

TABLE. 23. List of species found in each reservoir.

SPECIES.	LITTLE BARBROOK.	RAMSLEY.	
		Whole reservoir including Sts. a & b.	Sts. a & b.
<u>Dytiscus marginalis.</u>	1	2	2
<u>Agabus bipustulatus.</u>	5	6	6
<u>D.12.pustulatus.</u>		104	15
<u>Hydroporus palustris.</u>	2	9	9
<u>Halipus immaculatus.</u>	1		
<u>Gyrinus natator.</u>	9	1	1
<u>Ilybius fuliginosus.</u>	1		
<u>Helophorus flavipes.</u>	1		
<u>Hydrobius fuscipes.</u>		2	1
<u>Hydradephaga larvae.</u>	23	13	10
<u>Sialis larvae.</u>	9	4	
<u>Phryganea larvae.</u>	6	10	1
<u>Plectrocnemia larvae.</u>	5	6	1
<u>Nemoura larvae.</u>	8	4	1
<u>Coenagrion nymphs.</u>		1	1
<u>Notonecta obliqua.</u>		1	1
<u>Notonecta nymphs.</u>	3	6	6
<u>Triturus sp. adults.</u>		1	1
<u>Triturus sp. larvae.</u>		25	25
Total individuals.	74	195	81

TABLE.24. Animals other than Corixidae collected in seven sets of 20 S.N.S.s of the coarse net at Little Barbrook reservoir and seven sets of 22 S.N.S.s at Ramsley reservoir, during 1958.

Date.	<u>Agabus nebulosus.</u>	<u>Hydradephaga larvae</u>	<u>A. bipustulatus.</u>	<u>D. 12-pustulatus.</u>	<u>Phryganea larvae.</u>	<u>Plectrocnemia larvae.</u>	<u>Sialis larvae.</u>	<u>A. sturmi.</u>	<u>Hydrophilidae.</u>	<u>Nemoura nymphs.</u>	<u>Notonecta nymphs.</u>	<u>Cyrtus natator.</u>	<u>Hydroporus palustris.</u>
3.4.57.	2	3	1										1
17.4.57.	1												
1.5.57.	1	1		1									
15.5.57.	1	3				1							5
29.5.57.	2	9						1					12
12.6.57.	5	31		1									11
26.6.57.	1	64											2
10.7.57.		10		1									3
24.7.57.		4											1
21.8.57.	1		3	3			1						1
4.9.57.			1	2									1
18.9.57.									1				
30.10.57.		12											
13.11.57.		2											
24.11.57.		1											
28.3.58.		4			5					3			
11.4.58.		1								1			
25.4.58.		1	1										
9.5.58.		1											1
23.5.58.	1	1											
6.6.58.													11
4.7.58.		43	1										1
18.7.58.		32	1	2					1				
1.8.58.		20											2
15.8.58.	1	16											1
29.8.58.	29	17	3								1		3
12.9.58.	8	15									1	1	1
26.9.58.	4	9	1	5	1	1	1				1		1
10.10.58.	6	12	2				1				1		2
Totals.	63	297	13	16	6	2	3	1	2	4	4	1	61

TABLE.25. Animals other than Corixidae taken from Barbrook reservoir in the coarse net on those dates during 1957 and 1958 when all stations were sampled.

beetles and their larvae predominate. Table 26 shows the total catches of larger animals in the coarse net samples from section A100 to A300. Again beetles and their larvae predominate. It must be noted, however, that the totals given in this table were obtained from a total of 840 S.N.Ss. taken throughout the year. Thus the data suggest that even the beetles and their larvae were relatively scarce. By turning over stones on section A 100 to A 300 during September 1958, however, large numbers of A.nebulosus could be observed and this suggests that these beetles are more abundant than the net data indicate, either because they are chiefly nocturnal animals or because they are difficult to catch in a net. This illustrates the general point which should be borne in mind when considering the numbers of animals other than Corixidae taken in the net samples. That is, that different animal groups will differ in their amenability to net sampling, so that the data obtained cannot satisfactorily be used to compare the relative numbers of animals belonging to different groups. Nevertheless the net sample data, together with casual observations, do suggest that, apart from Corixidae, the water beetles A.nebulosus and Deronectes l2-pustulatus, together with their larvae, are the most abundant large animals found on section A 100 to A 300.

The catches of water beetle imagines in the fourteen traps at 1.0 m. depth on section A 100 to A 300 are shown in Table 27. The total catches over the whole trapping period probably give a fair indication of the relative abundances of the various species, except that, whereas the larger species were

Species or group.	Number collected in 840 S.N.S.s
T	
<u>Agabus nebulosus</u>	3
<u>A. bipustulatus.</u>	1
<u>Hydroporus palustris.</u>	5
<u>Deronectes 12-pustulatus.</u>	28
Hyradephaga larvae	105
<u>Phryganea larvae.</u>	1
<u>Plectrochemia larvae.</u>	2
<u>Nemoura cinerea nymphs.</u>	1
<u>Notonecta obliqua</u>	1

Table 26. Animals other than Corixidæ taken from stations A 100 to A 300 of Barbrook reservoir during net sampling in 1958.

Date of emptying traps.	<u>A.nebulosus.</u>	<u>A.bipustulatus.</u>	<u>Hydroporus palustris.</u>	<u>Deronectes 12-pustulatus.</u>	<u>Colymbetes fuscus.</u>	<u>Platambus maculatus.</u>	Totals.
2.4.58.	3						3
10.4.58.	2						2
16.4.58.	1						1
24.4.58.	21	3					24
30.4.58.	19	6	2	1			28
8.5.58.	123	31	2	4			160
14.5.58.	41	4	2	1			48
22.5.58.	37	6		7			50
28.5.58.	49	4	2	5	1		61
5.6.58.	104	16	4	2			126
11.6.58.	66	6		1			73
19.6.58.	200	44	33	1		1	279
25.6.58.	35	15	2			1	53
22.10.58.	4	2		10			16
Totals.	705	137	47	37	1	2	922.

TABLE.27. Animals other than Corixidae caught in the fourteen traps 1 m. depth in Barbrook reservoir during 1958.

usually dead when removed from the traps, most of the specimens of D.12-pustulatus and H.palustris were still alive. Thus these latter two species may be somewhat under-represented in the samples.

So far, only the larger insects which are caught in the coarse net have been considered. The smaller organisms cannot be obtained as a "by-product" of the corixid sampling but must be collected specially. For this reason the information regarding the smaller animals is rather less complete than that for the larger ones. The numbers of larval and pupal Chironomidae taken in the coarse net from Barbrook reservoir were small and have not been recorded. There were, however, large numbers of chironomid larvae in the reservoir, particularly the large Chironomus anthracinus whose larvae lived in the deep water and whose ~~imagines~~^{imagines} flew in large swarms above the reservoir banks in late May and early June. Also present were smaller forms, probably Tanytarsus spp., whose larvae formed mud tubes on the stones of the substratum at the 1.0 m. (3 ft.) depth. During the spring, summer and autumn the copepod, Cyclops vernalis and the cladoceran, Chydorus sphaericus, were seen in large numbers above and amongst the stones on section A 100 to A 300. The mite, Hydrozetes lacustris, was found in small numbers on stones taken from A 100 to A 300 and the lumbricid, Lumbriculus variegatus, occurred in those places where small quantities of alga and mud accumulated between the stones.

During April and May of 1959, an otter board was used to obtain plankton samples from just below the water surface about 10 to 20 m. offshore in Barbrook reservoir. The net used had

110 meshes per in. (40 per cm.). The plankton obtained was found to consist chiefly of the rotifer, Brachionus urceolaris, together with a small number of specimens of the copepod, Cyclops vernalis.

The fauna list for Barbrook reservoir is a relatively short one, particularly since the species of Coleoptera and Hemiptera only recorded in small numbers were probably chance immigrants from other habitats. Particularly noticeable is the absence of such groups as the molluscs, leeches and Platyhelminthes. This may be attributed to the fact that Barbrook reservoir is an upland water body with a very low base status. Comparison of the fauna list with that of Macan (1948) from an upland fishpond suggests that this is not the only relevant factor. Macan's survey was more intensive than that described here. For example, he used emergence traps to collect Diptera whereas in the present work Chironomidae were collected by occasional netting of swarming imagines on the reservoir banks. The habitats studied were also very different. Macan's pool having a more organic substratum and a denser and more diverse macroflora than can be found in Barbrook reservoir. This suggests that Barbrook reservoir is a somewhat rigorous environment for aquatic animals and that, in consequence, relatively few species are able to survive there.

It has not been possible in the present work to do more than collect together a number of casual observations on the feeding habits of C.germari and to carry out a preliminary study of the fore-gut contents of four species of aquatic Coleoptera.

During September 1958, specimens of Agabus nebulosus, A.bipustulatus, and Gyrinus natator were collected from various

places in Barbrook reservoirs. At the same time Deronectes
12-pustulatus and various aquatic larvae were collected from
Barbrook and Ramsley reservoirs. The animals collected were
killed with chloroform vapour and immediately preserved in
4% formalin solution. They were examined within a week of
collection. The fore-gut contents of each specimen were
examined and the number of individuals of each species containing
each type of food was determined in the way described by
Jones (1949, 1950). The results are shown in Table 28. These
data must be interpreted with caution for the following reasons:-

(i) Different food materials may be digested at different
rates and hence those materials most slowly digested would tend to
be recorded in an unduly large proportion of the sample.

(ii) Large food organisms may be broken into small, and
sometimes unidentifiable, fragments during ingestion whereas smaller
organisms are more likely to be ingested whole and to be readily
identifiable.

(iii) It cannot necessarily be assumed that all the material
present in the fore-gut of an animal is, in fact, food. Some of it
may have been ingested accidentally along with the food and may be
of little or no nutritive value to the animal containing it.

(iv) Conclusions based on samples taken at one time of
the year do not necessarily reflect the feeding habits of the animals
throughout the year.

(v) The technique used does not give any measure of the
relative weights of different foods taken, and therefore gives

	<u>A. bipustulatus.</u> (St. B.)	<u>A. nebulosus.</u> (St. B.)	<u>A. nebulosus.</u> (St. A25.)	<u>P. 12-pustulatus.</u> (Barbrook and Ramsley resrs.)	<u>Q. natator.</u> (St. B.)	<u>Q. natator.</u> (St. B - 10.)	<u>Phryganea larvae.</u> (Ramsley res.)	<u>Plectrocnemia larvae.</u> (Barbrook and Ramsley resrs.)	<u>Sialis larvae.</u> (Barbrook and Ramsley resrs.)
Total number examined.	14	78	78	44	38	22	8	8	3
No identifiable contents.	2	21	17	26	2	8	1	5	3
Leaf fragments.	1	5					4		
Alga (<u>Microspora</u> sp.).	11	43	35	6	33	1	6		
Detritus.	2	1	2				1		
Chironomid larvae and pupae.	5	22	20	4	1		5	1	
Corixid nymphs.	5	22	6						
Corixid adults.	3				1				
Cyclopoid copepods.	1	13	46	8	1			2	
Large Diptera (chiefly <u>Scopeuma</u>)	2	6							
Sciaridae (<u>Bradysia</u> sp.)	3	21	21		32	14	1		
Indeterminate insect fragments.	1	11	11	10	1				
Chironomidae imago.			9						
Acarines.	1	1		1					
Collembola.	1								
Cercopidae.	1								
Thysanoptera.	1								
Gyrinidae.			1						
Cladocera.							1		
<u>Agabus</u> sp. eggs.	1		1				1		

TABLE.28. Numbers of specimens of various predators containing each type of food material.

only a vague idea of the relative importance of each food.

(vi) This method gives little information about the exact nature of the food. For example, it does not show the extent to which the animals concerned are actively predatory and the extent to which they simply eat the dead bodies of animals killed by some other agency.

Even so, some useful conclusions can be drawn from the data. The numbers of aquatic larvae examined were very small, but the data do show that caddis larvae feed on animal as well as plant material. The data obtained from the Coleoptera are expressed in Figure 12, as percentages of each sample containing each of the commoner foods. The results from A.nebulosus and ~~A.bib~~ A.bipustulatus collected from station B show that these two species feed on similar foods in similar proportions, though the presence of adult Corixidae in A.bipustulatus but not in A.nebulosus may indicate that the larger species (A.bipustulatus) can deal more easily with larger-sized food organisms.

Comparisons between the fore-gut contents of samples of the same species from different parts of the reservoir are also of interest. The results show that a larger proportion of the A.nebulosus at station A 25 contained copepods and Chironomidae than of the A.nebulosus at station B. This reflects the abundance of these two foods at the two stations. Station B is an area of sandy shore with patches of J.bulbosus agg. where copepods and chironomid larvae are not numerous, whilst station A 25 is an area of steeply sloping stony bank on which copepods and chironomid larvae are abundant.

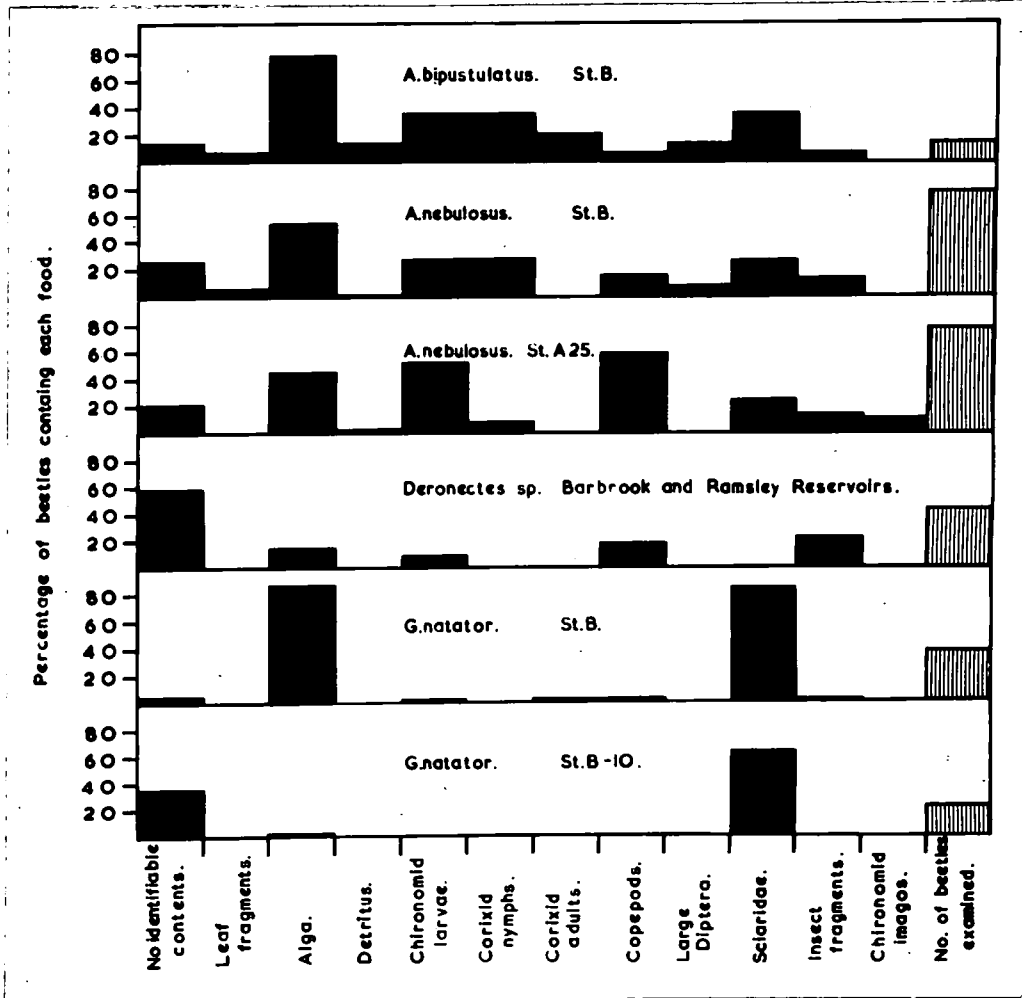


Figure.12. Percentage of water beetles of each species containing each type of food material.⁷

The bulk of the food of Gyrinus natator at stations B and B -10 was formed by small Diptera of the family Sciaridae, and genus Bradysia. These small Diptera occur in large numbers on the banks of the reservoir between May and September and often fall onto the water and become trapped there by surface tension effects. This shows that, although G.natator spends part of its time below the water surface, it feeds mainly at the surface on small floating insects. The presence of alga (Microspora sp.) in over 80% of the G.natator at station B where mats of this filamentous alga rest on top of the J.bulbosus agg. and break the water surface, and the virtual absence of alga in the specimens from B -10 where Microspora sp. is confined to the stones on the bottom, gives further proof that this species is a surface feeder.

The general conclusions are that during September, at least, G.natator feeds mainly on small floating insects whilst D.12-pustulatus feeds chiefly on small aquatic organisms such as copepods and chironomid larvae. A.nebulosus and A.bipustulatus, however, take a variety of foods, including rather larger animals such as Corixidae and their nymphs and the dipteran Scopeuma sp. To what extent the Corixid material found in these two species was taken by active predation and to what extent by eating dead corixids is, unfortunately, still not clear. On one occasion, however, a specimen of A.nebulosus was observed to attack an adult male of C.germari and this shows that the two Agabus spp. do attack living Corixidae.

It is not possible to determine the feeding habits of the Hydradephaga larvae by examining their gut contents. Specimens

of various sizes have been kept in jars together with a variety of other animals collected from the reservoirs. They will attack most small moving objects and have been observed to kill and feed upon chironomid larvae and corixid nymphs. They have also been observed to kill teneral adults of C.germari but have never been seen to kill adult corixids whose exoskeletons had hardened and darkened, though a number of attacks upon such Corixidae have been watched.

The fore-gut contents of many specimens of C.germari have been examined but the contents have usually consisted simply of unidentifiable granular material of a brownish, greenish or reddish shade. In a few specimens, however, portions of filaments of Microspora sp. have been found. For example, out of 18 individuals collected on 23.10.58, eight were found to contain small quantities of this alga amongst the fore-gut contents and out of 25 specimens collected on 25.4.59 four specimens contained portions of Microspora sp. Occasional adults of C.germari have been taken in the net with a chironomid larva or a Lumbriculus variegatus impaled on their mouthparts and chironomid larvae have been attacked by adults and by nymphs 3, 4 and 5, whilst in a sorting dish full of water. Nymphs 1 and 2 are kept in jars under laboratory conditions have been observed to feed on small chironomid larvae and also on instar 1 and 2 nymphs that had died. Neither adults nor nymphs, however, have been seen to attack living adults or nymphs, though egg cannibalism has been observed in this species under laboratory conditions. If a number of ovipositing females are kept together in a jar and provided with some vegetation to oviposit upon and if the eggs laid are examined daily, it is found that eggs which appeared quite sound when

laid may appear transparent after a few days. Microscopic examination of these eggs shows that they consist simply of a hollow shell and in some cases it is possible to locate the hole made in the shell by the stylets of the adults. Evidence that this also occurs in the field will be given later.

Specimens of C.germari in the field and in the laboratory have been observed manipulating sand, peat and alga with their palae but it has not been possible in such cases to see what, if anything, they were feeding on.

Thus it is clear that C.germari feeds on soft bodiea aquatic animals and probably also on the alga Microspora sp., but to what extent, if any it takes any other types of food is still not clear.

SECTION B.

BIOLOGY, ABUNDANCE, MORTALITY AND BIOMASS OF C.GERMARI.

X. THE LIFE HISTORY, DISTRIBUTION AND BIOLOGY OF C.GERMARI
IN BARBROOK RESERVOIR.

(1) Introduction and brief survey:-

(i) Annual cycle:- The annual cycle of C.germari in Barbrook reservoir is shown in Figure 13 and the evidence upon which it is based will be given below. Fig.13 is based on the 1958 sampling results.

(ii) Number of nymphal instars:- Rousseau (1921) has described the five nymphal instars of C.punctata and gives a synopsis of the characters by means of which the instars can be separated from one another. The following translation of part of Rousseau's synopsis has been made :-

"Instar 1:- Elytral rudiments not distinct. Posterior edge of mesonotum is continuous. Head not separated from thorax dorsally.

Instar 2:- Elytral rudiments small, not reaching the middle of the sides of the metanotum. Head separated from thorax.

Instar 3:- Elytral rudiments leave the external part of the apex of the short wing rudiments free and do not reach the level of the centre of the posterior edge of the metanotum.

Instar 4:- Elytral rudiments do not reach the posterior edge of the first visible abdominal segment. Wing rudiments reach the base of the second visible abdominal segment, their extremity is therefore not covered. The posterior edge of the metanotum is visible in its entirety.

Annual cycle of C.germari.

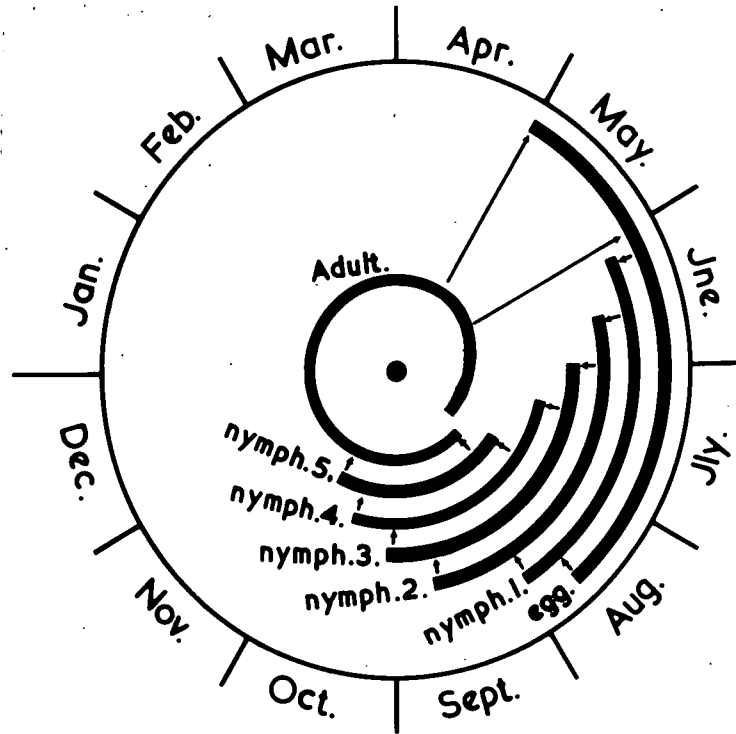


Figure.13.

Instar 5:- Metanotum transverse and is prolonged on either side as a wing rudiment whose extremity is hidden beneath the apex of the elytral rudiment. Strigil (where present in the adult male) is sometimes visible through the integument of the male instar 5 nymphs".

Rousseau's characters regarding the lengths of the elytral and wing rudiments relative to one another and to the abdominal and thoracic segments and also his observation that the head is not clearly demarkated from the thorax in instar 1, can be used to separate the nymphs of C.germari into five supposed instars. Simple outline diagrams of the anterior dorsal regions of each of these five stages are given in Figures 14, 15, 16, 17, and 18 for comparison with Rousseau's synopsis.

Samples of C.germari nymphs were thus separated into five supposed instars. Thirty-two specimens of each supposed instar were picked out at random and their lengths and head capsule widths were measured using a monocular microscope with a micrometer eyepiece. No overlap in either of these measurements was found between each successive pair of the supposed instars. It is therefore reasonable to conclude that C.germari has at least five nymphal instars. The mean measurements for each supposed instar together with their 5% confidence limits are shown in Table 29.

Dyar's law (Dyar 1890) assumes that, in Lepidopterous larvae, the width of the head capsule follows a regular geometrical progression in successive instars. The logarithms of the head mean head capsule widths of the supposed instars of C.germari

KEY TO FIGURES 14 TO 18.

P = Pronotum.

M = Mesonotum

Ma = Metanotum.

E = Elytral rudiment.

W = Wing rudiment.

A1 = First visible abdominal segment.

A2 = Second visible abdominal segment.

A3 = Third visible abdominal segment.

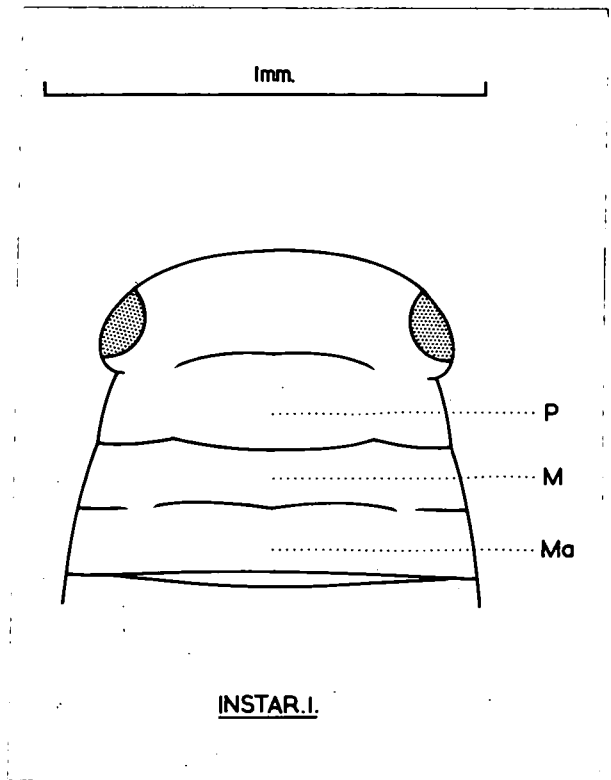


Figure.14.

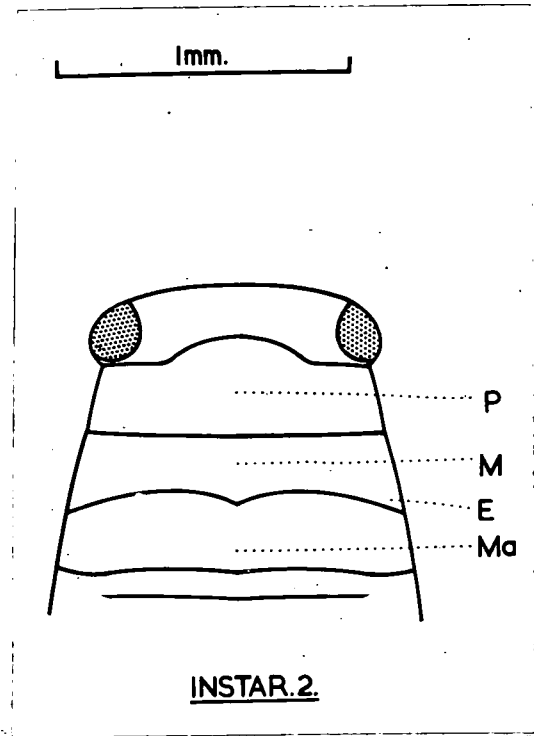


Figure.15.

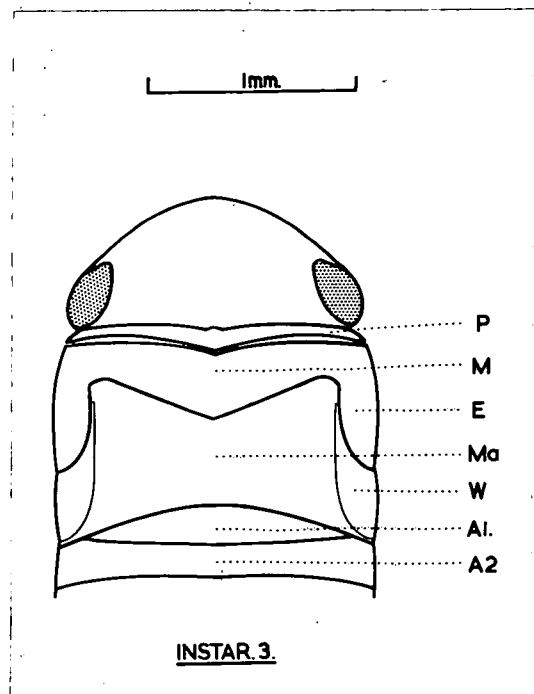


Figure.16.

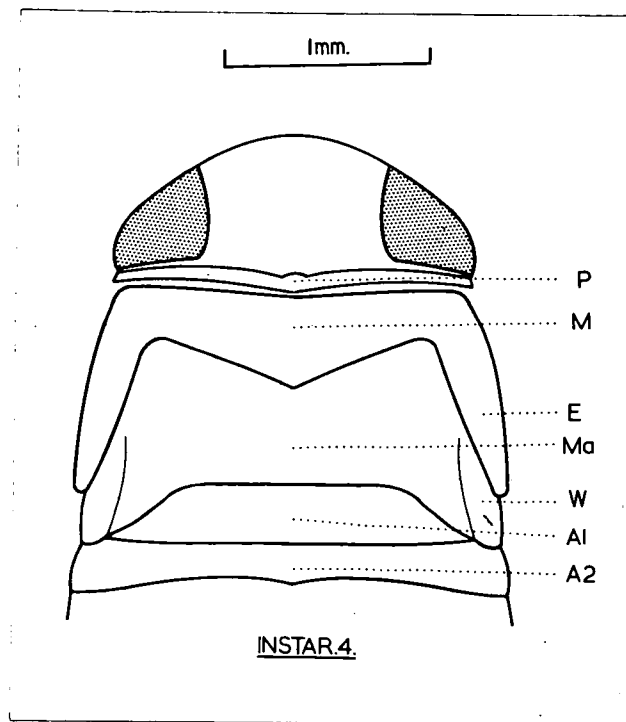


Figure.17.

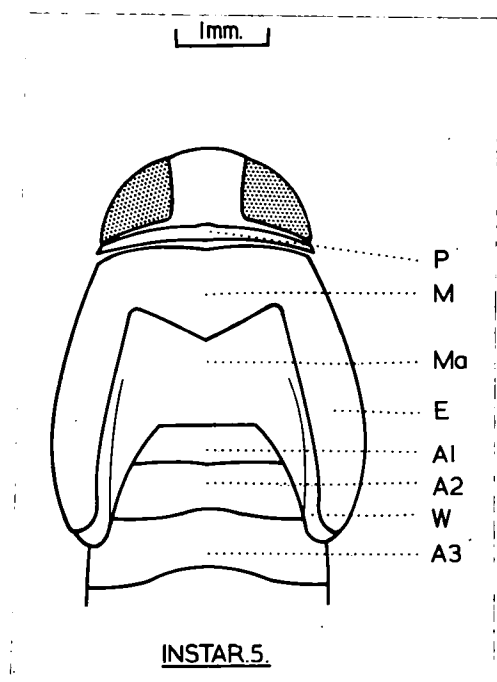


Figure.18.

Instar.	Mean length in mm. ± 5% confidence limits.	Mean head capsule width in mm. ± 5% confidence limits.
1	1.73 ± .015	0.18 ± .028
2	2.60 ± .158	1.05 ± .006
3	3.35 ± .026	1.40 ± .002
4	4.77 ± .011	1.83 ± .004
5	6.45 ± .039	2.18 ± .004

Table 29.

nymphs are shown in Figure 19. The figure approximates to a straight line and thus shows that Dyar's law is approximately true for the nymphs of C.germari and that no instar exists between the five already postulated for this species.

Thus the evidence shows that C.germari has five nymphal instars and this agrees with the statements of such writers as Poisson (1933), Griffith (1945) and Sutton (1947) regarding various other corixid species, though Caroli (1924) found only four instars in C.monticelli.

(iii) Number of generations per year:- The occurrence of more than one generation per year in certain species of Corixidae has been demonstrated by several writers. For example, Larsen (1938) found two generations per year in C.praeusta, Hungerford (1919) showed that the North American species Palmocorixa buenoi has two generations per year, and Poisson (1923) claimed that, in north-west France, C.striata (Linn.) has several generations per year.

The existence of only one oviposition period per season (See Figure 23), the distribution in time of the five nymphal instars (Figures 20 and 21), and the fact that the first teneral adults were found on July 24th and August 15th in the years 1957 and 1958 respectively, together with the fact that no fully developed eggs were found in the oviducts of the females until the spring following their emergence, show that C.germari has only one generation per year in Barbrook reservoir.

Logarithms of mean head capsule widths of the supposed instars. The extreme values for each group are also shown.

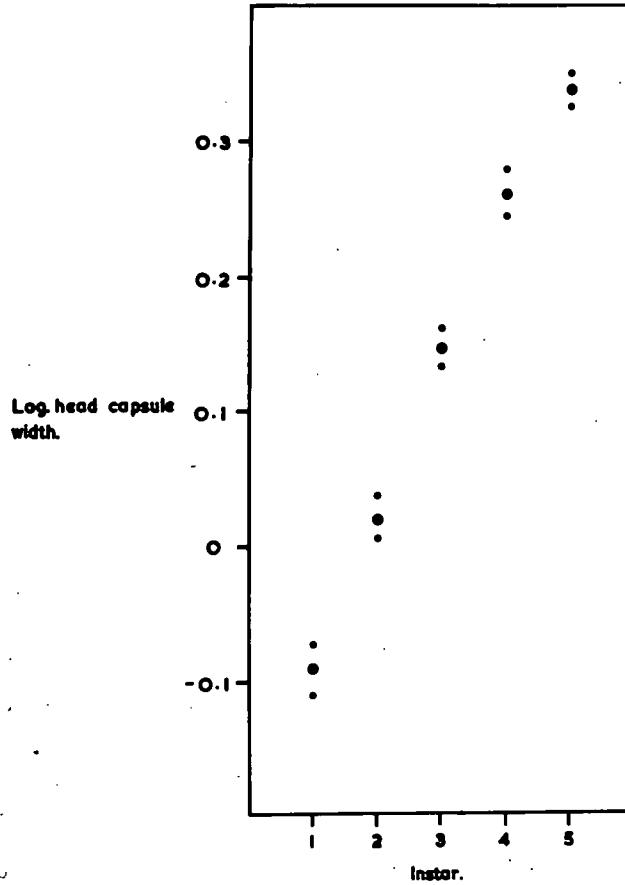


Figure.19.

Nymphal instars as percentages of nymphs caught.

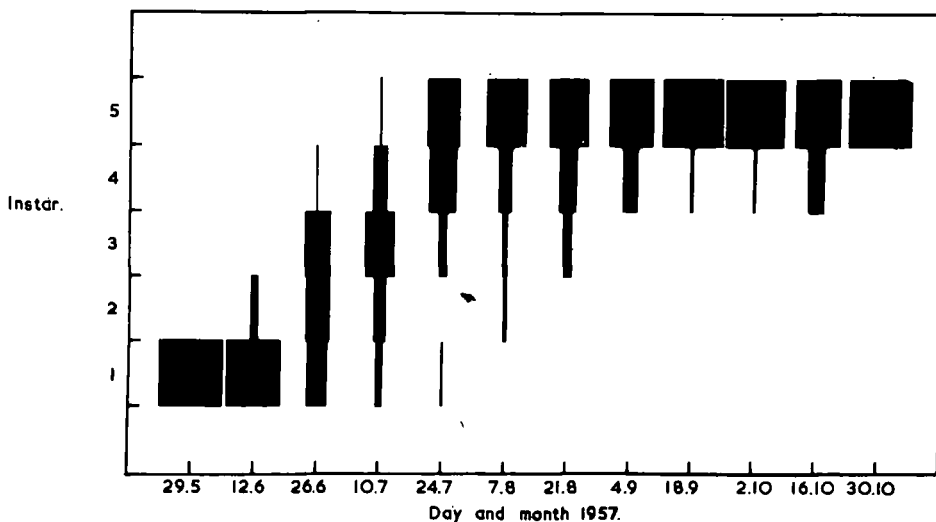


Figure.20.

Nymphal instars as percentages of nymphs caught.

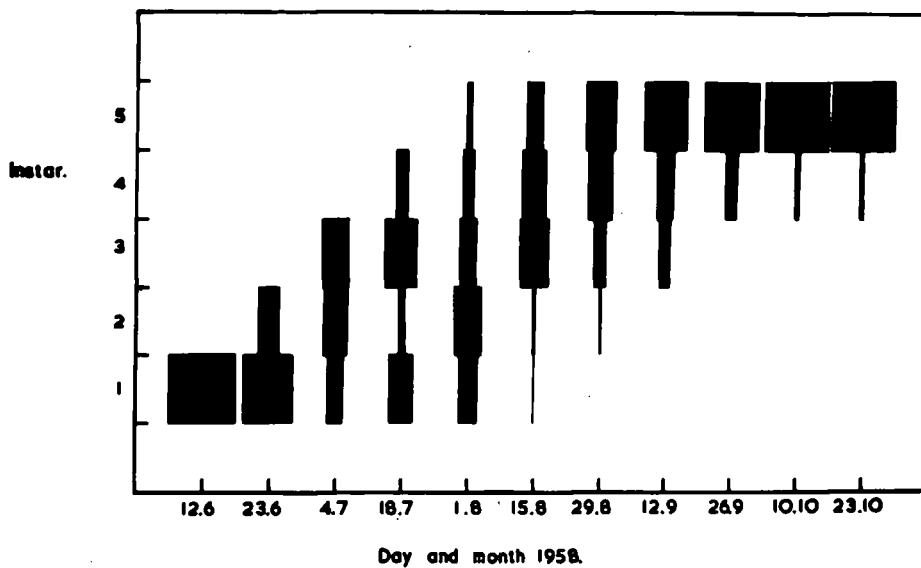


Figure.21.

(2) Distribution of the adults within the reservoir:-

The mean catches of C.germari adults per S.N.S. from various sections of the shore are shown in Tables 30 and 31 for the years 1957 and 1958. The data show that, during both years, the abundance of adults was considerably greater on section A 100 to A 300 than on any of the other sections. Also, the abundance on section A 100 to A 300 shows definite trends during the course of the season whilst the abundance on the other sections does not.

It is likely that the abundance of animals on stony shores will be related, to some extent, to the size, shape and arrangement of the component stones. Thus, within certain limits, a shore of smaller, irregular stones stacked together in an irregular manner will provide more crevices, to give shelter from predators and wave action, and a relatively larger area of exposed stone surface for oviposition, and for the grazing of food animals than will a shore composed of larger more regular stones fitted together in a more systematic way. Sections A 100 to A 300 and E 130 to A -10 can be used to test this hypothesis so far as C.germari is concerned. Section E 130 to A -10 has already been described as a length of shore made up of large cuboidal blocks of local sandstone hewn to shape and fitted closely together. There are, however, crevices up to 2 cm. ^(0.8 in.) wide and 40 cm. (16 in.) deep between some of these blocks, within which Corixidae and water beetles can be observed to move about. The data in Table 32 give some indication of the size of these stone blocks. For comparison, the weights of thirty stones picked up at random from section A 100 to A 300 have been determined. The density of these stones has been

	A100 to A300	E130 to A-10	B10 to C-20	D50 to E
S.N.S.s per sampling date.	15	14	12	12
Date.				
3.4.57.	8.0 ± 1.34	0.6 ± 0.66	0.8 ± 0.59	0.2 ± 0.36
17.4.57.	9.3 ± 2.11	0.1 ± 0.21	0.4 ± 0.32	0.3 ± 0.25
1.5.57.	10.2 ± 3.88	1.2 ± 0.85	0.8 ± 0.66	0.8 ± 1.08
15.5.57.	11.8 ± 3.80	0.6 ± 0.40	0.1 ± 0.02	0.1 ± 0.18
29.5.57.	6.2 ± 2.76	0.5 ± 0.44	0.1 ± 0.02	0.2 ± 0.36
12.6.57.	10.2 ± 3.84	2.1 ± 1.27	1.7 ± 1.32	0.7 ± 0.61
26.6.57.	0.4 ± 0.38	3.4 ± 1.54	0.5	2.1 ± 3.74
10.7.57.	0	0.1 ± 0.21	0.7	0.2 ± 0.33
24.7.57.	1.2 ± 1.10	0.3 ± 0.47	1.0	0.3 ± 0.38
7.8.57.	5.4 ± 2.79	2.2 ± 1.04	3.0	1.9 ± 1.66
21.8.57.	29.0 ± 5.16	1.0 ± 1.05	2.5 ± 1.12	1.6 ± 1.35
4.9.57.	20.5 ± 6.14	2.0 ± 1.29	4.4 ± 0.69	0.8 ± 0.83
18.9.57.	44.7 ± 12.83	0.9 ± 1.05	1.6 ± 0.87	0.1 ± 0.18
2.10.57.	70.0 ± 23.96	2.0 ± 1.17	7.6 ± 2.52	1.2 ± 0.84
16.10.57.	87.0 ± 13.21	2.1 ± 2.30	2.6 ± 1.07	1.1 ± 0.87
30.10.57.	92.5 ± 20.73	0.6 ± 0.49	1.3 ± 0.97	0.6 ± 0.78
13.11.57.	4.6 ± 2.22	0.9 ± 0.57	0.3 ± 0.31	1.6 ± 1.64
24.12.57.	0.6 ± 0.58	0.6 ± 0.94	0.4 ± 0.57	0.5 ± 0.42

TABLE.30. Mean catches of adults per S.N.S. on the various sections of shore during 1957, together with their 5% confidence limits.

On the dates 12.6.57 to 7.8.57 inclusive only 9 S.N.S.s were made on section D50 to E.

On the dates 26.6.57 to 7.8.57 inclusive only 12 S.N.S.s were made on section A100 to A300.

On the dates 10.7.57 to 7.8.57 inclusive only 3 S.N.S.s were made on section B10 to C-20 and on 26.6.57 only 6 S.N.S.s were made.

	A100 to A300	E130 to A-10	B10 to C-20	D50 to E
S.N.S.s per sampling date.	20	14	12	12
Date.				
20.1.58.	5.0 ± 0.73	0.8 ± 0.72	0.9 ± 0.09	0.9 ± 0.88
28.3.58.	8.0 ± 2.31	0.5 ± 0.43	2.7 ± 0.03	1.7 ± 1.18
11.4.58.	2.9 ± 1.29	0.6 ± 0.54	2.4 ± 1.66	1.8 ± 1.25
25.4.58.	9.9 ± 3.13	0.2 ± 0.33	1.3 ± 1.00	0
9.5.58.	10.5 ± 3.08	0.9 ± 0.76	4.5 ± 3.51	0.7 ± 0.73
23.5.58.	10.3 ± 1.90	4.9 ± 1.22	4.5 ± 2.79	1.3 ± 0.95
6.6.58.	2.6 ± 0.89	2.4 ± 0.77	5.3 ± 5.18	6.8 ± 4.61
4.7.58.	9.7 ± 1.02	2.9 ± 1.34	9.9 ± 4.06	17.0 ± 13.08
18.7.58.	4.1 ± 1.38	0.6 ± 0.61	6.5 ± 3.87	2.7 ± 1.75
1.8.58.	3.4 ± 1.20	0	1.9 ± 1.12	0.9 ± 0.73
15.8.58.	2.6 ± 1.75	0.1 ± 0.15	1.0 ± 1.23	0.3 ± 0.31
29.8.58.	10.6 ± 2.08	0.4 ± 0.29	1.2 ± 0.32	2.4 ± 1.92
12.9.58.	16.1 ± 4.63	0.9 ± 0.53	2.7 ± 1.27	1.5 ± 2.22
26.9.58.	64.8 ± 12.53	2.6 ± 0.97	6.5 ± 6.10	1.5 ± 0.78
10.10.58.	74.0 ± 14.13	1.0 ± 0.67	9.3 ± 3.84	3.2 ± 2.68

TABLE.31. Mean catches of adults per S.N.S. on the various sections of shore during 1958, together with their 5% confidence limits. On 20.1.58. only 15 S.N.S.s were made on section A100 to A300. On 4.7.58, 18.7.58 and 1.8.58 only 8 S.N.S.s were made on section E130 to A-10.

Length (cm.)	Breadth (cm.)	Depth (cm.)	Volume (cc.)
97	25	35	85,000
97	36	38	133,000
70	44	45	138,000
52	44	29	62,300
56	43	35	84,300
60	38	28	64,000
77	30	26	60,000
30	11	26	8,500
93	33	30	92,000
75	25	28	52,500
59	46	27	73,300
68	30	38	77,600
42	35	27	39,000
55	35	31	59,800
60	65	28	188,000
58	29	33	50,600
83	23	28	53,500
62	23	30	42,900
40	28	27	30,300
47	63	27	80,000
55	65	33	118,000
39	23	31	27,900
52	49	30	76,500
48	22	25	26,400
121	32	24	93,000
79	29	35	80,000
55	40	24	53,000
102	47	24	115,000
27	11	28	83,000
53	27	28	40,000

Mean volume = $72,900 \pm 13,900$ cc.

TABLE.32. Dimensions of 30 stone blocks selected at random from section E130 to A-10.

determined as approximately 2.5 g/cc. and hence the volumes of the stones have been calculated and are shown in Table 33. Comparison of these two Tables shows that there is a considerable difference in the mean size of the stones on the two sections of shore. Such differences would give rise to a large difference between the two shore sections in the number and size of available crevices and in the area of exposed stone surface per unit area of substratum, even if the shape and arrangement of the stones were similar on the two shore sections. The observed differences in stone shape and arrangement must further accentuate this effect. Thus the data suggest that the differences in abundance of C.germari between sections A 100 to A 300 and E 130 to A -10 may be a result of differences in the construction of the reservoir walls in those two sections.

The other two sections of shore for which abundance data are given in Tables 30 and 31 are, in one case, sandy shore and, in the other case, a wall built up of stones larger and more regular than those of section A 100 to A 300 and smaller and less regular than those of section E 130 to A -10. In both these cases the amount of shelter provided and the area of exposed stone surface per unit area of substratum are probably considerably smaller than on section A 100 to A 300, and might therefore be expected to give smaller catches of C.germari per S.N.S. than the latter section.

It can therefore be seen that the abundance of C.germari adults on different sections of the shore can be related to the physical nature of the substratum on those different sections of shore. Even so, it is important to note that C.germari reaches its

Weight (g.)	Volume (cc.)
2,660	1,073
276	117
250	102
1,610	650
730	294
300	124
454	183
326	138
418	169
1,460	589
965	389
722	291
226	91
283	114
173	76
531	215
510	206
156	63
261	103
248	100
2,470	998
453	176
219	89
156	63
142	57
163	66
1,950	786
965	389
552	223
566	228

Mean volume = 272 ± 101 cc.

TABLE.33. Weights and approximate volumes of 30 stones selected at random from section A100 to A300.

greatest abundance on precisely that part of the shoreline which is sheltered from wave action caused by the prevailing west and south-west winds and this suggests that the frequency with which severe wave action occurs on the various sections of shore may also be important in influencing the distribution of C.germari within the reservoir.

During 1958 the abundance of adult C.germari in the Ramsley and Little Barbrook reservoirs was measured in terms of the mean catch per S.N.S. The results are shown in Table 34 and they show that the abundance of the species in those two reservoirs was comparable to the abundance on sections E.130 to A -10, B 10 to C -20 and D 50 to E of Barbrook reservoir (See Tables 30 and 31). Ramsley reservoir has less macroflora and less organic material on the substratum than Barbrook reservoir, whilst Little Barbrook reservoir has more of both, but neither of these two reservoirs has any section of shore similar in construction to section A 100 to A 300 of Barbrook reservoir. This suggests that, so far as C.germari is concerned, the physical structure of the substratum is important.

(3) Distribution of the adults at different depths :-

Walton (1943) states that C.germari probably lives in deeper water than most other species and that, in one water body, he found it to be very abundant in water at least one metre deep. Data have been collected at Barbrook reservoir which support Walton's statements.

On twelve dates during 1957 net sampling was carried out at 0.5 m. depth as well as the usual 1.0 m. (3 ft.) depth. The results are set out in Table 35 and show that, on all occasions, the adults

Date	Mean catch per S.N.S. and 5% confidence limits	
	Little Barbrook	Ramsley
14.4.58	0.8 ± .51	0.5 ± .52
12.5.58	0.6 ± .51	0.3 ± .27
7.6.58	0.7 ± .48	0.2 ± .38
7.7.58	6.9 ± 3.61	0.4 ± .35
5.8.58	0.2 ± .06	0
30.8.58	6.4 ± 2.69	0.1 ± .14
30.9.58	4.3 ± 1.62	0.6 ± .09
21.10.58	1.5 ± .52	1.8 ± .09

Table 34. Abundance of C.germari adults in Ramsley and Little Barbrook reservoirs during 1958. Based on 20 S.N.S.s at each reservoir on each sampling date.

Date	No. of S.N.S.s at 0.5 m.	Mean catch per S.N.S. with 5% confidence limits where these could be calculated.	
		0.5 m.	1.0 m.
1.5.57	20	2.6	10.2 ± 3.88
15.5.57	20	1.9	11.8 ± 3.80
29.5.57	20	1.3	6.2 ± 2.76
12.6.57	20	2.6	10.2 ± 3.84
21.8.57	15	2.3 ± .52	29.0 ± 5.16
4.9.57	15	3.7 ± .59	20.5 ± 6.14
18.9.57	15	4.7 ± 2.70	44.7 ± 12.83
2.10.57	15	3.1 ± 1.76	70.0 ± 23.96
16.10.57	15	2.7 ± 1.03	87.0 ± 13.21
30.10.57	15	1.7	92.5 ± 20.73
13.11.57	15	0	4.6 ± 2.22
24.11.57	15	0.1	0.6 ± 0.58

Table 35. Comparison of the abundance of C. germari at 0.5 m. and 1.0 m. depth on section A 100 to A 300 of Barbrook reservoir.

were much more abundant at 1.0 m. (3 ft.) depth than at 0.5 m. (1.5 ft.): Popham (1943.a.) studied the depth distribution of C.dorsalis, C.fossarum and C.distincta in six Lake District habitats. He sampled at a range of depths from 0.5 to 3.5 ft. (0.15 to 1.1 m.) and found that nearly 90% of his 1123 specimens were taken at a depth of 0.5 ft. (0.15 m.) and that all the rest, apart from 3 specimens taken at 2.5 ft. (0.75 m.) were found at a depth of 1.5 ft. (0.46 m.).

During 1958, pairs of traps were operated in various depths of water from 0.33 m. (1 ft.) to 2.33 m. (7 ft.) between the net sampling stations A 200 and A 250. Two traps at 0.33 m. (1 ft.) suffered considerable damage and gave no useful results but the other pairs of traps were not damaged to any great extent and the total catches of each of these pairs of traps during each trapping period are shown in Table 36. Although such trap data must be interpreted with considerable reserve, the results show that C.germari is abundant at depths as great as 2.33 m. (7 ft.). The total catches at the various depths for the whole trapping season suggest that the abundance of adults reaches a maximum at a depth of about 1.0 m. (3 ft.) and then falls off slowly at greater depths, at least until a depth of 2.33 m. (7 ft.) is reached.

Thus, both net and trap sampling give results which agree with Walton's statement that this species lives at greater depths than most other British species appear to do. Comparison of the net sample data for C.germari in Barbrook reservoir with Popham's results for three other species gives a striking illustration of this point.

Date of emptying.	Days trapping.	Depth (m.).							Totals.
		.67.	1.00	1.33	1.67	2.00	2.33	Totals.	
2.4.58.	6	47	164	92	47	48	12	410	
10.4.58.	8	5	74	53	29	60	19	240	
16.4.58.	6	27	201	56	44	55	39	422	
24.4.58.	8	72	780	328	372	97	224	1873	
30.4.58.	6	224	427	195	420	277	231	1774	
8.5.58.	8	331	799	521	758	615	662	3686	
14.5.58.	6	176	482	255	208	337	302	1670	
22.5.58.	8	42	99	61	43	70	184	499	
28.5.58.	6	153	284	167	164	157	182	1117	
5.6.58.	8	200	457	287	358	425	285	2012	
11.6.58.	6	67	219	226	342	202	287	1343	
19.6.58.	8	356	500	666	658	530	576	3286	
25.6.58.	6	73	233	284	291	226	254	1361	
Totals.	80	1773	4728	3191	3734	2999	3267	19683	

TABLE.36. Catches of adults in traps at various depths during part of 1958.

Two traps were operated at each depth on each occasion.

(4) Sex ratios on section A 100 to A 300 :-

The sex ratios in the trap catches have already been considered and possible explanations of the remarkably high percentage of males in the spring and early summer trap catches as compared to the percentages in the net samples have already been put forward. It will therefore be assumed here that the sex ratios of the trap catches are not a true representation of the sex ratios in the field and attention will be concentrated on the net data.

The net sample ratios for each of those periods of the year when they might have been expected to be fairly stable, namely the spring to early summer and the autumn periods, have been analysed statistically. In each period the results were found by a Chi-squared test to be heterogeneous and it has been necessary to omit certain samples from each period in order to obtain homogeneity and hence to estimate the overall sex ratio for that period. This procedure is not very satisfactory but it has been necessary in order to obtain an estimate of the sex ratio for each period.

The samples of the old generation (spring to early summer) adults for 1957 were scored for sex and the results are shown in Table 37A. The total numbers of males and females for all of the samples were found and these were taken as representing the expected ratio of males to females. A Chi-squared test was then applied to the data and it was found that they were not homogeneous at the 5% level of confidence. Examination of the Table shows that the data, ^{on alternate} on alternate sampling dates give similar sex ratios but that the data for adjacent dates do not. It seems, in fact, that there

(A)

Date.	3.4.58.	17.4.58.	1.5.58.	15.5.58.	29.5.58.	12.6.58.	Totals
Males observed.	55	52	77	61	48	63	356
Females observed.	65	89	77	115	45	95	486
Totals.	120	141	154	176	93	158	842
Males expected.	51	60	65.5	75	39.5	67	
Females expected.	69	81	88.5	101	53.5	91	
Chi-squared.	.546	1.857	3.514	4.553	3.179	.415	

Expected ratio:- males:females :: 356:486 :: 42.5:57.5.

Total Chi-squared= 14.06 with 5 degrees of freedom.

Thus $P < .02$ and the results are not homogeneous at the 5% confidence level.

(B)

Date.	3.4.58.	1.5.58.	29.5.58.
Chi-squared.	.533	.058	.269

Expected ratio :- males:females :: 180:187 :: 49:51.

Total Chi-squared= 0.86 with 2 degrees of freedom.

Thus $P > .5$ and the results are homogeneous at the 5% confidence level.

(C)

Date.	17.4.58.	15.5.58.	12.6.58.
Chi-squared.	0	.380	.550

Expected ratio :- males:females :: 176:299 :: 37:63.

Total Chi-squared= 0.94 with 2 degrees of freedom.

Thus $P > .5$ and the results are homogeneous at the 5% confidence level.

TABLE.37. Old generation sex ratios for 1957.

was a fortnightly alteration between samples giving a sex ratio of about 1:1 and samples giving a marked excess of females. Separation of the data into these two groups and Chi-squared testing within each group (Table 37B and C) shows that each of these two groups is homogeneous. The reasons for this regular fluctuation in sex ratio remains obscure.

The old generation data for 1958 are shown in Table 38A. Again, a Chi-squared test shows that the data are not homogeneous at the 5% confidence level. The highest values of Chi-squared are given by the samples taken on 11.4.58, 25.4.58, 1.5.58 and 12.6.58. If these samples are omitted and the value of Chi-squared is recalculated (Table 38B) the data are found to be homogeneous and give a sex ratio of 57 males to 43 females. As the data for all the samples cannot be used to obtain a statistically satisfactory estimate of the sex ratio, the result obtained from Table 38B has been taken as the most reliable estimate available and has been used in subsequent calculations for which the sex ratio during the spring to early summer of 1958 is required.

The sex ratios of the new generation samples for 1957 and 1958 are shown in Tables 39A and 40A, respectively. The results for each of these years are heterogeneous and therefore certain samples have been omitted in order to obtain estimates of the sex ratios. The data for both years give sex ratios fairly close to a 1:1 ratio, though the 1957 sample data were found to be heterogeneous at the 5% confidence level when two of the samples had been omitted from Table 39B.

(A)

Date.	28.3.58.	1.4.58.	11.4.58.	17.4.58.	25.4.58.	1.5.58.	9.5.58.	15.5.58.	23.5.58.	29.5.58.	6.6.58.	12.6.58.	Totals.
Males observed.	88	14	41	87	92	140	113	142	118	132	36	88	1091
Females observed.	71	9	18	81	105	82	96	103	87	89	17	112	870
Totals.	159	23	59	168	197	222	209	245	205	220	53	200	1961
Males expected.	88	13	33	93	109	123	116	136	114	122	29.5	111	
Females expected.	71	10	26	75	88	99	93	109	91	98	23.5	89	
Chi-squared.	0	.177	4.40	.867	5.93	5.27	.174	.595	.316	1.84	3.23	10.71	

Expected ratio:- males:females :: 1091:870 :: 55:5:44.5. Total Chi-squared = 33.51 with 11 degrees of freedom.
 Thus $P < .001$ and the results are not homogeneous at the 5% confidence level.

(B)

Date.	28.3.58.	1.4.58.	17.4.58.	9.5.58.	15.5.58.	23.5.58.	29.5.58.	6.6.58.	Totals.
Males observed.	88	14	87	113	142	118	132.	36	730
Females observed.	71	9	81	96	103	87	89	17	563
Totals.	159	23	168	209	245	205	221	53	1283
Males expected.	91	13	96	119	140	117	126	30	
Females expected.	68	10	72	90	105	88	95	23	
Chi-squared.	.231	.197	1.970	.703	.067	.020	3.619	2.765	

Expected ratio:- males:females :: 730:563 :: 57:43. Total Chi-squared = 9.57 with 7 degrees of freedom.
 Thus $P > .20$ and the results are homogeneous at the 5% confidence level.

TABLE.38. Old generation sex ratios for 1958.

(A)

Date.	21.8.57	4.9.57	18.9.57	2.10.57	16.10.57	30.10.57	Totals.
Males observed.	206	131	323	569	693	646	2568
Females observed.	229	179	337	349	608	743	2445
Totals.	435	310	660	918	1301	1389	5013
Males expected.	222	158	337	468	663	707	
Females expected.	213	152	323	450	638	682	
Chi-squared.	2.354	9.411	1.188	2.643	2.767	10.727	

Expected ratio :- males:females ::2568:2445 ;: 51:49.

Total Chi-squared=29.09 with 5 degrees of freedom.

Thus $P < .001$ and the results are not homogeneous at the 5% confidence level.

(B)

Omitting the data for 4.9.57 and 30.10.57 and recalculating the values :-

Expected ratio :- males:females :: 1791:1523 ::54:46.

Total Chi-squared = 17.04 with 3 degrees of freedom.

Thus $P < .001$ and the results are still not homogeneous at the 5% confidence level.

TABLE.39. New generation sex ratios for 1957.

(A)

Date.	8.10.58	9.10.58	10.10.58	11.10.58	13.10.58	14.10.58	Totals.
Males observed.	691	910	740	906	946	808	5001
Females observed.	762	772	740	774	783	721	4552
Totals.	1453	1682	1480	1680	1729	1529	9553
Males expected.	763	883	777	882	907.5	802.5	
Females expected.	690	799	703	798	821.5	726.5	
Chi-squared.	14.31	1.738	3.709	1.375	3.439	.079	

Expected ratio :- males:females :: 5001:4552 :: 52.5:47.5.

Total Chi-squared=24.65 with 5 degrees of freedom.

Thus $P < .05$ and the results are not homogeneous at the 5% confidence level.

(B)

Omitting the data for 8.10.58 and recalculating the values :-

Expected ratio :- males:females :: 4310:3790 :: 53.2:46.8.

Total Chi-squared=8.92 with 4 degrees of freedom.

Thus $P > .05$ and the results are homogeneous at the 5% confidence level.

TABLE.40. New Generation sex ratios for 1958.

The sex ratios during the decline of the old generation and emergence of the new generation in 1958 are shown in Table 41. The data show the general trends in the sex ratio quite clearly. It can be seen, that, during the period when the old generation was observed to be decreasing in abundance, (See Table 48), the percentage of males amongst the survivors increased and this shows that the females died slightly earlier than the males. The sex ratios of the new generation adults give no indication that there is any difference in the time taken by nymphs of each of the sexes to reach the adult stage.

(5) Stridulation and Copulation.

Observation of C.germari under field and aquarium conditions has shown that the male generally attempts to copulate with a swimming female. The male seizes the female, the two animals rise together to the water surface and then, either the genitalia are engaged and the copulants swim to the bottom together, or, the animals part company and swim away from one another. It is therefore possible to obtain an approximate idea of the amount of copulation taking place in the field by noting whether many or few such pairs were observed at the water surface during each day's sampling. Such observations were made during 1958 and the following pattern was observed along section A 100 to A 300 :-

(a) Three pairs observed attempting to copulate on 17.4.58 when the water temperature was 5.0°C.

(b) Large numbers of pairs observed on 23.4.58, 24.4.58, 25.4.58 and 30.4.58 when the water temperatures were 9.0, 8.0, 9.0 and 10.5°C respectively.

Date	Number examined	Percentage of males.		
		Old generation.	New generation.	Whole sample.
20.6.58	105	56		56
23.6.58	108	66		66
26.6.58	95	72		72
4.7.58	194	66		66
10.7.58	125	45		45
18.7.58	81	53		53
24.7.58	77	69		69
1.8.58	67	83		83
7.8.58	34	88		88
15.8.58	51	84		84
21.8.58	148	96	54	62
29.8.58	211	100	60	70
4.9.58	154	100	54	61
12.9.58	322		56	56
18.9.58	537		51	51
26.9.58	1295		53	53
2.10.58	697		53	53

Table 41. Sex ratios during the decline of the old generation and emergence of the new generation in 1958. After 4.9.58 it was not possible to separate the remnants of the old generation from the new, so all specimens were treated as new generation material.

(c) After 1.5.58 the number of pairs observed decreased until by mid-May they were only seen very occasionally.

During 1957 very few pairs were observed attempting to copulate and it is therefore important to note that the winter of 1956 to 1957 was a very mild one and that when collecting began on 3.4.57 the water temperature had already reached 10.0°C.

Lassen (1938) states that the time of pairing in water bugs depends on the water temperature, and Poisson (1933) states that mating does not generally occur at temperatures lower than 11°C. This would explain the 1958 observations on C.germari and would suggest that a temperature of about 8°C is required by this species before copulating occurs on a large scale. It would also explain the failure to observe more than a few pairs attempting to copulate during 1957, for the relatively high water temperature early in the year would mean that the main copulation period of the season would be over by the time observations began. The belief that copulation is not attempted below a certain temperature value is further supported by the fact that males collected from the field on 3.3.58 and kept in jars at 20°C were observed to stridulate and attempt to copulate, although no such behaviour was occurring in the field at that time of the year.

Thus the present observations on C. germari support the view that a certain minimum temperature is required before copulation takes place but show that the minimum temperature for this species is several degrees lower than the 11°C observed in other species by Poisson.

The method and function of stridulation in the Corixidae has received a great deal of attention from a number of writers. Most modern authorities incline to the view of Mitis (1935) that, in the sub-family Corixinae, the sound is produced by rubbing a field of pegs on the fore femur over the sharp edge of the head capsule. Males of C.germari stridulating in aquaria have always been seen to make such a movement during sound production. Adult males of C.germari, collected from the field and kept in aquaria have been observed to stridulate at all times of the day but do so chiefly at dusk. These males have been observed to stridulate whilst swimming as well as when at rest.

Stridulation occurs only during the part of the year when copulation is taking place and it is therefore almost certain to have some significance in the process of reproduction. Its exact function, however, is not very clear. Leston (1955) and Schaller (1951) state that the stridulation of male Corixidae attracts the females for mating and have found that males reply to artificial sounds or the calls of other males. Similarly, Pringle (1954) states that the singing of Cicadas serves to assemble local populations into small groups for copulation. In the present work C.germari was observed in jars kept in the laboratory and the stridulation of the males was observed to excite other males and to cause them to stridulate too, but it did not have any noticeable effect on the females. The males showed little interest in resting females but when they encountered a swimming female copulation was usually attempted. Thus it would appear that the recognition and location of members of the opposite sex is primarily a response to a visual stimulus, at least over distances of a few centimetres,

and that the females play a passive part in the process. It is possible that stridulation may draw animals together from larger distances before visual recognition takes place. Thus, though these observations are not necessarily opposed to the conclusions of previous workers, they do suggest that it would be useful to assess the possibility that stridulation in the Corixidae is primarily a means of social stimulation between males.

(6) The egg and oviposition.

The eggs of the Corixidae have been described in a general way by Packard (1898). The number of fully developed eggs in the oviducts of the females of C.germari in Barbrook reservoir during the 1957 and 1958 seasons and also the percentages of the females collected in 1958 that were found to contain such eggs have been determined by dissecting samples of females collected from section A 100 to A 300. The results are shown in Tables 42 and 43. The fully developed egg within the oviduct has a firm integument, a peduncle, a basal attachment disc and the characteristic apical micropyle (see photograph 16) and can therefore be readily distinguished from the developing ova. The data in Table 42 clearly show an increase in the mean number of fully developed eggs within the oviducts throughout the oviposition period. This shows that the eggs are continually being developed during the oviposition period and thus the rate of change of the mean number of eggs in the oviducts will be related to the rate of egg production and the rate of oviposition in the following way :- If δa is the mean rate of accumulation of eggs in the oviducts of the population sampled, δd is the mean rate at which eggs are produced within the

Date.	Mean number of fully developed eggs per female.
3.4.57	6.8
17.4.57	9.0
1.5.57	9.2
15.5.57	11.3
29.5.57	10.3
12.6.57	11.6
26.6.57	15.4

Table 42. Mean number of fully developed eggs per female during 1957. After 26.6.57 the old generation females died and no eggs were found in the oviducts of the new generation females until 2.4.58.

Date.	Mean no. of fully developed eggs per female.	Percentage of females containing eggs.
28.3.58	0	0
2.4.58	0.3 ± .59	4
11.4.58	0.3 ± .37	10
15.4.58	1.8 ± .80	51
17.4.58	1.8 ± .69	41
25.4.58	8.3 ± 1.26	87
1.5.58	8.3 ± 1.05	96
9.5.58	8.9 ± 1.24	100
15.5.58	7.7 ± 1.00	100
23.5.58	7.6 ± 1.59	98
29.5.58	9.1 ± .99	98
6.6.58	10.0 ± 2.01	98
12.6.58	11.3 ± 1.13	99
20.6.58	10.2 ± 1.36	97
26.6.58	12.0 ± 1.29	100
4.7.58	9.2 ± 1.70	95
10.7.58	10.3 ± 1.66	95
18.7.58	9.9 ± 2.38	86
24.7.58	5.3 ± 2.05	55
1.8.58	5.2 ± 3.19	45
5.8.58	1.6	29

TABLE.43. Mean numbers of fully developed eggs per female and percentages of females containing such eggs during 1958.

the females and δ_o is the mean rate of oviposition by the population sampled, then :-

$$\delta_a = \delta_d - \delta_o$$

Thus when δ_a is positive $\delta_d > \delta_o$

and when δ_a is negative $\delta_o > \delta_d$

It must, however, be noted that this may not be quite true during periods when the oviposition rate is very low, for Poisson (1923) states that at low temperatures eggs are retained by the female and slowly degenerate. Nevertheless, counts of the fully developed eggs in the oviducts will give a rough measure of the relative rates at which egg production within the females and oviposition go on. It is clear that during 1957 the mean rate of egg production exceeded the mean rate of oviposition throughout the oviposition period. The reasons for this will be considered later. The data for the 1958 oviposition period (Table 43) show that in the early part of the season the rate of egg production exceeded the rate of oviposition so that eggs accumulated in the oviducts. Later on the mean number of eggs in the oviducts of the females fell, showing that the rate of oviposition had become greater than the rate of egg production. The same point is illustrated by the percentages of the females examined that were found to contain fully developed eggs in their oviducts (Table 43).

Banks (1939) has described the egg of C.germari. The egg illustrated in photograph 16 is one dissected out of the oviduct of a female and shows the small attachment disc, the micropyle region

KEY TO PHOTOGRAPHS 16 and 17.

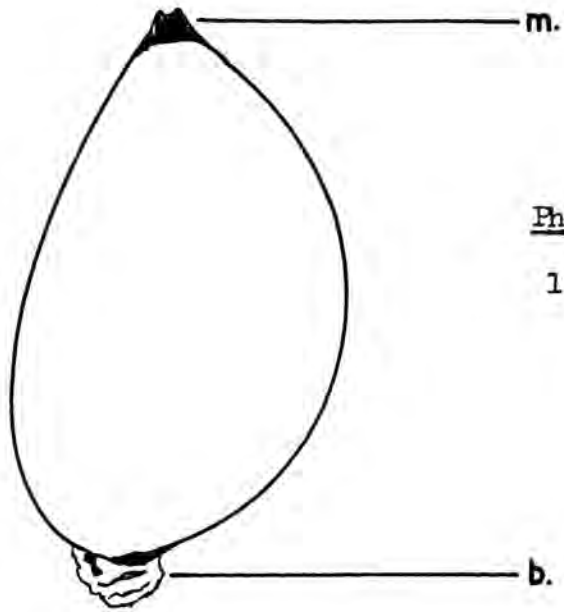
m = micropyle.

b = basal disc.

c = cement.

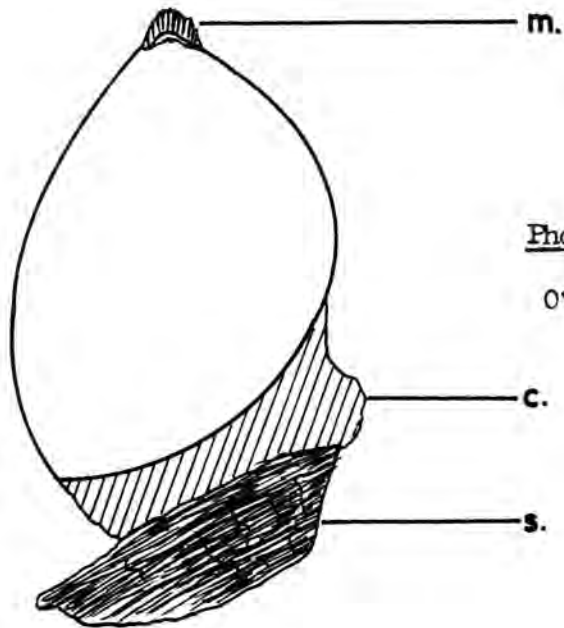
s = substratum.

The measurements refer to the length of the integument of the egg along its longest axis, excluding basal disc, cement and substratum.



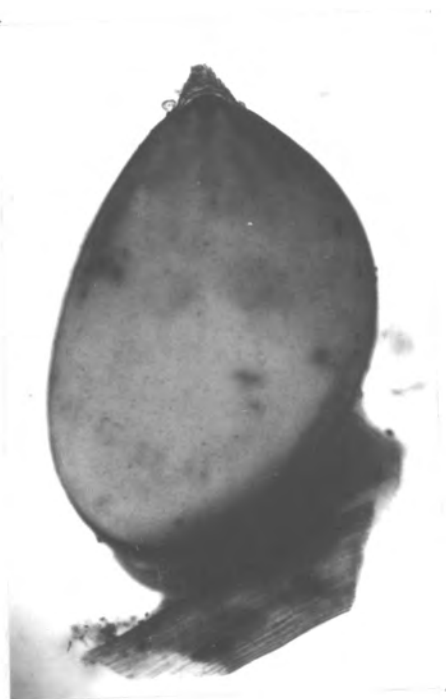
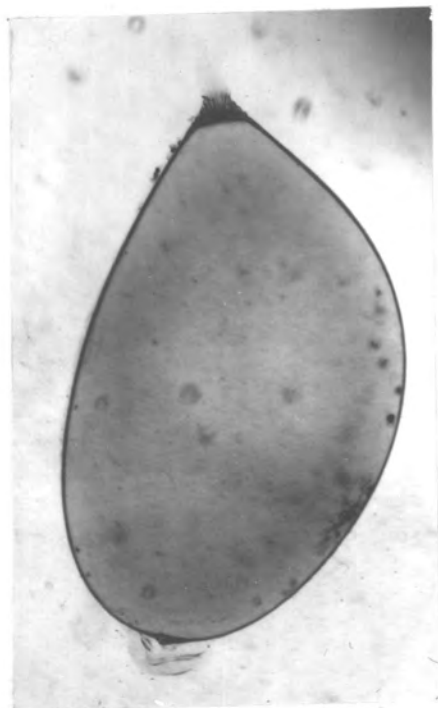
Photograph.16.

1.0 mm.



Photograph.17.

0.95 mm.



and the shape of the egg. Each egg is attached to the substratum by a substantial quantity of brown cement which completely hides the small basal attachment disc (Photograph 17). The shape of the egg is such that when the egg is attached to a plane surface the egg is inclined at an angle to that surface.

After about 8 days at 16°C the eyes of the instar 1 nymph can be seen through the integument of the egg as a pair of small reddish spots. Subsequently, the eyes become larger and the red dorsal abdominal glands and limbs of the nymph can be seen (Photograph 18).

Banks (1939) found that the eggs of C.germari hatched in about 20 days but did not state at what temperature. In the present work the time taken to hatch at a number of temperatures was determined. Seven jars were set up, each containing forty 2 x ½ inch glass specimen tubes half full of water. Water was then put in the jars until the water level in each jar coincided with the level in the tubes. Freshly laid eggs collected from the field were used in the experiment and one was placed in each tube. Each jar was then kept at constant temperature, the temperatures used being 5, 10, 20, 25 and 30°C. The seventh jar was kept at 5°C for seven days and was then kept at 25°C until hatching occurred. The jars were examined daily and the number of eggs hatching at each temperature on each day was noted. The results for the four highest temperatures are summarised in Figure 22, but hatching at 10°C took too long for daily observations to be continued and it is only possible to state that at that temperature hatching took between 46 and 56 days. Figure 22 shows that the relationship between hatching time and temperature is very roughly linear.

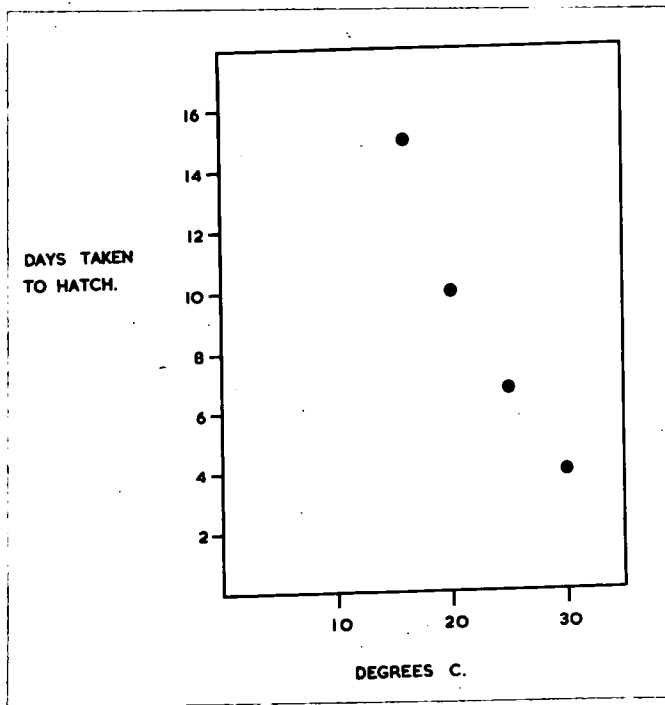


Figure.22. Relationship between temperature and time taken for eggs to hatch.

Poisson (1933) studied the effect of temperature on the embryonic development of C.lateralis. He found that between 0 and 9°C embryonic development was arrested and the eggs could be preserved for 10 to 12 months if cooled down in the early stages of development. The eggs of C.germari kept at 5°C for seven days did not show any signs of development, but when the temperature was raised to 25°C hatching occurred in 6 to 7 days. Other C.germari eggs kept at 5°C for 4 months did not show any signs of development during that period. These observations on the eggs of C.germari agree with Poisson's statements regarding the egg of C.lateralis. Now, assuming Figure 22 to approximate to a straight line and assuming that the number of degree-days above the threshold value required for complete embryonic development is very roughly constant at all temperatures studied, it is possible to calculate that the threshold value is about 8°C and that between 90 and 120 degree-days above this temperature are required for complete embryonic development by C.germari. Clearly the assumptions made above are not strictly true and the values used in the calculation are not sufficiently accurate to give very reliable estimates of the threshold value of the number of degree-days required for development, but the figures derived above do, at least, give a means of estimating very roughly how long the eggs of C.germari will take to hatch at any given temperature.

The results so far presented show that the eggs of C.germari can hatch even at the abnormally high temperature of 30°C (See Fig.3). Nevertheless, the results obtained suggest that there is a marked fall-off in percentage hatching success at temperatures above 20°C

and that the optimum temperature, under laboratory conditions, lies between 10 and 20°C. Thus, in the experiment described above, the percentages of eggs hatching successfully were 40, 47.5, 40, 35 and 5 at temperatures of 10, 16, 20, 25 and 30°C respectively.

At eclosion the integument of the egg is split from the micropyle region for about half to one-third of ^{the} length of the egg into a series of 6 to 8 petal-like strips (Photograph 19) and the nymph emerges through the space so formed. In the case of eggs hatching in the laboratory, the nymphs have occasionally been observed to be attacked by the fungus Saprolegnia sp. whilst in the process of emerging. This has not been observed in the field. Griffith (1945) found that the integument of the egg of R.acuminata was split into four strips at the apical end during eclosion. The number of strips is greater and rather more variable in the case of C.germari aggs.

Specimens of C.punctata, C.wollastoni and C.sahlbergi kept in jars in the laboratory were found to oviposit readily on a variety of materials including dead leaves, small twigs, Elodea sp, Juncus effusus stem, Equisetum stem, fibrous peat and even the glass sides of the jars. Leston (1955) studied C.punctata, C.dorsalis and C.falleni under laboratory conditions and found that these species would oviposit on pieces of Elodea canadensis and that they usually chose pieces more than 2 cm. long. He also found that females of C.castanea provided with Elodea and Juncus communis oviposited on

both with no suggestion of preference. In the present work it was found that specimens of C.germari kept in jars in the laboratory would oviposit on pieces of Chara and on J. effusus stems, the eggs usually being laid at night and placed on concealed parts of the plant material. As a result of this, it was assumed that C.germari had similar oviposition habits to the other species mentioned above. Therefore, in 1950 ^{standard-sized} standardized bundles of J. effusus stem were tied to stones wrapped in black mosquito netting, such as was used on the traps, and were submerged in the reservoir ^{along} section A 100 to A 300. The bundles of Juncus stem were examined at intervals of one week. On 30.4.58 no eggs were found on the Juncus bundles, but eggs were found on the traps at all depths and on the stones used to anchor the Juncus bundles. Examination of the ordinary stones of the substratum showed that eggs had been laid on them too, but handfuls of J. bulbosus agg. and dead stems of J. effusus and grass from section B 10 to C -20 were carefully examined without any eggs being found. These observations show that although C.germari will lay eggs on dead or living vegetation it shows a marked preference for stones.

On the same date 50 stones from 0.5 m. (1.5 ft.) depth were carefully removed from the stony bank of section A 100 to A 300. The orientation of each stone when lying on the bottom was noted and the numbers of eggs on different parts of each stone were determined. The results are summarised in Table 44. Division of the surface of each of a number of irregular stones into the four regions shown in this Table is a somewhat arbitrary matter and care must be exercised

	Total number of eggs.
Top of stone	0
Bottom of stone	199
Overhung sides and crevices	72
Vertical and upward-facing sides	22

Chi-squared =199
P < .001

Chi-squared =26.6
P < .001

Table 44. Parts of stones selected as oviposition sites. Fifty stones were examined and thirty-seven of them had eggs on. The figures quoted are the total numbers of eggs on the different regions of these thirty-seven stones.

in drawing conclusions from such data. Nevertheless, if, as seems reasonable, it is assumed that the top and bottom surfaces have about the same area, it is possible to compare the total number of eggs on each of these two parts of the stones by means of a Chi-squared test. Such a test has been applied to the data in Table 44 and shows that significantly more eggs are laid on the lower than on the upper surfaces of the stones. The eggs laid on the sides of the stones have been divided into those laid on overhanging sides or in crevices and those laid on upward-facing or vertical surfaces. A Chi-squared test shows that significantly more eggs are laid in the former than in the latter places.

Thus C.germari not only shows a preference for stones as oviposition sites but also shows a marked preference for the concealed or downward-facing surfaces of those stones.

The habit of ovipositing in concealed and therefore often dark places amongst the stones suggest^s that, during the oviposition period, the females of C.germari might differ somewhat from the males in their response to illumination. Such an effect would help to explain the high proportion of males in trap samples taken during the oviposition period. To test this possibility a simple experiment was performed. A small enamel dish was set up with a 1 cm. (.25 in.) to 1.5 cm (.37 in.) layer of Barbrook reservoir sand on the bottom covered by about 3 cm (.75 in.) depth of water. Twenty females of C.germari were placed in the dish and half the top of the dish was shaded by means of a piece of cardboard. The dish was then placed

in the sunlight in such a position that half of it was illuminated by the sun and half was shaded. After 15 minutes the number of insects in each half of the dish was determined. The position of the cardboard was then altered so that the halves of the dish under shade and sunlight were reversed and the experiment was repeated. This process was continued for five trials with each sex and the results are shown in Table 45. A Chi-squared test showed that there was no significant difference between the numbers of males in each of the two halves of the dish but that the females showed a significant tendency to position themselves in the less brightly illuminated half.

The rate of oviposition during 1958 was determined on section A 100 to A 300 by placing at a depth of 1.0 m. (3 ft.) a series of five stones of similar size and shape each of which was wrapped tightly in a piece of the blackened netting used on the traps. At intervals of seven days the stones were examined and all eggs laid on the stones and netting were removed and counted. The results are shown in Table 46 and Figure 23. It is only reasonable to assume that the oviposition rate on these stones at different times in the season is proportional to the rate on section A 100 to A 300 as a whole if it can be shown that even the highest number of eggs recorded per stone per week represented a considerably lower egg density than would be obtained on a similar stone from which the eggs were not periodically removed. Such a site was placed in the reservoir on 30.4.58 and when it was removed on 11.9.58 it had 566 eggs on it, of which 433 had hatched. This shows that the number of eggs deposited on the five sites during each week was limited by the oviposition rate of the animals and not by the egg carrying capacity of the sites. Hence

Trial	Males		Females	
	Shaded	Unshaded	Shaded	Unshaded
1	13	7	15	5
2	13	7	14	6
3	12	8	16	4
4	9	11	17	3
5	12	8	13	7
Totals	59	41	75	25
Chi-squared Probability	3.24 > .05		25.0 < .001	

Table 45.

Date.	Number of eggs removed on each date.					Totals.	Total eggs removed by each date as % of the season's total \pm 5% confidence limits.	
	i	ii	iii	iv	v			
25.4.58	0	0	0	0	0	0	0	
1.5.58	20	26	23	23	26	118	2.2	\pm 2.70
8.5.58	21	32	71	66	112	302	7.7	\pm 2.60
15.5.58	34	50	76	53	75	288	13.0	\pm 2.53
22.5.58	68	40	49	43	38	238	17.4	\pm 2.47
29.5.58	16	31	33	34	53	167	20.4	\pm 2.42
5.6.58	40	62	88	49	93	332	26.5	\pm 2.32
12.6.58	60	111	128	66	95	460	34.9	\pm 2.18
19.6.58	134	115	135	125	136	645	46.8	\pm 2.15
26.6.58	90	129	108	88	117	532	56.5	\pm 1.79
3.7.58	127	131	127	85	103	573	67.1	\pm 1.55
10.7.58	170	165	158	119	112	724	80.3	\pm 1.20
17.7.58	65	181	89	124	50	509	89.7	\pm 0.87
24.7.58	48	69	90	45	69	321	95.5	\pm 0.57
31.7.58	9	34	34	14	52	143	98.2	\pm 0.36
7.8.58	16	11	8	14	15	64	99.4	\pm 0.21
14.8.58	3	5	2	4	12	26	99.8	\pm 0.06
21.8.58	0	0	2	3	4	9	100	
28.8.58	0	0	0	0	0	0	100	

TABLE.46. Numbers of eggs laid on five stones (i to v) on section A100 to A300 during 1958.

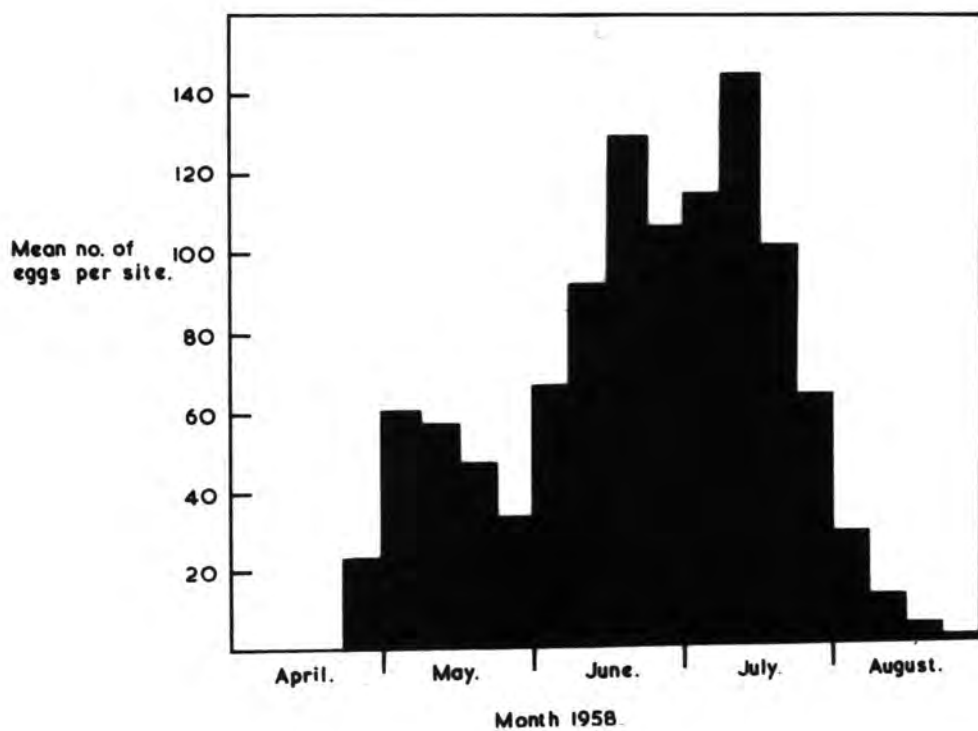


Figure.23. Oviposition rate on section A100 to A300 in 1958.

the data in Table 46 can be taken as a relative measure of the rate of field oviposition in 1958.

Figure 24 shows the mean number of eggs laid per site per week, the mean number of fully developed eggs per female found in samples of females, and the water temperatures during the 1958 oviposition period. Poisson (1933) states that the onset of oviposition in the Corixidae is governed by temperature and that it will not occur at temperatures lower than 9 to 10°C. Figure 24 shows that, although the females contained fully developed eggs before the temperature reached 9 to 10°C, no eggs were laid until that temperature^{was} reached. During 1959 oviposition sites were placed in the reservoir on 21.4.59 when the water temperature was 9.0°C. No eggs were found on the sites on 22.4.59 when the water temperature was 9.5°C, but eggs were found on 24.4.59 by which time the temperature had reached 11.0°C. Thus these data for C.germari agree with Poisson's statements regarding the Corixidae in general.

(7) Flight:-

Popham (1943 a) has shown that adult Corixidae are stimulated to flight by high temperatures, overcrowding and unsuitable backgrounds. He suggests that flight is a means of escaping from an unsuitable habitat or of reducing abundance in an excessively crowded habitat. A similar point is made by Brown (1954) who, on the basis of light trap collections, states that dispersion by flight takes place chiefly in the spring and the autumn. Brown suggests that the spring dispersion is of overwintered adults and probably occurs before

**MEAN EGGS PER FEMALE, OVIPOSITION RATE
AND WATER TEMPERATURE . 1958.**

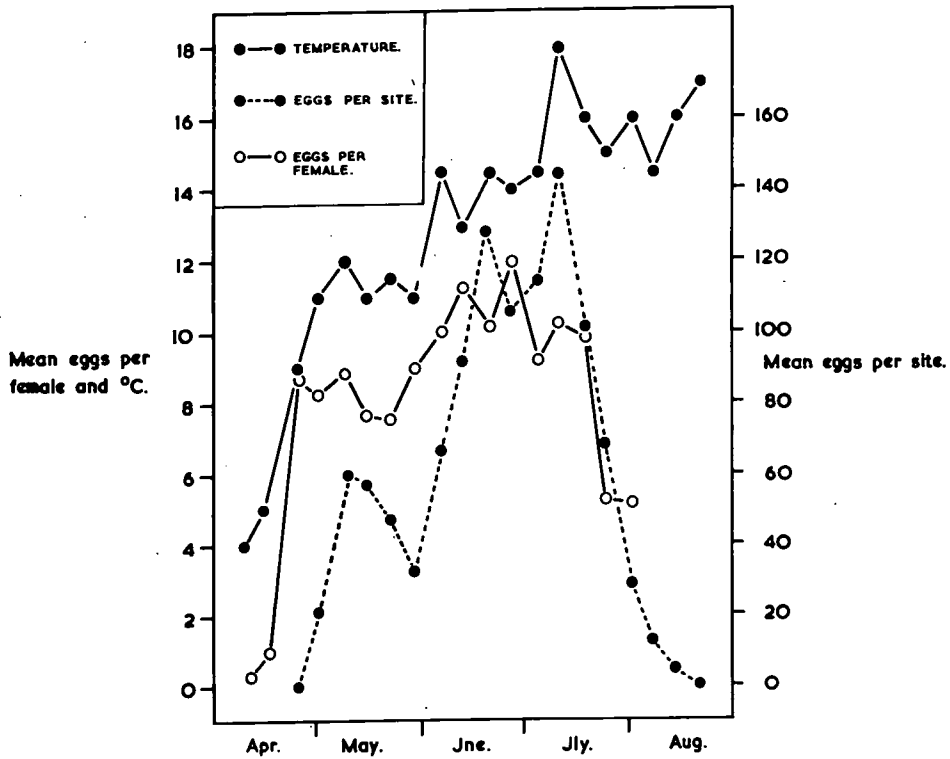


Figure 24.

breeding, whilst the autumn dispersion is of new generation adults and is probably a response to excessively high population densities.

Regarding the climatic conditions required for flight, Popham (1952a, 1952b) states that under normal conditions no flight occurs at temperatures lower than 15°C and he suggests that no flight occurs during the winter months. The fact that hot, still days appear to stimulate Corixidae to flight was noted by Macan (1939). Poisson, Richard and Richard (1957) claim that the greatest amount of flight activity coincides with large fluctuations of temperature, humidity, pressure and the proximity of storms. These three workers also claim that periods of flight activity are associated with full and new moons.

Attempts at flight by C.germari were observed at Barbrook on 3.10.57, 23.4.58, 30.4.58, 1.5.58, 22.4.59 and 23.4.59. The water temperatures for the last five dates were 9.0 , 10.5 , 11.0 , 9.5 and 10.0°C respectively, and on all dates the air temperature was about 20°C . This shows that C.germari will attempt to fly when the water temperature is lower than the 15°C postulated by Popham. Each of the days when attempts at flight were observed were hot days with relatively light winds. The insects were observed either to emerge from the water onto the shore and attempt to fly from there or to attempt to fly from the water surface. It was noticeable that during short periods when the sun was obscured by cloud the animals on the shore retreated into the water and those on the water surface submerged themselves. (Wigglesworth (1950) draws attention to

the importance of insolation as a means of raising the body temperatures of various insects to a suitable level for flight activity and also to the fact that when insects exposed to direct insolation are shaded their body temperature falls rapidly. Such effects will be particularly important in the case of aquatic animals whose body temperatures on emergence from the water are usually several degrees lower than air temperatures in the shade. In addition, C.germari does not carry out any preliminary wing vibration as a means of raising its body temperature prior to flight. Thus the pause between emergence from the water and attempted flight, which was observed by Popham and interpreted by him as a period of wing drying, may also be important, in the case of upland species, as a period when the body temperature is raised by insolation to a level sufficient for flight to occur. Also, if this be the case, then it is highly probable that suitable conditions for nocturnal flight occur very rarely in large upland water bodies such as Barbrook reservoir where the water temperatures and the night-time air temperatures are likely to be well below 20°C even during most of the summer.

Although large numbers of C.germari have been observed attempting to fly from Barbrook reservoir, almost all of them flew only a metre or two before falling back into the water or onto the shore and less than ten specimens have been observed to succeed in flying away from the reservoir. This suggests that flight from Barbrook reservoir has a negligible effect on the abundance of C.germari in the reservoir, a view which is supported by the fact that there was no detectable decrease in the catch per S.N.S. on the sampling occasion following

any of the observed "flight days" as compared to the catch per S.N.S. on the sampling occasion preceeding each "flight day".

The species composition of catches of flying or immigrant Corixidae have been studied by Thomas (1938), Brown (1951-2), Leston and Gardner (1953), Leston (1954) and Poisson, Richard and Richard(1957). The data given by these writers are from various places in the south of England except for the last three who worked in France. Although the species composition of each of the samples will depend to some extent on the species present and their relative abundance in each area, and possibly also on the relative susceptibilities of the various species to capture in light traps, comparison of the data shows that there is a general tendency for five species to predominate in these samples. These species, C.dorsalis, C.praeusta, C.lateralis and C.sahlbergi, are all lowland species which often occur in small water bodies which are liable to be unstable as regards water level and changes wrought by man. For species living in such places great mobility may be very useful as a means of maintaining or increasing the number of habitats occupied by the species and in remedying temporary extinction of the species in particularly unstable water bodies. For such species as C.germari which occur chiefly in larger, more stable water bodies large scale dispersion by flight may be a disadvantage owing to the fact that the larger type of water bodies favoured by this species will, in general, be scarce and hence the probability of flying individuals finding a suitable habitat to land in will be very small. During early June 1959 a preliminary experiment was conducted on C.germari, C.wollastoni and C.sahlbergi in an attempt to estimate the relative willingness of each of these species to fly. Two trials were

made for each species. For each species an enamel dish was set up containing bottom material from the habitat where the specimens of that species were collected. The dishes were filled with water to a standard level and the bottom material was arranged so as to form a sloping ramp coming up from the water at one end of each dish. Each dish was then illuminated by means of a 100 watt electric bulb shining obliquely onto the water at the shallow end of the dish from a distance of 1.5 ft. (0.5 m.). In the first trial 15 individuals of each species were put into the appropriate dishes and the number of specimens remaining in each dish was noted every half hour. The results are shown in Table 47. In the second trial, 10 individuals of each species were used. The results are shown in Table 48. No specimens of C.germari flew from the dish during either trial and a Chi-squared test showed that, in both trials, significantly more specimens of C.sahlbergi and of C.wollastoni than of C.germari flew from the dishes. This again suggests that C.germari is not a species that flies readily, though further trials at different times of the year would be required in order to prove this point conclusively. No physical reason has been found for the apparently poor powers of flight in this species, the wings are quite well developed and in the specimens so far dissected the flight muscles appeared to be adequately developed.

The evidence so far available therefore suggests that dispersion by flight is not important to C.germari as a means of reducing excessive abundance, though the relatively small numbers that do fly from Barbrook reservoir might be a means of establishing the species in new

Time (hours)	Temperature (°C.) of water	<u>C.germari</u>	<u>C.wollastoni</u>	<u>C.sahlbergi</u>
0	16.5	15	15	15
0.5	17.0	15	14	15
1.0	17.5	15	14	15
1.5	18.5	15	13	14
2.0	20.0	15	12	12
2.5	20.0	15	11	12
3.0	21.0	15	10	11
3.5	21.0	15	10	10
4.0	22.0	15	10	9

Table 47. The numbers of each of three species still present in the dish after each half hour period. The numbers of C.germari which flew and did not fly from the dish during the four hour period were compared with the corresponding values for each of the other species by means of 2 x 2 contingency tables. The values obtained were :- C.germari and C.sahlbergi, Chi-squared = 8.64 and $P < .001$; C.germari and C.wollastoni, Chi-squared = 6.00 and $P < .001$.

Time (hours)	Temperature (°C.) of water	<u>C.germari</u>	<u>C.wollastoni</u>	<u>C.sahlbergi</u>
0	19.5	10	10	10
0.5	20.0	10	10	9
1.0	21.0	10	9	6
1.5	21.0	10	7	5
2.0	22.0	10	6	4
2.5	22.5	10	4	4
3.0	22.5	10	3	1
3.5	22.0	10	3	1
4.0	22.0	10	2	1

Table 48. Explanation as for Table 47, except that the data for C.germari and C.sahlbergi gave Chi-squared = 16.36 and $P < .001$, the data for C.germari and C.wollastoni gave Chi-squared = 13.30 and $P < .001$.

habitats and of maintaining it in nearby habitats less favourable to it than Barbrook reservoir.

On 30.4.58 samples were taken of the specimens attempting to fly from the reservoir. Forty-three specimens were taken from the sandy shores at B, and 35 (81%) of these were found to be males. From the water surface on section A 100 to A 300 seventy-eight specimens were collected, of which 37 (47%) were males. A net sample of swimming specimens taken from section A 100 to A 300 ~~taken~~ on 1.5.58 contained 222 specimens of which 140 (63%) were males. The sex ratios of these three samples were tested by Chi-squared methods which showed that the two samples of insects which attempted to fly differed significantly from one another and from the sample of swimming specimens, so far as sex ratio was concerned.

The females collected on 30.4.58 whilst attempting to fly from the water surface were dissected and most of them had fully developed eggs in their oviducts. Thus if they had managed to fly to a new habitat they would have been able to lay fertile eggs.

(8) Parasites of C.germari.

An internal parasite occurred commonly in specimens of C.germari from Barbrook, Ramsley and Little Barbrook reservoirs. This is probably a gregarine protozoan but so far it has not been identified. This parasite has also been found in occasional specimens of C.praeusta, C.wollastoni and G. propinqua from Barbrook reservoir and in a specimen of C.venusta from Little Barbrook reservoir, but has not been found in

Corixidae from the Duckpool on Big Moor. A similar parasite has been found in specimens of C.distincta, C.wollastoni and C.carinata from upland reservoirs in Teesdale, Co. Durham.

The cysts of this parasite can easily be seen as spherical, white objects up to 1.0 mm. in diameter lying in the haemocoel of the host. Tables 49 and 50 and Figure 25 show the seasonal fluctuation in percentage of C.germari material from section A 100 to A 300 that contained these cysts. In 1957 and 1958 none of the specimens contained cysts at the beginning of the emergence of the new generation adults, though cysts were occasionally observed in instar 4 and 5 nymphs, but during the winter and spring the percentage increased and by early summer it reached a value of 90 to 100%. These figures, being based on counts of only one stage in the life cycle of the parasite, do not necessarily show the true infection rate in the host species and even if this point be ignored there is no indication that the parasite is directly responsible for the death of the host, for in 1958 90 to 100% of the hosts contained the parasite for about three months before the numbers of C.germari began to decrease. Even so, it is likely that the host suffers some loss of efficiency from the presence of the parasite and that the parasite influences the rate of breakdown of corixid material after death.

Several small field experiments were conducted to examine the possible effects of the parasite on the host. In only one case was it possible to demonstrate any marked difference in behaviour or performance between individuals containing cysts and those not containing cysts. On 23.4.58 seventy-six specimens of C.germari were collected

Date.	Percentage containing cysts $\pm 5\%$ confidence limits.	
	Old generation.	New generation.
3.4.57.	47 \pm 26.2	
17.4.57.	42 \pm 12.6	
1.5.57.	50 \pm 9.6	
15.5.57.	73 \pm 8.2	
29.5.57.	94 \pm 5.7	
30.5.57.	94 \pm 7.5	
2.6.57.	95 \pm 4.4	
26.6.57.	97 \pm 4.0	
25.7.57.		0
7.8.57.		17 \pm 9.6
21.8.57.		32 \pm 6.5
4.9.57.		26 \pm 6.1
18.9.57.		29 \pm 3.8
2.10.57.		29 \pm 5.0
16.10.57.		27 \pm 5.5
30.10.57.		35 \pm 5.8
13.11.57.		36 \pm 6.1
24.12.57.		46 \pm 20.7

TABLE.49. Percentages of specimens containing parasite cysts during 1957.

Date.	Percentage containing cysts \pm 5% confidence limits.	
	Old generation.	New generation.
20.1.58.	56 \pm 5.9	
5.3.58.	44 \pm 12.2	
20.3.58.	35 \pm 11.5	
2.4.58.	35 \pm 13.2	
11.4.58.	42 \pm 14.0	
15.4.58.	46 \pm 10.9	
17.4.58.	47 \pm 9.8	
25.4.58.	61 \pm 9.8	
1.5.58.	60 \pm 9.3	
9.5.58.	64 \pm 9.4	
15.5.58.	73 \pm 8.8	
23.5.58.	79 \pm 8.1	
29.5.58.	76 \pm 8.5	
6.6.58.	74 \pm 8.6	
12.6.58.	91 \pm 5.7	
20.6.58.	93 \pm 5.1	
26.6.58.	96 \pm 3.9	
4.7.58.	97 \pm 3.4	
10.7.58.	99 \pm 2.0	
18.7.58.	99 \pm 2.0	
24.7.58.	99 \pm 2.1	
1.8.58.	99 \pm 2.0	
7.8.58.	100	
15.8.58.	98 \pm 4.3	0
21.8.58.	100	0
29.8.58.	98 \pm 4.3	1 \pm 1.9
4.9.58.	87 \pm 14.6	2 \pm 2.8
12.9.58.		10 \pm 6.0
18.9.58.		11 \pm 6.3
26.9.58.		11 \pm 6.3
2.10.58.		13 \pm 6.7
10.10.58.		12 \pm 6.5
16.10.58.		18 \pm 7.7
4.11.58.		17 \pm 7.7
29.12.58.		35 \pm 9.9

TABLE.50. Percentages of specimens containing parasite cysts during 1958.

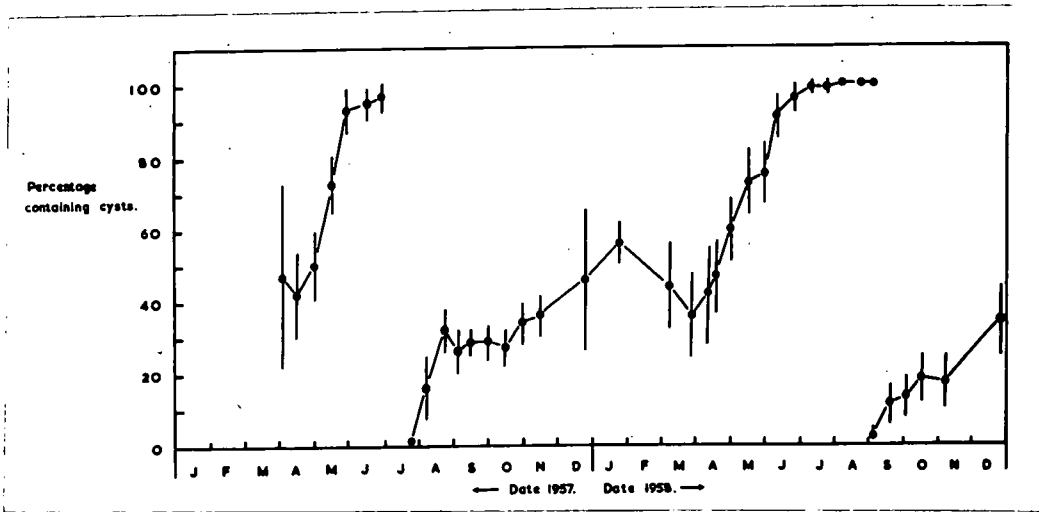


Figure.25. Seasonal fluctuation in percentage of adults containing parasite cysts.

from section A 100 to A 300 whilst attempting to copulate and 51% of these were found to contain parasite cysts. When the ratio :-
Number of specimens containing cysts : number not containing cysts,
was compared with similar ratios for the net samples taken on 17.4.58 and 25.4.58 by means of 2 x 2 contingency tables, Chi-squareds of 0.14 and 1.66 ($P > .70$, $P > .10$) were given. Thus the proportion of copulating specimens containing cysts did not differ significantly from the proportion in the net samples taken at the same time of the year. On 30.4.58 the proportion of cyst-containing individuals in a sample of C.germari attempting to fly from the shore at B was compared to the proportion in the net samples taken on 1.5.58. A Chi-squared value of 0.51 ($P > .30$) was given, thus showing no significant difference between the two sample ratios. A similar comparison between a sample of specimens attempting to fly from the water surface on section A 100 to A 300 on 30.4.58 and the net sample for 1.5.58, however, give Chi-squared = 35.13 ($P < .001$), which shows a significant difference between the two sample ratios. It has thus been shown that infection with the cysts of this parasite does not affect the readiness with which C.germari attempts to copulate or to fly from the shore, but that it decreases the readiness with which it will attempt to fly from the water surface. Observation of C.germari under laboratory conditions has shown that females containing cysts are able to lay viable eggs but it has not been possible to ascertain whether or not the parasite has any effect on the number of eggs laid or on the proportion that hatches.

The evidence available suggests that this parasite is well adapted to its host and that its effects, if any, on the host are too subtle to be readily detected by the methods used in the present work.

The immature stages of certain water mites are fairly common ectoparasites of Corixidae (Poisson, 1935), (Popham, 1943b), Kirkaldy, 1905, Lansbury 1955, Soar 1901, Leston 1955, Griffith, 1945) and Leston (1955) has shown that infection with these mites decreases the chances of a corixid individual overwintering successfully. These mites are not important in the water bodies studied for, of all the Corixidae collected, only two specimens (both of them C.praeusta from Station Delta of Barbrook reservoirs) were found to be carrying such ectoparasites.

XI. CHANGES IN THE ABUNDANCE OF C.GERMARI THROUGHOUT THE SEASON.

(1) General considerations.

Section A 100 to A 300 is the only part of Barbrook reservoir where C.germari is present in sufficient numbers for seasonal changes in its abundance to be assessed with any accuracy. It has been shown (Tables 30 and 31) that the abundance of the adults shows little variation throughout the season on sections of shore other than A 100 to A 300 and it has therefore been assumed that there is a negligible change in the abundance of adult C.germari on A 100 to A 300 as a result of movement between shore sections. The results obtained tend to justify this assumption. Regular estimates of the nymphs have not been made on sections other than A 100 to A 300 so this assumption does not necessarily apply to them and, therefore, the net estimates of nymph abundance on section A 100 to A 300 may not be a reliable measure of the number of nymphs produced there. An estimate of the total number nymphs produced during the season by the adults on section A 100 to A 300 has therefore been obtained from the oviposition and hatching success data.

(2) Abundance of the adults.

The data used are contained in Tables 30 and 51 and are illustrated in Figures 26 and 27. It will be seen that in Figure 26, which shows the mean catches of adults per S.N.S. \pm ^{5%}_A confidence limits, the abundance of the adults remained fairly steady from April to mid-June in 1957 and then fell off and reached a zero on 10.7.57. After this the new generation began to appear and a maximum abundance value was reached during the latter half of October. Following the attainment of the maximum abundance, the

Date.	Mean catch/S.N.S. \pm 5% confidence limits.	Date.	Mean catch/S.N.S. \pm 5% confidence limits.
20.1.58.	5.0 \pm 0.73	1.8.58.	3.4 \pm 1.20
28.3.58.	8.0 \pm 2.31	7.8.58.	1.7 \pm 0.72
X 1.4.58.	1.1 \pm 0.20	15.8.58.	2.6 \pm 1.75
X 11.4.58.	3.0 \pm 1.29	21.8.58.	7.4 \pm 2.57
17.4.58.	8.4 \pm 2.66	29.8.58.	10.6 \pm 2.08
25.4.58.	9.9 \pm 3.13	X 4.9.58.	7.7 \pm 2.30
1.5.58.	11.1 \pm 5.08	X 12.9.58.	16.1 \pm 4.63
9.5.58.	10.5 \pm 3.08	18.9.58.	26.9 \pm 5.81
15.5.58.	12.3 \pm 1.84	26.9.58.	64.8 \pm 12.53
23.5.58.	10.3 \pm 1.90	2.10.58.	34.9 \pm 6.26
29.5.58.	11.0 \pm 3.10	8.10.58.	72.7 \pm 14.85
X 6.6.58.	2.7 \pm 0.89	9.10.58.	84.1 \pm 2.77
9.6.58.	10.9 \pm 3.24	10.10.58.	74.0 \pm 14.13
12.6.58.	10.0 \pm 2.01	11.10.58.	84.0 \pm 11.77
X 20.6.58.	5.3 \pm 1.86	13.10.58.	86.5 \pm 15.66
X 23.6.58.	5.4 \pm 1.27	14.10.58.	76.5 \pm 13.67
26.6.58.	4.8 \pm 1.41	X 15.10.58.	61.5 \pm 12.27
X 4.7.58.	9.7 \pm 1.02	X 16.10.58.	48.7 \pm 13.48
10.7.58.	6.3 \pm 2.11	20.10.58.	73.0 \pm 20.11
18.7.58.	4.1 \pm 1.38	23.10.58.	59.7 \pm 9.73
24.7.58.	3.9 \pm 1.06	4.11.58.	47.5 \pm 7.83

TABLE.51. Mean catches of adults per S.N.S. on section A100 to A300 during 1958.

X denotes dates on which appreciable wave action was observed on section A100 to A300 (See Table.2.).

Abundance of adults at stations A100 to A300 in 1957.

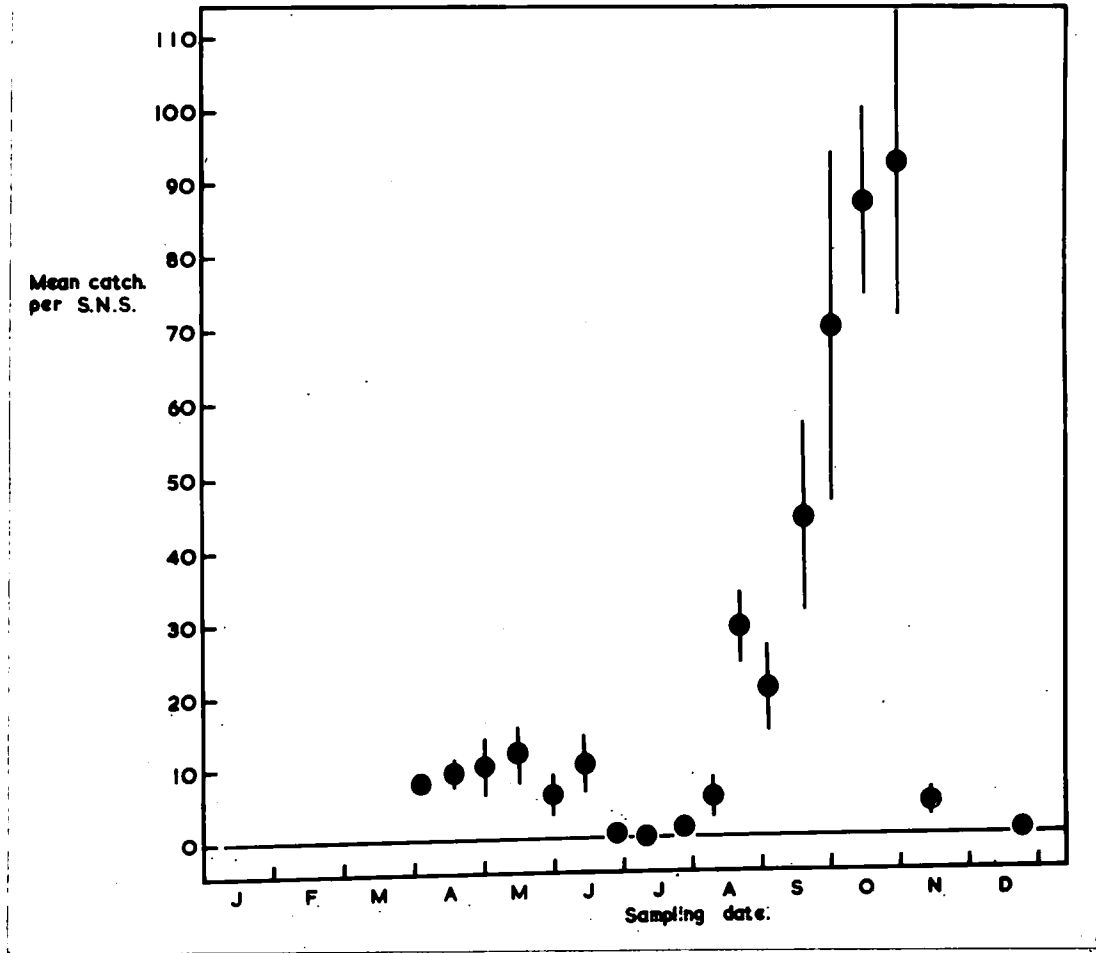


Figure.26.

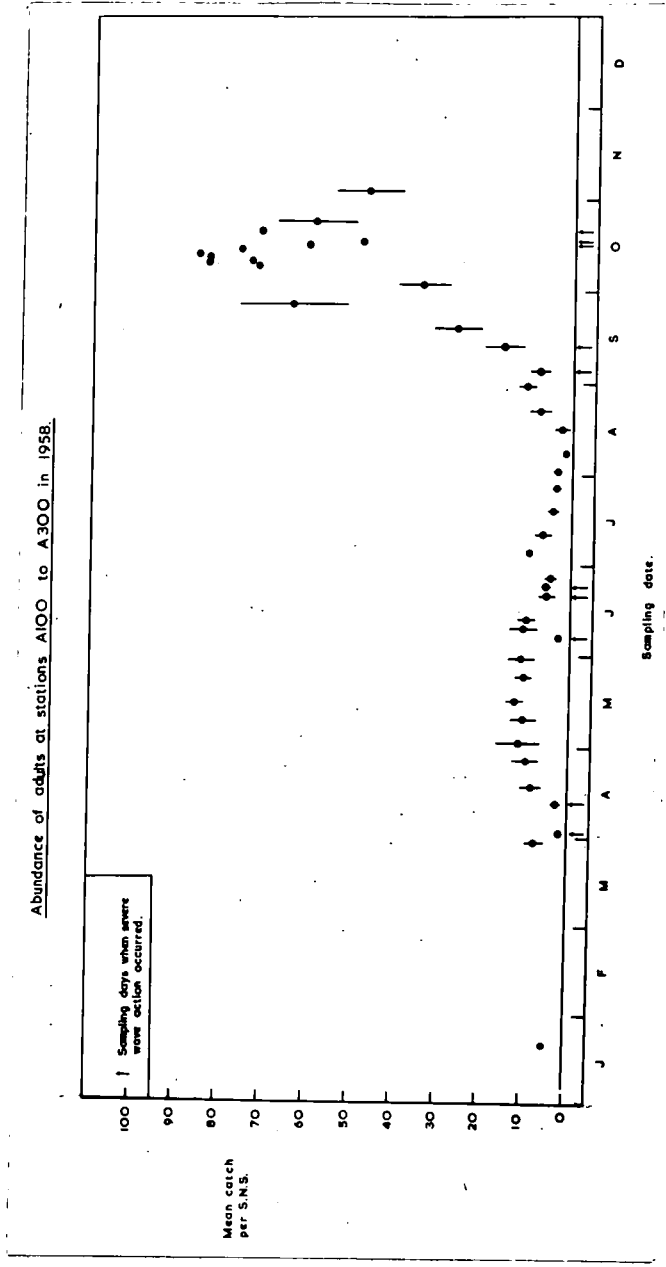


Figure.27.

catch per S.N.S. fell rapidly. The fall-off in July coincided with the water level falling below the level of the stony bank on section A 100 to A 300 and on the basis of the 1957 data alone it is not possible to tell whether the fall in abundance was due chiefly to mortality or to dispersion. The 1958 results, however, suggest that mortality is the main cause of this summer decline in abundance. As the autumn maximum of abundance was reached in 1957, the number of nymphs on section A 100 to A 300 became small and emergence of new generation adults could be regarded as virtually completed. The abundance values for 1958 are contained in Table 51 and are shown in Fig. 27. In this latter figure the 5% confidence limits are omitted from some of the October data for the sake of clarity. The 1958 abundance data show a similar basic pattern to those of 1957, but the old generation abundance fell off more slowly than in 1957. Although the emergence of the new generation began later in 1958 than in 1957, there was some overlap of the two generations in 1958 but none in 1957.

It will be noted, however, that Figure 27 shows certain dates on which the catch per S.N.S. was remarkably low. These low values were obtained on days when the wind speed and direction (see Table 51) were such as to cause severe wave action on section A 100 to A 300 and it is likely that on such days the corixids moved down into deeper water, or moved down amongst the stones of the substratum and thus became less amenable to net sampling. No such wave action occurred on section A 100 to A 300 on any sampling date during 1957.

It will also be noted that the decrease in abundance of the old generation was interrupted on 4.7.58 and 10.7.58 and this may be associated with the occurrence of severe floods in the S. Yorkshire and N.E. Derbyshire region on the night of 1.7.58 to 2.7.58. These floods caused the water level in the reservoir to rise about 1.0 m. (3 ft.) and then to fall back about 0.7 m. (2 ft.) within a period of twelve hours.

The fall-off in abundance of the old generation after 12.6.58 was largely a result of mortality for, during the period of fall-off; large numbers of dead and dying C.germari were to be seen floating on the water surface and others were observed swimming erratically in small circles near the water surface as though they were losing the ability to coordinate their movements. No attempts at flight were observed during this period.

(3) Abundance of the eggs.

The abundance of the eggs on section A 100 to A 300 during 1958 has been estimated indirectly by calculation from the net sample data for nymphs and adults and from direct counting of the eggs.

On 9.6.58, a day selected because it was a day when the catch per S.N.S. was not likely to be depressed as a result of wave action, two sets of 20 S.N.S.s were made with the fine net on section A 100 to A 300. The first set of sweeps caught a total of 48 adults and 171 instar 1. nymphs and the second set gave a catch of 50 adults and 174 instar 1. nymphs. These two sets of results agree very well and, on the basis of these data, instar 1. nymphs and

adults were assumed to be present in a 3.5:1 ratio. On the same date 20 stones were removed at random from 1.0 m. (3 ft.) depth on section A 100 to A 300 and 11.6% of these eggs were found to have hatched. Now if all the samples taken on days when the adult catch per S.N.S. was depressed by wave action are omitted, it is possible to combine the catch per S.N.S. data for the 1958 oviposition period and to obtain an estimate of the mean catch of adults per S.N.S. over the whole period. By interpolation on Table 46 it is possible to estimate what percentage of the season's eggs had already been laid by 9.6.58. The best estimate of the adult sex ratio during the 1958 oviposition period is Females:Males: 43:57.

By using these various pieces of information it is possible to calculate the total number of eggs laid on section A 100 to A 300 during 1958 in terms of coarse S.N.S. equivalents. This can be done in three ways :-

Calculation 1.

Data used :-

- (a) Of the eggs laid by 9.6.58, 11.6% had hatched by that date.
- (b) Up to 9.6.58 oviposition had been going on for 40 days.
- (c) The total number of oviposition days in 1958 was 99.
- (d) Along section A 100 to A 300 on 9.6.58, nymphs and adults were present in the ratio 3.5 : 1.
- (e) 43% of the adults present were females.

(f) During the 1958 oviposition period there were 10 adults per coarse S.N.S. unit.

Assumptions made :-

(i) There was a constant oviposition rate throughout the oviposition period.

(ii) There was negligible mortality of instar 1. nymphs prior to 9.6.58.

Calculation :-

$$\text{Nymphs per female on 9.6.58} = 3.5 \times 100/43 = 8.14$$

\div Hatched eggs per female
by 9.6.58.

$$\therefore \text{Eggs laid per female in 40 days} = 8.14 \times 100/11.6$$

$$\therefore \text{Eggs laid per female per day up to 9.6.58} \\ = 8.14 \times 100/11.6 \times 1/40$$

$$= 1.75$$

$$\therefore \text{Total eggs per female in the season} \\ = 1.75 \times 99 \times 173$$

There were 4.3 females per coarse S.N.S. during the 1958 oviposition period.

$$\therefore \text{Eggs laid per coarse S.N.S. unit in the season} \\ = 4.3 \times 173 = 747.$$

Thus the females oviposited at a mean rate of 1.75 eggs per day per female and in the whole season 747 eggs were laid per coarse S.N.S. unit.

Calculation 2.

Data used:-

(a) Of the eggs laid by 9.6.58, 11.6% had hatched by 9.6.58

(b) Along section A 100 to A 300 on 9.6.58 nymphs and adults were present in the ratio 3.5 : 1.

(c) 43% of the breeding adults were females.

(d) the breeding adults had an abundance of 10 per coarse S.N.S. unit.

(e) 33% of the season's eggs were laid by 9.6.58 (Derived from Table 46).

Assumptions made :-

(i) The rate of oviposition on the net covered stones, described on page 68, was proportional to the oviposition rate on section A 100 to A 300.

(ii) There was a negligible mortality of instar 1. nymphs prior to 9.6.58.

Calculations :-

Eggs laid per female up to 9.6.58 = $8.14 \times 100/11.6$

Total eggs laid per female during the whole season

$$= \frac{8.14 \times 100 \times 100}{11.6 \times 33} = -213$$

∴ Total eggs laid in the season per coarse S.N.S. unit = 213×4.3
= 916

∴ Mean oviposition rate = $213/99 = 2.15$ eggs per female per day.

Thus the females oviposited at a mean rate of 2.15 eggs per female per day and in the whole season 916 eggs were laid per coarse S.N.S. unit.

Calculation 3.

Data used :-

(a) 8.7 nymphs per fine S.N.S. were caught on 9.6.58.

(b) In the samples taken from 4.7.58 to 12.9.58 (omitting 15.8.58) the total catches of instars 3, 4 and 5 in fine and coarse nets were in the ratio 1 : 1.9.

(c) Of the eggs laid by 9.6.58, 11.6% had hatched by 9.6.58.

(d) 33% of the season's eggs had been laid by 9.6.58.
Assumptions made :-

(i) The rate of oviposition on the net covered stones described on page 61 was proportional to the oviposition rate on section A 100 to A 300.

(ii) The ratio of fine net catches to coarse net equivalents for instar 1. on 9.6.58 was proportional to the ratio for instars 3, 4 and 5 between 4.7.58 and 12.9.58.

(iii) There was negligible mortality in instar 1. nymphs prior to 9.6.58.

Calculation :-

Number of instar 1. nymphs per coarse S.N.S. unit on

$$9.6.58 = 8.7 \times 1.9$$

∴ Eggs per coarse S.N.S. unit laid during the whole season

$$= \frac{8.7 \times 1.9 \times 100^2}{11.6 \times 33}$$
$$= 432$$

∴ Mean oviposition rate = $432/99 \times 4.3 = 1.00$ eggs per female per day.

Thus the females oviposited at a mean rate of 1.00 eggs per female per day and in the whole season 432 eggs were laid per coarse S.N.S. unit.

Of these results, that given by Calculation 1 is rejected on the grounds that it is based on the unsound assumption that the

oviposition rate was constant throughout the season. The result given by Calculation 3. was rejected because it was inconsistent with other results in two particulars :-

(a) An oviposition rate of 1.000 eggs per female per day is remarkably low for, as will be shown later, females kept under laboratory conditions will lay eggs at a rate approaching this.

(b) It will be shown later that only about 58% of the eggs laid produced nymphs. This means that if only 432 eggs are laid per coarse S.N.S. unit the maximum possible number of nymphs ^{that} could have been taken by net sampling during 1958 would have been of the order of 250 per coarse S.N.S. unit, assuming no nymph mortality at all took place during the season. In fact mean catches of up to 300 or 400 nymphs per coarse S.N.S. unit were recorded during 1958. The magnitude of this discrepancy suggests that the result of Calculation 3 is not a reasonable one unless a large movement of nymphs from other parts of the reservoir to section A 100 to A 300 is postulated.

Calculation 2 has therefore been assumed to give the most reliable estimates of mean oviposition rate and total eggs laid during the 1958 season, but even these figures must be regarded as an underestimate because they rest on the assumption that no mortality occurred in instar 1. during the few days between the commencement of hatching and 9.6.58. The mean oviposition rate given by this calculation has been checked by means of two simple experiments :-

(i) On 14.5.58 fourteen females of C.germari were collected from the reservoir and were kept out of doors in a jar containing sand,

water and 4 in. (20 cm.) lengths of J. effusus stem. In eight days they laid a total of 78 eggs and hence the mean oviposition rate was 0.7 eggs per female per day.

(ii) For several weeks a field experiment was conducted in which a single female was placed in each of eight small netting cages containing stones. The cages were then placed in the reservoir at a depth of 1.0 m. (3 ft.) on section A 100 to A 300. After a number of days the cages were removed and the eggs on the stones in each cage and on the inside of the netting of each cage were removed and counted. This process was repeated six times over different periods of from 2 to 15 days, using newly collected females on each occasion. The results are shown in Table 52. The mean oviposition rate for the whole experiment was 1.0 eggs per female per day. In both of these experiments the conditions were obviously sub-optimal. In the first the animals lacked their preferred oviposition substratum and may also have been overcrowded and short of food, and in the second experiment the animals were constrained in cages and could not visit the surface to renew their physical gills. Although only two specimens died in the course of the first experiment and about 10% in the second this alone would cause the mean oviposition rate to be lower than in nature and also suggests that the survivors were living under unsuitable conditions and were probably ovipositing at a lower rate than normal. This therefore shows that the value of 2.15 eggs per female per day given by calculation 2 as the mean oviposition rate is a reasonable one.

Date when cages were emptied.	Duration of oviposition (days.).	Cage.										Totals.	Mean eggs / female / day.
		1	2	3	4	5	6	7	8				
27.5.58.	12	4	8	5	14	9	2	7	4	53	0.55		
29.5.58.	2	1	1	1	2	1	2	0	3	11	0.69		
10.6.58.	12	6	5	23	11	18	17	12	8	100	1.02		
25.6.58.	15	16	18	51	12	14	24	10	17	162	1.46		
9.7.58.	14	15	10	30	1	20	12	21	18	127	1.14		
23.7.58.	14	11	8	22	6	15	12	16	8	98	0.88		
Totals.	69	53	50	132	46	77	69	66	58	551	1.00		

TABLE.52. Oviposition rate of females in cages at 1.0 m.depth on section A100 to A300.

(4) Abundance of the nymphs :-

The estimates of nymphal abundance for 1958 have been shown in Table 9 and Figure 9 and although these are not very reliable estimates they do show the approximate abundance of the nymphs on section A 100 to A 300. They also show the way in which the abundance changed throughout the season and the bimodality of the abundance polygon in Figure 9 probably reflects the bimodality of the oviposition data (See Fig. 23).

XII. MORTALITY IN THE VARIOUS STAGES.

It has been shown that reasonably reliable estimates of the relative abundance of the different stages of C.germari can be obtained and these can all be expressed in terms of the coarse net S.N.S. Although this sampling unit gives no measure of the abundance of the stages per unit area of substratum it does give a method of comparing the relative abundance of the various stages throughout the season, and hence of measuring the mortality in each stage.

If the abundance of the old generation adults per S.N.S. is assumed to be constant for the periods 3.4.57 to 12.6.57 and 28.3.58 to 12.6.58, it is possible to combine the data for all sampling dates within each of those periods (omitting those dates in 1958 when the catch per S.N.S. was depressed by wave action) and obtain estimates of the abundance of the breeding adults in each year. By treating the data for the periods 16.10.57 to 30.10.57 and 8.10.58 to 14.10.58 in a similar way it is possible to obtain estimates of the number of new generation adults produced each year. The results are shown in Table 53.

The egg mortality was estimated by direct counting. Samples of eggs were taken on five occasions during 1958 by collecting 10 or 20 stones from a depth of 1.0 m. (3 ft.) on section A 100 to A 300 and removing all the eggs from each stone. The eggs from each stone

	Abundance in coarse S.N.S. units, 1957.	Abundance in coarse S.N.S. units, 1958.
Breeding adults.	9.3 ± 1.21	10.0 ± 0.80
New generation adults.	90.0 ± 11.85	79.6 ± 5.04

Table 53. Abundance of adults during 1957 and 1958, expressed as mean catches per coarse S.N.S. unit ± 5% confidence limits.

The eggs from each stone were then placed in a separate tube of 4% formalin solution. By examining the eggs at a magnification of x14 under a binocular microscope it was possible to separate the eggs into eight categories :-

(i) "Uneyed" :-

Apparently sound eggs which had not reached the stage of development at which the eyes of the developing nymph could be seen through the integument (Photograph 17).

(ii) "Eyed" :-

Apparently sound eggs in which the eyes of the developing nymph could be seen through the integument (Photograph 18).

(iii) "Hatched" :-

Eggshells showing the characteristic splitting into 6 to 8 strap-like strips from the micropyle to about halfway between apex and base, which is caused by the emergence of the nymph^m (Photograph 19).

(iv) "Hatching" :-

Eggs collected whilst the instar 1. nymph was in the process of emerging (Photograph 20). In no case was the partly emerged nymph found to have been attacked by fungus as were certain nymphs which died during emergence in laboratory cultures. Thus the eggs belonging to this category would probably have hatched satisfactorily if they had been left on the stones in the reservoir.

(v) "Fungal" :-

Eggs of C.germari were attacked by a fungus

identified as Saprolegnia sp. The fungus first became obvious when its zoosporangia protruded from the micropyle region of the egg in a dense tuft (Photograph 21). At a later stage the fungus disappeared leaving only a relatively smooth-edged and slightly dilated aperture at the micropyle end of the integument of the egg and, occasionally, a few fragments of hyphae or egg contents within the shell (Photograph 22). The aperture made by emerging fungus is easily distinguishable from that made by the emerging nymph, for it is smaller and does not cause splitting of the apical part of the integument into strips. It has not been possible to ascertain whether the fungus attacks healthy eggs or only those that are damaged or infertile.

(vi) "Hollow" :-

It has been noted that females of C.germari ovipositing under laboratory conditions will attack their own eggs and that the eggs attacked in this way appear to be hollow. Similar eggs have been found in the field samples (Photograph 23).

(vii) "Otherwise damaged" :-

A certain number of eggs in each sample consisted of damaged or incomplete shells. In some cases the micropyle region was still intact whilst the sides of the integument were split or holed and in such cases it was clear that the damage occurred before hatching. In other cases only the basal part of the integument remained and it was not possible to tell whether or not hatching had taken place before the damage occurred.

KEY TO PHOTOGRAPHS 18 TO 21.

e = eye of nymph.

d = dorsal abdominal gland of nymph.

h = head of nymph.

t = thorax of nymph.

i = integument of egg.

c = cement.

as = apical splits.

s = substratum.

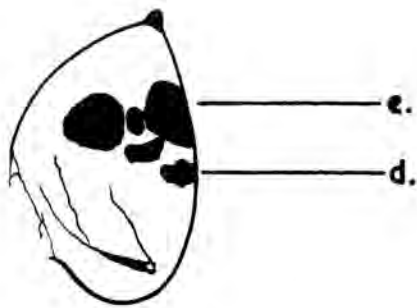
f = emerging fungus.

l = hole left by emergence of fungus.

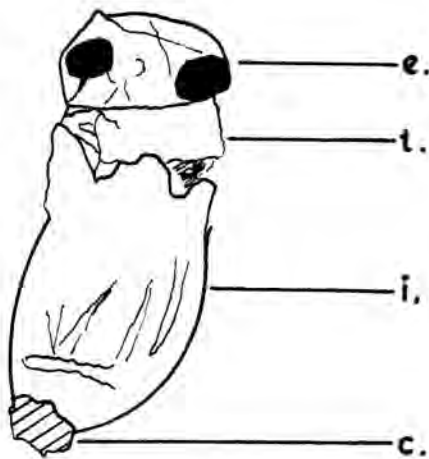
m = micropyle.

p = hole made by stylets of adult.

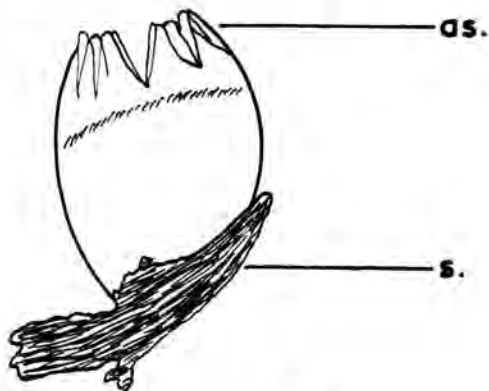
The measurements refer to the length of the integument of the egg along its longest axis, excluding cement, substratum, nymph or fungus.



Photograph.18. 0.95 mm.

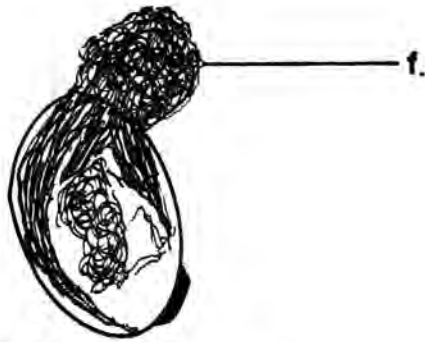


Photograph.19. 0.94 mm.

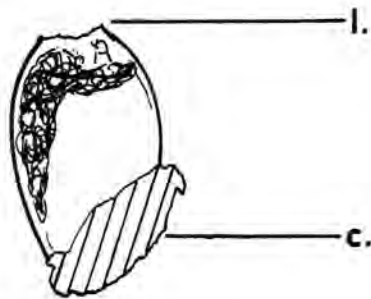


Photograph.20. 0.93 mm.

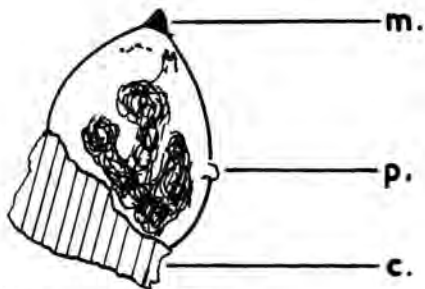




Photograph, 21. 0.86 mm.



Photograph, 22. 0.83 mm.



Photograph, 23. 0.86 mm.



(viii) "Deteriorated" :-

In the later samples eggs were found which were intact but discoloured. If these eggs were kept in the laboratory they did not hatch. Presumably these eggs were classified as "uneyed" in the earlier samples.

An analysis of the egg samples into these various categories is shown in Table 54.A. The same results are shown as percentages in Table 54.B. and illustrated in Figure 28. By 20.8.58 all but 1% of the eggs had hatched and the data obtained on that date have been taken as a measure of the egg mortality for the 1958 season. The smaller sample taken on 17.9.58 gave the same result and this shows that if any eggs or eggshells do become detached from the stones without leaving any trace this causes little or no error in the estimate of egg mortality.

One hundred apparently sound eggs were collected from the stones on section A 100 to A 300 on 17.7.58 and were kept in a jar in the laboratory until 30.6.59 to see whether any egg parasites emerged from them. Apart from instar 1. nymphs, Saprolegnia sp., and alga, no other organisms were found in the jar on any occasion when it was examined.

The overall egg mortality of 42% obtained from these egg counts shows that, of the 916 eggs per coarse S.N.S. unit laid during 1958, only about 531 hatched.

From the abundance and mortality values so far derived it is possible, ~~to say~~ by subtraction, to find out the mortality in the nymphs for 1958 and also the over-winter loss of adults for the

Date.	No. of stones	Eyed	Uneyed	Hatched	Hatching	Hollow	Fungal	Deteriorated	Otherwise damaged.	Totals
6.6.58	10	148	100	22	7	13	5		4	299
9.6.58	20	325	289	80	11	33	21		10	779
9.7.58	20	84	363	247	0	65	20		45	824
20.8.58	20	17	2	912	0	96	124	383	47	1581
17.9.58	10	0	0	369	0	49		213	29	660

(B)

Date.	Eyed.	Uneyed.	Hatched.	Hatching.	Hollow.	Fungal.	Deteriorated.	Otherwise damaged.
6.6.58	50±5.8	33±5.4	7.4±3.03	2.3±1.77	4.3±2.35	1.7±1.49		1.3±1.31
9.6.58	42±3.5	37±3.5	11.5±2.29	1.4±0.84	4.3±1.45	2.7±1.16		1.4±0.84
9.7.58	10±2.1	44±3.5	30 ± 3.19	0	8.0±1.89	2.4±0.34		5.5±1.59
20.8.58		1.0±0.50	58 ± 2.5	0	6.0±1.19	7.8±1.36	24±2.15	3.0±0.88
17.9.58		0	56 ± 3.9	0	7.4±2.04	31±3.6		4.4±1.60

TABLE.54. Analyses of egg samples.

(A) Numbers in each category.

(B) The same data expressed as percentages
5% confidence limits.

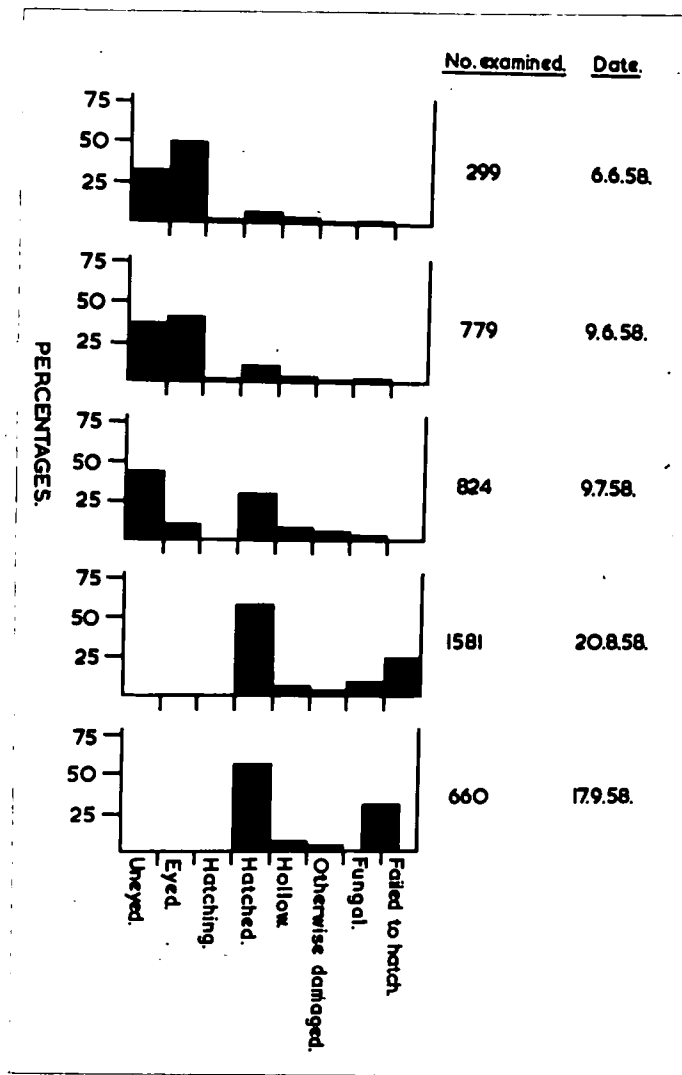


Figure.28. Analyses of 1958 egg samples.

winter of 1957 to 1958. During the spring of 1959 four sets of S.N.Ss. were taken on four consecutive days. The results are shown in Table 55 and, if these data are assumed to be adequate as a measure of the abundance of breeding adults during 1959, it is possible to make ^{an} estimate of the loss of adults during the winter 1958 to 1959. The causes of egg mortality have been classified on a percentage basis, but for the other stages it has only been possible to list the known or suspected causes of mortality without any indication of their relative magnitude.

It has already been shown that A.nebulosus and A.bipustulatus are probably predators on the adults and nymphs of C.germari, whilst the larvae of these beetles are predators on the nymphs of C.germari. The protozoan parasite cannot be excluded as a possible cause of death, though it is more likely to act in conjunction with other factors than on its own. Wave action is a mortality factor, for large numbers of dead and dying Corixidae can be found cast ashore at all times of the year on days following severe wave action and individuals have occasionally been observed in shallow water on a sandy, lee shore attempting to swim into deeper water but being steadily driven nearer the shore by each successive wave. Sudden fluctuations of water level can also be a cause of death, for on 3.7.58 following the floods of the night of 1 to 2.7.58, large numbers of corixids, many of them dead or dying, were found stranded amongst the grass and heather above the water level. Presumably these insects had moved up into the terrestrial vegetation whilst it was covered by flood water and had been left there when the water receded.

Date.	Mean catch of adults per coarse S.N.S. ± 5% confidence limits.
21.4.59	20.05 ± 2.43
22.4.59	21.05 ± 4.96
23.4.59	21.60 ± 5.64
24.4.59	21.80 ± 4.39
Total.	21.1 ± 2.14

Table 55. Abundance of C.germari adults during the spring of 1959.

A synthesis of the mortality data for C.germari is given in Table 56.

Stage.	No. present, in coarse S.N.S. units.	Mortality, in coarse S.N.S. units.	Description of mortality.	Possible causes of mortality.
New Generation. 1957.	90 ± 12	80	Overwinter loss.	Wave action. Predators. Flight? Parasite?
Breeding adults. 1958.	10 ± 0.8	10	Summer decline.	Senescence. Wave action. Predators. Floods. Parasite? Flight?
Eggs. 1958.	916	385	Egg mortality.	Fungus 8%. Attacked by adults 6%. Otherwise damaged 3%. Fail to hatch 24%.
Nymphs 1958.	531	433	Nymph mortality.	Wave action. Floods. Predators. (See above.)
New Generation. 1958.	80 ± 5	59	Overwinter loss.	
Breeding adults. 1958.	21 ± 2	21	Summer decline.	

TABLE.56. Abundance and mortality of C. Germari in terms of coarse S.N.S. units. Note that for the eggs and nymphs the values given are the total numbers passing through these stages in the course of the whole season.

XIII. THE WEIGHTS OF THE VARIOUS STAGES AND ESTIMATES OF BIOMASS.

So far this study has been concerned with the abundance and mortality of the various stages of C.germari in terms of numbers of individuals. Owing to the great differences in size and weight of the different stages, such numerical data do not give any measure of the weight of living material present at any one time or of the weight of that material lost by the species as a result of mortality during any particular period of time. Such information is useful because it gives a means of comparing the abundance and mortality in terms of a standard unit and also because a measure of the weight of living C.germari material present at any given time can be considered to be a rough measure of the amount of energy "locked away" in the form of C.germari individuals at that time.

The weight of each of the stages has been determined by weighing 10 groups of 25 individuals of each stage. Surface moisture was removed from the freshly killed animals on a filter paper and each group of 25 individuals was placed on a weighed piece of aluminium foil. The foil + insects was then weighed and hence the weight of the fresh insects was determined. This was termed "wet weight". The insects were kept on the foil and were dried at 105°C until no further loss in weight occurred. The weight of the foil + dry insects was then determined and hence the "dry weight" of the insects. In this way the mean "dry" and "wet" weights of groups of 25 individuals of each stage, together with 5% confidence limits, were determined.

The results are shown in Table 57, and Figures 29 and 30 show the mean values for all stages except the old generation adults.

Table 57 also shows the mean dry weight of each stage expressed as a percentage of the mean wet weight. The mean percentage dry matter of the eggs was considerably greater than that of the nymphs and this was probably partly accounted for by the fact that the eggs used were obtained from the oviducts of dissected females and such eggs would absorb water after oviposition (Banks 1949), so bringing their percentage dry matter value closer to that of the nymphs. In addition, the eggs were probably more heavily chitinised than the nymphs. The nine samples of teneral adults show that these insects have only about half the dry weight of the hardened and darkened new generation adults although there is little difference in the wet weight. The data also show that the males of C.germari are not as heavy as the females, and this would be expected from the relative sizes of the two sexes.

A simplified version of the abundance data for adults and nymphs in 1958 is shown in Figure 31 which is based on data from Tables 9, 51 and 53. The abundances shown in this figure can be converted into biomasses by using the weight data in Table 57 and Figure 32 shows the result of using the wet weight data for such a conversion. Comparison of Figures 31 and 32 shows that although the nymphs give the highest numerical abundance of the season (strictly speaking the eggs give the highest abundance value, but for convenience they are omitted from the present discussion) the autumn maximum of ~~adults~~ adults gives the greatest biomass value of the year.

Material.	No. of groups of 25 individuals.	Mean wet weight of 25 individuals \pm 5% confidence limits (mg.)	Mean dry weight of 25 individuals \pm 5% confidence limits (mg.)	Dry weight as a percentage of wet weight.
Eggs.	10	3.0 \pm 0.26	1.3 \pm 0.45	43
Nymph.1.	10	8.5 \pm 1.41	0.8 \pm 0.09	10
Nymph.2.	10	30.5 \pm 6.72	2.4 \pm 0.82	9
Nymph.3.	10	60.0 \pm 2.09	7.6 \pm 0.56	13
Nymph.4.	10	140.0 \pm 7.41	20.1 \pm 2.48	14
Nymph.5.	10	303.0 \pm 9.00	53.2 \pm 1.80	17
Teneral males.	5	473.0	63.5	13
Teneral females.	4	482.0	75.3	15
New generation males.	10	491.0 \pm 22.9	136.0 \pm 14.2	29
New generation females.	10	588.0 \pm 32.0	154.0 \pm 21.8	26
Old generation males.	11	630.0 \pm 69.2	100.0 \pm 3.4	16
Old generation females.	13	737.0 \pm 56.3	146.0 \pm 5.3	20

TABLE.57. Wet and dry weights of the stages of C.germari.

Wet weights of groups of 25 individuals.

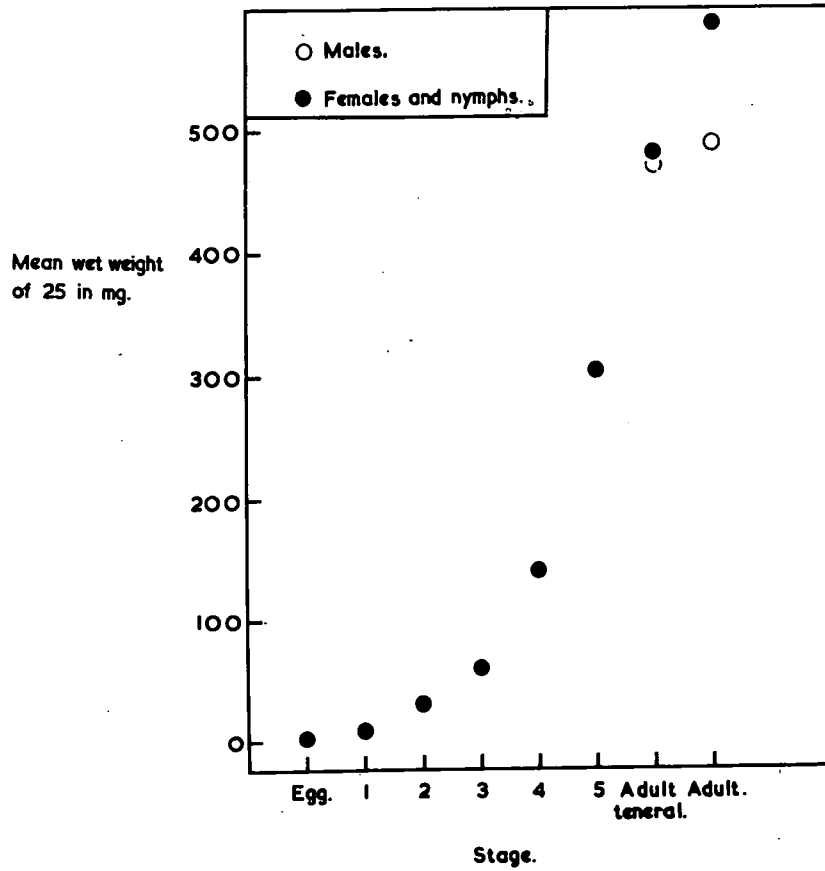


Figure.29.

Dry weights of the stages of C.germari.

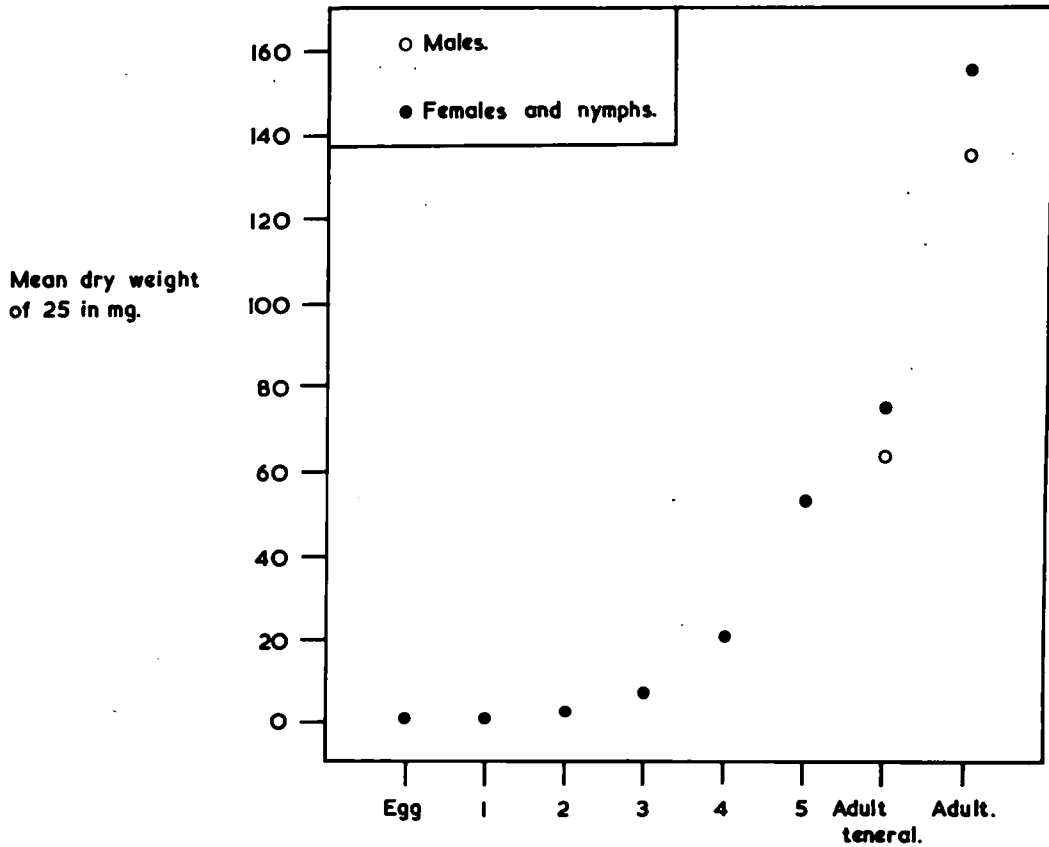


Figure 30.

Catches per S.N.S. 1958.

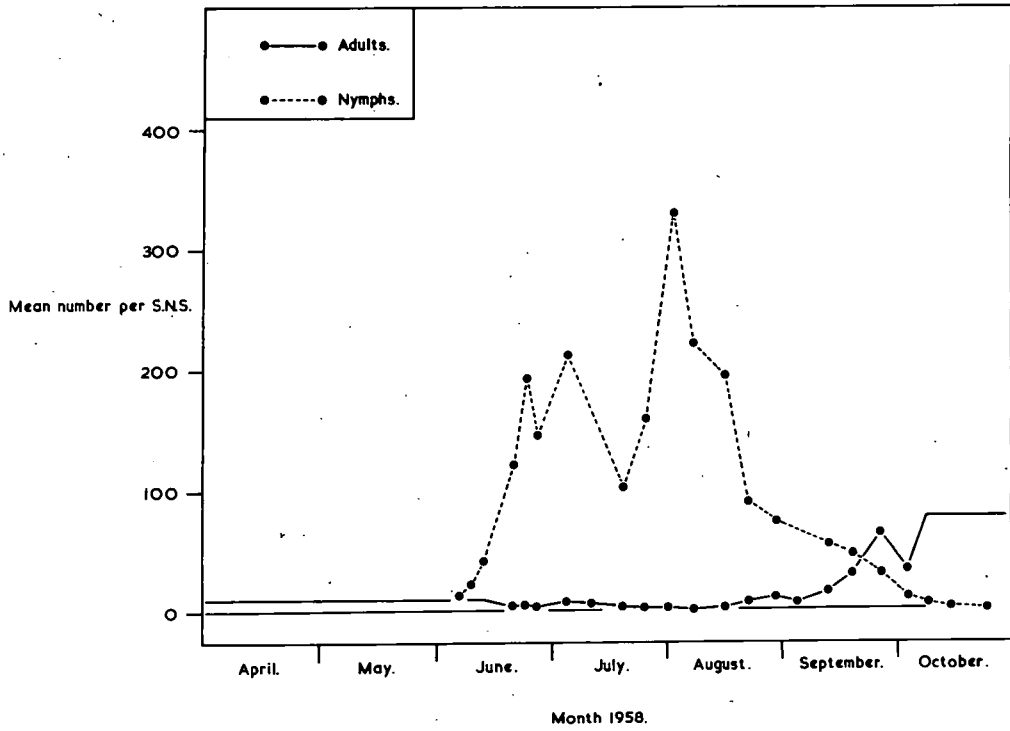


Figure.31.

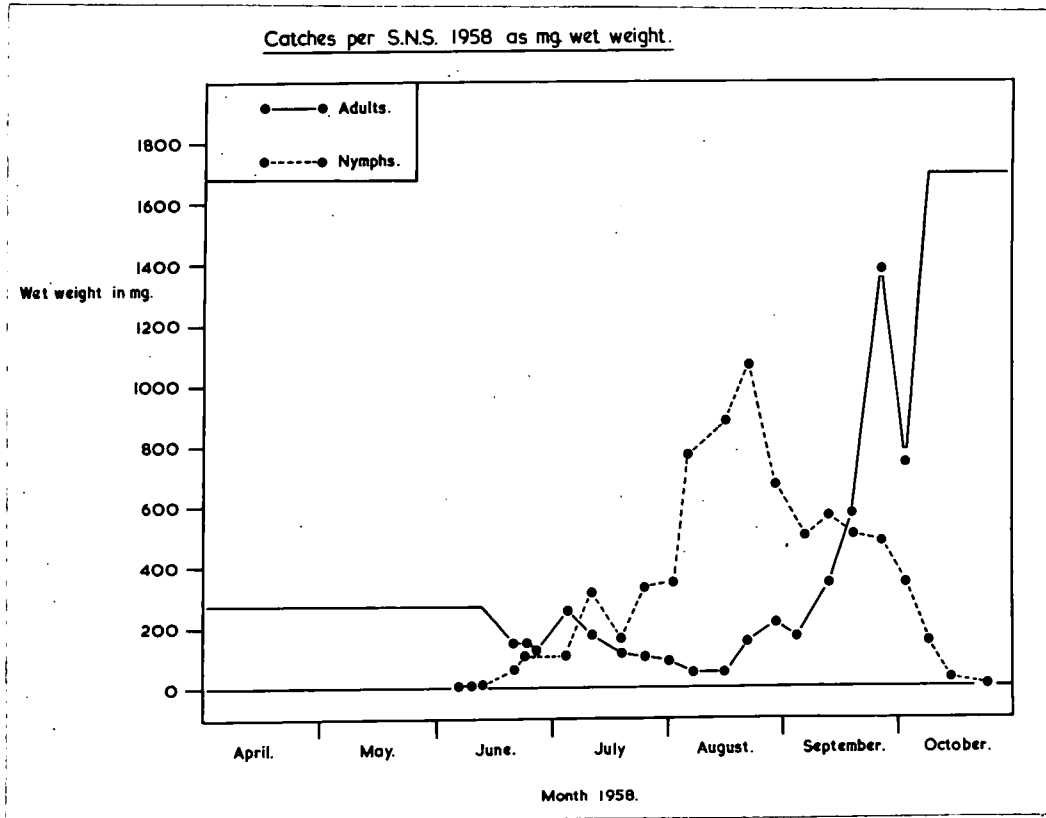


Figure.32.

The weight data can also be used to convert the figures in Table 56 to biomasses and the results given are shown in Table 58 where it has been assumed that the mortality of the nymphs is evenly spread over the five instars. If losses by flight are assumed negligible then this Table shows very clearly that the greatest turnover of C.germari material took place in the late summer and early autumn when the later nymphal instars and the new generation adults were being produced, and during the winter when the bulk of this material was returned to the environment as a result of mortality amongst the overwintering adults.

Stage	Wet biomass(mg.)		Dry biomass(mg.)	
	Produced.	Lost.	Produced	Lost
Autumn adults 1957	1429	1271	518	461
Spring adults 1958	273	273	49	49
Eggs 1958	109	46	48	20
Nymphs 1958	-	1871	-	291
Autumn adults 1958	1271	937	461	340
Spring adults 1959	573	573	103	103

Table 58. Quantities of C.germari reaching each stage and quantities lost in each stage expressed as mg.weight per S.N.S. unit.

XIV. APPROXIMATE ESTIMATES OF THE ABUNDANCE AND BIOMASS DATA
IN ABSOLUTE TERMS.

Attention has been paid to relative values of abundance and biomass, expressed in terms of a somewhat nebulous unit - the Standard Net Sweep. It is clearly desirable to obtain some idea of the meaning of these S.N.S. values in terms of the abundance and biomass of C.germari per unit area of substratum.

An attempt was therefore made to estimate a conversion factor for this purpose. Examination of Table 54A shows that the mean number of eggs per stone laid by 20.8.58 was about 80. It is known that by that date oviposition had ceased, so that a mean value of 80 eggs per stone can be considered to be approximately equivalent to a value of 916 eggs per coarse S.N.S. unit (See p. 85). If it is then assumed that the eggs are only laid on the stones of the top layer of the substratum it is possible to estimate the number of egg-carrying stones per m^2 of substratum and hence to find the mean number of eggs laid per m^2 of substratum during the 1958 season. Forty counts of the surface stones lying within a $1/16 m^2$ quadrat were therefore made on section A 100 to A 300 and a mean value of 27 ± 2.66 stones per $1/16 m^2$ was obtained. Thus, roughly $435 \times 80 (= 34,800)$ eggs were laid per m^2 of substratum during 1958. This value of 34,800 eggs per m^2 corresponds to a value of 916 eggs per coarse S.N.S. unit and hence values of all stages expressed as coarse S.N.S. units should be multiplied by $34,800/916 (= 38)$ to bring them to the

corresponding values per m^2 of substratum. This conversion factor is clearly an underestimate, for it rests on the assumption that no eggs are laid on stones below the layer visible when the substratum is viewed from above. On 22.5.59 the water level in Barbrook reservoir had fallen about a metre below top water level thus exposing substratum on which oviposition had already taken place. Examination of stones from this area of banking showed that, although some eggs were laid on the lower layers of stones, the great majority had been laid on the stones of the upper layer of the substratum. Thus, though the conversion factor is an underestimate it seems likely that the error involved is relatively small and therefore the conversion factor will, at least, show the order of magnitude of the abundance and biomass figures given earlier in this work.

Most of the abundance and biomass data are summarised in Tables 56 and 58. The values in these two tables have therefore been converted to the equivalent values per m^2 of substratum to give some idea of the absolute values of abundance, mortality and biomass shown by C.germari on section A 100 to A 300 of Barbrook reservoir.

Table 59 is derived from Table 56 and shows the numbers of the various stages produced per m^2 of substratum in the course of a season and the numbers per m^2 of each stage which die during a season. Table 60 is derived from Table 58 and shows the values from that table expressed to the nearest gram weight per m^2 of substratum.

It might be considered that the values given in these tables are excessively high, but Ancona (1933), on the basis of

Stage.	Produced.	Lost.
Autumn adults 1957.	3,420	3,040
Spring adults 1958.	380	380
Eggs 1958	34,808	14,630
Nymphs 1958	20,178	16,454
Autumn adults 1958	3,040	2,242
Spring adults 1959	798	798

Table 59. Approximate numbers of individuals of each stage produced and lost in each stage, expressed as individuals per m².

Stage	Wet biomass		Dry biomass	
	Produced	Lost	Produced	Lost
Autumn adults 1957	54	48	20	18
Spring adults 1958	10	10	2	2
Eggs 1958	4	2	2	1
Nymphs 1958	-	71	-	11
Autumn adults 1958	48	36	18	13
Spring adults 1959	22	22	4	4

Table 60. Approximate quantity of each stage produced and lost during the season, expressed in g. weight per m² of substratum.

observations by Pennafield, states that in Lake Texcoco (Mexico) the standing crop of corixid nymphs may reach a concentration of 200,000 per m^3 of water. The total production of nymphs in Barbrook reservoir during 1958 at a depth of 1.0 m. (3 ft.) was of the order of 20,000 per m^2 of substratum. Now the number of nymphs per m^2 of substratum at 1.0 m. (3 ft.) depth will be equal to the concentration per m^3 of water at that depth, so that the total annual production of nymphs in Barbrook reservoir at 1.0 m. depth on section A 100 to A 300 is only about 1/10th of the standing crop recorded in Lake Texcoco. The highest standing crop of nymphs recorded in Barbrook reservoir was the value of 300 to 400 per S.N.S. (11,000 - 15,000 per m^2 of substratum) obtained on 1.8.58.

In contrast, Popham (1952 a) counted the numbers of adults of C.distincta on known areas of pond bottom and found that in different parts of the pond the number of individuals per m^2 of bottom varied from 0 to about 10 on 17.5.57. At the corresponding time of the year, C.germari adults on section A 100 to A 300 of Barbrook reservoir had a density of about 380 per m^2 during 1958. Popham's data are based on direct counts of the specimens visible on the pond bottom and may therefore give a very low estimate of the abundance of C.distincta within the pond. In any case, Barbrook reservoir contains the most dense population of Corixidæ known to the present writer and a 38-fold difference between the Barbrook estimate and the figures obtained by Popham could well be explicable simply in terms of a real difference in the densities.

Mundie (1957) studied the Chironomidae of storage reservoirs which received water from the River Thames and were eutrophic. In one

of his reservoirs the highest estimate of standing crop made during the season was a value of 40,000 to 50,000 individuals per m^2 at 1.0 m. depth during March. At the same time a value of 34,000 individuals and 5.25 g. dry weight per m^2 was obtained at 6.8 m. depth. Comparison of these data with the figures for C.germari given in Tables 59 and 60 shows that though the annual production of eggs per m^2 by C.germari is smaller than the maximum standing crop of Chironomidae recorded by Mundie, the actual biomass of material produced by C.germari per m^2 of bottom is considerably higher than the biomass of Mundie's maximum standing crop. It must be noted, however, that this point has been somewhat over-emphasised by the treatment given above, for two reasons. Firstly, comparison has been made between the standing crop of chironomid larvae and the annual production of C.germari, though Table 60 shows that the standing crop of autumn adults of the latter gives a considerably higher biomass per m^2 than do the Chironomidae in Mundie's reservoir. Secondly, the figures given for C.germari are based on collecting from that part of the reservoir where the species is most abundant and are only applicable to the margins of the reservoir, whereas Mundie's figures are probably applicable to the whole margin of his reservoir down to a depth of at least 6.8 m. (19 ft.). Thus the abundance and biomass of chironomid larvae in the reservoir as a whole are probably a good deal higher than the comparable figures for C.germari in Barbrook reservoir.

XV. DISCUSSION.

In both 1957 and 1958 a marked decrease in catch per S.N.S. was observed after the autumn maximum had been reached. Walton (1943) made a similar observation for several corixid species and attributed the decrease in abundance to dispersion by flight. It is interesting to note that the species for which Walton gives diagrams to illustrate this autumn fall-off were C.falleni, C.nigrölineata, C.lateralis and C.sahlbergi, all species that are well known fliers (Leston 1954, Leston and Gardner 1953, Brown 1951-52, Popham 1952, Poisson, Richard and Richard 1957). The opinion has been expressed above that C.germari does not fly very much and several considerations suggest that the autumn fall-off of this species is not primarily a result of dispersion by flight. No flight was observed during the period of fall-off in 1957 or 1958 and, in both years, the possibility of flight taking place was small because the fall-off occurred when air and water temperatures were falling and there was little direct insolation. In addition, the catches per S.N.S. for the autumn of 1957 and the winter of 1957 to 1958 fell below the values obtained in the spring of 1958, and dispersion by flight would not give an adequate explanation of these observations. It is therefore likely that the autumn fall-off in the abundance of C.germari in Barbrook reservoir is to be explained in terms of a change in the distribution of this bug in the reservoir in response to falling water temperatures or decreased illumination or day-length.

Counts of the number of fully developed eggs per female (Tables 42 and 43) showed that the rate of development of eggs within the females exceeded the rate of oviposition throughout the 1957



oviposition period, whilst in 1958 most of the eggs developed within the females were laid before the decline of the old generation began. This can be related to the water levels during the two years. In 1957 the water level fell throughout the oviposition period, until by 10.7.57 none of the stony bank on section A 100 to A 300 was available for oviposition. It is likely that this caused a shortage of suitable oviposition sites and hence the females tended to retain eggs during the latter part of the oviposition period. In 1958 the water level remained near top water level throughout the oviposition period and the rate of oviposition exceeded the rate of development of eggs within the females during the latter part of the oviposition period, presumably because there was no shortage of oviposition sites during 1958.

The fall in water level during 1957 is also likely to have caused considerable egg mortality. Eggs laid on the stones of section A 100 to A 300 and then exposed above water would die through dessication or as a result of the instar 1. nymphs hatching onto dry land. In spite of this additional cause of egg mortality during 1957 as compared to 1958, the numbers of new generation adults produced in the two seasons were very similar (Table 53).

SECTION C.

ECOLOGICAL REQUIREMENTS OF C.GERMARI, WITH
REFERENCE TO OTHER SPECIES OF CORIXIDAE.

XVI. THE DISTRIBUTION OF C.GERMARI, THE CLOSELY RELATED SPECIES C.CARINATA AND THE ASSOCIATED SPECIES GLAENOCORISA PROPINQUA, WITH SPECIAL REFERENCE TO THE PENNINE REGION.

Tables 61 and 62 show species analyses of corixid samples from water bodies in the Pennine region. An attempt is made to examine these results in the light of previous records of C.germari, C. carinata and G. propinqua.

(1) Survey of the literature.

(i) General :-

C.germari and C.carinata were confused as a single species until their separation by Lundblad (1925). Hence, records published before that date are of little value so far as these species are concerned. These two species and G.propinqua are generally regarded as rather uncommon species and many of the more recent accounts of their habitats have been based on small numbers of specimens taken from relatively few places. In addition, many of the accounts are of little value in assessing the types of places inhabited by these species because they do not include adequate descriptions of the habitats. In attempting to survey the literature on this subject, one is therefore faced with the task of bringing together many small portions of information into a single statement. This is particularly difficult in the present instance because, in the case of little-known species, ~~and which are~~ the decision as to which features of the habitat are important to the species and which are not is very arbitrary and the features stressed vary from one writer to another.

Nevertheless, the literature gives several points on which various writers agree and an attempt is made below to present a brief

Date.	1 in.O.S. Ref.	Feet above sea.	<u>C.wollastoni.</u>	<u>C.nigrolineata.</u>	<u>C.sahlbergi.</u>	<u>C.lateralis.</u>	<u>C.praeusta.</u>	<u>C.punctata.</u>	<u>C.venusta.</u>	Totals.
22.4.55	111/285835	1200	1	24		1				26
22.4.55	111/273832	1360	2	6			1			9
22.4.55	111/275833	1325	2	3	5					10
21.5.57	84/992307	1600	20	22					2	44
23.5.57	84/750358	1900	10	4						14
22.4.55	111/284836	1200	14	3						17
22.10.56	84/757325	1800	8	2						10
22.10.56	84/757327	1800	57	6	1					64
22.4.55	111/273835	1355		2						2
8.10.56	84/758328	1800	12	1						13
8.10.56	84/757325	1800	40	1				4		45
8.10.56	84/765327	1800	43							43
22.10.56	84/757326	1800	8							8
1.11.56	84/753355	1750	6		8					14
23.5.57	84/753347	1750	1						1	2
23.5.57	84/751365	1950	5							5

TABLE.61. Species analyses of samples from Pennine peat pools.

Date.	1 in.O.S. Ref.	Feet above sea.	<i>C.wollastoni.</i>	<i>C.angrolinaea.</i>	<i>C.sahbergi.</i>	<i>C.lateralis.</i>	<i>C.praeuseta.</i>	<i>C.punctata.</i>	<i>C.venusta.</i>	<i>C.scotti.</i>	<i>C.distincta.</i>	<i>C.semistrata.</i>	<i>C.fossarium.</i>	<i>C.dorsalis.</i>	<i>C.germari.</i>	<i>G.propinqua.</i>	<i>C.carinata.</i>	Totals.
16.7.54	111/259855	1100	6												43	1		50
16.7.54	111/263855	1080	4												13	101		118
2.6.59	84/787432	1600	13												25	6		44
21.5.57	84/985310	1500	3													8	29	40
11.11.58	84/817431	1650	11	4													14	29
2.6.59	84/785415	1900	4													2	3	9
30.4.59	84/898434	1400	6		1											3	2	12
29.4.59	84/825430	1600	17				1									1	4	22
30.4.59	84/877446	1550	33						13							6	9	62
24.11.59	84/998328	1300	17						2		1					4		24
-9.58	84/780330	2000	46		4												2	52
24.11.58	84/989348	1100	5						1	5	13						2	26
30.4.59	84/825468	1350				1			61									72
28.10.58	84/736304	2500	30													2	87	119
6.6.57.	84/729283	1200	1			1											1	7
20.4.57	53/577777	800					3				24	4	1					68

TABLE.62. Species analyses of samples from Pennine reservoirs and tarns.

summary of the information given about the habitats occupied by each of the three species.

(ii) C. germari.

a. Size and depth of water bodies :-

Pearce and Walton (1939), Macan (1954^e) and Popham (1949) are agreed that C. germari usually occupies relatively large bodies of water. On the subject of depth, Macan (1954a) states that this species appears to live in water bodies of large size with a shallow, uniform depth. (Walton (1943) states that this species shows a marked preference for deep water (1 m. or more) and probably lives at greater depths than any other British species, with the possible exception of C. panzeri.

b. Base status :-

Macan (1954a) stated that this species is often found in base-deficient waters surrounded by peat, but it also occurs in base-rich waters as shown by the fact that Walton (1943) found it to be abundant in a calcareous reservoir and Macan (1954b) found it to be the most abundant species in a calcareous lake in Ireland.

c. Altitude :-

Brown (1948), referring to the distribution of C. germari and C. carinata in Scotland, stated that both species are probably widespread there and that they usually occur at altitudes of 1,000 ft. (300 m.) or more; though records of C. germari from the South of England suggest that altitude is less important to that species than to C. carinata. The fact that C. germari can occur in quite low lying water bodies was also shown by Crisp and Heal (1958)

who took this species from four Irish lakes, all of them at an altitude of less than 100 ft. (30 m.).

d. Bottom material and vegetation :-

Walton (1943) claimed that this species was usually found on a hard substratum with little or no macroflora. Popham (1949) also referred to the paucity of vegetation in the habitats of C.germari and Macan (1957) found this species in seven Scottish lochs all of which had bottoms of stones, gravel, sand or a mixture of all three.

e. Wave action :-

The observation that this species can occur in quite rough water was made by Walton (1943).

f. Bank profile :-

Macan's (1954a) statement regarding the uniformity of depth shown by the habitats occupied by C.germari (See a. above) suggests that these habitats must have relatively steeply sloping banks and Macan (1957) draws further attention to the fact that this species appears to prefer water bodies of fairly uniform depth with steeply sloping sides. The findings of Crisp and Heal (1958) agree with those of Macan on this point. Furthermore, Walton (1943) found two water bodies in which C.germari occurred in appreciable numbers and, although he states that the only two features shared by these two water bodies were the low value of dissolved organic matter and the hard bottom, it is clear from his habitat descriptions that these water bodies both had banks sloping steeply down into deep water round part, at least, of their margins.

(iii) C. carinata

a. Size and depth of water bodies :-

Brown (1945) studied the Corixidae of the Faeroe Islands and found only two species - C. carinata and C. wollastoni. He concluded that C. carinata was generally found in the larger, deeper pools with much open water, whilst C. wollastoni preferred pools with denser vegetation. Macan (1954^a) stated that C. carinata lives in deeper water than most of the other British peat pool species and he pointed out that the findings of Macan (1938) agree with those of Brown (1945) on this point.

b. Base status :-

The British records of this species are from base-poor upland water bodies. In Scandinavia, however, it is also found in low-lying pools near the sea (Lundblad 1925) and it is unlikely that such waters are base poor.

c. Altitude :-

Macan (1954) stated that, in Britain, C. carinata is an upland species, whilst Brown (1948) stated that in Scotland it is usually found above 1,000 ft. (300 m.) and expressed the opinion that altitude is probably more important to this species than to C. germari. Lundblad (1925) stated that, in Scandinavia, C. carinata is found in upland pools and also in pools near the sea.

d. Bottom material and vegetation :-

From the references to peat pools made by Macan (1954), and Brown (1945) it seems likely that the bottoms of the habitats

contained peat but no definite information is available on this point. Macan (1958, 1954a) and Brown (1945) both stated that C.carinata appears to prefer open water with relatively little macroflora.

e. and f. Wave action and Bank profile :-

No definite reference is made to these two features, but it seems very likely that the large upland habitats which have been described for C.carinata are subject to fairly severe wave action.

(iv) G.propinqua.

Very little information is available regarding this species. Pearce and Walton (1939) recorded the species from Cheshire and listed only six places in England, Wales and Ireland where it had then been found. Subsequent captures in Britain and Eire have been recorded by Walton (1943), Brown (1943), Brown (1946), Brown (1948), Popham (1949), Macan (1954 a and b), Macan (1957), Hanney (1958) and Crisp and Heal (1958). Most of these records refer only to small numbers of water bodies and are often based on very small numbers of specimens, so that only a sketchy picture of the type of habitat occupied by G.propinqua can be built up from them. The following synopsis is based on general statements made by some of the writers listed above.

a. Size and depth of water bodies :-

Pearce and Walton (1939) and Popham (1949) stated that this species generally lives in large water bodies, whilst Macan (1954 a.) stated that it probably inhabits deeper water than most peat pool species.

b. Base status :-

The general impression gained from the literature is that, in the British Isles, this species is confined to base-poor waters, usually peaty.

c. Altitude :-

Most of the habitats so far recorded have been upland ones, though the presence of G. propinqua in a water body near Cambridge (Hutchinson 1925) and in Irish bog pools less than 100 ft. (30 m.) above sea level (Crisp and Heal 1958) show that it is not confined to the uplands.

d. Bottom material and vegetation :-

Walton (1943) collected this species from a pool in Somerset and found that it was confined to open water. Popham (1949) stated that the habitats occupied by G. propinqua have very little vegetation.

e. Wave action :-

Walton (1943) stated that G. propinqua appears to be little affected by rough water conditions.

f. Bank profile :-

Crisp and Heal (1958) found G. propinqua in only six out of 20 water bodies studied on an Irish bog. Those six were the only ones, of the twenty examined, that had banks sloping steeply into deep water and it is therefore likely that this is an important feature of the type of habitat occupied by this species.

(2) Survey of the Corixidae of Pennine water bodies with special reference to C.germari, C.carinata and G.propinqua.

(i) General :-

This survey is concerned chiefly with upland waters in the Pennines but reference will also be made to other water bodies sampled by the present author.

As far as possible the collecting was carried out in the autumn and spring, since Corixid populations can be regarded as relatively stable during those seasons. This was not possible in all cases. The data used are based on general collections obtained by hand netting all round the margin of each of the smaller water bodies and at as many different places as possible around the margin of each of the larger water bodies. Particular care was taken to ensure that netting was carried out in water 1 to 2 m. deep (3 to 6 ft.) as well as in the shallows. The amount of time available for collecting at each place varied considerably and hence the total numbers collected from each one do not necessarily bear any relationship to the abundance of the Corixidae there.

In a number of cases several visits were made to a single water body and in such cases only one sample date is represented in the tables of results, that date being selected as one on which a large sample was taken at a time of the year when the population could be regarded as being relatively stable.

The results are shown in Tables 61 and 62, where each water body is referred to by a National grid reference. To simplify description the water bodies have been divided into three general

types :- peat pools, tarns and reservoirs. Each type is defined below:

(ii) Peat pools :-

Pools from .0005 (.00125 acres) to .012 ha. (.025 acres) in area, with maximum depths of 0.3 (1 ft.) to 2.0 m. (6 ft.) but usually less than 1.0m(3 ft.) deep. These pools usually have peat bottoms but, in some cases, the bottom consists partly or wholly of clay or finely divided mine debris. Stones, however, were rarely found on the bottoms of these pools. The peat pools are often situated in very exposed positions but, because of their small size, they rarely suffer severe wave action. The quantity of vegetation present varies a good deal from one pool to another, but most have a certain amount of Juncus effusus L., around their margins and some or all of the following present :- Sphagnum sp., Equisetum limosum L., Eriophorum angustifolium Honck, Potamogeton ^antans L., Glyceria fluitans (L), and mats of green filamentous algae. Pools of this type are the most common water bodies in the Pennines.

The duckpool on Big Moor also falls into this category.

(iii) Tarns :-

Three tarns were studied but one of them (83/677077) is rather unusual and will be described in another part of this work. The other two (84/729283 and 84/736304) are described below :-

84/736304 occupies about 1.0 ha. (2.5 acres) and is about 0.5 m. (1.5 ft.) deep, whilst 84/729283 has an area of 10 ha. (25 acres)

and a depth^{of} about 1.0 m. (3 ft.). Both of these water bodies have fairly steeply sloping margins and relatively uniform depth. In both cases the bottom is of sand with a covering of finely divided peat in most places and with stones littered about over the bottom. Neither tarn has any macroflora apart from a narrow marginal fringe of Eriophorum angustifolium at the south end of 84/736304. Both of ~~these~~ these tarns are in exposed positions and suffer severe wave action.

(iv) Reservoirs :-

In addition to the Barbrook, Little Barbrook and Ramsley reservoirs, eighteen Pennine reservoirs were studied and sample analyses from thirteen of these are given in Table 62. Two of these latter reservoirs (84/989348 and 84/828468) show certain deviations from the general description given below and these peculiarities will be dealt with in a later part of this work.

The South Pennine reservoirs studied are all associated with water supply and the North Pennine ones with mining activity. Both types of reservoir have been constructed by building a wall across a valley or on a hillside so as to retain the drainage water from the surrounding moorland. Thus, in all cases, part or all of the reservoir margin consists of a sandstone wall sloping steeply down into 0.5 (1.5 ft.) to 3.0 m. (9 ft.) depth of water, below which is a fairly level bottom of sand or clay which, in the case of all but the first three of the reservoirs listed on Table 62, is

overlayed by from 1 to 3 cm. (.25 to .75 in.) of finely divided peat. In all cases, the bottom is littered with loose stones. These reservoirs were all situated in exposed places and suffer severe wave action. In general, they contain no macroflora apart from occasional restricted areas of Glyceria fluitans, Juncus bulbosus agg., or Potamogeton natans. The only exceptions are Little Barbrook reservoir with its extensive marginal Glyceria beds, 84/787432 which has a steep bank with deep water and a sandy bottom at one side and a gently sloping bottom with much mud and an extensive bed of P.natans at the other side, and 84/780330 which contains a dense bed of P.natans but has a narrow strip of deep, open water along one side.

The South Pennine reservoirs are from 3.6 to 24 ha. (9 to 60 acres) in area, whilst the North Pennine reservoirs are generally rather smaller and range in area from 0.06 to 3.9 ha. (.15 to 10 acres).

(v) Distribution of the species between the different types of water bodies.

An attempt is made here to give a general summary of the corixid faunas of the different types of water body studied and to summarise those features of each type of water body which appear to have some bearing on the corixid species present in that type.

The bulk of the Corixidae collected from the peat pools (See Table 61) belonged to two species - C.wollastoni and C.nigrolineata. According to Macan (1954 a.) these species are typical of small peat pools above the altitude of 1,000 ft.(300 m.).

The other species listed can probably be regarded as strays from other habitats. The most striking feature is the complete absence of C.germari, C.carinata and G.propinqua from the peat pool samples.

Species analyses of the tarn and reservoir samples are given in Table 62 and by leaving water bodies 83/677077, 84/989348 and 84/828468 out of consideration for the time being, it is possible to draw a number of general conclusions.

The commonest species of the peat pool samples, C. wollastoni, occurred in quite large numbers in the tarns and reservoirs but a marked contrast between the peat pools and the larger water bodies was the scarcity of C.nigrolineata and the prominence of C.germari, C.carinata and G.propinqua in the samples from the tarns and reservoirs. The distribution of the latter three species between the individual tarns and reservoirs is rather striking, for C.germari and C.carinata were rarely found together in any individual water body, C.germari being confined to those with a predominantly sandy bottom and C.carinata to those with an accumulation of peaty material on top of the sand. G.propinqua was found in both peaty and sandy bottomed water bodies. The possibility that C.germari prefers hard and, therefore, presumably inorganic bottoms has already been referred to by Walton (1943) but the occurrence of this species in peat bottomed lakes in Eire has been demonstrated by Crisp and Heal (1958). Two possible reasons can, however, be put forward, to explain why, in the Irish lakes studied by Crisp and Heal, C.germari was found in water bodies which appear more typical

of C.carinata. Firstly, the water bodies concerned were at a very low altitude and C.carinata appears to be confined to high altitude's in the British Isles. Secondly, C.carinata has not yet been recorded from Ireland and may prove to be absent from the Irish fauna, in which case it is reasonable to suppose that the closely related C.germari would tend to occur in certain water bodies in Ireland that would be inhabited by C.carinata in other parts of the British Isles. The results also suggest that C.germari prefers rather larger and deeper bodies of water than C.carinata, for the water bodies in which the former was found range from 1.2 to 24 ha. (3 to 60 acres) in area whilst those in which C.carinata was found range from 0.06 to 4.0 ha. (.15 to 10 acres). Furthermore, the stony banks of the reservoirs containing C.germari slope down steeply into 1.0 (3 ft.) to 4.0 m. (12 ft.) of water whilst, with the exception of 84/985282 (depth at water's edge about 3.0 m. (9 ft.)), the reservoirs occupied by C.carinata were only 0.3 (1 ft.) to 1.5 m. (4.5 ft.) deep.

(vi) Common features of the water bodies occupied by C.germari, C.carinata and G.propinqua.

On the basis of the observations made at Barbrook, Little Barbrook and Ramsley reservoirs, at the water bodies listed in Tables 61 and 62, and the Irish lakes studied by Crisp and Heal (1958) it is possible to give a general summary of the features shared by the habitats in which these three species have been found. This survey will be made under the same headings as were used in the survey of the literature (pp. 103-108).

a. Size and depth of water bodies :-

The Pennine and Irish data show that these species occurred only in relatively large water bodies. It is also clear that the water bodies occupied by these species were generally deeper than the small peat pools from which these species were absent. It has been shown above (pp. 54 and 55) that C.germari on section A 100 to A 300 of Barbrook reservoir is more abundant at 1.0m(3 ft.) than at 0.5 m.(1.5 ft.) depth. Similarly, collections of Corixidae from 0.5 (1.5 ft.) and 1.0 m (3 ft.) depths on a steeply sloping bank in reservoir 84/985310 consisted almost entirely of C.carinata and C.wollastoni and comparison of the relative proportions of these two species at two different depths by means of a Chi-squared test showed that C.carinata formed a significantly larger proportion of the catch at 1.0 m.(3ft.) than at 0.5 m. (1.5 ft.) (See Table 63). Thus, for C.germari and C.carinata, and probably also for G.propinqua, water depth is an important feature of the habitat. This agrees with the statements of the other writers mentioned in the survey of the literature (pp. 103-108).

b. Base status :-

The Pennine water bodies where any of these three species were found all contain base-poor water, but the work of Walton (1943) and of Macan (1954 b.) showed that C.germari, at least, can also occur in base-rich waters.

Habitat.	Water depth.	<u>C.carinata.</u>	<u>C.wollastoni.</u>	Totals
Stony bank	1.0 m.	21	1	22
Stony bank	0.5 m.	18	12	30
Totals		39	13	52

Chi-squared = 8.509 $P < .001$

Thus there is a significant difference between the proportions of C.carinata and C.wollastoni at the two depths studied.

TABLE 63. The depth distribution of C.carinata and C.wollastoni on a stony bank in reservoir 84/985310 on 21.11.58.

c. Altitude :-

In the absence of data from low altitude reservoirs for comparison with the Pennine data, it is not possible to make any definite contribution to our knowledge of the altitudinal distribution of these species on the basis of the present work.

d. Bottom material and vegetation :-

It has been noted that C.germari tends to occur in water bodies with sandy bottoms, C.carinata in places where the sand is overlaid by peat and G.propinqua, in both types of place. One feature common to all the habitats where these three species have been found is, however, the presence of some stony or rocky material. The walls of the Pennine reservoirs are made of stones and the bottoms of both reservoirs and tarns are littered with stones, whilst in the Irish lakes which contained C.germari and G.propinqua the peaty banks are interspersed with areas of exposed rock surface. The importance of stones as oviposition sites for C.germari has been demonstrated at Barbrook reservoir and casual observations suggest that the same applies to C.carinata. With regard to G.propinqua, Crisp and Heal (1958) found that if the samples from water bodies containing C.germari and G.propinqua were separated into insects collected from rock surfaces and insects collected from peat surfaces and if the proportion of C.germari + G.propinqua to other species was compared between the two sets of sub-samples, then the C.germari and G.propinqua formed a significantly higher proportion of the catch from rock than from peat surfaces. Clearly it was desirable that this process should be repeated for G.propinqua and for C.germari separately and in April 1959 the area

was revisited and further samples were taken. On that occasion relatively few C.germari were collected, but G.propinqua was quite abundant. The results (Table 64) show that, relative to the other species present in the lakes studied, both C.germari and G.propinqua show a significant preference for rocky surfaces. Now these results and those already published were obtained at times of the year when these two species were ovipositing or were just about to begin oviposition, thus in the case of C.germari this preference for rock surfaces is likely to be an expression of the oviposition preference of the species. This may also be the case with G.propinqua but this species is largely predatory (Walton 1943) and may favour rock surfaces as resting places from which it can attack potential prey organisms, though it is difficult to see why rock surfaces should be superior to peat surfaces for this purpose.

Walton (1943) stated that G.propinqua is confined to open water and this observation is supported by observations on this species at Barbrook, Ramsley and Little Barbrook reservoirs (See pp.33-35 and Tables 14 - 19). C.germari and C.carinata were found both in open water and amongst vegetation but the species analyses of the samples from Barbrook reservoir (Tables 14 and 15) show that although C.germari was present in the densely vegetated station Delta, the proportion of other spp. present there was much higher than in the relatively open water of the rest of the reservoir. The same thing is shown by Table 65 which compares the proportions of C.germari and C.wollastoni in samples taken from a depth of 1.0 m. (3 ft.) on a stony bank with open water and from a depth of 0.5 m. (1.5 ft.) on a

(A)

	Peat	Rock	Totals
<u>G. propinqua.</u>	13	67	80
Other spp.(except for <u>C.germari</u>).	107	66	173
Totals	120	133	253

Chi-squared = 45.6 P < .001

(B)

	Peat	Rock	Totals
<u>C.germari</u>	0	11	11
Other spp.(except for <u>G. propinqua</u>)	107	66	173
Totals	107	77	184

Chi-squared = 16.3 P < .001

TABLE 64. Distribution of C.germari and G. propinqua between rock and peat surfaces in Irish Lakes, April, 1959.

(A) G. propinqua.

(B) C.germari.

Habitat	Water depth.	<u>C.germari.</u>	<u>C.wollastoni.</u>	<u>Totals</u>
Stony bank	1.0 m.	8	1	9
Potomogeton bed	0.5 m.	1	17	18
Totals		9	18	27

Chi-squared = 18.75 $P < .001$

Thus there is a significant difference between the proportions of C.germari and C.wollastoni in the two habitats studied.

TABLE 65. The distribution of C.germari and C.wollastoni in reservoir 84/787432 on 11.11.58.

muddy bottom in a dense P.natans bed. C.germari formed a significantly higher proportion of the catch from the former place than the latter, though this may partly be a reflection of the depth preference shown by C.germari. Similarly, Table 66 compares the relative proportions of C.carinata and C.wollastoni in the open water of a tarn and in a marginal fringe of E.angustifolium and shows that C.carinata formed a significantly greater proportion of the catch from open water than from amongst the vegetation. The contention that C.germari and C.carinata prefer open water is further supported by the fact that most of the water bodies in which they have been found contain relatively little vegetation.

e. Wave action:-

The Pennine and Irish habitats where any of these three species have been found by the present writer have always been relatively large water bodies in exposed places and subject to fairly severe wave action.

Walton (1943) states that both C.germari and G.propinqua can occur in waters subject to severe wave action. He also states that rough water "makes no difference" to G.propinqua and that C.germari, in one of his water bodies, could be found "abundantly in rough water where the wind was driving ^{up} waves half a metre high". The observations made at Barbrook reservoir, however, (see Table 51) suggest that Walton's remarks about C.germari require some qualification, for the Barbrook data do show that C.germari can be found on shores subject to severe wave action and that the species can be collected there when such wave action is in operation, but they also

Habitat	Water depth.	<u>C. carinata.</u>	<u>C. wollastoni.</u>	Totals
Open water.	0.5 m.	64	3	67
Eriophorum fringe.	0.5 m.	23	27	50
Totals.		87	30	117

Chi-squared = 56.63

$P < .001$

Thus there is a significant difference between the proportions of C. carinata and C. wollastoni in the two habitats studied.

TABLE 66. The distribution of C. carinata and C. wollastoni in tarn 84/736304 on 28.10.58.

show that fewer specimens than usual can be collected per unit effort under such conditions. In fact, it seems that the species tends to avoid the effects of severe wave action by moving into deeper water or descending amongst the stones of the substratum.

f. Bank profile :-

Macan (1957) distinguishes between water bodies whose bottoms slope gently from edge to middle and those with steeply sloping margins and relatively level bottoms. These he describes as "tin-hat" and "pill-box" types respectively. This distinction appears to be particularly important in describing the habitats occupied by C.germari, C.carinata and G.propinqua for all the water bodies in which any of these three species were found by the present writer belonged to the "pill-box" type.

(vii) Anomalous cases :-

Attention has been paid to the features common to all the water bodies where the present writer found one or other of these three species. There were, however, certain water bodies in which these species were rare or absent, even though these water bodies fulfilled some or most of the conditions which appear to be required by the three species. It is therefore necessary that some attention be paid to these water bodies in an attempt to see why they should be unsuitable for these three corixid species.

These anomalous cases consist of three listed on Table 62.- 83/677077, 84/989348 and 84/828468 and five others in the South Pennine region which are not included in Table 62. The map references

of these latter five are 111/320747, 111/355657, 111/358655, 111/360655 and 111/267854. Of these water bodies, 83/677077 can be immediately disposed of on the grounds that it is totally different from all the other large water bodies being studied. Although surrounded by moorland, it is a highly calcareous tarn with gently sloping margins, a fairly thick accumulation of mud in many places and beds of Phragmites communis Trin. at a number of points around its margins. Thus it is not surprising that this tarn should contain a radically different corixid fauna from the rest of the water bodies.

The remainder of the anomalous cases are all reservoirs and can be separated into two groups :- (1) Those where, in spite of the fact that at least one hour's netting was carried out in each case, negligible numbers of Corixidae were captured.

(2) Those where reasonable sized samples were obtained, but C.germari, C.carinata and G.propinqua formed a negligible proportion of the total catch. It is important to note, however, that, so far as their sizes, depths, bottom profiles, stony banks, densities of vegetation and bottom materials are concerned, these water bodies all appear likely to contain one or more of these three species.

Reservoir 111/267854 is situated at an altitude of 1070 ft. and receives water from reservoirs 111/259855 and 111/263855 (See Table 62). The only obvious respect in which it differs from the two latter reservoirs is that lime is added to

its water. During three visits in the summer and early autumn of 1954 no Corixidae were ever taken from it. Reservoirs 111/355657 and 111/360655 are small reservoirs at altitudes of 750 and 675 ft. (250 m. and 225 m.) respectively. Both have steeply sloping stony shores and bottoms of clay with little vegetation. These two water bodies receive water draining from farm land and have water pHs. on the alkaline side of neutrality. When they were visited in April 1959 no Corixidae were found in 111/355657 and only a single specimen of C.praeusta was obtained from 111/360655.

Reservoirs 111/320747 and 111/358655 are similar to the last two mentioned above and are situated at altitudes of 575 and 700 ft. (190 and 230 m.) respectively. When they were visited during April 1959, 12 specimens of C.dorsalis were taken from the latter and 32 specimens of C.dorsalis together with two specimens each of C.falleni and C.praeusta and single specimens of C.distincta and C.germari were taken from the former. Although these reservoirs have portions of steep stony bank apparently suitable for C.germari, Corixidae were scarce or absent in these areas and the bulk of the C.dorsalis material was collected from portions of gently sloping shore with a certain amount of vegetation cover. Similar results, but for a different species, were obtained from reservoir 84/828468 (See Table 62). This is a North Pennine reservoir associated with a mine which is still in operation. The mine and the reservoir are situated in a valley and the reservoir is situated lower down the valley than the mine and spoil heaps. It seems likely that the spoil heaps act as a source of enrichment for the drainage water flowing into the

reservoir. Netting on a stone bank sloping steeply into 1.0 (3 ft.) to 2.0 (6 ft.) m. of water yielded only 2 specimens of C.dorsalis and single specimens of C.germari and C.nigrolineata, but netting in gently sloping shallows (0.25 m. depth) inshore of a dense bed of P.natans on a bottom^{of}/clay, sand and mud gave 61 C.venusta, 6 C.dorsalis and 1 C.lateralis.

Reservoir 84/989348 appears to be a typical North Pennine reservoir with steeply sloping stone banks, little vegetation and a bottom of finely divided peat. Although specimens of C.carinata have been taken there, the most common species is C.distincta and this is found at a depth of about 0.5 m. on the stony banks. This reservoir is only about 2.5 miles (4.0 Km.) from reservoir 84/985310 and appears very similar to that reservoir in most respects. One difference between these two reservoirs, however, is that 84/985310 receives drainage water from base-poor rocks only, whilst just uphill of 84/989348 there is a narrow band of limestone and this feature may serve to raise the base status of the latter reservoir. The pH values given by water samples from these two water bodies were 3.9 and 4.6 respectively and this shows that, though the water in 84/989348 may be less acidic than that in 84/985310, it is still highly acidic.

The results from these various reservoirs are difficult to explain. It is clear that the base status of some, and perhaps most of these anomalous reservoirs is higher than that of the other water bodies studied, but the records of Macan (1954) and Walton (1943) show that high base status alone does not give an

adequate reason for the absence of C.germari. Another point which arises, however, is that most of the water bodies studied do not contain any fish, but that all of the anomalous water bodies, apart from 84/989348, contain trout and, in some cases, minnows as well. Walton (1943) showed that trout will eat C.germari and Popham (1944) showed that, under laboratory conditions, minnows will attack Corixidae. Even though trout and C.germari were both present together in the reservoir studied by Walton, it is possible that in certain water bodies the presence of trout might cause the extinction of C.germari in those water bodies. In such water bodies the only Corixidae likely to be found would be occasional visitors from other habitats and species such as C.dorsalis which live in relatively shallow water where they are less vulnerable to the attacks of large predators such as trout.

A further factor which may be important is the very small amount of flight which appears to be indulged in by C.germari, this probably means that the rate of spread of this species is relatively low and therefore that habitats quite suitable for this species may not contain it, simply because the species has never succeeded in reaching these habitats in sufficient numbers to colonise them successfully. Little is known about flight in C.carinata and G.propinqua, but, if they too should prove to fly very little, the same considerations will apply to them as to C.germari.

Thus various possible explanations of the anomalous water bodies can be given, but in the absence of further information,

these explanations must be regarded as rather speculative ones.

XVII. EXPERIMENTS ON RESPIRATION AND SWIMMING.

The experiments described here must be regarded as preliminary investigations but, though they are not very critical experiments the results are suggestive. The basic principle of all these experiments has been to take a number of species of Corixidae, representing a fairly wide variety of habitat types, and to compare the performances of these species in various activities relating to respiratory and swimming efficiency. The species that have been employed are C.germari, C.carinata and G.propinqua (deep, open water species), C.wollastoni (shallow peat pools), C.sahlbergi (small pools usually with dead leaves on the bottom) and C.distincta (lakes and ponds in places where a certain amount of organic matter accumulates). Not all of these species have been used in every experiment, but as wide a range of species as possible was used in each.

The first experiment on respiration was a comparison of the survival rates of different species when denied access to the water surface. Ten males and ten females of C.germari were each placed in 2 x 1 inch glass tubes. A piece of netting was tied over the mouth of each tube and the twenty tubes were then submerged in a trough of water. Care was taken to ensure that no bubbles of air were present in the tubes and the water temperature was maintained at 17°C. The tubes were examined at intervals and the total number of dead animals was noted on each occasion. This procedure was repeated using C.carinata, C.sahlbergi, C.wollastoni and C.distincta

and the results are shown in Table 67. If the times taken for 50% of the specimens to die are compared between species then the results show that 50% mortality was reached in less than 18 hours by C.sahlbergi, in 24 to 42 hours by C.germari and C.carinata and in 60 to 72 hours by C.distincta and C.wollastoni. Information about the oxygen tensions in the tubes during the experiment and the oxygen tensions experienced by these species in the field are required before detailed conclusions can be drawn, but the results ^{show} that, under the conditions of the experiment, there is no reason to believe that C.germari and C.carinata show any special mechanical or physiological adaptations to enable them to stay below the water surface any longer than some of the shallow water species do. Under field conditions, however, none of these species are likely to stay below the water surface for as long as they were compelled to do in this experiment and it is therefore necessary to examine not only the tolerance limits shown by the various species but also the length of time they stay down when allowed free access to the water surface. For this purpose two jars were set up for each species, one containing eight males and one containing eight females. The bottom material placed in each jar was collected from the same place as the insects kept in that jar and the water temperature in the jars was maintained at 17°C. The total number of surface visits made by the insects in each jar during each period of half an hour was determined over a total period of three and a half hours. Thus fourteen readings were obtained for each species.

Hours from start.	<u>C.sahlbergi</u>	<u>C.carinata.</u>	<u>C.germari.</u>	<u>C.distincta.</u>	<u>C.wollastoni.</u>	
18	18	5	2	1	1	
24	18	7	3	1	1	
42	20	15	15	3	3	
60		17	19	8	9	
72		19	20	13	10	
90		20		15	11	
144				17	16	
168				19	19	
180				20	20	

TABLE 67. Total number of dead specimens out of the initial 20 of each specimens of each species, after various time intervals. Experiment conducted at 20°C.

The results are summarised in Table 68 but those obtained for C.wollastoni have been omitted because, at the temperature of the experiment, this species spent most of its time at or near the water surface attempting to fly away and hence the number of surface visits recorded was unduly high. The results show that, on average, C.germari and C.carinata visited the surface less often than the two shallow water species, C.distincta and C.sahlbergi. In the case of C.germari this difference is significant at the 5% confidence level but more data is required before a definite conclusion can be reached regarding the difference in frequency of surface visits between C.carinata and the two shallow water species. It is therefore highly probable that C.germari possesses some behavioural adaptation which causes it to visit the water surface less often than the two shallow water species for which results have been obtained.

The horizontal swimming speeds of C.germari, G.propinqua and C.wollastoni were determined according to the method described by Popham (1953) and at the same time the number of leg strokes made per minute was determined for each species. The experiment was conducted at 10°C and thirty estimates of velocity and rate of striking were obtained for each species. From these data the number of leg strokes made per metre travelled was calculated for each species. The results are summarised in Table 69 and show that both C.germari and G.propinqua made significantly less strokes per minute and hence required less strokes to cover a metre than the two shallow water species did. In order to carry the argument

Species.	Mean number of surface visits per half hour by 8 individuals	
	Mean value.	5% confidence interval.
<u>C.germari</u>	2.06	1.859 to 2.268
<u>C.carinata</u>	4.59	4.146 to 5.063
<u>C.distincta</u>	5.87	4.667 to 7.224
<u>C.sahlbergi</u>	6.71	5.556 to 7.958

TABLE 68. Mean number of surface visits per hour by groups of 8 individuals of each species. Based on 14 trials per species at a temperature of 17°C.

	<u>G. prop-</u> <u>inqua.</u>	<u>C. germ-</u> <u>ari.</u>	<u>C. sahl-</u> <u>bergi.</u>	<u>C. wollast-</u> <u>oni.</u>
Mean velocity(cm/sec.)	3.2±.38	4.0±.33	3.1±.27	2.75±.36
Mean No.of strokes/sec.	213 ± 8.6	237± 7.4	280 ± 8.6	270 ± 8.5
Mean No. of strokes/m.	66.7	58.9	89.3	98.1

TABLE 69. Mean values for velocity, number of strokes per second and number of strokes per metre during horizontal swimming at 10°C. Based on 30 trials per species. 5% confidence limits are shown.

further, information is required about the amount of energy expended per leg stroke by each species. If it is assumed that the amount of energy used per leg stroke is the same for all four species, then it follows that C.germari and C.carinata swim more efficiently than C.sahlbergi and C.wollastoni and are therefore better suited to life in deep or rough water than the two latter species. What the results certainly do show is that, at the temperature of the experiment, C.germari swims significantly faster than the two shallow water species. This is of great importance, for it means that C.germari will be better adapted to life under rough water conditions than C.sahlbergi and C.wollastoni. It also suggests that C.germari will take proportionately less time over its visits to the surface than C.sahlbergi and C.wollastoni do. This last possibility was tested by placing a number of specimens of C.germari in an aquarium with 20 cm. (8 in.) depth of water above the surface of the substratum. Each time a specimen visited the water surface, the time taken to make the round trip from bottom to surface to bottom was measured. The experiment was conducted at 15°C and times were not recorded in cases where a specimen visited the surface and then swam about the aquarium before returning to the substratum. Twenty readings were obtained for C.germari and the process was then repeated for C.wollastoni and for C.sahlbergi. In each case the insects used were provided with bottom material from the places where they were collected. The results are summarised in Table 70. and show that, in 20 cm. (8 in.) depth of water, C.germari does take

	<u>C.germari.</u>	<u>C.sahlbergi.</u>	<u>C.wollastoni.</u>
Mean time taken(secs.)	6.3 ± 1.10	6.7 ± 0.99	8.9 ± 1.38

TABLE 70. Mean number of seconds taken to travel from the substratum to water surface and back again for the purpose of renewing the bubble gill. Based on 20 trials per species at 15°C in 20 cm.(8 in.) depth of water.

less time to visit the water surface and renew its bubble gill than C.sahlbergi or C.wollastoni, though the difference between C.germari and C.sahlbergi is not significant. In addition, it has been shown that C.germari visits the surface significantly less often than the two latter species. Thus, so far as the time factor is concerned, C.germari is likely to be able to make surface visitings an economical proposition at greater depths than C.wollastoni or C.sahlbergi.

XVIII. DISCUSSION.

Investigation of the Pennine habitats of C.germari, C.carinata and G. propinqua shows that the habitats of these three species can be typified to some extent. It is clear that water bodies suitable for occupation by these species are quite common in the Pennine region, in the form of reservoirs such as have been described above. Such reservoirs are widespread and by no means rare in the Pennines around the altitude of 1,000 ft.(300 m.). It is therefore likely that further collecting in this region will show that these three species are quite widespread there. It is further suggested that the reasons for these three species not hitherto being well-known in the Pennine region are that little attention has so far been paid to the corixid faunas of upland reservoirs and that inadequate attention has been given to the stony banks and deep water where these species are to be found most easily.

On the basis of the information already obtained about the biology of C.germari and the types of habitats it occupies, it is now possible to examine the various stages in its life history to see what adaptations fitting them for their habitat are shown by these stages.

It has been shown that C.germari generally lays its eggs on stones rather than on dead or living vegetation. This behaviour is clearly of value to a species living in places subject to severe wave action, for, in such places, eggs laid on vegetation are liable

to suffer dessiccation as a result of the vegetation being torn up and thrown ashore by waves. The stones of the substratum are likely to be moved about relatively little and are most unlikely to be cast ashore.

It is therefore of interest to note the peculiar form of the C.germari egg, for it is a relatively long, narrow egg with a very short pedicel and it shows bilateral symmetry such that, when the egg is attached to a plane surface, the long axis of the egg is inclined at an angle to that surface. The eggs that have been described for other species of Corixinae (Hungerford 1948, Poisson 1933, Packard 1898, Walton 1943) are of a variety of shapes but are generally radially symmetrical and their long axes therefore rise perpendicularly from the surfaces to which they are attached. Clearly, a long, narrow egg is ideally suited to being laid in crevices on stones, whilst the bilateral symmetry of the egg of C.germari means that when it has been laid within a crevice, or on a plane surface, its apex does not stand as far clear of the surface of the stone as would be the case with a long, narrow, radially symmetrical egg. The importance of this latter point is that the smaller the distance that the egg protrudes beyond the surface of the stone to which it is attached, the less danger there is of the egg being damaged by movement of the stones or by the scouring action of wave-driven particles of sand, peat or vegetation.

Popham (1941, 1943 a, 1943 b) showed that Corixidae tend to

match the colour shade of the background on which they were reared and that the adults select a background which matches their own colour shade. He further showed that, under laboratory conditions, specimens matching their background were less subject to predation by fish (Popham 1948) and to infestation by ectoparasitic mites (Popham 1943) than specimens not matching their background. It is therefore of interest to note that C.germari which lives on relatively pale, sandy bottoms is generally paler in colour than the closely related C.carinata which occurs in water bodies with peat-covered bottoms.

The most striking feature of the adults of C.germari is their ability to live at greater depths than most other British species. This fact has two consequences. Firstly, it has already been observed that this species is able to live on exposed shores in water bodies subject to severe wave action. The greater the depth at which an organism is able to live, the smaller are the chances of it being adversely affected by such wave action. This point is illustrated by the fact that the Barbrook reservoir traps at 0.3 m. depth suffered severe damage from wave action, but those at greater depths were damaged relatively little. Secondly, the water bodies usually inhabited by this species have all or part of their margins in the form of steeply sloping banks. In such a place, a species able to live only in relatively shallow water would only be able to live in a relatively narrow strip round the margin of the water body whilst a species such as C.germari that is able to

live at greater depths would be able to exploit a correspondingly broader strip and would therefore be able to attain greater numbers in the water body as a whole than would a species confined to the shallows.

In order to live at greater depths than most other species, C.germari must be, in some way, more efficient than those other species. Every time that a corixid visits the water surface to renew its bubble gill it must expend time and energy in making the journey and the greater the water depth the greater will be the quantities of time and energy required. Thus it might be expected that C.germari will show one or both of the following types of adaptation:- either some special respiratory adaptation that will enable it to visit the surface less often than the shallow water species, or else the ability to swim more rapidly and/or more efficiently than most of the shallow water species and so to expend relatively less time and/or energy in making its long journeys to the surface than is expended by the shallow water species in their shorter journeys.

The experiments on respiration and swimming suggest that C.germari is able to live at greater depths and in rougher water than certain other species with which it has been compared, because it swims more rapidly and possibly more efficiently than those other species. The experiments also show that C.germari visits the surface less often than the shallow water species, but the exact mechanism involved is not clear. Thus, results of preliminary experiments agree with inferences from study of the habits^{at} of C.germari.

SECTION D.

GENERAL DISCUSSION, SUMMARY AND REFERENCES.

XIX. GENERAL DISCUSSION.

A considerable amount of work has already been done on the British Corixidae. It is therefore necessary to justify yet another contribution on this subject and the aims of this discussion are to show the relevance of the present work to our knowledge of the Corixidae as a group and as a component of the fauna of upland water bodies, to show how such knowledge might possibly be given practical application and to consider certain developments of technique that would facilitate our expansion of this knowledge.

In the present work an attempt was made to describe the life history of C.germari in quantitative terms and to study certain aspects of the biology and distribution of this species. The studies of the biology and distribution have not raised any startling new facts but have, in many cases, provided quantitative evidence in support of the statements of previous workers on C.germari and the Corixidae in general. This is important because some of the statements previously made appear to have been based on subjective evidence and to have been rather speculative.

The studies on abundance and mortality have provided a picture of the abundance fluctuations shown by the species throughout its life history and have enabled some of the major causes of mortality to be listed, but two seasons' study are quite inadequate for the elucidation of the mechanism controlling the abundance of such an organism. Therefore this work cannot be regarded as a

study in "population dynamics" if that term be taken to imply study of the underlying causes governing the numbers attained by a given species in a particular habitat. The work must therefore be regarded as a quantitative life history study of C.germari which could serve as a basis for future work on the population dynamics of the species or for the use of the organism as a tool for study of the principles of population regulation. Such development of the work, however, would require more information about the ecological relationships between C.germari and the other animal species associated with it.

Upland reservoirs, such as Barbrook, provide a unique opportunity for work of this type because they contain relatively few species that reach appreciable abundance and hence a study of these few species would provide a relatively comprehensive picture of the interplay between the major components of the faunas of such water bodies. In order to do this, more information is required about sampling techniques.

The present discussion will therefore be directed towards two main ends :-

1. To examine two possible practical applications of our knowledge of the Corixidae and thus show the importance of detailed investigations of the biology and ecology of individual species and also the importance of attempting to gain understanding of the population dynamics of the Corixidae.

2. To discuss sampling techniques for free-swimming freshwater organisms, to assess the value of those used in the present work and to consider the developments of

technique likely to be required in future work on the Corixidae.

Previous descriptive work on the habitats of Corixidae shows that each species tends to occur in a restricted range of habitats. In view of this, the widespread occurrence of Corixidae and the clear-cut taxonomy of the British species, it might be expected that these animals would be useful as biological indicators. Macan (1938) demonstrated that Corixidae in lake bays showed a succession corresponding to the degree to which organic matter had accumulated in the various bays. The species studied could therefore be regarded as indicators of the amounts of organic matter in lake bays. In later work, (Macan) (1955) showed that species analyses of samples from fairly exposed lake shores could be correlated with the productivities of the lakes studied. It was, however, necessary to confine the collecting to exposed shores because, even in an unproductive lake, species typical of productive waters may be found in bays and vegetation stands whose productivities are higher than that of the lake in general. Macan's work has shown that some species of Corixidae can be useful indicators, but our present knowledge of the distribution of many species is on a purely descriptive and somewhat subjective level so that it is difficult to assess the exact meaning of the presence or absence of such species in particular water bodies. In such cases, only detailed study of the biology of each species and of the habitats it occupies will show exactly what the presence of that particular species actually indicates. Thus, in the series of lakes studied by Macan (1955) one or more of the species C.dorsalis (or C.striata),

C.scotti, C. falleni and C.fossarum occurred on the exposed shores of the lakes. These four species showed a succession corresponding to the degrees of productivity shown by the lakes, but Macan noted one anomalous case - in L.Meagh, the most eutrophic lake of the series, C.germari was the only corixid species found abundantly on the exposed shores. This might lead to the conclusion that C.germari is an indicator of highly eutrophic conditions. It is known, however, (Macan 1954a, 1954b) that this species also occurs in base-poor waters so that this explanation of the results is quite inadequate. The present work and that of Walton (1943) and Macan (1957) suggests that C.germari is associated with steeply sloping shores, severe wave action and sandy substrata with stones. The information given by Macan and Lund (1954b) and Macan (1955 and personal communication) shows that L.Meagh is a large, relatively shallow lake with very gently sloping margins. Macan and Lund (1954b) collected over sandy and stony bottoms. T.D.H. Catchpool (personal communication) states that the lake is in an exposed position and suffers very severe wave action. It is therefore probable that the presence of C.germari in Lake Meagh is an indication of some, or all, of these features rather than of the productivity of the lake. This exemplifies the need for greater knowledge of the individual species of Corixidae before many of the species can be used as biological indicators.

The present work shows that Corixidae are able to reach fairly high population densities in certain upland water bodies and it has been shown by Macan and Frost (1948) that trout tend to

avoid them as food. Thus Corixidae may be regarded as being of less value as potential fish food than certain other organisms present in upland water bodies. Therefore, if the abundance of the Corixidae (in such waters) could be reduced this might lead to greater production of insects more useful as trout food and hence to greater production of trout. To assess this and similar possibilities, detailed quantitative information is required about the abundance of Corixidae and other organisms in the water bodies concerned and about the factors controlling the abundance of those organisms.

Any attempt to make quantitative investigations raises the problem of finding a sampling technique which will enable the abundance of the organism concerned to be measured. This problem is particularly acute in the case of animals such as the Corixidae, which spend most of their time on the bottom but can swim fairly rapidly. Experience with the traps in Barbrook reservoir suggests that activity samplers are of doubtful value for measuring the abundance of such organisms and therefore a grab or net must be used. The grab has two disadvantages compared with a pond net. Firstly, it cannot be used on hard substrata such as are found in many upland reservoirs. Secondly, relatively fast-swimming organisms such as Corixidae and water beetles will tend to escape from the area covered by a grab before the grab closes and the ratio of escapes to captures will vary with the swimming speed of the insects which will, in turn, vary with the temperature and thus cause seasonal variation in sampling efficiency.

This latter effect will apply to a net as well but is likely to be less important in that case, for Macan (1949) has shown that a pond net is a more efficient means of sampling active, free-swimming insects than a hand grab is. In the present work, nets were found to give a satisfactory measure of the abundance of C.germari but in the course of the work it became evident to the present writer that our knowledge of the mode of operation of the plankton net and the common pond net was very scanty. It is therefore suggested that, in order to be sure that the accuracy of quantitative results obtained by net sampling is adequate to allow the population dynamics of a free-swimming organism to be studied, our knowledge of the exact meaning of those results must be deepened. In particular, it is important to examine such problems as the relationship between mesh size and the size of the animals caught; the relationship between numbers caught, the swimming speed of the animals and the net velocity; the relationship between filtering efficiency, net shape, mesh size and net velocity; and, in the case of insects such as the Corixidae, the relative importance of the filtering efficiency of the net and the ability of the net to stir up the water and raise animals from the bottom to a position where they can be caught by a subsequent stroke of the net. It would then be possible to obtain some idea of the accuracy of net sampling and of the netting technique likely to be most efficient in any given situation.

It should be fairly straightforward to devise ways of obtaining information about the operation of nets but, in the case of certain corixid species, other sampling problems arise. The

evidence suggests that C.germari fly relatively little and that it is justifiable to assume that losses from the reservoir by flight are negligible. With many other species this assumption cannot be made and in studying the population dynamics of such species it will be necessary to take into account the interchange of individuals between water bodies. The mercury vapour light trap is the most obvious method of studying flight in Corixidae (Thomas 1938, Leston and Gardner 1953, Leston 1954, Poisson, Richard and Richard 1957) but this technique has many inadequacies. Light traps will miss species that fly by day and may be selective in their action by night. Thus the presence of a species in light trap collections is proof that that species does fly but the absence or scarcity of other species in such collections does not give any indication of the extent to which those species do or do not fly. Thus the interpretation of light trap captures is very difficult and, even if some means could be devised to find out exactly what species in what proportions were in the air at any given time, the difficulty of relating these data quantitatively to fluctuations in abundance within individual water bodies would still remain. Before it becomes possible to study the population dynamics of species that fly about a great deal it is therefore essential that further attention be paid to problems relating to the measurement of flight activity in Corixidae.

XX. SUMMARY.

General.

1. The general methods of approach used in previous work on the biology and ecology of Corixidae are reviewed. The present work was chiefly an attempt to study the life history of Corixa germari (Fieb) in a single water body between Spring 1957 and Spring 1959.
2. Most of the work was carried out at three base-poor South Pennine reservoirs and one peat pool, all situated at altitudes of about 1,000 ft. (300 m.).
3. Particular attention was paid to Barbrook reservoir. This reservoir occupies 12.9 ha., has steep stony sides and a bottom of sand. It contains little vegetation and is subject to severe wave action.
4. Twenty-one species of Corixidae were found in the reservoirs but in Barbrook reservoir C.germari formed about 98% of the material collected. In the other two reservoirs C.germari showed less marked predominance.
5. The other animals identified from each reservoir have been listed. In Barbrook reservoir the main components of the fauna are Rotifera, Copepoda, Cladocera, water beetles, Chironomidae and C.germari.
6. In Barbrook reservoir C.germari is infected by an endoparasitè, probably a gregarine Protozoan. The presence of this parasite has no clearly marked effect on the host.

Sampling methods.

1. The abundance of the eggs of C.germari was measured by direct counting in the field.

2. Net sampling was found to be a satisfactory method of measuring the abundance of the adults and nymphs. The first two nymphal instars were sampled with a net that had 24 meshes per cm., the other swimming stages with a net that had 6 meshes per cm. Data from laboratory and field were used to relate the catches in the two nets.

3. Activity traps were found unsatisfactory as a means of measuring the abundance of Corixidae in Barbrook reservoir.

Food and predators.

1. C.germari has been observed to feed on chironomid larvae, small lumbricids and its own eggs. Filaments of the alga, Microspora sp., have been found in the fore-guts of specimens of C.germari.

2. Examination of the fore-gut contents of water beetles from Barbrook reservoir showed that during September the imagines of Agabus nebulosus and A.bipustulatus feed chiefly on chironomid larvae and pupae, corixid nymphs and small Diptera. Laboratory observations showed that the larvae of these beetles attack Corixidae and chironomid larvae.

Life history and distribution within the reservoir.

1. C.germari has five nymphal instars.
2. In Barbrook reservoir C.germari has one generation per year.
3. Net sampling showed that, in Barbrook reservoir, the adults of C.germari were more abundant on a bank of relatively small irregular stones than on banks of larger more regular stones or on gently sloping sandy shores. This may be partly due to the fact that the former place suffered less wave action than the others.
4. Data from net and trap sampling show that the adults of C.germari were more abundant at 1.0 m. depth than at 0.5 m. depth and that from 1.0 m. to 2.67 m. the abundance fell off very little.
5. The sex ratios given by the net samples show various inconsistencies but suggest that the sex ratio is fairly close to 1:1 throughout the autumn, winter and spring. The old generation males tended to outlive the old generation females in 1958.

Reproduction.

1. A temperature of at least 8°C appears to be required before copulation takes place.
2. Laboratory observations showed that stridulating males excite other males and cause them to stridulate too. Stridulation does not appear to have any effect on females. Over distances of a few centimetres, males appear to respond to a visual stimulus and

attempt to copulate with swimming females but not with resting ones. It is suggested that stridulation in Corixidae may be a means of social stimulation between males.

3. Eggs develop within the females throughout the oviposition period.

4. The egg of C.germari has been described by Banks (1939).

5. Laboratory experiments showed that hatching takes about 15 days at 16°C and that between 10 and 30°C the relationship between hatching time and temperature is roughly linear. Below 8°C hatching is indefinitely suspended.

6. In the laboratory, the highest percentage hatch was given between 10 and 20°C.

7. In the field C.germari showed a preference for stones as oviposition sites and most of the eggs are laid on the undersides of the stones or in crevices. During the oviposition period the females showed a tendency to occupy more poorly illuminated places than the males.

Flight.

1. Attempts at flight by C.germari have been observed in the field but very few specimens were observed to succeed in leaving the reservoir. Experiments in the laboratory showed that C.germari was less willing to fly than C.wollastoni or C.sahlbergi.

Abundance and mortality.

1. In 1957 and 1958 the overwintered adults of C.germari gave catches of about 10 per Standard Net Sweep. In 1958 these overwintered adults produced about 916 eggs of which 58% (531) hatched. Of the nymphs produced 80 survived to become adults in the autumn and 20 of these adults survived to breed in 1959. Wave action and predation appeared to be important causes of adult and nymph mortality. Of the eggs, 8% were attacked by fungus, 6% were attacked by the adults, 24% appeared to be undamaged but failed to hatch and 3% showed damage but the cause of the damage could not be determined.

2. The wet and dry weights of the various stages of C.germari were determined and the relative abundance data were converted into biomasses.

3. Preliminary estimates of the number of eggs per m^2 of substratum during 1958 have made it possible to convert the relative biomass and abundance data into approximate values per m^2 of substratum. The catch per Standard Net Sweep corresponds roughly to the number of Corixidae per $1/38 m^2$.

Distribution and ecological requirements.

1. References in the literature to the ecological distribution of C.germari, C.carinata and Glaencorisa propinqua have been reviewed and the present author's records of these three species have been considered in the light of this review. These three species all

appear to prefer relatively large deep water bodies with steeply sloping banks, some stone present and little vegetation. C.germari was found in water bodies with sandy bottoms, C.carinata in those whose bottoms were overlaid by peat and G.propinqua was found in both types of water body.

2. The adaptations to environment shown by C.germari have been considered. The shape of the egg is well suited to the type of oviposition site used and the type of oviposition site is ideal for places where severe wave action occurs. The ability of C.germari to live at greater depths than most corixid species probably enables it to survive severe wave action. Preliminary experiments suggest that C.germari visits the water surface less often and swims more rapidly than the shallow water species. This probably accounts for its ability to live at depths of 1.0 m. or more.

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* = Originals not consulted.

APPENDICES.

APPENDIX I.

IDENTIFICATION OF MATERIAL.

As far as possible, the material collected has been submitted to competent authorities for determination. A list of the material so examined, together with the names of the authorities, is given below :-

<u>Species or Group.</u>	<u>Authority.</u>
Corixidae.	Dr. T.T. Macan.
Coleoptera.	Dr. J. Balfour-Browne.
Acarina.	Dr. O. Evans.
Annelida.	Mr. S. Prudhoe.
Sciaridae (Diptera).	Mr. P. Freeman
<u>Chironomus anthracinus</u> (Diptera).	Dr. J.H. Mundie,
Crustacea.	Dr. W.J.B. Smyly.
Plecoptera.	Dr. H.B.N. Hynes.
Trichoptera.	Mr. J.P. Leader.
Algae.	Dr. G. Leedale.
Fungi.	Dr. P. Watson.
<u>Juncus bulbosus</u> agg.	Mr. P.E. Allen.

Dr. J. Théodoridès kindly agreed to examine the endoparasite of C.germari but was unable to do so because all the living material sent to him deteriorated in transit.

APPENDIX II.

STATISTICAL METHODS USED. (Methods recommended by

Mr. Wallington of the Mathematics

Department, Durham Colleges).

I. Normal Distribution.

(i) 5% confidence limits of the mean :-

Given a set of n samples whose values are $x_1, x_2, x_3, \dots, x_n$ and whose mean is \bar{x} .

Then $\bar{x} = \sum x/n$

And the standard error of the mean = $\frac{\sqrt{\sum x^2 - \frac{(\sum x)^2}{n}}}{\sqrt{n}}$

Thus the mean and its 5% confidence limits are given by :-

$$\bar{x} \pm t' \times \frac{\sqrt{\sum x^2 - \frac{(\sum x)^2}{n}}}{\sqrt{n}}$$

when t' is the value of t corresponding to a probability of 0.05 and n degrees of freedom. This value of t can be obtained from tables but, for most practical purposes, it can be assumed that where $n > 30, t = 2.0$.

(ii) To test the significance of the difference between two means :-

Given two sample means \bar{x}_1 and \bar{x}_2 , based on n_1 and n_2 samples respectively,

then if :- $\bar{x}_1 - \bar{x}_2 \Big/ \frac{\sum (x_1 - \bar{x}_1)^2}{n_1} + \frac{\sum (x_2 - \bar{x}_2)^2}{n_2} > 2.0$.

the difference is significant at the 5% confidence level.

(Normal distribution methods have been used to calculate the values given in Tables 4, 6, 10, 29, 30, 31, 32, 33, 34, 35, 43, 51, 53, 55, 57, 69 and 70).

The first part of the document discusses the importance of maintaining accurate records of all transactions. It emphasizes that every entry should be supported by a valid receipt or invoice to ensure transparency and accountability.

Furthermore, it is noted that the records should be kept for a minimum of seven years, as required by the relevant tax authorities. This period allows for thorough audits and the resolution of any potential disputes.

In addition, the document highlights the need for regular reconciliation of accounts. By comparing internal records with bank statements and other external sources, any discrepancies can be identified and corrected promptly.

It is also stressed that the records should be organized in a clear and logical manner. This will facilitate the retrieval of information and make the process of reporting to the authorities much more efficient.

Finally, the document concludes by stating that maintaining accurate records is not only a legal obligation but also a key to the success of any business. It provides a solid foundation for financial planning and decision-making.

The following table provides a summary of the key points discussed in the document. It is intended to serve as a quick reference for all stakeholders involved in the financial management of the organization.

It is important to note that this document is a general guide and should not be taken as legal advice. For specific advice, please consult with a qualified professional.

The information provided here is for informational purposes only and does not constitute an offer or recommendation of any financial product or service.

We appreciate your attention to these matters and encourage you to reach out if you have any questions or need further assistance.

II. Poisson Distribution.

A set of samples consisting of small discrete numbers approximates to a Poisson distribution but the square roots of the numbers will approximate to a normal distribution.

Given a set of small discrete numbers

$t_1, t_2, t_3, \dots, t_n$. to find the mean and 5% confidence limits of the mean the values $t_1, t_2, t_3, \dots, t_n$. must be converted into the values $s_1, s_2, s_3, \dots, s_n$., such that $s = \sqrt{t}$.

Hence find \bar{s} and its standard error by the normal distribution method given above. Now find the values of:- ($\bar{s} + 2x$ standard error of s .) and :- ($\bar{s} - 2x$ standard error of s .)

These are the 5% confidence limits of \bar{s} and $\bar{s}^2 = \bar{t}$..

(This method has been used to calculate the values given in Table 68).

III Correlation and regression.

(i) Correlation coefficient :-

To test for correlation between two sets of values x and y the correlation coefficient, r , is calculated. When n is the number of x, y pairs considered and \bar{x}, \bar{y} are the means of x and y respectively, then :-

$$r = \frac{\frac{1}{n} \sum xy - \bar{x} \bar{y}}{\sqrt{\frac{1}{n} \sum x^2 - (\bar{x})^2} \times \sqrt{\frac{1}{n} \sum y^2 - (\bar{y})^2}}$$

Now when $r = 1$ there is a perfect positive correlation between x and y , and when $r = -1$ there is a perfect negative correlation. To test the significance of a given value of r it is necessary to calculate t .

$$t = \frac{r\sqrt{n-2}}{\sqrt{1-r^2}}$$

Now the probability of the correlation being significant can be determined by reference to a table of values of t , the table being entered at the $n - 2$ degrees of freedom level.

(ii) Regression lines :-

If two sets of measurements x and y appear to be significantly correlated it is possible to calculate approximate values of y corresponding to given values of x by means of the regression line of y upon x . The formula of the best-fitting straight line is :-

$$y - \bar{y} = b (x - \bar{x}) \text{ where } b = \frac{\sum yx}{\sum x^2}$$

Thus the value of y corresponding to a given value of x is :-

$$y = \bar{y} + b (x - \bar{x}).$$

(Correlation and regression methods have been used on p.25).

IV. Proportions and percentages.

If a sample of n items is taken and a proportion p of those items is (for example) parasitised, then the standard error of that proportion is given by :- $\sqrt{p(1-p)/n}$

Hence the 5% confidence limits of the proportion = $2x\sqrt{p(1-p)/n}$.

If it is required to express the proportion as a percentage of n then the 5% confidence limits of the proportion must be multiplied by 100 to give the 5% confidence limits of the corresponding percentage. (This method has been used to calculate the values given in Tables 7, 11, 46, 49, 50 and 54).

V. Chi-squared methods.

(i) If a given sample is separated into two or more classes it is possible to test whether or not the number of individuals falling into each particular class differs significantly from a particular expected value. This test is made by calculating the value of Chi-squared where :-

$$\text{Chi-squared} = \frac{(\text{Observed value} - \text{Expected value})^2}{\text{Expected value.}}$$

The probability that the difference between the observed and expected values is due to pure chance is then obtained by reference to a table of Chi-squared by entering the table at the one degree of freedom level.

If $P < 0.05$ the difference is taken to be significant.

In this way a Chi-squared can be calculated for each class and these Chi-squareds can then be added to give the Chi-squared value of the whole sample. In Table 37 a value of Chi-squared has been calculated for each sex on each sampling date and by adding these together a total Chi-squared for each date can be found, and by adding the latter together a Chi-squared

value for the whole Table can be found. In such a case there are N degrees of freedom where N = Number of sampling dates - 1.

(ii) 2 x 2 Contingency tables :-

Given two samples, each of which can be separated into two classes, it is possible to set out the results in a contingency table as represented below :-

	Class A.	Class B.	Totals.
Sample 1.	a	b	n_3
Sample 2.	c	d	n_4
Totals.	n_1	n_2	n_T

It is then possible to find out whether the ratio a : b given by sample 1. differs significantly from the ratio c : d given by sample 2. by using the formula :-

$$\text{Chi-squared} = \frac{n_T (ad - bc)^2}{n_1 \times n_2 \times n_3 \times n_4}$$

Such a table has one degree of freedom.

(Chi-squared methods have been used in Tables 12, 37, 38, 39, 40, 44, 45, 47, 48, 63, 64, 65 and 66).

APPENDIX III.

THE LENGTHS OF ADULT SPECIMENS OF C.GERMARI FROM BARBROOK
RESERVOIR.

Hungerford (1948) points out that specimens of C.germari examined by him were 7.4 mm. long whereas Macan (1939, 1956) and Stichel (1935) quote ranges of 7.5 - 10.0 and 7.5 - 8.0 mm. respectively for this species.

In the present work it became clear that the adult specimens of C.germari taken from Barbrook reservoir were also unusually small and samples of 50 specimens of each sex were collected, killed and immediately measured by means of a low-power (x7) microscope with a micrometer eyepiece. The results are shown in Table A. It can be seen that the lengths of all the females examined fell within the ranges given by Macan and by Stichel but that about 25% of the males measured less than the minimum value quoted by those two workers.

Clearly, the lengths may vary according to the techniques employed by different workers, but in this case it seems more likely that C.germari shows a rather abnormal (for Corixidae) amount of variation in size from one habitat or area to another and that Barbrook reservoir is a habitat which produces relatively small specimens.

Males.

Length in mm.	Frequency
7.2 - 7.3	2
7.3 - 7.4	3
7.4 - 7.5	7
7.5 - 7.6	9
7.6 - 7.7	12
7.7 - 7.8	7
7.8 - 7.9	7
7.9 - 8.0	2
8.0 - 8.1	1

Females.

7.5 - 7.6	2
7.6 - 7.7	3
7.7 - 7.8	9
7.8 - 7.9	11
7.9 - 8.0	7
8.0 - 8.1	9
8.1 - 8.2	7
8.2 - 8.3	1
8.3 - 8.4	1

TABLE A. Distribution of lengths in samples of male and female specimens of C.germari from Barbrook reservoir.

