ECOLOGICAL STUDIES OF THE COMMON LEECHES OF RUTLAND WATER

by

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A thesis submitted in candidature for the degree of Doctor of Philosophy at the University of Leicester

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I dedicate this thesis to my mother Fatima, my late father Hamid, my sisters Suhaila and Elham, and my brothers Khalid, Wail and Shamil Al-Hayaley.

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1. INTRODUCTION

Leeches are common carnivores in many freshwater ecosystem with roles ranging from outright predation to intermittent ectoparasitism. Despite their abundance most researchers have concentrated on their life cycles and prey preferences without considering their significance in the energetics of freshwater ecosystems.

In this account, I examine the energy budgets, abundance and population dynamics of three predatory species, <u>Erpobdella octoculata</u> (L.), <u>Helobdella stagnalis</u> (L.) and <u>Glossiphonia complanata</u> (L.) in the relatively simple and immature ecosystems of a new reservoir, Rutland Water, in Leicestershire, England. This study forms a part of the investigation of the benthic invertebrates of Rutland Water being conducted by members of the Zoology Department, University of Leicester.

1.2 Taxonomic criteria and distribution of species recorded in Rutland Water

The class Hirudinea comprises three orders (Moore,1959), namely Rhyncobdellae, Gnathobdellae and Pharyngobdellae, which together contain ten families, 140 genera and 500 species (Sóos, 1969, 1970). Most species

are confined to freshwater but both terrestrial and marine taxa occur throughout the world. Sixteen species, all freshwater, have been recorded in the British Isles (Elliott & Mann, 1979). Seven species have been recorded from Rutland Water during this study (Table 1) of which the commonest are <u>Helobdella stagnalis</u>, <u>Erpobdella octoculata</u> and <u>Glossiphonia complanata</u>. All identifications were made using this key by Mann (1964).

1.2.1 Family Erpobdellidae

Five British species belong to this family. They possess no jaws but have large mouths which contain muscular ridges which facilitate the ingestion of whole prey. The genital pores are separated by a consistent number of annuli in each species. There are four pairs of eyes arranged in two transverse rows.

1.2.1.1 Erpobdella octoculata (L.)

The genus <u>Erpobdella</u> can be distinguished from other British erpobdellids (<u>Dina lineata</u> and <u>Trocheta</u> spp.) by having all annuli of the same breadth. In addition <u>Trocheta</u> spp. have the genital pores separated by 5 - 6 annuli.

TABLE 1

Species occurring in Rutland Water

Rhyncobdellae

Family Glossiphoniidae

<u>Helobdella stagnalis</u> (Linnaeus, 1758) <u>Glossiphonia complanata</u> (Linnaeus, 1758) <u>Glossiphonia heteroclita</u> (Linnaeus, 1761) <u>Hemiclepsis marginata</u> (O.F. Müller, 1774) <u>Theromyzon tessulatum</u> (O.F. Müller, 1774) Family Piscicolidae <u>Piscicola geometra</u> (Linnaeus, 1758)

Pharyngobdellae

Family Erpobdellidae

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Erpobdella octoculata (Linnaeus, 1758)

<u>E. octoculata</u> has the genital pores separated by $2\frac{1}{2}$ - $3\frac{1}{2}$ annuli which in <u>E. testacea</u> are separated by $3\frac{1}{2}$ - $4\frac{1}{2}$ annuli (Mann, 1952). In addition <u>E. octoculata</u> has the dorsal surface with a variable amount of black pigment which is lacking in <u>E. testacea</u>.

Confirmation of identification can be obtained by dissecting the atrial cornua.

Johansson (1910) described three varieties of this species depending on the amount of black pigment on the dorsal surface. The variety atomaria has the dorsal surface marked by a black reticulum with the light spot small and regularly rounded off, the variety pallida has no pigment at all on the dorsal surface and the variety vulgaris has a small amount of black pigment, not forming a complete Mann (1952) found var. vulgaris and var. atomaria reticulum. occurred in approximately equal numbers and there was no difference in their geographical distribution in collections made in Britain. He concluded that he was dealing with a single systematic unit in which the members develop a variable amount of black pigmentation depending on some external or internal factor at present unknown. Mann (op. cit.) reported that var. pallida has not been recorded in Britain and the variety is regarded by Sóos (1966) as being confined to Eastern Europe. Dall (1979) reported the occurrence of only vulgaris and atomaria in Denmark.

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In the present study, both varieties were encountered and their identity confirmed by dissection of the atrial cornua in approximately 20 of each variety.

<u>E. octoculata</u> is found throughout Europe (Sóos, 1967). It occurs in all kinds of freshwater habitat, in hard and soft water, in lotic and lentic water bodies (Maitland, 1966; Wilkialis, 1970; Elliott, 1973b; Lang, 1974; Dall <u>op</u>. <u>cit</u>.). It occurs in particularly high numbers in habitats subjected to moderate organic pollution (Elliott op. cit; Aston & Brown, 1975).

1.2.2 Family Glossiphoniidae

This family includes seven British species. They lack jaws and the mouth is a small slit in the oral sucker. The total number of annuli is less than 80, arranged in groups of three so that the pattern on the dorsal surface, where present, is repeated every three annuli. There are two to eight eyes and when there are eight eyes they are placed in two longitudinal rows.

1.2.2.1 Helobdella stagnalis

This species is readily differentiated from all other British Glossiphoniidae by the presence of a dorsal chitinous scute lying a short distance behind the

anterior sucker. This species possesses only a single pair of eyes.

It is one of the most widespread species in the world being recorded from every continent except Australasia and Antarctica (Sóos, 1969) and is widely distributed in the British Isles. The species is tolerant of very diverse conditions. Thus Bennike (1943) reported <u>H. stagnalis</u> living in oxygen concentrations as low as $0.69 \text{ ml } 0_2 \text{ l}^{-1}$ while various authors (e.g. Williams, 1961; Maitland, 1966; Sapkarev, 1968) reported from very acid water (pH < 4.0). It is most abundant, however, in eutrophic, alkaline, lentic water bodies (Sawyer, 1968; Scudder & Mann, 1969; Tillman & Branes, 1973) and is particularly abundant in waters of large surface area (Mann, 1961).

1.2.2.2 Glossiphonia complanata (L.)

This species is differentiated from all other British Glossiphoniidae by the presence of two distinct dorsal longitudinal lines and three pairs of eyes which are arranged in two nearly parallel rows. Elliott and Mann (1979) describe variations in the eye pattern but no examples of any of these have been encountered in this study.

It is Holarctic in distribution (Kleem, 1975), and shows a strong preference for lentic waters (Soos, 1967).

It is reportedly tolerant of oxygen concentration as low as $0.69 \text{ ml } 0_2 \text{ l}^{-1}$ (Bennike, <u>op</u>. <u>cit</u>.). Scudder and Mann (1968) and Wilkialis (1970) relate the distribution and abundance of this species to the availability of snails which form its exclusive prey. Since snails are generally dependent on a high level of calcium, the leech is similarly restricted as noted by Mann (1957, 1961).

1.2.2.3 Glossiphonia heteroclita (L.)

This leech is amber with three pairs of eyes, the first pair closer to the mid-line than either of the other two pairs. These two characteristics differentiate it from <u>G</u>. <u>complanata</u> and other British Glossiphoniidae. In addition, <u>G</u>. <u>heteroclita</u> is translucent, and more or less brownish yellow while <u>G</u>. <u>complanata</u> is clearly marked with green and brown.

It occurs in Europe and Central and East Africa (Sóos, 1969). It shows a strong preference for hard water (Mann, 1964) and occurs chiefly in lentic habitats containing large numbers of snails. It appears to differ from <u>G. complanata</u> in preferring stagnant water (Wilkialis, 1964; Sawyer, 1968; Sóos, 1969).

1.2.2.4 Theromyzon tessulatum (O.F. Muller)

This species is easily recognised by the presence of eight eyes arranged longitudinally in two parallel rows on each side of the mid-line.

It is Holarctic in distribution (Sóos, 1969). It rarely occurs in running water but is not restricted to a particular type of lentic habitat (Williams, 1961; Wilkialis, 1970). Maitland (1966) reported that this species is much less dependent on the alkalinity and hardness of the water than are most other species. It feeds on the blood of water birds and has been recorded on domestic and wild ducks, swans, bitterns, curlews and great crested grebes (Mann, 1951), so its distribution among various habitats presumably reflects the distribution of the hosts (MacCarthy, 1975).

1.2.2.5 Hemiclepsis marginata (O.F. Müller)

This leech can be recognised by the presence of only two pairs of eyes of which the anterior are much smaller and closer together than those of the posterior pair. Further, this is the only British glossiphoniid in which the head and anterior sucker are markedly wider than the following body segments.

It is Palaearctic in distribution (Kleem, 1976) and occurs in the muddy-sandy bottoms of lakes and

rivers (Mann, 1955; Maitland, 1967; Wilkialis, 1970). This leech feeds on the blood of fishes and amphibians and the presence of this species is to a great extent dependent on the presence of suitable hosts (Mansfeld, 1934; Mann, 1955; Maitland, 1966).

1.2.3 Family Piscicolidae

This family contains one British species. It has no jaws. Both anterior and posterior suckers are usually distinctly marked off from the body. The body is cylindrical with many narrow annuli. There are two pairs of eyes.

1.2.3.1 Piscicola geometra

This species is recognised by the presence of two pairs of eyes which are parallel to one another and by the general appearance of the family noted above. The pulsatile vesicles present on the margin of the posterior half of the body.

It is Palaearctic in distribution but has also been found in North and South America possibly as a result of introduction (Sóos, 1967). It is a widely distributed leech, particularly in well oxygenated fast running water, and is rarely found in a standing water,

except in the surface zone of lakes and ponds (Mann, 1962). It is ectoparasitic on a wide range of fishes, and the presence of this species is to a great extent dependent on the presence of its hosts (Brightwell, 1842; Bennike, 1943; MacCarthy, 1975).

1.3 Previous studies of leeches

The systematics, taxonomy and distribution have occupied the attention of a number of biologists over many years (e.g. Sóos, 1967; Sapkarev, 1968; Elliott & Mann, Detailed investigations of the biology and ecology 1979). of leeches in Britain have been confined principally to the population dynamics of a few species. Mann (1953; 1957a, 1957b) studied E. octoculata, H. stagnalis and G. complanata in Berkshire. Elliott (1973a) studied E. octoculata in Cumbria and Murphy and Learner (1982) studied the same species in Wales. The population dynamics of H. stagnalis were studied by Learner and Potter (1974) in Wales. Outside Britain the life cycle and production of E. octoculata was studied in Denmark by Dall (1979), and Tillman and Barnes (1973) studied the life cycle of H. stagnalis in Lake Utah in U.S.A. Davies and Reynoldson (1976) compared the life cycle of H. stagnalis in two different areas in Canada. These studies are detailed in Chapter 4 (Population Dynamics).

The studies of food of non-parasitic species have been confined to the numbers of individuals eaten and prev preference. Thus Davies and Everett (1975) in Canada examined the total range of prey taken by the leeches Nephelopsis obscura, Erpobdella punctata, Helobdella stagnalis and Glossiphonia complanata and they found that H. stagnalis fed on Enchytraeidae, Copepoda, Cladocera, Lymnaea sp. and Gammarus lacustris. G. complanata fed on Enchytridae, Lymnaea sp. and Helisoma sp. Young and Ironmonger (1979a) studied the natural diet of E. octoculata in some British lakes and they found that Chironomids and Oligochaetes were the predominant diet of these leeches. Furthermore, feeding activity was lowest in winter and fairly low in late summer/early autumn. Young and Ironmonger (1980) studied the food of E. octoculata, H. stagnalis and G. complanata in the laboratory, and they found that E. octoculata fed exclusively on Chironomids and Oligochaetes; H. stagnalis fed on a wide variety of prey, including Oligochaetes, Chironomids, gastropods, Asellus sp. and mayflies, and G. complanata fed on Gastropods, Oligochaetes and Chironomids. Serological investigations of the diet of H. stagnalis and G. complanata in the British lakes were reported by Young (1980, 1981). He found that the Oligochaetes and Chironomids were the most favoured prey for H. stagnalis and Gastropods and Oligochaetes were the most favoured prey for G. complanata. The effect of temperature

on predation was studied by Hilsenhoff (1963) in the U.S.A. for the leech <u>H</u>. <u>stagnalis</u>, and he found that predation on <u>Tendipes plumosus</u> increased with rising temperature. Green (1974) in England found that <u>E</u>. <u>octoculata</u> would feed at temperatures as low as 2^oC. He further reported a constant rate of predation between 7^o, and 12^oC.

Estimation of respiration is confined to a single comparison between five British species by Mann (1956). Studies of the effects of pH, NaCl concentrations and oxygen tension on respiration of <u>Poecilobdella viridis</u> were recorded by Nagabhushanam & Kulkarni (1977) in India at a temperature of 26^oC.

There are few reports of research on applied aspects of leech ecology. In an attempt to control <u>Hirudo</u> <u>nipponia</u> in the U.S.A. Keegan, Poore, Weaver and Suzuki (1964) investigated the tolerance of this species to hydrocarbon and organophosphorus insecticides. They found that Chlordane was the most toxic of materials tested, while DDT was the least toxic. Meyer (1969), also in the U.S.A., studied the effect of three insecticides, isopropoxyphenyl, methylene borate, and dimethyl phosphate on <u>Erpobdella</u> <u>punctata</u>, <u>Illinobdella moorei</u>, <u>Piscicola salmositica</u>, <u>Piscicola parasitica</u> and <u>Theromyzon</u> sp. He found that <u>P. parasitica</u> showed least resistance. Kleem (1976) studied the possible importance of leeches as intermediate or final hosts of parasitic protozoans, trematodes, cestodes, nematodes and nematomorphs in the U.S.A.

1.4 The study of energetic requirements

Over the last forty years, the value of investigating the energy budget of a population has become generally accepted (cf. Slobodkin, 1962; Petrusewicz & Macfadyen, 1970). The basic philosophy is that all parameters and interactions can be defined in terms of energy transfer and transformation. Biological parameters such as oxygen consumption and biomass can thus be equated and compared (Lindeman, 1942).

Engelmann (1966) recognised three lines of approach to the investigation of energy requirements of ecological systems, which can be loosely defined as the study of the individual, the population and the trophic level. The first of these is most appropriate to investigations of physiological responses to varying conditions while the third is applicable to studies of energy flow in a community or ecosystem. The second, that of the population energy requirements, is most satisfactory for determining the functional role of a population in a community as well as providing a satisfactory basis for comparisons with other populations of the same species at different points in space or time, and with populations of other species at the same point in the space-time continuum.

The comparison of different biological parameters in energy terms is possible only if it is assumed

that the laws of thermodynamics are applicable to ecological systems. This has been discussed by a number of workers (e.g. Slobodkin, 1960; Phillipson, 1966, 1975). It has been shown that energy transformation conforms to the first law of thermodynamics (Weigert, 1968). While all available evidence indicates that the second law is also obeyed (Phillipson, 1966).

The energetic relationship may be written in biological terms as:

C = P + R + FU
where C = food consumed
 P = production
 R = respiration which is used as a
 measure of the energy used in
 metabolic activity
 FU = energy lost through egestion,
 excretion, ecdysis, etc.

This equation comprises parameters which can all be measured independently. Nonetheless if measurements are made of any three parameters, the fourth can be derived by difference. It follows that by determining all parameters, an internal check on the accuracy of the experimental determinations may be made.

Studies on ecological energetics have focused on many different freshwater species including

<u>Asellus aquaticus</u> L. (Fitzpatrick, 1968; Prus, 1972; Adcock, 1975), <u>Gammarus pulex</u> L. (Nilson, 1974), <u>Acroneuria</u> <u>californica</u> Banks (Heiman & Knight, 1975), <u>Tegula</u> <u>funebralis</u> (Paine, 1971) and <u>Nepa rura</u> (Waitzbaner, 1978). The only study on leeches reported in the literature is of <u>Malmiana nuda</u>, an ectoparasitic Piscicolid, by Mace and Davis (1972) in Canada.

1.5 Outline of present study

Investigations of Rutland Water in 1975 - 1977 (<u>vide</u> Bullock, Clark & Ison, 1982) showed that leeches were generally abundant and were likely to be of considerable importance in the energy balance of the benthic invertebrate community. It was therefore decided to investigate the three species <u>Helobdella stagnalis</u>, <u>Glossiphonia complanata</u> and <u>Erpobdella octoculata</u>, which were in sufficient numbers for valid population estimates to be made.

The aims of the study were:

- To determine the abundance and population structure of the three species.
- To estimate food consumption, respiration, production and egestion rates for selected individuals under laboratory conditions.
- To produce a tentative energy budget for each of the three species.

To achieve these aims, research was carried out in three parts. First, the populations were monitored in Rutland Water over two years by means of a series of grab samples at monthly intervals. These were supplemented by hand collection of samples along the shore line of the dam. Seasonal variation in abundance, population structure and biomass were determined from these samples. Secondly, individuals were maintained in the laboratory and quantitative estimates of food consumption, egestion and respiration rates were made for a range of sizes of leeches at three temperatures.

Thirdly, the field and laboratory studies were then integrated to obtain overall estimates of energy consumption by each of the three species.

2. MATERIALS AND METHODS

2.1 Description of study area

Rutland Water lies in eastern England in the county of Leicestershire (0[°] 37'W, 52[°] 45'N) (Fig. 1) at a distance of 30 Km from Leicester and 45 Km from Peterborough. The water (Fig. 2) is a pumped storage reservoir designed by the Anglian Water Authority to supply water to the Greater Peterborough and Northampton areas. The dam lies at the eastern end of the reservoir just west of the village of Empingham. A large central basin lies behind the dam and from this the reservoir extends westwards along the valleys lying on either side of the Hambleton peninsula. A limnological tower lies in the central basin and is used to monitor physico-chemical parameters at all depths.

The reservoir is one of the largest man-made water bodies in Europe, with a surface area of 1260 ha when full. It has a capacity of 124 x 10^6 m³, is over 8 Km long with a perimeter of 39 Km. The maximum depth is 34 m in the central basin. The reservoir bottom consists of soft mud except near the dam, where much of the floor is a more solid clay. Along the shore near the dam, the floor is totally covered with stones.

The water supply to the reservoir comes from two sources. The greater part, some 60%, was pumped from the

Fig. 1 Map of Rutland Water Authority area in eastern England, showing the location of Rutland Water.

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FIG.1

Fig. 2 Rutland Water showing the four transects (broken lines)

- D = Dam transect
 T = Tower transect
- N = North arm transect
- S = South arm transect



Fig 2 The main features of Rutland water

river Welland, which runs to the south of the reservoir and then turns north east to enter the Wash (Fig. 1). A pumping station also exists on the river Nene but less water has been pumped from this source because the concentrations of sulphates and nitrates exceeded the W.H.O. recommended limits until late 1977. The remaining 40% of water was provided by the natural catchments of two streams, the north and south Gwash which run into the reservoir. At the start of filling in February 1975, the water came from the natural catchment only, but in the last three months of 1976 the water was obtained from both sources with water pumped from the Welland, making a major contribution (Low, 1982). The reservoir was almost full by July 1977, when the first water was taken into Since 1977, the water level has been maintained supply. about 1 m below maximum capacity, except that evaporation in the summer months has resulted in some small drop in level.

The only macrophytes are <u>Potamogeton crispus</u> and <u>Elodea canadensis</u>, both of which occurred as isolated individuals near the shore. Both species were present in the Gwash before the reservoir filled. During the summer of 1977, <u>Enteromorpha intestinalis</u> formed extensive growths around the shore line and in June 1977 <u>Hydrodictyon</u> sp. was common in the littoral zone but did not occur in floating mats. In autumn 1977 <u>Cladophora</u> sp. encrusted with epiphytic disease was common floating in isolated clumps (Ferguson, pers. comm.).

2.2 Limnological characteristics (Data supplied by the Anglian Water Authority)

2.2.1 Temperature

Water temperature was measured at least fortnightly and usually weekly at the limnological tower from the bottom (<u>c</u> 25 metres) to 1 metre below the water surface throughout the period. In January 1978 the surface was frozen for several days although not at the depth (1 m) at which surface temperature is measured.

During 1978 (Fig. 3) the water column was thermally stratified, albeit rather weakly, for much of the period June to August. For the rest of the year the temperature difference throughout the water column was small and in winter there was little or no difference between the surface and the bottom. In the summer of 1979 the temperature fluctuated and thermal stratification existed from June to the beginning of August when the difference between the surface and the bottom was again $c 5^{\circ}C$.

A steady increase in surface water temperature occurred from approximately 2°C in January 1978 to a peak in late August of approximately 17°C, but in 1979 the lowest temperature was 1°C in January, rising to a peak of 18°C in early August (Fig. 3).

Fig. 3 Mean water temperatures in Rutland Water from January 1978 to October 1979. Measurements were recorded at weekly intervals at the limnological tower from 1 - 25 m.





FIG.3

2.2.2 Oxygen

The oxygen concentration was close to saturation in the whole water column throughout the colder months in both years (Fig. 4). The concentration in the hypolimnion progressively declined throughout the summer as the water temperature increased. The minimum observed percentage saturation during the two years near the bottom was 30% saturation at 11° C.

2.2.3 Major ions

The concentration of some of the major nutrients were determined by the Anglian Water Authority and presented in Table 2. In comparison with other freshwater bodies (Table 3) the reservoir may be considered an eutrophic hard water body.

2.3 Sampling technique

There are many variables which affect the collection of samples in freshwater, such as the nature of the substrate, the depth of the water, the organisms which are being studied, climatic conditions and the objectives of the study. Hence the first problem is selection of suitable techniques. No absolute quantitative method has

Fig. 4 Percentage oxygen saturation in Rutland Water. Lines link points of identical saturation over the period May - October 1978 and May - August 1979. Measurements were recorded at weekly intervals at the limnological tower from 1 - 25 m. (Data supplied by Anglian Water Authority)





TABLE 2 Chemical characteristics of Rutland Water (supplied by the Anglian Water Authority)

	Year	Minimum	Maximum	Median	Mean value	Std. dev.	No. of values
pH value	1977-1978	7.95	8.80	8.40	8.39	0.244	34
	1978-1979	7.80	8.45	8.20	8.19	0.202	11
Alkalinity	1977-1978	130	205	180	178.08	12.79	34
(CaCO ₃) mg 1 ⁻¹)	1978-1979	170	200	180	181.5	7.88	10
Calcium	1977-1978	108	139	122	121.39	5.915	31
(mg 1 ⁻¹)	1978-1979	109	121	115	114.81	3.25	11
Magnesium	1977-1978	10	11.7	11	11.5	0.337	31
(mg 1 ⁻¹)	1978-1979	11.2	11.9	11.6	11.5	0.221	11
Sodium	1977-1978	32.3	43.7	38.1	38.158	2.713	31
(mg 1 ⁻¹)	1978-1979	36.9	43.0	40.3	40.32	1.792	11
Potassium	1977-1978	7.75	10.8	8.9	8.968	0.570	31
(mg 1 ⁻¹)	1978-1979	8.87	9.3	9.08	9.085	0.330	2
Chloride/Chlorinity	1977–1978	55	62	58	58.38	1.55	3 4
(mg 1 ⁻¹)	1978–1979	56	62	58	58.27	1.79	11
Sulphate (SO ₄)	1977-1978	162	178	171	170.87	4.05	33
(mg 1 ⁻¹)	1978-1979	164	173	169	169.10	3.24	10
Dissolved	1977-1978	0.01 <u>4</u>	0.27	0,068	0.089	0.057	3 4
phosphate (mg l ⁻¹)	1978-1979	0.013	0.094	0.027	0.033	0.020	10
Electrical conductivity (µS cm ⁻¹)	1977-1978 1978-1979	735 670	990 815	842.5 770	847.35 759.09	57.118 43.52	34 11

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Concentration of the major ions in Rutland Water compared with Burton well water (Macan & Worthington, 1951), Esthwaite Water (Macan, 1970), Wistow Lake (Adcock, TABLE 3

1975) and Foremark Reservoir (Severn-Trent Water Authority). All results in mg 1^{-1} unless stated otherwise.

	C	Mg	Na	ХI	caco ₃	ប	so4	ር
Rutland Water	122	11	38.1	8.9	180	58	171	0.06
Burton Well Water	159	39	51	57	280	06	378	No data
Esthwaite Water	8.3	3.5	4.7	0.9	18.3	7.6	6.6	No data
Wistow Lake	98	15	21	4.8	194	40.6	97.5	53
Foremark Reservoir	21.7	No data	19.3	5.1	160	37	104	No data

been described in the literature as applicable to leech populations, although many different methods and techniques for collecting leeches have been described.

Searching time has been used frequently and can be used to sample riffle areas and the shores of lakes and rivers. It involves a thorough check for leeches in their favoured habitat, and is made reasonably quantitative by searching for a fixed period of time. Authors vary in their choice of time. Mann (1953) used periods of 45 - 60 min, Williams (1961) 30 - 45 min, Maitland (1970) 60 min. A possible defect of this technique is that at low leech densities a greater area can be searched, thus affecting strict comparability. An alternative is to make a thorough search within a predetermined area. In this study, search samples were taken within an area of 1 m^2 to assess densities of <u>G. complanata</u> and <u>F. octoculata</u>.

Other investigators have collected leeches by vigorous sweeping of a pond net in the marginal area of the water body (Scudder & Mann, 1968; Macphee, 1971; Maitland & Kellock, 1972; Aston & Brown, 1975). This method can be used on the banks of rivers and lakes and, although it samples a large volume, it is not suitable for deep water. Further it is unlikely to give a satisfactory estimate of a given area.

Lang (1974) is the only author to dive for his samples during his work in Lake Geneva (Western Germany &

Switzerland). He placed some tiles on the substratum at seven stations around the lake. He then collected all leeches and other macrobenthos from beneath each tile, once a month.

Artificial substrates can be used, but while this method is useful for collecting specimens (Arthur & Horning, 1969; Mason, 1970), it does not give truly quantitative data as the area sampled cannot be estimated with any accuracy.

Adequate estimates of densities can only be achieved in water of any depth by sampling with a grab, taking a known area of substrate. Bennike (1943), Scudder and Mann (1968), Sapkarev (1968), and Milbrink and Wideholm (1973) found that the Ekman grab was the most useful device for average freshwater conditions. Flagman <u>et al</u>. (1970) compared many different grabs and found that the Ekman grab gave the highest number of benthic macroinvertebrates per unit area.

There are nevertheless problems with such a method. The grab swings from side to side as it is lowered and is likely to strike the bottom obliquely, thus reducing the degree of penetration and efficiency of sampling. Further a small pebble or woody fragment is sufficient to prevent complete closure of the jaws. To add to these difficulties, when sampling relatively deep water in windy weather it is not possible to use the ordinary Ekman grab because during

the time it takes for the messenger to reach the release catch, wave action may have raised the boat and hence lifted the grab off the substrate or dragged the grab over on its side.

In the present study it was decided to use a modification of the Ekman grab (Rawson, 1947). This apparatus closes automatically on reaching the substrate without the use of a messenger. This saves much time in deep water and ensures closure while the grab is still in contact with the substrate. It also improves stability so that the grab does not meet the bottom obliquely but, of course, does nothing to cope with stones, etc., trapped between the jaws.

2.4 Sampling pattern and frequency

Samples were collected approximately monthly from September 1977 to October 1979, using the Ekman grab operated from a boat. On the first two occasions, samples were taken with an unmodified Ekman grab, but thereafter the Rawson modified grab was used.

Four study transects were selected on the reservoir and these were designated as the Dam, the North Arm, the South Arm and the Tower (Fig. 2). On the first two sampling occasions, eight grabs per transect were collected, but from November 1977 the number of samples was

increased to 46 in all, with 10 samples taken on the Tower transect and 12 on each of the other three. The minimum depth from which samples were taken by the Ekman grab was 1 metre.

From August 1978 until October 1979, four samples were taken monthly near the dam, each of 1 square metre in area and up to 30 cm in depth, to collect <u>E. octoculata</u> and <u>G. complanata</u>. These samples were taken by carefully lifting every stone in the area and removing each leech that was present. This sampling technique was used because of the strong preference of the two species for the underside of stones, which are infrequent on the soft bottom of the reservoir and cannot be sampled with the Ekman grab. Also only low numbers of both species were recorded from the transect samples during the first year.

2.5 Sorting

Samples were collected into labelled buckets, brought back to the laboratory, and placed immediately in a cool room $(10^{\circ} \pm 1^{\circ}C)$. Each sample was washed in a sieve $(17 \text{ mesh cm}^{-1}, \text{ aperture 355 } \mu\text{m})$ with a jet of water to remove clay and fine debris, and the residue hard-sorted.

The leeches were identified and recorded, and separate records made of those which carried eggs or juveniles attached to their ventral surface, or showed a

clearly visible clitellum. Each leech was weighed alive, after removing moisture with a filter paper for 30 sec, on a direct reading electrical balance (Mettler H30) reading to the nearest 0.1 mg. The sorting and weighing were usually completed within three days of the samples being collected.

The dry weight of each leech was determined separately after drying the leech at 80°C and a vacuum of 400 mm Hg in a vacuum oven for 12 hr. Winberg and Duncan (1971) recorded temperatures from 50° to 100°C for drying biological samples. The dried leeches were reweighed using an electro microbalance (EMB) reading to the nearest 0.01 mg.

3. ABUNDANCE AND DISTRIBUTION

3.1 Introduction

Distribution and abundance are closely related. A factor which affects the distribution of an organism may also affect its abundance and thus these two characteristics may be treated as different aspects of the same phenomenon (Anderwartha & Birch, 1954). Recently interest in the study of distribution and abundance of freshwater macrobenthos has increased, mainly because it may be used to monitor the impact of pollutants on aquatic communities (Moore, 1979) and detect the source of pollution (Nalepa & Thomas, 1976; Edmonds & Ward, 1978). Investigators have tried to relate the presence or absence of specific indicator species to varying degrees of water quality (Patrick, 1949; Olive, 1973; Ruggiero & Merchant, 1979).

Most studies on distribution and abundance of freshwater invertebrates have been undertaken at the level of the community. In Canada, Moore (1980) studied the factors which influence the densities of a community of benthic invertebrates in a shallow eutrophic freshwater bay. He concluded that the increasing availability of algae in the littoral regions was strongly correlated with oligochaete densities, but had no effect on the abundance of Chironomidae. He reported also that differences in the timing of emergence of different chironomid species were partly related to water temperature and the organic content of the substrate.

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Edmonds and Ward (1979) studied the distribution of profundal benthos in the Colorado Front Range Reservoir (Horsetooth Reservoir) and found that there was a strong positive relationships between total faunal density values and organic content of the substrate. Furthermore, they reported that chironomids decreased and oligochaetes increased in abundance with increasing depth.

Ruggiero and Merchant (1979) found that the distribution of benthic macroinvertebrates in the Patuxent River (Maryland, U.S.A.) was more closely related to substrate than to water chemistry. Streit and Schröder (1978) investigated the dominant groups of benthic invertebrates in Lake Constance (West Germany and Switzerland). Thev examined the reaction of invertebrates to the fluctuating water level in the lake and found that some species (including the leech species H. stagnalis, E. octoculata and gastropods Radix ovata) increased in density with increasing water level in spring, while others such as G. complanata, Dreissena polymorpha and the Trichoptera showed no response to water fluctuation. Maitland (1979) studied the distribution of zoobenthos in Loch Leven in Scotland, and recognised the existence of two communities correlated with different substrate types, mud and sand. The mud associated community included Hydra sp., and a number of chironomids, mainly Chironomus spp., Polypedelum sp., and Procladius sp., while the sand associated community was characterised by the presence of large numbers of Nematoda, Oligochaeta (Naididae and Enchytraeidae) and various Diptera (Strictochironomus spp., Cryptochironomus spp., Tanytarsini and Ceratopogonidae).

Relatively little is known about the factors governing the distribution and abundance of leeches in any particular body of water. Mann (1955) studied the distribution and abundance of leeches in 58 water bodies, 29 in Berkshire and 29 in the English Lake District. He recorded total alkalinity, dissolved organic matter, pH of substrates and water, and the surface area of each water body. He found that \underline{E} . <u>octoculata</u> was the most numerous leech in soft water and H. stagnalis the most numerous in hard (calcium rich) eutrophic water, while G. complanata was the most abundant in moderately fast flowing rivers with a high calcium content. Young and Ironmonger (1981) have provided numerical data on the distribution and abundance of the three species of leeches inhabiting the stony littoral of 100 British lakes of diverse trophic status during March/ April 1978. The numbers, biomass and mean weight were analysed for correlation with a wide range of physical factors (surface area, altitude and latitude) taken from Ordinance Survey maps and chemical characteristics (pH, sodium, potassium, calcium, magnesium, sulphate and chloride). Significant positive correlations were found for all of the chemical characteristics, with the exception of E. octoculata numbers, and H. stagnalis mean weight. They reported furthermore that the three species occur over a wide spectrum of calcium content, although only E. octoculata is found in lakes with a very low content.

The reservoir is more or less uniform in terms of physico-chemical characteristics of the water (Table 2) and that we are dealing with a single system in which most of the variables described by Mann (<u>op</u>. <u>cit</u>.) and Young and Ironmonger (<u>op</u>. <u>cit</u>.) do not change in the reservoir, so it was decided to investigate the effect of the nature of the substratum, the organic content of the four sites of the reservoir, and the influence of the depth of water on leech distribution, because no previous survey has considered them concurrently.

3.2 Method

Abundance sampling

Samples of the substrate were collected with the Ekman grab on four occasions along the four transects, at approximately the same collection points as were the benthic samples. Visual estimates of the composition of the substrate were made for each sampling according to the following categories: clay, mud, clay and mud, clay and detritus, mud and detritus, mud and stones, detritus, and algae.

The loss on ignition of each substrate sample was determined on two occasions for the four transects, by drying each sample in an oven for 2 days at 60° C. Each sample was then weighed, placed in a muffle furnace and heated at 550°C for twenty four hours, and reweighed. The

difference between the dry weight before and after combustion is the loss on ignition, which is the weight of organic material in the sample.

To examine the effect of depth, samples were recorded as shallow (\leq 2m depth) and deep (>2m depth).

3.3 Results

The numbers of individuals collected in each sample on each occasion are shown in Appendix A. The total of 1,072 samples were collected over the two years. From these, 1,861 leeches were isolated and the relative abundances of the three species was 80% H. stagnalis, 18% E. octoculata and 2% G. complanata. The mean and variance were calculated for each transect, on each occasion, for each species, and in many cases the variance was greater than the mean (exceptions included those occasions when no leeches were recorded in a transect). This suggested that the data required transformation before statistical analysis could be applied. A regression of log (variance +1) on log (mean +1) for the three species gave regression coefficients of 2.130 (H. stagnalis), 1.804 (E. octoculata) and 1.933 (G. complanata) (Figs. 5,6 & 7). Applying Taylor's (1961) power law, these values indicate that a log transformation is applicable for all three species.

The samples were analysed to determine whether there was any significant variation in abundance with sampling occasion and transects, using a 2-way analysis of variance on log transformed data. Table 4 shows the result of the analyses for the three species. There are

Fig. 5 Relationship between variance (s^2) and the sample mean (\bar{x}) of <u>H</u>. <u>stagnalis</u> from Rutland Water. Regression equation: $\log (s^2 + 1) = 2.12975 \log (\bar{x} + 1) - 0.06936$ n = 35

r = 0.972



Fig. 6 Relationship between variance (s^2) and the sample mean (\bar{x}) of <u>G</u>. <u>complanata</u> from Rutland Water. Regression equation: log $(s^2 + 1) = 1.93339 \log (\bar{x} + 1) - 0.04035$ n = 17 r = 0.964



Fig. 7 Relationship between variance (s^2) and the sample mean (\bar{x}) of <u>E</u>. <u>octoculata</u> from Rutland Water. Regression equation: $\log (s^2 + 1) = 1.80411 \log (\bar{x} + 1) - 0.05832$ n = 77r = 0.826



Source of	Degrees of	H. sta	gnalis	E. octo	oculata	G. comp	olanata	
variation	freedom .	Mean squares	Variance ratio	Mean squares	Variance ratio	Mean squares	Variano ratio	e e e
Transects	m	0.636	8.000 ^{xxx}	0. 3.06	8.743 ^{xxx}	0.011	1.100	S.
Occasions	23	0.933	11.735 ^{xxx}	0.030	0.857 NS	0.006	0.600	NS
Transects x Occasions	69	0.1056	1.327 ^x	0.036	1.028 NS	0.008	0.800	SN
Residual	976	0.0795		0.035		0.010		

TABLE 4 Analyses of variance for three species of leeches in Rutland Water.

xxx = P<0.001 ^x = P<0.05

NS = Not significant

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TABLE 5 Ranked mean values (log (x +1) transformed data) for all sampling occasions for <u>H</u>. <u>stagnalis</u> with those means which are not significantly different linked by a continuous line

	Occasion	Mean	SE of single mean = <u>+</u> 0.0415
1	Feb 79	0.019	
2	Feb 78	0.039	
3	Mar 79	0.040	
4	May 79	0.061	
5	Apr 79	0.062	
6	Dec 78	0.067	
7	Nov 78	0.077	
8	Jun 79	0.090	
9	Apr 78	0.100	
10	Jan 78	0.110	
11	Oct 78	0.118	
12	Mar 78	0.144	
13	Sep 78	0.161	
14	May 78	0.176	
15	Jun 78	0.189	
16	Nov 77	0.209	
17	Aug 78	0.223	
18	Jul 78	0.249	
19	Sep 77	0.262	1
20	Jul 79	0.291	
21	Oct 77	0.317	
22	Aug 79	0.430	
23	Oct 79	0.553	
24	Sep 79	0.556	2
			-

highly significant differences between transects (P<0.001) and between occasions (P<0.001) for <u>H</u>. <u>stagnalis</u> and the interaction between transects and occasions was just significant (P = 0.05). The analysis for <u>E</u>. <u>octoculata</u> shows a significant difference between transects (P<0.001) but no significant effect from either occasions or the interaction (P>0.05). <u>G</u>. <u>complanata</u> showed no significant response to either variable.

Tests between the means of transects and of occasions were carried out by means of a multiple range Table 5 shows the mean number of H. stagnalis recorded test. on each occasion in order of magnitude. Those means which do not differ significantly (P = 0.05) are linked by a continuous line. Thus abundance estimated for February 1979 through November 1977 are not significantly different from each other, being linked by a continuous line. September and October 1979 were significantly greater than the rest of the months, except August 1979, The picture from the analyses in general shows that summer and autumn months do not differ significantly from each other, but are significantly greater than winter and spring samples. This difference reflects recruitment to the population and the effect of temperature (cf. Chapter 4). There are some anomalies in that some months do not appear in the expected sequence. Thus September and October 1978 would be expected to occur in the same pattern as August, September and October 1979, but instead do not differ significantly from winter and spring samples, suggesting poor recruitment in that year.

The analyses of variance showed a significant difference between transects for both <u>H</u>. <u>stagnalis</u> and <u>E</u>. <u>octoculata</u>. The multiple range test (Table 6) indicated that <u>H</u>. <u>stagnalis</u> was less common in the dam transect, than in the other three transects. <u>E</u>. <u>octoculata</u> had the same pattern of distribution with a lesser abundance near the dam than elsewhere.

It is noteworthy that the dam transect differs from the other three transects in that the substratum is mainly clay, as opposed to mud and detritus in the other three transects (Table 7). Further, the organic content (loss on ignition) is markedly less in the dam samples than the other three (Table 8). The reduced numbers of leeches in the dam transects is possibly a direct consequence of the substratum or is indirectly a response to reduced prey density.

The analysis of variance was again used to compare the occurrence of leeches in deep water (> 2m) and in shallow water ($\leq 2m$) (Table 9). The analyses for H. <u>stagnalis</u> and <u>E. octoculata</u> showed the abundance was clearly related to water depth with both species more abundant in shallow water, while no significant difference was found for <u>G. complanata</u>.

As a consequence of the above result and the previous results (Table 4), the <u>H</u>. <u>stagnalis</u> data were analysed with respect to season, transects and depth. In this case, seasons were taken as three month periods, e.g. May, June & July = summer (cf. Table 11).

TABLE 6 Mean number of leeches (log (x +1) transformed) in the four sites of Rutland Water, lines to the left represent the values not significantly different from each other.

	Number of samples	<u>H. stagnalis E</u>	. <u>octoculata</u>
Dam	280	0.116	0.037
S. arm	280	0.196	0.075
N. arm	236	0.205	0.102
Tower	276	0.240	0.109

N. arm	Tc Tc	
		We r
4	S	б
Ø	7	I
З	2	ł
15	12	4
ε	ω	12
15	12	12
I	1	1
I	2	2
C		
0*	40	40
4 8 6 1 9 4 1 9 8 4 8 9 7 9 8 1 9 8		7 7 7 8 12 1 12 13 48 148

TABLE 7

Ď	am	. N	min	ູ ເ	arm	TC	Wer
9/12/78	26/4/79	19/12/78	2 /4/79	19/12/78	26/4/79	19/12/78	26/4/79
0	e	17	12	17	ľ	10	m
m	თ	31	28	19	11	11	12
9	10	17	14	11	თ	13	١
6	თ	14	21	8	10	11	14
80	ω	15	17	00	20	17	16
11	13	11	16	12	23	27	17
4	2	15	16	17	14	15	17
10	15	11	40	10	18	12	18
8	11	12	18	13	11	49	18
12	10	25	34	11	ı	12	15
7	10	29	24	11	14		
		10	27	13	16		
- 7.09	60.6	x = 17.25	22.25	<u></u> x = 12.5	14.6	x = 17.7	14.44
וו א א	8,09	וו או	19.75	 	3.55	וו א (16.07

Loss on ignition (% oven dry weight of 1 mg samples). Samples taken on two occasions at four transects TABLE 8

TABLE 9 Mean numbers of leeches (log (x +1) transformed) in shallow ($\leq 2m$) and deep ($\geq 2m$) samples.

	Species	Shallow	Deep	VR
<u>н</u> .	<u>stagnalis</u>	0.206	0.159	6.197 ^x
<u>E</u> .	octoculata	0.102	0.046	34.44 ^{xx}
<u>G</u> .	complanata	0.009	0.007	0.2 NS

xx = P < 0.01
x = P < 0.05
NS = Not significant</pre>

The result of this more complex analysis confirms the difference between both depth and transects (Table 10). The result also revealed a highly significant effect of season but no significant effect from either the interaction of transects with depth and season with transects. A multiple range test (Table 11) shows in general markedly higher densities from May to October than from November to April, although the differences are not clear-cut. Populations were significantly higher in the period August -October 1979 than at any other time, while November 1978 -January 1979 and February - April 1979 were significantly less than all other periods, except February to April 1978. The remaining data form a graded set with overlapping nonsignificant ranges. Considering the interaction between depth and season, all shallow water densities from May to July and August to October are significantly greater than the February to April shallow water values (Table 12), as well as the November 1978 to January 1979 deep water samples.

A similar analysis of the data for E. <u>octoculata</u> showed significant effects of both transect and depth as found earlier (cf. Table 4) and also of the season with depth interaction (Table 13).

A multiple range test (Table 14) in general shows that <u>E</u>. <u>octoculata</u> occurred in shallow water most of the season. Thus all deep samples except winter 1978 are significantly less than summer 1978, late summer 1978 and late summer 1979 shallow samples.

TABLE 10 Analysis of	variance for <u>H</u> .	stagnalis to examine	the effect of dep	th.	
Items	SS	DF	<u>MS (s²)</u>	VR	
Transects	2.002	£	0.667	8475 ^{XX}	
Depth	0.7423	1	0.7423	9.432 ^{xx}	
Transects x depth	0.412	ſ	0.137	1.740 NS	
Season	19.865	7	2.8378	36.058 ^{XXX}	
Season x transects	2.580	21	0.1228	1.560 NS	
Season x depth	1.9437	7	0.2777	3.529 ^{XX}	
Residual	75.93	965	0.0787		
Totals:	103.232	1007			1

xxx = P<0.001
xx = P<0.01
NS = Not significant</pre>

TABLE 11Ranked mean values (log (x +1) transformed data)
to test the effect of depth on season for
H. stagnalis

Season

Mean

Late Winter	1979 (Feb - Apr)	0.0399	
Winter 1979	(Nov - Jan)	0.0717	SE of single
Late Winter	1978 (Feb - Apr)	0.0840	$\frac{1}{2}$ + 0.0237
Summer 1979	(May - July)	0.1540	
Winter 1978	(Nov – Jan)	0.1590	
Late Summer	1978 (Aug - Oct)	0.1670	
Summer 1978	(May - Jul)	0.1910	
Late Summer	1979 (Aug - Oct)	0.543	

TABLE 12Ranked mean values (log (x +1) transformed data)
to test the effect of interaction of season x
depth for <u>H</u>. stagnalis

Season	Mean
Late Winter 1979 D	,0.033
Late Winter 1978 S	0.045
Late Winter 1979 S	0.0468
Winter 1979 D	0.0518
Late Summer 1978 D	0.0903 SE = ± 0.0336
Winter 1979 S	0.0912
Summer 1979 D	0.1132
Late Winter 19 7 8 D	0.1235
Winter 1978 D	0.1342
Summer 1978 D	0.1824
Winter 1978 S	0.1840
Summer 1979 S	0.1948
Summer 1978 S	0.213
Late Summer 1978 S	0.242
Late Summer 1979 D	0.5174
Late Summer 1979 S	0.5692

D = Deep

S = Shallow

Item	SS	DF	WS	VR
Transects	0.977	ſ	0.326	13.588 ^{xx}
Depth	0.879	l	0.879	36.625 ^{xx}
Transect x depth	0.186	С	0.062	2.58 NS
Season	0.288	7	0.041	1.708 NS
Season x transects	0.630	21	0.03	1.25 NS
Season x depth	0.638	7	0.0911	3.795 ^{xx}
Residual	23.52	964		
Totals:	27.118	1007		

TABLE 13 Analyses of variance for <u>E</u>. <u>octoculata</u> to examine the effect of depth

xx = P<0.01
NS = Not significant</pre>

TABLE 14 Ranked mean values (log (x + 1) transformed data) to test the effect of interaction of season x depth for <u>E</u>. <u>octoculata</u>

Season x depth

Late Summer 1978 D	0.018
Winter 1978 S	0.019
Summer 1979 D	0.033
Summer 1978 D	0.041
Late Winter 1979 D	0.051
Winter 1979 D	0.054
Late Summer 1979 D	0.057
Late Winter 1978 D	0.064 SE = 0.01865
Winter 1978 D	0.070
Late Winter 1978 S	0.081
Summer 1979 S	0.086
Late Winter 1979 S	0.086
Winter 1979 S	0.100
Summer 1978 S	0.145
Late Summer 1979 S	0.154
Late Summer 1978 S	0.159

In general H. stagnalis and E. octoculata

occurred at shallow water ≤ 2m throughout the study period and were more abundant in summer, and late summer seasons. Nevertheless the transect locality influenced the abundance and distribution of the leeches with the dam transect tending to show decreased abundance.

3.4 Discussion

The aim of this section was to investigate the variation in distribution and abundance of the leech species in Rutland Water and to provide a basis for further field work. The only factors considered are the composition and organic content (loss on ignition) of the substratum, and the depth of water. There are other factors which influence the distribution and abundance of leeches (cf. Sawyer, 1974) such as water chemistry, temperature and dissolved oxygen. These were not measured in relation to specific sampling points but A Ferguson (personal communication) has found no significant variation in water chemistry throughout the water body.

The data for <u>H</u>. <u>stagnalis</u> and <u>E</u>. <u>octoculata</u> show a clear preference for three of the four transects, with numbers in the dam transect significantly lower. The evidence on the abundance of prey organisms offers no explanation for this difference, since potential prey are equally abundant in all four transects. If then there are no differences in the water body, it must be concluded that

the leeches are showing a behavioural response to the type of substratum and prefer a mud and detritus substratum as opposed to the clay substratum with a low organic content which characterises the dam transect.

This conclusion is at variance with the generalisation of Elliott and Mann (1979) that leeches are scarce on muddy substrata. Maitland (1979) concluded that H. stagnalis was equally abundant on a sandy substratum with low organic content and a muddy substratum with a high organic content. Maitland's data were gathered over a 10 day period in October, a time at which juveniles are dispersing and numbers are greatest, and it is consequently difficult to attach great significance to his result. It is perhaps more germane to consider the possible relationship between substratum selection and prey availability. Here again Maitland's results indicate abundant potential prey on both substrata. Mackay (1976) and McLachlan (1969) have both reported a significant correlation between the abundance of chironomid larvae and both increasing organic content and substratum composition. In the latter, they reported that clay is discriminated against in favour of muddy or sandy/silty substrata. It is therefore possible that the observed distribution in Rutland Water reflects an adaptation for leeches to locate substrate more likely to be favoured by their prev.

Mann (1961) concluded that <u>G</u>. <u>complanata</u> was very abundant and distributed evenly when the calcium content of the water is high, while Wilkialis (1970)

related the abundance of this species to the number of snails in any given piece of water. The two views are in agreement in that the abundance of snails is positively correlated with the calcium content of the water (e.g. Tucker, 1958). Hence there is an implicit relationship between the abundance of this species and its food (snails) particularly Lymnaea peregra L. (cf. Young & Ironmonger, 1979). Although the reservoir is alkaline (pH \geq 8) with a calcium content of 122 mg 1⁻¹ (Table 3) only low densities of <u>L</u>. peregra were recorded in Rutland Water, except for a brief upsurge in July and August 1978 (Bullock <u>et al</u>., 1982). It is therefore not surprising that <u>G</u>. <u>complanata</u> is recorded infrequently in the grab samples.

<u>G. complanata</u> was found, however, in reasonable abundance amongst large stones at the edge of the reservoir (Chapter 4) and <u>L. peregra</u> was similarly present in this littoral zone. Thus it may be suggested that the primary factor governing the distribution of <u>G. complanata</u> in Rutland Water is the availability of suitable prey.

The leeches were generally abundant in June, July, August, September and October. At this time there was continuous breeding and leeches were more active. Both these aspects were almost certainly mediated by increased water temperature which, as shown in Chapters 5 and 6, also caused increased metabolic activity.

In the present study, <u>H</u>. <u>stagnalis</u> and <u>E</u>. <u>octoculata</u> occurred in the shallow water more than deep water. This may reflect the availability and quality of prey, which are more abundant in the shallow water (J.Bullock,

personal communication), the higher temperatures in shallow water and the better oxygenation through wave action.

The relative abundances of the leeches in Rutland Water are 80% <u>H</u>. <u>stagnalis</u>, 18% <u>E</u>. <u>octoculata</u> and 2% <u>G</u>. <u>complanata</u>. These figures are similar to those figures reported by Lang (1974) of 61 , 26 and 10% respectively in Lake Geneva. Similarly, Streit and Schröder (1978) reported the same sequence of abundance in Lake Constance without guoting figures.

The only other available evidence deals with distribution rather than abundance. Thus, Mann (1961) reported <u>H. stagnalis</u> occurring in the greatest number of lakes in the Lake District and Southern England. Young and Ironmonger (1981) found <u>E. octoculata</u> the most widespread in Britain. Both papers are based on short surveys and the latter was conducted in April when <u>H. stagnalis</u> are least abundant.

To summarise the result, substratum composition, organic content and depth of water affect the distribution and abundance for both <u>H</u>. <u>stagnalis</u> and <u>E</u>. <u>octoculata</u>. The distribution of <u>G</u>. <u>complanata</u> appears to be more immediately related to that of its gastropod prey.

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4. POPULATION ECOLOGY

4.1 Introduction

The study of a field population of any animal requires adequate estimates of their density. These are generally obtained by the collection of samples which neither greatly deplete the population nor cause excessive damage to the habitat.

The first study of the population ecology of leeches in Britain was that of Mann (1953,1957a & b) who dealt with three species, <u>H</u>. <u>stagnalis</u>, <u>G</u>. <u>complanata</u> and <u>E</u>. <u>octoculata</u>, in Whiteknights Lake in Berkshire, England. Elliott (1973a) has provided a comprehensive study of the population ecology of <u>E</u>. <u>octoculata</u> in a small stony stream in the English Lake District. Learner and Potter (1974) studied the life cycle and production of <u>H</u>. <u>stagnalis</u> in a shallow eutrophic reservoir in South Wales. Young and Ironmonger (1982) conducted a comparative study of <u>E</u>. <u>octoculata</u>, <u>G</u>. <u>complanata</u> and <u>H</u>. <u>stagnalis</u> in two lakes, one of which is an upland oligotrophic lake in Wales and the second of which is a lowland eutrophic mere in England.

Outside Britain, Tillman and Barnes (1973) studied the life cycle of <u>H</u>. <u>stagnalis</u> in Lake Utah in U.S.A., and Davies and Reynoldson (1976) compared the life cycle of <u>H</u>. <u>stagnalis</u> in two different areas in Canada. Lang (1974) studied the life cycle of three species,

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<u>H. stagnalis, G. complanata and E. octoculata</u> in Lake Geneva in Switzerland. Dall (1979) in Denmark studied the life cycle and production of <u>E. octoculata</u> and <u>E. lestacea</u>.

In the present study, the life cycle was studied together with the changes in both population density and biomass. These were measured over the course of two years and the data then used to calculate population energy budgets for the three species of leeches.

4.2 Life cycle of H. stagnalis

The sampling method and collection of the leeches have been discussed in section 2.3. All leeches were weighed and the data presented as frequency diagrams in 2 mg weight classes (Fig. 8) on the 24 sampling occasions from September 1977 to October 1979.

<u>H</u>. <u>stagnalis</u> lays its eggs in a thin transparent cocoon which it fastens to the ventral surface of its body (Mann, 1957b). None of the leeches carried eggs or young when sampling began in September 1977. The population was composed mostly of small individuals (modal value 2 - 4 mg) which had progressed to a modal value of 4 - 6 mg by November 1977, but with some leeches reaching 14 - 16 mg. In January and February 1978, the population declined on reaching the range (maxmimum 8 - 10 mg). In March and April 1978 the leeches increased in weight with some individuals attaining 16 mg, although many remained

Fig. 8 Weight frequency histograms for <u>H</u>. <u>stagnalis</u> from Rutland Water at each sampling date. The number of mature leeches is shown in solid lines.





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S 79

small. Egg cocoons were recorded first in May when about 20% of the overwintering population were carrying eggs. By June 1978, 40% of the overwintering population carried eggs and young. In July 1978 a new group of small leeches appeared which comprised about 10% of the total population, which was the offspring of the overwintering population. 15.5% of the overwintering population still carried young and the number of ovigerous individuals was clearly declining. The August 1978 polygons showed that there has been considerable growth of the offspring but it does not reach maturity. In September 1978 there was a high percentage (23.6) of young (0 - 2 mg) of leeches and more than 80% of leeches are ≤ 6 mg and were actually the progeny of that year.

The pattern was repeated in the second year (1978 - 1979) except that in June 1979, 81% of the overwintering population carried eggs and young, and the first young released in July comprised 24% of the total population and young-carrying adults were present in August, the percentage of young liberated in September 1979 was 16.3%. The growth occurred from September -December in both years with the mean temperature ranging from 15.3 - 7.5°C and the production of eggs in both years commenced when the temperature was 11°C. The breeding season of <u>H</u>. <u>stagnalis</u> in Rutland Water commenced in May and extended through to August, and this is similar to the findings of Bennike (1943) and Wilkialis (1970), but in conflict with Mann (1957b) who reported that the breeding

season of <u>H</u>. <u>stagnalis</u> began when the overwintering adults produced a brood in Spring and then died. Some of their offspring grew rapidly and bred in the Summer, and the final overwintering populations were composed of survivors of both Spring and Summer generations. Learner and Potter (1974) reported that their result from Eglwys Nunydd Reservoir in Wales was similar to that described by Mann. In Canada, Davies and Reynoldson (1976) found the life cycle at Marion Lake and Newsome Pond was extended from mid-March to mid-September with two broods being produced per year. In Newsome Pond on the other hand, only a single generation was completed in a year.

Lang (1974) reported a similar life cycle to that of Mann (<u>op</u>. <u>cit</u>.) in a study of a population in Lake Geneva, Switzerland. Tillman and Barnes (1973) reported, in their study of <u>H</u>. <u>stagnalis</u> in Utah Lake, U.S.A., that a short breeding season and the overwintering adults provided both Spring and Summer generations and they showed that gonad development of this leech had two distinct periods of egg and sperm production. Young and Ironmonger (1982) showed that a period of 69 - 72 days was necessary to complete a generation from egg to egg in the laboratory at a constant temperature of approximately 16° C. In Rutland Water, <u>H</u>. <u>stagnalis</u> was found carrying young rather than eggs in July for both years, and if the leeches carrying eggs were present in July, it would be expected that some leeches would be carrying young in September and October respectively.

It is difficult to explain that young leeches produced in July will grow rapidly and give a second brood by late in September or beginning of October, as it needs more than two months. Even though breeding commenced at the beginning of May, we would expect to observe an egg carrying adult late in July, but this has not been shown for July in both years and Fig. 8 confirmed that Rutland Water was devoid of any leeches carrying eggs or young in September for both years.

The life history of <u>H</u>. <u>stagnalis</u> at Rutland Water is different to that described by Mann (1957b), Learner and Potter (1974) and that of Young and Ironmonger (1982) in the following respects:

1. Mann; Learner and Potter, and Young, and Ironmonger reported that breeding seasons commenced in April, whereas at Rutland Water breeding commences in late May with a water temperature above 11^oC.

2. Mature leeches, i.e. leeches carrying eggs or young, reported by Mann; Learner and Potter, and Young and Ironmonger were less than 4 mg live weight, while in the present study no leech reached maturity at less than 4 mg.

3. Mann; Learner and Potter, Young and Ironmonger reported that young appeared at the beginning of June, whereas at Rutland Water young appeared in July, because reproduction in Rutland Water begins later.

Most workers included water temperature data except Mann (<u>op</u>. <u>cit</u>.) and they related the breeding

of <u>H</u>. <u>stagnalis</u> to temperature as the main factor (Tillman & Barnes, 1973; Learner & Potter <u>op</u>. <u>cit</u>; Sawyer, 1972) indicating that rising temperature induces breeding activity. Bennike (1943) showed that the breeding season was short when the water temperature is $12 - 13^{\circ}$ C. Learner and Potter (<u>op</u>. <u>cit</u>.) found that breeding started in April when the temperature was above 10° C, and Young and Irongmonger (<u>op</u>. <u>cit</u>.) showed that the breeding season started in April when the water temperature was above 11° C on the two years.

In the present study the temperature reading (Fig. 3) for the month of April in the two years never exceeded 7° C, and in both years the temperature exceeded 10° C after mid-May. Hence egg deposition or breeding of <u>H. stagnalis</u> found in Rutland Water commenced in May when the temperature was over 11° C in both years, and the temperature is considered to be a trigger for the commence-ment of the breeding season.

4.2.1 Population density

The mean population density of <u>H</u>. <u>stagnalis</u> was calculated from the total samples taken on each occasion (32 samples in September and October 1977, and 46 in all other months). The graph for the population density is presented in Fig. 9 as number per m^2 , and indicates low population numbers throughout the Winter in both years and

Fig. 9 The mean population density of <u>H</u>. <u>stagnalis</u> in Rutland Water from September 1977 to October 1979.



the densities declining particularly in February when the lowest densities were recorded (4.8 m^{-2}) in 1978, and (2.9 m^{-2}) in 1979. The population started to rise in density from March in both years before any reproduction occurs. This may have been due to leeches not being collected in the grab samples, and observations show that many leeches were concealed under stones during the cold period of the year. In June for the two years the population begins to increase through recruitment of juveniles, and the trend continues through the Summer of each year. The highest population densities were recorded in September of each year $(178 \text{ m}^{-2} \text{ and } 199 \text{ m}^{-2} \text{ respectively})$. These high densities were due to recruitment of juveniles to the population.

It appears that the population density of <u>H</u>. <u>stagnalis</u> in Rutland Water is very low when compared to the data reported in the literature. Hilsenhoff (1962) recorded a total population density of 262 - 615 ind/m²/yr in Lake Winnebego in the U.S.A. Learner and Potter (1974) recorded a density of 343 - 1376 ind/m⁻²/yr⁻¹ in a shallow eutrophic reservoir in South Wales. Young and Ironmonger (1982) in the eutrophic lake Crosemere recorded a mean number of 720 m⁻² in August and 80 m⁻² in April. Thut (1969) working in Lake Washington recorded a density of mean monthly estimates of 44 m⁻² yr⁻¹. Table 15 shows the different densities obtained by some workers and in comparison with them indicates that density in Rutland Water was lower.

Author	Maximum density	Minimum density	Method of collection	Location
Hilsenhoff 1967	615 m ⁻² yr ⁻¹	262 m ⁻² yr ⁻¹	£kman grab	Winnebago Lake, U.S
Sapkarev 1963	1527 m ⁻² July	22.2 m ⁻² February	£kman grab	Mendota Lake, U.S.A.
Thut 1969	60 m ⁻² October	30.0 m ⁻² February	£kman grab	Washington Lake, U.S.A.
Learner & Potter 1974	1336 m ⁻² yr ⁻¹	343 m ⁻² yr ⁻¹	Fixed-handle grab	Eglwys Reservoir, Wales, U.K.
Present study	178 m ⁻² September	2.9 m ⁻² February	Ekman grab	Rutland Water, U.K.

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Bennike (1943) concluded that in Lake Fures, the highest population density was commonly encountered in the surface zone (0 - 1.5m) from May to September, and migration to greater depths did not occur during the rest of the year; the littoral H. stagnalis being killed by winter ice. While Davies and Reynoldson (1976) showed in their studies in both Newsome and Marion Lake in Canada that H. stagnalis migrates to deep water in Winter and from deep water to the shallow littoral zone in Spring. In our present study, the density markedly increases in the breeding season and decreases in Winter. Although we have the same number of samples both in the deep and in the relatively shallow water, and no sign of migration showed in the Winter (cf. section 3), and we would expect a high density at Winter time in the deep water, but the situation showed no sign of high density, so the leech might be very sensitive to temperature and when cold spells are expected, the leech will conceal itself underneath the stones and will stay there until the temperature becomes suitable.

4.2.2 Population Biomass of H. stagnalis

The monthly estimates of total population biomass (mg DW m⁻²) were obtained by dry weighing all leeches collected and converting this figure to mg m⁻² (Fig. 10). The data show a peak of biomass from July to September in each year, which is due to recruitment and a

Fig. 10 Population biomass (mg DW m⁻²) of <u>H</u>. <u>stagnalis</u> in Rutland Water from September 1977 to October 1979.



FIG 10

high growth rate in this period. The biomass gradually declined from November 1977 until February 1978, and from October 1978 to April 1979, and this was due to mortality as well as to failure to sample leeches concealed under stones, and perhaps to the leeches not feeding at low temperatures. Young and Ironomonger (1982) reported that an increasing temperature accelerates the rate of growth and metabolism.

4.3 Life cycle of E. octoculata

The results of the samples collected from September 1977 to October 1979 by means of the Ekman grab are presented in Fig.11. Due to the low numbers of this species in the grab samples, an alternative sampling method was used. Leeches were collected by hand from an area of one square metre and a depth of 30 cm near the dam, from August 1978 to October 1979 (Fig.12). Both Figures 11 & 12 show that the mature individuals, identified by the presence of a clitellum, were present from May to October in each year; their weights ranged from 55 to 150 mg. Cocoon deposition was observed in July and empty cocoons were first recorded in August, and by September and October most of the juveniles had emerged. At this time, the population density was at a maximum and three size classes can be distinguished:

1. Small leeches (0.5 - 10mg) which have newly joined the population and were the progeny of the current year.

Fig. 11 Weight frequency histograms for <u>E</u>. <u>octoculata</u> from Rutland Water at each sampling date taken by Ekman grab. The number of mature leeches with clitellum are shown in dotted lines.



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FIG.11

= 5 animals

Fig. 12 Weight frequency histogram for <u>E</u>. <u>octoculata</u> from Rutland Water at each sampling date taken by hand. Solid areas indicate leeches with clitellum.















0.78

S-78



670

5.79

A-79

















mg(weight Class)

FIG.12

Medium sized individuals (15 - 55 mg) which have been present throughout the preceding year but were not mature.
Large leeches, 55 mg in size, which are mature and were presumably two years old.

In November each year the picture showed clearly that the large leeches, which had bred earlier, had mostly disappeared and very few survived to breed in the next year. The losses were high among the young leeches between November and February, while the growth was high from February until June. The medium weight had low mortality from November until July, and the growth was high from February until June, as indicated by the upward extension of the polygons in Figures 11&12. By May 1978 some of the medium sized leeches had reached maturity (indicated by the development of a clitellum) while others appear to mature later in the year.

It is evident (Fig.12) that young leeches of <u>E</u>. <u>octoculata</u> reach maturity in their second year under the conditions at Rutland Water. Mann (1953) in the Foundry Brook, Berkshire (England) reported that <u>E</u>. <u>octoculata</u> were breeding after one year as well as after two years, and lived for two years. The very few which failed to breed in their first year, lived for three years, breeding in their second and third years. Lang (1974) working at Lake Geneva, Switzerland, reported a similar life cycle to that reported by Mann (<u>op</u>. <u>cit</u>.). Dall (1979) in his work

in Lake Esrom, Denmark, found that 85 - 90% of <u>E</u>. <u>octoculata</u> reproduced after one year, and only a few individuals survived and reproduced for the first time after two years. Young and Ironmonger (1982) found a similar life cycle to that reported by Dall (<u>op</u>. <u>cit.</u>), with 81% in Crosemere and 75% in Llyn-y-Gadair reproducing and then dying after one year.

In Wilfin Brook, Cumbria, a maximum life cycle of about two years was recorded (Elliott, 1973 a and b) and <u>E</u>. <u>octoculata</u> did not breed in the first year, but all bred in their second year. Aston and Brown (1975) recorded a similar life cycle at an unpolluted site in the river Trent, but an annual cycle at another site on the Trent which was organically polluted.

The life cycle in Rutland Water is thus similar to that found by Elliott (<u>op</u>. <u>cit</u>.) and by Aston and Brown (<u>op</u>. <u>cit</u>.) at an unpolluted site on the river Trent.

The number of cocoons deposited and leeches liberated has been investigated in the laboratory. Twenty mature active leeches were kept individually in small jars, β cm in diameter, with resting stones and aerated lake water, in a 15 (\pm 1) ^OC constant temperature room. Six leeches out of twenty did not produce any cocoon and later died. Table 16 showed the estimation of numbers of eggs and young per cocoon, and cocoons per leech, was made, and the number of young produced by the leeches in the present

	No. of cocoons	No. of eggs/cocoon	No. of leeches liberated
1	3	5	13
2	6	4	14
3	10	4.1	27
4	8	5.1	27
5	6	4.1	13
6	7	4.1	30
7	8	4.5	28
8	4	3 .7 5	9
9	3	5.3	8
10	6	4.1	13
11	5	4.8	14
12	7	4.8	24
13	7	5.0	24
14	4	4.25	10
No. of cocoons/leech		No. of eggs/cocoon	No. of leeches
6 ± 0.54 (3 - 10)		$4.5 \stackrel{+}{-} 0.14$ (2 - 7)	$18.14 \stackrel{+}{=} 2.13$ (8 - 27)

TABLE 16E. octoculata mean numbers of cocoons/leech,
eggs/cocoon and number of leeches liberated

Mean number of leech produced for \underline{E} . octoculata with comparison with other authors TABLE 17

study was compared with other authors (Table17).

4.3.1 Population density of E. octoculata

The density of E. octoculata was monitored in Rutland Water by two methods (section 2). The graph for the population density is presented in Fig. 13 as number per m^2 , and indicates a density which declined from November 1977 until February 1978, due to mortality and the nature of the leeches to stay underneath the stones The density started to increase during the cold period. from February 1978 until April 1978, and this may be due to the fact that the leeches came out from underneath the stones. A second decline in density appeared from April to August, and the picture was clear in 1979: this was attributable to the mortality of the mature leeches which died after breeding. The data from dam samples indicates a higher population than from the grab samples. However the picture showed clearly that the density was at a maximum in October 1978 for the dam samples, and that was due to the addition of new recruitment; and a decline in density until March 1979; a slight increase in density from March 1979 until June without adding any young: this increase was due to the movement of the leeches from underneath the stones. The density further decreased due to mortality of the mature leeches, and in September 1979 the density began to increase through recruitment of juveniles, but

Fig. 13 The mean population density of <u>E</u>. <u>octoculata</u> in Rutland Water from September 1977 to October 1979

- ▲ samples taken by Ekman grab
- samples taken by hand



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the density of <u>E</u>. <u>octoculata</u> near the dam in September 1979, did not attain the level of September 1978, but was less.

There is a fluctuation in population density in some months, such as May 1978 and December 1978, and this must be due to the leeches not being available for collection in the grab. Despite the small numbers of leeches collected in the present study, and the fluctuation in density, the picture showed a high density after recruitment, and low density during Winter and the breeding season. The lowest population density recorded was 3.8 m^{-2} in January 1978, and the highest density was 26 m^{-2} . Near the dam, the lowest density was 12.5 m^{-2} and the highest density was 36 m^{-2} .

These appear to be very low densities when compared with some authors. Elliott (1973a) recorded a maximum density of 4000 m⁻² in October and a low density of 700 m⁻² in June. Dall (1979) recorded 1550 m⁻² density in August and a density of 75 m⁻² in February. Aston (1975) showed a different population density: a high density in the polluted part of the river Trent for three stations gave 136.1 m⁻², 380.5 m⁻² and 245.6 m⁻², while near the unpolluted area, two stations gave low densities of 22.5 m⁻² and 41.0 m⁻² respectively.

4.3.2 Population biomass

The monthly estimates of total population biomass (mg DW m^{-2}) were obtained by dry weighing all leeches collected and converting this figure to mg m^{-2} (Fig. 14). The data show the total biomass for E. octoculata taken by the two methods of sampling and the monthly variations in the biomass show a different pattern to that of the population density. The period from November 1977 to February 1978 showed a decline in the total biomass, similar to the decline in population density which is due to three factors: (1) the mortality of large leeches after they have laid their cocoons, as shown in Fig. 12 : (2) a high mortality of leeches in all weight classes at this period, as shown in the population density section, and (3) the movement of the leeches to the underside of stones for a period of time during the Winter. Population biomass increased from April 1978 to July 1978 as a result of rapid growth in all size classes. The biomass reached 250 mg⁻² in June 1978, following a decline in May caused by smaller numbers in the samples of that month, possibly as a result of aggregation. The biomass declined from July until March 1979, despite the addition of numerous juveniles in September and October. The second year followed much the same pattern, with the peak again being reached in June 1979. Unlike the previous year, the biomass remained high throughout August and September,

- Fig. 14 Population biomass (mg DW m⁻²) of <u>E. octoculata</u> in Rutland Water from September 1977 to October 1979.
 - ▲ samples taken by Ekman grab
 - samples taken by hand



FIG.14

although July is greatly reduced due to a very low population density.

The data from the dam samples shows a similar pattern: the population biomass declined from August 1978 until March 1979, and then increased gradually from April to July 1979 as a result of rapid growth of individual leeches and little variation in population density. The general trend, as revealed by both sampling methods, was for a minimum biomass in February and a maximum in July.

Elliott (<u>op</u>. <u>cit</u>.) recorded the maximum biomass in June or July, and the minimum in February or March, whilst Dall (<u>op</u>. <u>cit</u>.) recorded two separate minima of biomass, one in Winter (January, February) and the other in August, with a maxima in June and October. The latter results differ from Elliott's findings and the present study, because the cocoons hatched in July and these juveniles had a very fast growth rate from July to October, thus giving a high biomass.

4.4 Life cycle of G. complanata

The number of individuals of <u>G</u>. <u>complanata</u>, obtained by taking monthly samples of 1 m^2 of stony substrate near the dam, were used to study the population structure and the data are presented as frequency diagrams in 5 mg live weight classes from August 1978 to August 1979 (Fig. 15).

Fig. 15 Weight frequency histograms for <u>G</u>. <u>complanata</u> from Rutland Water at each sampling date taken by hand from an area of 1 m^{-2} . Solid area indicates leeches carrying eggs or young.



Like <u>H</u>. <u>stagnalis</u>, <u>G</u>. <u>complanata</u> lays its eggs in a thin transparent cocoon which it attaches to its underside. On hatching, the juveniles remain attached to the parent for about a month. The parent feeds little, if at all, during this period and dies soon after the juveniles leave.

None of the leeches carried eggs or young when sampling began in August 1978, the population consisted mainly of small individuals (generally <15 mg), with some large leeches which presumably did not breed in 1978. The juveniles grew rapidly from August 1978 until November 1978, attaining a modal size class of 15 - 20 mg. At the same time, there was a high overall mortality with numbers falling from 78 m^{-2} to 39 m^{-2} between September and November. The number of leeches remained low in Winter from December 1978 to February 1979, and this is a similar pattern of events to the findings for H. stagnalis and E. octoculata. The breeding season began in mid-April 1979, when the water temperature was 6⁰C. In May, more leeches were carrying egg cocoons and some were carrying young (water temperature 10[°]C). In June no egg-carrying leeches were found, and most leeches over 20 mg weight were carrying young. By this time some young had been released and appear in the population as individuals <15 mg in weight (water temperature >12°C). In July, no leeches were carrying eggs or young, and many juveniles had entered the population. Some large leeches (>35 mg) remained in the
population. It is improbable that these belong to the 1979 generation, and since all leeches die after reproducing (cf. Mann, 1957a), it seems possible that some of the leeches persist for a further Winter before reproducing.

The outline of the life cycle of G. complanata is similar to that described by Young and Ironmonger (op. cit.) when they reported an annual breeding cycle with about 72% of leeches dying after one year in the productive lake, and 88% of the leeches dying in the unproductive lake, and some of both populations surviving into the next year and then breeding. Mann (op. cit.) recorded a population which produced eggs in two broods, with two year old leeches reproducing in March, and one year olds reproducing in April and May. At the end of the first year, 100% of the first brood were breeding, but only 40% of the second brood. At two years old, almost all leeches had bred and then died shortly after reproducing, and 5 - 6% of the population survived to breed again at three years of age. Lang (1974) reported three generations present in Lake Geneva, similar to the findings of Mann (op. cit.), with two broods per year, with a breeding season from March to June, and all mature leeches breeding at the same time. In the present study, the breeding season is shorter, with the older leeches (more than one year old) breeding earlier, and there was no evidence for the production of two distinct broods.

4.4.1 Population density of G. complanata

The population density of <u>G</u>. <u>complanata</u> was estimated from August 1978 to August 1979. The graph is presented in Fig. 16 as number per m^2 , and indicates a marked decrease from September 1978 to February 1979, when the lowest density was recorded. As in the cases of <u>H</u>. <u>stagnalis</u> and <u>E</u>. <u>octoculata</u> numbers tended to be minimal in the Winter as well, and this may have been due to mortality first, and due to the movement of young off stones. An increase was recorded in March 1979 which was possibly due to the movement of leeches to the stones (Young & Ironmonger, 1982), and the decrease continued until June when the first juveniles of the 1979 generation appeared.

Young and Ironmonger (<u>op</u>. <u>cit</u>.) reported some evidence for an increase in population numbers in the Autumn without the addition of any young, and this was attributed to the movement of leeches onto stones.

4.4.2 Population biomass of G. complanata

The mean population biomass was calculated from all individuals and is presented in Fig. 17. The pattern is the same as that for population density, with low population biomass in Winter with little or no growth occurring. The population fell steadily until March 1979

Fig. 16 The mean population density of <u>G</u>. <u>complanata</u> in Rutland Water from August 1978 to August 1979.





Fig. 17 Population biomass (mg DW m⁻²) of <u>G</u>. <u>complanata</u> in Rutland Water from August 1978 to August 1979.



FIG.17

when the population biomass increased due to a relatively high density of leeches. The biomass decreased again in April, probably as a result of the mortality of large leeches following breeding. In May and June, the biomass increased as a result of growth and, to a limited extent, the addition of juveniles to the population. In July and August, the biomass declined because of the loss of first reproductive large leeches.

The highest population biomass was recorded in September 1978, and was 91 mg dry weight⁻² and the lowest was 20 mg dry weight m⁻² recorded in February 1979. There is no data on biomass available in the literature to compare with these results.

4.5 Summary

Population structure, density and biomass for three species: <u>H</u>. <u>stagnalis</u>, <u>E</u>. <u>octoculata</u> and <u>G</u>. <u>complanata</u>, were investigated in Rutland Water. Because of the strong preference of the animals to live under stones, collections were made by hand near the dam for the two species, <u>E</u>. <u>octoculata</u> and <u>G</u>. <u>complanata</u>.

The life cycle of <u>H</u>. <u>stagnalis</u> was predominantly annual with the overwintering population breeding in May, June and July, when the temperature was above 11° C. The population density varied between 200 - 5 individuals m⁻² with the biomass 215 - 5 mg dry weight m⁻²; high density

and biomass was due to the addition of new recruitment to the population and the lowest density and biomass was recorded in Winter.

<u>G. complanata</u> had a similar life cycle to that of <u>H</u>. <u>stagnalis</u>. It lived for one year and the majority then bred. A small percentage which failed to mature may have survived to the next year. The density varied between 19 and 4 individuals m^{-2} with a biomass of 90 - 20 mg dry weight m^{-2} .

<u>E</u>. <u>octoculata</u> did not breed in their first year but all reproduced in their second year before dying. Cocoon deposition began in June and terminated in August. The highest population density was recorded in September as 31.5 individuals m^{-2} and the lowest in January with 3.8 individuals m^{-2} . The population biomass was highest in June 1978, being 250 dry weight m^{-2} and was very low in Winter (February) being 30 mg dry weight m^{-2} . It is suggested that water temperature in terms of growing season is at least one of the most important determinants for the beginning of the breeding season.

5. RESPIRATORY STUDIES

5.1 Introduction

The utilisation of energy in metabolic activity is an essential component of the energy budget of any organism. The metabolism of stored energy can be measured in terms of temperature changes or of the chemical reactions which involve gaseous uptake and release. These gaseous exchanges are quantitatively related to the energy liberation from each particular chemical substance. When the substance is known the measurement of one of the three variables defines the remaining two (Petrusewicz & Macfadyen, 1970).

In most, if not all, studies of whole organism metabolism under aerobic conditions, it is preferable to measure oxygen consumption rather than either carbon dioxide evolution or temperature change. The heat produced is very difficult to measure in small animals, and no convenient method for this determination is available (Southwood, 1978). Oxygen uptake varies less with different energy sources than carbon dioxide output (Petrusewicz et al., <u>op. cit</u>.) and is thus more reliable when the nature of the metabolised compounds is unknown.

In order to estimate the respiratory activity of a field population, it is necessary to determine the respiration rates of all the life stages or size classes in

the population, and their relation to temperature. These values can be applied to the field data comprising population density and size class structure. This involves either a large number of determinations of respiratory activity or the acceptance of an overall population estimate in which a number of assumptions are made concerning the relationship between respiration rate and weight, and respiration rate and temperature (Phillipson, 1963). Whilst it may be preferable to explore the latter approach, there are few data at the present time on which to base an objective estimate of their reliability, and it is necessary to obtain more detailed estimations in order to make this assessment (Phillipson, <u>op</u>. <u>cit</u>.).

5.2 Previous studies on leeches

While much has been published on the respiration of several aquatic invertebrates, very little data **are** available on the respiratory rates of leeches. Lindeman (1932) studied the relationship of oxygen uptake in <u>Hirudo</u> <u>medicinalis</u> to the oxygen tension of the water and found that the oxygen consumption of this leech was independent of the oxygen tension between 20 and 100% saturation of oxygen at "room temperature". Mann (1956) measured the oxygen consumption of five species of fresh water leeches, <u>Helobdella</u> <u>stagnalis; Glossiphonia complanata; Piscicola geometra;</u> <u>Erpobdella octoculata</u> and <u>E. testacea</u> and found that oxygen

consumption by the last three species is related to oxygen tension of the water, while a degree of independence is shown by <u>H. stagnalis</u> and <u>G. complanata</u>. His experiment was conducted only at the rather high temperature of 20° C.

Nagabhushaman and Kulkarni (1977) investigated the effects of pH, NaCl concentration and oxygen tension on the respiration of <u>Poecilobdella viridis</u> at 26° C. They found that the respiration rate increased significantly with progressive elevation of oxygen tension of the medium. They also found no significant change in the respiratory rate at a pH between 5.5 to 7.0, but respiration rate was decreased in pH of 4.6 and 8.2 - 9.1, while increasing salinity caused the rate to rise. Ramamurthi (1968) reported that the related leech <u>P. granulosa</u> had a minimal oxygen consumption in 25% sea water, with a maximum oxygen consumption in 50% sea water,

5.3 Techniques for measuring oxygen consumption

Most measurements of oxygen uptake have been made with manometric apparatus in which the carbon dioxide released by the animal is absorbed by an alkali such as potassium hydroxide, so that when oxygen is taken in, the total mass of gas in the closed respiration chamber is reduced. The rate of oxygen uptake is then measured as the reduction in the volume or the pressure of gas in the chamber, or from a combination of both measurements (Petrusewicz <u>et al.</u>, <u>op. cit</u>.).

Umbreit et al. (1972) reviewed many respirometers used in estimating oxygen uptake which depend on manometric systems. The Warburg respirometer has been commonly used and this operates using the constant volume principle. The reference arm of the manometer was open to the atmosphere and hence subject to variation in atmospheric This system has been superseded by the differentpressure. ial type of respiometer originally designed by Barcroft In this system a chamber of similar volume to the (1908).respiration chamber was placed on the reference arm of the This system is thus isolated from changes in manometer. atmospheric pressure, and consequently the respirometer was more accurate for low respiration rates.

Gilson (1963) designed a respirometer in which the volume of oxygen used by the animal is determined by adjustment of a micrometer syringe. The syringe was calibrated in µl and gave a direct volume reading. Lawton and Richards (1970) showed that the Gilson apparatus gives comparable results to the cartesian diver, Warburg and Winkler methods of measuring respiratory rates of aquatic invertebrates. Many authors, for example, Heiman and Knight (1975); Adcock (1975), Dussart and Kay (1980) have shown that the Gilson respirometer is suitable for ecological work in measuring the oxygen uptake in aquatic benthos. It was therefore decided to use the Gilson respirometer to measure the consumption of oxygen by leeches.

5.4 Materials and methods

5.4.1 The Gilson respirometer

The apparatus comprises 20 reaction or respirometer flasks, each linked to a separate manometer which in turn links with a single reference or compensation Fig.18 shows the basic arrangement for a single flask. reaction flask. The reaction flask (14) is connected to a manometer (5) which in turn connects to the reference flask (1). The system is thus isolated from atmospheric changes and is further stabilised both by being maintained at a constant temperature and by all flasks being immersed in a water bath. Any change in the system should be the result of respiration in the reaction flask which will reduce the pressure in the reaction flask side of the manometer. The restoration of the manometer fluid to the original mark is achieved by means of a micrometer screw plunger (6) which is graduated in µl and hence the value of oxygen utilised is measured directly.

5.4.2 Procedure

Animals from Rutland Water were kept in glass aquaria in well aerated reservoir water, and were maintained at the temperature at which respirometry was to be carried out, i.e. 5° , 10° and 15° C for 7 - 14 days. The leeches

FIG.18

Diagram of Gilson differential respirometer to show the arrangement of valves

- 1. Reference flask
- 2. Disconnect valve
- 3. Operational valve
- 4. Index
- 5. Glass manometer
- 6. Micrometer
- 7. Capillary tygon tubing
- 8. Ground glass joint
- 9. Filter paper in centre well
- 10. Water with animal
- 11. 'Seelskrew'
- 12. Gassing manifold inlet
- 13. Water level
- 14. Reaction flask



FIG.18

were separated into groups of individuals, to avoid cannibalism. Small individuals of <u>H</u>. <u>stagnalis</u> have a relatively low respiration rate and in order to obtain reliable estimates, groups of up to four individuals were respired in a single flask; while individual specimens of E. octoculata and G. complanata were used.

5.4.3 Operational procedure for the Gilson respirometer

- 1. The water bath was brought to operating temperature and the reference flask of 270 cm³ was partly filled with 140 cm³ deionised water to leave an air space of 130 cm³ which is equal in volume to the sum of the air spaces of 20 reaction flasks (each 7.5 cm³ flask contained 1 cm³ of water).
- 2. A small piece of filter paper (Whatman No. 1) and two drops of KoH solution (5 gm KoH to 100 gm water) was placed in the central well of each reaction flask.
- 3. One cm³ of filtered fully oxygenated reservoir water was added to each reaction flask.
- Leeches were placed in each reaction flask except those used as controls (see (6) below).
- 5. The joints were treated with a high vacuum grease and the flasks immediately placed on the Gilson apparatus and held in place with two springs.

- 6. Six control flasks were used in each experiment. They were positioned at the four corners of the water bath with a further two in the centre (i.e. flasks 1, 3, 10, 11, 19, 20). Each control flask was set up in the same way as above, except no animal was inserted.
- 7. All flasks were immersed in the water bath. The micrometers attached to the volume control plungers were set at the 100 µl mark to allow for possible negative readings. The index was set at the meniscus in each manometer and the system was allowed to equilibrate for 45 min before it was closed to the atmosphere.
- 8. Readings were taken at 30 min intervals. On each occasion, the meniscus of each of the twenty manometers was returned to the starting point (indicated by the index) by adjusting the volume to equilibrate pressures with the graduated plunger. The volume change was then read from the micrometer on the plunger.
- 9. At the termination of each run, the system was opened to the atmosphere and each animal was removed from the reaction flask, killed in ethanol, placed in a foil pan and dried for 12 hr at 80°C in a vacuum oven at 400 mm Hg pressure. The dry weight was measured to the nearest 0.01 mg on an electromicrobalance.

The respirometer was operated in a constant temperature room to eliminate the effect of temperature oscillations on the manometric system (Carver & Gloyne, 1971). Adcock (1975) noticed that vessels adjacent to the stirrer motor and refrigeration unit at the rear of the apparatus

were subjected to localized heating, and this effect was reduced by fitting an aluminium baffle between the apparatus and the units.

5.5 Oxygen uptake

Throughout the respiration estimation, the leeches in the Gilson were virtually inactive (this was observed by raising the flasks above the surface of the water bath briefly). The rate of oxygen uptake thus reflects the resting rate of oxygen utilisation of the three species. Dry weight measurements have been used throughout the experiments as water content might affect the exact weight of individuals. However, Figs. 19,20 & 21 showed the relationship of live to dry weight is effectively linear over the whole weight range for the three species, and hence the use of dry weights probably increases precision only marginally.

5.5.1 Calculation of oxygen uptake

The mean change in oxygen content in the nearest three control flasks was used to correct the readings for the reaction flasks. Thus controls 1, 3 and 10 were used to correct readings of reaction flasks 2 and 4 - 9 inclusive, while the mean change for flasks 11, 19 and 20 was used to correct readings for the flasks 12 - 18 inclusive. The corrected volumes were then plotted against time and appeared to be linearly related. Consequently a number of data sets

Fig. 19 Relationship between dry weight and live weight of <u>H. stagnalis</u> from Rutland Water. Regression equation: $Y = \frac{0.00124 + x}{4.17712}$ r = 0.99095 n = 173where y = dry weight (mg) x = live weight (mg)



Dry weight(mg)

Fig. 20 Relationship between dry weight and live weight of <u>G. complanata</u> from Rutland Water. Regression equation: $y = \frac{x + 2.39971}{5.79776}$ r = 0.9875

n = 47
where y = dry weight (mg)
x = live weight (mg)



Fig. 21 Relationship between dry weight and live weight of <u>E</u>. <u>octoculata</u> from Rutland Water. Regression equation: $y = \frac{x + 1.03445}{5.58665}$ r = 0.9922n = 82where y = dry weight (mg) x = live weight (mg)



were subjected to linear regression and a high degree of correlation obtained in all cases ($r \ge 0.95$; $r^2 \ge 0.90$). It was therefore concluded that a linear regression analysis would provide an adequate description of all data. The respiration rate (μ l O_2 ind⁻¹ h⁻¹) is then directly available as the regression coefficient. All calculations were performed using a Wang 729 programmable calculator.

5.6 Results

The respiration rate (μ l 0₂ ind⁻¹ h⁻¹) was regressed on the dry weight of the individual, using a log/ log transformation. Strong positive correlations were found in all cases (r > 0.925, P < 0.001) (Table 18, Figs. 22 - 30).

Similar calculations of the relationship between metabolic rate (μ l O₂ mg⁻¹ h⁻¹) and dry weight (log/ log transformed) show a negative correlation at each temperature (Table 19, Figs. 31 - 33) but the percentage variation accounted for by the independent variable (dry weight) is much less (r² = 0.26 - 0.66) than in the regression of respiration rate (r² > 0.82). This weaker correlation is frequently encountered in the literature (Mcfarlane & McLusky, 1972, r² = 0.31 - 0.75, on chironomid larvae; Adcock, 1975, r² = 0.173 - 0.96, on <u>Asellus aquaticus</u>).

Figs. 34 - 36 summarise the values displayed in Figs. 22 - 30 of log respiration rate on log dry weight (and show that, respiration rate increased logarithmically with dry weight, so that the larger animals have the greater oxygen consumption). Metabolic rate conversely declined with increasing size irrespective of temperature (Figs. 31 - 33).

ABLE 18 Regression coef ions (n) and si weight (mg) for ures Species	fficient ignifica r E. oct Temp.	(b), intercept (a) nce of relationship oculata, <u>H</u> . <u>stagnal</u> b [±] SEb	, correlati between re is and <u>G</u> . <u>G</u>	on coeffici espiration r complanata u r	ent (r) ate (µ1 nder th) n	number_l of_pbservat- 02 ind_l h_l) and dry ee different temperat- P
pobdella octoculata	15 10 5	$\begin{array}{c} 0.77664 \stackrel{+}{\pm} 0.0398 \\ 0.64882 \stackrel{+}{\pm} 0.03675 \\ 0.55842 \stackrel{-}{\pm} 0.02176 \end{array}$	0.02848 0.06835 0.034403	0.931536 0.926999 0.963393	60 533 53	P < 0.001 P < 0.001 P < 0.001
lobdella stagnalis	15 10 5	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	0.05027 0.01342 0.01835	0.90876 0.96471 0.98170	64 52 44	P < 0.001 P < 0.001 P < 0.001
ossiphonia complanata	15 10 5	$\begin{array}{c} 0.70343 \stackrel{+}{2} 0.02368 \\ 0.69377 \stackrel{+}{2} 0.02436 \\ 0.63029 \stackrel{+}{2} 0.02076 \end{array}$	0.04024 -0.01330 0.01743	0.97124 0.96996 0.96992	55 60 803	P < 0.001 P < 0.001 P < 0.001

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Figs. 22 Oxygen consumption (μ l O₂ ind⁻¹ h⁻¹) against dry & 23 weight (mg) for <u>E. octoculata</u> from Rutland Water at 5^o and 10^oC. Linear regressions are given in Table 18.





- Fig. 24 Oxygen consumption (μ l O₂ ind⁻¹ h⁻¹) against dry weight (mg) for <u>E</u>. <u>octoculata</u> from Rutland Water at 15^oC. Linear regressions are given in Table 18.
- Fig. 25 Oxygen consumption (μ l O₂ ind⁻¹ h⁻¹) against dry weight (mg) for <u>H</u>. <u>stagnalis</u> from Rutland Water at 5^OC. Linear regressions are given in Table 18.







Figs. 26 Oxygen consumption (µl O_2 ind⁻¹ h⁻¹) against dry & 27 weight (mg) for <u>H</u>. <u>stagnalis</u> from Rutland Water at $10^{\circ}C$ and $15^{\circ}C$. Linear regressions are given in Table 18.



۱°c







Log(d.wt.+1)

Figs. 28 Oxygen consumption (μ l O₂ ind⁻¹ h⁻¹) against dry & 29 weight (mg) for <u>G</u>. <u>complanata</u> from Rutland Water at 5^oC and 10^oC. Linear regressions are given in Table 18.



Fig. 30 Oxygen consumption (μ l O₂ ind⁻¹ h⁻¹) against dry weight (mg) for <u>G</u>. <u>complanata</u> from Rutland Water at 15^oC. Linear regressions are given in Table 18.


Regression coefficient (b), intercept (a), correlation coefficient (r), number of observations (n) and significance of relationship between metabolic rate (μ 1 0₂ mg⁻¹ h⁻¹) and dry weight (mg) for <u>E</u>. <u>octoculata</u>, <u>H</u>. <u>stagnalis</u> and <u>G</u>. complanata under three different temperatures TABLE 19

Fig. 31 Weight specific oxygen consumption $(\mu \mid 0_2 \text{ mg}^{-1} h^{-1})$ as a function of dry weight (mg) for <u>E. octoculata</u> from Rutland Water at three temperatures. Linear regressions for each temperature are given in Table 19.



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Fig. 32 Weight specific oxygen consumption $(\mu \mid O_2 \mid mg^{-1} \mid h^{-1})$ as a function of dry weight (mg) for <u>H. stagnalis</u> from Rutland Water at three temperatures. Linear regressions for each temperature are given in Table 19.



Fig. 33 Weight specific oxygen consumption (µl 0₂ mg⁻¹ h⁻¹) as a function of dry weight (mg) for <u>G. complanata</u> from Rutland Water at three temperatures. Linear regressions for each temperature are given in Table 19.



(1+dejaM)20J

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Fig. 34 Summary of oxygen consumption (µl O_2 ind⁻¹ h⁻¹) as a function of dry weight (mg) for <u>E</u>. <u>octoculata</u> from Rutland Water at three temperature investigated. The linear regressions are given in Table 18, and a summary of the tests for significance are given in Table 22.



(l+dsəy)607

FIG.34

- Fig. 35 Summary of oxygen consumption (µl O_2 ind⁻¹ h⁻¹) as a function of dry weight (mg) for <u>H</u>. <u>stagnalis</u> from Rutland Water at three temperatures investigated. The linear regressions are given in Table 18 and a summary of the tests for significance are given in Table 20.
- Fig. 36 Summary of oxygen consumption (µl O_2 ind⁻¹ h⁻¹) as a function of dry weight (mg) for <u>G</u>. <u>complanata</u> from Rutland Water at three temperatures investigated. The linear regressions are given in Table 18 and a summary of the tests for significance are given in Table 21.



Log(d.wt.+1) ••



In the present study the regression lines of the respiration-weight data for the three temperatures for each of three species were examined by using a covariance analysis (Ostle, 1963) to show if a single line would adequately describe the relationship for each species over all three temperatures (Tables 20 - 22). The following results were obtained:

(I) In all species the three regression lines are not homogeneous (P<0.001).

(II) The regression coefficients differed significantly $(P \lt 0.05)$. Thus no overall equation could be derived.

Hence, for each species the regression equations of the relationship between size and metabolism vary with temperature.

5.6.1 Q_{10} and weight

To examine the response to temperature or the relationship between the respiration rate and temperature, Vant Hoff's equation was used to calculate the temperature coefficient (Q_{10}), the equation is written as:

$$\log Q_{10} = (\log v_1 - \log v_2) \frac{10}{t_1 - t_2}$$

where v_1 and v_2 are the respiration rate at temperature t_1 and t_2 .

The temperature changes were $5^{\circ} - 10^{\circ}$, $10^{\circ} - 15^{\circ}$, and 5° to 15° C, and each weight class used in the

66.

rat rat	significance bodella stagn e (μl 0 ₂ ind	of the rela $1 \frac{1}{h}$ b	fferent tempe	espiratory w ratures. x	eight to dry = dry weight	weight of ir (mg), y = re	idividual spiration
Temperature	DF (n - 1)	$\Sigma(x - \overline{x})^2$	$\Sigma(x-\overline{x})(y-\overline{y})$	$\Sigma(y - \bar{y})^2$		Residuals	
ວ ່					s.s.	DF(n - 2)	М. S.
15	63	1.07450	0.78935	0.70216	0.12227	62	0.00197
10	51	1.33459	0.92149	0.68365	0.04739	50	0.00094
5	43	1.31797	0.71837	0.40628	0.01473	42	0.00035
			sum of res	iduals = S ₁	0.18439	154	0.00119
Within temp	157	3.72706	2.42921	1.79207	0.20878	156	0.00133
		increase	in sum of res	$iduals = S_{j}$, 0.62439	2	0.01219
Between	2	0.05237	0.19028	0.42914 S	0.26221	1	0.26221
Total	159	3.77943	2.61949	2.22123 S ₁	r 0.40569	158	0.00256
Test for	homogeneity	: VR = (S _T -	s1)/4/(s1/15	(4) = 46.49	l5 P <0.001		
Test for	identity of	slopes: VR =	(s ₂ /2)/(s ₁ /1	.54) = 10.243	36 P < 0.001		

rate	(µ1 0 ₂ ind 1	h ⁻¹)					
Tempgrature	DF (n - 1)	$\Sigma(x - \overline{x})^2$	$\Sigma(x-\overline{x})(y-\overline{y})$	$\Sigma(y - \overline{y})^2$		Residuals	
5					s.s.	DF(n - 2)	Μ.S.
15	54	6.27787	4.41605	3.29307	0.18668	53	0.00352
10	52	2.87475	1.99442	1.47067	0.08700	51	0.00170
5	69	2.65402	1.67282	1.12077	0.6639	68	0.00114
			sum of res	iduals = S ₁	0.34007	172	0.00201
Within temp	175	11.80664	8.08329	5.88451	0.35037	174	0.00201
		increase	in sum of res	iduals = S,	, 0.01030	2	0.00515
Between	2	6.23746	5.92857	4.03119 S	, 1.603785	Ч	1.60378
Total	177	18.0441	14.011869	9.91570 S ₁	r 0.96500	176	0.00548

Test for identity of slopes: $VR = (S_2/2)/(S_1/172) = 2.6142 \quad 0.01 < P < 0.05$

Tempgrature	DF(n - 1)	$\Sigma(x - \overline{x})^2$	Σ(x-x)(y-y)	$\Sigma(y - \overline{y})^2$		Residuals	
0					s.s.	DF(n - 2)	Μ.S.
15	59	4.70442	3.65368	3.27007	0.43244	58	0.007455
10	52	5.79922	3.76269	2.84098	0.39969	51	0.007836
5	52	5.88717	3.28754	1.97801	0.14216	51	0.002787
			sum of res	iduals =	S ₁ 0.87429	160	0.006089
Within temp	163	16.39081	10.70391	8.8906	1.09894	162	0.006780
		increase i	n sum of res.	iduals =	S ₂ 0.12465	2	0.062320
Between	2	0.73689	0.427906	1.3538	5 ₃ 1.1053	1	1.105300
Total	165	17.127707	11.131816	9.44286	s _τ 2.20795	164	0.013463

population was expressed as the median dry weight of all specimens in the class and then interpolating this value in the equations relating dry and live weight for the three species (Figs. 19, 20 & 21). The mean respiration rate for each of the weight classes was then calculated from the respiration rate-dry weight regression equations (Tables 18& 19) at each of the experimental temperatures. A selection of these values is presented were treated similarly (Tables 23,24 & 25, Figs. 37-42).

The temperature coefficient Q_{10} was calculated for each species for all size classes and is shown in Tables 26,27 & 28 and indicates that the temperature response for <u>H</u>. <u>stagnalis</u> and <u>G</u>. <u>complanata</u> was almost constant over the range 5° - 15°C being 1.83 - 1.76 and 1.29 - 1.33 respectively. In <u>H</u>. <u>stagnalis</u> an interesting trend in the temperature response appears in Q_{10} values for the lower component of the temperature range 5° to 10°C in comparison to the higher component 10° to 15°C. The Q_{10} values increase with increasing weight while in the higher range the converse occurs. <u>G</u>. <u>complanata</u> shows similar trends, with Q_{10} 5° to 10°C rising from 0.85 - 1.25 with increasing weight and Q_{10} 10° - 15°C decreasing from 1.95 -1.42.

The same results were obtained for the temperature response for the metabolic rate as shown in Tables 26,27 & 28). The result for <u>E</u>. <u>octoculata</u> show greater values of Q_{10} in the large animals and smaller values for the small leeches over all temperature ranges, although this

. 67.

Weight c	lass	Median	Respiration	rate (µ1 0 ₂	== ind ⁻¹ h ⁻¹)	Metabolic	cate (μ1 0 ₂ π	ng ⁻¹ h ⁻¹)
(live wt	(gm	wt (dry wt)	5°C	10°C	15°C	5°C	10 ⁰ C	15°C
1 - 5		0.722	0.466	0.665	0.628	0.619	0.866	0.827
6 - 10	~	1.617	0.863	1.184	1.254	0.546	0.765	0.771
11 - 15		2.512	1.182	1.644	1.832	0.497	0.701	0.733
16 - 20	0	3.407	1.478	2.063	2.378	0.460	0.651	0.704
21 - 25	10	4.586	1 . 828	2.573	3.061	0.423	0.601	0.674
26 - 3C	0	5.197	1.997	2.822	3.402	0.406	0.580	0.662
31 - 35	10	6.092	2.232	3.172	3 . 889	0.386	0.552	0.645
36 - 4C	0	6.987	2.453	3.506	4.361	0.368	0.528	0.631
41 - 45	10	7.882	2.664	3.827	4.822	0.352	0.507	0.618
46 - 50	0	8.777	2.866	4.138	5.273	0 338	0.489	0.606
51 - 55	10	9.672	3.060	4.438	5.715	0.325	0 472	0.596
56 - 60	0	10.563	3.246	4.729	6.146	0.313	0.456	0.586
61 - 65	10	11.462	3.427	5.014	6.574	0.302	0.442	0.578
66 - 70	0	12.357	3.602	5.291	6.993	0.293	0.429	0.569
71 - 75	10	13.252	3.772	5.561	7.406	0.283	0.417	0.562

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dry weight	-1 h ⁻¹)	15°C	1.135	0.968	0.852	0.764	0.693	0.635	0.585	0.543	0.505
.) and median	rate(μ1 0 ₂ mg	10°C	0.801	0.717	0.656	0.609	0.571	0.539	0.512	0.488	0.466
1 0 ₂ mg ⁻ 1 h ⁻ 1 ratures.	Metabolic r	5°C	0.69	0.599	0.533	0.482	0.442	0.408	0.378	0.353	0.330
olic rate (µ three tempe	nd ⁻¹ h ⁻¹)	15°C	0.304	0.662	0.993	1.306	1.604	1.889	2.165	2.433	2.693
h ⁻¹), metab stagnalis at	rate(µl O ₂ i	10°C	0.187	0.491	0.769	1.028	1.274	1.508	1.732	1.949	2.158
(µl O ₂ ind ⁻¹ asses of <u>H</u> .	Respiration	5°C	0.166	0.395	0.597	0.799	0.947	1.103	1.25	1.391	1.524
ation rate 1e weight cl	Median	سر (dry wt)	0.227	0.706	1.185	1.664	2.143	2.622	3.100	3.579	4.058
TABLE 24 Respir of nir	Weight class	(Bill Me Me III)	0.1 - 1.9	2.0 - 3.9	4.0 - 5.9	6.0 - 7.9	8.0 - 9.9	10.0 - 11.9	12.0 - 13.9	14.0 - 15.9	16.0 - 17.9

Weight class	Median	Respiration	rate (µl O ₂	ind ⁻¹ h ⁻¹)	Metabolic 1	rate (µl 0 ₂	mg ⁻¹ h ⁻¹)
live wt mg)	wt (dry wt)	5°C	10°C	15°C	5°C	10°C	15°C
1 - 5	0.931	0.575	0.531	0.742	0.607	0.631	0.940
6 - 10	1.448	0.830	0.805	1.060	0.573	0.601	0.870
11 - 15	2.656	1.356	1.384	1.731	0.516	0.550	0.757
16 - 20	3.518	1.692	1.761	2.17	0.487	0.524	0.700
21 - 25	4.381	2.006	2.117	2.584	0.463	0.503	0.655
26 - 30	5.243	2.302	2.455	2.979	0.443	0.485	0.618
31 - 35	6.106	2.58	2.780	3.358	0.426	0.469	0.586
36 - 40	6.968	2.851	3.093	3.724	0.411	0.456	0.557
41 - 45	7.831	3.108	3.396	4.078	0.397	0.444	0.533
46 - 50	8.693	3.357	3.689	4.422	0.385	0.433	0.511
51 - 55	9.555	3.597	3.974	4.757	0.375	0.423	0.495
56 - 60	10.417	3.831	4.252	5.084	0.365	0.414	0.473
61 - 65	11.280	4.058	4.525	5.403	0.355	0.406	0.457
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Fig. 37 Effect of temperature on mean oxygen consumption $(\mu \mid O_2 \text{ ind}^{-1} \text{ h}^{-1})$ of fifteen size classes of <u>E. octoculata</u> from Rutland Water. Mean oxygen consumption calculated from the regression equations in Table 18. Weight classes (mg live weight) are shown in Table 23.



Fig. 38 Effect of temperature on mean oxygen consumption $(\mu \mid O_2 \text{ ind}^{-1} \text{ h}^{-1})$ of nine size classes of <u>H. stagnalis</u> from Rutland Water. Mean oxygen consumption calculated from the regression equation in Table 18. Weight classes (mg live weight) are shown in Table 24.





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Fig. 39 Effect of temperature on mean oxygen consumption $(\mu \mid O_2 \text{ ind}^{-1} \text{ h}^{-1})$ of fourteen size classes of <u>G. complanata</u> from Rutland Water. Mean oxygen consumption calculated from the regression equation in Table 18. Weight classes (mg live weight) are shown in Table 25.



FIG.39

Fig. 40 Effect of temperature on the metabolic rate $(\mu \mid O_2 \mid mg^{-1} \mid h^{-1})$ of five weight classes of <u>E. octoculata</u> from Rutland Water. Mean specific oxygen consumption calculated from the regression equation in Table 19. Weight class (mg live weight) are shown in Table 23.



Fig. 41 Effect of temperature on the metabolic rate $(\mu \mid O_2 \mid mg^{-1} \mid h^{-1})$ of nine weight classes of <u>H. stagnalis</u> from Rutland Water. Mean specific oxygen consumption calculated from the regression equation in Table 19. Weight class (mg live weight) are shown in Table 24.



Fig. 42 Effect of temperature on the metabolic rate $(\mu \mid O_2 \text{ mg}^{-1} \text{ h}^{-1})$ of five weight classes of <u>G. complanata</u> from Rutland Water. Mean specific oxygen consumption calculated from the regression equations in Table 19. Weight class (mg live weight) are shown in Table 25.

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TABLE 26	Temperature weight class and metaboli	coefficients ((es of <u>E</u> . <u>octocu</u> c rate (μl O ₂ π	l ₁₀) calculated <u>lata</u> using the ng ⁻¹ h ⁻¹) agains	for the two ten regression of 1 t temperature.	nperature ranges respiration rate	for fifteen ($\mu 1 \ 0_2 \ ind^{-1} \ h^{-1}$)	
	5 - 15	5 - 10	10 - 15	5 - 15	5 - 10	10 - 15	
I	1.347	1.806	. 0.891	1.336	1.957	0.911	
11	1.453	1.882	1.125	1.412	1.963	1.015	
III	1.549	1.934	1.241	1.474	1.989	1.093	
IV	1.608	1.948	1.328	1.530	2.002	1.169	
٧	1.674	1.981	1.415	1.593	2.018	1 257	
١٧	1.703	1.996	1.453	1.630	2.040	1.302	
VII	1.742	2.019	1.503	1.670	2.045	1.365	
NIII	1.777	2.042	1.547	1.714	2.058	1.428	
IX	1.81	2.063	1.587	1.755	2.074	1 485	
Х	1.839	2.084	1.623	1.792	2.093	1.535	
XI	1.867	2.103	1.658	1.833	2.109	1.594	
XII	1.893	2.122	1.689	1.872	2.122	1.651	
XIII	1.918	2.140	1.719	1.913	2.142	1.71	
ΧIV	1.941	2.157	1.746	1.941	2.143	1.759	
XV	1.963	2.170	1.773	1.985	2.171	1.816	

	5 - 15	5 - 10	10 - 15	5 - 15	5 - 10	10 - 15
	1.83	1.27	2.64	1.64	1.35	2.01
	1.67	1.54	1.82	1.61	1.43	1.82
	1.66	1.65	1.67	1.60	1.51	1.69
	1.63	1.65	1.61	1.59	1.60	1.57
	1.69	1.81	1.59	1.57	1.67	1.47
	1.71	1.87	1.57	1.55	1.83	1.31
_	1.73	1.92	1.56	1.54	1.91	1.24
11	1.75	1.96	1.55	1.53	1.99	1.17
	1.76	2.01	1.55	1.53	1.99	1.17

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for fourteen	
ire ranges	
culated for three temperatu	three temperatures.
Temperature coefficients ($ m Q_{10}$) calcu	weight classes of <u>G</u> . <u>complanata</u> at t
FABLE 28	

5	15	5 - 10	10 - 15	5 - 15	5 - 10	10 - 15
1.2	29	0 85	1.95	1.55	1.08	2.22
1	27	0.94	1.73	1.52	1.1	2.10
-	2 7	1 04	1.56	1.47	1.13	1.89
1.	28	1.08	1 52	1 44	1 15	1.78
Ι.	28	1.11	1.49	1.41	1.18	1.69
Γ.	29	1.14	1 47	1.40	1 19	1.62
Ι.	30	1.16	1.46	1.38	1.21	1.56
Ξ.	30	1.17	1.45	1.36	1.23	1 49
	31	1.19	1 44	1.34	1.25	1 44
-	31	1.21	1.43	1.33	1.26	1.39
Γ.	32	1.22	1.43	1.32	1.27	1.37
Γ.	32	1.23	1.42	1.30	1.28	1.31
Γ.	33	1.24	1.42	1.29	1.30	1.27
Γ	.33	1.25	1.42	1.27	1.32	1.23

is less marked in the 5° - 10° C range animals and smaller values for the small leeches over all temperature ranges.

Thus for the three species, it can be seen that the large size classes show a greater response to temperature (as measured by Q_{10}) than do the smaller leeches.

5.7 Discussion

Various relationships between respiration rate and body weight have been described in poikilotherms. These include: -

(1) The surface law, basically propounded by Sarrus and Rameaux (1839, cited by Brody, 1945) and later by Bertalanffy (1957). This effectively states that respiration rate is directly proportional to two-thirds the power of **live** weight.

(2) The power function of body weight $0.75 \stackrel{+}{-} 0.015$, this relationship suggested by Hemmingsen (1960) which states that the respiration rate was proportional to the power of 0.75 of the body weight.

Studies of many invertebrates are consistent with Bertalanffy's (1957) respiration coefficient (e.g. Adcock, 1975 for A. <u>aquaticus</u>; Prus, 1977; Halcrow & Boyd, 1967, for <u>Gammarus oceanicus</u> and Cairns, 1978, for <u>Sericesthis</u> <u>nigrolineata</u>). But others are consistent with Hemmingsen's respiration coefficient of 0.75 (e.g. Davies, 1966, for the

68.

gastropods <u>Patella vulgaris</u> and <u>P. aspersa</u>; Rao, 1980, <u>Cellana</u> radiata).

In the present study the relationship between oxygen uptake and dry weight is again linear on a log/log plot but the regression coefficients do not conform to either of the above relationships. The regressions for the three temperatures for each species are significantly different. This is in agreement with the observations of Rao and Bullock (1954) that respiration rate varies with temperature in poikilotherms. This is further supported by Berg and Ockelman (1959) who found that the respiration rate varied seasonally in freshwater <u>Limnaea</u> spp, and by Laybourn and Strachan (1980) who found a similar temperature effect in the benthic marine copepod Cyclops bicuspidatus.

There is currently no explanation for various b-values found among poikilotherms, but Newell (1973) demonstrated that environmental and endogenous factors influenced the rate of respiration and these factors included activity, body size, exposure to air temperature and nutritional level.

Comparison of the rate of oxygen uptake for the three species of leeches with these values obtained by Mann (1956) is difficult as he worked with only one temperature (20° C). However, his results are consistent with the present findings. The regression coefficients for <u>H. stagnalis</u> of 0.81 and <u>G. complanata</u> of 0.715 are similar to those found in the present study at 15°C (cf. Table 18).

69.
The regression coefficient for <u>E</u>. <u>octoculata</u> of 1.06 is much higher than that obtained in this study of 0.776 at 15° C and implies that the oxygen consumption per unit weight was actually lower in the smaller animals. It is possible that the larger leeches were responding to a lower oxygen concentration by ventilatory movements.

There are different views of the relationship between Q_{10} and animal size. The first of these is suggested by Akerlund (1969) in his work on the snail, <u>Marisa</u> <u>cornvariatis</u> is that Q_{10} values are inversely related to body weight, i.e. large animals are less influenced by temperature than small animals. Rao and Bullock (1954) sugggested that Q_{10} values are directly proportional to body weight, in that oxygen consumption commonly increases with increasing weight. They supported their conclusion with data from various sources. The third view is that the Q_{10} of poikilothermic invertebrates is constant with increasing size. This was demonstrated by Pamatmat (1969) in his work on the intertidal bivalve <u>Transella tentilla</u>.

In the present study, <u>E</u>. <u>octoculata</u> shows an increasing Q_{10} with increasing body weight as was reported by Rao et al. (<u>op</u>. <u>cit</u>.) but it is noteworthy that the Q_{10} values for the low temperature range (5^o - 10^oC) are greater in all cases than that for the higher range (10^o - 15^oC).

<u>H. stagnalis</u> and <u>G. complanata</u> have similar patterns of Q_{10} values increasing with size over the temperature range 5^o - 10^oC and decreasing over the range

 $10^{\circ} - 15^{\circ}$ C, although the decrease is very slight over much of the size range. This is in agreement with Heubner (1973) who found that Q_{10} varied inversely with size between 15° and 30° C, but directly with size between 5° and 10° C in the prosobranch <u>Polinices duplicatus</u>. She suggested that large snails are more sensitive to temperature changes in the low range and small animals are more affected when warm.

There is a discrepancy in Q_{10} values for many different species and there is no explanation for the variation of Q_{10} with both temperature and animal size. Huebner (op. cit.) suggested that alteration in isozymes proportions as well as change in animal activity may be responsible for general respiratory response to temperature.

It is difficult at the present time to suggest a mechanism for the different temperature responses of <u>H. stagnalis</u> and <u>G. complanata</u> to that of <u>E. octoculata</u>. It is possible that different physiological mechanisms are involved and a possible factor is the presence of haemoglobin in the Glossiphoniidae which is absent in <u>E. octoculata</u>.

Further research is required on metabolic temperature response of leeches, especially for higher and lower temperatures.

6. FEEDING STUDIES

6.1 INTRODUCTION

Identification of the food that is being eaten by a particular species in a habitat is an essential preliminary to estimating quantitative consumption. This information can be used in a variety of ways, including the construction of an energy budget. In this case

$$C = P + F + FU$$

where C is consumption, P is production, R is respiration and FU is faeces and urine excretion.

Hence, if estimates are made of any three parameters, the fourth can be derived. Using this system, internal checks on the accuracy of the experimental determination of these parameters may be made.

Several methods may be used to identify and measure the food actually consumed (Klekowski & Duncan, 1975). First, food preference experiments may be carried out in the laboratory on animals acclimated to laboratory conditions. In this method, a wide variety of possible foods are presented to the animal over a given time. This method can be used to estimate the amount of food eaten per unit time.

A second method is the analysis of gut contents. This method requires dissection of the gut of the animals and identification of ingested organisms or their remains, identified. However, this method is only satisfactory for those animals that consume their 'prey' whole, such as <u>E. octoculata</u>, but it is not suitable for sanguivores such as <u>G. complanata</u> and <u>H. stagnalis</u>.

A third method is a serological technique which involves the identification of a prey species through antigen anti-sera reactions in a precipitin test, using a serum of a sensitised mammal. This method may be linked by the fact that, unless certain assumptions are made, they cannot be quantified (Southwood, 1978), so the method is less useful for quantitative studies on food consumption, unless it is known that only one individual is normally eaten per period of detectibility (Klekowski & Duncan, 1975).

The feeding studies on leeches, reported in the literature, are divided between these three methods. Food preferences were studied by Young and Ironmonger (1980) in England, for the three species <u>E. octoculata</u>, <u>G. complanata</u> and <u>H. stagnalis</u>, by exposing potential prey organisms to leech attack in dishes, in the laboratory. The prey organisms included 42 taxa, and the experiment ran for 10 days. In the U.S.A., Hilsenhoff (1963) studied predation by <u>H. stagnalis</u> on the larval dipterans <u>Tendipes plumosus</u>, and Cross (1976) studied the predation rate of <u>H. stagnalis</u> and <u>Erpobdella punctata</u> on a mixed population of tubificids. Davies and Everett (1975) in Canada, examined the food of four species, <u>G. complanata</u>, <u>H. stagnalis</u>, <u>Nephelopsis</u> <u>obscura</u> and <u>Erpobdella punctata</u> on a range of 11 prey taxa in a laboratory experiment.

Gut contents were used to study the food preferences of <u>E</u>. <u>octoculata</u> by Elliott (1973b) and Young and Ironmonger (1979) in England.

Serological techniques were used by many authors. In Canada, Davies <u>et al</u>. (1978, 1979) studied predation by <u>N</u>. <u>obscura</u> and <u>H</u>. <u>stagnalis</u>. Worna <u>et al</u>. (1981) examined the preyutilization by <u>G</u>. <u>complanata</u> and <u>H</u>. <u>stagnalis</u>. In England, Young (1980, 1981) determined the food of <u>H</u>. <u>stagnalis</u> and <u>G</u>. <u>complanata</u> in productive and unproductive British lakes. Young (1982) investigated the food niches of the lake-dwelling triclads and the three species, <u>H</u>. <u>stagnalis</u>, <u>G</u>. <u>complanata</u> and <u>E</u>. <u>octoculata</u> in the littoral zone of British lakes of different trophic status.

The leeches are reported in the literature as feeding on a wide variety of prey specimens, e.g. <u>H. stagnalis</u> is widely reported to feed on chironomid larvae (Bennike, 1943; Hilsenhoff, 1963; Moore, 1966; Sapkarev, 1968; Wilkialis, 1970; Lang, 1974; Cross, 1976; Davies <u>et</u> <u>al</u>., 1979; Young, 1980; Young <u>et al</u>., 1980; Worna <u>et al</u>., 1981), together with <u>Asellus aquaticus</u> (Wilkialis, 1970; Lang, 1974; Davies <u>et al</u>., 1979; Young, 1980; Young <u>et al</u>., 1980; Worna <u>et al</u>., 1979; Young, 1980; Young <u>et al</u>., 1980; Worna <u>et al</u>., 1981), and some molluscs (Mathers, 1948; Kleem, 1975; Davies <u>et al</u>., 1979; Young, 1980; Young <u>et al</u>., 1980). A claim by Moore (1912) that it feeds on the blood of fish, frogs and humans, may be discounted.

<u>G. complanata</u> feeds primarily on molluscs (Pawlawski, 1936; Mathers, 1948; Moore, 1964; McCarthy, 1975; Kleem, 1975; Davies, 1975; Young <u>et al.</u>, 1970; Young, 1981; Worna <u>et al.</u>, 1981) and is also reported to feed on chironomid larvae (Mathers, 1948; Williams, 1961; Young <u>et</u> al., 1980; Young, 1981; Worna <u>et al.</u>, <u>op. cit.</u>).

The third species, <u>E</u>. <u>octoculata</u> has been reported to feed extensively on chironomid larvae and oligochaetes (Bennike, 1943; Elliott, 1973b; Green, 1974; Lang, 1974; Aston & Brown, 1975; Young <u>et al.</u>, 1979, 1980, and Young, 1982).

In the present study, two main experiments have been used to determine the food taken by the three species of leeches. First, experiments were designed to evaluate the total range of prey taken by each species. The potential prey were chosen because they are represented the most abundant aquatic macrobenthos found in Rutland Water (Bullock <u>et al.</u>, 1982). Secondly, by knowing the type of prey eaten extensively, estimates were made on a dry weight basis of food eaten by every leech per unit time.

The aims of the present study of feeding were: 1. To determine the quantity of food taken by each size class of the leeches.

2. To determine the effect of day-length and water temperature on feeding.

3. To use the data to compare the energy budgets of the three species of leeches.

6.2 Method

6.2.1 Prey preference experiment

This experiment was designed to establish the range of prey taken by the three leech species on Rutland Water. The leeches, together with their potential prey, comprising <u>A</u>. <u>aquaticus</u>, <u>Gammarus pulex</u>, <u>Lymnaea peregra</u>, <u>Physa heterostropha</u>,Oligochaeta and larvae of chironomidae, were collected from Rutland Water, and transported to the laboratory in buckets filled with reservoir water.

For the experiment, ten containers of 250 cm³ capacity were used for each of the six prey taxa, with the intention of using five for each leech species, and five as controls. Ten individuals of a single prey taxon were placed in each container, together with 150 cm³ of filtered reservoir water. A small stone (4 - 5 cm diameter) was placed at the centre of each container, to provide a resting and sheltering place, and all containers were aerated with air stones from a compressed air supply.

All leeches were starved for 14 days and only medium-sized leeches were selected for the study. Four individuals of <u>H</u>. <u>stagnalis</u> (4 - 6 mg) or <u>E</u>. <u>octoculata</u> (40 - 50 mg) were allocated to each container, but a shortage of <u>G</u>. <u>complanata</u> (40 - 60 mg) necessitated the use of only two individuals of this species.

The containers were maintained at 10° C in a light regime of 12 hr light: 12 hr dark. The containers

were checked daily for three days. On each occasion, the numbers of live prey were recorded and all losses replaced.

After the three days, all remaining prey were removed from the containers, the water changed, and the leeches starved for a further 14 days. The prey taxa were then reintroduced, placing the taxon in each container as on the first occasion.

6.2.2 Results

The result for the two three-day periods have been amalgamated to show the mean mortality in each prey taxon with each predator over a period of six days (Table 29).

The mortality of each taxon in the presence of each predator was compared with the control mortality, using the Mann-Whitney U-test. The tests show a significant departure for the null hypothesis, as follows: -

1. <u>H. stagnalis</u> on Oligochaeta only.

2. G. complanata on Lymnaea peregra only.

3. E. octoculata on Oligochaeta and larval Chironomidae.

6.3 Food consumption rate

This experiment is designed to estimate the weight of food consumed by a leech in unit time and the effect of temperature and light on the consumption rate. <u>H. stagnalis</u> and <u>E. octoculata</u> are both feeding on oligochaetes <u>Tubifex</u> tubifex, while <u>G. complanata</u> feeds on a gastropod, particularly

betv	y preference veen control	experime mortalit	utes, m nts, a y and e	wilcoxc	intal mort	ple test. ality is	given wit	the sign:	stical c ificance	lifference level.
Potential prey	<u></u> 1	<u>I. stagnal</u>	<u>is</u>		บ	<u>complanat</u>	157	ш	<u>octocu</u>]	ata
	Control mortal- ity	Experi- mental mortal- ity	U value	ρı	Experi- mental mortal- ity	U value	<u>с</u> ,	Experi- mental mortal- ity	U value	С.
Oligochaeta (Tubificid)	1.55	4.333*	23	< 0.05	0.833	19	>0.05	13.833	25	<0.05*
Lymnaea peregra	0.666	0.333	17.5	>0.05	2.333	25	< 0.05*	0.666	13	>0.05
<u>Physa hetero-</u> stropha	0.333	0.166	17.5	>0.05	0.333	12.5	> 0.05	0.5	15	> 0.05
<u>Asellus</u> aquaticus	0.833	0.666	14.5	>0.05	1.0	14.5	> 0.05	0.666	14.5	> 0.05
Gammarus pulex	0.5	0.5	13.5	>0.05	0.5	13.5	> 0.05	0.833	16.5	>0.05
Chironomidae	2.166	2.83	17.0	> 0.05	2 . 5	17.0	> 0.05	12.833	25	< 0.05*

★significant at 5%

<u>L</u>. <u>peregra</u> (Section 6.2), so those taxa were used as the test foods, although the first two species are known to have a much wider dietary range.

The leeches were collected from the reservoir with their food organisms and kept in constant temperature rooms at 5° , 10° and 15° C with an adequate supply of food for a minimum of two weeks. For H. stagnalis and E. octoculata, five size categories were selected, while four size categories were used for G. complanata, each category was fed at each of the three test temperatures (5°, 10° and 15° C) and replicated four times. The number of E. octoculata was varied to allow for possible variations in voracity (see Table 31). In the light of experience with this species, it was decided that such variation was unnecessary and the remaining two species were treated with a constant number of individuals, four per replicate, regardless of size. The experiment was conducted in 250 cm³ glass vessels (as in the previous experiment), containing 125 cm³ of filtered reservoir water and a pebble (4 - 5 cm diameter) to provide attachment and cover for the leeches. Thirty control vessels for each species were half filled with filtered reservoir water and ten were held at each of the experimental temperatures.

The oligochaetes were weighed alive after being blotted dry by laying them on filter paper for one minute. They were then placed in each experimental container (approximately 45 mg dry weight for <u>H</u>. <u>stagnalis</u> and 75 mg dry weight for <u>E</u>. <u>octoculata</u>), and similar weights of prey were added to the control containers. For <u>G</u>. <u>complanata</u>,

six <u>L</u>. <u>peregra</u>, each of 150 - 170 mg live weight (= c 20 mg dry weight of soft tissue), were placed in each vessel.

The relation between dry weight and fresh weight in the oligochaete was established using 36 samples of <u>T</u>. <u>tubifex</u>. Each sample was blotted dry and weighed on a Mettler H30 balance. The samples were then dried overnight in a vacuum oven at 80° C and 400 mm Hg pressure. The samples were then cooled and weighed on an electromicrobalance. The regression of dry weight on fresh weight gave the relation dry weight (mg) = 13.5774 + 0.1132 fresh weight (mg) (r = 0.99726, P<0.001), Fig. 43.

The relation between live weight (including shell) and the dry weight of soft tissues in <u>L</u>. <u>peregra</u> was established similarly. Snails were weighed, after blotting dry on filter paper. They were then killed by immersion in boiling water for several minutes, the soft tissues were removed with forceps and dried in the vacuum oven. After cooling, the tissues were reweighed and a sample linear regression calculated. This gave dry weight (mg) = 4.73998 + 0.09848 ***** fresh weight (mg). (r = 0.759; n = 34, P<0.001). Fig. 44.

The experiment was run twice for each species of leeches for every temperature for three days, using two different light-dark regimes; one with a 16 hr : 8 hr lightdark cycle, and the second with 8 hr : 16 hr light-dark cycle to detect any effect of light regime on food consumption. The illumination was provided by 80 watt fluorescent light strips fixed on the top of the cabinet. A red dull light of 40 watt was used during dark. Periods of illumination

Fig. 43 Relationship between dry weight and live weight of Tubificidae from Rutland Water. Regression equation: Y = 13.5174 + 0.1132X r = 0.997 n = 36 where Y = dry weight (mg) X = live weight (mg)



Fig. 44 Relationship between dry weight of soft tissues of snails (mg) and live weight of snails (mg) of <u>Lymnaea peregra</u> from Rutland Water. Regression equation: Y = 4.73998 + 0.09848X where Y = dry weight of soft tissues (mg) X = live weight of snail (mg)

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were controlled by a time switch.

The experiment was inspected at least once a day. When the food supply had been virtually exhausted, more food of known weight was added. Any replicate in which a leech died was terminated immediately and restarted with new leeches and food.

At the end of the experiment the remaining food in the experimental and control vessels was blotted dry (as above) and dry weights measured.

6.3.1 Calculations

All weights of food organisms were converted to dry weight using the regression equations cited earlier. Since the controls had shown an overall reduction in weight this was used to calculate an expected weight of prey organisms at the end of the experiment using simple proportions, i.e.

$$\frac{\hat{w}_{pe}}{w_{pb}} = \frac{w_{ce}}{w_{cb}}$$

where W = dry weight, p = prey, c = control, b = beginning of experiment and <math>e = end.

Hence, the expected final dry weight (\hat{W}_{pe})

is $W_{pb} \neq W_{ce}/W_{cb}$ The weight of prey consumed is $W_p = \hat{W}_{pe} - W_{pe}$

6.3.2 Results

The results are summarised in Tables 30 - 32 and are presented more fully in Appendix B. The data suggest that the total food uptake was linearly related to the size of the leech in each species. This relation was examined by regression analyses of total food uptake on estimated dry weight (mg) of the leeches (Tables 30 - 32).

6.3.3 Food consumption and day length

The effect of light on feeding in the present study was tested for <u>H</u>. <u>stagnalis</u> and <u>E</u>. <u>octoculata</u> at three temperatures using a special analysis (Ostle, 1963), to show if a single line would be adequately described the relationship for each species. No analysis was made for <u>G</u>. <u>complanata</u> because the observed number of prey consumed under both light regimes were identical in each size class at both 10° C and 15° C, while there was no feeding at 5° C (Appendix B).

The analysis of the results are given in Tables 33 and 34 and the test includes the following: -

I. Homogeneity: - This tests the hypothesis that an overall equation may adequately represent the relation between the two variables in both light regimes.

II. Identity of the slopes: - This tests the hypothesis that the slopes of the regression lines are identical.

The result of the tests were as follows: A. In <u>H</u>. <u>stagnalis</u> at 5° C the regression lines are not homogeneous(P<0.01) and thus cannot be represented by a single regression equation. The slopes of the line were not significantly different.

Temp-	Weight class	Median	Mean food consumption mg/ind/day with SE	Correlatio	n coefficient	Y = a + bx
c1 a r n1 c	(8m)	METGUL	16hr light 8hr light	l6hr light	8hr light	
5°C	2 - 2.5	2.25	0.032 [±] 0.01 0.093 [±] 0.018	0.7614	0.7426	Y = 0.013655 + 0.01753x (16hr
	3 - 5	4	$0.093 \pm 0.025 0.144 \pm 0.026$			light)
	6.5 - 7.5	7	0.127 ± 0.012 0.190 ± 0.009			
	8.5 - 9.5	6	0.170 ± 0.019 0.201 ± 0.026			Y = 0.07045 + 0.01561x (8hr)
	10 - 12	11	0.210 ± 0.048 0.24 ± 0.03			10:00.
10°C	2 - 2.5	2.25	0.127 ± 0.03 0.12 ± 0.02			
	3 - 5	4	0.236 ± 0.027 0.215 ± 0.01			
	6.5 - 7.5	7	0.287 ± 0.012 0.278 ± 0.013	0.804	0.941	Y = 0.101734 + 0.023348x
	8.5 - 9.5	6	$0.29 \pm 0.007 0.39 \pm 0.017$			r = 0.87463
	10 - 12	11	0.323 ± 0.021 0.375 ± 0.009			
15°C	2 - 2.5	2.25	0.209 ± 0.036 0.175 ± 0.019			
	3 - 5	4	$0.292 \pm 0.34 0.283 \pm 0.03$			
	6.5 - 7.5	7	$0.32 \pm 0.010 0.304 \pm 0.033$	0.744	0.794	Y = 0.111489 + 0.033415x
	8.5 - 9.5	6	0.352 ± 0.012 0.343 ± 0.005			r = 0.77435
	10 - 12	11	0.548 ± 0.08 0.532 ± 0.07			

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TABLE 30 Linear regression equation derived for the food consumption of the leech <u>H</u>. <u>stagnalis</u> under two light regimes at

emp-	Weight class	Median Weicht -	Mean food c mg/ind/da	onsumption y	Correlation	coefficient	,4 + 11 >
	(no. of leeches)	127811C	l6 hr light	8hr light	l6hr light	8hr light	
5°C	2 - 10 (10)	ور	0.11 ± 0.015	0.108 ± 0.028			
	15 - 20 (5)	17.5	0.261± 0.076	0.182 ± 0.036			
	30 - 40 (5)	35	0.342 [±] 0.014	0.317 ± 0.024	0.586	0.465	Y = 0.1574 + 0.0042x
	50 - 60 (5)	55	0.451 [±] 0.068	0.781 ± 0.040			r = 0.519
	70 - 80 (3)	75	0.276 [±] 0.056	0.33 ± 0.061			
0°C	2 - 10 (10)	9	0.243 [±] 0.026	0.24 ± 0.05			
	15 - 20 (5)	17.5	0.253± 0.076	0.255 ± 0.051	0.829	0.840	Y = 0.2091 + 0.00693x
	30 - 40 (5)	55	0.545 [±] 0.051	0.535 ± 0.024			
	50 - 60 (5)	35	0.657 0.003	0.665 ± 0.058			r = 0.835
	70 - 80 (3)	75	0.665 [±] 0.053	0.642 ± 0.047			
5°C	2 - 10 (10)	9	0.323± 0.028	0.31 ± 0.044	·		
	15 - 20 (5)	17.5	0.404 [±] 0.008	0.3 ± 0.067			
	30 - 40 (5)	35	0.611 [±] 0.055	0.585 ± 0.051	0.910	0.660	Y = 0.2852 + 0.0068x
	50 - 60 (5)	55	0.698± 0.06	0.734 ± 0.074			
			-	J			

esh weight of Dry weight ech used (mg) tissues of (mg 12.5 20.004 22.5 20.74 45 21.72 65 22.71 12.5 22.71 12.5 20.004 12.5 20.74 45 22.5 20.74 45 20.74 65 21.72	of soft Mean number of snail Dry weight consumed snail consumed per leech per leech per day) per day (mg)	0.041 0.82	0.041 0.85	0.041 0.89	0.041 0.931	0.67 1.34	0.087 1.80	0.108 2.34	0.108 2.45
	esh weight of Dry wei ech used (mg) tissues	12.5 20.	22.5 20.	45 21.	65 22.	12.5 20.	22.5 20.	45 21.	65 21.

Summary of the amount of food consumed by G. complanata in Rutland Water. TABLE 32

Summary of sum of squures and products and relevant tests described in the text to test the significance of the relationship of food consumption at two different light regimes TABLE 33

ortups ortup $(1, 2)$ <th< th=""><th>output $(1, 0)$ $(1, \infty)$ $(1, \infty)$</th><th></th><th></th><th></th><th>7,2</th><th></th><th>۲ ,</th><th>Re</th><th>iduals</th><th></th></th<>	output $(1, 0)$ $(1, \infty)$				7,2		۲ ,	Re	iduals																																																																																																																																																																																												
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36 0.0002Sum of residuals $S_2 = 0.000495$ 7 1 0.0003 <tr co<="" td=""><td>Test for homogenity : VR = 4.153 (P < 0.01) Test for identity of slopes : VR = 0.365 N.S (P > 0.05) Test for identity of slopes : VR = 0.365 N.S (P > 0.05) Test for identity of slopes : VR = 0.06733 18 0.001 Vithin 19 203.8 4.0225 0.16712 0.0190 18 0.001 Within 39 4.07.6 9.5167 0.28982 0.067228 37 0.001 Test for homogenity : VR = 1.601 N.S (P > 0.05) Test for homogenity : VR = 1.601 N.S (P > 0.05) Test for homogenity : VR = 1.601 N.S (P > 0.05) Test for identity of slopes: VR = 2.84 N.S Nithin 19 203.8 6.5153 0.37575 0.16746 18 0.000 Within 39 4.07.6 13.3444 0.73796 0.13337 18 0.000 Within 39 4.07.6 13.3444 0.73796 0.30107 37 0.000 Within 39 4.07.6 13.3444 0.73796 0.30107 37 0.000 Within 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Test for homogenity : VR = 0.171 N.S (P > 0.65) Test for homogenity : VR = 0.171 N.S (P > 0.05)</td><td></td><td>Total</td><td>39</td><td>407.6</td><td>6.7558</td><td>0 21756 S₇</td><td>r = 0.10558</td><td>38</td><td>0.00277</td></tr> <tr><td>Test for identity of slopes : VR = 0.365 N.S (P>0.05) Test for identity of slopes : VR = 0.00190 18 0.00105 8h light 19 203.8 4.0225 0.16712 0.0190 18 0.00103 Sum of residuals $S_1 = 0.0623$ 35 0.00103 Within 38 407.6 9.5167 0.28982 0.067228 37 0.00492 Total 39 407.6 9.5167 0.29004 $S_T = 0.06728$ 37 0.00178 Total 39 407.6 9.5167 0.29004 $S_T = 0.06784$ 38 0.00178 Total 19 203.8 6.5153 0.29764 $S_T = 0.06784$ 38 0.0075 Test for homogenity : VR = 1.601 N.S (P> 0.05) Test for identity of slopes: VR = 2.84 N.S Total 19 203.8 6.5153 0.37575 0.16746 18 0.0093 8h light 19 203.8 6.5153 0.37575 0.16746 18 0.0093 Within 38 407.6 13.3444 0.73796 0.13337 18 0.00032 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Test for identity of slopes : VR = 0.0228 N.S (P > 0.05)</td><td></td><td></td><td></td><td></td><td>Sum of</td><td>residuals S_l</td><td>= 0.30083</td><td>36</td><td>0.00835</td></tr> <tr><td>Increase in sum of residuals S2 = 0.00024 1 0.00024 Total 39 407.6 13.3444 0.74059 ST 38 0.00799 Test for homogenity : VR = 0.171 N.S (P > 0 05)</td><td>Increase in sum of residuals $S_2 = 0.00024$10.000Total39407.613.34440.74059$S_T = 0.3037$380.007Test for homogenity : VR = 0.171N.S(P > 0.05)Test for identity of slopes : VR = 0.0228N.S(P > 0.05)</td><td>U</td><td>groups</td><td>38</td><td>407.6</td><td>13.3444</td><td>0.73796</td><td>0.30107</td><td>37</td><td>0.00813</td></tr> <tr><td>Total 39 407.6 13.3444 0.74059 $S_{T} = 0.3037$ 38 0.00799 Test for homogenity : VR = 0.171 N.S (P > 0.05)</td><td>Total 39 407.6 13.3444 0.74059 S_T = 0.3037 38 0.007 Test for homogenity : VR = 0.171 N.S (P > 0 05) Test for identity of slopes : VR = 0.0228 N.S (P > 0.05)</td><td></td><td></td><td></td><td>Increas</td><td>e in sum of</td><td>residuals S₂</td><td>= 0.00024</td><td>1</td><td>0.00024</td></tr> <tr><td>Test for homogenity : $VR = 0.171 N.S (P > 0.05)$</td><td>Test for homogenity : VR = 0.171 N.S (P.> 0 05) Test for identity of slopes : VR = 0.0228 N.S (P>0.05)</td><td></td><td>Total</td><td>39</td><td>407.6</td><td>13.3444</td><td>0.74059 S_T</td><td>= 0.3037</td><td>38</td><td>0.00799</td></tr> <tr><td></td><td>Test for identity of slopes : VR = 0.0228 N.S ($P > 0.05$)</td><td></td><td></td><td>Test</td><td>for homogen</td><td>ity : VR = 0</td><td>.171 N.S (P</td><td>0 05)</td><td></td><td></td></tr>	Test for homogenity : VR = 4.153 (P < 0.01) Test for identity of slopes : VR = 0.365 N.S (P > 0.05) Test for identity of slopes : VR = 0.365 N.S (P > 0.05) Test for identity of slopes : VR = 0.06733 18 0.001 Vithin 19 203.8 4.0225 0.16712 0.0190 18 0.001 Within 39 4.07.6 9.5167 0.28982 0.067228 37 0.001 Test for homogenity : VR = 1.601 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light$19$$203.8$$6.8291$$0.36221$$0.13337$$18$$0.0076$$Within$$38$$407.6$$13.3444$$0.73796$$0.30107$$37$$0.008$$Total$$39$$407.6$$13.3444$$0.73796$$0.30107$$37$$0.00024$$1$$0.00024$$Total$$39$$407.6$$13.3444$$0.74059$$S_7$$0.00024$$1$$0.00024$$1$$0.00$</math></t<>	Bh light19203.85.49420.167120.0190180.001 $Vithin$ Sum of residuals S_1 0.0623 360<001		16h light	19	203.8	4.0225	0.1227	0.0433	18	0.0024	Sum of residuals $S_1 = 0.0623$ 360.00173within38 407.6 9.5167 0.28982 0.067228 37 0.00182 Total39 407.6 9.5167 0.28982 0.06492 1 0.00492 Total39 407.6 9.5167 0.29004 $S_T = 0.06784$ 38 0.00178 Total39 407.6 9.5167 0.29004 $S_T = 0.06784$ 38 0.00178 Test for homogenityVR = 1.601 N.S (P> 0.0536 1 0.00492 1 0.00492 Test for homogenityVR = 1.601 N.S (P> 0.0536 1 0.00742 1 0.00742 Test for identity of slopes:VR = 2.84 N.S 16766 18 0.0074 Test for identity of slopes:VR = 2.84 N.S 0.16746 18 0.0074 Within 19 203.8 6.5153 0.37575 0.16746 18 0.0074 Within 19 203.8 6.8291 0.36221 0.13337 18 0.0074 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S</td> <td></td> <td></td>	16h light.19203.86.51530.375750.16746180.0098h light19203.86 82910.362210.13337180.0008h light19203.86 82910.362210.13337180.0008h light19203.86 82910.362210.13337180.0088h light19203.86 82910.362210.13337180.008WithinSum of residuals $S_1 = 0.30083$ 360.008Increase in sum of residuals $S_2 = 0.30083$ 370.008Total39407.613.34440.74059 $S_T = 0.30024$ 10.0007Total39407.613.34440.74059 $S_T = 0.3037$ 380.007Test for homogenity : VR = 0.171 N.S (P > 0 05)Test for identity of slopes : VR = 0.0228 N.S (P > 0.05)			Test	for identit	y of slopes:	VR = 2.84 h	4 . 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Test for homogenity : VR = 4.153 (P < 0.01) Test for identity of slopes : VR = 0.365 N.S (P > 0.05) Test for identity of slopes : VR = 0.365 N.S (P > 0.05) Test for identity of slopes : VR = 0.06733 18 0.001 Vithin 19 203.8 4.0225 0.16712 0.0190 18 0.001 Within 39 4.07.6 9.5167 0.28982 0.067228 37 0.001 Test for homogenity : VR = 1.601 N.S (P > 0.05) Test for homogenity : VR = 1.601 N.S (P > 0.05) Test for homogenity : VR = 1.601 N.S (P > 0.05) Test for identity of slopes: VR = 2.84 N.S Nithin 19 203.8 6.5153 0.37575 0.16746 18 0.000 Within 39 4.07.6 13.3444 0.73796 0.13337 18 0.000 Within 39 4.07.6 13.3444 0.73796 0.30107 37 0.000 Within 39 4.07.6 13.3444 0.73796 0.30107 37 0.000 Within 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Total 39 4.07.6 13.3444 0.74059 Sr = 0.00024 1 0.000 Test for homogenity : VR = 0.171 N.S (P > 0.65) Test for homogenity : VR = 0.171 N.S (P > 0.05)		Total	39	407.6	6.7558	0 21756 S ₇	r = 0.10558	38	0.00277																																																																																																																																																																																												
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At 10° and 15° C, the regression for the two regimes was homogeneous and the slopes of the lines were not significantly different (P>0.05), thus an overall equation may be used to represent the two lighting regimes at each temperature.

B. The analysis for \underline{E} . <u>octoculata</u> (Table 34) shows that the regression lines were homogeneous and the slopes of the lines were not significantly different, thus an overall equation of food on live weight for these animals can be described by a single equation at each temperature.

6.3.4 Food consumption and temperature

The mean consumption rates for each of these size classes for the three species were calculated from the regression equations at each temperature (Tables 30, 31 & 32). Thus a linear regression equation was calculated for each for consumption rate against temperature. This relationship for each temperature for each species is adequately described by a straight line and are given in Table 35.

The results showed clearly that the individual food consumption shows a positive, linear correlation with temperature change, with consumption rates increased from 5° to 15° C.

The consumption rates of the three species were compared on the basis of consumption rate per one mg body weight at three temperatures and it seems clear that \underline{G} . <u>complanata</u> consumes more than the other two species.

Summary of sum of squares and products and relevant tests described in the text to test the significance of the relationship of food consumption at two different light regimes for \underline{E} . <u>octoculata</u> at three temperatures. TABLE 34

Groups	DF(n-1)	7/2-212	5/2-21/1-1	5/2	Re	siduals	
	DF (II - 1)	(x x) 7	(-) (x-x)-	(1-4)- (SS	DF(n-2)	M.S.
16h light	19	12443.2	71.38300	1.19162	0.78212	18	0.04345
8 h light	19	12443.2	33.58082	0.41799	0.32736	18	0.01818
			Sum of	residuals S ₁	= 1.10948	36	0.03081
Within groups	38	24886.4	104.96382	1.60961	1.16690	37	0.03153
		Increase	in sum of	residuals S ₂	= 0.05742	1	0.05742
Between groups	1	0	0.01508	0.03115 5.	0	C	C
Total	39	24886.4	104.9789	1.64076 S.	r = 1.19792	38	0.03152
	Test	for homogeni	ty: VR = (S	T-S1)/2/S1/3	6 0 1.4352 N.	S (P>0.05)	
	Test	for identity	of slopes	= 1.863 N.S	(P > 0.05)		
16h light	19	12443.2	87.4785	0.89409	0.2791	18	0.0155
8h light	19	12443.2	85.0221	0.82198	0.24104	18	0.01339
			Sum of	residuals S ₁	= 0.52014	36	0.01444
Within groups	38	24886.4	172.5006	1.71607	0,52037	37	0.01406
Bottoon		Increase	in sum of	residuals S ₂	= 0.00023	1	0.00023
groups	1	0		°.3	0 =	0	0
Total	39	24886.4	172.5006	· 1.71631 S.	r= 0.52061	38	0.0137
	Test	for homogeni	ty: VR = [(S _T -S _{1/2})](S ₁ ,	(36)] = 1.627	4 N.S (P>0	.05)
	Test	for identity	of slopes	: VR = (S _{2/1}	$/s_{1}/36 = 1.5$	927 N.S (P>	. 0.05)
l6h light	19	12443.2	89.3913	0.77029	0.1281	18	0.00711
8h light	19	12443.2	80.4962	1.16549	0.6447	18	0.03581
			Sum of	residuals S ₁	= 0.7728	36	0.02146
Within groups	38	24886.4	169.8875	1.93578	0.77603	37	0.02097
		Increase	in sum of	residuals S ₂	= 0.00323	1	0.00323
Between groups	1	0		ŝ	0 =	0	0
Total	39	24886.4	169.8875	1.96665 S.	r= 0.8069	38	0.02123
	Test	for homogeni	ty: VR = (S	T-S1)/2/S1/30	6 = 0.7945 N.	S (P 0.05)	
	Test	for identity	of slopes	$VR = (S_2/1)/3$	$s_1/36 = 0.150$	5 N.S (P 0.	.05)

TABLE 35 Linear the th consum	regression equations derive ree temperatures investigate ed, X mg live weight of leec	d for the food consumption d in Rutland Water. Y = mg h.	of the three species under dry weight of food
Species	5°C	10 ⁰ C	15 ⁰ C
	Linear regression equation	Linear regression equation	Linear regression equation
<u>H</u> . <u>stagnalis</u>	Y = 0.07045 + 0.01561X	Y = 0.102 + 0.0223X	Y = 0.1188 + 0.02376X
l mg weight consumed	0°086 mg	0.124 mg	0.142 mg
G. complanata	I	$\dot{\mathbf{Y}} = 0.7985 + 0.00204\mathbf{X}$	Y = 1.2309 + 0.0207X
l mg weight consumed		0.800	1.2516
E. octoculata	Y = 0.1574 + 0.00421X	Y = 0.2091 + 0.00693X	Y = 0.2852 + 0.0068
l mg weight consumed	0.162	0.216	0.293

6.4 Faeces production

The faeces of the leeches could not be distinguished from those of <u>Tubifex</u> <u>tubifex</u> and <u>Lymnaea</u> <u>peregra</u> in the feeding experiment. For these experiments, leeches were classified according to size. For <u>H</u>. <u>stagnalis</u>, four size classes were used, with 30 individuals per replicate for the first two size classes and 20 individuals for the third and fourth size classes. Three size classes were used for <u>G</u>. <u>complanata</u> with 10 individuals per replicate and five size classes in <u>E</u>. <u>octoculata</u> with 20 individuals in the smaller size class and 10 individuals for the <u>four</u> largest size classes (see Table 36). Each size class of each species was tested at 5^o, 10^o and 15^oC except that the 5^{o} C temperature was omitted for <u>G</u>. <u>complanata</u> since it had already been demonstrated that this species does not feed at this temperature. Each combination was replicated four times.

The leeches were placed in 125 cm³ of autoclaved reservoir water with a generous supply of food. After 24 hr, the leeches were transferred to a clean container in 100 cm³ of sterile filtered reservoir water. After a further 24 hr, the leeches were removed, blotted dry and weighed. The water was filtered through a preweighed fine glass fibre filter (Whatman type GF/A) which retains particles down to 1 μ m in diameter. The filter papers were dried overnight in a vacuum oven at 80°C and 400 mm Hg pressure. The papers were cooled in a desiccator and reweighed. The difference

in weight was taken to be the faecal output (dry weight). 6.4.1 Results

The faecal production of the three species are summarised in Tables 36, 37 and 38 as dry weight 24 hr^{-1} ind⁻¹, together with linear regression equations of faecal production on live weight. Only in the case of <u>H</u>. <u>stagnalis</u> is there a consistent correlation between weight of leeches and quantity of faeces. In other cases, although there is a general upward trend in faecal production with increasing weight, the variation was such that the regression equations were either non significant or only just attaining significance (P = 0.05). Consequently in order to relate faeces production to food consumption, the regression equation in Table 35 was used to calculate expected food consumption in each replicate and these were used to estimate the apparent percentage assimilation. The mean percentage assimilation was then calculated for each temperature and shows little variation.

Examination of the data indicates that the quantity of faeces generally increased with temperature, although variation tends to obscure this, and this is compensated by the increased consumption rate with increasing temperature. Consequently the apparent percentage assimilation remains effectively constant.

It is not surprising to find the faeces production in sanguivorous species is low, particularly since only solid material was measured and no measurement was made of any soluble egesta. It would, however, be expected that

TABLE 36 Faecal production (mg ind⁻¹) in 24 hr for <u>E. octoculata</u> at three temperatures, with expected consumption (calculated from Table 35) and apparent assimilation

Group		50	C			10	0°C			15	°C	
D 7 1 0	Mean wt of leech (mg)	Faeces prod- uced (mg)	Food con- sumed (mg)	Apparent % assimil- ation	Mean wt of leech (mg)	Faeces prod- uced (mg)	Food con- sumed (mg)	Apparent % assimil- ation	Mean wt of leech (mg)	Faeces prod- uced (mg)	Food con- sumed (mg)	Apparent % assimil- ation
20	8.04 7.986 9.95 9.135	0.012 0.006 0.009 0.008	0.192 0.191 0.199 0.199 0.195	96 96 96	9.415 7.515 7.625 8.85	0.008 0.021 0.009 0.012	0.274 0.261 0.262 0.27	97 92 95	9.01 8.51 9.92 9.07	0.0075 0.042 0.012 0.006	0.346 0.343 0.353 0.347	97 87 96
10	23.4 22.4 22.8 29.56	0.009 0.000 0.012 0.031	$\begin{array}{c} 0.256 \\ 0.252 \\ 0.253 \\ 0.282 \end{array}$	96 100 89	29.39 22.27 28.01 24.44	0.035 0.016 0.028 0.014	0.413 0.363 0.403 0.378	91 93 96	23.5 28.07 21.22 27.73	0.029 0.061 0.009 0.015	$0.4581 \\ 0.476 \\ 0.429 \\ 0.474 \\ 0.4$	93 87 98
10	35.05 36.08 38.74 38.24	0.025 0.00 0.032 0.009	0.305 0.309 0.320 0.318	91 100 90 97	33.64 35.59 37.92 38.40	0.009 0.031 0.033	0.442 0.455 0.472 0.475	98 93 96	39.06 34.08 38.06 37.07	0.052 0.035 0.008 0.012	$0.551 \\ 0.517 \\ 0.544 \\ 0.542 \\ 0.54$	90 93 97
10	55.09 54.08 51.94 53.05	0.022 0.002 0.027 0.005	$\begin{array}{c} 0.389\\ 0.385\\ 0.376\\ 0.381\\ 0.381 \end{array}$	94 98 98	54.03 54.07 58.77 56.75	0.041 0.032 0.041 0.00	0.583 0.583 0.616 0.602	93 94 93 100	51.55 55.09 57.80 55.55	0.03 0.06 0.007 0.014	0.636 0.659 0.678 0.663	95 99 97
10	76.67 77.76 79.9 72.7	0.034 0.00 0.026 0.031	0.480 0.485 0.493 0.463 7	92 100 94 93 93	73.81 76.05 77.21 71.05	0.021 0.038 0.045 0.011	0.721 0.736 0.744 0.701 ×	97 94 94 98 94.6	78.7 74.05 74.30 74.3	0.095 0.0121 0.005 0.011	0.821 0.789 0.791 0.79	88 98 98 98
Linear Dî faec veight	regression es on live	Y = 0.0 r = 0.4 0.05 < P	006 + 0.0 149 < 0.1	002×		Y = 0.0 r = 0.4 0.01 < F	0129 + 0. 4531 5 ≤0.05	0003×		Y = 0.0 r = 0.1 N.S.)18 + 0.0 1898	002×

	1	0 ⁰ C			1500		
Mean Weight (mg)	Faeces produced (mg)	consumed (mg)	% Apparent assimilation	Meight (mg)	Faeces produced (mg)	Food consumed (mg)	% Apparent assimilation
12.06	0.09	0.823	89	11.0	0.11	1.458	92
14.5	0.105	0.828	87	13.1	0 095	1.502	93
14.4	0.008	0.827	66	12 1	0 105	1.481	92
13.0	0.07	0.825	66	13.9	0.08	1.518	94
33	0.11	0.865	87	32	0 12	1.893	93
38	0.095	0.876	89	35.5	0.096	1.961	95
35.4	0.085	0.869	06	31	0.11	1.871	64
37.7	0.095	0.875	89	39	0.21	2.038	89
66.1	0.12	0.933	87	60.9	0.11	4.492	9.5
67.7	0.045	0.9366	95	69.7	0.13	2.674	95
65.4	0.105	0.932	88	63.8	0.04	2.552	98
6.5.9	0.11	0.933	88	66.7	0.09	2.612	96
			$\tilde{x} = 90$				$\tilde{x} = 93.8$

TABLE 37 Faecal production (mg ind⁻¹) in 24 hours for <u>G</u>. complanata at two temperatures with expected consumption

elgnt ces on Linear regression of faece Y = 0 0224 + 0.0025 r = 0.5318 0.05<P<0.1

Y = 0.111 + 0.00008xr = -0.0465N.S. TABLE 38 Faecal production (mg ind⁻¹) in 24 hr for <u>H. stagnalis</u> at three temperatures, with expected consumption (calculated from Table 35) and apparent percentage assimilation

Group			5°C			10	0°C			150	c	
SIZE	Mean wt of leech (mg)	Faeces prod- uced (mg)	Food con- sumed (mg)	Apparent % assimil- ion	Mean wt of leech (mg)	Faeces prod- uced (mg)	Food con- sumed (mg)	Apparent % assimil- ion	Mean wt of leech (mg)	Faeces prod- uced (mg)	Food con- sumed (mg)	Apparent % assimil- ion
30	3.17 3.63 4.39 4.06	0.006 0.003 0.0023 0.0023	0.1199 0.1271 0.1389 0.132	95 97 97 100	2.21 2.34 2.516 2.67	0.005 0.004 0.003 0.003	0.151 0.154 0.158 0.158 0.162	96 96 97	2.22 2.36 2.74 2.78	0.005 0.003 0.003 0.007	0 172 0 173 0.184 0.185	97 98 96
30	4.4 4.8 4.08 4.08	0.005 0.0027 0.0033 0.002	0.1391 0.1454 0.1346 0.1346	96 98 98	4.06 4.85 4.34	0.007 0.005 0.0035 0.0035	0.1925 0.210 0.1988 0.1968	96 97 97	4.33 4.01 4.18 4.8	0.01 0.03 0.0087 0.003	0.2217 0.214 0.2181 0.232	95 96 86
20	7.42 7.22 7.85 7.56	0 004 0.0063 0.0075 0.0045	0.1862 0.1831 0.193 0.1885	96 96 97	7.51 7.55 7.41 7.2	0.0125 0.0086 0.005 0.005	0.2695 0.2704 0.267 0.2626	95 96 95	7.1 7.76 7.58 7.58	0.013 0.016 0.005 0.008	$\begin{array}{c} 0.287\\ 0.303\\ 0.305\\ 0.2989\end{array}$	95 94 97
	10.02 10.96 10.57 11.00	0.006 0.0045 0.004 0.0065	0.2769 0.2415 0.2354 0.242	97 = 97	10.96 10.64 11.0 11.935	0.012 0.0075 0.0053 0.011	0.2444 0.3393 0.3473 0.3682 ×	95 97 98 = 96.5	$10.51 \\ 10.63 \\ 10.69 \\ 10.95$	0.02 0.0105 0.0125 0.008	$\begin{array}{c} 0.3685\\ 0.3714\\ 0.3792\\ 0.2602\\ \overline{x}\end{array}$	94 97 96
Linear of faec weight	regressic es on liv	Y = 0.01).006 + 0).4149 <p <0.05<="" td=""><td>.002×</td><td></td><td>Y = 0. r = 0. 0.05 <</td><td>00254 + 0 6504 P < 0.01</td><td>.0006×</td><td></td><td>Y = 0. r = 0. 0.0014</td><td>0027 + 0 6325 < P < 0.01</td><td>.00095×</td></p>	.002×		Y = 0. r = 0. 0.05 <	00254 + 0 6504 P < 0.01	.0006×		Y = 0. r = 0. 0.0014	0027 + 0 6325 < P < 0.01	.00095×
r = cor	relation											

correlation coefficient a macrophage like <u>E</u>. <u>octoculata</u> would produce a greater quantity of faeces.

Generally predators are considered as having high absorption efficiencies. Thus Macfadyen (1967) discussed three major trophic groups of animals and concluded that carnivores (predators) are characterised by a high absorption efficiency while, on the other hand, herbivores have an intermediate level and detritivores have the lowest efficiency.

No authors appear to have made any attempt to measure faecal production and hence no data are available for comparison. P. Calow (pers. comm.) has recommended a value for percentage assimilation greater than 90%.

6.6 Discussion

The first step in a feeding study is to determine the prey taxa selected by a predator. The six groups of prey organisms selected in the present study represent the most abundant food organisms available to the three species of leeches in Rutland Water and include the main food items attributed to these species in the literature. The prey preference trial revealed that <u>H. stagnalis</u> fed extensively on <u>Tubifex tubifex</u>; this agrees with various authors (Davies & Everett, 1975; Young <u>et al</u>., 1980, 1981; Wrona <u>et al</u>., 1981) who reported heavy predation on oligochaetes.

Although Young <u>et al</u>. (op. cit.) and Wrona (op. cit.) also recorded a broader dietary range including gastropods, isopods and chrionomid larvae, none of these was taken in the present experiment. <u>G. complanata</u> fed extensively on <u>L. peregra</u> but on neither oligochaetes nor chironomid larvae contrary to the results by Davies and Everett (op. cit.) and Young <u>et al</u>. (op. cit.). <u>E. octoculata</u> preyed only on oligochaetes and chironomid larvae. It did not take either <u>Asellus aquaticus or Gammarus pulex</u>, although both have been reported as prey (Young <u>et al</u>., op. cit.).

The more restricted diets found in this experiment, reported by the authors cited above, is not readily explained. Wrona (op. cit.) used a serological technique on field collected specimens and Y.T. Daoud (pers. comm.) has confirmed that both <u>H</u>. <u>stagnalis</u> and <u>E</u>. <u>octoculata</u> take <u>Asellus</u> spp. in Rutland Water. Young <u>et al</u>. (op. cit.) used a similar technique to that used in this study. There is one difference, however, in that in my study, the leeches were maintained for at least one week: <u>T. tubifex</u> (both <u>H. stagnalis</u> and <u>E. octoculata</u>) or <u>L. peregra</u> (<u>G. complanata</u>), this may have resulted in habituation to a single food type.

There is no explanation why the leeches select some prey and ignore others. Wrona <u>et al</u>. (op. cit.) concluded that the preferential selection for prey exhibited by the leeches may be due to prey differences in palatability or quality as a food source or to differences in the leeches' ability to capture the prey. One factor not included which

affects the selection of prey by predators in both the field and laboratory is the preys' activity. Thus all authors are in agreement that oligochaetes, chironomid larvae and gastropods are the most common food for the leeches and all these prey taxa are very sluggish and hence are easily captured.

There are many factors affecting the rate of food consumption by invertebrates, such as temperature, availability of food and the physiological state of the individual (Petrusewicz <u>et al.</u>, op. cit.). For the leeches the day-length and water temperature are claimed to be most important factors, causing variability in food consumption. Thus Young (1980, 1981) reported the lowest food consumption during the winter months in all three species and Wrona <u>et</u> <u>al</u>. (op. cit.) confirmed that consumption activity was at a minimum in winter months. Both authors reported an abundance of prey in the winter months. Hilsenhoff (1963) showed that the predation rate of <u>H</u>. <u>stagnalis</u> on <u>Tendipes plumosus</u> was minimal at 4^oC and increased to a maximum at 25^oC. Similarly, in the present study the consumption rate increased from 5^oC to $15^{\circ}C$.

Elliott (1973b) claimed that day length was the causative factor governing the feeding activity in <u>E. octoculata</u> rather than water temperature. He inferred that, although leeches were active in periods of darkness, 12 hr of day light was necessary to promote this activity. The data he presents are, however, readily explained in terms of leech inactivity in response to decreased water temperature.

Further, Greene (1974) reported a slightly more active consumption by <u>E</u>. <u>octoculata</u> at lower light intensities, but the difference was not statistically significant. This is substantiated in the present study, where food consumption was strongly correlated with temperature but unaffected by day length.

It is therefore concluded that the leeches are to some degree restricted in their diet and hence will be affected by the availability of prey. Further, a major environmental factor controlling feeding rate is that of water temperature.

7. ENERGY BUDGET OF THE THREE SPECIES

7.1 Introduction

The population dynamics of field populations of the three species, <u>H</u>. <u>stagnalis</u>, <u>G</u>. <u>complanata</u> and <u>E</u>. <u>octoculata</u> have been described earlier (Chapter 4). The respiratory metabolism, feeding preference and quantitative feeding biology were studied in the laboratory (Chapters 5 & 6). These approaches can be combined to estimate the energy budget of each species. It is necessary to convert all items in the energy budget to units of energy.

7.1.2 Energy equivalents

The energy content of the three species and of their food were determined using a commercial version of Phillipson's (1964) ballistic microbomb calorimeter and the procedure described by Phillipson was followed with two modifications. First, no water was introduced into the bomb so that there was a dry atmosphere, and secondly the bomb, after pressurising, was checked for leaks by immersion in a beaker of water to a point below the teflon junction. This procedure also cooled the bomb after pressurisation.

Material for calorific determination was dried in a vacuum oven at 80° C for 24 hrs. These were ground to a fine powder and compacted into pellets of 10 - 30 mg dry weight. These materials were stored in a desiccator over silica gel overnight. On the following day,

the pellet was placed on a preweighed platinum foil pan and weighed on an electromicrobalance $(\stackrel{+}{-} 0.001 \text{ mg})$ to give the weight of pellet by difference. The pan and pellet were placed on the pan support of the calorimeter and a 4 cm length of 0.1 mm diameter platinum wire was attached to the firing electrodes and bent to bring it contact with the pellet. The calorimeter was sealed, charged with oxygen to a pressure of 28 bars, and cooled and checked for leaks by immersion in water.

The bomb was seated on a brass ring containing eight thermocouples and the whole apparatus was insulated by an inner metal and an outer polystyrene jacket. After the temperature had equilibrated, the pellet was ignited by passing a current through the platinum wire. The corresponding temperature rise of the exterior of the bomb was detected by the thermocouples and this produced a deflection on a chart recorder. This was measured to the nearest 0.5 mm, and since the deflection is proportional to the calorific value of the pellet, this was easily calculated. Any ash remaining on the foil pan was weighed again so that the result could be expressed on an ash-free dry weight basis.

The bomb was calibrated using standard thermochemical benzoic acid with a known calorific value of 26.3584 joules mg^{-1} . A total of six pellets were fired in which the calorific equivalent of each millimetre of deflection was calculated as calibration factor mean = 12.705 \pm 0.072 J mm⁻¹.

7.1.3 Results

The calorific values of the three species of leeches were determined by sorting each into two size classes (Table 39). Five determinations for each size class of each species were made and they are presented in Table 39. Application of simple t-tests revealed no significant difference between the two size classes in any species. These results are similar to those of Calow and Woolhead (1977) when they reported only minor differences in energy content between newly hatched and larger freshwater triclads. A one-way analysis of variance indicated a significant difference between species ($F_{2,27} = 3.555$, 0.01 < P < 0.05) and a subsequent multiple range test revealed that <u>H</u>. <u>stagnalis</u> had a significantly higher mean value than did <u>E</u>. <u>octoculata</u> (P < 0.05).

The only available data to compare with these results are those of Prus (1970) who obtained values of 22.784 J mg⁻¹ dry weight for <u>Dina microstoma</u>. This lies within the range of the result cited here.

The calorific values of two major food items, Tubificidae and Lymnaea peregra, were determined in an identical manner. L. peregra was removed from its shell before vacuum drying, but otherwise the procedure was identical to that followed with the leeches. The mean values (Table 39) are based on six (Tubificidae) and seven (L. peregra) determinations.
Mean energy equivalents of materials used in the individual energy budget of the leeches TABLE 39

Sample		J mg ⁻¹ dry wt.	J mg ⁻ l ash-free dry wt.	ц
<u>G. complanata</u> small leeches large leeches		21.509 ± 0.573 20.802 \pm 0.363 t = 1.042	23.621 ± 0.287 24.397 \pm 0.696 t = 1.031	ហហ
<u>H. stagnalis</u> small leeches large leeches		22.163 $\frac{1}{2}$ 0.684 21.913 $\frac{1}{2}$ 0.583 t = 0.278	24.040 ± 0.735 25.561 ± 0.664	ហហ
E. <u>octoculata</u> small leeches large leeches		21.425 ± 0.623 21.07 ± 0.443 t = 0.464	23.387 $\frac{1}{2}$ 0.589 22.966 $\frac{1}{2}$ 0.468 t = 0.559	ഗവ
L. <u>peregra</u> Oligochaetes		16.488 ± 0.229 19.569 ± 0.453	19.392 ± 0.522 21.334 ± 0.522	7 6
	G. complanata	H. stagnalis	E. octoculata	
	24.009	24.800	23.177	

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7.2 Population respiratory metabolism

The energy which is assimilated can either be incorporated into the individual as tissue for growth or reproduction or to utilise in performing work. The work necessary for maintenance of the individual is usually measured by estimating oxygen consumption.

The total respiration of the leech populations were estimated in the following manner:

 The numbers of leeches of each size class on each sampling occasion and the mean dry weight of individuals in each class had been estimated (Chapter 5).

2) The mean temperature of the reservoir water in each month was estimated as the mean of the 2 - 4 readings recorded by the Anglian Water Authority (<u>vide</u> Fig. 3).

3) The appropriate respiration equation was chosen as being that for the temperature closest to the lake temperature for each occasion.

4) The total daily respiration (R) on each occasion was then estimated as $\sum_{i=1}^{N} n_i$ antilog $[a + b (\log w_i)]$ where n_i is the number of individuals of mean weight, w_i , in size class i (i = 1 to N) and (a + bw) is the appropriate respiration equation.

5) The total respiration between two sampling occasions, t, and t_2 is then $(t_2 - t_1) (R_{t_1} + R_{t_2})/2$.

The total respiration for each month was summed to give the annual respiration of the whole population (Tables 40, 41 & 42). The oxygen consumption for the whole population for one year was then converted to Kilo Joules (kJ) yr^{-1} , using an oxycalorific coefficient of 20.19745 (Ivlev, 1934; 1 ml 0, corresponds to 4.825 cal = 20.19745 J).

Table 40 demonstrates clearly that a high peak of oxygen consumption occurred in June/July of the first year and August/September of the second year, for the population of <u>H. stagnalis</u> and declined during winter, from December - April in each year, which was 8.38 kJ yr⁻¹ with 6.82 kJ yr⁻¹ in the second year.

In <u>E</u>. <u>octoculata</u> the consumption of oxygen was at a maximum in June for both years and the minimum consumption occurred from December - March in each year (Table 41). The annual respiratory loss was again higher in the first year (8.05 kJ) than in the second year (7.531 kJ).

The annual respiratory loss for <u>G</u>. <u>complanata</u> was 13.02 kJ, and the high peak of respiration loss was recorded in September. Again it is at a minimum throughout the winter season (Table 42), from November - February.

The low respiratory loss during the winter season for all three species partly reflects the low population biomass as well as the low water temperature, while the high peak of respiratory loss in the summer is a result of increased temperature and the presence of large individuals in great numbers, hence the respiration rate of

)le (t ₂)	$\frac{1}{1000} (t_2 - t_1) (R_{t_2} + R_{t_1}) R_{t_1} (\mu_1 \circ_2)$	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	15 42 (2729.088 + 844.728) 75650.136 10 28 (844.728 + 341.214) 16603.188 5 28 (341.214 + 136.41) 6686.736 6686.736 65696.736 65696.736	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	365 337912.78
Second sample (t ₂)	a Date Tempgrature	19/10/77 28/11/77 14/1/78 21/2/78 31/3/78 31/3/78 17/4/78 19/6/78 19/6/78 15 25/7/78 15 15 15 15 15 15 15 15 15 15 15 15 15	24/10/78 15 21/11/78 10 19/12/78 5	22/5/79 24/4/79 22/5/79 18/6/79 23/7/79 20/8/79 15 15 15 15 15	978/79
st sample (t ₁)	Temperature C	7 77 8888888 155 155 155 155 155 155 155 155	8 78 15 78 10	80000000000000000000000000000000000000	Total Year 2 19

TABLE 40 Calculation of annual respiration of <u>H</u>. <u>stagnalis</u> in Rutland Water

ר UNYCALOFILIC EQUI

Oxygen consumed per total leeches per year = 8.381 kJ 1977 - 1978 = 6.824 kJ 1978 - 1979 = Ξ = = Ξ = =

Calculation of annual respiration of \underline{E} . <u>octoculata</u> in Rutland Water TABLE 41 •

First si	ample (t ₁)	Second	sample (t ₂)			
Date	Tempe ratu o _C	ire Date	Temperature ^O C	$(t_2 - t_1)$	(^{Rt} 2 - ^{Rt} 1)	K (JAT 02)
13/9/77	15	19/10/77	15	37	(337.756 + 430.521)	14213.124
19/10/77	15	28/11/77	15	40	(430.521 + 692.861)	22467.64
28/11/77	10	14/1/78	ഹ	47	(692.861 + 226.131)	21596.312
14/1/78	Ŋ	21/2/78	Ŋ	38	(226.131 + 177.046)	7660.363
21/2/18	ſ	31/3/78	ŝ	38	(177.046 + 442.586)	11773.008
31/3/78) ሆ	17/4/78) ሆ	17	(442,586 + 1281,439)	14654 212
7/4/78	ու	17/5/78	10	30.	(1281.439 + 1594.276)	43135.725
31/5/1C		10/6/78	ן ר זי		(1594.276 + 3415.672)	87664_147
19/6/78	י קר סיר	25/7/78	15	36	(3415.672 + 1703.659)	92147.958
	י ת ק ק	21/8/1C) ער דר	27	(1703.659 + 2073.472)	
01 /1 /C2	ר אר הייר	12/9/78	15	22	(2073.472 + 1247.739)	36532.496
) 1) 			
	Year l l	.977/78		365		965.821865
06/0/01	36	87/01/20	15	42	(1247.739 + 1274.867)	52975.23
		01/11/10		30	(1274 863 + 577 962)	25932.94
01 /01 /82			р ц Н	0 C	(577 A67 1 755 061)	18667 077
8//TT/T2	21	19/12/10	חנ			10001 • 166 1000 × 1
19/12/78	പ	22/2/19	ŋ	00	(7%C*000 + TO6*CC/)	
22/2/79	ഹ	14/3/79	'n	20	(300.542 + 338.681)	6392.23
14/3/79	ъ	24/4/79	۵	41	(338.681 + 710.693)	21510.732
24/4/79	Ś	22/5/79	10	28	(710.693 + 1468.893)	30514.708
22/5/79	10	18/6/79	15	27	(1468.893 + 1945.544)	46094.899
18/6/79	15	23/7/79	15	35	(1945.544 + 831.272)	48594.28
6L/L/20	15	20/8/79	15	28	(831.272 + 2114.493)	41240.71
20/8/79	15	12/9/79	15	23	(2114.493 + 1934.238)	46560.406
	[[]]			365		323000 03
	Year 2 I	61 /81 6		COr		372902.92
	Oxycalori	fic equivalen	t = 20.19745 j			

Oxygen consumed per total leeches for first year = 8.05 kJ 1977 - 1978 = 7.53 kJ 1978 - 1979

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	(² 0 IN) X	11298.71 116958.66 93893.533 48566.28 81875.32 28478.91 57559.54 47862.69 57559.54 82676.353 37589.04 644902.9
	$x_{t_2} + x_{t_1}$	(1417.083 + 5039.015) (5039.015 + 3315.175) (3315.175 + 2207.974) (2207.974 + 1141.425) (1141.425 + 855.534) (1141.425 + 855.534) (855.534 + 2704.330) (270.330 + 1110.056) (1110.056 + 1624.955) (1624.955 + 2638.715) (2638.715 + 11712.672) (11712.672 + 1876.237)
(+ +)	, ⁻² - ⁻ 1,	35 34 34 34 35 35 35 36 36 36 36 36 36 36 36 36 36 36 36 36
sample (t ₂)	Tempgrature	115 10000000000000000000000000000000000
Second	Date	6/9/78 4/10/78 7/11/78 6/12/78 26/2/79 3/4/79 8/5/79 8/5/79 12/7/79 2/8/79
sample (t ₁)	Tempgrature	117 10000000000000000000000000000000000
First :	Date	2/8/78 6/9/78 4/10/78 7/11/78 6/12/79 26/2/79 3/4/79 8/5/79 4/6/79 12/7/79

Calculation of annual respiration of G. complanata in Rutland Water

TABLE 42

Oxycalorific equivalent = 20.19745 J

Oxygen consumed per total leeches per year = 13025 kJ 1978 - 1979

the leech population increased and fluctuated widely with temperature changes.

7.3 Annual food consumption and faeces production

Calculations of annual food consumption and faeces production are based on daily estimates using the field data for the numbers of leeches of each size class on each sampling occasion, and the mean dry weight of individuals in each class. The consumption of T. tubifex by H. stagnalis and E. octoculata and L. peregra by G. complanata were estimated using the equations in Table 35 which represent the food consumed by the leech at three temperature 5° , 10° and 15°C, these equations were chosen as being that for the temperature closest to the reservoir temperature for each occasion. The total food consumption and faeces production between two sampling occasions was estimated in a way similar to that of annual respiratory metabolism. The total energy consumed and faeces produced are presented in Tables 43, 44 and 45. The difference in annual population consumption between the two years for <u>H. stagnalis</u> and <u>E. octoculata</u> is reflected in the difference of population structure between them, thus in year one despite the lower density, the population was dominated by individuals which had a higher biomass.

The faeces production has the same pattern, its' production was highest in the first year and lowest in the second year.

	$A = P + R$ $P = 52.52 - 8.381$ $P = 44.144 \text{ kJ } \text{yr}^{-1}$ where A = assimilation R = respiration P = production	$P = 45.104 - 6.824$ $P = 38.279 \text{ kJ } \text{yr}^{-1}$
μ ¹ 02 consumed	38913.34 34110.97 6374.23 9457.53 6667.55 18493.8 48703.87 83954.48 65598.95 55714.351 414942.11 = 8.381 kJ	75050.136 16603.188 6686.736 6659.51 1528.366 7350.797 4871.09 10943.18 39985.61 72925.81 95308.42 $337912.78 = 6.824 kJ$
ng) Faeces produced (mg)	7.338 9.766 7.949 1.598 2.038 3.600 9.107 13.203 13.203 10.825 83.537	17.002 2.915 1.572 1.614 0.348 0.78 1.422 6.015 7.60 12.378 15.135 66.782
Pood consumed (n	244.607 325.54 53.276 53.276 53.276 53.276 53.276 53.276 120.015 303.581 542.772 542.772 360.855 2767.656	566.737 97.16 52.416 53.787 11.61 25.994 47.404 200.508 253.418 412.608 504.528 504.528
Date	(13.9-19.10) 77 (19.10-28.11) 77 (28.11-14.1) 78 (14.1-21.2) 78 (21.2-31.3) 78 (31.3-17.4) 78 (17.4-17.5) 78 (17.5-19.6) 78 (19.6-25.7) 78 (19.6-25.7) 78 (25.7-31.8) 78 (21.8-12.9) 73 Total 365	(12.9-24 10) 78 (24.10-21.11) 78 (21.11-19.12) 78 (19.12-22.2) 78 (12.2-14.3) 79 (22.5-14.3) 79 (24.4-22.5) 79 (22.5-18.6) 79 (22.5-18.6) 79 (23.7-20.8) 79 (20.8-12.9) 79 (20.8-12.9) 79 (20.8-12.9) 79

TABLE 43 Energy balance for <u>H</u>. stagnalis

ate	Food consumed	(mg) Faeces produced (mg)	μ^{1} 02 consumed	
-19.10) 7	7 84.786	4.239	14213.124	A = P + R
0-28.11)7	7 121.86	6.093	22440.0	
1-14.1) 7	8 127.629	6.381	21596.312	P = 35.836 - 8.05
-21.2) 7	8 58.691	2.934	7660.363	
-31.3) 7	91.504	4.575	11773.008	$P = 27.835 \text{ kJ } \text{yr}^{-1}$
-17.4) 7	8 93.798	4.69	14654.212	ı
-17.5) 7	8 248.025	12.40	43135.725	where A = assimilation
-19.6) 7	8 377.306	18.867	82664.142	R = respiration
-25.7) 7	376.488	18.824	92147.958	P = production
-21.8) 7	198.815	9.94	50990.256	
-12.9) 7	8 151.426	7.571	36532.496	
tal 36	5 1930.328	96.512	398728.596 = 8.05 kJ	
-24.10) 7	8 238.896	11.945	52975.23	A = P + R
0-21.11)7	8 120.876	6.044	25932.94	
1-19.12)7	101.57	5.079	18667.922	P = 35.102 - 7.53
2-22.2) 7	9 209.365	10.468	34336.347	
- 14 2) 7	9 48.5	2.425	6392.23	P = 27.572
-24.4) 7	9 140.015	7.001	21510.732	
-22.5) 7	9 191.226	9.561	30513.751	
-13.6) 7	9 248.603	12.43	46094.899	
-23.7) 7	9 225.243	11.262	48594.28	
-20.3) 7	9 173.586	8.679	41324.71	
-12.9) 7	9 190.291	. 9.515	46560.406	
tal 36	5 1888.171	94.409	372902.92 = 7.53 kJ	

TABLE 44 Energy balance for \underline{E} . octoculata

				_
Date	.Food consumed (mg)	.Faeces produced (mg)	μ102 consumed	1
(2.8-6.9) 78	1359.61	108.77	11298.71	A ★ P + R
(6.9-4.10) 78	1321.39	105.71	116958.66	
(4.10-7.11)78	856.596	68.528	93893.53	P = 104.561 - 13.025
(7.11-6.12)78			48566.28	
(6.12-26.2)79			81875.32	P = 91.536 kJ yr ⁻¹
(26.2-14.3)79			28478.91	where A = assimilation
(14.3-3.4) 79			38143.86	R = respiration
(3.4-8.5) 79	670.76	53.661	47862.69	P = production
(8.5-4.6) 79	1322.93	105.83	57559.54	
(9.6-12.7) 79	800.21	64.017	82676.353	
(12.7-2.8) 79	561.645	44.93	37589.04	ł
Total 365	6893.141	551.446	644902.9 = 13.0	25 kJ

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TABLE 45 Energy balance for G. complanate

7.4 Calculation of production

In the absence of information on population production, the component of energy budget is considered here as follows:

The total energy assimilated (A) is estimated directly as the food consumed minus the faeces produced. The assimilation is then converted to the joules equivalent, after using the conversion of the Lymnaea food for <u>G. complanata</u> 16.488 J mg⁻¹ and 19.569 J mg⁻¹ for <u>H. stagnalis</u> and <u>E. octoculata</u>. The total annual respiration of <u>H. stagnalis</u> population for the two years were 8.381, 6.824 kJ and the total annual respiration for <u>E. octoculata</u> for the two years 8.05, 7.53 kJ. The total population respiration for <u>G. complanata</u> was 13.025 kJ. Similarly, the the total population assimilation for the three species for the two years was calculated as 52.535, 46.053, 35.885, 35.1 and 104.561 kJ for the whole population.

Thus,

$$\dot{A}_p = P_p + R_p$$

where A_p : population assimilation in the field
 $P_p = A_p - R_p$

The population production is presented in Tables 43 - 45 for the 3 species which was based on the estimation of total respiration with the total assimilation, the population production for <u>H. stagnalis</u>, <u>E. octoculata</u> and <u>G. complanata</u> were 44.154, 38.279, 27.835, 27.571 and 91.536kJ for the whole population.

8. GENERAL DISCUSSION

Three dominant predatory leeches were studied in Rutland Water over two years. This study was concentrated on distribution and abundance, and population biomass and structure, together with estimates of respiration, food consumption and faeces production to calculate energy budgets. From these data, estimates of production were obtained for each species. Ideally, such estimates can be compared with estimates of production obtained directly from field data (Engelmann, 1966), but the low numbers of leeches obtained in samples make such estimates unrealistic.

The problem in population estimates is that the use of a grab sampler did not take into consideration the tendency of leeches to hide beneath stones. The problem was overcome by using hand collecting in the littoral zone in the second year to study quantitatively the population ecology of both <u>E. octoculata</u> and <u>G. complanata</u>.

The leeches were abundant in the summer period particularly after breeding, but the numbers in the grab samples declined greatly in winter. This is doubtless

partly due to mortality but numbers rose again in the spring prior to reproduction, suggesting that the leeches were available for capture during the winter period (cf. Fig. 9). This suggests that the leeches may burrow into the substratum when temperatures are low.

The distributions of the leeches was limited to both the type of substratum and organic content. This resulted in the dam transect, which had a clay substratum, supporting low densities of all three species. The other three transects supported higher densities on a generally mud/detritus substratum. The abundance of the leeches was clearly related to water depth with both <u>H. stagnalis</u> and <u>E. octoculata</u> more abundant in shallow water (≤ 2 m). Nonetheless, the distributions of all species were highly aggregated and this resulted in apparent violent oscillations in <u>E. octoculata</u> which occurred in relatively low numbers.

The life cycle of <u>E</u>. <u>octoculata</u> took two years to complete, as has been reported by Elliott (1973a) although Mann (1955) and Young <u>et al</u>. (1982) reported an annual cycle. The difference in duration may be a result of physico-chemical differences in the water bodies, as has been demonstrated by Aston and Brown (1975).

<u>H. stagnalis</u> has an annual life cycle with extended breeding season as has been reported by Bennike (1943) and Wilkialis (1970). No evidence was found of two generations per year as reported by Mann (1957b), Learner <u>et al.</u> (1982). Again, this difference could be a response to physico-chemical variation.

<u>G. complanata</u> was only sampled effectively for one year. On the basis of this evidence, there is only one generation in a year in Rutland Water. This agrees with the findings of Young <u>et al</u>. (1982) but differs from Mann's (1957a) report of two generations in the year.

Reproduction began in May to June in all three species at a time when the water temperature exceeded 10^oC. It is possible that this is a direct response to temperature, but also may reflect the increased availability of prey at this time.

Respiration rates were measured in the laboratory at three temperatures $(5^{\circ}, 10^{\circ} \text{ and } 15^{\circ}\text{C})$. In all three species, oxygen consumption increased logarithmically with dry weight, and increased with rising temperature. These relationships were used to estimate population respiration rates in the field. This extrapolation is likely to underestimate true respiratory activity, since the leeches were more or less quiescent in the respirometer. Also, there is an element of approximation in applying the equation for the temperature nearest to the known field temperature.

Measurement of food consumption was carried out in the laboratory under three temperatures for different size classes of leeches. The weight of food consumed was measured and linear regression equation of consumption on biomass of leeches were fitted. These equations were then used to estimate consumption in field populations in the same way as that used to estimate the annual respiration

estimates. The energy consumed for <u>H</u>. <u>stagnalis</u> were 54.160 kJ yr^{-1} (1977 - 1978) and 47.477 kJ yr^{-1} (1978 - 1979), for <u>E</u>. <u>octoculata</u> 37.774 kJ yr^{-1} and 36.949 kJ yr^{-1} , and for <u>G</u>. <u>complanata</u> 113.654 kJ yr^{-1} (1978 - 1979). The figure for <u>G</u>. <u>complanata</u>, is certainly overestimated, because the assumption was made that if one snail was killed, the entire mass of soft tissues were consumed. This is untrue, but it was impossible to estimate the amount of food remaining.

Although faecal production was measured in the laboratory and could therefore be applied to the field populations, it was not possible to measure excretory losses which include not only normal nitrogenous excretion but also mucous secretion. This therefore implies an overestimation of production. Also, it is acknowledged that the further subdivision of production into growth and reproduction has not proved feasible in this study.

It follows from the preceding account that with respiration underestimated, consumption probably overestimated and excretion underestimated, the estimates of production are certainly excessive. Nonetheless, they do indicate the order of magnitude of the impact of leeches on benthic organisms which has not been attempted before.

Further research on aspects of the energy flow is necessary. First, the energy input to the population should be studied, especially the quality and availability of food. These measurements must be based on a full understanding of the feeding biology of the animal concerned.

Secondly, the energy balance of the individual animal at different temperatures should be determined to emphasise the effect of temperature on the energy parameters. More detailed work is required on the ecology of the leech population in order to assess the absolute effect of temperature (low and high) on food, respiration and life cycle.

SUMMARY

1. Three species of leeches, <u>Helobdella stagnalis</u>, <u>Erpobdella</u> <u>octoculata</u> and <u>Glossiphonia complanata</u> were studied in Rutland Water. The 1072 grab samples taken over the period of two years showed that <u>H</u>. <u>stagnalis</u> was the most abundant species with densities ranging from 180 m⁻² (in September) to 4 m⁻² (in February), while <u>E</u>. <u>octoculata</u> had densities from 30 m⁻² (in October) to 3 m⁻² (in January). <u>G</u>. <u>complanata</u> was only recorded at very low densities in the grab samples. This species was therefore studied on a stony substratum close to the water edges, where a maximum density of 18 m⁻² was recorded in September which declined to 4 m⁻² in February. The distribution and abundance was related to water depth, while the substratum type also had a considerable effect on their distribution.

2. <u>H. stagnalis</u> and <u>G. complanata</u> completed their life cycle in one year with continuous breeding from June - September. No evidence was found of two generations per year. <u>E. octoculata</u> reached maturity in their second year. The life cycle observed in the present study are compared with those described in previous accounts.

3. Respiration rates were measured at three temperatures, 5° , 10° and 15° C. Log/log linear regressions were calculated for oxygen uptake on dry weight; the regression coefficients were significantly different from each other at each temperature. The mean respiratory metabolism was estimated for the densities described in paragraph one as 7.778 kJ m⁻² yr⁻¹ for E. octoculata and as 7.603 kJ m⁻² yr⁻¹ in <u>H. stagnalis</u>, while <u>G. complanata</u> was 13.025 kJ m⁻² yr⁻¹.

4. Feeding experiments revealed that <u>H</u>. <u>stagnalis</u> fed extensively on <u>Tubifex tubifex</u>, <u>E</u>. <u>octoculata</u> fed extensively on both <u>T</u>. <u>tubifex</u> and chironomid larvae, while <u>G</u>. <u>complanata</u> fed on <u>Lymnaea peregra</u>. The food consumption rate was measured at three temperatures and showed a significant increase at increased temperatures, but no effect of day length was detected. Faeces production was measured and the apparent percentage assimilation were calculated as 97% for <u>H</u>. <u>stagnalis</u>, 95% for <u>E</u>. <u>octoculata</u>, while <u>G</u>. <u>complanata</u> had 92%.

5. The energy equivalents of leeches were measured as follows: 24.8 Jmg^{-1} dry wt of <u>H</u>. <u>stagnalis</u>; 23.177 Jmg^{-1} dry wt of <u>E</u>. <u>octoculata</u> and 24.009 Jmg^{-1} dry wt of <u>G</u>. <u>complanata</u>. The energy equivalent for <u>L</u>. <u>peregra</u> was 16.488 Jmg^{-1} dry wt and 19.569 Jmg^{-1} for <u>T</u>. <u>tubifex</u>. No significant difference between large and small individuals in their energy equivalent was detected. The mean energy consumed by <u>H</u>. <u>stagnalis</u> estimated at 50.818 kJ m⁻² yr⁻¹ and, for <u>E</u>. <u>octoculata</u> at 37.362 kJ m⁻² yr⁻¹ and by <u>G</u>. <u>complanata</u> 113.654 kJ m⁻² yr⁻¹.

Production was estimated from the annual food consumption minus faeces production and annual respiration, and were 41.692 kJ m⁻² yr⁻¹ for <u>H</u>. <u>stagnalis</u>; 27.703 kJ m⁻² yr⁻¹ for <u>E</u>. <u>octoculata</u>, and 91.536 kJ m⁻² yr⁻¹ for <u>G</u>. <u>complanata</u>.

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APPENDIX A

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APPENDIX A. The numbers of <u>G</u>. <u>complanata</u> in each sample from Rutland Water on each sampling occasion between 1977 - 1979

The numbers of <u>H</u>. stagnalis in each sample from Rutland Water on each sampling occasion between 1977 - 1979 APPENDIX A

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The numbers of <u>E</u>. <u>octoculata</u> in each sample from Rutland Water on each sampling occasion between 1977 - 1979 APPENDIX A

APPENDIX B

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APPENDIX 1	

TABLE 1	mg/live w	eight and the r	weight of food	: mg/dry weigh	ıt.				
Weight Class		16hr light	- 8hr dark		° C•	8hr light	- 16hr dark		
(mg)	Food added (mg)	Food remainder	Food loss	Control	Food added (mg)	Food remainder	Food loss	Control	
2-2.5(4) 2-2.5 2-2.5 2-2.5 2-2.5	44.87 45.43 44.71 45.33	41.53 40.93 40.24 40.93	3.34 4.50 4.49 4.38	3.74 4.98 2.91 4.18	44.87 44.53 44.76 44.76	39.97 40.36 40.07 40.87	4.9 4.17 4.57 3.89	3.51 3.05 3.18 3.14	
3-3.5(4) 3-3.5 3-3.5 3-3.5 3-3.5 	44.55 44.19 44.53 45.32	40.79 38.95 40.52 40.11	4.76 5.24 4.01 5.21	- - - - - - - - - - - - - - - - - - -	44.08 44.53 44.76 44.76	39.28 40.13 38.53 39.86	4.8 4.4 5.89 4.9	0.022	
6.5-7(4) 6.5-7 7-7.5 7-7.5	45.77 45.21 44.6 45.04	40.19 40.34 39.39 39.83	5.58 4.87 5.21 5.21	x = 3.6/8	44.76 44.59 44.93 44.93	39.8 39.12 38.87 39.00	4.96 5.47 5.93 5.93	x = 3.261	
8-8.5(4) 8-8.5 9-9.5 9-9.5 -9.5	44.6 44.3 45.1 45.1	40.71 38.31 39.28 39.5	5.89 5.02 5.6		44.34 44.08 44.7 44.7	38.8 37.45 39.34 39.32	5.54 6.63 5.19 38	1	
10-10.5(4) 10-10.5 10-11 11-12	45.77 44.19 44.19 44.19	37.85 38.45 39.48 38.42	7.92 5.74 5.39 5.77		44.87 44.59 44.3 44.3	37.47 38.79 39.13 38.3	7.8 5.8 6.0		

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Weight Class	1s	t 3 days: 16hr	light - 8hr d	lark	10 Č	2nd 3 days: 8hr	light - 16hr darl	×
(mg)	Food added (mg)	Food remainder	Food loss	Control	Food added (mg)	Food remainder	Food loss	Control
2-2.5 2-2.5 2-2.5 2-2.5	44.1 44.3 44.87 44.64	37.96 39.32 40.00 40.24	6.13 4.97 4.46	33.56 3.56 3.67 3.67 2.79	44.94 44.73 44.73 44.61	39.04 39.93 39.93 40.11	4455 9.83 7.83	3.69 3.18 5.56 2.77
3-3.5(4) 3-3.5 4.5-5 4.5-5	44.5 44.48 44.48 44.3 44.3	37.28 37.85 38.69 38.49	7.21 6.63 5.91 5.81	3.51 3.51 3.1 2.69 2.69	44.8 44.3 44.5 44.5	38.29 38.38 38.3 38.3	6.51 5.92 6.4 6.2	3.55 3.14 3.19 4.24 4.24
6.5-7(4) 6.5-7 7-7.5 7-7.5	44.21 44.3 44.6 44.4	36.9 37.6 37.8 37.2	7.31 6.7 6.8 7.2	000 r	44.31 44.25 44.41 44.4	37.4 37.15 37.76 37.0	6.91 7.1 6.65 7.4	
8-8.5(4) 8-8.5 9-9.5 9-9.5	44.32 44.45 44.4 44.5	37.22 37.65 37.3 37.3	7.1 6.8 7.1 7.2		44.35 44.37 44.50 44.50	37.04 36.57 37.96 36.9	7.31 7.8 7.2 7.6	
10-10.5(4) 10-10.5 10-11 10-12	44.87 44.7 44.53 44.54	37.07 38.02 36.83 36.94	7.8 6.68 7.7		44.78 44.40 44.20 44.20	36.88 36.2 36.05 36.05	7.9 8.2 8.15 8.15	

TABLE 3								
Weight Clace		l6hr light	- 8hr dark	15 C		8hr light -	- 16hr dark	
(ge)	Food added (mg)	Food remainder	Food loss	Control	Food added (mg)	Food remainder	Food loss	Control
2-2.5 2-2.5 2-2.5 2-2.5	44 3 44.26 44.6 45.1	38.31 36.31 36.93 38.18	5.99 7.95 7.67 6.92	4.35 4.63 5.27 3.90	44.94 44.3 44.3 44.3	37 8 37.1 37.1 38.1	7.14 7.2 7.09 6.2	4.9 4.2 5.1 5.1
3-3.5(4) 3-3.5 4-4.5 4-4.5	44.51 44.08 44.82 44.30	36.9 36.13 35.48 36.68	7.61 7.95 9.34 7.62		44.87 44.42 44.7 44.6	36.48 37.19 35.6 36.5	8.39 7.23 9.1 8.1	5.1 4.23 4.23 7.23
6.5-7(4) 6.5-7 6.5-7 6.5-7.5	44.87 44.47 44.94 44.99	36.59 35.96 36.73 36.19	8.33 8.51 8.8	- + 10.4 = X	44.3 45 44.78 44.53	35.1 36.1 36.48 37.13	9.2 8.9 7.4	967.4 × -
8-9(4) 8-9. 8-9	44.91 44.8 44.4 44.6	36.41 35.7 35.7 35.5	8.5 9.1 9.1	1	44.76 44.35 44.35 44.71	35.86 35.55 35.25 35.41	8.9 9.1 9.3 1.2	
10-11(4) 10-11 10-11 11-12	44.87 44.93 44.51 44.53	36.15 32.23 31.31 34.23	8.72 12.7 13.2 10.3	I	44.7 44.38 44.76 44.20	33.5 33.48 30.8 30.8	11.2 10.9 9.8 13.4	1

APPENDIX B - Estimation of food consumption for the leech <u>E</u>. <u>octoculata</u> at three different temperatures. The weight of leech in mg live weight and the weight of food in mg dry weight.

Weight class	No. of leeches _		16hr light -	8hr dark	(5 [°] C)		8hr light - 1	6hr dark(5°C)
		Food added	Food remainder	Food loss	Control	Food added	Food remainder	Food loss	Control
2-10 2-10 2-10 2-10	10	77.81 75.77 76.34 76.40	70.21 67.40 67.50 66.66	7.6 8.37 8.84 9.80	6.52 6.41 6.62 6.61	76.00 78.04 78.60 78.26	69.77 72.49 75.77 75.32	6.23 5.55 2.88 2.94	0.56 1.62 1.40
15-20 15-20 15-20 15-20	2	77.24 77.47 76.34 75.89	55.43 67.98 70.38 68.35	10.819.495.967.54	4 4 4 9 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7	77.23 77.23 76.52 76.44	71.7 71.16 73.06 73.23	5.53 6.25 3.46 3.21	2.49 0.25 0.70
30-40 30-40 30-40	Ś	77.24 76.00 75.89 77.33	66.44 65.43 65.18 67.51	$10.8\\10.57\\10.71\\9.82$	$\frac{6.31}{x} = 5.335$	76.9 77.92 76.8 77.3	70.57 71.21 71.7 71.8	6.33 6.71 5.1 5.5	$\tilde{x} = 1.14$
50-60 50-60 50-60	2	77.02 76.23 76.45 77.33	62.01 64.79 65.00 67.12	15.01 11.74 11.45 10.21		77.34 76.91 77.82 77.30	63.24 65.7 64.51 64.48	$14.1 \\ 11.21 \\ 13.31 \\ 12.82 \\ 12.82$	
70-80 70-80 70-80 70-80	e	77.58 77.70 77.38 76.45	71.00 70.20 69.07 67.54	6.58 7.50 8.31 8.91		77.58 78.33 78.26 77.24	72.21 74.87 75.32 72.47	5.29 3.46 2.94 4.77	

Weight class	No. of leeches	16	hr light - 8h	r dark(10	(0 ₀ (8hr	· light - l6hr	dark(10 ⁰	()
		Food added	Food remainder	Food loss	Control	Food added	Food remainder	Food loss	Control
2-10 2-10 2-10 2-10	10	76.56 76.60 77.47 77.7	62.52 58.90 60.57 61.90	14.04 17.70 16.90 15.8	7.7 4.08 4.7 9.17	77.13 78.38 77.56 77.28	65.41 61.34 58.86 64.77	11.72 17.04 18.70 14.51	7.59 7.05 9.14 8.45
L5-20 L5-20 L5-20 L5-20	5	77.47 77.9 78.53 78.72	61.51 66.81 66.23 67.62	15.96 11.09 12.3 11.1	10.98 7.02 9.17 12.11 11.43	77.58 77.41 77.43 77.90	63.59 67.20 65.51 65.58	$13.99 \\ 10.21 \\ 11.92 \\ 12.32 $	6.45 9.22 9.62 7.82 10.39
30-40 30-40 30-40 30-40	Ś	77.5 78.31 78.4 77.26	60.88 59.5 60.98 62.16	$16.62 \\ 18.81 \\ 17.42 \\ 15.1 \\ 15.1$	$x = \frac{11.61}{8.797}$	78.49 78.04 77.51 77.52	63.05 60.81 61.17 61.27	15.44 17.23 16.34 16.25	x = 8.273
50-60 50-60 50-60	Ŋ	77.32 77.4 78.1 77.3	59.01 56 19 60.88 59.38	$18.31 \\ 21.21 \\ 17.22 \\ 17.92 \\ 17.92 \\ \end{array}$		77.52 77.91 77.41 76.51	59.61 57.09 60.21 59.4	$17.91 \\ 20.82 \\ 17.2 \\ 17.11$	
70-80 70-80 70-80 70-80	m	76.79 77.61 77.42 77.51	62.16 61.43 63.3 63.3	$14.63 \\ 16.18 \\ 14.12 \\ 14.21 \\ 14.21$		78 21 77.32 77.41 78.31	64.69 62.11 64.1 64.1	13.52 15.21 13.31 14.2	

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Weight class	No. of leeches	:C	dur Ligne - lo	hr dark(1	ó°с)	1 6 h	ır light - önr	dark(15 ⁰ C)	
		Food added	Food remainder	Food loss	Control	Food added	Food remainder	Food loss	Control
2-10 2-10 2-10 2-10	10	77.41 77.23 77.81 77.21	59.2 61.01 58.27 57.1	18.21 16.22 19.54 20.11	10.57 5.88 6.5 6.23	78.14 76.90 78.60 78.60	58.74 61.70 58.09 61.00	19.4 15.2 20.51 17.6	3.94 11.21 11.49 11.7
15-20 15-20 15-20	2	78.13 77.2 77.4 77.18	62.9 62.43 62.53	15.23 14.77 14.82 14.65	12.2 7.36 11.91 8.18 8.18	78 83 78.26 76.90	62.51 64.93 65.48 63.34	16 32 13 33 11 42 13.9	7 92 9.82 9.75 10.59
30-40 30-40 30-40	Ŋ	77.21 77.32 78.42 77.51	57.49 61.4 59.99 59.68	$19.72 \\ 15.92 \\ 18.43 \\ 17.83$	$\overline{x} = 8.799$	77.92 78.94 77.70 79.06	56.82 63.6 59.49 60.75	20.2 15.34 18.21 18.31	$\hat{x} = \frac{1.95}{9.237}$
50-60 50-60 50-60	Ś	77.77 77.71 77.54 77.33	55 47 59.59 59.05 59.12	22.3 18.12 18.49 18.21		77.58 77.90 77.49 77.47	54.18 58.7 59.19 57.37	23.4 19.2 18.3 20.1	
70-80 70-80 70-80 70-80	с С	78.56 77.66 77.31 77.22	62.33 66.37 61.89 60.67	16.23 16.29 15.42 16 55		77.13 76.56 78.04 76.11	60.03 63.36 59.94 63.91	17.1 13.2 18.1 14.2	

APPENDIX B - Estimation of food consumption for the leech <u>G</u> complanata at three different temperatures.

TABLE 7

	16hr	light - 8	hr dark (at	5°C)				8hr lig	çht - 16hr dé	ark	
Weight class	No. of snails	No. of snails	mg dry wt of	Con	ltrol	Weight class	No of snails	No. of snails	mg dry wt of	Cont	crol
with no. of leeches	added with wt class	eaten/ leech/ day	snails eaten/ leech	Added	Mortal- ity	- with no of	added with wt class	eaten/ leech/ day	snails eaten/ leech	Added	Mortal- ity
	(150-160)						(150-160)				1
10-15(4) 10-15 10-15 10-15	مەمە	0000	0000	, a o o o o	00000	10-15(4) 10-15 10-15 10-15	مەمە	0000	0000	٢	00000
	(160-165)			<u>، م، م</u>			(160-165)			o o (000
20-25(4) 20-25 20-25 20-25	००००	0000	0000	୰୰୰ୣ	00000	20-25(4) 20-25 20-25 20-25	مەمە			୕ୢ	0 0 0 0 O
	(110-111)						(110-111)				
40-50(4) 40-50 40-50 40-50	۵۵۵۵	0000	0000			40-45(4) 40-45 40-45 40-45	००००				
	(180-185)						(180-185)				
60-70(4) 60-70 60-70 60-70	مەمە	0000	0000			60-70 60-70 60-70 60-70	୰ଡ଼ଡ଼ଡ଼				

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	Mortal- ity		00000	00	00000				
	Control		مەمەمە	עסע	مەمەر				
hr dark	mg dry wt of snails eaten/ leech		0.82		0.85		0.89		0.971
ight - 16	rcan/ leech/ day		0.041		0.041		0.041		0.041
8hr 1	No. of snails eaten/ four leeches/ 3 days		00		00		00		00
	No. of snails added with wt class	(150-160)	୰ଡ଼ଡ଼ଡ଼	(160-165)	مەمم	(170-175)	مممم	(180-185)	مەمم
	Control Mortal- ity		00000	99	۵۵۵۵۵ مومو				
10°C)	mg dry wt of snails eaten/ leech		0.82		0.85		0.89		0.931
· dark (at	Mean/ leech/ day		0.041		0.041		0.041		0.041
light - 8hr	No. of snails eaten/ four leeches/ 3 days		00		00		-0-0		0011
16hr	No. of No. of added with wt class	(150-160)	୰ଡ଼ଡ଼ଡ଼	(160-165)	୰୰ଡ଼୰	(170-175)	୰ଡ଼ଡ଼ଡ଼	(180-185)	مەمە
	Weight class with no. of leeches		10-15(4) 10-15(4) 10-15(4) 10-15(4) 10-15(4)		20-25(4) 20-25(4) 20-25(4) 20-25(4)		40-50(4) 40-50(4) 40-50(4) 40-50(4)		60-70(4) 60-70(4) 60-70(4) 60-70(4)

	Mortal- ity		xi 9000000000000000000000000000000000000						
	Control								
8hr light - 16hr dark	Mean no. of snaiïs eaten/ leech/ day		0.067		0.087		0.108		0.108
	No. of snails eaten	(150-160)		(160-165)	-0	(170-175)	7070	(180-185)	7777
	No. of snails added		୶ଡ଼ଡ଼ଡ଼ୄ		مەمە		مەمە		ڡڡڡڡ
	Weight class with no. of leeches		10-15(4) 10-15(4) 10-15(4) 10-15(4)		20-25(4) 20-25(4) 20-25(4) 20-25(4)		40-50 40-50 40-50		62-73 60-70 60-70
	Mortal- ity		100010001						
	Control		0 " *: فىمەمەمەمەم						
16hr light - 8hr dark (at 15 ^o C)	Mean no. eaten/ leech/ day		0.067		0.087		0.108		0.108
	Mean/ leech/ 3 days	(150-160)	0.250 0.250 0.250 0.250	(160-165)	0.25 0.25 0.25 0.5	(170-175)	0.5 0.5 0.25 0.25	(180-185)	0.5 0.5 0.25 0.25
	No. of snails eaten/ four leeches				7777		8099		1155
	No. of snails added		୰୰ଡ଼୰		مەمەم		ڡڡڡڡ		୰୰୰୰
	Weight class with no. of leeches		10-15(4) 10-15(4) 10-15(4) 10-15(4)		20-25(4) 20-25(4) 20-25(4) 20-25(4)		40-50(4) 40-50(4) 40-50(4) 40-50(4)		60-70(4) 60-70(4) 60-70(4) 60-70(4)

ABSTRACT

Ecological Studies of the Common Leeches of Rutland Water by M.H. Majeed.

Three species of leeches (<u>Helobdella stagnalis</u>, <u>Erpobdella</u> <u>octoculata</u> and <u>Glossiphonia</u> <u>complanata</u>)were studied in Rutland Water (England) between September 1977 and October 1979. Samples were taken by Ekman grab at monthly intervals and by hand collecting from unit areas near the shore. For each sample, the number and size distribution was recorded of each species, and these data were used both to analyse the effect of depth and substratum on distribution and to provide base-line data on the life cycles and population structure for estimating the parameters of the annual energy budgets.

The abundance and distribution were clearly related to water depth and to the type of substratum. Maximum densities were recorded from July to October, while the lowest densities were recorded in January to March.

The life cycle of both <u>H</u>. <u>stagnalis</u> and <u>G</u>. <u>complanata</u> were predominantly annual, while <u>E</u>. <u>octoculata</u> took two years to complete its cycle.

The respiration rates of the three species were determined using a Gilson respirometer operated at 5°, 10° and 15°C. Oxygen consumption increased with dry weight of leeches over all three temperatures, and in each species the three regression equations were significantly different from one another. The monthly respiratory metabolism was calculated for each species by applying the regression equation for the nearest temperature to the recorded population structure and from these values, annual respiration was determined.

Food consumption was measured at 5°, 10° and 15°C and direct relationships between food consumption and both body weight and temperatures were found. No effect of day length was demonstrated. The apparent percentage assimilation was calculated, and was more than 90% in all three species. Monthly consumption was calculated by applying the appropriate regression equation of food consumption on body weight to the data for population structure at the nearest temperature to that in the field. This value was multiplied by the apparent assimilation efficiency to give the monthly assimilation rate and these values were summed to determine the annual assimilation.

Annual production for each species was calculated using annual assimilation, minus annual respiratory metabolism.

Problems encountered in this study have been discussed.