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THE POPULATION DYNAMICS AND PRODUCTIVITY OF *ASELLUS AQUATICUS* (L) IN LOCH LEVEN, KINROSS

BY

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Thesis submitted for examination for the degree of Doctor of Philosophy, University of Stirling.

August 1976

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I should also like to thank the staff of the Institute of Terrestrial Ecology, Wetlands Research Group, Edinburgh for the use of boats and equipment and for help and encouragement.

ABSTRACT

The population dynamics of Asellus aquaticus (L) in the shallow rocky areas of Lock Leven has been studied in the context of the information supplied by the International Biological Programme project on the loch.

From the qualitative and quantitative results a picture of the life cycle in this particular loch has been built up, from which it has been concluded that the cycle has no synchrony with day length or other external factor, other than temperature. Once the temperature is high enough to allow successful copulation and rearing of young the animal reproduces as often as possible, under the constraint of temperature regulating duration of growth to sexual maturity, development time of eggs and the intermoult period between releasing young and readiness for copulation.

The timing of breeding activity and the period of reproductive stasis were comparable to other temperate studies and mid-way between studies from colder and warmer climates.

Productivity data was calculated and compared with other results in the literature, from which it was suggested that food substrates available in the habitat influenced the production efficiency irrespective of the amount of available cover - which had a greater effect on the standing crop. Laboratory food preference tests

and assimilation experiments indicated that Asellus eats the most easily ingested food substrate from the habitat, irrespective of its assimilability.

Growth experiments using a variety of food substrates under various conditions indicated that growth was affected by the type of food available. From this it was suggested that the production efficiency values observed in the various studies from the literature varied according to the food substrate available: where a highly assimilable one was present, such as benthic algae, the production efficiency was high; where a poorly assimilable one was present, such as macrophyte remains, the production efficiency was lower.

The significance of Asellus to the Loch Leven ecosystem is reappraised in the light of the results, especially as a source of food for trout and perch.

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CHAPTER 1

INTRODUCTION

1.1 The Project Aim

A study has been made to determine the significance of Asellus aquaticus L., in the Loch Leven ecosystem, the major components of which were studied in the International Biological Programme project which started in 1966 and culminated in the symposium of 1973 (Royal Society of Edinburgh, 1974).

Maitland and Hudspith (1974) sampled the Zoobenthos in the sandy littoral area of the Loch but found only a small Asellus population density of 71 m^{-2} (54.0 mg dry wt m^{-2}) in 1970 and similarly low values for 1971. Their samples taken in October 1968 suggested that there might be denser populations in the mud areas (57% of the loch area) than in the sand areas (42%) but even at 113 individuals m^{-2} (52 mg dry wt m^{-2}) the population is small, though such a short sampling programme can only indicate the general distribution and abundance.

From this data it would seem that Asellus has a low standing crop and is at so low a density that its importance as a food organism is minor; however, in contrast to this is data provided by Thorpe (1974) on the trout and perch populations. He found that Asellus dominated the food ration of trout in June and July in terms of numbers of Asellus to total numbers of all food items, and similarly for perch in June, July and August.

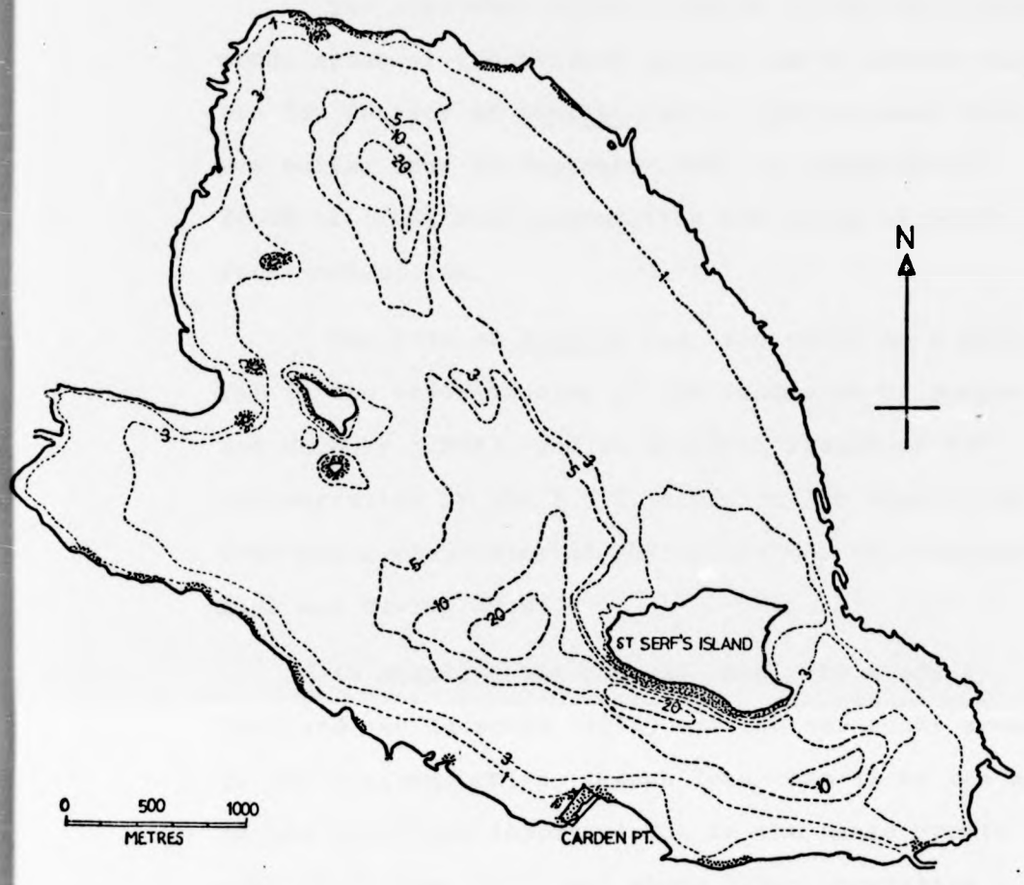

FIG.1. Map of Loch Leven showing the distribution of shallow rocky areas. Carden Point and the approximate position of the area surveyed for figure 2 are indicated.

= shallow rocky areas.

= area surveyed in detail.

----- = depth contours (depth shown in metres.)

The available organic matter in the sandy and muddy areas of the benthos is too low to assume that the low density of Asellus has a high turnover rate, yet during June to September 1971 it represented 24.2% of trout food consumption and 33.8% of perch food consumption.

The role of Asellus has been noted as a major gap in the understanding of the ecosystem by Morgan and McLusky (1974), and is mainly a result of the concentration by the I.B.P. study on the simplified food chain comprising of phytoplankton, chironomidae, fish and diving ducks.

In sampling the mud and sand, the study by Maitland and Hudspith (1974) omitted the rocky areas of the littoral which, though less than 1% of the area of the loch, are important due to the dense growth of epilithic algae in a loch where other vegetation - emergent or submerged - is scarce: in 1972 emergent vegetation occupied only 5% of the shoreline and less than 0.01% of the total loch area (Britton, 1974).

Asellus is known to prefer a vegetated substrate to either mud or sand (Andersson, 1969). It has been recorded as feeding on alga similar to the Cladophora glomerata (with its associated epiphytes) found in Loch Leven, in several other studies (e.g. Andersson, 1969; Berglund, 1968; Moore, 1975; Wolff, 1973).

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Thus it is logical to suggest that the rocky areas may be the source of the Asellus found by Thorpe (1974) in the fish diets. This is supported by the fact that some of the main feeding areas of the trout are thought to be the rocky shelf areas around St. Serfs Island, the north bay, and along the south shoreline (see map Fig.1). (Thorpe, personal communication).

This study is an attempt to test the suggestion that the rocky shallow areas are a source of Asellus in far greater quantities than are produced by the sand and mud areas, and to evaluate the significance of Asellus in the Loch Leven ecosystem. To this end a qualitative sampling programme and a subsequent quantitative one were undertaken, resulting in population dynamics and productivity data as well as details of the life cycle of Asellus in Loch Leven. Comparisons of this productivity data with results from other workers suggested work on food preference and assimilation followed up by growth experiments to evaluate the meaning of comparative differences between Asellus productivity data from the different studies.

1.2 The Sampling Site

The main physical and chemical characteristics of Loch Leven have been described respectively by Smith (1974) and Holden and Caines (1974). The loch itself (Fig.1) is a shallow (mean depth 3.9m), well

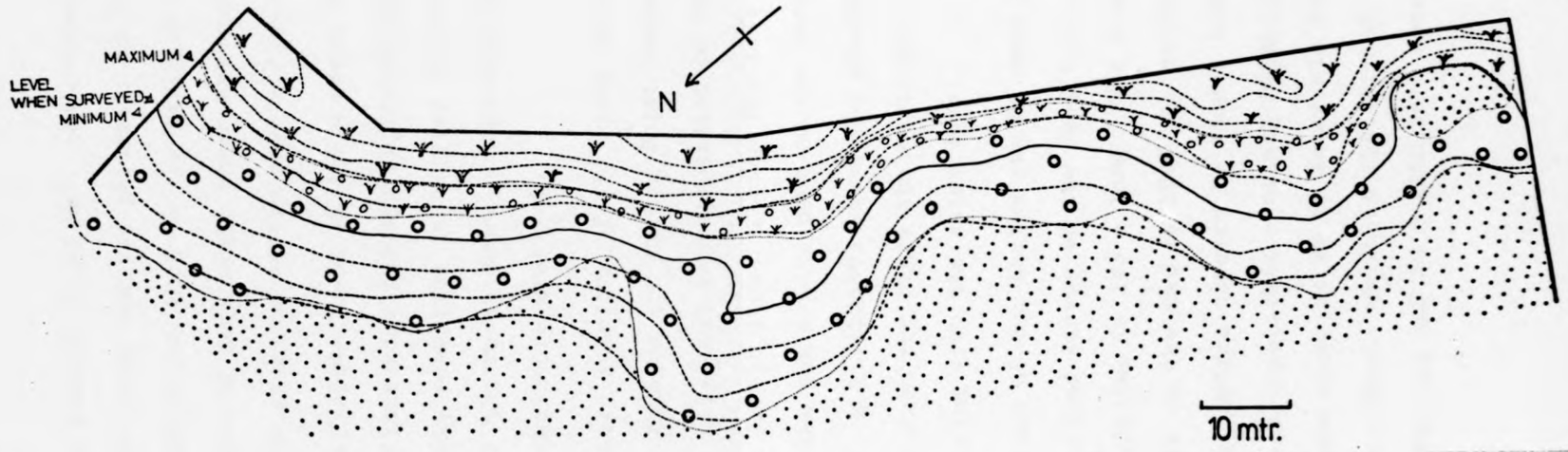


FIG.2. Detailed survey of the area of Carden Point indicated on figure 1. Survey carried out 30.8.75.

---------- = Boundaries of substrate types:

= stones and boulders

= grass and associated plants

= mixture of stones and terrestrial plants

= sand

-------- = Contours at +/- 25cm intervals from water level.

mixed eutrophic loch of 13.31 km^2. An estimated 1% of the bottom is stony and the perimeter is affected by the situation of the loch in the plain of Kinross (30 km north-west of Edinburgh) where exposure to prevailing winds produces severe wave action.

The modal water level is 107 m above sea level, but the level fluctuates through approximately 0.5 metre about this level, resulting in varying exposure of the higher areas of the rocky shore - magnified by the slightness of the shore gradient.

Preliminary sampling of the rocky littoral of several of the islands and Carden Point indicated that the latter was a typical representative of the substrate type in the loch. Carden Point is a wide promontary in the south-east part of the loch (O.S. grid ref: N.T. 153996) where the gradient is such that even 15 m from the shore the depth may be only 1 to 1.5 m varying with the water level.

The nature of the bottom can be seen from Fig.2, which is a detailed survey of the east side of Carden Point. The baseline is 145 m long. The total area of stony substrate on the map is 1996 sq. metres with a further 444 sq. metres covered by stones interspersed with terrestrial vegetation - mainly Potentilla sp. The contours are shown at 25 cm intervals above and below the water level, which at the time of the survey (30 August 1975) was 106.83 m (350.26') above sea level:

a low value but normal for August. Thus the level would be expected to fall another 0.05 m and rise by about 0.4 m if following the average pattern for 1949-1967 (Smith, 1974).

The stony areas are strewn with rocks varying from half a metre across, down to sandy gravel, forming a shelf area extending up to 40 m from the permanent turf of the shore.

CHAPTER 2

POPULATION DYNAMICS

2.1 Qualitative Dynamics

A detailed knowledge of the quantitative and qualitative changes in the population structure throughout the year is fundamental to the study of the significance of that organism in terms of energy flow in an ecosystem.

Unfortunately, in the wealth of literature relating to sampling the benthos there is little mention of a method of effectively quantitatively sampling a substrate such as that at Carden Point, with its irregular rocks varying in size from gravel to quite large boulders. Macan (1958) has given a summary of the available methods:

1. Lifting by hand of individual stones (with quantification from either the area of the stone or the time allowed for sampling).
2. Provision of a known area of removable substrate for colonisation.
3. Boxes and cylinders. A given area is enclosed and the animals within it removed.
4. Fixed nets. A known area upstream is disturbed and the animals dislodged from it are washed into the net (in running water only).
5. Nets that are pushed forward through the substratum.

Each has its own inherent difficulties and inaccuracies and was in turn tried and rejected as a means of quantitatively sampling the substrate. Thus initially a sampling programme was begun which aimed only at qualitatively sampling the population structure. At the same time a quantitative method was sought using both the available literature and field experiments.

The technique used was that of lifting individual stones while enclosed in a net, so that all the animals clinging to the stone could be picked off and all those caught in the net added to them. In this way it was hoped to take a sample of animals which, although non-quantitative, would qualitatively reflect the composition of the population. In order to avoid bias, stones of various sizes were lifted and as many animals as it was practical to sort, were collected.

Samples were taken in this way at approximately fortnightly intervals through the period June to September 1974 and March to October 1975, with less frequent sampling before and after these periods, and during the September 1974 to March 1975 period when recruitment had ceased.

In the laboratory the animals were sorted from any vegetation and ovigerous females placed in individual containers so that any expulsion of brood contents would not be lost. Samples were preserved

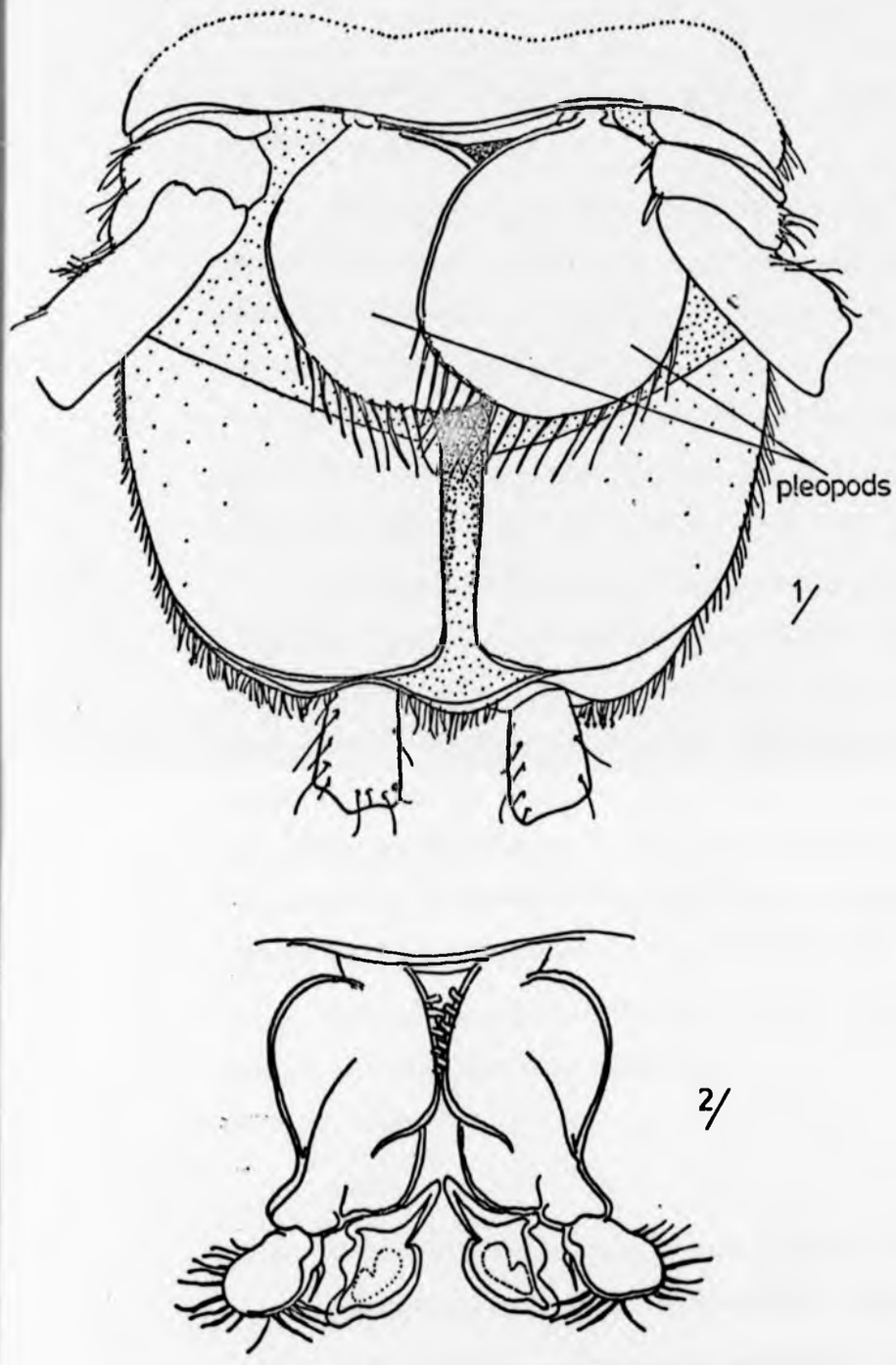


FIG 3. Drawings of the sexual pleopods of Asellus aquaticus:

1/ Female, showing underside of abdomen;

2/ Male, showing 2nd pleopods only.

(The size scale depends on the size of the individual.)

in 5% formalin solution with glycerine added to prevent hardening.

Measurement was made from the median supra-anal projection of the abdomen to the front edge of the cephalon, between the antennae. Any arch in the body was flattened and any build up of fluid pressure in the segments released in order not to affect the measurement, which was to the nearest 0.5 mm above, using an eyepiece graticule in a binocular microscope.

Sex was determined by examination of the sexual pleopods (Fig.3), although for convenience in handling large numbers of animals, those below the 4.5 mm size class were classed as juveniles in the 1974 samples. There is justification for this in terms of growth rate similarity in males and females up to this size (Needham, 1937) but since it produced the anomaly of ovigerous juveniles it was lowered to -4.0 mm for 1975.

The brood pouches of all ovigerous females were opened and the contents classified into four arbitrarily defined stages:

1. EGGS
2. EARLY EMBRYOS - loss of egg membrane and embryonic membranes, limbs poorly developed.
3. LATE EMBRYOS - limbs well developed, antennae developed, locomotory movement co-ordinated.
4. BROOD POUCH EMPTY - contents released. (But may also include females with embryos dead and rejected.)

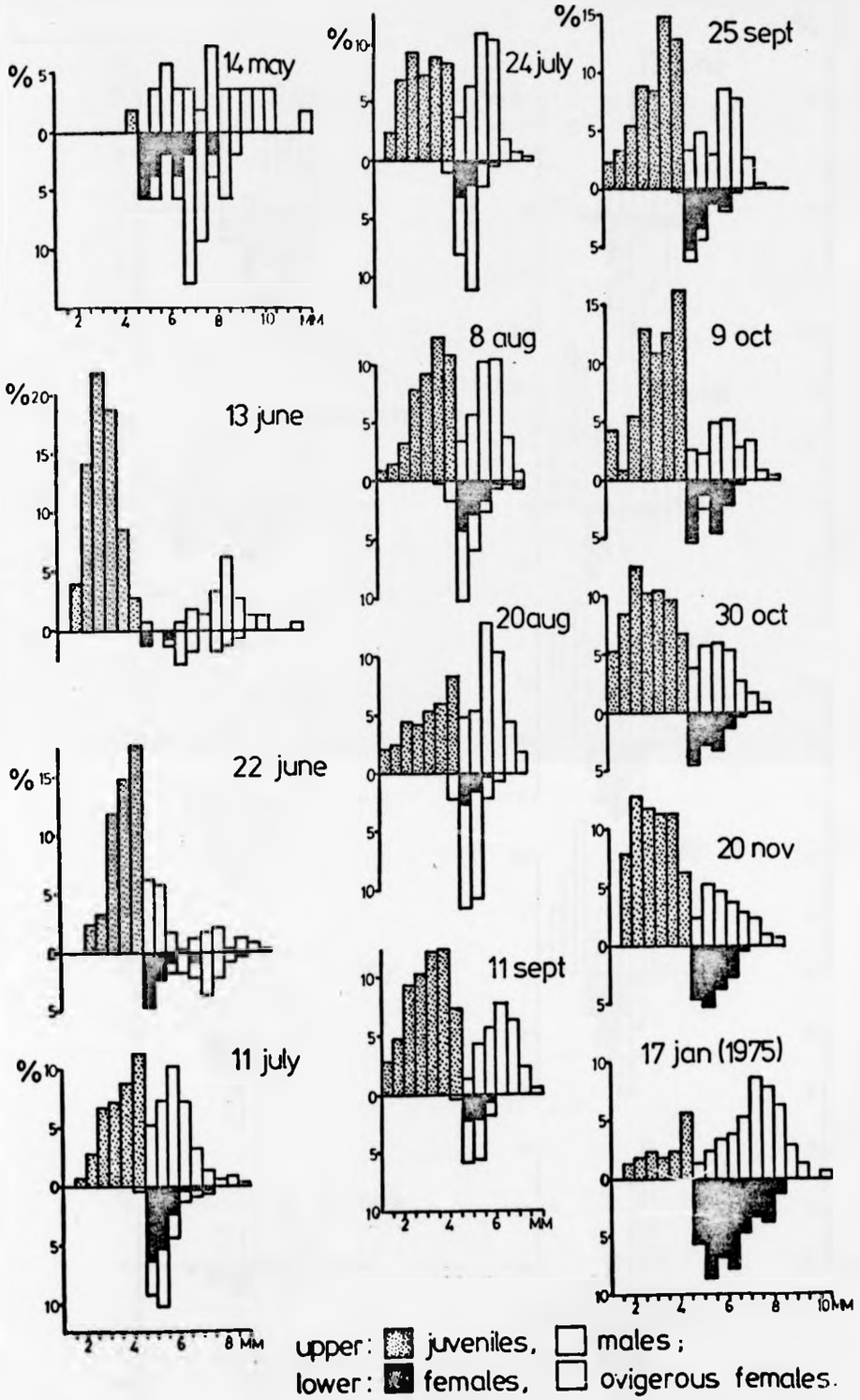
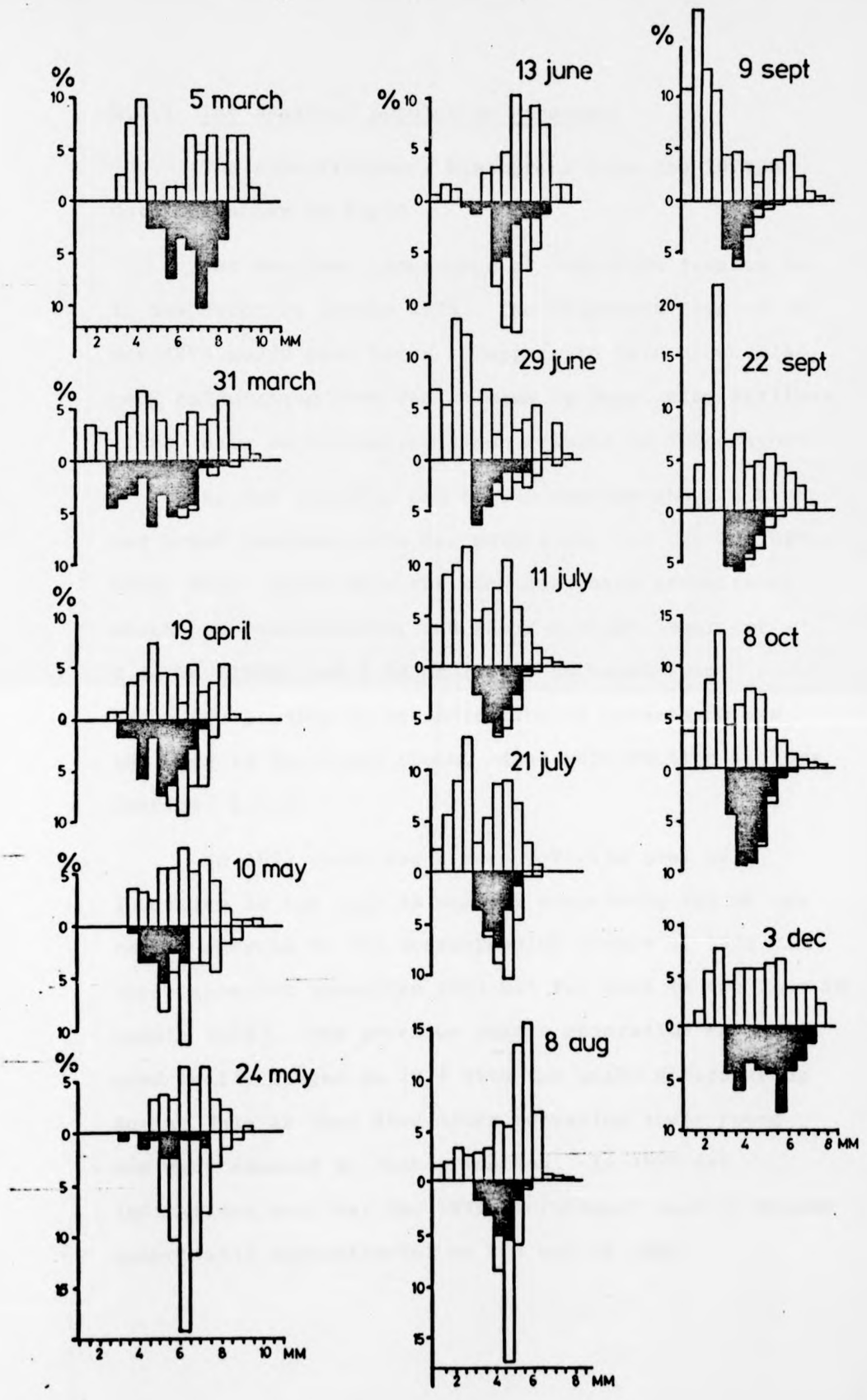


FIG 4. Length-frequency histograms of Asellus aquaticus at Carden Point. Each size-class is expressed as a percentage of the total sample. (1975 results on facing page)


%
5 march
31 march
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10 may
24 may
13 june
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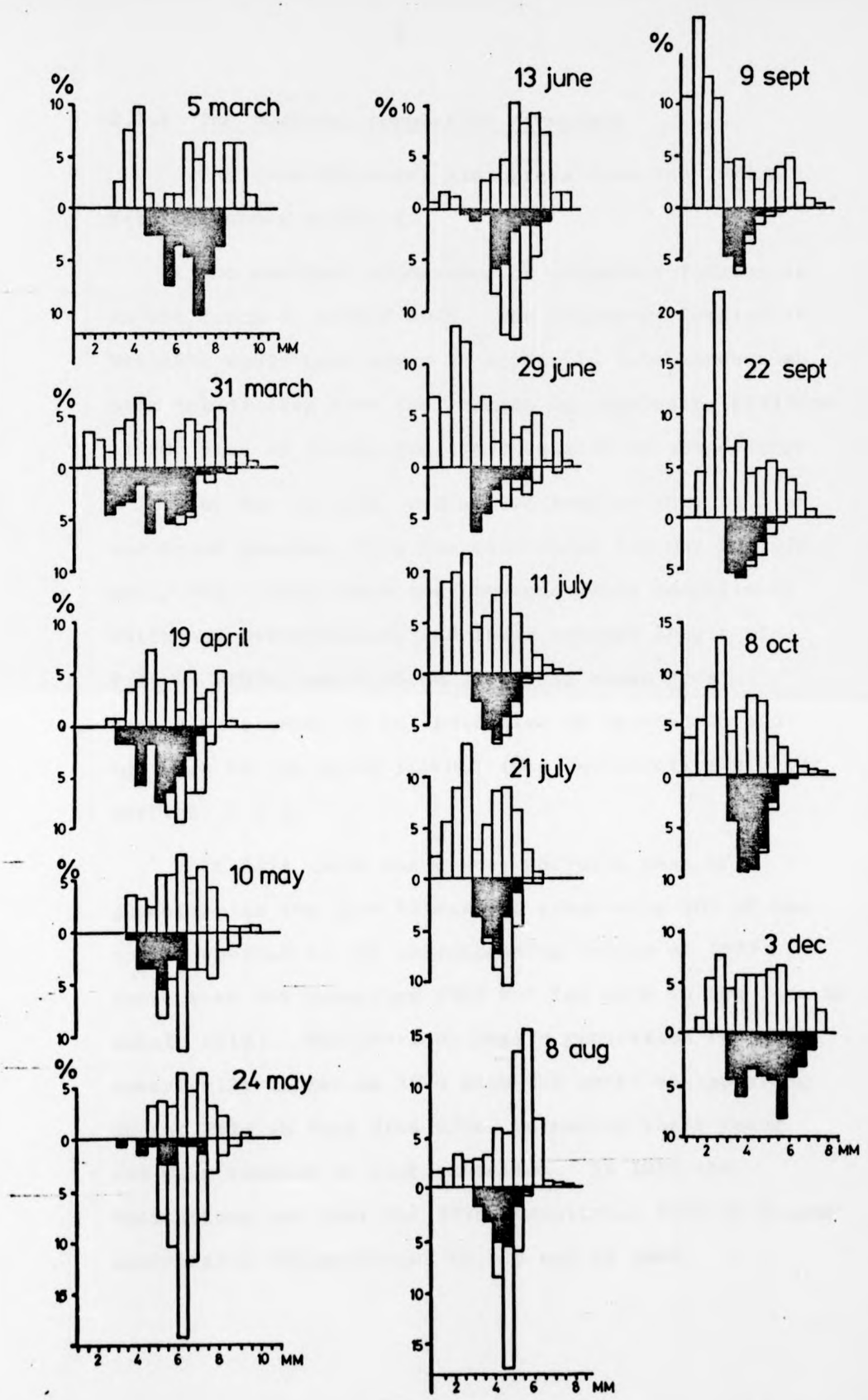
11 july
21 july
8 aug
9 sept
22 sept
8 oct
3 dec
MM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8 aug
9 sept
22 sept
8 oct
3 dec
MM

2.1.1 The seasonal population structure

The size-frequency histograms from the 1974/5 data are shown in Fig.4.

The earliest appearance of ovigerous females is in the March 31 sample 1975. The ovigerous females in May 1974 would have begun to appear in late March also, back calculating from the release in June using Williams (1960) data on incubation times related to temperature.

By May 14/1974, 64% of the females above 4.5 mm had brood pouches, with the equivalent for May 24/1975 being 84%. These were the previous years recruitment which had overwintered, and their average length of 7.44 mm (1974) and 6.43 mm (1975) is known from fecundity studies to be indicative of between 80 and 100 eggs in the brood pouch, (see reproductive biology section: 2.1.2)

In 1974 there was a very definite peak of juveniles in the June 13 sample, comprising 70% of the total, whereas in the corresponding sample of 1975 there were few juveniles (8%) but far more in the June 29 sample (61%). The previous year's generation was numerically larger in 1974 with the peaks disappearing during July as they died after releasing their young and were removed by fish predation. In 1975 the indications are that the 1974 recruitment died or became numerically insignificant by the end of June.

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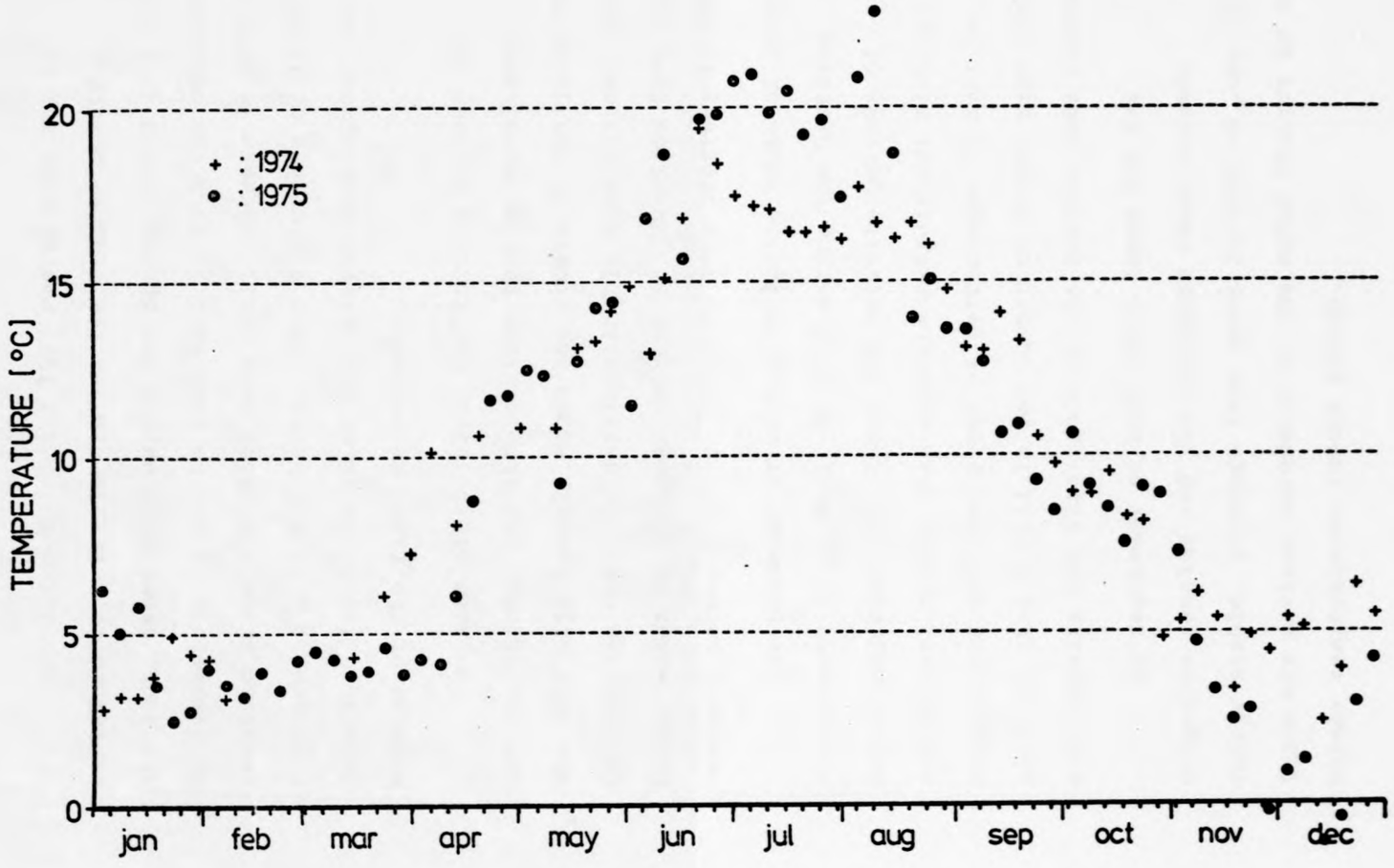

FIG 5. Graph of temperature variation in Loch Leven during 1974 and 1975. (Data supplied by the Institute of Terrestrial Ecology, Edinburgh.)

The lateness of the 1975 recruitment may be explained by referring to the temperature data for the loch, especially during the Spring period (Fig.5). By comparison it can be seen that in 1975 the temperature remained below 5°C until late April, whereas in 1974 it rose past 5°C in mid March. This difference of 15-20 days is a likely cause of the delayed development and release of the first recruitment.

Because of the clear distinction between the new recruitment and the previous year's recruitment, the 1974 data clearly shows the growth of the juveniles up into the sexually distinguishable size classes, before being masked by the next release of juveniles from the sexually mature females. This is less distinct in 1975.

The presence of several definite peaks of juvenile recruitment (e.g. Sept. 9/1975) during the breeding period suggests that there are definite periods of recruitment rather than constant recruitment although since these are histograms of percentages it must be realised that a fall in the number of larger size classes will magnify the importance of the smaller size classes.

By September of both years there are few ovigerous females and the histogram shape becomes fairly stable, although from March 31/1975 to June 13/1975 there are obvious movements of the modal classes as the warmer temperatures induce growth.

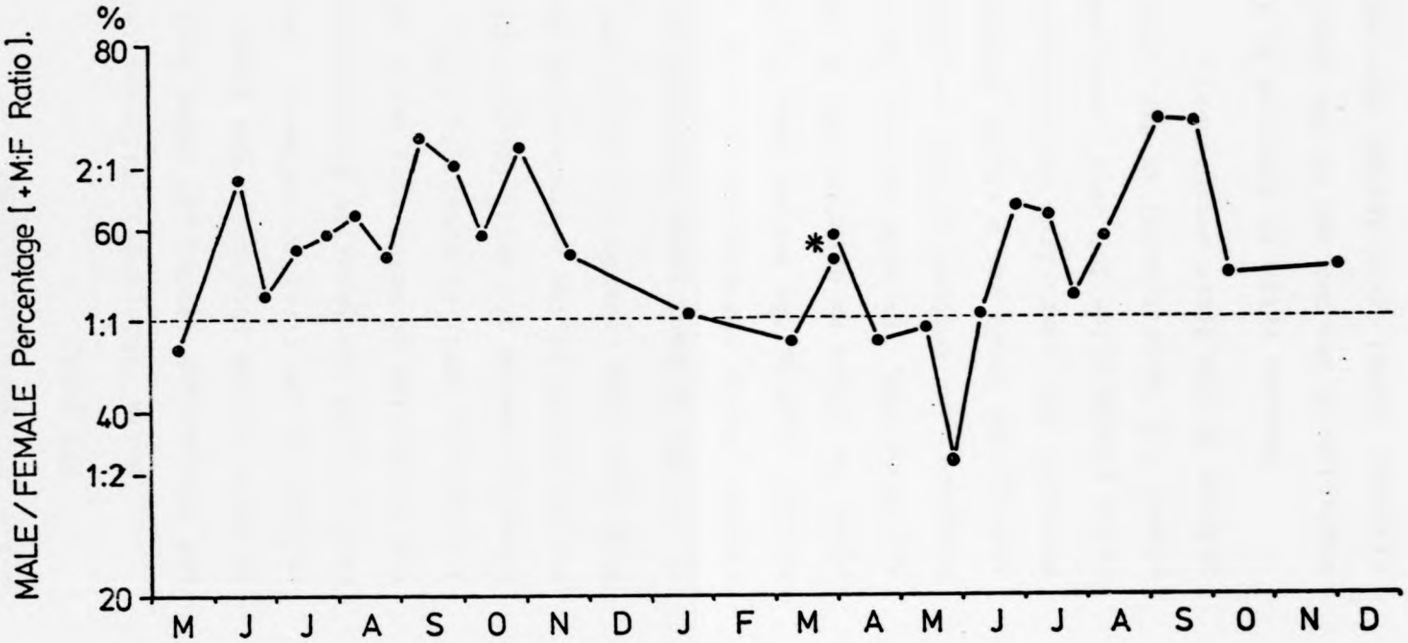

FIG 6. Graph showing seasonal variation in the sex-ratio; males expressed as a percentage of total population above 4.5mm (up to *) or 4.0mm (after *).

2.1.2 Reproductive Biology

Sex ratio

Seitz (1953,1954), Williams (1960), Steel (1961) and Fitzpatrick (1968) all found that the proportion of males in the population was lowest just before the release of the first recruitment. Once this recruitment entered the sexually distinguishable size-classes the proportion of males rose again and remained around 1:1 (Steel, 1961; Fitzpatrick, 1968) throughout the breeding season and until February/March when fertilization of the overwintering females takes place. From this time onwards the proportion of males decreases.

The present study indicates a similar pattern (Fig.6) though changing erratically from sample to sample. During the period when recruitment was taking place the males as a percentage of the population rose to around 60%, reaching the 2:1 (male:female) ratio in September and October of 1974 and September 1975. After this period there was a steady return to a 1:1 ratio by February and, apart from the March 31/1975 sample, the ratio stayed below 1:1 until June, reaching a low of almost 1:2 (male:female) in May, just prior to the release of the first recruitment.

The sex ratio is affected by three mechanisms. Migration of one sex out of the habitat can be discounted: Williams (1960) investigated this and found no evidence of it, nor was any found in the present study. Thus the

balance between the sex ratio of the recruitment and differential mortality must determine the overall ratio. Obviously the former only operates during the recruitment phase so that differential mortality must be responsible for the decline in males once copulation in the overwintering population has taken place. The females survive for 2 to 3 months more in order to produce the initial recruitment but the males die soon after copulation. This has the ecological advantage of efficiently utilizing the food resources of the environment since only the females will be competing for the available food at a time when plant growth is slow and assimilation efficiency of food is depressed by low temperatures (see Feeding and Assimilation, section 4.).

The redress of the balance once recruitment begins, and its rise to 2:1 (male:female) must be a result of more males being produced than females, or a higher mortality in females. It is likely that as most of the females are ovigerous during the breeding season, they may be at a physical disadvantage when evading the heavy predation by trout and perch at this time of the year, so that mortality due to predation is greater in females.

Seitz (1953) worked on the sex ratio of the broods of Asellus and found that although some monogenic broods (i.e. broods consisting of only one sex) are produced, the majority are mixed, with a

preponderance towards one sex or the other.

The control of this is unknown, so that its operation in producing the variation in sex ratio found here is uncertain. Certainly Collinge (1947) found that high temperatures and a nutritive diet favoured a bias towards female production in certain land isopods and Kinne (1952) found the temperature prior to oviposition to be a controlling factor of the intra-brood sex ratio of Gammarus duebeni, but unless the mechanism is the reverse of Collinge's findings - and his seems the more logical bias - the effect seems incompatible with the results found. Thus the differential mortality due to predation by fish may be the most important factor.

Although no direct evidence has been found, it is possible that cannabalism may also be a factor. When kept in the laboratory at high densities there was considerable mortality due to cannabalism, often involving damaged or weakened individuals. Due to the different growth pattern whereby the males continue growing whilst the females divert production to reproductive products, females are generally smaller than males. Thus they may fall victim more easily to cannabalism. Collinge (1945) describes in detail the devouring of a female by a large male, lending some support to the theory.

TABLE 1. Analysis of data on developmental stages of brood-pouch contents from 1974 and 1975 samples.

SAMPLE DATE	EGG		EMBRYO STAGE: EARLY		EMBRYO STAGE: LATE		EMPTY		NO B.P.		TOTAL
	No	%	No.	%	No.	%	No.	%	No.	%	
14 may	18	64.29	-	-	-	-	-	-	10	35.71	28
13 jun	5	27.78	3	16.67	4	22.22	3	16.67	3	16.67	18
22 jun	6	12.48	7	14.56	9	18.72	4	8.32	22	45.76	48
11 jul	122	34.95	17	4.87	6	1.72	15	4.30	189	54.15	349
24 jul	56	24.56	70	30.70	27	11.84	20	8.77	55	24.12	228
8 aug	107	23.78	27	6.00	33	7.33	87	19.33	194	43.11	450
20 aug	58	42.33	27	19.71	15	10.95	15	10.95	22	16.06	137
11 sep	9	7.50	21	17.50	28	23.33	19	15.83	43	35.83	120
25 sep	3	4.84	1	1.61	6	9.68	3	4.84	49	79.03	62
9 oct	-	-	-	-	2	5.56	2	5.56	32	88.89	36
30 oct	-	-	-	-	-	-	1	0.72	138	99.28	139
20 nov	-	-	-	-	-	-	-	-	78	100.0	78
17 jan	-	-	-	-	-	-	-	-	74	100.0	74
5 mar	-	-	-	-	-	-	-	-	34	100.0	34
31 mar	4	5.97	-	-	-	-	-	-	63	94.03	67
19 apr	15	29.41	-	-	-	-	3	5.88	33	64.71	51
10 may	44	61.11	-	-	-	-	-	-	28	38.89	72
24 may	14	17.07	25	30.49	17	20.73	11	13.41	13	15.85	82
13 jun	12	14.12	17	20.00	6	7.06	18	21.18	32	37.65	85
29 jun	5	19.23	4	15.38	6	23.08	1	3.85	10	38.46	26
11 jul	17	10.06	3	1.78	4	2.37	16	9.47	129	76.33	169
21 jul	28	33.33	7	8.33	1	1.19	8	9.52	40	47.62	84
8 aug	41	19.71	20	9.62	6	2.88	59	28.37	82	39.43	208
9 sep	7	26.92	2	7.69	1	3.85	4	15.38	12	46.15	26
22 sep	2	4.88	7	17.07	-	-	3	7.32	29	70.73	41
8 oct	-	-	-	-	-	-	8	4.79	159	95.21	167
3 dec	-	-	-	-	-	-	-	-	57	100.0	57

Variation in reproductive activity

It has been indicated from the histograms (Fig.4) that once the overwintering females have died and the first recruitment reaches sexual maturity, the reproductive activity is not constant: juveniles are not recruited at a constant rate. This is further illustrated by data from the analysis of brood pouch contents.

Table 1 shows the variation in brood pouch composition over the two year period. Considering the egg-carrying females only, it can be seen that there is a high value as the overwintering females are fertilized with a peak in the early part of May (in 1975; and by extrapolation, in 1974). This rapidly falls as the eggs develop and are released, but builds up again as the earliest released juveniles reach sexual maturity. The death of the overwintering females will accentuate part of the peak for the maturing initial recruitment so that it is conceivable that although there are two high values in July and August 1974 and July and September 1975, these represent only one period of reproductive activity and the bimodality is caused by the loss of the previous generation females.

The effect of the variation in reproductive activity on the population can be seen from Fig.7, which compares the seasonal variation in both egg-carrying females and juveniles. The general pattern

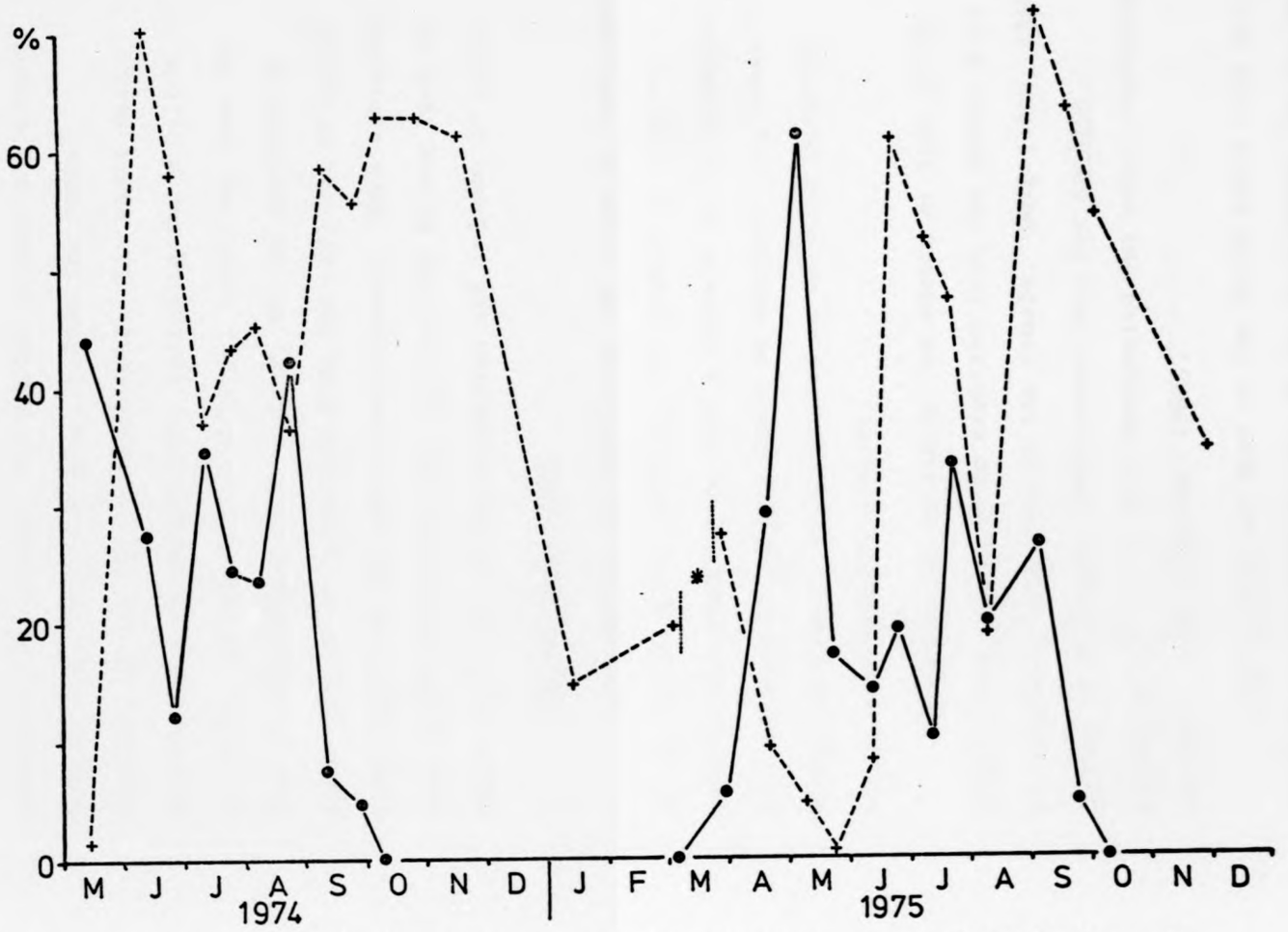

FIG 7. Seasonal variation in (•—•) egg carrying females as a percentage of all females, and (+---+) juveniles as a percentage of the total population. (pre * juvenile 4.5mm, after * juvenile 4.0mm.)

is that there are two peaks of juveniles each year. The first follows the release of the broods of the overwintering females, the second follows the second peak of egg production arising from the sexual maturity of the first recruitment. The small peak of juveniles in August 1974, following the previous argument, is possibly an artifact resulting from the loss of the larger size classes, but is possibly an early release of juveniles from the earliest released individuals of the year's recruitment. Such variation must occur within the main pattern due to the lack of exact synchrony of fertilization and release of young.

Reproductive rate

In addition to describing the stage of development of the brood pouch contents, the number of eggs or embryos was recorded so that a measure of the capacity for increase of Asellus could be derived. A greater number of females were examined in 1974 and produced the more dependable results.

Considering initially the number of eggs in the brood pouch, it is to be expected that the number will be related to the size of the female. Berg (1938, 1948 - quoted in Williams, 1960) noted this for Asellus aquaticus but it is well documented for other crustacean species. (See Williams, 1960).

The numbers of eggs in the brood pouch have been related to the body length of the incubating female for the 1974 and 1975 breeding periods (Fig.8). The

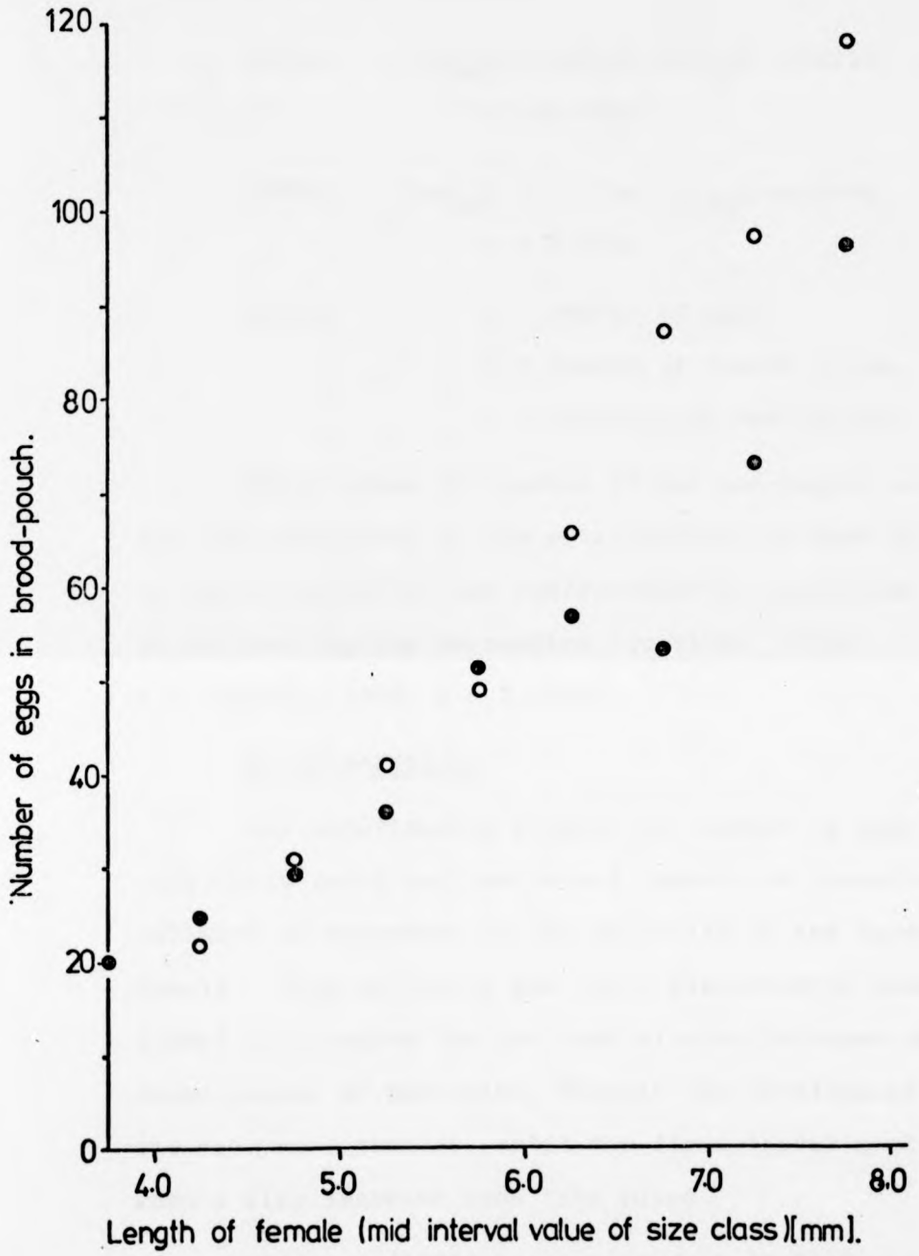

FIG 8. Graph of the relationship between number of eggs and the length of the incubating female: 1974 and 1975.

relationship is not linear and is best expressed as a log to log relationship:

1974: $\log_{10} n = 2.8163 \log_{10} l - 0.4278$

$r = 0.9963$

1975: $\log_{10} n = 2.0708 \log_{10} l + 0.0876$

$r = 0.9845$

where n = number of eggs

l = length of female in mm.

r = correlation coefficient

Fig.8 shows the curves of the non-logged values but the similarity of the relationships is best shown by the closeness of the coefficients of regression (b) in the two log-log regression equations (1974: b = 2.8163; 1975: b = 2.0708).

Brood mortality

The relationship between the number of eggs in each brood pouch and the actual numbers of juveniles released is dependent on the mortality in the marsupium itself. This mortality was first discussed by Janke (1926) as a reason for the lack of size increase of the brood pouch, or marsupium, despite the development of the embryos - that is, until the first larval moult when a size increase does take place.

Williams (1960) criticizes Janke's findings and from work of his own lowers Janke's estimation of brood pouch mortality of 47% to a more realistic figure of 20%.

TABLE 2a: Mean brood numbers and percentage brood mortality in relation to size of incubating female: 1974 data.

SIZE RANGE	BROOD STAGE	Nº EXAM'D	MEAN BROOD Nº.	STAND. ERROR	% MORTALITY EGG - L.E.
4.01-4.5	EGG	33	21.88	1.8922	
	EE	5	18.20	4.5886	35.10
	LE	5	14.20	3.2156	
4.51-5.0	EGG	135	30.77	0.8676	
	EE	49	30.18	1.3243	25.38
	LE	47	22.96	1.8262	
5.01-5.5	EGG	134	40.71	1.0090	
	EE	77	32.86	1.2205	24.32
	LE	43	30.81	2.0343	
5.51-6.0	EGG	45	48.13	2.4805	
	EE	19	45.05	3.4298	17.93
	LE	12	39.50	4.4081	
6.01-6.5	EGG	11	65.36	6.0122	
	EE	9	73.11	3.2600	27.83
	LE	6	47.17	8.7328	
6.51-7.0	EGG	3	87.00	14.1917	
	EE	3	71.00	20.6467	23.56
	LE	6	66.50	13.4033	
7.01-7.5	EGG	1	97.00	-	
	EE	3	89.00	13.5277	15.12
	LE	6	82.33	12.3255	
7.51-8.0	EGG	1	118.00	-	
	EE	2	109.50	1.4991	12.29
	LE	2	93.50	11.4977	

TABLE 2 b: Mean brood numbers and percentage brood mortality in relation to size of incubating female: 1975 data.

SIZE RANGE	BROOD STAGE	Nº EXAM'D	MEAN BROOD Nº	STAND. ERROR	% MORTALITY EGG - L.E.
4.01-4.5	EGG	28	24.71	1.8860	
	EE	10	25.80	2.4856	39.30
	LE	3	15.00	1.9977	
4.51-5.0	EGG	49	29.10	1.6729	
	EE	32	27.22	2.0206	20.10
	LE	12	23.25	3.2072	
5.01-5.5	EGG	34	35.68	2.7320	
	EE	16	29.31	2.5375	7.51
	LE	5	33.00	4.8390	
5.51-6.0	EGG	4	50.75	6.0200	
	EE	9	39.33	3.2267	63.88
	LE	3	18.33	7.4249	
6.01-6.5	EGG	8	56.88	3.9316	
	EE	13	41.38	5.7634	36.27
	LE	4	36.25	6.7850	
6.51-7.0	EGG	1	53.00	-	
	EE	6	54.00	10.6353	21.51
	LE	5	41.60	12.3792	
7.01-7.5	EGG	1	73.00	-	
	EE	2	58.50	17.5011	38.70
	LE	4	44.75	14.2300	
7.51-8.0	EGG	2	96.00	7.0004	

Jones and Naylor (1971) studied the marine isopod Jaera spp. in a similar way and noted a 50% mortality in the four species studied.

The results of the present study are shown in Tables 2a and b. The overall mean value for 1974 is 22.69% (range 12.29-35.10) between eggs and late embryos, with 1975 being 32.47% (range 7.51-63.88). Here again, the greater number of gravid females considered in 1974 lends greater confidence to the former figure so that the low figure of 20% from Williams (1960) seems to be confirmed. Steel (1961) made similar observations and from his published data a value of 27% (range 10% to 41%) can be calculated.

There seems to be some disagreement in the literature as to the fate of the lost progeny. Janke (1926) reports seeing eggs passed out of the brood pouch, but he maintained his animals on sieves so that eggs could pass through. He notes that these eggs are abnormal but Williams (1960) claims some evidence that animals maintained on sieves do drop their eggs, possibly due to some irritating effect of the mesh.

Steel (1961) could observe few free eggs, so suggested that they are eaten by the female or by the embryos once they are capable of feeding, or that they die and decay in the brood pouch. In the present study dead (opaque) eggs have been found, but not in large numbers. Steel concludes that the manner of the loss and its causes are unknown, while Williams decides that

accidental loss during walking, movement of the brood pouch lamellae and movements of the embryos themselves are the cause.

Both explanations seem to disregard the feeding of the embryos in the brood pouch. At first the developing embryos feed on the food reserve provided in the egg and so do not increase in mass, but take up more room as they change shape and develop appendages. Janke (1926) states that this increase in required space is accommodated by a loss of eggs, and presumably embryos, from the brood pouch. There is an intermittent aeration of the eggs/embryos supplied by the maxillipeds which produce a flow of water in the brood pouch. Janke denies any suggestion that this provides a flow of detritus for food but dies not suggest an alternative source of food. The function of the maxillipeds is solely to turn and brush the embryos, using especially the coxpodites of the maxillipeds, thus keeping them free of fungal attack.

However, it seems reasonable to suggest that once the mouthparts of the young develop they may utilize any fungus growing in the brood pouch. In fact, considering the cannabalistic tendencies of Asellus it may be that the 20-30% mortality represents a considerable source of food to the young as they develop. In laboratory experiments early embryos died when kept separately in 15^{o}C water in glass tubes; however, when 5 embryos were placed together it was found that they

developed to the juvenile stage quite rapidly but only one or two survived, the rest 'disappearing' i.e. being eaten.

It seems reasonable to conclude then, that eggs or embryos are rarely expelled from the brood pouch, that they are either eaten directly or eaten once attacked by fungi and bacteria, by the remaining young - which may in fact depend on this mortality as a source of food.

2.1.3 Summary of life cycle from field observations

Length of breeding season

The breeding season is usually defined as the period during which ovigerous females or females with empty brood pouches occur in the population. Williams (1960), discussing pre-1960 studies and his own findings, shows a plasticity in the timing of the breeding cycle which relates to geographical factors. As examples he quotes a breeding season from April to September in Konisberg (= Kalingrad) (Leichman, 1891 - quoted in Maercks, 1930), in Loch Lomond (Weerekoon, 1956) and in Warsaw (Rosenstadt, 1888 - quoted in Maercks, 1930) and Maercks himself found the season in Berlin to be March/ April to September.

Williams' (1960) own data from Flintshire, Cheshire and Anglesey indicated February to October, a longer season: as was also found by Fitzpatrick (1968, from Durham area) and Steel (1961, from the Thames).

This would seem to be the situation in a temperate climate, intermediate between the north European situation with its short season limited to Spring and Summer (e.g. Andersson, 1969; Lakes Erken and Pajep Måskejaure, Sweden) and the more equable southern European situation with breeding occurring all year round, though usually with a period of maximum (e.g. Balesdent-Marquet, 1955).

It is interesting to note, though at present inexplicable, that there is a small anomaly from Sweden and Denmark in that taking Andersson's (1969) results (egg-bearing females found May-August), Berglund's (1968; egg-bearing females found February to September in pond Billingdammen) and Wesenberg-Lund's (1939; egg-bearing females found all year round in Denmark) there would seem to be a complete range of breeding seasons in a much smaller latitude range. Much more climatic and population dynamics data would be needed from each site to begin to explain this.

Fig.7 shows that in 1975 the breeding season began in late March and extended to October. In 1974 the release of the first recruitment in early June suggests that initiation of breeding was in late March, using Williams (1960) data on incubation times related to temperature.

Loch Leven therefore fits into the intermediate temperate situation. However, there is a difference

between this and other results from the British Isles. Williams (1960 - Flintshire, Cheshire and Anglesey), Fitzpatrick (1968 - Durham) and Steel (1961 - River Thames) found that breeding was inhibited only from November to January, but in Loch Leven inhibition extends from October to February. The geographical plasticity of the breeding season suggests that temperature is the limiting factor; however, although the Thames has a smaller temperature range of approximately 3°C to 20°C (Berrie, 1972) than Loch Leven which is 0°C to 22°C with only rare ice formation; and although Fitzpatrick (1968) shows a stable 40 cm deep minimum temperature of 3.7°C, these may not be the direct cause of the difference.

Vitagliano Tadini and Montalenti (1965) have suggested that the important parameter in determining the period of reproductive stasis is the gradual decrease or gradual increase in total day length with respect to an initial 12 hour day. However, since initiation of reproduction occurs at the equinox period it is difficult to see how the difference between the Loch Leven study and those further south may be explained in terms of differences in day length.

Asellus in Loch Leven was observed to feed mainly on benthic algae rather than on decaying macrophytes as found in most of the other studies. Thus the climate may affect the food availability or food condition for Asellus thereby delaying its ability to breed.

Thus the underlying cause of the plasticity of the breeding season, though shown to be connected with climate, cannot be positively identified from the present study. However, the results suggest that it is the temperature which is controlling the reproductive stasis.

Number of broods

To determine the number of broods produced by an individual it is necessary to know the sequence of events in reproduction. Since reference will be made to these events, the concise and well authenticated account from Williams (1960) is reproduced here for reference:

> 'some time before the female is ready to oviposit she is seized by the male who, using his first and fourth peraeopods, places her, dorsal side uppermost, between his legs. The female is kept in this position by the male's fourth pair of peraeopods. This association of male and female is known as precopulation and it may last for less than a day to more than a week, depending on the temperature, the nearness of the female to oviposition, and other factors. Before oviposition the female must moult, and ... this takes place in two phases. During the first phase the posterior part of the old cuticle is cast, revealing the open vaginae situated ventro-laterally on the fifth thoracic segment. Copulation may occur as soon as this phase has been completed, and is effected principally by the endopodites of the second pleopods of the male. In copulation, the male extends either its left or right endopodite downwards and forwards into the gap between the respectively left or right fourth and fifth female peraeopods, and introduces sperm into the vagina of that side. As soon as the endopodite has discharged all its sperm it is withdrawn, and the process repeated by the endopodite of the other side. The whole process may occur several times, but between each discharge there is a pause whilst

> the sperm sacs of the endopodites are refilled by the penes. When copulation has completely finished, the male and female separate, and the female undergoes the second phase of her moult. In this phase the anterior part of the old cuticle is cast revealing the large oostegites which form a brood pouch beneath the anterior part of the thorax. The oostegites arise from the bases of the first four pairs of peraeopods, but very rarely ... only the first three pairs of peraeopods may possess oostegites. Fertilization is internal. The eggs are released into the brood pouch shortly after the second phase of the female moult has been completed, and are incubated for a varying period of time. Females which are incubating eggs are said to be ovigerous. The eggs develop within the brood pouch into juveniles which are released when they are approximately 1 mm long. After the release of the juveniles the female undergoes a further moult whereby she loses her brood pouch, her oostegites being reduced once more to small club shaped lamellae. The moult preceding oviposition has been termed the 'Parturialhäutung' by Emden (1922); the moult following the release of the juveniles has been termed the 'Zwischenhäutung' by Haemmerli-Boveri (1926). In the breeding season these moults are normally consecutive, whilst in the non-breeding season successive moults occur without the production of a brood pouch.'

The first recruitment of juveniles is released into the population by the overwintering females in June. The long development time is due to the low temperatures in the loch at that time, but when these juveniles reach a sexually mature state (mid July 1974, late July 1975) the loch temperature is at its maximum and stays in excess of 15^{o}C until late August/early September. At these temperatures development time from oviposition to release is from 2-3 weeks and the initial recruitment itself may have released juveniles by mid August.

As well as the time taken to incubate a brood (Parturialhäutung-Zwischenhäutung) it is important to consider the intermoult period : Zwischenhäutung-Parturialhäutung. Williams (1960 found this period to be much more inconsistent than the incubation period and to vary from 8 days (between first and second broods of a female matured in its first year) to $1\frac{1}{2}$-2 weeks between the late Summer and Autumn broods of females producing 3 broods in their first year. It should be possible to derive an average value from the Loch Leven data.

Returning to Fig.7 the pattern is that a peak of ovigerous females in March/April gives rise to a peak of juveniles in June (1974, slightly later in 1975). Considering 1974 data only, this peak of juveniles matures and a second peak of ovigerous females appears in mid July, again followed by a peak of juveniles. These juveniles have little chance of becoming sexually mature and incubating a brood due to falling temperatures in late August, therefore the peak of ovigerous females in late August must be the primary recruitment incubating a second brood and releasing it late August/early September. With a temperature of just over 15°C the incubation period should be approximately 3 weeks so that between release in late July and oviposition in early/mid August there is a period of approximately 2 weeks which must be the duration of the intermoult period.

Whilst complicated by the lack of perfect synchrony in release and oviposition, this estimate from population data must reflect the average length of time between Zwischenhäutung and Parturialhäutung.

This data clarifies the problem of whether the bimodal peak of ovigerous females was an artifact due to the loss of the overwintered females. This suggestion now seems unlikely.

The 1975 data shows only two peaks of juvenile recruitment but as in 1974 there are peaks of egg-carrying females in late July and early September so that a similar cycle of events must have occurred.

Thus in Loch Leven the overall pattern is that overwintering females release their broods in June. From the size data it is likely that they do not produce another and are absent from the population by the end of July, whether by 'natural causes' or by fish predation which will naturally tend to eliminate the larger individuals.

Their offspring are sexually mature by July and release their own offspring about the third week in July. After a two week intermoult period, oviposition and incubation leads to a second brood being released in September.

The offspring of the June recruitment show no sign that they breed that year; early ones may do, but

in general they just grow in size until the low temperatures of winter arrest growth.

Obviously the lack of synchrony must produce a considerable amount of variation but in general, specimens released in the Spring breed twice before overwintering and once after; whereas specimens released later in the breeding season breed only after overwintering.

Reference to other studies shows that there is as much variation in the number of broods produced as there is in the breeding season timing. Steel (1961) found a simple situation where females released in Spring breed in Autumn, overwinter and die after producing a Spring brood. Those females released in Autumn overwinter and produce only one brood before dying. Work done by Fitzpatrick (1968) in the Durham area produced similar results. Low temperatures in the environments studied by Andersson (1969) produced a similar situation, individuals either living for two years and reproducing in the second, or living one year and reproducing once only.

In contrast, Williams (1960) found a much more complicated situation with Spring released juveniles producing 3 broods before overwintering and 3 broods afterwards so that the maximum number of broods was 6, with smaller numbers if released later in the breeding season. In his habitats, however, the first release of

juveniles took place in April/May so that the period of time during which juveniles were being recruited was much longer than in Loch Leven, where recruitment began in June.

Variation in temperature regime from habitat to habitat is a possible cause of this variation: higher temperatures shorten times of incubation and growth to maturity and possibly also alter the length of the intermoult period so that more broods can be produced per unit time. Variation in the timing of temperature changes can alter the length of the available breeding time, allowing more broods to be produced.

Variation in predatory pressure may account for the loss of large overwintered females from the population in Loch Leven, whereas they were of considerable importance in Williams' study, producing 2 more broods.

Food availability and quality may also be factors affecting reproductive capacity and more information on the feeding of Asellus in Loch Leven is supplied later.

2.2 Quantitative Dynamics

2.2.1 Introduction

A solution to the difficulty of quantitative sampling was indicated by terrestrial studies (Southwood, 1966); from which it seemed possible that a capture/recapture technique might provide useful population estimates so that combination with qualitative data

would produce an estimate of the population biomass and the magnitude of its seasonal variation.

The limitations of the technique are related to the capture/recapture method used and to the sampling methods, so that, throughout the study, note must be taken of the following assumptions which underlie most methods of analysis of the Lincoln Index Type (from Southwood, 1966):

1. The marked animals are not affected by being marked and the marks will not be lost.

2. The marked animals become completely mixed in the population.

3. The population is sampled randomly with respect to its mark status; this assumption has two aspects: firstly that all the individuals of the different age groups and both sexes are sampled in the proportion in which they occur; secondly, that all the individuals are equally available for capture irrespective of their position in the habitat.

4. Sampling must be at discrete time intervals and the actual time involved in taking the samples must be small in relation to the total time. (Only applicable to multiple recapture methods).

On the basis of these assumptions the method described below was evolved. Subsequent reference will be made to the fulfilment of these assumptions.

2.2.2 Marking the animals

Neutral red was found to be an ideal marking agent. Although a poor stain at the pH of the loch water it was readily taken up by decaying leaves, and when these were eaten by Asellus the stain produced two deep crimson bands of coloration, one on either

side of the gut. This corresponds to the position of the two pairs of hepato-pancreatic caeca - structures which fulfill the role of the vertebrate liver and pancreas and play a prominent part in primary food absorption (Vonk, 1960).

This staining was found to persist, even when no stained food was available, for several days; it did not affect the behaviour of the animals, and was immediately recognisable when sorting animals in a transparent tray over a diffuse light source.

When alive and healthy the body itself was clear of stain, but on death the stain coloured the rest of the body pale pink - providing a useful indication of unhealthy specimens before release.

On placing in 5% formalin for preservation the animals produced a crimson regurgitation from the mouth, providing a useful check during sorting and preservation of the samples.

2.2.3 The Capture/Recapture Method

To avoid disturbing the area of the experiment animals were taken from close by on the day preceding the release.

In the laboratory a number were measured in the range 4.0 mm to 9.0 mm to the nearest 0.5 mm above (using an eyepiece graticule in a dissecting microscope); however, no attempt was made to determine the sex of the

individuals as this increase in handling caused some damage and subsequent mortality.

Measured individuals were placed in polythene screw topped containers with decaying willow leaves stained with neutral red, and aerated overnight at a temperature similar to the loch temperature.

The following day they were transported to Loch Leven, the leaves removed and the animals checked so that any mortalities could be taken out and noted. An area of stony substratum under a depth of approximately 25 to 40 cm of water was selected such that there were stones with a covering of Cladophora in the area. Then two steel quadrat frames were placed side by side to delimit an area $\frac{1}{2}$ x 1 m. Within this area the marked animals were released. The frames were 20 cm deep and rested on the stones of the bottom so that it was easy to ensure that the individuals all landed on stones within the area. The frames did not prevent movement across the boundaries of the area but as the experiment was carried out during a period of the day when Asellus is inactive it was expected, and indeed observed, that they crawled under the stones immediately and no other movement was seen during the 2 hour period allowed for intermingling with the resident population under the stones.

The quadrats were then cleared of as many animals as possible by lifting and enclosing each stone in a net

so that animals adhering to it could be picked off, then netting up the gravel and examining it in a white container on the shore.

On returning to the laboratory the samples were sorted in transparent photographic dishes with an illuminated opal glass plate beneath so that marked animals could be seen clearly. The animals sorted from the samples were preserved, with marked separated from unmarked ones since the stain bleaches in formaldehyde.

On the first sampling occasion (August 8/1974) 5 quadrats of $\frac{1}{2}$ x $\frac{1}{2}$ m were cleared for comparison with the mark/recapture experiment. In the calculations these are used as the qualitative sample; however on subsequent occasions the recapture samples, minus the marked (i.e. imported) individuals, were taken as the qualitative sample to eliminate error caused by patchiness in the distribution and no quadrat samples were taken.

This method most nearly conforms to the basic assumptions previously noted:

1. The mark is persistent over the time period of the experiment and the animals seem in no way affected by it. It is considered a minor hazard that the stain is present in the faeces and if marked animals are contained with unmarked animals the stain is taken up by the unmarked animals due to coprophagy. This only happens after a suitable time has elapsed for microbial recolonization of the faecal pellets and thus this does not cause problems in this experiment.

2. Mixing in the population is aided by scattering evenly over the area. All experiments were carried out around midday when the animals are not generally active on the rocks but lie adpressed to the undersides. When the released animals fall onto a stone they immediately clamber under the stone, thus entering the general population.

3. Elimination of sampling bias is attempted by not just sampling the area but by trying to completely remove all Asellus from within the two quadrat frames. (N.B. It is irrelevant that two quadrat frames are used, they are placed together to delimit a $\frac{1}{2}$ x 1 metre area, which is a convenient size to work with.)

4. Assumption 4 relates to repeat recapture methods and is not relevant here.

2.2.4 Calculation of Results

Although the basic capture/recapture method is centred around the 'simple Lincoln Index' (Lincoln, 1930 - quoted in Southwood, 1966)

where $P = \frac{an}{r}$

P = estimate of total population

n = number of individuals in second sample

a = total number marked and released

r = total recapture of marked animals,

it has been shown by Bailey (1951, 1952) that it develops an unacceptable bias where there are small values of r (i.e. $r < 20$). A modification suggested by Bailey (1952), using the same notation, is:

$$P = a\,(n+1) \,/\, (r+1)$$

For practical purposes an estimate of the variance of P is given by:

$$\text{var } P = \frac{a^2\,(n+1)(n-r)}{(r+1)^2\,(r+2)}$$

However some allowance needs to be made for the marked animals being brought in from outside the sample area.

Taking:

$$p = \frac{a\ (n+1)}{r+1}$$

let $\check{X}$ be the total population, since P is the total population plus imported marked individuals:

$$P = \check{X} + a$$

Then:

$$\check{X} + a = \frac{a\ (n+1)}{r+1}$$

$$\check{X} = \frac{a\ (n+1)}{r+1} - a$$

$$= \frac{a\ (n+1) - a\ (r+1)}{r+1}$$

$$= \frac{an + a - ar - a}{r+1}$$

$$= \frac{a\ (n-r)}{r+1}$$

whereas var P becomes var $\check{X}$ without change

$$\text{var}\ \check{X} = \frac{a^2\ (n+1)\ (n-r)}{(r+1)^2\ (r+2)}$$

Since there is only a single estimate on each occasion the standard error is $\sqrt{\text{var}}$ and the 95% confidence limits will increase as the size of the estimate increases, without reflecting the relative accuracy of the estimate. Therefore, as a measure of confidence in the estimates relative to each other, the coefficient of variation will be given:

$$\text{C.V.} = \frac{S}{\check{X}} = \frac{\sqrt{\text{var}}}{\check{X}}$$

Initially the total number of marked and recaptured animals were used to calculate the total population size, but since the efficiency of capturing small animals is poor and the number of large animals is small, it was decided that a more accurate method would be to split the results into 0.5 mm size classes and work from the most accurate estimate. The criterion for this was the value of the standard error as a percentage of the estimate: the smallest being considered the more accurate.

The quantitative sample data was used to apportion the animals to their size classes so that biomass per square metre could be calculated using the length to dry weight relationship for individual specimens as outlined in Appendix 1.

2.2.5 Results of the Capture/Recapture Programme

Using the total data the population estimates for the delimited area used in the recapture method were as shown in Table 3.

TABLE 3: Summary of data and calculated values for capture/recapture samples, using total values.

DATE	a	r	n	$\check{X}$	var	C.V.
08.08.74	400	81	339	1258.5	158.6	0.1260
20.11.74	192	84	554	1061.7	124.4	0.1172
05.03.75	108	44	125	194.4	35.8	0.1839
18.04.75	215	95	203	241.9	33.8	0.1395
24.05.75	191	46	172	512.0	86.6	0.1691
13.06.75	179	18	205	1761.7	413.5	0.2347
11.07.75	212	74	983	2569.4	306.7	0.1193
08.08.75	225	92	724	1529.0	168.9	0.1105
08.10.75	200	65	880	2469.7	313.7	0.1300
03.12.75	210	114	225	202.7	26.9	0.1300

[$\check{X}$ is the estimate of the number of individuals in the half square metre taken as a sample area, and the units of a, r and n are the numbers of animals released or captured within that half square metre.]

As the values shown in Table 3 are for the half square metre sample area, it is necessary to double the population estimate ($\check{X}$) to produce a population estimate in terms of numbers per square metre. To convert to biomass these estimates can be apportioned to size classes using the size class distribution of the qualitative sample, represented by the unmarked specimens in the sample 'n'. (The first sample, 8 August 1974 is not included since the qualitative sample was taken at the same time but from an adjacent area and hence is

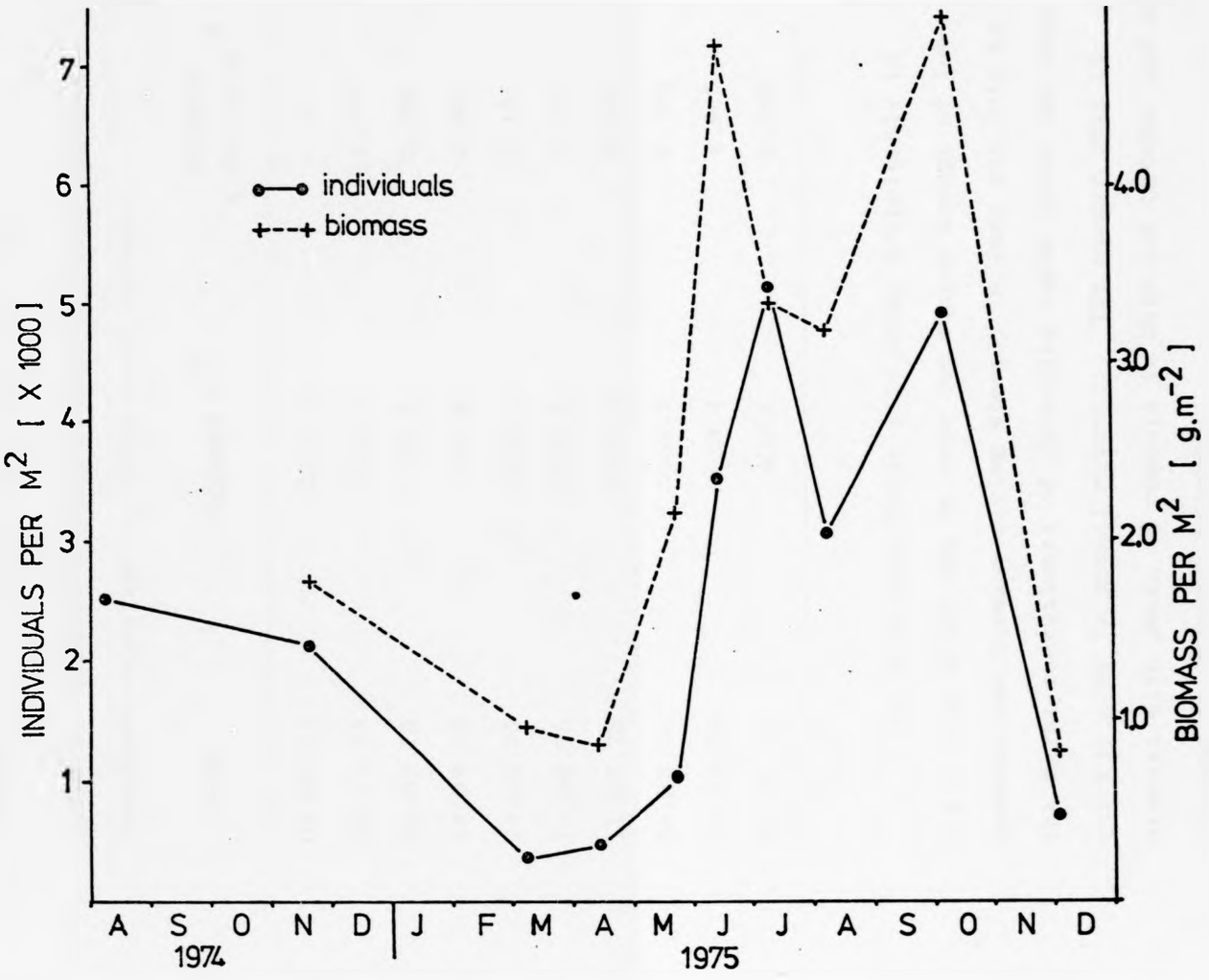

FIG 9. Graph of data from Table showing seasonal variation in numbers and biomass at Carden Point.

subject to error due to the uneven distribution of Asellus). The results are shown in Table 4.

TABLE 4: Numbers m^{-2} and biomass m^{-2} from capture/recapture experiments, using total values.

DATE	NUMBERS m^{-2}	BIOMASS g dry wt m^{-2}
08.08.74	2517.1	-
20.11.74	2123.3	1.777
05.03.75	388.8	0.954
18.04.75	483.8	0.864
24.05.75	1024.1	2.161
13.06.75	3523.5	4.775
11.07.75	5138.9	3.360
08.08.75	3058.1	3.171
08.10.75	4939.4	4.939
03.12.75	405.4	0.829

The data from Table 4 is shown graphically in Fig.9 from which can be seen the winter trough of low numbers and biomass rising steeply in June and July as the first recruitment of juveniles takes place and they quickly grow to sexual maturity. The summer peak is bimodal with peaks of numbers in July and October and of biomass in June and October.

The October peak of biomass is the greatest but by less than 0.20 g/m^2, whereas the earlier peak of numbers

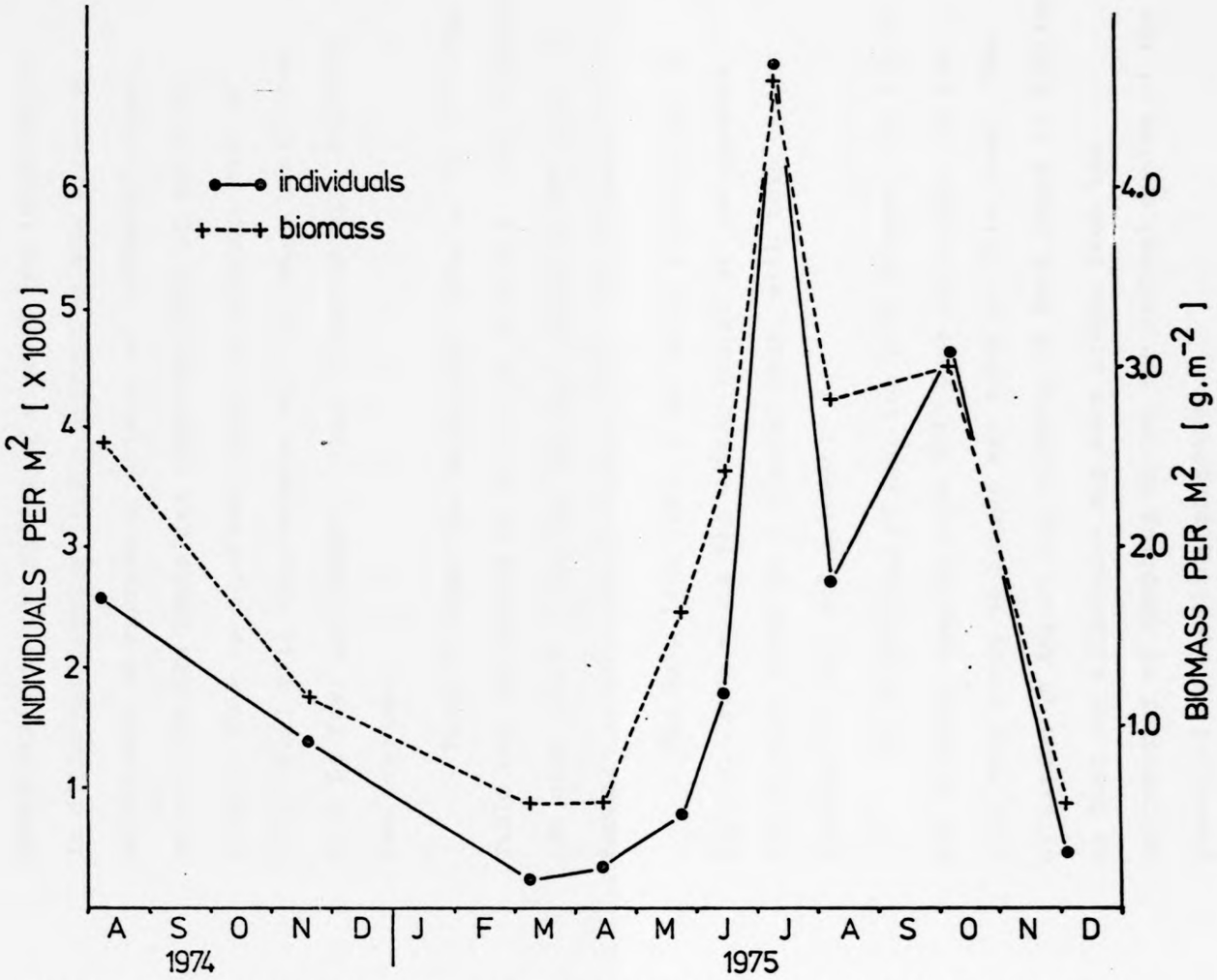

FIG 10. Graph of data from Table showing seasonal variation in numbers and biomass at Carden Point. (Using modified method of calculation.)

is the greater by approximately $200/m^2$.

The modified method of calculation, by its sensitivity to the differing size of the individuals in different samples, takes account of the variable efficiency of capture of animals of different sizes, especially the upper and lower extremes of the size range. This is important since the average size of individual will vary between Winter: when small ones will be few; and Summer: when juveniles will dominate the samples.

Table 5 shows the equivalent data to the previous Table but calculated as described in 2.2.4. For reference the size class producing the most accurate estimate is shown.

The data from Table 5 are shown graphically in Fig.10. Here again the Winter trough of low numbers and biomass rises to a bimodal peak, with both curves peaking in July and October.

It is noticeable that the peak between the August and December samples from 1975 does not appear in the 1974 data since no sample was taken at this time. The situation in August and December of both years is similar so that the difference may have arisen from the infrequency of sampling during the initial months of the quantitative sampling programme.

TABLE 5: Numbers m^{-2} and biomass m^{-2} from the capture/recapture experiments, using modified method. The size-class giving the most accurate estimate is also shown.

DATE	SIZE-CLASS USED IN CALCULATION	TOTAL POPULATION NUMBERS m^{-2}	TOTAL POPULATION BIOMASS g dry wt m^{-2}
08.08.74	- 6.0	2579.7	2.584
20.11.74	- 6.0	1393.9	1.166
05.03.75	- 7.5	243.0	0.597
18.04.75	- 6.0	329.7	0.592
24.05.75	- 6.0	775.4	1.636
13.06.75	- 6.0	1776.5	2.408
11.07.75	- 5.0	7012.3	4.586
08.08.75	- 5.5	2722.5	2.823
08.10.75	- 5.0	4606.8	3.006
03.12.75	- 6.0	496.9	0.573

2.3 Discussion of the Qualitative and Quantitative Population Dynamics

From a qualitative sampling programme much information can be extracted relating to population composition in terms of size classes, sexes and reproductive stages so that a picture of the breeding cycle of the animal may be built up. However, care must be taken that wrong conclusions are avoided; for example, a loss of adult size classes from the population may look like an influx of juveniles into the population when seen on histograms such as are given in Fig.4.

Quantitative samples provide estimates of absolute numbers which are essential for clear understanding of changes in population composition. In the present study the concurrent operation of qualitative and quantitative sampling programmes has enabled much information to be extracted as well as enabling cross reference between results. Thus a measure of the effectiveness of the quantitative method is given by the close relationship between changes in absolute numbers and life cycle phenomena derived from the qualitative data.

Thus the June release of juveniles into the population is accompanied by a dramatic increase in the numbers of animals per square metre and the biomass. Direct comparison of the biomass and numbers curves is not possible since the scales are not comparable, due to the non-linear relationship between length and dry weight and the varying size distribution in the population. However, comparison of the timing of changes in biomass and numbers can be made.

The bimodality of both curves, with peaks in July and October, corresponds closely to the two most important times of release of juveniles. There is no necessity to suggest any hormonal or other mechanism of synchronisation of release: given that there is a certain temperature below which the animals cannot successfully breed, the onset of reproductive activity in the water

will be synchronised by the rising temperatures during Spring. Similarly it follows that knowing the temperature regime, it should be possible to predict the life cycle in the field if all the intervals of the cycle are known (Parturialhäutung to Zwischenhäutung - i.e. the incubation period, Zwischenhäutung to Parturialhäutung - the intermoult period) and the time taken for growth to maturity, as well as a quantification of their relationship to temperature.

There is no indication that the observed synchrony is any more than the result of the animals repeating the incubation and intermoult cycle as often and as rapidly as the ambient temperature permits.

CHAPTER 3

PRODUCTIVITY

3.1 Introduction

Population dynamics in terms of numbers and biomass can only go so far in describing a population. When considering that population as a component part of an ecosystem it becomes necessary to extend the description to encompass the energy involved in the population, not only in the population level as it stands at any one time (standing crop) but in terms of energy flow through the population. Thus it is possible to quantify not only the energy content of the population at any one time, but also to quantify that produced and then lost in any form (e.g. predation) over a period of time prior to sampling.

The basic information for this quantification is contained within the population dynamics data. Other information is extracted from the literature where it is of such a nature that it is likely to be constant for the species and where it can be substantiated by several studies.

3.2 Method of Growth Increments

Fitzpatrick (1968) derived a productivity estimate for Asellus aquaticus but experienced considerable difficulty as he considered it to be breeding over an extended period, thus falling in between the two simple cases of animals breeding continuously and those breeding once, at a particular time of the year.

TABLE 6 : Calculation of production due to growth when recruitments are seperated.
(R1 = Initial recruitment, R2 = Late recruitment.)

SAMPLE DATE (month)	NUMBER IN RECRUITMENT $N(m^{-2})$	MEAN INDIVIDUAL DRY WEIGHT $\bar{w}$(mg)	WT. INCREMENT SINCE PREVIOUS SAMPLE $\bar{w}$(mg)	MEAN N^o/m^2 DURING PERIOD t $\bar{N}$(thousands)	PRODUCTION INCREMENT $\bar{N}\,\bar{w}(g\ m^{-2})$
R1					
JUNE*	85.50	0.1822	–	–	–
JULY	7012.31	0.6540	0.4718	3.5489	1.6744
AUGUST	2722.53	1.0369	0.3829	4.8674	1.8637
SEPT**	603.36	1.7843	0.7474	1.6629	1.2429
				R1 Production Increment ($g\ m^{-2}$)	4.7810
R2 (Assuming that after 9 September R1 is numerically insignificant).					
SEPT 9**	3046.67	0.3037	–	–	–
SEPT 22	4100.00	0.7195	0.4158	3.5733	1.4858
OCTOBER	4606.75	0.6525	-0.0670	4.3534	-0.2917
DECEMBER	496.86	1.5320	0.5007	2.5518	1.2777
MARCH	243.00	2.4568	1.3036	0.3699	0.4822
APRIL	329.71	1.7955	-0.6613	0.2864	-0.1894
MAY	775.40	2.1099	0.3144	0.5526	0.1737
				R2 Production Increment ($g\ m^{-2}$)	2.9383

Total annual production due to growth = 7.7193 $g\ m^{-2}$.
Since mean calorific value = 3.0355 Kcal/g dry wt. (Fitzpatrick, 1968)
Total annual production due to growth = 23.4319 Kcal m^{-2}
= 98.1094 KJ m^{-2}.

* Taking up to 3.5mm size class (inclusive) as R1.
** Taking up to 5.0mm size class (inclusive) as R2.

However, the population dynamics data presented in Fig.4 and Fig.7 provides sufficient information to consider recruitment in terms of two main component recruitments: the June initial recruitment and the September late recruitment, so that each can be considered separately as being released at a particular time of the year.

As has already been discussed (2.3) the synchrony of release is not perfect; however, the inaccuracy involved is likely to be small compared with the inaccuracy inherent in the method of Saito (1965: as used by Fitzpatrick, 1968) where a mortality rate derived from Winter falls in population size is applied to a situation where predation in Summer is very high relative to Winter levels.

Thus separated, the recruitments can be treated as age classes with declining numbers due to mortality and increasing mean individual weight due to growth. Crisp (1971) has described a method by which it is possible to sum the increments in weight of the age classes, allowing for the decline in numbers, so that the total production due to growth is derived. By calculating the mean weight increment between sample dates and the mean number of animals during the period between samples, the method estimates the production lost due to mortality or emigration before the end of the period as well as that remaining. The steps in this computation are shown in Table 6.

As well as growth, reproduction is a component of production and it is thus necessary to estimate how much energy was diverted from growth into reproductive products. As is usual, the productivity due to sperm production is not considered as it is impossible to derive from the measurements taken. The assumption is made that the energy value is small enough to be disregarded and 'reproductive products' is taken to mean eggs only.

Saito (1965) estimated the number of offspring produced by his population of terrestrial isopods by considering the number of adult females at each sample date, the proportion of these that were ovigerous, and the number of eggs produced by a female of the mean size at that time. He assumes an arbitrary figure of 50% for the calorific value of the yolk consumed in respiration before release so that the calorific value of the egg produced is twice that of the young released, and thus estimates the calorific value of the reproductive products of the whole population.

Using the numerical data presented in the quantitative dynamics section (2.2.5) and the qualitative sample data, it is possible to derive corresponding values for the number of females with eggs, the mean size of such females, and the numbers of eggs these females would on average carry, for each month. As shown in Table 7 the yearly egg production is potentially 27.54×10^3 eggs m^{-2}.

TABLE 7: The number of ovigerous females and deposited eggs per m^2 during the breeding season of 1975.

DATE	NUMBER OF OVIGEROUS FEMALES m^{-2}	MEAN LENGTH	NUMBER OF EGGS/FEMALE	ESTIMATED TOTAL EGG NUMBERS m^{-2} thous'
10 May	186.02	6.82	65.19	12.13
13 June	114.02	4.73	30.56	3.48
11 July	131.15	5.12	34.00	4.46
8 Aug	176.57	4.74	30.69	5.42
9 Sept	78.97	4.37	25.93	2.05
			Total number of eggs =	27.54×10^3

Since the young are released at a length of 1.1 mm which corresponds to 0.0259 mg dry weight the total potential release would be 713.29 mg dry wt m^{-2}; this converted to calories using a caloric equivalent of 3.0355 Kcal/gm dry weight (a mean of the values for males and females given by Fitzpatrick (1968)) would be 2.165 cal m^{-2}. Making Saito's (1965) assumption that the energy consumed by the young is equal in calorific content to that of the released young, the energy contained by the eggs is estimated at 2.165 + 2.165 = 4.33 Kcal m^{-2} year.

The potential release and the actual release are not usually the same due to infertility of eggs and cannabalism of the developing embryos - components of the brood pouch mortality estimated to be 32.47% between eggs and late embryos in 1975. However, since at least some

of this loss is converted to body weight due to consumption by the offspring (see 2.1.2), it will be regarded as an unknown quantity of small enough magnitude to be omitted from the calculations. This estimate can be added to the estimate of production due to growth to give a combined productivity for growth and reproduction of 116.24 KJ m^{-2} yr^{-1}.

3.3 The McNeill-Lawton Relationship

From an examination of results from productivity studies on 42 poikilotherms and homeotherms (including Fitzpatrick's (1968) data on Asellus aquaticus, Saito's (1965) data on Ligidium japonica and data on Asellus militaris from Teal (1957) McNeill and Lawton (1970) produced regression equations for annual production and annual respiration for short and long lived poikilotherms (short $\leq$ 2 years $<$ long). Used with caution these equations are suggested as a short cut way of predicting energy flow through a population in which either annual production or annual respiration is known and the other is impossible to determine by any other method. It depends upon very accurate data for numbers of animals per unit area. In the present study it forms a useful check, being a second way of determining annual productivity from the same basic data.

The relationship necessitates the determination of the oxygen consumption of Asellus at different temperatures. Extensive work on this was carried out by

Fitzpatrick (1968) and it was decided that his data could be used rather than laboriously repeating the determinations. He found that:

where: $y = mm^3\ O_2\ ind^{-1}\ hr^{-1}$

and: x = dry wt (mg.)

then:

at 10°C

$$\log_{10} y = 0.6314 \log_{10} x - 0.2168$$

at 15°C

$$\log_{10} y = 0.6890 \log_{10} x - 0.1147$$

at 20°C

$$\log_{10} y = 0.7647 \log_{10} x - 0.1307$$

and at an unspecified temperature, for ovigerous females:

$$\log_{10} y = 0.8107 \log_{10} x - 0.1712$$

Strangely, Fitzpatrick concludes ".... it can be seen (from his graph of the 3 lines) that they are very similar, showing no progressive increase or decrease in respiratory rate with temperature.", and thus concludes that the Q_{10} for Asellus aquaticus is 1.0. This conclusion hardly seems justifiable from consideration of the slope coefficients of the lines, though he omits confirmatory statistics and there is insufficient data in the text for a test to be made.

Therefore in using the formulae on the Loch Leven data, the 10°C and 20°C lines are used and the year apportioned appropriately. The numbers of animals in

TABLE:8 Number of individuals and total oxygen consumption for each size class; data used in calculation of total annual respiration.

	-1.5	-2.0	-2.5	-3.0	-3.5	-4.0	-4.5	-5.0	-5.5	-6.0	-6.5	-7.0	-7.5	-8.0	-8.5	-9.0	-9.5	-10.0	-10.5
JAN		9.01 1.13	13.43 2.48	17.93 4.54	13.43 4.41	17.93 7.37	44.87 22.42	53.88 32.03	85.32 59.31	80.82 64.75	94.25 86.03	76.31 78.52	94.25 108.48	94.25 120.36	58.38 82.14	22.44 34.65	9.01 15.17		4.5 8.90
FEB		5.42 0.68	8.08 1.49	10.78 2.73	8.08 2.56	10.78 4.43	26.98 13.48	32.40 19.26	51.30 35.66	48.59 38.94	56.67 51.73	45.89 47.22	56.67 65.23	56.67 72.37	35.10 49.39	13.49 20.83	5.42 9.13		2.7 5.36
MAR					6.00 1.97	18.00 7.40	24.00 11.99	9.00 5.35	6.00 4.17	21.00 16.83	12.00 10.95	27.00 27.78	39.00 44.89	30.00 38.31	18.00 25.33	15.00 23.16	15.00 25.26	3.0 5.48	
APR				3.05 0.77	9.16 3.01	18.32 7.53	33.58 16.78	30.53 18.15	39.69 27.59	42.74 34.25	36.63 33.44	39.69 40.84	33.58 38.65	21.37 27.29	18.32 25.78	3.05 4.71			
MAY					6.15 2.02	0.00 0.00	12.31 6.15	30.77 18.28	92.31 64.17	104.62 83.83	196.93 179.75	129.24 132.99	110.77 127.50	49.23 62.87	30.77 43.29	6.15 9.50	6.15 10.36		
JUN	9.50 0.55	28.50 3.11	19.00 3.33	9.50 2.44	19.00 6.69	57.00 26.29	199.50 116.63	304.00 219.37	408.50 356.29	266.00 275.58	247.00 299.86	152.00 213.26	28.50 45.77	28.50 51.96					
JUL	277.71 16.02	624.86 68.17	585.57 120.49	802.29 205.71	501.43 176.45	763.72 352.30	1018.3 595.29	1141.7 823.87	702.00 612.28	316.29 327.68	115.71 140.47	46.29 64.94	15.43 24.78				KEY		
AUG	38.77 2.24	47.39 5.17	81.85 14.36	73.23 18.78	129.23 45.48	163.70 75.51	400.62 234.20	624.63 450.73	521.24 454.63	430.78 446.29	180.93 219.65	17.23 24.17	8.62 13.84	4.31 7.86			ind./m^2 $mm^3O_2/m^2/hr.$		
SEP	222.69 16.44	418.08 52.22	450.84 83.36	651.69 164.88	418.08 137.42	467.22 192.07	320.58 160.19	249.87 148.52	222.69 154.81	184.86 148.13	168.48 153.79	86.97 89.49	32.76 37.71	5.46 6.97					
OCT	169.57 12.52	231.74 28.94	401.31 74.20	616.09 155.87	401.31 131.91	700.87 288.13	774.35 386.94	678.26 403.16	322.18 223.98	158.26 126.81	73.48 67.07	45.22 46.53	22.61 26.02	11.50 14.69					
NOV	51.80 3.82	76.13 9.51	140.00 25.89	214.38 54.24	152.25 50.04	254.28 104.53	268.10 133.97	240.45 142.92	134.93 93.80	98.53 78.95	48.48 44.25	36.40 37.46	24.15 27.80	10.33 13.19					
DEC		7.57 0.95	25.22 4.66	37.83 9.57	42.88 14.09	58.01 23.85	45.40 22.69	47.92 28.48	52.96 36.82	73.14 58.61	37.83 34.53	32.79 33.74	25.22 29.03	10.09 12.89					

TABLE 9: Calculation of annual oxygen consumption from monthly summed respiration rates.

MONTH	$mm^3 O_2/m^2/hr.$	Hours in month	Ltrs $O_2/m^2/mth.$
JAN	732.7050	744	0.5451
FEB	440.5696	672	0.2961
MAR	248.8785	744	0.1852
APR	278.7829	720	0.2007
MAY	740.7231	744	0.5511
JUN	1621.1122	720	1.1672
JUL	3528.4636	744	2.6252
AUG	2012.9108	744	1.4976
SEP	1546.0083	720	1.1131
OCT	1986.7787	744	1.4782
NOV	820.3802	720	0.5907
DEC	309.9024	744	0.2306
		ANNUAL RESPIRATION =	10.4808

49.8886 Kcals/m^2 (1ml C_2 = 4.76 cals; Ivlev, 1934)

Then when:

$$\log P_{(ann)} = 0.8262 \log R_{(ann)} - 0.0948$$

(McNeill & Lawton, 1970)

$$P_{(ann)} = 20.32 \text{ Kcal}/m^2/yr.$$

$$= 85.0798 \text{ KJ}/m^2/yr.$$

where:

$P_{(ann)}$ = Annual Production

$R_{(ann)}$ = Annual Respiration

each size class is determined for each month and the total oxygen consumption per hour calculated using the appropriate consumption rate for the size and temperature. This data is shown in Table 8, and the final total annual respiration and production shown in Table 9.

3.4 Discussion of Productivity Study

Two estimates of the productivity of Asellus aquaticus have been derived, one in section 3.2 (116.24 KJ $m^{-2}yr^{-1}$) and one in section 3.3 (85.08 KJ $m^{-2}yr^{-1}$). Of these, the McNeill-Lawton one must be the least sensitive to field parameters special to this population since it is merely an estimate based on an empirical relationship. In addition it relies heavily on the oxygen consumption as determined by laboratory measurements being relevant to field consumption rates whereas the basal or resting metabolism or any standard condition chosen in the laboratory is likely to be similar to only a few field conditions. Activity levels will affect oxygen consumption unpredictably, and there will be cyclic variations in oxygen requirements related to condition and state of the breeding cycle. Fitzpatrick (1968) indicated that gravid females had a different rate of oxygen consumption per unit weight than non-gravid females and Lang and Ruzickova-Langova (1951) found differences in the quantity of consumed oxygen between Summer and Winter, as well as daily fluctuations with minima around 11 a.m. to 1 p.m. and maxima at 5-6 p.m.

Thus the annual oxygen consumption is likely to be inaccurate and the McNeill-Lawton regression equation for annual production and annual respiration can only magnify this inaccuracy since the 95% confidence limits on the regression coefficients are high. Thus even when the poikilotherms are sorted into short and long lived species, the confidence limits for the short lived ones (relevant to Asellus aquaticus) are $\pm$ 0.4312 for log $P_{(ann)}$ and $\pm$ 0.4598 for log $R_{(ann)}$ in the equation

$$\log P_{(ann)} = 0.8262 \log R_{(ann)} - 0.0948$$

Nevertheless, it may provide a useful estimate of annual production where no other method is possible, so long as its limitations are accepted. It is useful here as a second method of calculating productivity from the same basic biomass data.

The estimate of 116.24 KJ $m^{-2}yr^{-1}$ derived from growth increments combined with reproduction data may be expected to be more sensitive to the individual character of this population since it takes into account more information derived from the sampling programme and should therefore be the more accurate estimate. However, there is a further refinement which may be made, since as well as production in terms of growth and reproduction there is a quantity of material which is lost as exuviae each time the animal moults to increase in size. Some estimate of this can be made using data from other studies.

Fitzpatrick (1968) estimated that a female requires 11 moults to reach maximum size and a male requires two more. This, combined with an exponential relationship between the weight of the exuvium and the size of the animal producing it, and a calorific value for exuviae of 0.816 Kcal/g dry produced an energy loss as exuviae equivalent to 40% of the assimilated energy over a year. Teal (1957) used a value of 10% of the energy passing through his population of Asellus militaris, based on his study of chironomid moulting, but suggested that the value would probably be less than 10%. Fitzpatrick's value will be used to refine the productivity estimate by calculating an equivalent value for energy loss as exuviae and adding it to the original estimate. Since the energy loss per square metre per year in Fitzpatrick's study was the equivalent of 17.21% of that used in growth, the 116.24 KJ $m^{-2}yr^{-1}$ for growth and reproduction in the present study becomes 133.12 KJ $m^{-2}yr^{-1}$ when an equivalent value is added.

Taking the calorific value of exuviae as quoted, the weight of exuviae is equivalent to 4.9391 g $m^{-2}yr^{-1}$ so that the total estimated production, when converted to dry weight values, is 14.09 g $m^{-2}yr^{-1}$ and the annual production/mean biomass ratio ($P_{(ann)}/\bar{B}$) for the year is 7.05. It must be emphasised that these values are for the study area at Carden Point and although they are proposed as an estimate for the type of rocky substratum found in some areas of the loch, they cannot be generalised as values for the whole loch.

There are few studies on Asellus with which to compare either the levels of production or the $P_{(ann)}/\bar{B}$ ratio, which is an index of the efficiency of biomass production. Andersson (1969) studied two Swedish populations of Asellus aquaticus: finding the production in Lake Pajep Måskejaure (1966-7) to be 16.70 g $m^{-2}yr^{-1}$ (= 212.25 KJ $m^{-2}yr^{-1}$) and in Lake Erken 31.60 g $m^{-2}yr^{-1}$ (= 401.62 KJ $m^{-2}yr^{-1}$) with $P_{(ann)}/\bar{B}$ ratios of 1.96 and 2.03 respectively. The latitude and temperatures were such that in these studies there was a single recruitment and a life span of two years in the more northern Lake Pajep Måskejaure and one year in Lake Erken. However, the habitat consisted of abundant vegetation (mosses, Nitella sp, Isoetes sp, Potamogeton sp, Myriophyllum sp. and Ranunculus sp; with Cladophora aegagrophila dominating the Lake Erken site.)

Thus it may be justified to say that the vegetation provided abundant food and cover so that biomass was high but that the cold climate slowed growth and restricted reproduction so that productivity was slow relative to more temperate populations such as that of Loch Leven. Thus although the productivity per unit area was greater than at Carden Point, its efficiency of production in terms of unit biomass was smaller. (Hence mean biomass was 8.52 and 15.59 g dry wt m^{-2} compared with 1.997 g dry wt m^{-2} for Carden Point (mean of sample totals); but with a $P_{(ann)}/\bar{B}$ of 1.96 and 2.03 compared to 7.05).

Teal (1957) worked with Asellus militaris and found a productivity of 437.5 KJ $m^{-2}yr^{-1}$ in a temperate cold Spring, and from his data can be calculated a $P/\bar{B}$ of 12.60. Here again there was a greater productivity than at Carden Point, but in this case it came from a small biomass ($\bar{B}$ = 2.73 g dry wt m^{-2}) with a high production efficiency.

Whilst it is likely that the efficiency of production is limited to a large extent by the temperature regime induced in Andersson's (1969) lakes by the climate and in Teal's (1957) case by the Spring water temperature, other factors are likely to be involved. It is known that Asellus has a wide variety of food substrates on which it can survive: as a detritivore it can live on amorphous detritus, macrophyte remains, fungal growth (e.g. sewage fungus), benthic algae, etc. It is possible that the varying nature of the food source affects the efficiency of its conversion to production and thereby affects the $P/\bar{B}$ ratio.

From the varying standing crop, productivity and production data detailed above a pattern suggests itself. The hypothesis can be formed that an abundant availability of food and cover creates the conditions necessary for a high mean biomass or standing crop, and warm temperatures and particular food characteristics as yet undefined but relating to their conversion to production, result in a high production efficiency.

Teal (1957) worked with Asellus militaris and found a productivity of 437.5 KJ $m^{-2}yr^{-1}$ in a temperate cold Spring, and from his data can be calculated a $P/\bar{B}$ of 12.60. Here again there was a greater productivity than at Carden Point, but in this case it came from a small biomass ($\bar{B}$ = 2.73 g dry wt m^{-2}) with a high production efficiency.

Whilst it is likely that the efficiency of production is limited to a large extent by the temperature regime induced in Andersson's (1969) lakes by the climate and in Teal's (1957) case by the Spring water temperature, other factors are likely to be involved. It is known that Asellus has a wide variety of food substrates on which it can survive: as a detritivore it can live on amorphous detritus, macrophyte remains, fungal growth (e.g. sewage fungus), benthic algae, etc. It is possible that the varying nature of the food source affects the efficiency of its conversion to production and thereby affects the $P/\bar{B}$ ratio.

From the varying standing crop, productivity and production data detailed above a pattern suggests itself. The hypothesis can be formed that an abundant availability of food and cover creates the conditions necessary for a high mean biomass or standing crop, and warm temperatures and particular food characteristics as yet undefined but relating to their conversion to production, result in a high production efficiency.

If this hypothesis is correct, Teal's spring should have conditions favouring growth and reproduction (high $P_{(ann)}/\bar{B}$) but lacking abundant food and/or cover. Despite its classification as a cold spring, Teal's temperate spring showed a constancy of temperature common to many such springs in that although not rising above 12°C it did not drop below 8°C. Thus while lacking the high temperatures and correspondingly fast development rates of Carden Point, breeding should be unrestricted by temperature, and growth possible all year round: contributing to the high production efficiency.

The available food and cover in Teal's spring consisted of decaying allochthonous leaf material and benthic algae. At the ambient temperatures the leaf decay would be slow and as it has been suggested (though from limited experimental material) by Barlöcher and Kendrick (1973 a, 1975) that it is the fungal fraction of such material that is the actual food source of a detritivore, so this material would provide little food but good cover and living space. The filamentous and colonial green algae parallel the Cladophora glomerata of Loch Leven so that it seems reasonable to conclude that, as expected from the hypothesis, Teal's high production efficiency indicates a favourable temperature regime and a high quality food resource (benthic algae), but the low biomass indicates low food availability, despite available cover or living space.

Carden Point has no macrophytic vegetation and little allochthonous material, however - there is a dense coating of benthic algae on the rocks. The rocks themselves are used as cover in that the animals spend long periods under the rocks, but when grazing on the alga they are without cover unless the algal tufts are very dense. Again considering the hypothesis stated above, this could be the reason that the standing crop is low (1.997 g dry wt m^{-2}); however the production efficiency at 7.05 is considerably higher than Andersson (1969) found in Sweden, though not as high as Teal (1957) found. It is also higher than general values for benthic invertebrates (e.g. 4.0 from Shorygin, 1952 - quoted in Winberg, 1971).

The temperature in the Summer months allows fast development to maturity and the length of the breeding season is greater than in the Swedish lakes. It cannot be overlooked, however, that the production efficiency may have some connection with the ability to utilize the food substrate so that the food available in the form of benthic and epiphytic algae may be highly assimilable, providing an abundant food source despite the lack of cover.

Thus while the productivity of Asellus at Carden Point has been estimated, it immediately leads on to questions regarding the different food substrates utilized and their assimilability and usefulness as a substrate for production of biomass.

CHAPTER 4

FOOD PREFERENCE AND ASSIMILATION

4.1 Introduction

The productivity and respiration data calculated in the previous chapter provide the parameters necessary to calculate annual assimilation:

When A = annual assimilation

$P_{(ann)}$ = annual production

$R_{(ann)}$ = annual respiration

$$A = P_{(ann)} + R_{(ann)}$$

$$= 133.12 + 209.04$$

$$= 342.16 \text{ KJ } m^{-2}yr^{-1}$$

However, although the assimilated energy is the basis for all the energy processes of the animal, it is merely a quantity of energy whose relationship to actual consumption of material is complicated by many factors. One of the most important of these is the efficiency of assimilation, itself dependent on factors such as the type of substrate consumed and the temperature of the animal.

This provides the basis for the suggestion in the previous discussion that the type of food available may affect the production efficiency. A high productivity relative to the biomass level infers that the animals are maximizing their use of the environment, and one way that this could be brought about is by the efficient use of the available food substrates.

By understanding more fully the feeding strategy of Asellus it was hoped to relate the variability of production efficiency recorded from several environments to the variable assimilability of the available food substrates and decide whether Asellus was able to optimise feeding by preferentially consuming easily assimilated foods or whether preference was related to some other factor.

4.2 The Feeding of Asellus and related animals

Andersson (1969) related the distribution and abundance of Asellus aquaticus in Lakes Pajep Måskejaure and Erken to the nature of the bottom: hard bottoms have the lowest numbers of individuals and the lowest average individual weight. Soft bottoms have an intermediate position with vegetated ones having the highest values.

Whilst accepting that vegetation will provide a greater living space for the fauna he also related the distribution to the food preference of Asellus for vascular plant remains and filamentous algae - following Williams' (1962) description of their preferred food substrates. In Lake Pajep Måskejaure the vegetation consisted of Isoetes lacustris, and in Lake Erken it was mainly Cladophora aegagrophila. From samples of Asellus and Cladophora taken together he showed a definite correlation between numbers of Asellus and dry weight of Cladophora per m^2.

Berglund (1968) showed that the abundance of Asellus in his trout pond had a direct correlation with the abundance of vegetation, in this case Nitella opaca (a charophyte) and a Nitella/Drepanocladus callescens mixture.

From a wide range of literature, Asellus is generally described as feeding on decaying vegetation, microscopic algae and decaying animal material. It seems versatile in deriving nourishment from whatever organic material is available in the habitat; and since allochthonous leaves and decaying marginal vegetation often dominate the aquatic littoral they often form the predominant food source.

Thus where benthic alga predominates in the habitat one would expect this to dominate the food profile of consumption. In fact Moore (1975) has demonstrated that in a Cladophora glomerata dominated habitat Asellus fed mainly on the epiphytic diatoms of the Cladophora filaments - finding the cell walls of the latter too tough for attack, or at least less desirable than the epiphytes.

Moore also noted the selectivity of the feeding behaviour relative to chemical constituents of the algae. Thus the blue-green algae were avoided: these are often found to be distasteful to invertebrates. This selectivity by taste is comparable to the results of Barlöcher and Kendrick (1973 b) who found the food

preference of Gammarus pseudolimnaeus to be a consequence of the fungus type dominating the decomposer fraction.

It is well established that the fungal and bacterial fractions of the detrital material are the actual assimilated fractions (e.g. Hynes, 1963; Newell, 1965; Fenchel, 1969; Hargrave, 1970). The leaf material is mostly structural carbohydrates: cellulose, hemi-cellulose and lignin, with little protein (Kaushik and Hynes, 1971). Their nutritive value to an animal is dependent upon the ability of the consumer to digest them. Few freshwater invertebrates can (Monk, 1975) and even if the necessary enzymes are present, the rate of passage through the gut may be too fast for their digestion (Hargrave, 1970).

The colonisation of such material by saprophytic fungi and bacteria means that the protein content is boosted by the microbial proteins (Kaushik and Hynes, 1968; Matthews and Kowalczewski, 1969) - readily digested by detritivores. Thus the animal is capable of selecting a particular fungal food substrate, seen as a selection of a particular leaf type due to the characteristic pattern of fungal colonisation of leaves. Selection of the fungal type occurs even if the fungus is innoculated on an atypical leaf type (Barlöcher and Kendrick, 1973 b).

Barlöcher and Kendrick (1973 a) took the selectivity of fungal types a stage further and showed that the animals gained weight at a faster rate on certain fungi than on others, and that their survivorship was also affected by different fungal food types. In a later study (1975) they determined the assimilation efficiency of Gammarus pseudolimnaeus on many of these fungi.

On comparison of their results a complicated picture emerges. All the fungi are easier to assimilate than elm or maple leaves, whether in terms of ash free dry weight, protein or calories. However, with animals fed on Aspergillus niger or Tetracladium marchalianum the mortality rate was as high as in the controls, which were not fed at all; that despite the fact that in terms of ash free dry weight and calories Tetracladium had the highest assimilability. In contrast, Humicola grisea gave the highest survivorship and gain in weight and at the same time had a high efficiency of assimilability, however derived.

It seems, then, that there is a complex interrelationship between the food substrate preference of an animal and the effectiveness of that substrate as food in terms of assimilability and usefulness for weight gain or survivorship.

The following experiments were designed to examine the food preferences of Asellus amongst a selection of

natural food items as well as a pure fungal culture. At the same time the assimilation efficiency was determined for comparison. The growth experiments set up to determine the effectiveness of the substrates are described later.

4.3 Food Preference Studies

4.3.1 Substrates used in experiments

Three common leaf types were chosen as food substrates: the willow (*Salix fragilis*), the oak (*Quercus* sp) and the elm (*Ulmus gladra*). In each case sufficient leaves for all the experiments were collected from around the base of a single tree, taking newly fallen rather than partially decayed ones. This was to ensure uniformity since it is known that leaves vary in composition with differences in site, in successive years, at different positions in the crown and also during the period that they remain on the tree (Ovington, 1956).

Discs were cut using a 1 cm diameter cork borer and the soluble contents leached out by aeration in several changes of distilled water over 3 days. The discs were then dried in a dessicator and stored in airtight jars with silica gel crystals to maintain dryness.

For comparison, one of the hyphomycetes used by Barlocher and Kendrick (1973 a and b, 1975) *Humicola grisea* was also included. Whereas they provided whole colonies, the method used here was to culture the fungus on a liquid malt extract medium in petri dishes at 25°C

until a continuous mat of hyphae was produced. This was washed carefully in distilled water for 24 hours at 4°C to wash away all the medium and suspend growth. From the mat, discs were cut, again using the cork borer.

Since the natural food substrate in Loch Leven is Cladophora glomerata and associated epiphytes, this was also included as a substrate. By laying a layer of washed algal clumps thinly and evenly on nylon netting and drying in a dessicator it was possible to peel off fairly even mats of dry algae which were stored in airtight jars and then cut into 1 cm x 1 cm squares for use in experiments.

4.3.2 Simple choice experiments

The initial experiments were conducted using a simple choice method similar to that of Barlöcher and Kendrick (1973 b). In each of several petri dishes were placed 5 Asellus of similar size (approximately 5-8 mm) in 10 mm depth of filtered loch water at 15°C The experimental animals were starved for 24 hours prior to the experiment to ensure that they would feed during the experiment.

In each dish were placed food discs (one of each type being tested), each separated from the others and away from the edge of the dish. In the case of Cladophora and the leaves they had been soaked in filtered loch water for 3-5 days in order that they should not float. Not all the available substrates were offered in each experiment.

The dishes thus set up were left for 15 minutes and then at each quarter hour interval they were observed and the number of animals on each food type noted. Ten such counts were usually taken. ($2\frac{1}{2}$ hours)

The total count for the experiment was:

No. Animals/dish x No. dishes x No. observations

and the percentage of these scored by each food type was calculated. The results are summarized in Table 10.

TABLE 10: Results of the simple choice experiments. The numbers given are the percentages of the total counts which were recorded on each of the food substrates offered.

EXP'T NO.	OAK	ELM	WILLOW	FUNGUS	CLAD-OPHORA	NEITHER	TOTAL COUNTS
1	5.47	22.40	7.20	57.33	N.O.	7.60	750
2	15.25	26.75	20.25	N.O.	35.25	2.50	400
3	11.80	48.40	33.60	N.O.	N.O.	6.20	500
4	N.O.	23.20	9.60	65.80	N.O.	1.40	500
5	N.O.	N.O.	N.O.	65.25	33.50	1.25	400

NOTE: 1. 'Neither' indicates that the animals were not on any substrate but were moving around the dish.

2. In experiment ~~#~~ 5 two fungal discs and two Cladophora squares were offered so that there should be sufficient area to prevent crowding and disturbance of the animals.

3. 'N.O.' indicates that this particular substrate was not offered in that particular experiment.

In taking the percentage of times that animals were on any food type, given the choice of several, as a measure of the preference of the animal for that food type, one is making certain assumptions. One is that the presence of an animal on a type indicates that it prefers that type to all others available. The animal does not, however, necessarily know of the presence of the other types. An animal may use a disc for shelter, in which case there would be no difference between any of the substrates. Shelter includes both negative phototaxis and the animals' natural tendency to cling to something when in a smooth bottomed dish.

Assuming that taking not one but ten observations over $2\frac{1}{2}$ hours will cancel some of these effects and give the general preference order, the animal can be seen to have a definite order of preference, given any combination: Fungus > Cladophora > Elm > Willow > Oak.

As indicated, there were some counts of animals moving about the dish. Generally animals on less preferred substrates were more inclined to leave the disc and move around, perhaps searching for other food. However, on occasion animals on highly preferred substrates moved off and sometimes moved onto supposedly less preferred

discs. The ideal case would be where animals had a tendency to move which was inversely related to the palatability of the substrate, resulting in a gradual gravitation towards the highest preferred substrate, from which movement would be minimal. Unfortunately it was not always the case that animals sought out a disc in order to feed and this must be at least part of the reason why the gravitation to highly preferred substrates was not perfect.

4.3.3 Consumption of different substrates

Instead of measuring preference in terms of behaviour given choices of different substrates, it is possible to directly measure consumption by weighing the discs before and after being offered to animals. This is easier with the leaf discs than with fungus or Cladophora.

Eight glass dishes each with 5 animals between 4 and 6 mm long were used; the animals having been starved for 24 hours prior to the experiment. In each dish a disc of willow, elm and oak were offered for 24 hours, and then their loss of weight calculated from the difference between the dry weights before and after offering (drying at 20°C in a dessicator). Controls run identically but without animals were used to correct any effect due to leaching.

Since the microbial biomass in leaves treated as above is small (Barlöcher and Kendrick 1973 a) the preference in this case is due to chemical or physical

differences in the leaves themselves. The results are shown in Table 11.

TABLE 11: Leaf preference by differential consumption - means from 40 animals.

LEAF TYPE	CONSUMPTION (mg dry wt/animal)
Elm	0.5201
Willow	0.2907
Oak	0.1552

The preference scale confirms part of that found in the first experiment:

Elm > Willow > Oak

4.4 Assimilation Studies

The amount of energy that a consumer may derive from the food eaten depends largely on the efficiency with which it can assimilate the food. As has already been inferred, the greater part of plant detrital material is indigestible structural carbohydrate, the protein content being small. Thus in terms of dry weight the assimilation efficiency of such material must be low, e.g. 5% for Hyalella azteca feeding on elm leaves (Hargrave, 1970); 10-20% for Gammarus pseudolimnaeus feeding on elm or maple leaves (Barlöcher and Kendrick, 1975). Since 80-95% of the consumption may be egested without incorporation into the body tissue of the animal it is important to know precisely what proportion of the

food substrate being eaten is actually being assimilated, otherwise misinterpretation might occur. For instance, an animal may assimilate more nutrient material from a small quantity of one substrate than from a larger quantity of another, even though the consumption rates would suggest that the latter was the more important substrate.

Although many varied techniques for the estimation of consumption and assimilation rates using marker - both radioactive and non-radioactive - have been developed (see Grodzinski et al., 1975), a simple gravimetric method should provide accurate estimates when investigating an animal with discrete fecal pellets and a substantial intake of solid food. Precedent for this approach was taken from Prus (1971) on Asellus aquaticus, Carefoot (1973) on Ligia pallasii, Hubbell, Sikora and Paris (1965) on Armadillidium vulgare and Nilsson (1974) on Gammarus pulex.

The same substrates were investigated as were used in the food preference experiments (4.3.1). However, in the case of the fungus Humicola grisea, a different technique was used, and this is described subsequently.

4.4.1 Leaf material and Cladophora

The assimilated fraction of the substrate was calculated from the difference between the consumption and the faeces produced by animals kept in small open dishes containing 25 cm^3 of water. Specimens were starved for 24 hours before the start of the experimental period,

and then exposed to known weights of food material either individually or in groups of 5. This latter represents a density of 500 individuals m^{-2}, low in the annual range from 240-7000 m^{-2} in the loch itself but the maximum feasible in a simple container without incurring large mortality rates, presumably as a result of cannabalism. Since both leaf and Cladophora material had been stored dry at 20°C it was weighed and then soaked in filtered loch water for 24 hours at 4°C so that it should be negatively buoyant and thus both suitable and available for the animal on the bottom of the dish.

The experiments were carried out in constant temperature rooms with a 12 hour photoperiod. Duplicate dishes each containing both food material and Asellus faeces (to provide the same fungal innoculum as the Asellus specimens they came from, i.e. those used in the experiments) were used as controls so that when the experiment was terminated (usually when at least half of the disc had been consumed in most of the dishes) there were blanks from which the weight change effected by the immersion time and fungal growth could be assessed. All the food remains were dried at 60°C for 24 hours and then weighed. After a 24 hour period to allow gut evacuation, the faeces were removed using a pipette, dried and weighed (in small foil trays). Often it was necessary to allow the fecal pellets to settle to the bottom of a centrifuge tube so that the pellets could be pipetted from the narrow tube bottom.

Thus the consumption could be calculated by difference and the assimilation and assimilation efficiency calculated from the standard formulae:

$$A = C - F\,U$$
(soluble excretion + secretion discounted)

$$\text{Assimilation efficiency} = \left(\frac{A}{C} \times \frac{100}{1}\right) \%$$

where A = assimilation, C = consumption and

FU = rejecta (faeces + urine)

The length and wet weight of the animals was also taken.

A disadvantage of this technique is that error may arise from retention of material in the gut both before and after the experimental period. Evidence suggests that in many invertebrates, especially detritus and deposit feeding ones, there is a dependence on ingestion to force material through the gut (Hargrave, 1972). This error was reduced by providing excess food before the pre-experimental starvation period, and starving for an equal period at the end of the experiment so that if material was retained it might be expected to be similar in quantity before and after the experiment.

4.4.2 Fungal material

The fungal material could not be treated as was the leaf and algal material since it is living and would grow over the extended period of the experiment, making use of the soluble organic substances produced by the animals excretion. This would cause error since the

correction factor from the control would be large and affected by the different sizes of the uneaten and the partially eaten discs. Where the correction factor is small, in the cases of leaf and Cladophora material, the difference should be negligible.

However, the fungal hyphae are pale, resulting in a pale gray fecal pellet. Thus, since it is possible to distinguish these from the brown pellets produced from leaf material, it was possible to use a short term experimental method similar in some respects to that used by Barlöcher and Kendrick (1975) but facilitated by the preparation of the fungus as hyphal discs.

Again, individuals in small dishes were used but they were not starved, having been fed on a leaf diet. For four hours they were fed fungal discs prepared and weighed, blotted dry, after which they were replaced by leaf material. All faeces derived from the fungus were collected at regular intervals, dried at 60°C for 24 hours, and weighed. By having preweighed the discs and then drying at 60°C for 24 hours when removed from the experiment it was possible to determine the weight loss (i.e. consumption) using a wet weight to dry weight ratio produced by weighing, drying and reweighing a large number of controls.

4.4.3 Results of Assimilation Experiments

To simplify the results, a proportion of the experiments were carried out using willow leaf substrate only, rather than repeating the experiments on all the substrates. This concentration of effort on willow allowed a greater number of replicate experiments for statistical analysis of the results. Willow was chosen since it is a common food of Asellus under field conditions and one which in the laboratory is accepted readily and easily stored and worked with. Preference studies showed it to be a preferred substrate but not the most nor the least preferred, therefore it was chosen as a typical or standard substrate for the experiments relating temperature to consumption, assimilation and assimilation efficiency.

The experiments investigating assimilation efficiency related to animal density and food substrate type involved all the food types including willow, and are considered together in the section following the willow experiments.

Results of experiments involving willow only

1. Consumption rate related to temperature

The following results were calculated from these experiments:

$5^{o}C$: $C = 3.139$ mg.ind^{-1}200 hr^{-1} (st.dev. = 2.622; N = 31)

$10^{o}C$: $C = 1.479$ mg.ind^{-1}200 hr^{-1} (st.dev. = 1.275; N = 37)

$15^{o}C$: $C = 1.293$ mg.ind^{-1}200 hr^{-1} (st.dev. = 0.969; N = 30)

The increase of the variance with the mean required the transformation of the data to logarithmic values before comparing means. The validity of this transformation was tested using a variance ratio or F test.

From the data it can be seen that there is an increasing consumption rate with decreasing temperature. Transformation to logarithmic values produces an insignificant ($P < 0.05$) F test value so that parametric comparisons can be made. The 5^{o} to 10^{o}C difference is very significant but the 10^{o} to 15^{o}C difference is not significant (at $P = 0.05$).

The greater standard deviation for the 5^{o}C results may be a contributing factor to the magnitude of the difference but the tendency of the data is to suggest that consumption is inversely related to temperature but that only below 10^{o}C does it operate significantly.

2. Assimilation related to temperature

Again taking an arbitrary 200 hr period the assimilation rates at these temperatures were:

5^{o}C: $A = 0.5312$ mg.ind^{-1}200 hr^{-1} (st.dev. = 0.562; N = 31)

10^{o}C: $A = 0.3108$ mg.ind^{-1}200 hr^{-1} (st.dev. = 0.348; N = 37)

15^{o}C: $A = 0.3339$ mg.ind^{-1}200 hr^{-1} (st.dev. = 0.336; N = 30)

Again transformation was necessary. In this case the F test showed significance for the variances of 10^{o}C and 15^{o}C at the $P = 0.05$ level but not at the $P = 0.02$ level and this was considered acceptable for the comparison

to be made. The differences of $5^{o}C$ to $10^{o}C$ and $10^{o}C$ to $15^{o}C$ were found to be insignificant ($P = 0.05$), indicating that the assimilation rate is not related to temperature between $5^{o}C$ and $15^{o}C$.

3. Assimilation efficiency related to temperature

The assimilation efficiencies on willow as a food substrate at the three temperatures were:

$5^{o}C$: A.E. = 15.29% (st.dev. = 8.498; N = 32)

$10^{o}C$: A.E. = 19.73% (st.dev. = 12.317; N = 38)

$15^{o}C$: A.E. = 30.84% (st.dev. = 18.897; N = 30)

Here also, the F test was significant for the variances at $10^{o}C$ and $15^{o}C$ ($P = 0.05$) but not at the $P = 0.02$ level and so the transformation was considered valid for the comparisons. The $5^{o}C$ to $10^{o}C$ increase was not significant ($P = 0.05$) but the $10^{o}C$ to $15^{o}C$ increase was very significant ($P < 0.01$). Thus the data indicates a rise in assimilation efficiency with increasing temperature.

Results of experiments using all the substrates

Table 12 gives the assimilation efficiencies at $15^{o}C$ for all the substrates investigated at both densities.

TABLE 12: Results of determinations of the assimilation efficiency of single, and groups of five animals in a similar sized experimental area (equivalent to densities of $100m^{-2}$ and $500m^{-2}$ respectively). The figure in brackets is the standard error of the mean. ($T^{o}C = 15^{o}C$)

SUBSTRATE	SINGLE ANIMAL	FIVE ANIMALS
Humicola grisea	86.31 (3.29)	-
Elm leaf	54.44 (6.71)	23.16 (1.41)
Willow leaf	30.84 (3.45)	24.08 (3.59)
Oak leaf	27.15 (6.16)	39.61 (9.01)
Cladophora	26.83 (2.71)	28.15 (3.14)

When considering the significance of the above results it is necessary to consider the number of failures as well as the number of successful experimental results. Considered thus, the result that gives cause for doubt is the 'oak leaf/single animal' one, which had a less than 50% success rate. The failures were due to the weight of collected faeces exceeding the value calculated for consumption.

In these experiments, due to the hard texture of the oak leaf material there was very little consumption, even when exposed for long periods, in the majority of cases less than 0.2mg and often less than 0.1mg. In comparison with such small consumption and an even smaller assimilation the errors arising from the retention of faeces during the starvation period and the correction

factor for weight change due to leaching and fungal growth become unacceptable. This is not so in, for example, the elm experiments where consumption was usually in excess of 1.0 mg and often over 2.0 mg. Thus the validity of this result is open to doubt but not the overall method or results.

4.5 Discussion of Food Preference and Assimilation Experiments

When considering the order of preference of *Asellus* for food substrates:

Fungus > *Cladophora* > Elm > Willow > Oak

the most relevant factor seems to be the ease of ingestion of the material as represented by the texture. Of the leaves, oak is the brittlest - staying intact for long periods of immersion in the natural environment. Both elm and willow leaves soften with prolonged immersion in water: in the latter case the epidermal layers often peel off, especially from the underside. There would seem by observation to be little to distinguish between elm and willow in terms of texture.

The filamentous nature of the *Cladophora* will make the material more easily broken up and ingested, as will be the case for the fungal hyphae. However, the cell walls of the latter are not composed entirely of cellulose, having some chitin and other materials. It is possible that these are more palatable to *Asellus* and as well as the texture are part of the reason why fungus is preferred wherever offered.

Ingestibility is not the only factor involved in substrate preference. Where two substances are texturally similar, as in the case of elm and willow, one would expect no preference between them if texture were the only factor. As Table 10 shows, there is a definite preference for elm whenever the two are offered together. Here then it is reasonable to assume that some other stimulus is involved, possibly a chemical one relating to the composition of the leaf or of any fungal material that might have developed on it.

Comparing the preference scale:

FUNGUS > CLADOPHORA > ELM > WILLOW > OAK

with the order of assimilability for single animals:

FUNGUS > ELM > WILLOW > OAK > CLADOPHORA

indicates that they are the same for all the substrates except Cladophora, which is second in preference only to fungus but which seems to be least efficiently assimilated. Cladophora is seen to be much less assimilable than elm, over which it is preferred.

Even if the order of assimilability were the same as the order of preference it would not be justifiable to conclude that an animal chooses a food substrate for its assimilability due to the overriding consideration of the texture of foods. When an animal passes so much material through its gut with such a short retention time it may be that the softer, more easily broken up

substrates are more accessible to enzyme penetration than tougher ones, so that a substrate which from chemical considerations might be expected to be easily assimilated may have a poor assimilation rate due to the resistance of its physical structure to penetration by enzymes.

Thus the texture of the food may be the most important factor determining the food preference. Cladophora may be an example of the role of texture in preference but seems to disprove the suggestion that an easily ingested substrate is probably easily penetrated by enzymes. In fact, the Cladophora material when leached and washed and dried, probably consists of little other than cellulose cell wall material and such material is barely attacked, except by long exposure to cellulases, and the short retention times of detritivores are usually insufficient.

For this reason the Cladophora material is probably unsatisfactory as a representative of the situation in the field where it is usually alive and encrusted with epiphytic organisms and semi-decayed filaments. No way was found of quantifying this material in such a way that it could be fed to Asellus quantitatively, so that the dried and leached filaments had to be substituted. In the growth experiments that follow, live material had to be used to prevent rapid decay and deoxygenation and the difference is evident from the results, which suggest that live Cladophora and the associated epiphytes and detritus would be more easily assimilated.

When considering assimilation and its relationship to temperature rather than substrate, it is to be expected that a higher temperature will increase the efficiency of enzyme attack on the substrate, and that the passage of material across the gut membranes will be enhanced at 15°C. This may continue to higher temperatures since the optimum for enzymic reactions may be 10°C or more above this; but the experimental set up would not allow higher temperatures under identical conditions.

Since the assimilation does not seem to vary as the temperature - and hence the assimilation efficiency - falls, it follows that consumption must increase, as the results show: there is a 100% increase in uptake at 5°C over 10°C.

This effect would seem to be advantageous in ensuring that in the Summer months when the population is at its densest and food may be competed for, the animals can make more efficient use of whatever they are able to consume. This is especially important as Summer is the time of year when production of reproductive material, high growth rates and increased respiration make large demands of energy input.

The relationship between density and assimilation efficiency shown significantly in elm and willow but not in oak and Cladophora is less easy to understand. Prus (1971) found the opposite effect and suggested that a higher assimilation efficiency would give an advantage

in high density conditions when food was scarce. If the results of the present study are correct it could equally be argued that if a lower assimilation efficiency produced a slower growth rate then the effect would give an advantage to low density populations increasing in size, since the same amount of food would produce larger animals and hence more offspring as shown in the Reproductive Biology section (2.1.2). Thus the effect would produce a simple feedback control to increase the density of low density populations.

Since this explanation is dependent on a relationship between assimilation efficiency and growth rate it can be left aside at this stage for discussion in the growth experiment section.

Two important points arise from these experiments which have important bearing on the subject of the thesis:

1. Relating to the population dynamics: in the warmer Summer months when energy demand on the individual is at a maximum and the population is at a high density so that food resources may be short - there is a compensatory increase in assimilation efficiency brought about by the higher temperature.

2. Relating to the production efficiency: when feeding on a substrate which is less efficiently assimilated, there is no compensatory increase in consumption. Since assimilation rate falls the available energy for growth and reproduction must fall, as is investigated in the following chapter.

CHAPTER 5

GROWTH EXPERIMENTS

5.1 Introduction

Just as the distinction between the rate of production (or productivity) of organic matter by a community and the standing crop, consisting of the organic matter of the community itself, is a fundamental one, so also is the distinction between the rate of production and the production efficiency ($P/\bar{B}$, where $\bar{B}$ is the mean biomass present per unit area over the year).

Production is the increase in biomass which occurs in a given period of time, whether or not all of it survives to the end of that period (Mann, 1969); but the production efficiency is the ratio of the production to the biomass of the organisms producing it and is therefore independent of the finite amount of production - inasmuch as a small efficient community could have a larger production than a larger but less efficient community.

In the discussion to the productivity section (3.4) it was suggested that a possible key to the different productivity data from the literature and the present study might lie in the differing food substrates available and the resultant production efficiencies. In support of this it has been shown that different food substrates are not treated indiscriminately by Asellus: certain food types are preferred - notably fungal cultures and algal material, and others are

slowly ingested and then only when the other alternatives are not available. The preferred algal material corresponds to some of the algal material available at Lake Erken (Andersson, 1969) where the $P/\bar{B}$ was higher than in Lake Pajep Måskejaure in which macrophytes dominated; and to benthic algae in Root Spring (Teal, 1957) where the $P/\bar{B}$ was up to 12.60 compared with 7.05 found in the present study.

In addition it has been suggested in the last section (4.5) that the animals have a rate of ingestion independent of the assimilation efficiency so that the energy input is lower with a poorly assimilable substrate than with a more assimilable one.

Finally in the last section the suggestion was made that a density dependent assimilation effect might operate through the growth rate to control population size - providing that a link between assimilation efficiency and growth rate can be assumed.

To show that a substrate is easily assimilable goes only part way to showing that it gives a higher production efficiency than a less assimilable one, even though this is suggested by the fact that a lower assimilation efficiency can mean a lower rate of assimilation due to constant consumption rates.

Since:

Assimilation = Production + Respiration

and production is in terms of growth in body material (plus moults, etc.) and reproductive products; by

equalising the respiration as far as possible by keeping a constant temperature, the effect on growth of an organism of feeding with different substrates can be seen as a direct indication of the effect of that substrate on the production efficiency. A substrate efficiently converted to biomass will give a high growth rate and vice versa.

The growth experiments that follow were set up to observe whether or not such an effect was produced and to give comparative results for several of the substrates concerned in the feeding experiments. Long term experiments were chosen so as to minimise short term variations in growth.

5.2 Methods

Early in the period of study, preliminary growth experiments were carried out with the intention of determining what pattern growth took so that the larger scale experiments could be set up accordingly. Although the data from these experiments is not given (since it is repeated and extended in the ones that follow), they confirmed Prus' (1972) findings that the lifespan shows approximately rectilinear growth. The implications of this to the treatment of the results is discussed in the results section (5.3).

To parallel the feeding experiments the growth experiments were set up so that single animals and group cultures could be observed, and so that the effect of substrate and temperature could also be compared.

5.2.1 Single animal culture

White translucent plastic cartons were used for this experiment. They had push-on lids which prevented evaporation, and when one third full they contained approximately 100 cm^3 of water - considered adequate for the experiment. Into each was placed a small Asellus, 100 cm^3 of filtered loch water and a portion of food substrate in excess of the animals requirements until the next measurement. Again the food substrates from 4.3.1 were used with the exceptions of fungus, which was not used, and Cladophora which was used live and fresh from the loch rather than leached and dried.

Ten replicates for each food type were set up at 5°C, 10°C and 15°C in constant temperature rooms with a 12 hour photoperiod.

5.2.2 Group cultures

For these experiments large (1L) glass jars were used. Into each were placed 30 Asellus of as uniform small size as possible (usually about 3-4 mm long), a quantity of substrate in excess of requirements, and approximately 800 cm^3 of filtered loch water. These jars were kept under aeration in 5°C and 15°C constant temperature rooms as in the previous experiment.

At approximately monthly intervals the animals were measured using an eyepiece graticule in a binocular microscope, avoiding excessive handling as much as possible. Food was renewed when almost consumed

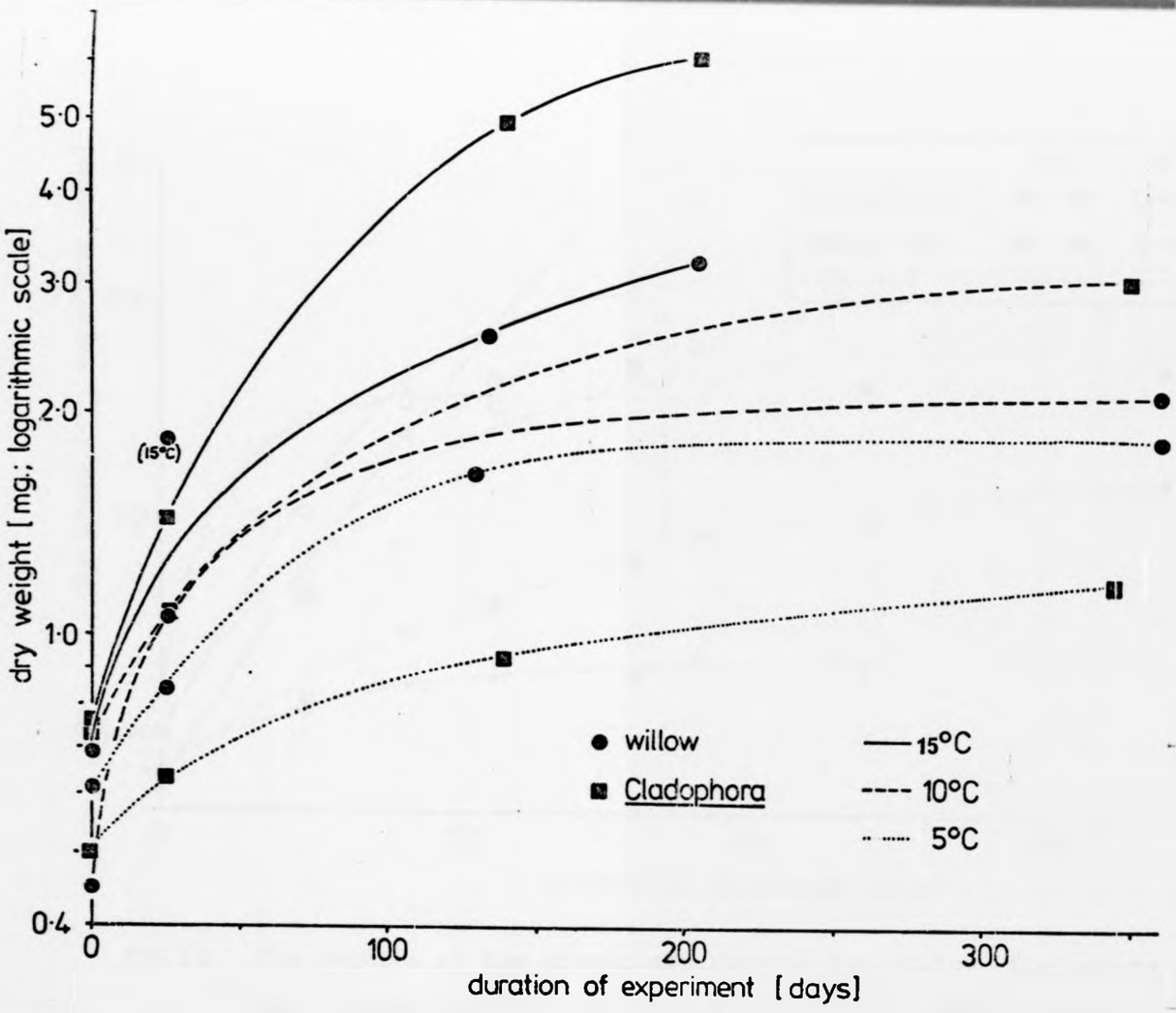

FIG 11. The results of the growth experiments for Willow and Cladophora as substrates, fed at 5°C, 10°C and 15°C. (Individual culture)

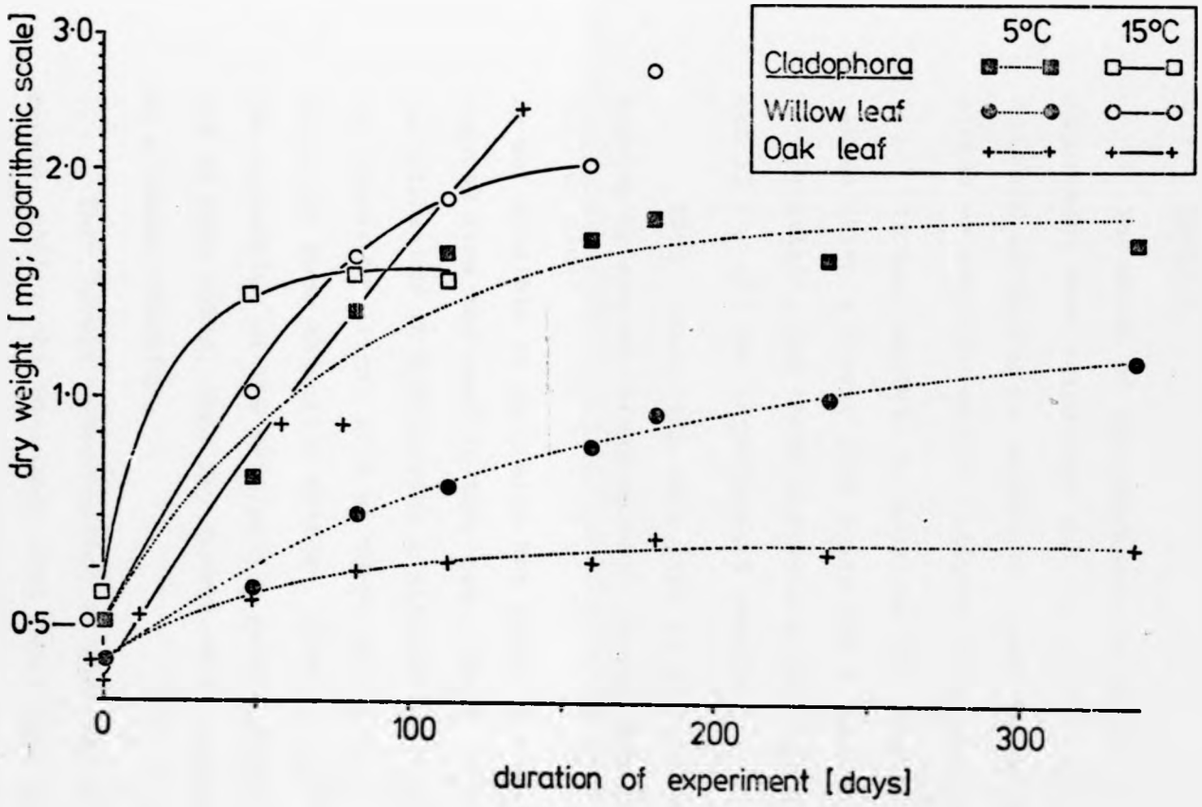

FIG 12. The results of the growth experiments for Willow, Cladophora and Oak as substrates, fed at 5°C and 15°C. (Group culture)

and build up of faeces and excretory products prevented by changing the water when renewing the food.

5.3 Results

The means of the measurements for each experiment were calculated and the results grouped and compared according to substrate types, temperature and single or multiple animal cultures (see appended data).

It was possible to describe the data by means of curves using a linear time scale and a logarithmic scale of dry weight, and these curves are shown in Figs. 11 and 12 for all the experimental results.

When considering data with so few points, the drawing by eye of 'ideal curves' through the points may well be close to the reality of the relationship but it is not possible to determine how close or how far removed from the reality they are. There is some justification in considering a straight line through the linear by linear plot of these points as being the safer and more objective method. This is supported by the suggestion of the preliminary growth experiments and of Prus (1972) that the growth curve approximates to a linear function.

This linear approximation to what are essentially curves, offers the advantage that there is a ready check on the closeness of fit provided by the correlation coefficient. Thus in Table 13 where the slopes of these linear approximations are considered, the correlation

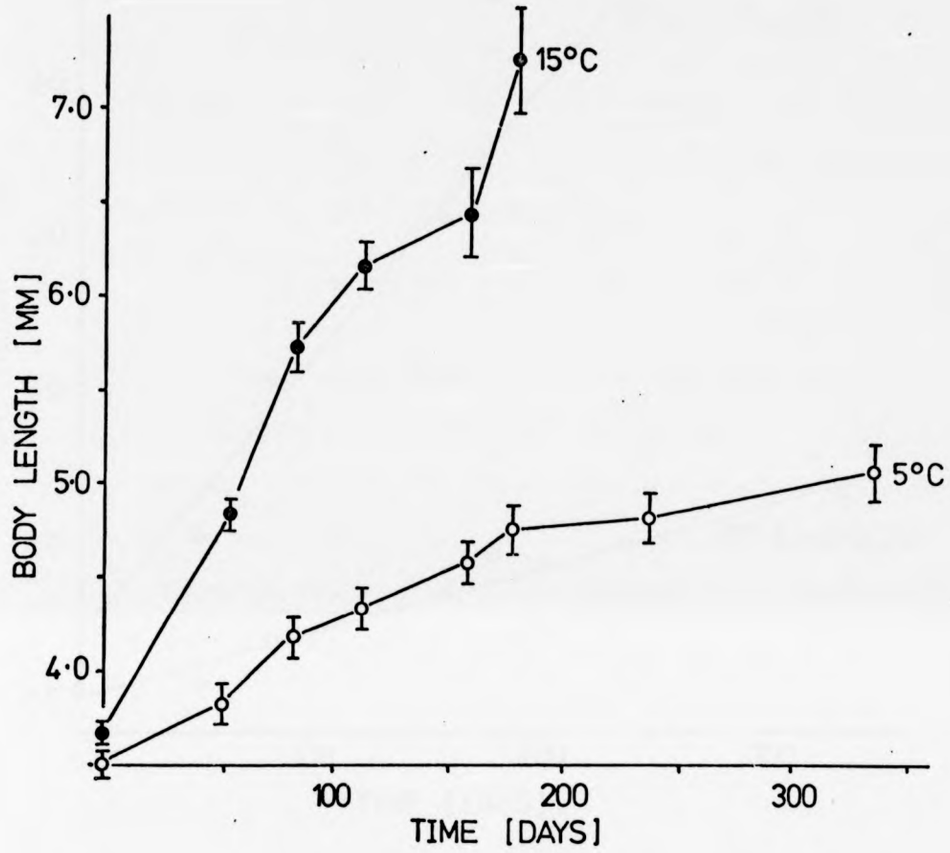

FIG 13 a. The average increase in body length of an individual during a growth experiment. (Substrate: willow leaf; group culture.) Vertical lines represent 2 standard errors.

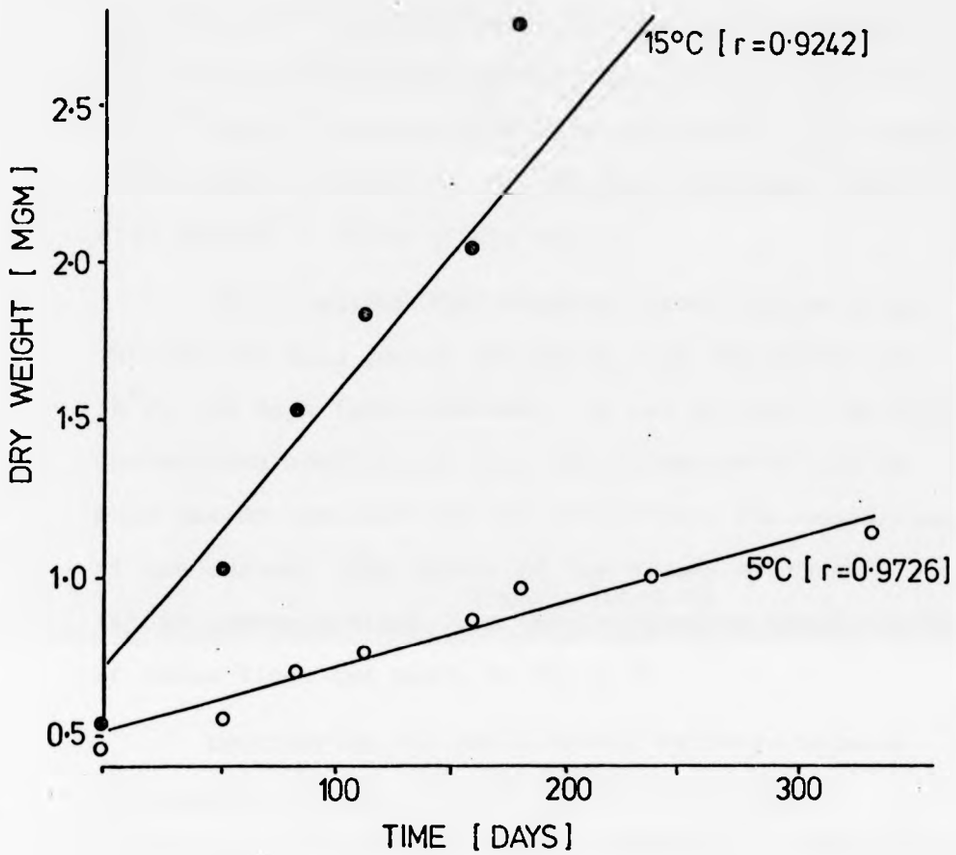

FIG 13 b. Graph of the data from figure 11a converted to dry weight. The calculated regression lines are shown, with the correlation coefficient (r).

coefficient is given and its significance indicated. Where it is not significant then the linear approximation may be considered an invalid approximation. Fig.13a shows as an example the results of the group cultures at 5°C and 15°C with willow as a substrate. The growth is in terms of length. Fig.13b shows the same results with growth in terms of dry weight.

Whilst noting that sigmoid curves can be drawn through the data points (in which case the result at 15°C, 179 days looks dubious), it can be seen from the correlation coefficient that the closeness of fit is good and so this will be the method used for comparison of the curves. The values of the slopes of these linear approximations, and the significance of the correlation coefficients of these lines are shown in Table 13.

Considering the individually cultured animals the growth rate at 10°C and 15°C is higher with Cladophora than with willow as a substrate. The growth rate falls as the temperature falls, but in the case of willow at 5°C the fall from 10°C is slight and at this temperature the growth rate on willow is higher than that on Cladophora. However, the correlation coefficient is not significant at the 95% level for willow at 5°C so that this result is in doubt.

A similar pattern is shown in the experiments where several animals are grown together, although some problems were encountered with deoxygenation and

TABLE 13. The Coefficients of the Slope of the regression lines from the growth experiments. The level of significance of the Correlation Coefficient is given as a measure of the validity of the linear approximation (see explanation in text).

	SINGLE CULTURE						GROUP CULTURE					
	5°C		10°C		15°C		5°C		10°C .		15°C	
	SLOPE	SIGN. OF r	SLOPE	SIGN. OF r	SLOPE	SIGN. OF r	SLOPE	SIGN. OF r	SLOPE	SIGN. OF r	SLOPE	SIGN. OF r
Cladophora	0.0019	*	0.0065	*	0.0271	**	0.0031	*	----------		0.0076	n.s.
Willow leaf	0.0032	n.s.	0.0039	n.s.	0.0109	*	0.0021	***	----------		0.0083	**
Oak leaf	----------		----------		----------		0.0005	*	----------		0.0139	*

Key to significance: n.s. = not significant.

* = $P < 0.05$

** = $P < 0.01$

*** = $P < 0.001$

cannibalism at 15°C and this may be responsible for the non-significance of the linear approximation to the Cladophora results. At 5°C the effects of the three food substrates can be seen: Cladophora giving the highest growth rate, oak the lowest, with willow intermediate. The problems already mentioned meant that the 15°C experiments were very much shorter in duration and much reduced in animal numbers. Since it is not possible to say whether the mortality was equally affecting all sizes it is unlikely that the 15°C results are as accurate as the rest; for instance were larger animals to be more susceptible then the growth rate would apparently be depressed, and vice versa.

Taking an overall view of the results the depression of the growth rate by group culturing can be seen in all but the 5°C Cladophora experiment. There is a 257% difference between individually grown and group cultured animals at 15°C fed on Cladophora and the percentages of 31% for willow at 15°C and 51% for willow at 5°C are significant falls in the growth rate resulting from the higher density. In all cases the quantity of food was not limiting.

5.4 Discussion of the growth experiments

The comparison of linear approximations, where these are considered to be valid approximations to the growth pattern (as assessed by the significance of the correlation coefficient, as described), indicates that the hypothesis that a higher assimilation rate would

produce a faster rate of growth is correct. The results with Cladophora confirm the suspicion that dead, leached and dried filaments (as used in the feeding experiments) - being almost entirely carbohydrate cell-walls - do not give a true indication of the food value of the living material with its associated epiphytic community (as was used in the growth experiments). Furthermore it would be logical to suggest that the fungal culture - had it been possible to feed it under the conditions of the experiment - would have produced even faster growth rates, due to its higher assimilability by the animal.

The faster growth rates at higher temperatures is an expected result of an increased rate of matabolism and the higher assimilation efficiencies would provide extra assurance of the provision of enough energy input to meet respiration as well as production requirements at these higher temperatures.

When considering the density effect it is to be noted from the appended data that the sizes of the animals at the beginning of the experiments were not exactly the same and thus the variation caused by the initial phase of the sigmoid growth pattern may play some part in the differences shown in the results. However, the variation in initial size is not considered to be so large as to substantially alter the results and the linear approximations should allow valid comparisons of the growth through the size ranges considered. However, these results cannot be applied to the early growth phase - more experimental results with small animals and calculations involving instantaneous growth

rates at these sizes would be necessary for this.

Nevertheless, the results shown indicate a lowering of the growth rate in group cultures compared to single animal cultures. This is confirmation of the findings of the assimilation studies - that assimilation efficiency and hence assimilation is depressed, thereby limiting individual growth.

The interpretation suggested for this density effect on assimilation efficiency and growth is the one briefly mentioned in the previous discussion section (4.5): that the result of the increased growth on a low density population is to increase the size of the reproducing female and thus produce an increased reproductive potential as a response to the low population density. That this conclusion should contradict Prus' (1971) data and conclusion is inexplicable, but it is possible that at the very high densities (equivalent to 1500, 3000 and 6000 ind m^{-2}) the density dependence produced a different effect; so that the lower densities produced a higher assimilation efficiency to boost the reproductive potential - this effect reaching a plateau of low assimilation efficiencies at the optimum density for the environment - then as the density increases above this optimum the assimilation efficiency increases again to protect the population at times of food shortage as Prus suggested. This hybrid explanation encompassing the two effect is, however, speculative and would need to be investigated by a series of experiments under identical conditions using the whole range of densities since the contradiction could arise from

experimental differences.

The more important point for the main theme of the study is, however, that the different food substrates did produce different growth rates and that the reasonable extension of this is to say that different food substrates produce different production efficiencies.

CHAPTER 6

GENERAL DISCUSSION

GENERAL DISCUSSION

Studies of the numerical dynamics of populations of animals, even when accompanied by productivity data, may be little more than quantitative exercises if they do not go on to suggest why the dynamics function as they do. Production data may fit into place in an ecosystem model but often little attention is directed as to why the production and production efficiency are at the levels found, even when data from other workers provides different results from these parameters. Resorting to the philosophy that each ecosystem is so complex and each so different from the other that generalisations and comparisons of specific points are invalid, is not a reasonable argument when such a wealth of data is accumulating.

The present project considers the population dynamics and theproduction of Asellus and attempts to go further than stating the results and filing it amongst the other available results. The question is asked, 'Why are the productivity, the standing crop and the resultant production efficiency different in the several studies of Asellus so far recorded?' Then, by investigation of certain parameters: the type of food available in the habitats, the variable assimilation efficiency with differing food substrates and its effect on growth rate, the study attempts to answer that question as far as possible.

Support is shown for the hypothesis that the different major food substrates available in the habitat affect the energy uptake of the animal. Asellus eats that food which is most easily ingested from the environment around it, apparently eating to the limits of its physical capacity unknowing and regardless of the assimilability of that food. This strategy of consumption means that if the substrate is highly assimilable the production efficiency will be high, and if it is poorly assimilable then the production cfficiency will be low.

Applying this to other studies on Asellus the postulated high assimilability of natural algal material provides a clue to the increased production efficiency in Lake Erken (with Cladophora aegagrophila), over Lake Pajep Måskejaure (macrophytes dominant) (Andersson, 1969), and the very high production efficiency of Root Spring (with its benthic algae) (Teal, 1957). No doubt other factors are involved; the very high production efficiency at Root Spring is probably an effect not only of the availability of benthic algae but also of the lack of low winter temperatures being as it is, a constant temperature spring. Temperature and other climatic factors may affect the other studies in the same way that they affect the duration of the breeding season (section 2.1.3), but one factor, and one of major importance, must be the food types present in the habitat.

Not only has this been suggested by comparison of results, but it has been indicated by laboratory investigation where it was found that various food substrates produced different growth rates, there being some indication that higher growth rates were associated with more assimilable substrates.

The major aim of the project, as stated in section 1.1, was to test the suggestion that the rocky shallow areas of the loch are a source of Asellus in far greater quantities than are produced by the sand and mud areas. In doing this, not only would the anomaly of a low standing crop in the overall loch but high numbers in trout and perch diets be explained, but also a truer picture of the significance of Asellus in the loch ecosystem could be proposed. This evaluation of the significance of Asellus would replace that given in the papers by Maitland and Hudspith (1974) and Morgan and McLusky (1974) at the conclusion of the main part of the I.B.P. study on the loch.

The productivity data produced by the present study was discussed in section 3.4 where the annual productivity of Asellus at Carden Point was determined to be 14.09 g $m^{-2}yr^{-1}$ with a $P/\bar{B}$ ratio of 7.05 (during the period 1974/5). Comparing this with the values for chironomid larvae, the organism investigated as the main food item for trout and perch on the I.B.P. study, the results are as shown in Table 14.

TABLE 14: A comparison of the production of larval chironomid populations and Asellus aquaticus in Loch Leven.

ORGANISM	YEAR	PRODUCTION	SUBSTRATE TYPE
Chironomid			
Chironomid larvae:			
Glyptotendipes	1970	894	sand
	1971	110	
Stictochironomus	1970	24	sand
	1971	206	
Polipedium	1971	13	mud
Chironomus	1971	515	mud
Glyptotendipes	1971	38	mud
Total (5 spp.)	1971	455.34	sand and mud
Asellus aquaticus	1974/5	133	rocky shallows

(Chironomid data taken from McLusky and McFarlane (1974) and calculated from Maitland and Hudspith (1974) and Charles et. al., (1974).

As can be seen from the comparison of the production data for larval chironomids and the results of the present study, the value for Asellus, whilst much smaller than the production of Glyptotendipes (sand) in 1970 and Chironomous (mud) in 1971, was comparable in order of magnitude to the other chironomid values. It must be emphasised, however, that this is a comparison of the productivity per unit area where found. Thus in

a square metre of shallow rocks the production of Asellus (133 KJ $m^{-2}yr^{-1}$) exceeds the production of Glyptotendipes (1971 data - 110 KJ $m^{-2}yr^{-1}$) in a square metre of sand. However, since sand covers 42% of the loch area the absolute production of the chironomid will exceed that of Asellus since there is only 1% of the loch area with a rocky substratum.

This restricted distribution casts doubt on the value of comparisons within an ecosystem where to standardise comparisons of production and standing crop values the data for a small area must be spread over the whole loch area. Thus estimating from Maitland and Hudspith's (1974) mean value for Asellus of 54 mg dry wt m^{-2} from the sand during 1970, and from the comparison of the mud and sand values from their survey in 1968, and by adding the data from the present study, the standing crop of Asellus over the whole area of the loch is 5.09 KJ m^{-2} (using a mud:sand:rock ratio of 57:42:1), whereas in the rocky shallows the value is 25.40 KJ m^{-2}. This latter value is a mean with a range during the year of 7.28 to 58.29 KJ m^{-2}. Thus although the average standing crop in the loch is low, the animal is concentrated in certain areas, and within these areas the standing crop is five times higher than elsewhere and the productivity is comparable in order of magnitude to other food organisms of trout and perch.

As chironomid larvae are the most common food organism of predatory fish and ducks in the loch and are found over the whole of the loch area, the I.B.P. programme of study concentrated on the energy pathway of phytoplankton to chironomid larvae to trout, with other predators such as perch and ducks also being studied.

The net production of herbivorous chironomids was found to be 525 KJ $m^{-2}yr^{-1}$; the minimum consumption values of trout and perch were 144 and 398 KJ $m^{-2}yr^{-1}$ (Laughlin, 1974). Thus the consumption of the predatory species amounts to 562 KJ $m^{-2}yr^{-1}$ and the total production of chironomids is only 525 KJ $m^{-2}yr^{-1}$. Assuming the estimated values approximate to the ecological values, there is still a shortfall indicated whereby the predators could not derive their energy requirements from the chironomids alone.

The production value of 133 KJ $m^{-2}yr^{-1}$ for Asellus derived by this study is for the shallow rocky areas, no study having produced a corresponding production value for the sand and mud areas. For this reason it is proposed to estimate a value from the P/B ratio from the present study and using the mean standing crop value already estimated. It must be stressed, however, that part of the result of the thesis has been to show that the $P/\bar{B}$ ratio varies with food conditions as well as other climatic factors so that it is unlikely that the

$P/\bar{B}$ ratio is the same in the rest of the loch as it is in the rocky littoral. It is likely that in the absence of abundant benthic algae the main food supply will be particulate detritus so that the $P/\bar{B}$ ratio would be smaller, perhaps in the order of 2-3. However, since there is no other quantitative measure available other than the 7.05 derived from the present study, it can be used to give an estimate of production from the standing crop ($\bar{B}$) of 35.88 KJ $m^{-2}yr^{-1}$.

Adding this value to the production of chironomid larvae one gets a combined invertebrate production of 561 KJ $m^{-2}yr^{-1}$ compared to a demand for consumption of 562 KJ $m^{-2}yr^{-1}$. It is not suggested that the production of chironomids and Asellus satisfies the demand of the predator populations - the model produced is simple and one need only look at Thorpe's (1974) data on stomach analysis of fish to see that as well as Asellus and chironomids the trout and perch populations consume quantities of perch fry, molluscs, Gammarus and other invertebrates. However, for comparative purposes it is of interest that taken over the whole area of the loch the demand for consumption approximates to the production of these invertebrates. The approximation is close enough to suggest that the production of chironomids and Asellus is very effectively harvested by the predators so that the yield to these predators may be a large proportion of the production, and predatory

pressure high. This has already been suggested when, to explain the disappearance of overwintering females from the population after production of the primary recruitment, it was necessary to suppose that predatory pressure on large animals was such that they did not survive to produce the 2 or 3 broods that Williams (1960) suggested that they were capable of producing. Again, in section 2.1.2, where the sex ratio was discussed, it was proposed that the predatory pressure on the population was such that the ovigerous females, being slower and larger, were at a disadvantage and so many were taken that a considerable increase in the proportion of males in the population was observed without any other likely explanation.

Considering the rocky areas specifically, the production of 133 KJ $m^{-2}yr^{-1}$ of Asellus is almost sufficient to satisfy the minimum trout consumption if no other predator was acting in that area; on the same basis Asellus could satisfy 33% of the minimum consumption requirement of perch. Study of the predatory behaviour of the trout would indicate whether the discrepancy between demand and supply means that all the trout move around in the loch and therefore feed part of the time over the rocks and part of the time over the sand and mud, or whether a hierarchy is set up whereby certain individuals take up 'beats' or territories over areas of particular production, supplementing their diet

from the other invertebrates there and excluding other fish from the area. As the fish samples for stomach analysis were taken from the rocky areas only, it is not possible to speculate much in this direction; however, if the fish were moving extensively in the loch as part of their feeding behaviour the proportion of food items in the stomachs might be expected to follow the pattern for the whole loch, whereas if the fish were feeding exclusively in the rocky shallow areas one would expect the pattern of food items to reflect that of the rocky littoral itself.

Taking the loch as a whole, 6% of the chironomid/ Asellus production is from Asellus whereas in the rocky areas where chironomid production is minimal, Asellus could be 92% of the minimum consumption of the trout population per square metre. In fact Thorpe (1974) found that between July and September 1971 Asellus formed 24.2% of the total consumption of trout, thus suggesting that these fish were not feeding exclusively over the rocky areas but were certainly taking in a higher proportion of Asellus than present in the loch as a whole. They therefore may represent fish captured while feeding over the rocks as a part of a pattern of behaviour encompassing a much greater area.

There has been some speculation that the fish samples were biased since they were netted over shallow rocky areas; Charles et. al. (1974) illustrated the

magnitude of the difference this might cause when they compared the percentage by volume of larval chironomidae in the diet of trout and perch caught in deep water (66%: trout; 92%: perch - May to September, 1968) with Thorpe's data from the shallow water net samples (14%: trout; 12%: perch - July to September, 1971). However, other factors such as differences in the methods of collection and examination may account for part of the difference and, as in the case of Asellus in the diet of fish caught over the rocky shallows: the diet must be biased in some way towards the food types available immediately before capture. Also it must be considered important that the fish were collected over these shallow areas not only because of the ease of netting in such conditions but also because of the concentration of the fish in these areas. The indications are, therefore, that the netted fish, and hence the stomach analyses of Thorpe (1974), are representative of the whole population for which a part of the normal feeding behaviour is to spend some time feeding over the shallow rocks.

Thus the position of Asellus in the Loch Leven ecosystem can be seen to be one of considerably greater importance than originally thought during the I.B.P. study. The shallow rocky areas of the loch are a source of detrital material and/or shelter for a diverse fauna amongst which are several food items of trout and perch:

Asellus, Gammarus, molluscs, leeches, trichoptera and various annelids. Of these Asellus is of considerable importance since not only is it found in large numbers for part of the year (e.g. in excess of 7000 individuals per m^2 in July 1975) but it has certain advantages as a food source for predators for although its calorific value is in the middle of the range of aquatic animals tabulated by Prus (1970), it has behavioural patterns which make it easier to catch than, for instance, Gammarus. Whilst the small individuals move amongst the algal strands on the rocks, the larger ones often position themselves on the distal ends of the strands, in a position readily seen by the fish. Moreover, when disturbed in this poisition they will often release their hold and swin downwards - forming an easy prey item which the fish could easily become conditioned (short-term) to searching for. Similar behaviour was noted by Berglund (1968) who concluded that part of the reason that Asellus formed 90% of the food in the stomachs of his trout was the mobility of Asellus in the uppermost layers of the bottom vegetation (Nitella opaca) and its habit of climbing to the highest terminal branches of the Nitella.

As a rapid converter of most allochthonous and autochthonous detrital material to readily utilised food for predatory fish Asellus is adapted to take advantage of whatever organic material is entering the environment and make it available to the higher trophic levels. No

measure has been made of the import of organic material to the loch but the shallow areas under consideration are the recipients of deciduous leaf material as well as decomposing fragments of shoreline vegetation, including material from wave eroded shore areas. All this is in addition to the benthic algae and the associated epiphytic growth.

Thus the littoral area is of importance not only to the inhabitants of the littoral itself but also to predators. In Loch Leven, as in all other water bodies, the littoral area is an important influence on the ecosystem of the whole water body. In Loch Leven this arises from the abundance of food substrates in the form of benthic algae and autochthonous and allochthonous detritus. Of the diverse and abundant fauna associated with this energy input, Asellus aquaticus has been shown to be of major importance as a direct link between the various food substrates and the larger predatory organisms such as trout and perch which are of interest to man.

APPENDICES

1. The Length to Dry Weight Relationship.

On seven sampling days a number of animals were set aside for determination of a relationship between body length (the parameter used throughout the study) and the dry weight, for use in biomass determinations.

The animals were kept without food for 24 hrs to allow some gut evacuation - total evacuation was not possible, probably due to an increased retention time when a food source was absent. The animals were measured alive (see section 2.1 for details) and then kept seperately in small petri dishes. They were killed by the addition of a few drops of 40% formaldehyde solution to the water in the dishes. Each animal was then placed in a foil planchet and dried for 48hrs at 60°C in a drying oven.

The dried animals were cooled in a dessiccator and then weighed to the nearest microgramme using an electrical microbalance.

Since the weight was measured directly, the relationship is for the length to the total dry weight, not to the ash-free dry weight. The resulting relationships are shown in table I.

Summation of these lines produces the pooled data line:

$$\log_{10} (\text{dry weight}) = 2.4748 \log_{10} (\text{length}) - 1.6891$$

The extreme closeness of fit of the data to the individual lines (as indicated by the correlation coefficients in table I) means that the F test for comparison of this pooled data line with the seperate lines is inappropriate: it will indicate significant difference even though in reality the lines are very close. However, calculations were made of the range of values produced by the two lines with the most dissimilar slope coefficients, as a percentage of the values obtained using the pooled data line.

TABLE I. The results of the length/dry weight determinations as used to calculate the pooled data line. Values are shown as constants in the equation:

$$\log_{10} (\text{dry weight}) = b \log_{10} (\text{length}) + a$$

DATE	b	a	COEFFICIENT OF CORRELATION	NUMBER OF ANIMALS
21 xi 73	2.3778	-1.6268	0.9844	75
14 v 74	2.9527	-2.1356	0.9854	13
9 iv 75	2.7694	-1.9172	0.9865	24
24 v 75	2.7820	-1.9291	0.9477	24
30 vi 75	2.5943	-1.7549	0.9865	25
21 vii75	2.3536	-1.5853	0.9670	24
7 viii75	2.8762	-1.9888	0.9644	24
Pooled Data Line:	2.4748	-1.6891		

The results showed that at no time during the year was the range produced more than 2% of the overall weight for any size class and thus the pooled data line was considered valid for use in calculating biomass data from length measurements.

2. Data from the Assimilation experiments

Substrate: Willow leaf;
Temperature: 5°C.

DRY WEIGHT	DURATION (HOURS)	ASSIM'N mgm.	CONSUM'N mgm.	ASSIM'N EFFICIENCY %
4.2469	45	0.2297	2.0070	11.44
4.2902	168	0.3185	2.6955	11.81
2.5013	45	0.2767	1.5837	17.47
9.1374	168	0.0117	0.1837	6.37
3.9990	168	0.0216	0.7236	2.99
4.2469	168	0.2102	2.2852	9.20
2.9244	72	0.3487	2.1569	16.17
4.1348	72	0.2364	2.0144	11.74
3.7727	168	0.5284	1.3004	40.63
4.0009	168	0.0035	0.8775	0.40
2.9067	168	0.1790	1.6730	10.70
2.9087	168	0.7057	2.9757	23.72
1.8106	45	0.2475	1.2015	20.60
3.2472	72	0.1171	1.5881	7.37
3.4007	72	0.1851	1.4871	12.45
3.3062	72	0.6562	1.7822	36.82
3.6014	45	0.5520	2.3850	23.14
3.6034	72	0.2431	1.2561	19.35
2.9717	336	0.0097	0.2597	3.74
3.1783	336	0.1973	1.2223	16.14
4.3276	96	0.2343	1.4103	16.61
4.4988	96	0.4320	2.4840	17.39
2.9914	336	0.1240	0.5630	22.02
3.1134	96	0.1051	1.1321	9.28
3.1724	96	0.2238	1.6308	13.72
1.4799	336	0.1922	1.1502	16.71
3.2236	336	0.1771	0.8511	20.81
1.8972	96	0.1666	1.0286	16.20
3.4125	96	0.0923	0.7063	13.07
2.9579	336	0.1062	0.6802	15.61
2.5466	336	0.4257	2.3677	17.98

Substrate: Willow leaf;
Temperature: 10°C.

DRY WEIGHT	DURATION (HOURS)	ASSIM'N mgm.	CONSUM'N mgm.	ASSIM'N EFFICIENCY %
3.1704	264	0.1951	0.4731	41.24
2.1254	264	0.2260	1.0250	22.05
1.9464	264	0.1291	0.3901	33.09
1.4799	480	0.3260	1.4180	22.99
2.8556	168	0.6826	2.1946	31.10
2.5092	168	0.0306	1.5526	1.97
2.5328	96	0.1897	0.7937	23.90
1.6905	264	0.0028	0.5758	0.49
2.6548	264	0.0141	0.5881	2.40
1.2503	168	0.0692	0.7242	9.56
1.4498	264	0.1361	0.7891	17.25
1.5431	264	0.0631	0.9211	6.85
2.2789	168	0.3312	2.0302	16.31
1.1897	264	0.1136	0.8046	14.12
1.1013	264	0.1661	1.3521	12.28
1.5626	96	0.0761	1.2601	6.04
1.7305	168	0.1073	0.9513	11.28
2.2356	96	0.1025	0.9885	10.37
1.6698	168	0.1360	1.2570	10.82
1.0903	96	0.1147	0.6547	17.52
1.6531	96	0.1828	1.0498	17.41
1.9302	264	0.0958	0.6088	15.74
1.7783	480	0.1239	0.2899	42.74
1.2184	168	0.1729	0.6809	25.39
1.4646	480	0.3249	0.6869	47.29
1.4445	96	0.6540	2.4020	27.23
1.0824	96	0.2392	0.9542	25.07
1.2438	96	0.5185	2.2895	22.65
2.1077	168	0.9321	2.6491	35.19
1.2637	264	0.0418	0.2928	14.28
1.5626	96	0.3215	1.7695	18.17
1.1080	96	0.1842	0.7622	24.17
2.3380	264	0.0512	0.2262	6.72
1.5862	96	0.3206	1.6746	19.14
1.8086	168	0.1467	1.2567	11.67
1.5045	168	0.1782	1.0132	17.59
1.9201	480	0.2228	0.4288	51.96

Substrate: Willow leaf;
Temperature: 15°C.

DRY WEIGHT	DURATION (HOURS)	ASSIM'N mgm.	CONSUM'N mgm.	ASSIM'N EFFICIENCY %
1.8617	96	0.2035	1.8325	11.10
1.6915	264	0.1151	0.6581	17.49
1.9739	264	0.5656	2.2016	25.69
1.1448	480	0.2111	0.4941	42.72
1.7196	264	0.4819	1.5559	30.97
1.4246	480	0.4348	0.6998	62.13
2.1687	264	0.0938	0.5888	15.93
2.0900	264	2.3295	2.7275	85.41
3.0976	168	0.2611	1.5551	16.79
4.7527	168	0.8265	1.7875	46.24
1.1847	480	0.2998	0.5698	52.61
2.0054	168	0.2877	0.9137	31.49
2.9323	96	0.2197	1.0647	20.63
1.5803	168	0.4185	1.5644	26.75
1.7279	96	0.1718	0.9388	18.30
0.9964	168	0.3921	1.8921	20.72
1.3166	96	0.2115	1.4115	14.98
2.2809	96	0.0908	1.1198	8.11
1.1164	168	0.3223	1.6283	19.79
1.7436	96	0.0969	1.1449	8.46
2.5092	480	0.0994	0.2744	36.23
1.2000	216	0.4969	1.1169	44.49
2.2500	216	0.3938	0.5728	68.75
1.0000	216	0.0282	0.5472	5.15
2.7500	216	0.1184	0.2444	48.45
1.0800	216	0.2817	0.8807	31.99
4.6200	216	0.2885	0.8885	32.47
1.3000	216	0.1648	0.4758	34.64
1.3600	216	0.1755	0.7845	22.37
4.1000	216	0.0682	0.2252	30.28

(5 animal cultures, totals for assimilation and consumption given.)

MEAN LENGTH mm.				
5.62	312	0.7008	3.4198	20.49
5.25	312	1.8549	6.7069	27.66

Substrate: Cladophora;
Temperature: 15° C.

LENGTH mm.	DURATION (HOURS)	ASSIM'N mgm.	CONSUM'N mgm.	ASSIM'N EFFICIENCY %
(single animal cultures)				
8.6	168	0.3514	1.2934	27.16
7.8	168	0.5717	2.4457	23.37
6.7	168	0.2860	1.3260	21.56
6.8	168	0.2578	1.4148	18.22
6.7	168	0.4266	1.3306	32.06
5.3	168	0.1903	0.6323	30.09
8.0	168	0.9216	2.0496	44.96
6.5	168	0.6550	2.0890	31.35
8.1	168	0.5095	1.8595	27.39
6.8	168	0.1587	1.3237	11.98
6.2	168	1.0182	2.6732	38.08
7.8	168	0.1182	0.7492	15.77
(5 animal cultures, totals for assimilation and consumption given.)				
MEAN LENGTH mm.				
4.88	144	0.2349	1.8549	12.66
5.00	144	0.3627	1.0877	30.54
4.88	144	0.7125	2.1515	33.12
6.48	144	0.7789	2.0549	37.90
6.60	144	0.6501	2.1141	30.75
6.52	144	1.0416	3.8396	27.13
9.18	144	0.8675	3.0945	28.03
8.40	144	0.3874	2.8244	13.72
11.73	144	0.8809	2.2299	39.50

Substrate: Elm leaf;
Temperature: 15°C.

LENGTH mm.	DURATION (HOURS)	ASSIM'N mgm.	CONSUM'N mgm.	ASSIM'N EFFICIENCY %
(single animal cultures)				
4.7	216	1.6134	2.0024	80.57
5.3	216	2.3728	2.8558	83.09
7.0	216	0.6786	1.2086	56.15
5.6	216	0.9704	1.3606	71.33
7.4	216	0.8489	0.8949	94.86
10.2	216	0.0643	0.6233	10.32
5.5	216	0.1610	0.7770	20.72
4.6	216	0.3424	0.8494	40.31
6.2	216	0.9392	1.2772	73.54
6.7	216	0.1261	0.6631	19.02
9.5	216	1.8674	2.1584	86.52
5.1	216	0.6332	1.6562	38.23
7.0	216	0.1746	0.4926	35.44
6.5	216	1.1410	1.9100	59.74
6.0	216	0.0096	0.6016	1.60
8.9	216	0.4304	0.7734	55.65
4.8	216	2.5469	3.4779	73.23
6.6	216	1.8499	2.3219	79.67
(5 animal cultures, totals for assimilation and consumption given.)				
MEAN LENGTH mm.				
5.48	312	1.3784	6.5724	20.97
5.28	312	2.3891	8.6101	27.75
5.04	120	0.2226	0.9476	23.49
6.60	120	1.0678	4.4858	24.03
8.80	120	1.0452	5.3462	19.55

Substrate: Humicola grisea;
Temperature: 15°C.

LENGTH mm.	DURATION (HOURS)	ASSIM'N mgm.	CONSUM'N mgm.	ASSIM'N EFFICIENCY %
(single animal culture)				
7.4	4	0.3267	0.3427	95.33
9.3	4	0.5451	0.6881	79.22
6.9	4	0.0725	0.1915	37.86
8.1	4	0.4489	0.6269	71.61
6.4	4	0.7740	0.8600	90.00
7.9	4	0.5414	0.6594	82.10
8.5	4	0.4608	0.4848	95.05
10.2	4	1.5725	1.7755	88.57
8.1	4	1.6974	1.7544	96.75
7.4	4	1.2624	1.3444	93.90
6.6	4	0.3928	0.4708	83.43
9.9	4	0.9447	1.0687	88.40
11.0	4	1.5603	1.6593	94.03
10.0	4	1.4596	1.5906	91.46
8.7	4	1.1614	1.2324	94.24
10.0	4	1.0794	1.0854	99.45
7.3	4	0.5522	0.6592	83.77
7.6	4	0.9855	1.1155	88.35
Substrate: Oak leaf; Temperature: 15°C.				
(single animal culture)				
8.9	216	0.4039	0.7709	52.39
5.4	118	0.0178	0.1978	9.00
5.0	118	0.0078	0.1728	4.51
6.3	118	0.1287	0.2917	44.12
6.9	118	0.2529	0.4189	60.37
7.7	118	0.0507	0.2277	22.27
6.4	118	0.3335	0.5205	64.07
7.2	118	0.1250	0.3610	34.63
6.3	118	0.0096	0.1986	4.83
5.4	118	0.0004	0.1504	0.27
6.8	192	0.0140	0.1020	13.73
5.4	192	0.0290	0.2220	13.06
6.3	192	0.0730	0.2460	29.67
(5 animal cultures, totals for assimilation and consumption given.)				
MEAN LENGTH mm.				
5.50	312	0.9762	1.9822	49.25
5.32	312	0.2697	3.7297	7.23
4.88	120	1.7785	4.7845	37.17
6.48	120	0.4605	1.0635	43.30
9.20	120	2.3454	3.8394	61.09

3. Data from the Growth experiments

Section 1: The individually cultured animals

Substrate: Willow Leaf;

Temperature: 15°C.

DATE	DAYS	LENGTH (mm.)	WEIGHT (mgm.)	NUMBER OF ANIMALS
12 v 75	0	4.13	0.6845	10
6 vi 75	25	6.14	1.826	9
23 ix 75	134	7.071	2.589	7
2 xii75	204	7.75	3.248	6
Temperature: 10°C.				
12 v 75	0	3.49	0.451	10
6 vi 75	25	4.94	1.066	10
9 v 76	363	6.50	2.102	3
Temperature: 5°C.				
12 v 75	0	3.93	0.6052	10
6 vi 75	25	4.48	0.8389	10
23 ix 75	134	5.92	1.668	10
7 v 76	361	6.14	1.825	8
Substrate: Cladophora;				
Temperature: 15°C.				
12 v 75	0	4.30	0.7563	10
6 vi 75	25	5.56	1.429	8
28 ix 75	139	9.20	4.968	2
2 xii75	204	10.00	6.105	2
Temperature: 10°C.				
12 v 75	0	4.24	0.7305	10
6 vi 75	25	4.95	1.066	9
9 v 76	348	7.567	3.062	4
Temperature: 5°C.				
12 v 75	0	3.64	0.5006	10
6 vi 75	25	4.00	0.6324	9
26 ix 75	139	4.675	0.9307	8
5 v 76	344	5.15	1.181	4

Section 2: The group cultured animals

Substrate: Willow Leaf;
Temperature: 15°C.

DATE	DAYS	LENGTH (mm.)	STANDARD DEVIATION OF LENGTH.	WEIGHT (mgm.)	NUMBER OF ANIMALS.
26 vi 75	0	3.66	0.3578	0.5110	30
23 vii75	47	4.84	0.3970	1.013	29
27viii75	82	5.73	0.5998	1.539	22
26 ix 75	112	6.16	0.5629	1.841	19
12 xi 75	159	6.44	0.7732	2.055	9
2 xii75	179	7.28	0.5679	2.783	4
29 i 76	237	6.80	-	2.351	1
Temperature: 5°C.					
26 vi 75	0	3.50	0.3596	0.4543	30
24 vii75	48	3.82	0.5136	0.5643	29
27viii75	82	4.18	0.5600	0.7050	29
26 ix 75	112	4.33	0.6012	0.7693	29
12 xi 75	159	4.57	0.6153	0.8790	28
2 xii75	179	4.76	0.6619	0.9723	28
29 i 76	237	4.82	0.6864	1.0020	26
7 v 76	336	5.08	0.8057	1.1420	28
Substrate: Cladophora:					
Temperature: 15°C.					
26 vi 75	0	3.80	0.4287	0.5569	30
23 vii75	47	5.50	0.5909	1.391	26
27viii75	82	5.59	0.5994	1.447	22
26 ix 75	112	5.55	0.7234	1.422	4
Temperature: 5°C.					
26 vi 75	0	3.67	0.3610	0.5110	30
24 vii75	48	4.39	0.5532	0.7962	24
27viii75	82	5.36	0.6724	1.3050	26
26 ix 75	112	5.75	0.6658	1.5520	28
12 xi 75	159	5.86	0.5730	1.6270	28
2xii 75	179	6.03	0.5474	1.7460	28
29 i 76	237	5.71	0.4851	1.5250	25
7 v 76	336	5.85	0.4925	1.6200	20

Substrate: Oak Leaf;
Temperature: 15°C.

DATE	DAYS	LENGTH (mm.)	STANDARD DEVIATION OF LENGTH.	WEIGHT (mgm.)	NUMBER OF ANIMALS.
15 ix 75	0	3.40	0.3818	0.4230	25
26 ix 75	11	3.67	0.3700	0.5110	24
12 xi 75	58	4.67	0.5283	0.9274	7
2 xii75	78	4.66	0.5857	0.9228	5
29 i 76	136	6.90	-	2.4360	1
Temperature: 5°C.					
26 vi 75	0	3.51	0.3022	0.4575	30
24 vii75	48	3.76	0.3348	0.5425	30
27viii75	82	3.90	0.4426	0.5940	30
26 ix 75	112	3.95	0.4214	0.6130	29
12 xi 75	159	3.95	0.5474	0.5474	28
2 xii75	179	4.07	0.4683	0.6600	28
29 i 76	237	3.99	0.4170	0.6285	26
7 v 76	336	4.05	0.5519	0.6521	21

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