

POPULATION AND PRODUCTION STUDIES
OF
TWO SPECIES OF WOODLICE
(ISOPODA : ONISCIDEA)

A thesis presented for the
Degree of Doctor of Philosophy
in the University of Leicester

by

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June 1986

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INTRODUCTION

Introduction

Ecology has been defined by Odum (1967) as "the study of the structure and function of ecosystems". He suggests that a great deal of attention has been focused on the structural, descriptive approach, whereas few studies of the functioning of ecosystems have been attempted. This is no longer an accurate statement as great progress has been made in the last twenty years. However, in the case of the study of woodlice there are numerous gaps in their holistic study some of which this thesis attempts to correct.

Odum (op cit) further states that by structure he means: (a) the composition of the biological community, including species, numbers, biomass, life history and distribution in space of populations, (b) the quantity and distribution of abiotic materials such as nutrients and water, and (c) the range of conditions of existence. such as temperature gradients and light. Functions are defined as: (a) the rates of production plus rates of respiration; (b) the rates of biogeochemical cycling, e.g. nutrient flow, and (c) biological or ecological regulation.

The two approaches to the study of ecosystems are both necessary. The structural approach serves to describe the existence of organisms and materials. Odum (op cit) & Macfadyen (1963) have stressed that, although biomass in different ecosystems may be widely different, the energy flow produced may be very similar. Strict comparisons of numbers alone are, therefore, of limited use when one wishes to fully understand the working of ecosystems. The functional approach, whereby rates of energy flow per unit area of habitat per unit time are measured for various organisms, will enable stricter comparisons to be made both within and between ecosystems.

The present study attempts to compare the ecology of two common species of woodlice in two different habitats. This subject was chosen because of the importance of these organisms in promoting energy flow in ecosystems, because

of their large populations, because of the need for greater knowledge of their ecology in the field. A second factor in choosing this study is that woodlice offer some unique advantages for teaching. They are readily accessible in the field for sampling and collecting, even in urban areas, and they are of a convenient size for observation and experimental work. Finally, a body of knowledge on other aspects of the ecology and biology of terrestrial isopods, especially their environmental physiology, forms a valuable background for field studies.

The terrestrial isopods are exceptional invertebrates because their population structure is strongly influenced by a variety of environmental factors and yet individuals are capable of surviving for periods up to four years (McQueen 1976). These characteristics, combined with ready availability and ease of laboratory culture, have yielded a number of quite complete population studies that have given considerable information about reproduction, growth and mortality. Because much of this information influenced the research undertaken here, and is not available elsewhere, a comprehensive review of the literature pertaining to isopod ecology is necessary here before some of the gaps in the total ecology of isopods are filled.

Following the literature review the present study attempts an overview of the biology and behaviour of two common isopods Oniscus asellus (Linnaeus) and Porcellio scaber Latreille. This is followed by studies of population density and biomass by means of samples taken regularly over two years by day and night and within three distinct habitats on Nene College, Moulton Park Campus. The behaviour, respiratory and feeding studies were undertaken in laboratory conditions. Thus a model of the ecology of these two isopoda is undertaken which has not been undertaken by any other researcher.

Growth

Laboratory work by both Heeley (1941), and Standen (1970), working with Trichoniscus pusillus (Brandt) have shown that the Oniscidea pass through about seven juvenile stadia during which flagellum segments, pereion segments, and legs are added. From the eighth moult onwards the animals are recognised as adults. Laboratory studies by Heeley (1941) on T. pusillus, Hatchett (1947) on Armadillidium vulgare (Latrielle), Cylisticus convexus (De Geer), Porcellio scaber, and Trachelipus rathkei (Brandt), Brereton (1957) on P. scaber, Becker (1936) on P. scaber, Merriam (1971) on A. vulgare, and McQueen & Carnio (1974) on Porcellio spinicornis (Say) indicate that growth rate is inversely related to body size or weight. Furthermore, Becker (op cit), on P. scaber, and McQueen et al (op cit) on P. spinicornis, show a strong correlation between growth rate and temperature. Merriam (op cit) also showed that growth rate is related to food quality.

A number of field studies reflect the growth patterns observed in the laboratory. Hatchett (op cit), studying a natural population of Cylisticus convexus, in Michigan, suggests that the young are released from the brood pouch in the early spring and attain adult size (8 mm) by early August. The difficulty with this interpretation is that Hatchett's growth data indicate that 25 weeks are required at 20°C before an animal reaches 8 mm in length. There is not enough time for this to occur during the first summer and it must be assumed that contrary to Hatchett's interpretation, C. convexus, must have been 14 months old before reaching maturity. Hatchett also noted that during years of high rainfall mean size was greater. Brereton (op cit) found a similar pattern in a naturally occurring population of P. scaber. Young were released into the population during August and September, some growth occurred in Autumn and, after they overwintered as animals of about 3 mm, spring growth allowed the recruits to attain adult length (6 mm) by June. Adult growth patterns were difficult to follow because of low growth rates and recruitment from the

juvenile population, but Brereton suggests that some animals might survive 3 or 4 years. Sutton (1968), studying P. muscorum in England, found recruitment during July and August, rapid autumn growth, no winter growth, and rapid spring growth to reach maturity by June when reproduction was possible. Radu & Tomescu (1976), studying Protracheoniscus politus in Israel, also found that maturity was reached during the second summer and they suggested that a 3-year life cycle was possible. Paris (1963) found that A. vulgare in California followed the same pattern. Recruitment began in April and animals grew throughout the year so that the first recruits reached adult length (8 mm) during the next breeding season. They suggest that animals can live for as long as 4 years.

Al-Dabbagh and Block (1981), in a study of A. vulgare on a Breckland (England) grassland, found one or two broods per annum depending on whether the grass was grazed or ungrazed. In the ungrazed tussocky grassland each cohort participated in two annual breeding seasons. The use of grazing as a management tool to maintain the diversity of insect populations in certain chalk grasslands has been advocated by Morris (1973). Rotational grazing was thought to conserve the characteristic fauna of grazed and ungrazed habitats. Morris (op. cit.) recorded considerable differences in isopod numbers throughout the year for grazed (292m^{-2}) and ungrazed areas (7233m^{-2}) which differ by a factor of 25. Southwood (1971) showed that the short grass total macro-invertebrate fauna had a marginally higher density than the long grass sward. More work needs to be done on the possible correlation between population density, physical structure of vegetation and microclimates.

Laboratory experiments by Sunderland, Hassall and Sutton (1976) suggest that the effect of temperature, together with the temporal separation of early and late recruits was the most likely cause of cohort splitting in P. muscorum.

Mortality

Two laboratory studies have produced survivorship curves for terrestrial isopods. Brereton (1957), studying P. scaber reared at about 20°C, found that 82% of the eggs survived to produce juveniles. After release from the brood pouch 10% of the emerged animals survived the first 50 days, 6% of the cohort survived the next 200 days, and almost 100% of the survivors died during the remaining 250 days. McQueen & Carnio (1974), working with P. spinicornis reared at 20°C, found that 60% of the individuals survived the first 50 days, of these 50% survived the next 100 days, and almost 100% of the survivors died during the next 550 days. The rates of survivorship recorded in these and other studies were strongly influenced by a variety of factors. Brereton (op cit) found that survivorship in young animals was inversely related to population density. McQueen [?]et al (op cit) reported that P. spinicornis always suffered 100% mortality if individuals were unable to find a habitat with a relative humidity (RH) ranging from 92% to 98%, and they also found that survival increased as temperature increased from 0°C to 25°C and decreased with further increases in temperature. Reichle & Van Hook (1971) made similar observations with A. vulgare and C. convexus. Finally, Merriam (op cit) found that food type strongly influenced the survival of laboratory populations of A. vulgare.

Several field studies include estimates of survival rates. Hatchett (1947) suggests that C. convexus might survive for 3 years in the field, and that females make up about 65% of the population. Brereton (op cit) found that a naturally occurring P. scaber population living on a tree exhibited survivorship rates that were very close to those found in the laboratory. Fifty days after emerging from the brood pouch 12% of the population survived, after 18 months 5.8% survived, and after 30 months 1.7% survived. Brereton also found that the sex ratio increased from 1:1 to 9:1 in favour of the females, suggesting that males suffer greater mortality than females. Because the field

and laboratory data in Brereton's study agreed so well he concluded that mortality from external sources such as predation must be small in naturally occurring populations. Paris (1963), using A. vulgare, reported a brood mortality of 8%, followed by a survivorship of 19% after 6 months, 11% after 1 year, and less than 1% after 4 years. With increased age the sex ratio increased in favour of the males, suggesting increased female mortality due to deaths during breeding. Sutton (1968, 1972) found that 20% of the T. pusillus population survived the first 3 months and 7% survived at least 2 years, while more than 35% of a P. muscorum population survived the first 6 months of life and 2% survived 2 years. He also noted that the drought conditions which occurred during 1964 did not cause higher mortality in either population, than that which occurred in 1967, although survival in T. pusillus during 1965 was high, but the cause was unknown. Radu & Tomescu (1974) reported similar mortality patterns for P. politus, where 5% of the animals survive 18 months and less than 1% survive more than 30 months, while with increased age the sex ratio favoured females.

Wallwork (1975), in a comparative survey of energy content in different members of the soil fauna, contrasted the relatively high energy content of predatory species with the lower values that he considered were characteristic of saprophages. He attributed the differences largely to difference in the mobility of members of the two groups, the more mobile predators requiring more energy rich food reserves than the relatively sedentary saprophages that utilize continuously available food. Hassell (1976) in his study of P. muscorum found values that fell close to the upper end of the range given by Wallwork (op cit) for saprophagous species possibly reflecting the fact that this is a particularly active species of isopod (Sutton 1972). Rate of growth in P. muscorum was affected by food quality (Sunderland et al 1976). High food quality available to one generation can influence the ratio of fast to slow growing females and thereby alter the rate of population increase, Sutton & Holditch (1984.) The fast growing females being the surface active species.

Population Limitation

Almost all of the major isopod studies isolate factors that the authors believe are primarily responsible for population limitation, and in every case the key factor is unique. A number of studies suggest that climatic conditions are important. Hatchet (1947) believed that rainfall increases growth rates in C. convexus, which could influence the time necessary to reach maturity. Paris (1963) noted that most of the mortality in juvenile A. vulgare is caused by flooding that is induced by winter rains. Since both sources of mortality are avoided by individuals that obtain suitable refuges, both may be density dependent. Sutton (1968) show that summer drought prevented T. pusillus from breeding during the summer of 1964, but this probably had no limiting effect as the population compensated with reduced mortality and returned to normal levels within a year. Finally, McQueen & Carnio (1974) suggest that on the basis of a laboratory-derived demographic model a population of P. spinicornis living in Ontario could be regulated by minor shifts in annual temperature and humidity.

A number of biotic factors may also be important. Clark (1970) and Sutton (1970, 1972) have shown that various vertebrate and invertebrate predators are capable of inflicting considerable mortality on isopod populations, and Clark demonstrated that predation by Bufo was density dependent at high densities. However, there is no field evidence to suggest that predation might result in population limitation, particularly for P. spinicornis, which tend to occupy wall and cliff habitats which are relatively free of potential vertebrate predators. There are also a number of host-specific parasites that infect terrestrial isopods, and Sutton (1972) found infection rates of 30% by Dipteran larvae in some P. scaber populations, but the effects of parasite infections on isopod field populations have not been demonstrated, and no parasites have been found in P. spinicornis. There is, however, one reported case of significant pathogen infection. Paris (1963) found that the pathogenic fungus Entomophthora sp. reduced a California A. vulgare population

from 5000m² over a 6-month period to 150m². Cannibalism may also be important. Brereton (1957) showed that most mortality in P.scaber occurred soon after release from the brood pouch, and that cannibalism by adults is common in the laboratory. Brereton argues that since adults and juveniles share the same refuges in the field, the rates of cannibalism may be high. Finally, Stachurski (1968, 1972) presents good evidence to show that Ligidium hypnorum, inhabiting small islands that grow and contract with annual rainfall and drying, are limited by the availability of food in Poland.

There appear to be as many explanations for population limitation as there are studies, but there is some general agreement on the life-history patterns exhibited by naturally occurring populations. Young are produced during the spring and summer, and mortality during brooding ranges from 0% to 10%. Either one or two breeding peaks are possible and this is probably controlled by environmental conditions (Sutton et al 1984). At least a year is required before sexual maturity is reached and only about 10 to 20% of the recruits survive this period. Individuals may survive for 3 or 4 years, but 1-year-old animals contribute most to the production of new recruits. It may be noted that within the guidelines established by this description of life-history patterns, almost all studies relate specific exceptions and most of these appear to result from unique combinations of food quality, temperature, and other essential factors. One of the objectives of the work presented here is to attempt to learn more about the relationships that determine these exceptions.

One of the major problems encountered when attempting to interpret data from isopod field studies is that there is a lack of information about growth, reproduction, and survival under a variety of controlled conditions. Only Brereton (1957) and Hatchett (1947) present this kind of information and it is available for only one set of climatic conditions, making it impossible to draw conclusions about field populations which experience a variety of climatic conditions.

Sunderland et al (1976) suggest that the mortality rate during the life of a cohort was not shown to be dependent upon initial cohort density. The high mortality in the first two months of life was as much as 81% of recruitment. The overall pattern of decline in density was exponential for all cohorts but survivorship patterns of the constituent groups of a cohort were different.

Energetics

In contrast to the foregoing population studies, very few researchers have worked on the functional approach to the study of isopods. Watson (1966) calculated that O.asellus and P.scaber ingested, on average, 10.106 g dry weight per annum, assimilated 3.025 g and egested 7.081g. dry weight. Phillipson & Watson (1965) noted the relationship between live weight and length where a change occurs at approximately 20mg weight and 7.5mm length which also coincides with a change in the respiratory rate to live weight relationship in O.asellus. The high oxygen uptake at live weights less than 20mg. is clearly associated with growth. They also found seasonal differences in respiratory rates in both sexes. The highest respiratory rates per unit weight occurred between March and August and were more than twice as high as those obtained for the winter months. They calculated that an oxygen consumption per unit weight per unit time was between 4.992 and 5.328 mm³ O₂ / mg / dry/wt.

White (1968) working with T. rathkei found the biomass of the population in deciduous forest fluctuated from 0.09 to 0.35 gm⁻² averaging 0.208gm⁻². This average is equivalent to 148.93J m⁻².

White (op cit) and Watson (op cit) both indicate the consumption of a relatively large quantity of leaf litter, which passes rapidly through the gut, making available a large faecal substrate favourable for micro-organisms to work on.

Terrestrial isopods exploit a wide variety of foods. They show a preference for certain types of plant material, the preference being expressed by more frequent visits if given a choice and by higher rates of ingestion. Rushton & Hassall (1983) Beck and Brestowsky (1980) found that O. asellus grew better on freshly fallen leaves than on overwintered leaves of Quercus and Fagus.

An inverse relationship between ingestion and efficiency of absorption has been reported by various authors (Dallinger & Wieser, 1977; Rushton & Hassall, op cit) Dallinger and Wieser (op cit) fed Porcellio laevis with Betula litter loaded with different amounts of copper and found that the amount of organic matter absorbed remained fairly constant although the rate of ingestion varied almost eight-fold. The picture that emerges from these and other data eg. Hubbell et al, (1965) is that isopods may maintain a certain constancy of absorption rate when feeding on one particular food under different environmental or nutritional conditions, but may also absorb different types of food of enormously varying rates. This ability enables isopods to achieve an optimal composition of nutrients and energy from mixtures of food of which each single component may be deficient in some respect.

Weiser (1984) shows that isopods have the ability to use coprophagy in order to improve the nutritional value of the primary food and are able to match the variability of the rates of energy uptake by the variable rates of energy dissipation.

The gaps in the total ecology of isopods which this study attempts to fill include the behaviour and nocturnal activities, the abiotic variables together with population and production studies. No other researcher has attempted this holistic approach.

BIOLOGY OF ISOPODS

The Biology of WoodliceClassification

Phylum	-	<u>Arthropoda</u>
Class	-	<u>Crustacea</u>
Sub-class	-	<u>Malacostraca</u>
Order	-	<u>Isopoda</u>
Sub-order	-	<u>Oniscidea</u> Latreille, 1829

The Crustacea comprise the third largest class of animals, coming after the Insecta and the Gastropoda, and most of the 26,000 species are aquatic, the greater part of these living in marine environments. The Sub-order Oniscidea is the only crustacean group to have become completely terrestrial in habit. (Edney, 1954).

That all the woodlice are grouped in the Oniscidea reflects the assumed belief that they are derived from three separate invasions from the sea (Sutton, 1972). One being largely a failure, the Tylidae, not found in Britain, one being quite successful giving rise to the large family Trichoniscidae and a third stemming from a form similar to Ligia giving rise to all the slaters and pillbugs represented by Oniscus, Porcellio and Armadillidium with their many relations, Vandel 1965). As they are directly evolved from a marine habitat (Hurley, 1959), they have no intermediate fresh-water stage to which they might be obliged to return for reproductive purposes.

This independence has been made possible by the retention of the marsupium or brood pouch - a feature of the marine forms, which allows the eggs to be incubated in a fluid environment, and protects the embryos from desiccation until they are able to fend for themselves. By allowing the Oniscidea to disperse more widely, rather than be restricted to habitats

that would allow a return to freshwater, the brood pouch is one of the few features that have any advantage for the terrestrial existence of woodlice.

Body Structure

The British woodlice vary in size from the Trichoniscidae which are in almost all cases under 5mm., to the species Ligia oceanica which may measure up to 30mm.

Woodlice have a dorso-ventrally compressed, rigid, exo-skeleton and seven pairs of jointed limbs. The body is considered to have three tagmata which are sometimes referred to as the head, thorax and abdomen but as these parts do not correspond, either in function or number of segments present, to those of the Insecta, they have been given the more specific terms of:-

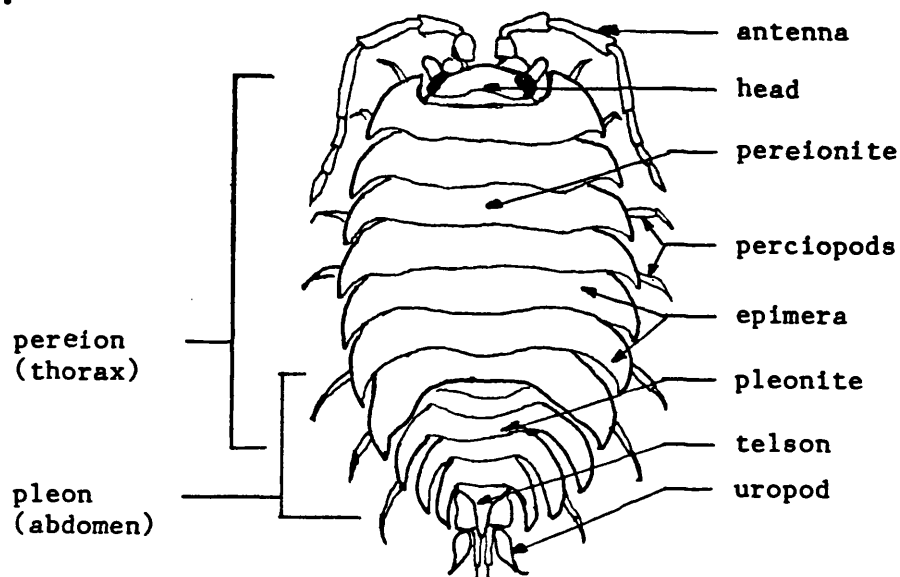
- 1) The Cephalon (head) consisting of five somites.
- 2) The Pereion (thorax), consisting of eight somites and sometimes known as the mesosome.
- 3) The Pleon (abdomen), consisting of six somites, which is always shorter than the pereion and is terminated by the pointed telson which is fused to the sixth somite.

The Cephalon has two pairs of antennae, one pair being minute antennulae which consist, usually, of only three segments and are vestigial. The true antennae are larger, having a basal section or peduncle of five segments and a distal section or flagellum that has a variable number of segments, the number being of taxonomic value in mature animals.

Although it is difficult to provide physiological evidence, the antennae appear to be sensory organs (Sutton, 1972).

The mouth is surrounded by four pairs of appendages which are derived from the limbs of the gnathal segments of their ancestors:-

A.



B.

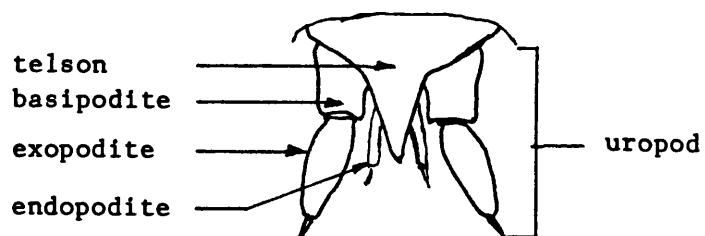


Fig. 1 A Dorsal view of *Oniscus asellus* showing major external features;
 B *Porcellio scaber* dorsal view of telson and uropods.
 (After Sutton 1972)

- 1) A pair of dissimilar mandibles which carry the strongly sclerotized teeth and an articulated spur known as the lacinia mobilis. Behind the teeth there are a number of minute bristles or penicils.
- 2) The First Pair of Maxillae
- 3) The Second Pair of Maxillae
- 4) A Pair of Maxillipeds

These parts form the
floor of the mouth

The detailed structure of the maxillipeds and the varying number of penicils are of taxonomic importance.

The lower lip is formed by the maxillipeds which are actually morphological appendages of the first somite of the pereion and are fused at the centre line, and the upper lip is formed by the labrum which is a transversely hinged sclerite of the head.

When feeding, the food is held and abraded by the maxillae and maxillipeds so that the mandibles are able to gain a purchase and tear off particles of a suitable size for ingestion.

The similarity of oniscoid mouthparts to those of biting insects is a good example of convergent evolution.

Most species have a pair of compound eyes, being composed of many ommatidia, placed on the side of the head. Some species are only endowed with simple ocelli while others have no eyes at all.

The Pereion

Each of the eight somites is composed of a tergite or dorsal plate and a sternite or ventral plate, and carries a pair of pereopods (walking legs) that have six segments which are known proximo-distally as basi-; ischio-; mero-; carpo-; pro- and dactylo-podites.

The projecting lateral extensions of each of the tergites, that are present in some species, are known as epimera.

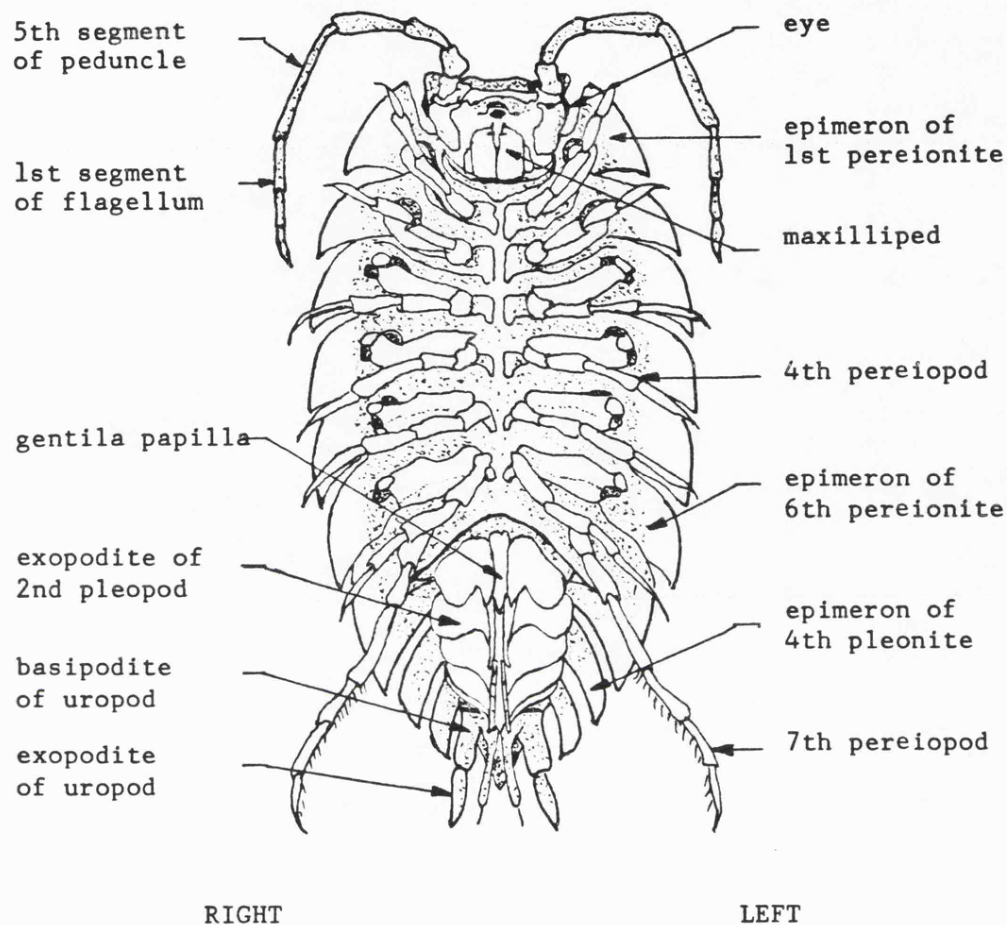


Fig. 2 *Oniscus asellus*; ventral view showing major external features.
(After Sutton 1972)

During the period of reproduction, the gravid females develop four broad lamellae, known as oostegites, that project in pairs from each side of the ventral surface between the second and fifth pair of pereopods, overlapping at the centre to form a brood pouch in which the cleidoic eggs and embryoid young are carried.

The Pleon

The pleon has five biramous appendages known as pleopods and the pointed telson which is fused to the sixth pereionite carries a pair of biramous uropods.

The external and internal rami of the pleopods which are known as the exo- and endo-podites respectively, are flat except for the first two pairs in the males which are modified to form organs of copulation. The males also have a median structure formed from the vasa deferentia, which although not an intromittant organ, is known as the penis or genital papilla. These structures also have great taxonomic value.

Some genera also have invaginations branching into the pleopods which are known as pseudotracheae. Each of these arises from a single pore of the pleopod and thus increases the surface area available for the exchange of respiratory gases with relatively little water loss (Sutton, 1969).

The pseudotracheae resemble the tracheae of insects except that they lack the spiracular mechanism which controls the opening in the latter, and have been shown to be important sites for oxygen absorption and the species with pseudotracheae are better able to function in dry air than those without pseudotracheae (Verrier, 1932; Reinders, 1933; Becker, 1936).

There are three types of pseudotracheae, the first of which is primitive and is less efficient than the more advanced type which have better developed branching (Modlinger, 1931). The second type generally occurs in such genera as Metoponorthus, Porcellio and Armadillium. The

third type has not yet been investigated experimentally but it is believed that all three types have evolved independently (Vandel, 1965).

Although it cannot live long if the pleopods are blocked, O. scaber is able to survive for long periods if the oxygen pressure is increased, even if the air is dry but survival is greater in moist air thus implying that oxygen may be absorbed through the integument if it is kept moist, a fact that has been further confirmed by the reduction of respiration in dry air (Spencer & Edney, 1954).

The Exoskeleton

The innermost layer of the rigid exoskeleton is composed of living cells which secrete the material that forms the lifeless cuticle overlying it. The cuticle itself also has two layers, the thick endocuticle composed of the polysaccharide chitin and a protein known as arthropodin and over this the epicuticle or outer layer.

The skeletal plates are made rigid by the deposition of calcium carbonate and the tanning of the arthropodin to form sclerotin but the intersegmental plates lack this deposition and so remain pliable, thus permitting movement.

In general the integument of woodlice does not have the waxy layer which renders the cuticle impervious to water although there are suggestions that an endocuticular wax may be present in species such as Venezillo arizonicus that inhabit drier environments (Edney, 1968).

The surface of the cuticle is never smooth but is sculptured and may or may not bear spines according to species. In the case of P. scaber and O. asellus there is a wealth of sculptural detail of great taxonomic potential (Sutton, 1969) The bodies forming the irregularities are calcareous, as evidenced by Sutton's (op cit) experiments in which he treated the animals with EDTA (ethyldiaminetetra acetic acid), a decalcifying

agent, which dissolved the granules thus indicating their chemical nature. Apart from the loss of rigidity, the removal of the granules had no effect on the cuticle. Although stating that the function of the granules and the sculpturing upon which the granules appear remains a matter for speculation, Sutton (opcit) suggests that the former may be a means of storing or secreting excess calcium, and the latter could have evolved to prevent the surface of the body from coming into contact with the soil water in much the same way that aquatic insects create an aquafuge surface. It has also been suggested that they may be sense organs connected with thigmotaxis (Sutton, 1972) and that they might possibly be humidity receptors.

Internal Structure

The Nervous System of woodlice corresponds to the general arthropod pattern, having a pair of ganglia above the oesophagus which receive stimuli via the nerve tracts from the eyes and antennae. These ganglia connect with the sub-oesophageal ganglia from which a double nerve cord runs ventrally along the length of the body, having in each pereion segment a pair of more or less fused pair of ganglia followed by a fused pleon ganglia.

The Digestive System has a short oesophagus from which the gut joins the proventriculus. The latter is a complex sclerotized structure which grinds the food, filtering off juices and small particles which pass into the heptopancreas which consists of four large, lobed, digestive glands (Fig. 3).

The rest of the gut following the proventriculus is of ectodermal origin and consequently 'hind gut' although it is often mistaken mid gut.

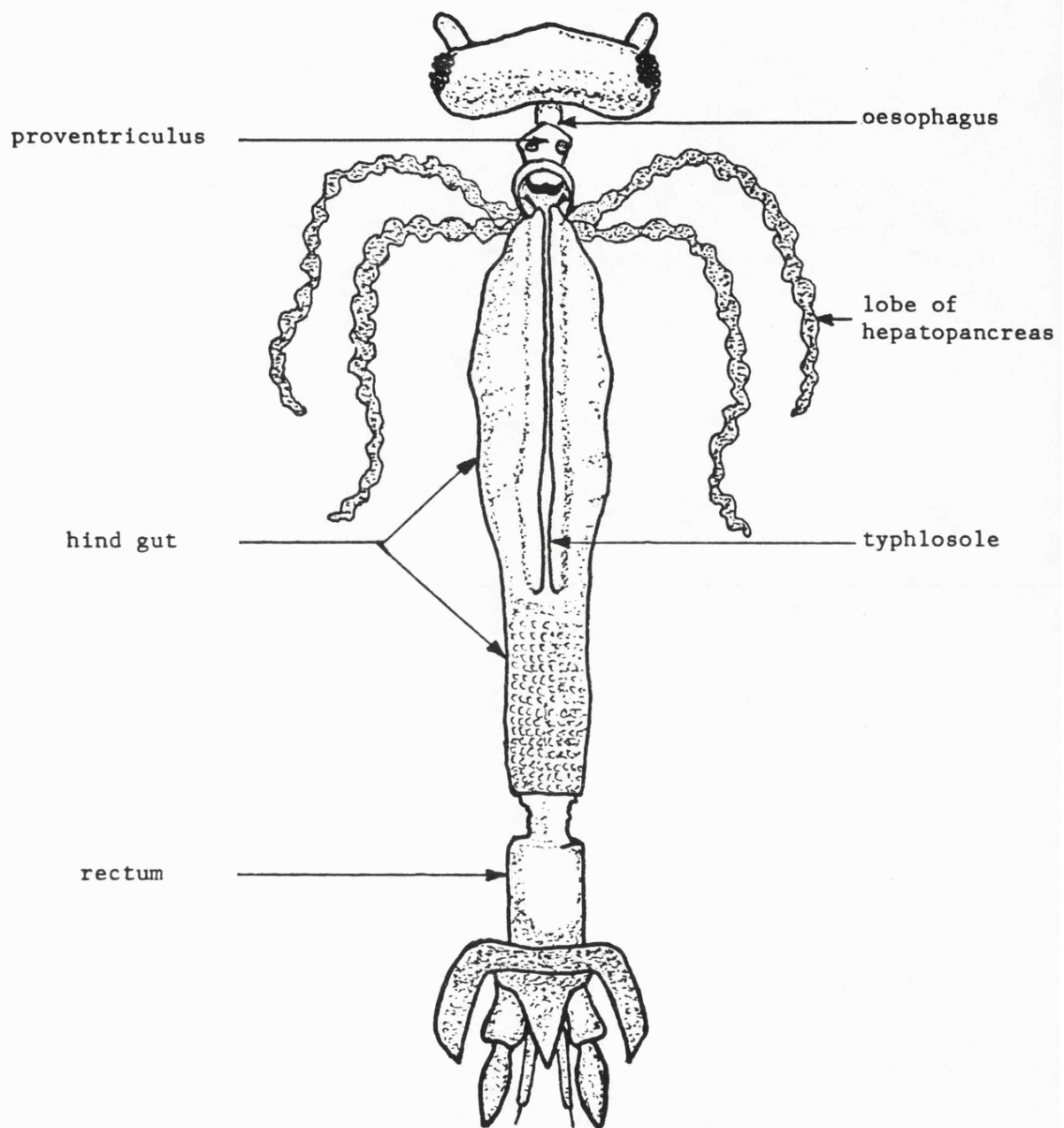


FIG. 3 *Oniscus asellus*; dorsal view of the dissected digestive system.
(After Sutton 1972)

The hind gut has a typhlosole running its length and is terminated by a short rectum which opens through the anus underneath the telson (Fig 3).

The Reproductive System in the males has a pair of tri-lobed testes which open via a common duct into the genital papilla. In the female the paired ovaries are connected through oviducts to the brood pouch which develops during the reproductive period (Figs. 4 & 5).

The Circulatory System has a dorsal heart and aorta which pumps blood forwards and laterally along a series of arteries into blood spaces known as haemocoelae which also hold the tissues and organs. The blood drains back through the haemocoelae to the gill area where it is reoxygenated before returning to the heart which is situated near the rear of the body.

The Tegumental Glands which take up about one third of the body space in Oniscus asellus (Sutton, 1972) are not present to the same extent in all woodlice and their variation in size and number is independent of evolutionary position, respiration, humidity requirements, age, sex or moulting stage (Gorvett, 1956).

Their function has been the subject of investigation for about 100 years with various theories being hypothesized, although most of these were discounted by Gorvett (op cit) when he proposed his theory of limited defence against what are potentially their greatest predators - spiders. Since then, however, Stevenson (1961) has said that they appear to secrete a substance necessary for the hardening of the cuticle after moulting.

The latest finding appears to be that of Stevenson and Murphy (1966) who say that as the food is consumed it is mixed with a mucopolysaccharide secreted from tegumental glands in the head.

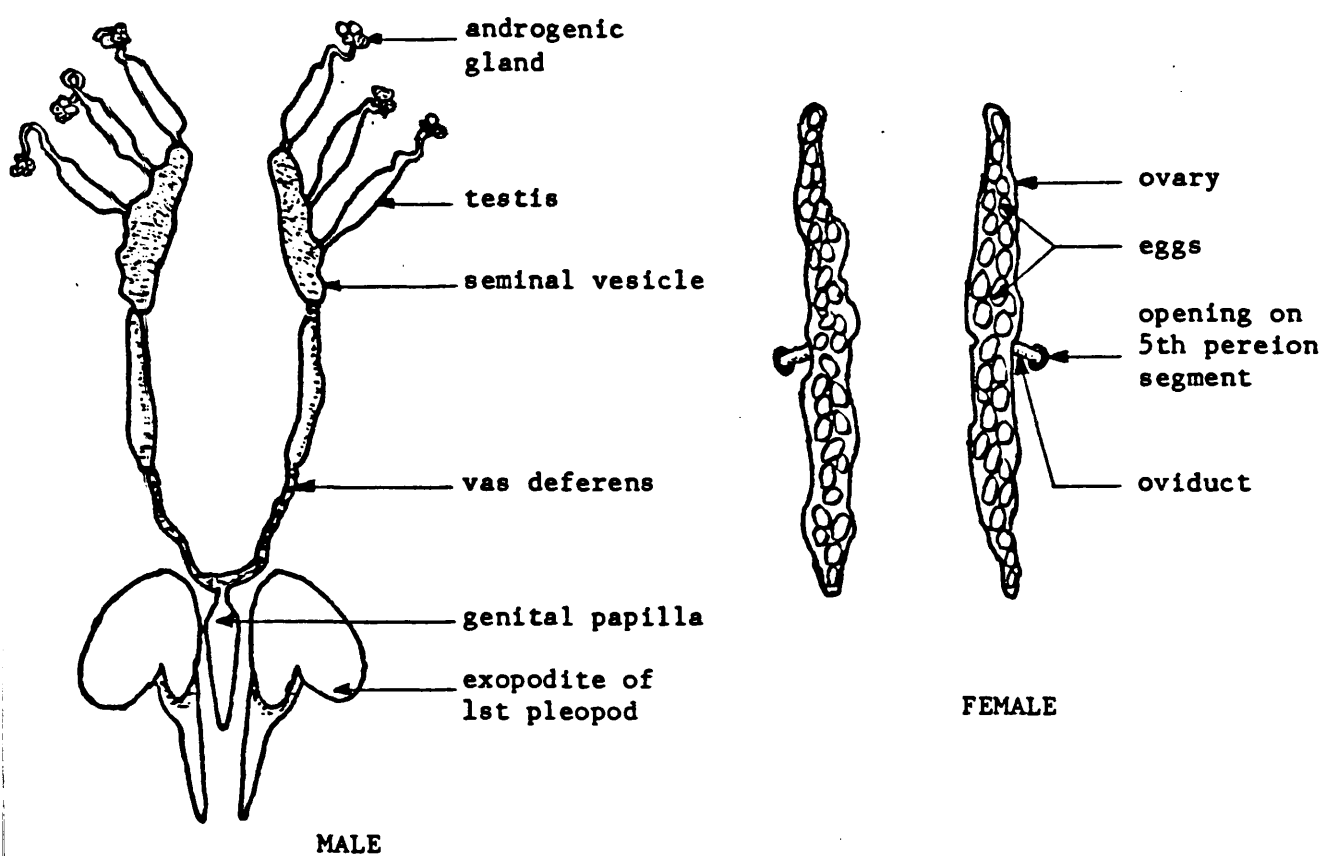


FIG. 4 Oniscus asellus; dissections of the male and female reproductive systems
(After Sutton 1972)

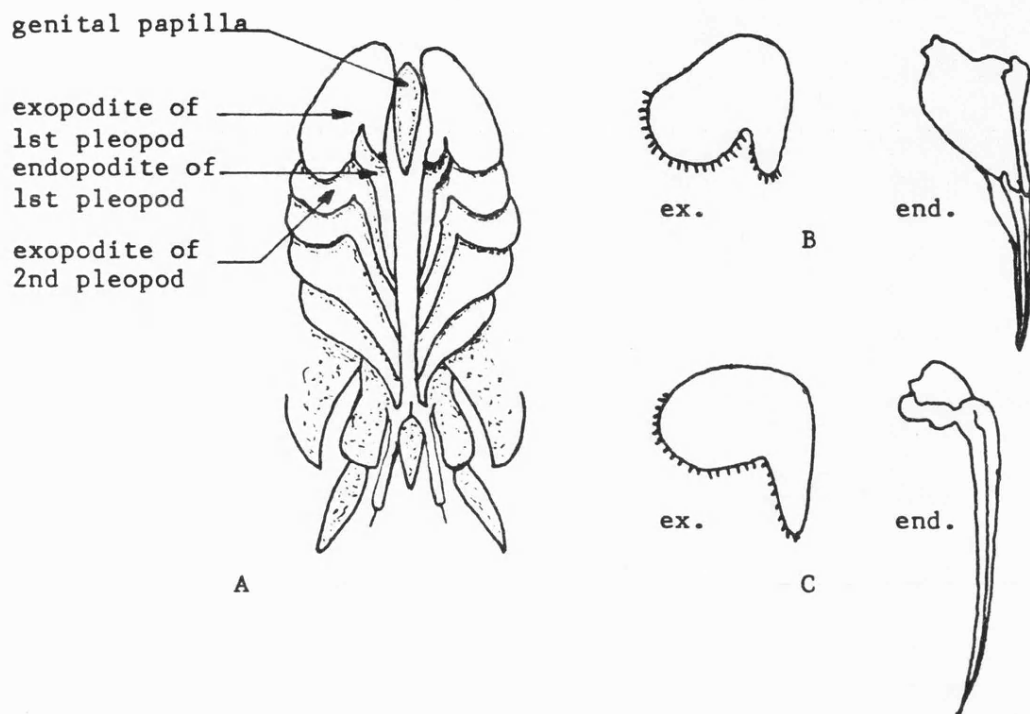
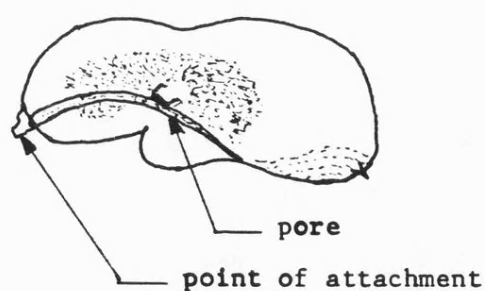


Fig. 5 Oniscus asellus; male genitalia,
 A ventral view of the pleon showing the genitalia in position;
 B exopodite and endopodite of the 1st pleopod of the right side;
 C exopodite and endopodite of the 2nd pleopod of the right side.



Porcellio scaber; exopodite of the 1st pleopod of female to show pseudotracheal field.
 (After Sutton 1972)

The species distribution and habitat range in the British Isles.

The Oniscidea are the only members of the Crustacea which have evolved a completely terrestrial life. Nevertheless, within the group there are great differences in the capacity to withstand desiccation. The Ligiidae are restricted to the inter-tidal zone of marine littorals and of fresh-water habitats. The Trichoniscidae are found in permanently damp places such as the leaf-litter of some forests, while many Oniscidae are found in drier habitats such as under logs and stones. The most moisture independent are the Armadillidiidae which are found in chalk grass land and sand dunes and are considered to be the most highly evolved of all in this respect (Sutton 1972). Furthermore, among both the Oniscidae and Armadillidiidae, physiological experiments have revealed difference in tolerance to desiccation but whether these are related to habitat differences is not known (Edney 1954). Climate influences distribution in a multitude of ways but most of its effects, rainfall for example, are indirect. Rainfall operates through its effect on food supply and soil conditions. Of the direct effects, summer heat and winter frost are probably the most important. Other factors which could affect distribution are pH and calcium content, soil type and drainage, food and shelter.

Forty two species of woodlice have been described for Great Britain and Ireland (Edney 1953; Sutton 1972), although only 29 of the 42 species listed can, with any confidence, be regarded as native; the rest have all been accidentally introduced by man. Some of these have become naturalised but others are aliens in Britain (Sutton 1972). Most species have a wide but very patchy distribution in Britain, many being recorded only from gardens and other habitats, such as greenhouses, created by man. Many of these species are found all over the world, and it is suggested that their wide distribution is the result of fairly recent carriage by man (Vandel 1960; Van Name 1936).

Only five species occur frequently on the College site, while one other P.spinicornis was occasionally found. These five species show quite clear habitat differences as discussed below.

The recorded distribution of the species of woodlice found in the sample sites.

In summary form the distribution is as follows: Porcellio scaber, Latreille (Oniscidae) is presumed to be a west European form (Sutton (op cit)) common in central and west Europe and extending east as far as the Balkan countries. It gives way in south-west Germany to P. conspersum which does not occur in the British Isles. P. scaber is also found in North America, chiefly in temperate zones, and in Kamchatka, South Africa, New Zealand (Meinertz 1950), the Galapagos, Bermuda, Juan Fernandez, Brazil, Greenland, Alaska (Van Name 1936), Hawaii and Rapa Island in the Pacific Ocean, and Australia. This wide but discontinuous distribution suggests that P.scaber has often been introduced by man (Sutton op cit).

The Porcellionidae divide into two great series; the Trichoniscus - group which forms pseudo-tracheae on all five pairs of pleopods, and the Porcellio - group which have pseudo-tracheae on the first two pairs only. The first group is thought to originate in the Australasian region and are found throughout the Near and Far East, Europe and Northern Africa (Sutton op cit). Trachelipus rathkei belongs to this group (Vandel 1943). The origin of the bitracheate forms is thought to be E. Africa. The bitracheate forms have evolved from the quinquetracheate ones, and have spread throughout the Mediterranean region and the whole of Europe (Vandel op cit). P. scaber belongs to this group. Thus the two forms meet in Europe. T. rathkei occurs, though rarely, in fields beside woods, while P.scaber occurs commonly in woods.

Philoscia muscorum (Scopoli 1763), is presumed to be a west-European form, but it extends south to Italy and Spain. In Germany it is most common towards the west and is absent in large areas of central and east Germany (Meinertz 1950). It is most abundant in disused grassland habitats (Sunderland, Hassell and Sutton, 1976).

Trichoniscus pusillus (Brandt 1833). This is the more northerly European form (Edney 1954), extending east to the Balkan Islands. It occurs also in North America (Van Name 1936).

Armadillidium vulgare (Latreille 1804) occurs throughout western Europe and is replaced in the Baltic countries by A. opacum. It occurs commonly in eastern Denmark but is almost entirely absent in the west (Meinertz op cit), and as it is reported to be particularly abundant in Britain on calcareous soils (Edney 1953) it is perhaps intolerant of acid soils because of its need of calcium, having the heaviest exo-skeleton of all species. It occurs in North America as far west as Colorado and certain central and South American cities and in greenhouses in Canada (Van Name 1936). The family is best represented in the equatorial region and the southern hemisphere, and occurs throughout the Pacific Islands (Jackson 1941)

The species being discussed are all found commonly over the general region of western Europe. This is a region which has passed through birch and pine to a climax temperate deciduous forest. The difficulties of understanding the interrelations of animals in the unstable communities dominated by man are great. There are advantages in turning to the vestiges which remain in Europe of climax communities, for here might be found relationships between individuals and species which have evolved with the communities themselves.

The two species studiedOniscus asellus L.

Up to 16mm long and 8 mm wide, Oniscus asellus is one of the largest and most common of the British woodlice. Their colour varies, some having brighter and more conspicuous markings than others, but in general, they are a slatey-grey with lighter, irregular raised markings or welts.

The antenna of this species has a very fine pile of hairs and the last segment of the peduncle is about seven times as long as it is wide. The flagellum which has only three segments, the middle often being the shortest, is shorter than the last segment of the peduncle. (Fig. 7)

The head, which is carinate along the anterior margin, has very strong lateral lobes, their upper surface being concave. Without these lobes the head is twice as wide as it is long and is prominently rounded in front. The head is protected at the sides by the forward projecting margins of the epimera of the first pereionite.

The telson is triangular with a substantial median process that is almost twice as long as the width of the base. The exopodites of the uropods are flattened, lance-shaped, having rounded apices and are two and a half times as long as they are wide. The almost tubular endopodites are much narrower and their bases cannot be seen from above as they are concealed by the telson.

The species are ubiquitous being found in large numbers, generally in aggregations beneath logs, stones, bark and other places where there is a supply of decaying cellulose material. It is one of the few species that can tolerate acid soils. The average brood size is thirty.

Porcellio Scaber L.

Almost twice as long as they are wide, this species may grow to 17mm in length (Fig. 6). They are usually a dark slate-grey but show variations ranging from brick orange to an almost lime green speckled with black, especially in the young.

The last peduncular segment of the antennae, which are minutely scaled, is about six times as long as it is wide. The flagellum is about three-quarters of the length of the last segment of the peduncle.

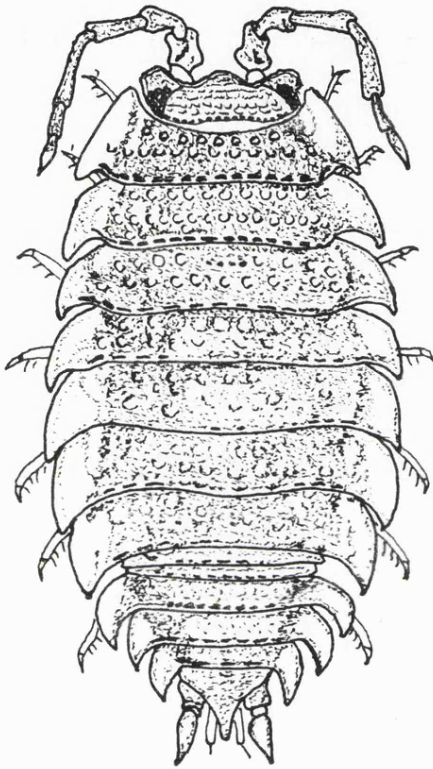
The frontal lobe of the head which bears strong, apically rounded lateral lobes, with concave ventral surfaces, is triangular.

The dorsal surfaces of both the head and the body are strongly tuberculate, irregularly so on the body, but more or less in transverse rows on the head.

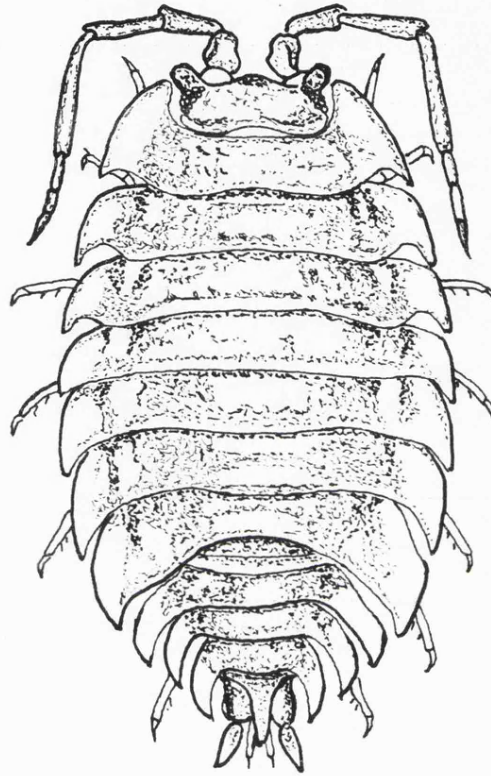
The telson with its rounded apex is very obvious and the exopodites of the uropods are flattened and about two and a half times as long as they are wide, while the endopodites are shorter but about five times as long as their own width and nearly tubular.

This species has pseudotrachae which are easily seen on the first two pair of pleopods, and it is more tolerant of the lower levels of humidity than Oniscus asellus which does not possess pseudotrachae.

P.scaber is widely distributed, being found under stones and bark and in stone walls. It appears to migrate during the summer to the bark of trees where it feeds on Scoliciosporum chlorococcum (Vězda). It can tolerate dessication better than O.asellus and can be found on sand dunes and acid heathland.



A



B

Fig. 6&7 Dorsal view of A Porcellio scaber (Male), length 12mm;
B Oniscus asellus (Male), length 13mm.

(After Sutton 1972)

Methods of Keeping Woodlice in the Stock Culture

During this study woodlice populations were maintained in cultures in the College animal house in normal lighting regimes and a mean temperature of 15°C.

The animals were kept in small glass terraria 26cms x 12cms x 20cms. which were closed with a glass lid. A pad of wet gauze was placed in each terrarium to maintain humidity and a piece of bark added to provide shelter. Food, in the form of partly decomposed leaf litter comprising mainly ash (Fraxinus excelsior) and sycamore (Acer pseudoplatanus), was spread over the floor. In addition, the lichen, S.chlorococcum, removed from the trunks of trees and kept in a stock bottle was supplied every three days.

In this way an environment was provided which had a high humidity and a dark resting place. A humus layer developed slowly and this was retained in the terraria. Apart from supplying food and wetting the gauze pad at regular intervals, this system regulated itself and required no further attention.

When a census was necessary the whole contents of a terrarium was tipped onto a white topped sorting table and the humus systematically searched for woodlice. After measuring and recording the animals, the terraria were re-established with the old humus and fresh food supply and new gauze pad.

Life histories of O.asellus and P.scaber

Two cultures containing 20 female specimens were set up as described previously and weekly observations made over one year 1980. Throughout the period fresh collections of breeding females were taken from the environment and examined in the same way to act as controls. These were assigned a distinguishing mark with quick drying paint so as to identify them from the experimental animals.

The table below shows the breeding stage and moults (averages) for the two species.

Table 1 Breeding cycle of O.asellus and P.scaber.

	Time of Molt forming brood pouch	Embryonic period	Larval period	No. liberated	Period between 1 & 2 stadia	Period between 2 & 3 stadia	Period between liberation of 1st & 2nd broods	
<u>Oniscus</u>	Mid.Apr.	34	8	32				First brood
<u>asellus</u>	to				68	55	63	
	Mid.Aug.	29	8	26				Second brood
<u>Porcellio</u>	End March	38	7	17				First brood
<u>scaber</u>	to				64	-	57	
	End July	28	8	14				Second brood

Explanatory notes on the Table

- (a) Date of moulting is the mean date as moulting takes place in two parts with an interval of 2 - 3 days between.
- (b) Embryonic period is the period between the moult forming the marsupium and the bursting of the egg membrane within it.

- (c) Larval period is the time between the bursting of the egg membrane and the release of the brood from the marsupium.

From the results given in the table it is possible to draw the following conclusions:

- (a) The duration of the respective stages in breeding was remarkably constant for both species.
- (b) There is a difference, however, between the larval period in each species in that the first brood embryonic period is longer than the second and the second brood is smaller than the first. This may be due to poor climatic conditions and a shortage of food in the wild, early in the year. However the figures are averages and not all females had a second brood.
- (c) The average ratio of the larval period to the embryonic period in the brood pouch is almost identical being 1:4 and 1:4.5 respectively. In some species of woodlice the ratio increases in direct proportion to the average sizes of the broods. (Heeley 1941).
- (d) The occurrence of moults during the non-breeding time of the year did not show the same regularity as those in the breeding season.
- (e) P.scaber only liberated approximately half the number of larvae as O.asellus .

Summary for the two species:

Oniscus asellus

Showed great uniformity throughout especially the embryonic stages which in no instance varies more than 6 days from the average of 31.5 days.

Porcellio scaber

Showed equal uniformity especially in the larval stages in the first brood which was almost exactly one week in duration. The size of the second brood is smaller than the first and the duration of the embryonic period is also reduced

by one quarter. The total developmental stages within the brood pouch are practically the same as Oniscus asellus; consequently females of both species formed brood pouches, liberated their young at the same time and underwent their second moult within a few days of each other.

It was found that the rate of breeding and the duration of the different periods in the captive specimens varied in no instance from those of specimens freshly collected from the field.

STUDY AREA

The Study Area

Work was undertaken in two contrasting areas chosen for their position, flora and soil types (Fig 8).

Spinney Hill Woods

Samples were confined to two shelter belt woodlands between Nene College grounds and All Saints Middle School and alongside The National Leathersellers Centre on the northside of the college. Map references OS 1:50000 sheet no. 152 764636, 766638, and 763640 as shown on Fig 8. In addition research was carried out on the ha-ha a sunken boundary wall of Victorian origin (Fig 8 B)

The present-day Moulton Park was originally a royal deer park that was established some seven hundred years ago to supply the needs of the Crown for fresh meat, timber and wood at Northampton Castle. Shelter belts and fine specimen trees remain.

General observations were made on the stand structure canopy cover 80% and the flora cover estimated using Domin's (1960) scale of abundance. This information can help to identify the probable management regime of a site and the age of woodland. The main constituents of the litter and a modal value was taken of this variable quantity which averaged 5cm in depth. The litter layer was not always clearly defined but is taken to be the unconsolidated layer of material, including the fermentation and humus zone, on the soil surface. Surface stones and logs were noted since these provide shelter for many species of cryptozoans which move out onto the leaf carpet at night.

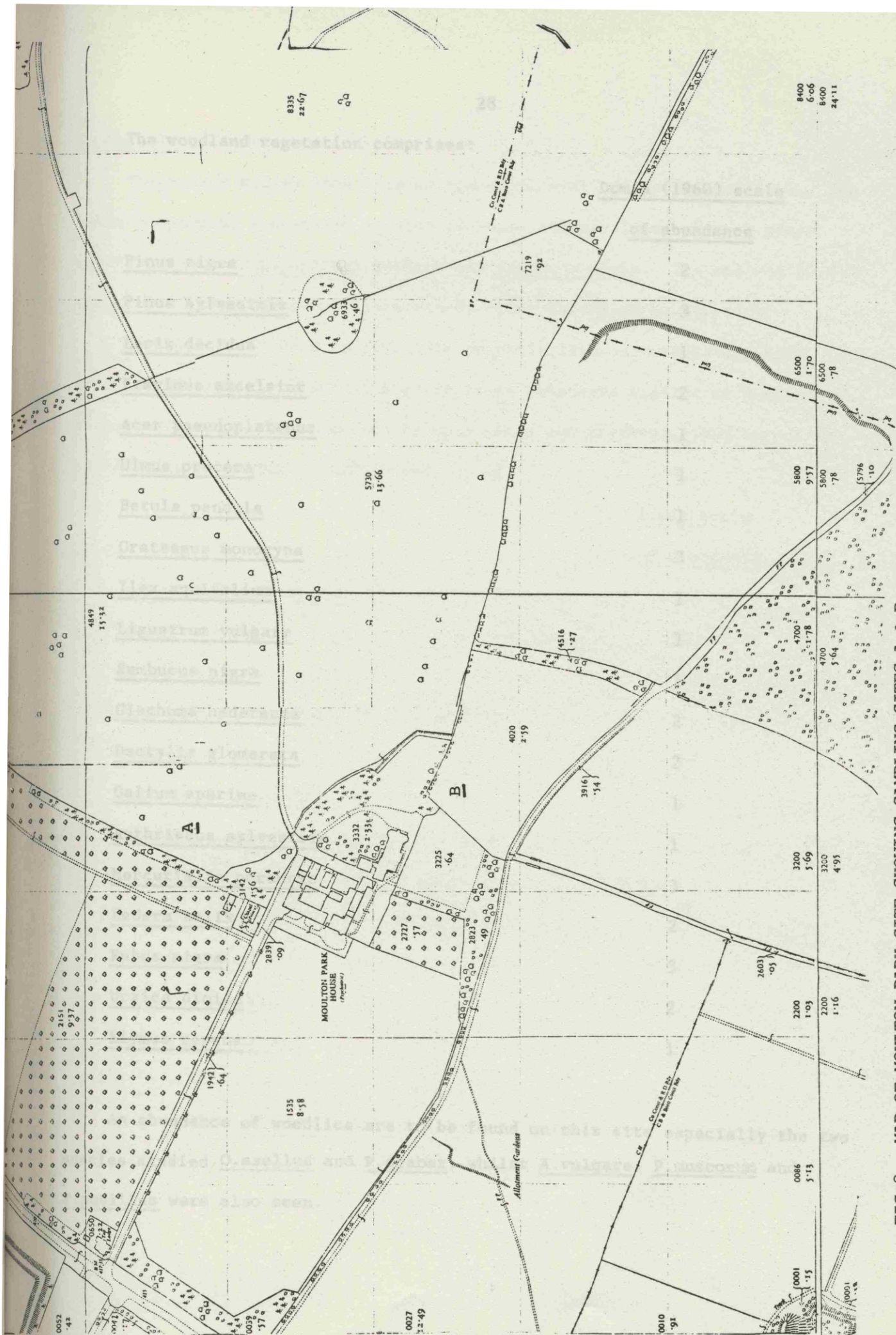


FIG 8 MAP OF MOULTON PARK SITE SHOWING SAMPLING SITES A & B

The woodland vegetation comprises:

	<u>Domin (1960) scale</u>
	<u>of abundance</u>
<u>Pinus nigra</u>	2
<u>Pinus sylvestris</u>	3
<u>Larix decidua</u>	1
<u>Fraxinus excelsior</u>	2
<u>Acer pseudoplatanus</u>	1
<u>Ulmus procera</u>	1
<u>Betula pendula</u>	1
<u>Crataegus monogyna</u>	3
<u>Ilex aquifolium</u>	1
<u>Ligustrum vulgare</u>	1
<u>Sambucus nigra</u>	1
<u>Glechoma hederacea</u>	2
<u>Dactylis glomerata</u>	2
<u>Galium aparine</u>	1
<u>Anthriscus sylvestris</u>	1
<u>Mercurialis perennis</u>	3
<u>Hedera helix</u>	2
<u>Rubus nigra</u>	3
<u>Urtica dioica</u>	2
<u>Elymus repens</u>	1

An abundance of woodlice are to be found on this site especially the two species studied O.asellus and P.scaber, whilst A.vulgare, P.muscorum and T.pusillus were also seen.

Ha-ha wall and surrounds

The second survey site lies on the south side of the main college. The ha-ha is part of a degraded section of broad stone walling amongst dense undergrowth of Ulmus procera suckers and Sambucus nigra. The wall is 80 m. long 1.5 m. high and is overshadowed by other shrubs of cultivation.

The wall dates back to late 18th or early 19th century having been re-built several times and much of it is an extensive scatter of tumbled stones. The site is surrounded by open field and trackway. The immediate surrounding vegetation cover is made up of:

	<u>Domin scale</u> <u>of abundance</u>
<u>Aesculus hippocastanum</u>	2
<u>Ulmus procera</u>	3
<u>Sambucus nigra</u>	2
<u>Acer pseudoplatanus</u>	2
<u>Syringa vulgaris</u>	1
<u>Anthriscus sylvestris</u>	1
<u>Glechoma hederacea</u>	2
<u>Lamium album</u>	1
<u>Galium aparine</u>	1
<u>Urtica dioica</u>	2
<u>Arum maculatum</u>	1
<u>Dactylis glomerata</u>	2

The woodlice P.scaber and O.asellus are abundant and P.muscorum also occurs.

Climate

On each sampling date the relative humidity and temperature were recorded for each site (Appendix 4), and relevant information from the College Meteorological Station was recorded monthly (Appendix 5). The relative humidity of the litter was measured using an aspirated hygrometer. Temperature measurements were made using a thermistor soil probe at the surface and at a depth of 5cm.

The prevailing climatic conditions are an essential influence on woodlice activity and distribution (Edney, 1954; Cloudsley-Thompson, 1956; Brereton, 1957; Nair, 1984; Warburg, 1984), although climatic conditions are greatly ameliorated in a wood and the insulating effect of woodland litter on the soil is well known (Brereton, 1957; George 1970, Wallwork, 1975).

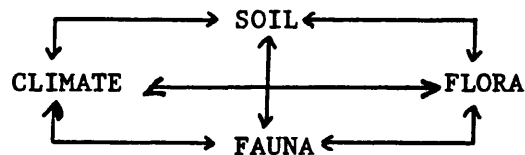
For this reason micro-climatic studies are more important than general climatic conditions as these stenohygric animals are restricted to narrow limits of variation in atmospheric humidity. The results are discussed fully in the chapter on population dynamics. (Chapter 4).

The influence of micro-climate on the litter fauna is, in the main, a direct one. There are indirect effects, for example when climate influences the character of the vegetation or through weathering processes, the soil type. Climate can interact with biotic factors, such as intra-specific competition for shelter or breeding sites. This kind of interaction may provide a mechanism for regulating population size in isopods in grass-land where periodic flooding or drought can restrict the number of sites available for colonisation (Paris 1963).

The importance of soil properties as possible controlling factors

The most important soil properties are those which act uniformly over a long period and thus bring about a definite effect which influences the fauna selectively. Much has been written on soil biology (Kevan 1955); Kuhnelt 1961; Macfadyen 1963; Wallwork 1975), and all agree that the controlling factors are temperature, moisture content, and vegetation. Although botanists stress the importance of the pH and mineral status as controlling factors, zoologists appear much less concerned. It has been claimed by Sutton (1972) that woodlice are most numerous in calcareous and alkaline soils. Furthermore, it is well known that the behaviour of woodlice is strongly influenced by atmospheric humidity (Cloudsley Thompson 1977)

In ecology the general interdependence of the great complex of factors should not be neglected. This can be illustrated:



The relationship between vegetation and soil seems to be studied according to a set procedure which logically is:

- (a) Qualitative vegetation and soil surveys to establish the basic trends of vegetation development and stability and the related general soil properties.
- (b) The study of the available soil nutrients and mineral cycling via autoecological and detailed synecological studies.

This is the work pioneered by Tansley (1917) and Braun-Blanquet (1932), and faunal studies should fit into this scheme. In other words a holistic view should be taken. This is why a study of the vegetation of the sites was undertaken using a Domin (1960) scale of abundance.

Although this study is mainly concerned with organisms within the woodland litter, many of the species found within the litter also move into the underlying soil at certain times eg. during cold weather, thus for these species, the nature of the soil may have a direct influence upon their distribution.

Many soil characteristics are to a large degree dependent upon the bedrock. Many of the soil nutrients may be derived from breakdown of the bedrock, and some of these, particularly calcium are known to affect the distribution of some isopods. Soil structure and drainage may also be influenced by the bedrock, with soils overlying clay frequently having impeded drainage, in contrast to soils overlying sands or chalk.

Although soil conditions can directly affect conditions in the litter layer e.g. by drainage influence, this is only a minor link in the complex interrelationship between soil, litter and vegetation. The nature and composition of the litter, hence habitat conditions, are dependent upon the woodland vegetation, which in turn is dependent upon the soil.

1. The bedrock was identified from 1:50,000 geological maps of the British Isles and was found to be boulder clay.
2. Soil classifications are based on a soil survey of England and Wales and was in Group 29. B.W. Avery, D.C. Findlay & D. Mackney (1974).

Soil texture descriptions are based upon widely accepted definitions, obtained from physical inspections of soil samples. (Avery et al, op cit). These soil texture descriptions rely particularly on proportions of particles in different size classes and can be described as silty clay/silt.

The present study, by detailed soil analysis, attempts to see if the edaphic factors are partly responsible for controlling populations of woodlice and determining their choice of habitat.

Methods

Random core samples measuring 7.5cm x 4.5cm were taken from the top 5cm of soil and litter on both sites. These samples were air dried and tested by the following standard techniques and repeated three times.

(a) Total N by Kjeldahl digestion.

This is the standard and widely used method for N in proteinaceous material and a modified method gives nitrate $\text{NO}^{'2}$ and nitrate $\text{NO}^{'3}$.

(b) Organic C by digestion with potassium dichromate and sulphuric acid which is the chemical oxygen demand method as used in water quality analysis.

(c) P and K extracted by a mixture of 0.5 M acetic acid and 0.5 M ammonium acetate.

This is a technique using a buffer solution which is used to simulate the conditions of acidity around a root system and gives an indication of the amount of these elements available.

(d) Exchangeable Ca determined by leaching with neutral N ammonium acetate pH by Pye electric meter.

Ecologists often refer to 'pH of soil' which is incorrect. A soil can, indeed, be acidic, alkaline or neutral but pH refers to the hydrogen ion concentration of an aqueous solution. The so called 'soil pH' is obtained by extracting soil with deionised water and measuring the pH of the resulting solution. In order to compare these values the mass of soil, time of extraction, volume of water and temperature were all strictly controlled and kept constant.

(e) To estimate the water content of the soils aliquots of 5g were placed in foil containers of known weight and dried to constant weight at 90 C. The results are presented in Table 2.

TABLE 2

Results of soil analysis

	Organic C%	Total N%	P p.p.m.	K p.p.m.	pH	Ca/m.equiv. per 100g.	Water %
<u>Woodland</u>	26.9	1.43	6.2	91	5.1	11.6	28.0
<u>Ha-ha Wall</u>	18.3	1.42	24.0	210	6.3	16.9	18.5

(Average of three samples in each and every case.)

Discussion Table 2

The results for the surrounds of the ha-ha wall are probably inflated because of the close proximity of the original house, more recent builders' rubbish and leaching from the limestone wall. The latter probably accounts for the higher pH of this site and higher Ca.

The results from the woodland soil are more abnormal. The C:N ratio is fairly high whilst the other site is near to the norm of 12:1 (Kuhnet, 1961). The importance of N content lies in the fact that it serves as a nutrient for the organisms taking part in the decomposition although too much could be toxic. There is ample litter (carbon) from the deciduous trees and the influence of tannins in the litter slows down the rate of decomposition (Bocock, 1963). A low pH of soils can slow up microbial activity and decomposition.

Carbonic and other acids in the soil water can be neutralised to some extent by the secretions of the calciferous glands which are found in the bodies of several species of woodlice, millipede, centipede and earthworm. But there must obviously be some source of calcium if adequate replenishment of these glands is to be effected. The woodland study area had the lower soil calcium content.

Calcium probably influences woodlice in three ways:

- (a) by controlling pH;
- (b) as an essential item of diet since all species have the integument calcified to a greater or less degree (Healey, 1941);
- (c) by affecting permeability of body tissue as calcium ions have a strong influence in controlling the passage of solutes through living membranes.

It is interesting to note that the woodland study site had the least species abundance and the ha-ha wall area and surrounds had most species diversity and abundance (pers obs). This latter site, in addition to the above had free

drainage, adequate organic matter, neutral and calcareous reaction, high calcium content, good aspect and a warmer soil. (See Fig 15 and Table 14.)

The results indicate that woodlice populations are affected by soil acidity/alkalinity but not significantly by moisture content. Numbers were lower in the more acid woodland site (pH 5.1). Previously, quantitative assessments of pH and animal populations have merely indicated larger numbers of nematodes, earthworms, molluscs and arthropods on base rich than on acid soils. (Cloudsley-Thompson and Sankey, 1953, 1956). Sutton's claim, (1972), has therefore been verified by these results. More research, however, needs to be pursued in this area to confirm these results with a large survey and to investigate if high populations can be correlated with high pH and whether this can be attributed to metabolic requirements of lime, the effect of pH on soil structure, or its indirect effects on the vegetation.

From these results it seems quite likely that the structure and nutrient status of the soils can partly control the abundance of woodlice and possibly the other invertebrates living in them.

Soil structure, vegetation type and chemical characteristics are relatively static features of the soil environment. Their effects on the soil fauna are essentially qualitative, ie they determine the presence or absence of a species in a particular place. Micro-climate factors, on the other hand, are dynamic in character, with diurnal and seasonal periodicities. Their effects are not only qualitative but also quantitative. They promote cyclical shifts, horizontally and vertically, in the centres of population density (Wallwork (1975)).

BEHAVIOUR STUDIES

Behaviour Studies

The conquest of land by arthropods illustrates a number of fundamental points of behaviour in the response of the animals to stimuli provided by the biotic and abiotic conditions of their physical environment. The terrestrial arthropods can be divided on an ecological basis into two main groups. The first includes isopods, diplopods and chilopods which in dry air lose water rapidly by transpiration through their integuments (Cloudsley-Thompson 1956, Edney 1957). Consequently these stenohygic animals are restricted by behavioural mechanisms to damp, dark habitats which they leave only at night when the temperature falls and the relative humidity of the atmosphere increases (Cloudsley-Thompson 1952).

The second group includes most insects and arachnids: these are comparatively independent of moist surroundings because their integument possesses an impervious epicuticle which prevents desiccation at normal temperatures (Wigglesworth 1950). These animals are termed euryhygic.

In making their advance onto land the Isopoda left the more stable marine environment to face the problems of life on land. These problems may be summarised as follows:-

The need for:

- (a) structural support;
- (b) a means of extracting oxygen from air;
- (c) an alternative way of diffusing toxic excretory products;
- (d) maintaining a tolerable dilution of the body salts in the haemolymph;
- (e) a temperature control system;
- (f) modified reproductive mechanisms;
- and (g) calcium carbonate for their exo-skeleton.

The cuticle of the isopod exo-skeleton was probably evolved by their marine ancestors as a form of protection while still maintaining a permeable

surface between their body fluids and that of their aquatic environment. But while the exo-skeleton supports the body it is no answer to the two main hazards of a terrestrial habitat which are 1) overhydration and 2) desiccation, the latter being particularly important as they are small animals with a relatively large surface area to body mass and consequently susceptible to excess transpiration.

Although some species, eg A.vulgare, are now thought to have a cuticular layer of wax (Edney 1968), most species lack an impervious integument and are cryptozoic. As Warburg (1965, p184) phrases it they are "able to survive on land by avoiding typical land conditions".

The behaviour patterns which have evolved to overcome these problems, such as becoming photonegative (except under certain environmental conditions or stimuli) and thus finding the dampness that is associated with the dark, whilst having an important survival value restricts the extent to which the species have been able to exploit their terrestrial environment. Despite this, they may be found in habitats as diverse as the Algerian Desert, where Hemilepistus reaumuri (Audouin & Savigny) spends the daylight hours at the bottom of a deep burrow, and the nests of ants, to which the myrmecophilous Platyarthrus hoffmannseggii (Verhoeff) is attracted by formic acid and a positive hygrokinesis which is possibly combined with a high photoklinokinesis (Warburg 1964).

That water loss through the integument is lethal was demonstrated by Fraenkel & Gunn (1940) who were able to keep animals alive in a moist chamber for days with hardly any change in weight. By contrast those which were maintained in a desiccating chamber lost approximately one quarter of their original body weight in 24 hours, despite the fact that losses of faeces and carbon dioxide were relatively small.

As this is so, the choice of habitat is largely determined by the humidity requirements, which vary with each of the species, with the needs

of the four most common British species standing in the following order from high to low humidity requirements:

Philoscia muscorum > Oniscus asellus > Porcellio scaber >

Armadillidium vulgare (Edney 1957).

The last named has the ability to conglobate, ie roll into a ball, a tendency which is thought to be a mechanical response evolved to reduce transpiration losses by reducing the amount of body surface exposed to the air (Allee 1926; Cole 1946). Allee also found that P.scaber and O.asellus were more likely to 'bunch' than forms that are able to conglobate. By bunching (see page 44) they do in fact create their own micro-climate (Warburg 1964) as well as affording protection from predators, and the fact that aggregations of woodlice are found in the field points to this phenomenon as a survival mechanism. Wolsky (1933) found that P.scaber would aggregate around moist cotton-wool if direct access was available but if prevented from touching it, no aggregation occurred, causing him to conclude that this was a chance mechanism although it has since been shown that there is a mutual attraction of woodlice for each other by means of a chemical stimulus (Kuenen & Noteboom 1963).

Fraenkel & Gunn (1961) argue that this mechanism is a negative response to other stimuli, having shown that the average linear velocity of moving woodlice was greater in dry air than in moist air. They use the analogy that traffic which has been flowing swiftly on the open road, with a reasonable space between each car, becomes involved in a nose to tail stream of traffic when the speed limit is reduced such as when entering areas having a lower speed limit.

The increase in speed in dry air was also shown by Waloff (1941) working on P.scaber who added that they also made more frequent changes in direction, and that the combination of the two responses returned them to areas of high humidity. This was also noted by Gunn (1937) who showed that excessive activity in P.scaber in dry air, brought it to more humid conditions where

the activity ceased. Den Boer (1961) found that the activity of P.scaber decreased as the temperature dropped, and that the decrease in activity correlated with the actual drop in temperature.

Trichoniscus pusillus (Brandt) shows another method of avoiding desiccation - that of burrowing deep into the soil during dry periods. Although they escape the effects of desiccation, they are without food which results in a cessation of growth and a failure to breed in the following spring (Sutton 1968).

Cloudsley-Thompson (1956) showed that at temperatures just above freezing point, the reactions of isopods to humidity are much reduced and do not differ significantly from one another which may explain why O.asellus, P.scaber and A.vulgare are usually considered as being representatives of widely differing habitats, and yet have been found on the same rubbish tip but in different micro-habitats within it (Edney 1954).

As woodlice are characteristically negatively phototactic (Sutton 1972), the diel alternation between night and day acts as a stimulus in the maintenance of the physiological regulation of their nocturnal activity and the length of day is the factor which determines the number of hours during which they are active. Cloudsley-Thompson (1952) showed that the pattern is maintained for several days after the woodlice had been subjected to continuous light and that even after the reaction disappeared it was easily restored by re-exposing them to a fluctuating regime of light and dark.

The degree of nocturnal activity may also be correlated with the ability to withstand water loss through transpiration (Cloudsley-Thompson op cit) and wind has been shown to inhibit the nocturnal emergence of woodlice, perhaps because of its drying effect upon the moist air currents which surround the transpiring animals, although this relationship may not hold true below 5.5°C (Cloudsley-Thompson 1958).

Field observations of P.scaber (George 1970) show a shortened period of activity in step with the shorter nights of summer but also a

lack of clear relationships between activity and changes in temperature and relative humidity. This decrease in humidity reaction allows the species to walk in drier places at night and the increase in humidity ensures that they return safely to their moist habitat thus avoiding possible desiccation by the sun's rays or predation by daylight. This is discussed more fully in the population studies Chapter 4 (p 70 ff).

We have two apparent influences:

- i) negative photo response; and
- ii) positive humidity response.

Both normally co-ordinate an isopod's activities:

- i) Causes an avoidance of light; and
- ii) causes a seeking of appropriate humidities by increased activity at the 'wrong' humidity.

Now clearly the humidity response is proximal. Failure results in death. Light response is distal (long range) but generally complementary.

Under dry conditions P.scaber becomes active and the photo-negative is over-ridden. The animal does not become photo-positive.

Should habitats dry up, the tendency to become photo-positive in dry air enforces a move which may result in the finding of another damp habitat, whereupon the photoreaction is reversed once more (Sutton 1978).

Henke (1930) working on A.cinereum was the first to show that temperatures reversed the response to light and that negative phototaxis could be reinduced by a return to a lower temperature. Edney (1953) working with four species including the two under discussion here, claimed that the tendency to move to a drier environment at higher temperatures was an attempt to reduce body temperature by increasing the rate of transpiration. This reaction occurred occasionally if the animals were trapped in a very humid micro-climate which became hot as a result of insolation thus forcing the woodlice to come out into the sunshine where, owing to evaporation and convection, the body temperature falls. This can only be a temporary

measure, however, as the excess transpiration would deplete the body's water reserves causing too high a concentration of body salts in the haemolymph.

The fact that the response to humidity is correlated with the water balance of the animal, as well as with ambient temperature, led several workers to suggest that isopods respond to saturation deficit of the air (Edney 1968, Cloudsley-Thompson 1956). Some isopods, however, respond to relative humidity rather than to saturation deficit (Warburg 1964).

All of these behaviour patterns appear to be safety mechanisms evolved to relieve the compulsion to remain in a dark environment when other factors reach the limits of tolerance.

The behaviour mechanisms which are described as humidity responses are correlated with saturation deficits rather than the relative humidity. Although no specific organ has been identified as being concerned with measuring humidity, Waloff (1941) suggests that the increased concentration of body salts upon evaporation of water stimulate proprioceptors which may act as 'hygrometers of the body'. This seems a very dangerous way for isopods to live.

Lockwood (1968) emphasises the difficulties involved in assessing the evaporation rate of woodlice because of the fluctuation in the degree of cuticle permeability under the effect of temperature and hydration plus the fact that water is also lost with excretory products.

Isopods having evolved without a freshwater stage, are unlikely to have evolved a means of disposing of excess water without a proportional loss of body salts, which would be difficult to replace on dry land (Lockwood op cit).

It may be noted that body fluid loss through transpiration is usually replaced by ingesting moist food which they prefer. Other means of replacing lost moisture in the event of food shortages have been found. Spencer & Edney (1954) showed that woodlice were capable of both oral and

anal drinking and postulated that anal intake is probably a function retained from their marine origins.

They also seem to have developed a wider range of tolerance rather than to have evolved adaptations for the maintenance of isotonic balance. The osmotic changes which are particularly significant during the moult when they are associated with calcium mobility (Widmann 1935; Parry 1953) are similarly tolerated.

Apart from water loss as a by-produce of excretion, and through the permeable cuticle, it has been suggested that secretion by the tegumental glands could also be a potential source of loss although, as previously mentioned, they are only activated by severe mechanical or other stimuli (Gorvett 1956).

The following section is concerned with the investigation of some of these responses and how the behavioural adaptations to life on land are connected with the physiological and morphological adaptations discussed above.

It is quite clear that woodlice have a wide range of structural and physiological adaptations to enable them to survive on land, but only in the damper terrestrial habitats. Their behavioural reactions are finely tuned to environmental conditions and Edney (1954,1967) suggested that the principal adaptations of terrestrial isopods are not physiological, but behavioural.

In sum, these behavioural responses include locomotory responses to: humidity, temperature, light, wind, solid objects, and chemical odours. Other behavioural responses include feeding, reproduction, and drinking, moulting and defensive mechanisms.

The following trials were carried out in an attempt to interpret the distribution of terrestrial isopods in field trials in terms of their behavioural reactions and their physiological needs.

An attempt is made to answer the following questions:

Do woodlice aggregate around obstacles as a defence mechanism or is

there an attraction of chemical stimuli? Are they more active in dry or moist air? What is the effect of temperature, darkness and light on their behaviour? An attempt is made to place these responses in order of priority.

Aggregation in Woodlice

Thigmokinesis is a characteristic response of cryptozoans and has been carefully investigated by Friedlander (1963).

It is well known that many species of woodlice form large aggregations under the influence of environmental conditions and a number of behavioural studies have been concerned with this problem (Allee 1926, Gunn 1937, Waloff 1941). Allee (op cit) was the first to show experimentally that this behaviour results in a reduction of water loss and so may have survival value.

There appear to be two types of aggregation between which the earlier literature does not distinguish, namely "bunching" and "grouping" (Edney 1949). When they bunch, woodlice pile up on each other forming an aggregation for a considerable time. In the present study individuals of O.asellus are known to have stayed bunched for up to four hours in choice chambers. This behaviour is described by Allee (1926) who showed that bunching produced a drop in respiratory rate. He also showed that a low temperature induced bunching and a high one reduced it, but that the relative humidity of air affected it even more markedly. Edney (1960) states that bunching results in a reduction of water loss and increased survival in dry air and that the mechanism of the aggregation is uncertain and may be a form of social behaviour brought about by thigmokinesis. The aquatic Asellus spp. are poor swimmers and flood waters are likely to carry them downstream. Under these conditions the animals cluster together, hanging on to the substratum and to each other and so are better able to resist the current. All individuals behave alike and this results in bunching formation without differentiation of behaviour and without organisation (pers obs).

In grouping, animals come to lie close together, sometimes with their lateral plates touching or overlapping. This happens under low shelter such as logs and stones but also in vessels in the laboratory.

Bunching can reduce water loss but it appears that grouping cannot

present the same advantage since each kind of aggregation may occur under low as well as high air humidities. It seems that aggregation is not a direct humidity response. The results obtained by Freidlander (op cit) suggest that aggregations may be partly due to the attraction of mechanical contact with each other and show that O.asellus can distinguish between different surface roughness. Allee (op cit) records partial success in controlling the site of bunching by fixing a recently killed woodlouse to the floor of a container around which isopods bunched, although woodlice do not aggregate around dead bodies under field conditions. Woodlice may well be sensitive to chemical stimuli which is investigated below.

Cloudsley-Thompson (1956) showed that O.asellus was sensitive to chemical stimuli as they discriminated in favour of water as opposed to one per cent sucrose solution using chemo-receptors in the terminal antennal segments.

The present study is an attempt to investigate the nature and mode of action of stimuli which induce aggregation.

This work was carried out prior to Takeda's (1983) work being Published.

Method

Specimens of O.asellus and P.scaber were obtained from the field on the day of the tests.

All the tests were carried out in 150 mm x 75 mm crystallising dishes floored with damp filter paper to maintain humidity. Tests were made in the laboratory. One group of animal antennae were amputated to see if this affected aggregation and this was completed one hour before the test as the stimuli received via the antennae activate the neuro-secretory cells of the brain (Takeda 1984).

I. Assessment of Aggregation Behaviour in different conditions

The tendency of O.asellus and P.scaber to aggregate was measured by placing ten animals at a time into a crystallising dish. At 30 min intervals

over a period of five hours from 10.00 am to 3.00 pm the number of aggregated animals was recorded. Any assemblage of two or more animals in physical contact was counted as an aggregation. After each recording the aggregations were gently dispersed with a fine damp brush. The following trials were completed:

- (a) RH 80% Temperature 21°C
- (b) RH 100% Temperature 21°C
- (c) RH 85% Temperature 10°C (control conditions)
- (d) RH 95% Temperature 21°C with antennae amputated
- (e) RH 85% Temperature 21°C with obstacles
- (f) Chemical Stimuli of own faeces
RH 85% Temperature 21°C

The control conditions of 10°C and RH 85% are the mean average conditions for site litter layer (top 5 cm). Temperature was standardised at 21°C with variable humidities as this is considered to be the more important factor (Edney op cit).

II Effect of physical contact stimuli on aggregation

Pieces of plasticine given a rough surface of gravel and measuring 2 cm x 1 cm x 2 cm were prepared. These obstacles were placed around the sides of a crystallising dish and one in the centre. The test was carried out as for I. above.

III Aggregation due to chemical stimuli

A third series of investigations were carried out to test whether other stimula were responsible for this aggregation response. Brossut (1974) found an active principle which stimulated separate animals to form a group

and named it the aggregation phenomenon. A great deal of research has subsequently established this phenomenon in mammals and insects (Shorey 1976; Takeda 1984).

This test was designed to see if the species were attracted to chemicals emanating from them.

A series of choice chambers were set up as before but with an isopod faecal extract introduced. 300 mg wet faeces was homogenized with acetone in a glass mortar. The test was carried out with filter paper impregnated with the extract of the faeces and with a clean filter as a control. Ten species of O.asellus and P.scaber were introduced into the chambers as before after being cleaned with cotton-wool impregnated with 70% alcohol to remove contaminated materials from the body surface.

Results (Table 3)

The results show that the proportion of O.asellus aggregating under given conditions does not differ from the proportion (0.73) aggregating under the normal conditions (of 85% RH and 10°C).

The alternative hypothesis is acceptable and shows that the proportion of O.asellus aggregating under given conditions does differ from the proportion (0.73) aggregating under the normal conditions (of 85% RH and 10°C) and in a directional sense.

The results (Table 3) are compared with the control treatment and for departure from the control using a simple test based on the assumption of binormality. The final statistic, z , is distributed normally and hence $z = 1.96$ has probability of 0.005 in a two-tailed test while for $z = 2.576$, $P = 0.01$ and for $z = 3.291$, $P = 0.001$.

It is therefore concluded that only a and b show any significant departure from the 'control'.

Having noted that animals at 21°C, whether at 80% RH or 100% RH, show a tendency to greater aggregation than those at 10°C, it is worth comparing the effects of amputation (d) with these two treatments (a) and

Aggregation in *O. asellus*

Conditions	Proportion aggregating in "experimental" sample p_1	Sample size n_1	Proportion aggregating in "control" sample p_2	Sample size n_2	Estimate of population proportion $\hat{\pi}$	Test statistic z	Probability levels (from tables of normal dist. ⁿ .)
a) Normal animals at 80% RH 21°C	0.94	100	0.73	100	0.835	4.00	$p < 0.1\%$
b) Normal animals at 100% RH 21°C	0.88	100	0.73	100	0.805	2.677	$p < 1\%$
d) Amputated at 95% RH 21°C	0.71	100	0.73	100	0.720	0.315	$p > 5\%$
e) Normal animals with obstacles at 85% RH 21°C	0.70	100	0.73	100	0.715	0.470	$p > 5\%$
f) Choice H ₂ O supernatant at 85% RH 21°C	0.67	100	0.73	100	0.700	0.926	$p > 5\%$

$$\hat{\pi} = \frac{n_1 p_1 + n_2 p_2}{n_1 + n_2}$$

$$z = \frac{|p_1 - p_2|}{\sqrt{\hat{\pi} (1-\hat{\pi}) \left(\frac{1}{n_1} + \frac{1}{n_2} \right)}}$$

Aggregation in *P. scaber*

Conditions	Proportion aggregating in "experimental" sample P_1	Sample size n_1	Proportion aggregating in "control" sample P_2	Sample size n_2	Estimate of population proportion	Test statistic z	Probability levels
a) Normal animals at 80% RH 21°C	0.07	100	0	100	0.035	2.693	< 1%
b) Normal animals at 100% RH 21°C	0	100	0	100	0	0	-
d) Amputated at 95% RH 21°C	0.10	100	0	100	0.05	3.244	< 0.1%
e) Normal animals with obstacles at 85% RH 21°C	0	100	0	100	0	0	-
f) Choice H ₂ O supernatant at 85% RH 21°C	0	100	0	100	0	0	-

Note: Case c (not listed) represents control group at 85% RH and 10°C in proportions aggregating

(b). The resulting z value of 4.493 is highly significant ($P < 0.001$) from which it is concluded that amputation does reduce the degree of aggregation if the temperature is maintained at 21°C. Similar results appertain when comparing (a) and (b) with (e) and (f)

The results in Table 4 show that there is no difference between the experimental and control groups in some cases but that in others the alternative hypothesis is accepted as there is a greater proportion aggregating in the experimental groups than in the control group. On the basis of this data results for cases (a) and (d) are significant (at 1% and 0.1% levels respectively) but the remaining **cases are** not significant. Table 4 (a) and (d) are theoretically significant but in practice are meaningless because of the very small numbers involved and the control group has no aggregation.

Discussion

These results (Table 3) show that considerable aggregation occurs in O.asellus and a significantly greater proportion in (a) and (b) than in the control. There was no significant difference in the remainder.

In P.scaber (Table 4) there was no significant aggregation except in cases (a) and (d) which is in agreement with field observation (see Chapter 4). As P.scaber is less susceptible to desiccation than O.asellus (Edney 1954) this is understandable. Aggregation may provide protection against excessive water loss but as shown by Takeda (1984) the tendency to aggregate is not a response to such conditions only. P.scaber on the other hand show little tendency to aggregate regardless of humidity since this species is less susceptible to desiccation than O.asellus (Edney op cit). It appears that the behavioural mechanism has been lost in this relatively advanced isopod.

Where O.asellus are in the lower humidity chamber (Result (a)) they aggregated more than in the saturated atmosphere (Result (b)) and thus appeared to be less mobile. Aggregations of isopods change in relation to humidity.

In relatively low humidity, isopods aggregate rapidly and form dense aggregations. This is useful to protect the body against water loss Takeda (1984). The correlation of aggregation both with humidity and temperature suggests that responses of isopods to each other are closely linked with the responses to environmental stimuli as suggested by Warburg (1968).

The fact that antennae-less O.asellus (Result (d)) aggregated less (0.71) than normal ones suggests that the antennae do not contain some of the sense organs which are sensitive to stimuli associated with aggregation. Cloudsley-Thompson (op cit) showed that sensitivity to humidity is not controlled from the antennae and in fact no humidity receptors have been identified. Tactile receptors account for Result (e) where O.asellus was induced to aggregate around obstacles. The presence of the obstacles did not increase the total aggregation significantly although the woodlice were no longer dependent on each other for rough surfaces to aggregate against. Attachment to a substrate may serve as protection against predators (Gorvett 1956; Wieser 1963) and may help to keep aggregates intact.

Result (f), where both species had a choice between liquid extract of crushed faeces or distilled water, gives conflicting results. O.asellus were observed to be more agitated at first and took some time to aggregate with a consequent lower aggregation than in any of the other trials. After the first two half-hourly counts they did not move into the supernatant side again. It is suggested that these isopods respond to olfactory stimuli that help to guide them into suitable shelter Takeda (op cit) Much more sophisticated work needs to be carried out to investigate what is probably one of the factors responsible for aggregating in woodlice. Aggregation phenomena have been demonstrated in social insects such as cockroaches Brösent (op cit). It is possible that one of the active principles responsible for the initiation and maintenance of aggregation in some

woodlice is secreted from the tissues of the gut and incorporated in the faecal materials Takeda(op cit) although this is not supported by these results.

The terrestrial isopods seem to advance from the sea to the land environment from the primitive type of Ligia to P.scaber and finally to A.vulgare, the most suitable type for land adaptation in Europe. The biological significance of the aggregation phenomenon seems to be to protect the body from water evaporation on land. The phenomenon was probably introduced to these isopods at the time of migration to the land, and as a result, their land adaptation becomes possible. Body growth becomes accelerated as a secondary effect of aggregation Takeda (op cit).

24 Hour Investigation to Assess the Humidity Preference of Oniscus
asellus and Porcellio scaber

Method

Six plastic containers (internal base size 25 cm x 17.5 cm) were prepared, each having one half of the floor covered with damp filter paper, and the other half covered with dry, fibre glass filter paper. Both sheets of filter paper were taped to the base to prevent the animals crawling underneath in response to their negative phototaxis, and a 2 cm space was left between the two areas of paper.

Ten specimen of O.asellus were introduced to each of three containers and ten P.scaber into the other three. All containers were kept in darkness.

Two containers, one with O.asellus and the other with P.scaber, were maintained at 10°C, another pair at 15°C and the final pair at 20°C. Observations were made at half-hourly intervals over a period of 24 hours, using a torch with a yellow filter to which neither species responds. A record was made of the position and activity (settled or moving) of the woodlice and they were gently dispersed each time by means of a fine brush.

Results

The contingency tables, Tables 7-10 and Figs IX-XIV show that there is a heterogeneity from these data between the activity of both species of woodlice and their environmental conditions especially numbers settled in humid conditions in all three temperature regimes.

There is a significant correlation between the state of activity and the moisture level of the filter paper, the frequencies observed in each half of the containers indicating that they have a strong preference for the wet filter paper. This is indicated by the fact that they settle on the wet paper, whilst on the dry proportionally more are active as they attempt to reach conditions within their range of preference, in response to their hydro-kinetic tendencies.

NOTE: In the following tables of results, in each cell the upper figure records the observed frequency, the middle figure records the expected frequency, and the lower figure records the contribution of that cell to the total $\sum \frac{(O-E)^2}{E}$

In each case the calculated expected frequency is the uncorrected value as is the contribution to $\sum \frac{(O-E)^2}{E}$; corrected values were obtained using the SUPASTAT statistics package.

Table 7 Showing 2 x n contingencies of observed frequencies of Oniscus asellus in differing environmental conditions at intervals of 30 minutes over a 24 hour period

	Dry 10°C	Dry 15°C	Dry 20°C	Humid 10°C	Humid 15°C	Humid 20°C	Totals
Oniscus asellus (moving)	18 4.87 35.442	5 0.96 16.918	7 2.08 11.653	23 19.47 0.641	8 23.37 10.109	12 22.25 4.725	73
Oniscus asellus (settled)	78 91.13 1.893	14 18.04 0.903	34 38.92 0.622	361 364.53 0.034	453 437.75 0.540	427 416.75 0.252	1367
TOTALS	96	19	41	384	461	439	1440

NOTE: expected frequency of moving, dry, 15°C is <1 and expected frequency of moving, dry, 20°C and 10°C is <5 - hence χ^2 test is not valid.

Table 8 Showing 2 x 2 contingencies of observed frequencies of *Oniscus asellus* in differing environmental conditions at intervals of 30 minutes over a period of 24 hours. Derived from Table 7

(i) Amount of movement v level of humidity

	Dry	Humid	Totals
Moving	30) 7.91) 61.712	43) 65.09) 7.498	73
Settled	126) 148.09) 3.296	1241) 1218.91) 0.400	1367
Totals	156	1284	1440

$$\frac{\chi^2 = 72.91}{69.643 \text{ (corrected)}} \quad df = 1, p < 0.001$$

(ii) Amount of movement v temperature

	10°C	15°C	20°C	
Moving	41) 24.33) 11.416	13) 24.33) 5.279	19) 24.33) 1.169	73
Settled	439) 455.67) 0.610	467) 455.67) 0.282	461) 455.67) 0.062	1367
TOTALS	480	480	480	1440

$$\chi^2 = 18.82 \quad df = 2 \quad p < 0.001$$

(no correction necessary)

(iii) Analysis of preferences

	No in Dry	No in Wet	TOTALS
Ob	156	1284	1440
Exp	720	720	1440
O - E	-564	+564	833.6

$$\frac{(O-E)^2}{E} = \chi^2 = 883.6$$

Number degrees of freedom = 1

Critical value from tables (5%) = 3.841

Result is very highly significant

(iv) Number moving v number static

	Moving	Static	TOTALS
Obs, O	73	1367	1440
Exp, E	720	720	1440
O - E	-647	+647	

$\frac{(O-E)^2}{E}$	581.401	581.401	1162.803
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χ^2	1162.8
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Number degrees of freedom = 1

Critical value from tables (5%) = 3.841

Result is very highly significant

Table 9 Showing 2 x n contingencies of observed frequencies of Porcellio scaber in differing environmental conditions at intervals of 30 minutes over a 24 hour period

	Dry 10°C	Dry 15°C	Dry 20°C	Humid 10°C	Humid 15°C	Humid 20°C	Totals
Porcellio scaber (moving)	26) 5.05) 86.982	*6) 3.77) 1.320	*12) 4.22) 14.367	24) 25.62) 0.102	18) 26.90) 2.943	6) 26.45) 15.811	92
Porcellio scaber (settled)	53) 73.95) 5.936	53) 55.23) 0.090	54) 61.78) 0.981	377) 375.38) 0.007	403) 394.10) 0.201	408) 387.55) 1.079	1348
TOTALS	79	59	66	401	421	414	1440

* NOTE: expected frequency of moving, dry, 15°C < 5
expected frequency of moving, dry, 20°C < 5

χ^2 test likely not to be valid.

Table 10 Showing 2 x 2 contingencies of observed frequencies of Porcellio scaber in differing environmental conditions at intervals of 30 minutes over a period of 24 hours. Derived from Table 9

(i) Amount of movement v level of humidity.

	Dry	Humid	Totals
Moving	44) 13.03) 73.576	48) 78.96) 12.144	92
Settled	160) 190.96) 5.021	1188) 1157.03) 0.829	1348
TOTALS	204	1236	1440

$$\chi^2 = \frac{91.569}{88.636 \text{ (corrected)}}$$

$$df = 1 \quad p < 0.001$$

(ii) Amount of movement v temperature

	10°C	15°C	20°C	Totals
Moving	50) 30.7) 12.188	24) 30.7) 1.449	18) 30.7) 5.232	92
Settled	430) 449.3) 0.832	456) 449.3) 0.009	462) 449.3) 0.357	1348
TOTALS	480	480	480	1440

$\chi^2 = 20.16$

$df = 2 \quad p < 0.001$

(No correction necessary)

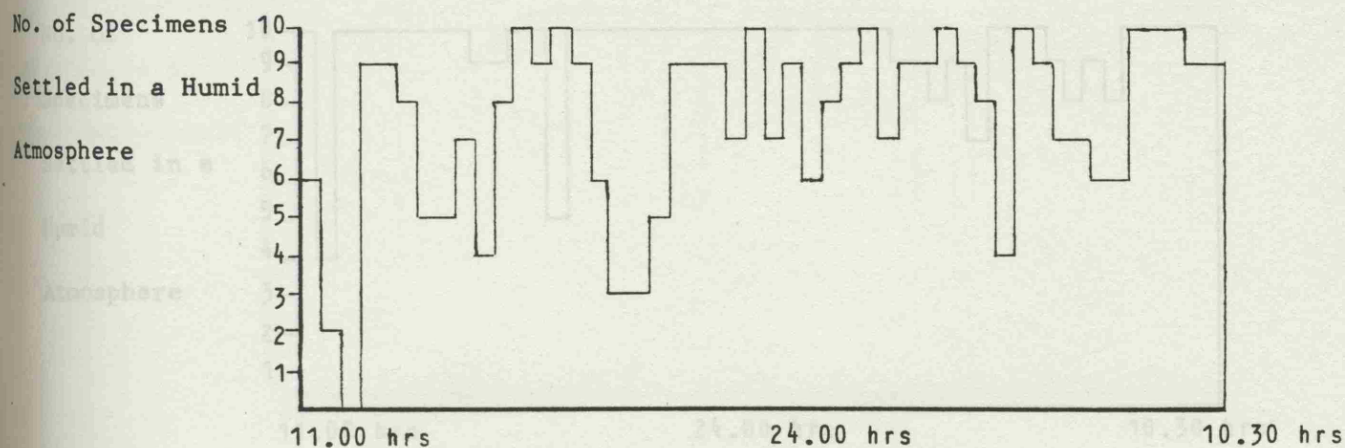
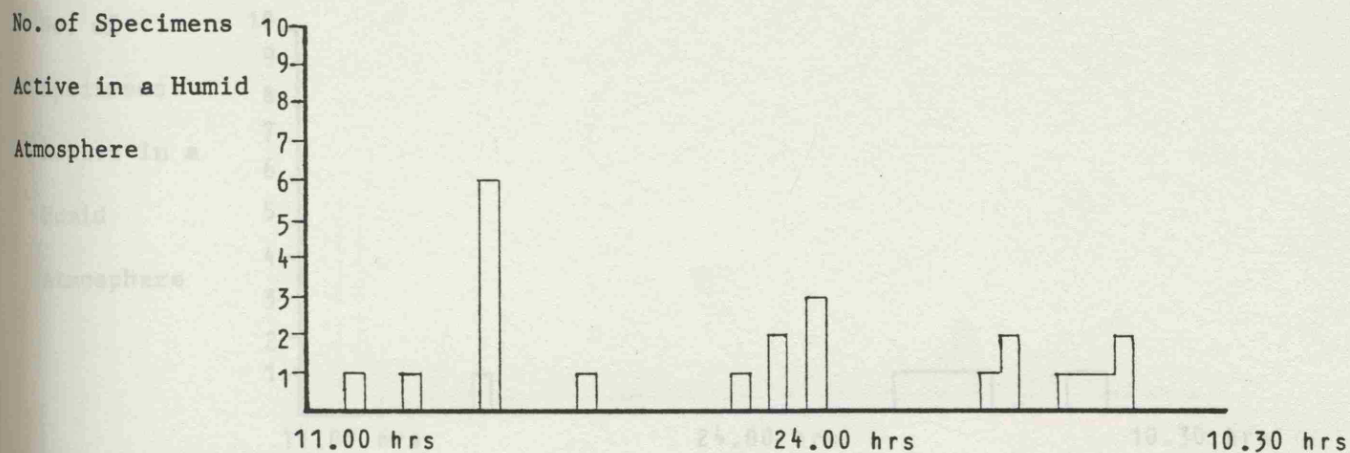
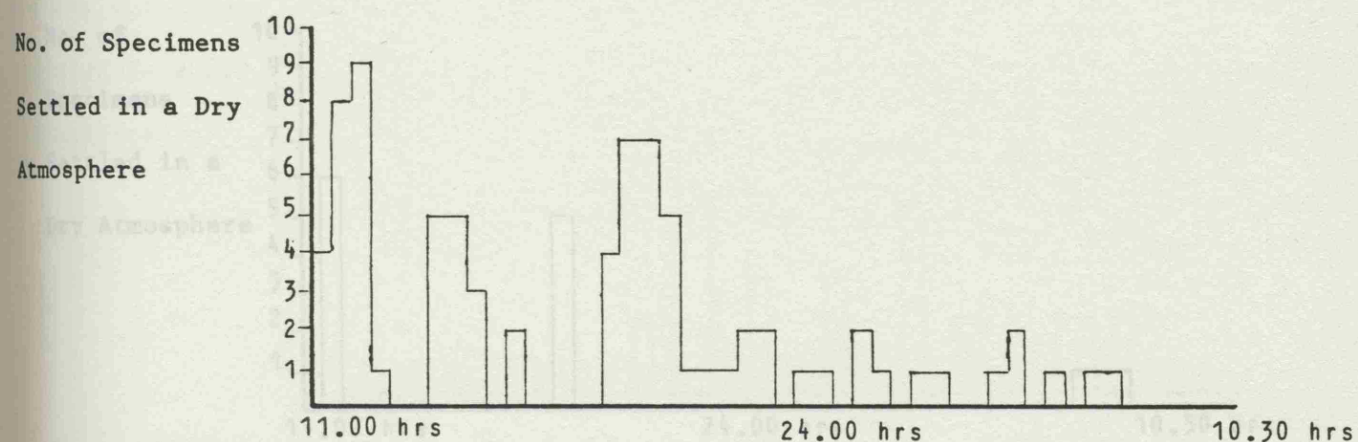
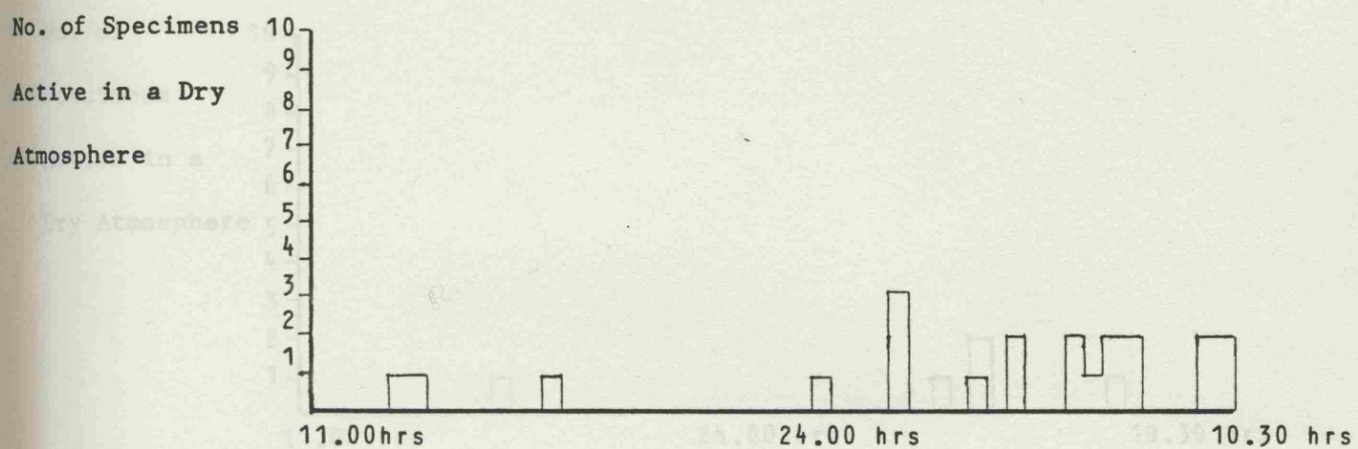


Figure-IX. To show the distribution and activity of 10 Oniscus asellus specimens, at half-hourly intervals during a 24 hour period at a temperature of 10°C.

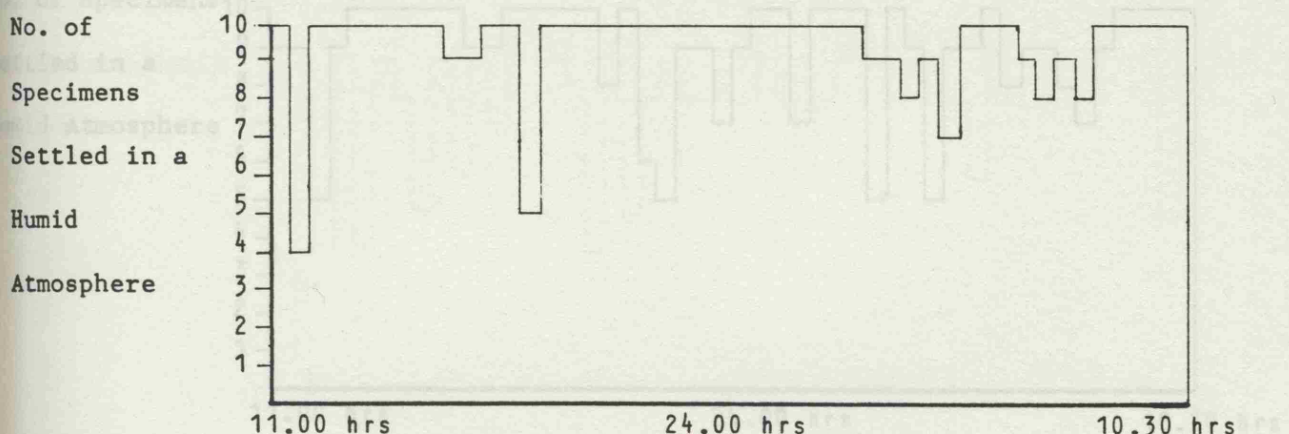
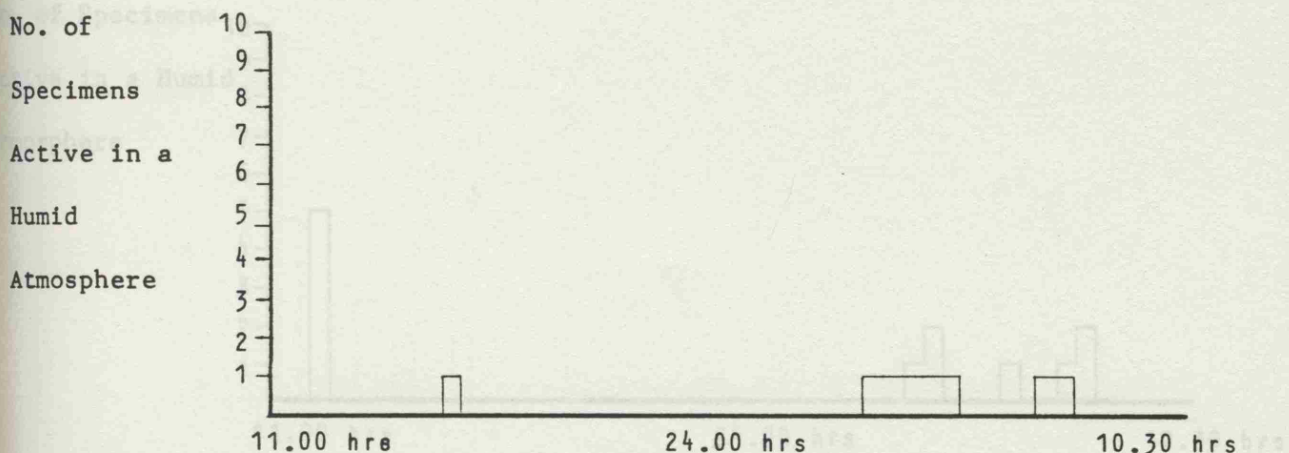
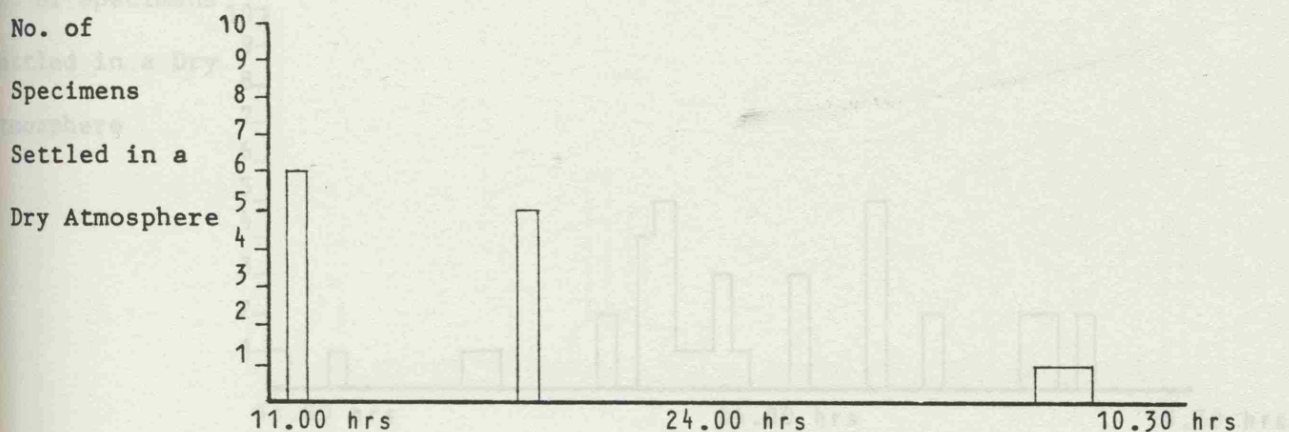
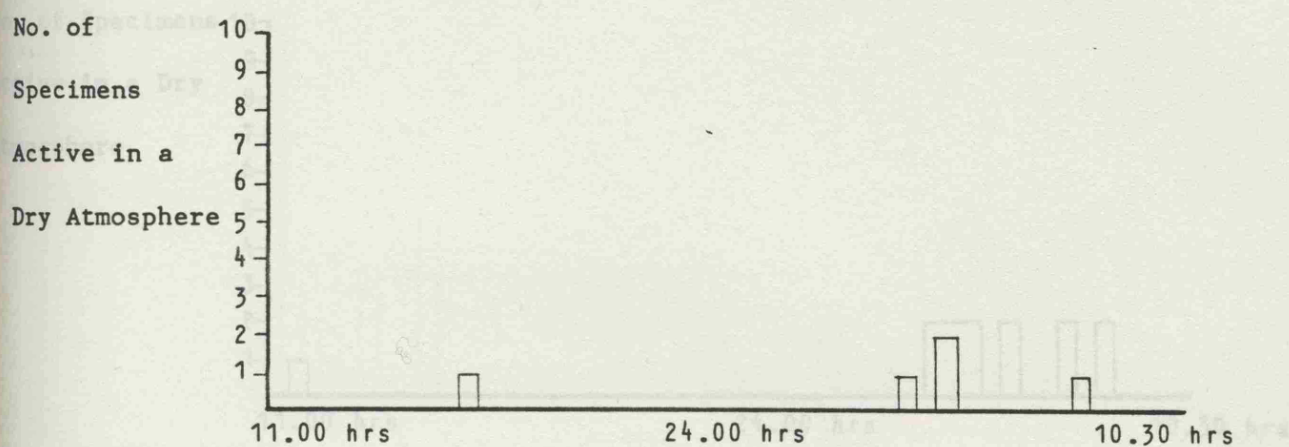


Figure X. To show the distribution and activity of 10 *Oniscus asellus* specimens, at half-hourly intervals during a 24 hour period at a temperature of 15°C.

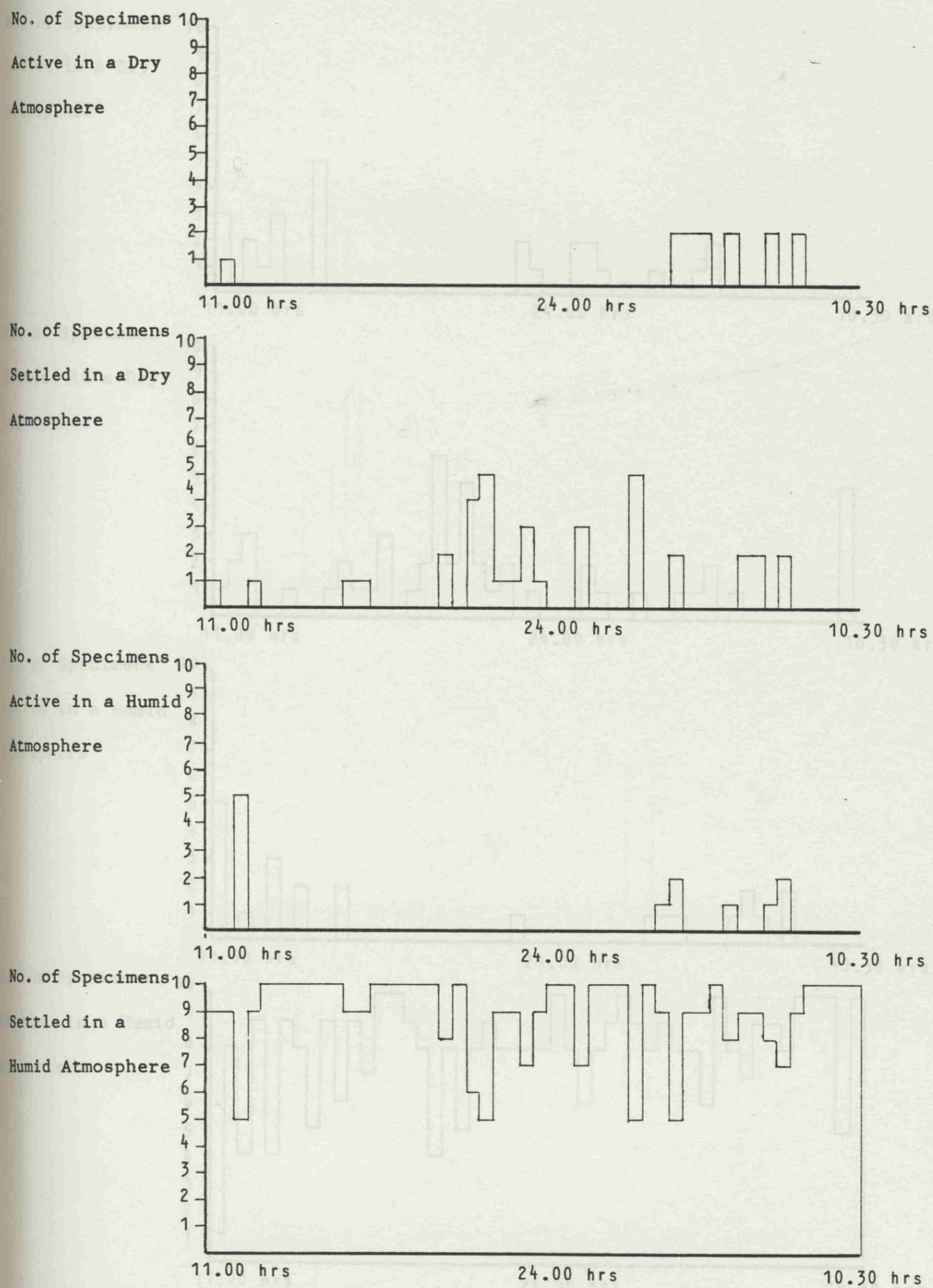


Figure XI. To Show the distribution and activity of 10 Oniscus asellus specimens, at half-hourly intervals during a 24 hour period at a temperature of 20°C.

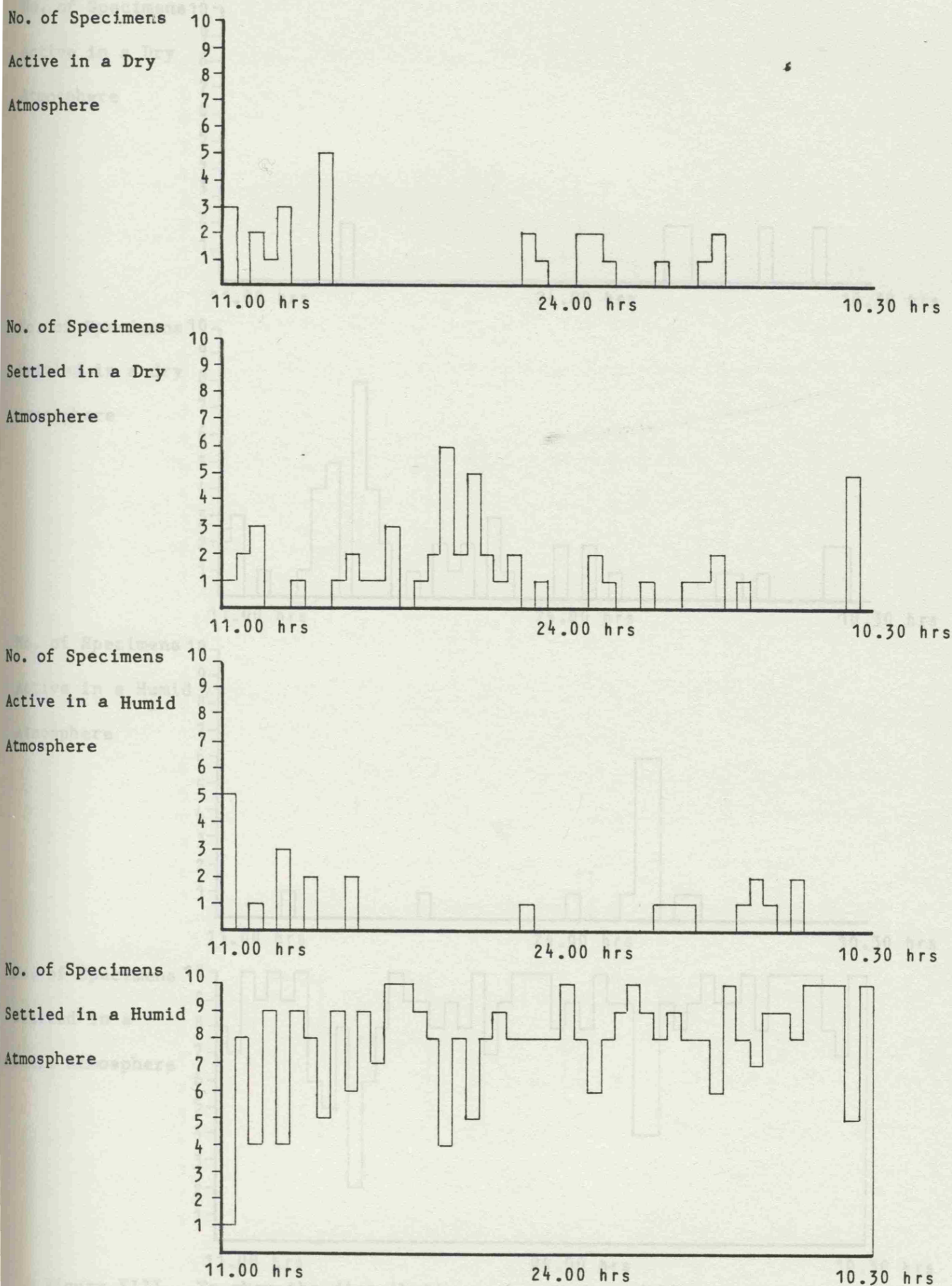
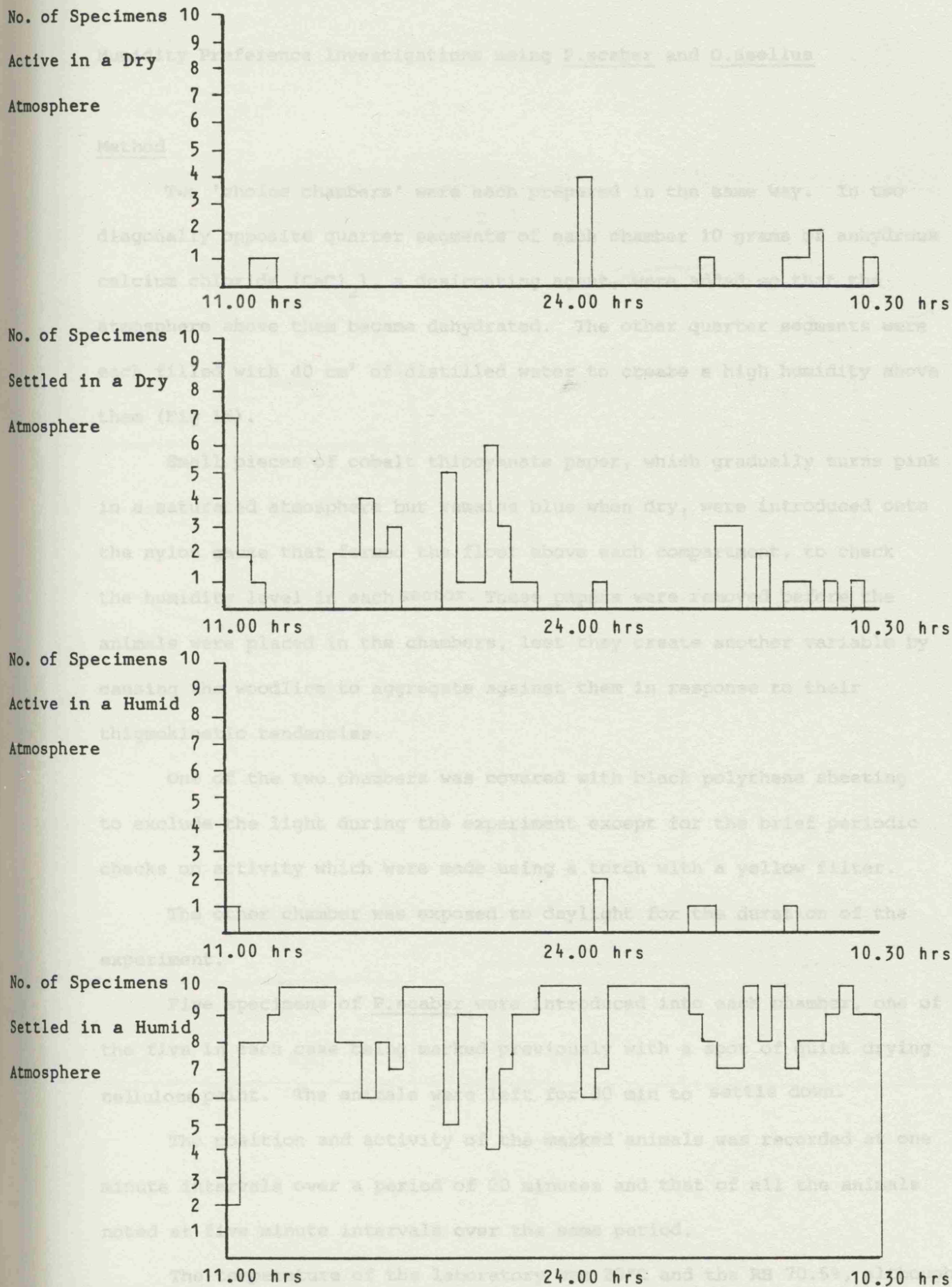


Figure XII. To show the distribution and activity of 10 *Porcellio scaber* specimens, at half-hourly intervals during a 24 hour period at a temperature of 10°C.



Humidity Preference Investigations using P.scaber and O.asellus

Method

Two 'choice chambers' were each prepared in the same way. In two diagonally opposite quarter segments of each chamber 10 grams of anhydrous calcium chloride (CaCl_2), a desiccating agent, were added so that the atmosphere above them became dehydrated. The other quarter segments were each filled with 40 cm³ of distilled water to create a high humidity above them (Fig 15).

Small pieces of cobalt thiocyanate paper, which gradually turns pink in a saturated atmosphere but remains blue when dry, were introduced onto the nylon gauze that formed the floor above each compartment, to check the humidity level in each sector. These papers were removed before the animals were placed in the chambers, lest they create another variable by causing the woodlice to aggregate against them in response to their thigmokinetic tendencies.

One of the two chambers was covered with black polythene sheeting to exclude the light during the experiment except for the brief periodic checks on activity which were made using a torch with a yellow filter.

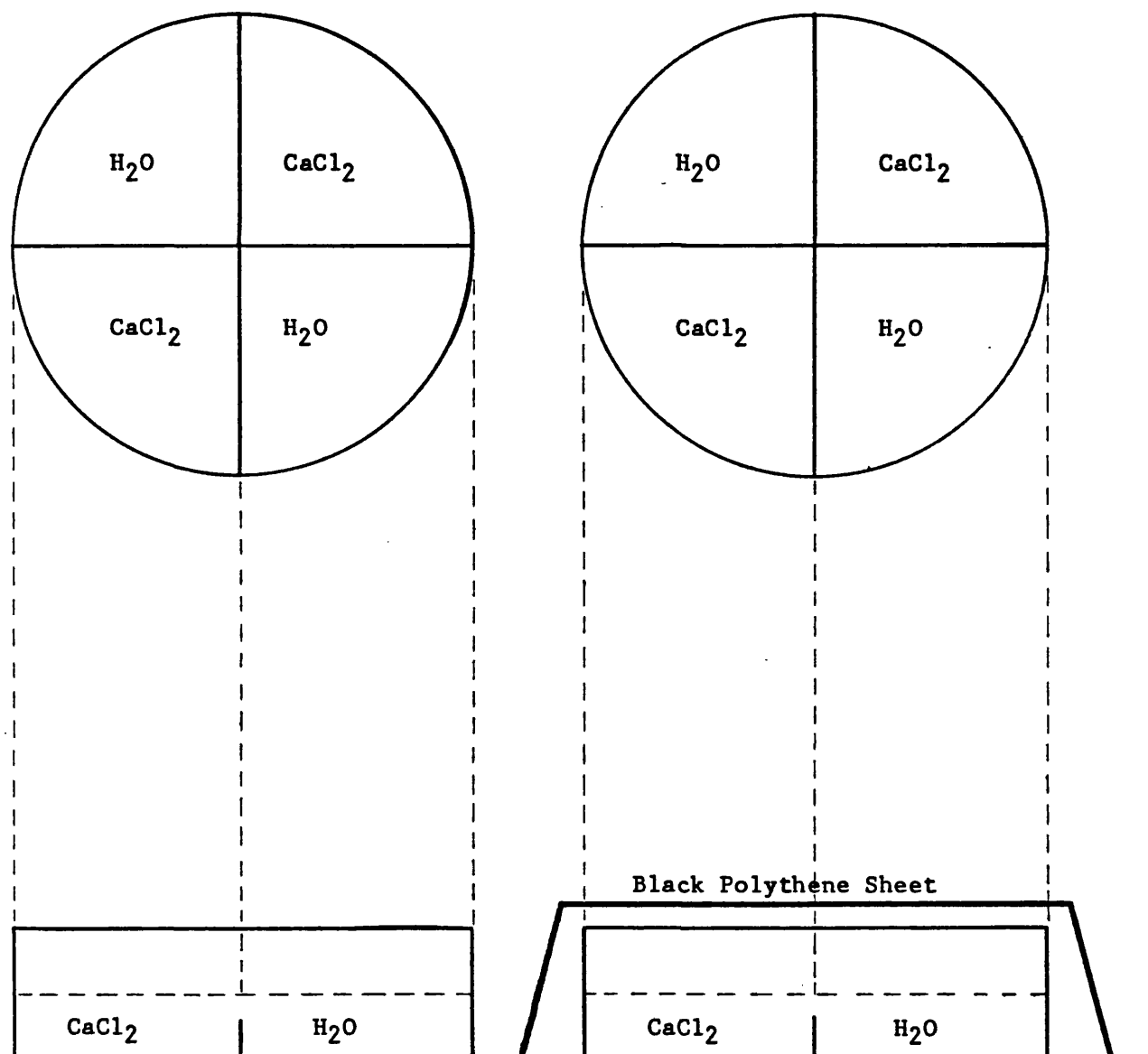
The other chamber was exposed to daylight for the duration of the experiment.

Five specimens of P.scaber were introduced into each chamber, one of the five in each case being marked previously with a spot of quick drying cellulose paint. The animals were left for 30 min to settle down.

The position and activity of the marked animals was recorded at one minute intervals over a period of 20 minutes and that of all the animals noted at five minute intervals over the same period.

The temperature of the laboratory was 20°C and the RH 70.5%, although the latter did not affect the atmosphere within the chamber.

Figure 15 To show choice chambers used in humidity preference/activity
experiment (page 52)



The experiment was repeated using 5 adult specimens of O.asellus in each chamber and then repeated at 12°C in a controlled temperature chamber, again using both species.

Table 11a Showing the frequencies of distribution and activity level of
O.asellus and P.scaber in various experimental conditions

(i) Amount of movement v level of humidity at two temperatures

Derived from Table 7 O.asellus at 20°C

	Humid	Dry	Totals
Moving	4) 7.56) 1.073	4) 0.44) 28.444	8
Settled	64) 60.44) 0.209	0) 3.56) 3.556	64
TOTALS	68	4	72

Calculated value of $\chi^2 = 34.245$ (25.023 corrected)

But one expected frequencies of < 1 so test not valid.

(ii) P.scaber at 20°C

	Humid	Dry	Totals
Moving	10) 17.11) 2.955	12) 4.89) 10.343	22
Settled	46) 38.89) 1.300	4) 11.11) 4.551	50
TOTALS	56	16	72

Calculated value of $\chi^2 = 19.073$ (16.552 corrected)

(iii) O.asellus at 12°C

	Humid	Dry	Totals
Moving	15) 20.4) 1.450	8) 2.5) 11.599	23
Settled	49) 43.5) 0.681	0) 5.4) 5.444	49
TOTALS	64	8	72

Calculated value of $\chi^2 = 18.313$ (15.814 corrected)

(iv) P.scaber at 12°C

	Humid	Dry	Totals
Moving	15) 19.25) 0.938	6) 1.75) 10.321	21
Settled	51) 46.75) 0.386	0) 4.25) 4.25	51
TOTALS	66	6	72

Calculated value of $\chi^2 = 15.896$ (12.376 corrected)

Table 11b Showing the frequencies of distribution and activity level of O.asellus and P.scaber at 12°C and 20°C giving the amount of movement v level of light

(i) O.asellus at 20°C

	Light	Dark	Total
Moving	6) 4) 1.000	2) 4) 1.000	8
Settled	30) 32) 0.125	34) 32) 0.125	64
TOTALS	36	36	72

Calculated value of $\chi^2 = 2.25$ (1.266 corrected)

(ii) P.scaber at 20°C

	Light	Dark	Total
Moving	7) 11) 1.455	15) 11) 1.455	22
Settled	29) 25) 0.640	21) 25) 0.640	50
TOTALS	36	36	72

Calculated value of $\chi^2 = 4.19$ (3.207 corrected)

(iii) O.asellus at 12°C

	Light	Dark	Totals
Moving	22) 11.5) 9.587	1) 11.5) 9.587	23
Settled	14) 24.5) 4.500	35) 24.5) 4.500	49
TOTALS	36	36	72

Calculated value of $\chi^2 = 28.174$ (25.555 corrected)

(iv) P.scaber at 12°C

	Light	Dark	Totals
Moving	10) 10.5) 0.024	11) 10.5) 0.024	21
Settled	26) 25.5) 0.010	25) 25.5) 0.010	51
TOTALS	36	36	72

Calculated value of $\chi^2 = 0.0672$ (0 corrected)

Table 12 Additional analysis giving temperatures combined

(i) O.asellus

	Humid	Dry	Totals
Moving	10) 28.4) 11.936	113) 103.6) 34.325	132
Settled	12) 2.6) 0.856	0) 9.4) 9.400	12
TOTALS	31	113	144

$$\chi^2 \text{ (corrected)} = 42.786$$

(ii) O.asellus

	Moving	Settled	Totals
Light	28) 15.5) 10.081	44) 56.5) 10.081	72
Dark	3) 15.5) 2.765	69) 56.5) 2.765	72
TOTALS	31	113	144

$$\chi^2 \text{ (corrected)} = 23.678$$

(iii) P.scaber

	Moving	Settled	Totals
Humid	25) 36.4) 3.586	97) 85.6) 19.889	122
Dry	18) 6.6) 1.527	4) 15.4) 8.467	22
TOTALS	43	101	144

$$\chi^2 \text{ (corrected)} = 30.606$$

(iv) P.scaber

	Moving	Settled	Totals
Light	17) 21.5) 0.842	55) 50.5) 0.942	72
Dark	26) 21.5) 0.401	46) 50.5) 0.401	72
TOTALS	43	101	144

$$\chi^2 \text{ (corrected)} = 2.122$$

Hence, we accept the alternative hypothesis in cases (i), (ii) and (III) ($p < 0.001$) but accept the null hypothesis in cases (iv); ie for cases (i), (ii) and (iii) the activity and conditions are associated, but in case (iv) there appears to be no more activity in light or dark conditions.

TABLE 12a

Summary of Tables 8 and 10

SPECIES	TABLE	VARIABLES	CALC χ^2	CONCLUSIONS
<u>O. asellus</u>	8 (i)	mobility v humidity	72.91	p < 0.001 p < 0.001 p < 0.001
	8 (ii)	mobility v temperature	18.82	
	8 (iii)	dry v humid	883.6	
	8 (iv)	mobile v static	1162.8	
<u>P. scaber</u>	10 (i)	mobility v humidity	91.569	p < 0.001
	10 (ii)	mobility v temperature	20.16	

TABLE 12b

Summary of Tables 10 and 11

Species	Temp	Table	Variables	Calc χ^2	Conclusions
<u>O. asellus</u> @ 20°C		11a) (i)	mobility v humidity	(34.245 (25.023	χ^2 not valid
<u>P. scaber</u> @ 20°C		11a) (ii)	mobility v humidity	(19.073 (16.552	p < 0.001
<u>O. asellus</u> @ 12°C		11a) (iii)	mobility v humidity	(18.713 (15.814	p < 0.001
<u>P. scaber</u> @ 12°C		11a) (iv)	mobility v humidity	(15.896 (12.376	p < 0.001
<u>O. asellus</u> @ 20°C		11b) (i)	mobility v light	(2.25 (1.266	p > 0.05
<u>P. scaber</u> @ 20°C		11b) (ii)	mobility v light	(4.19 (3.207	p < 0.05
<u>O. asellus</u> @ 12°C		11b) (iii)	mobility v light	(28.174 (25.555	p > 0.001
<u>P. scaber</u> @ 12°C		11b) (iv)	mobility v light	(0.0672 (0	p < 0.05

(continued/. . .)

TABLE 12c

Summary of Tables 10 and 11

(continued)

	Species	Derivation	Table	Variables	Calc χ^2	Conclusions
Temperatures Combined	<u>O. asellus</u>	11a) (i) + (iii)	11(i)	Mobility v humidity	42.786	p < 0.001
	<u>O. asellus</u>	11b) (i) + (iii)	11(ii)	Mobility v light	23.678	p < 0.001
	<u>P. scaber</u>	11a) (ii) + (iv)	11(iii)	Mobility v humidity	30.606	p < 0.001
	<u>P. scaber</u>	11b) (ii) + (iv)	11(iv)	Mobility v light	2.122	p > 0.05

NOTE: Where two values are given in the column headed "Calc χ^2 " the upper value represents the uncorrected value and the lower the corrected value (this required when the contingency table is 2 x 2).

Experiment to determine the percentage activity of O.asellus and P.scaber in dry air and in humid air.

Method

Two choice chambers were prepared, one with water below the nylon gauze and the other floored with CaCl_2 , to create a humid atmosphere in the former and a dry atmosphere in the latter. The diagonally opposite quarter segments of each of the chambers were blacked out using polythene sheeting which was cut to size and taped over the chambers (see Fig 15).

Five specimens of O.asellus were introduced to each of the chambers and their position and activity noted at one minute intervals over a period of 20 minutes (longer might have proved lethal over the CaCl_2).

The experiment was repeated with specimens of P.scaber. The temperature of the laboratory was 20°C. Animals were only assessed as being active when they came from under the dark segments thus clearly showing movement.

Table 14

	Humid	Dry	Totals
<u>O.asellus</u>	22) 14.9) 3.413	46) 53.1) 0.956	68
<u>P.scaber</u>	6) 13.1) 3.868	54) 46.9) 1.083	60
Totals	28	100	128

$$^2 \text{ (uncorrected) } = 9.320$$

$$^2 \text{ (corrected) } = 8.507$$

Number of degrees of freedom = 1

Critical value (5%) = 3.841

Result is highly significant ($p < 0.01$)

Results

The results show that activity, denoted by the number of appearances made, was 54% for P.scaber and 46% for O.asellus in the dry atmosphere compared with only 6% and 22% respectively in the humid atmosphere, figures which corroborate the previous research that has shown that there is an increase in activity in dry air.

Treating percentages as frequencies (ie experiment using 100 animals)
 χ^2 (corrected) = 8.057.

Calculated value of χ^2 significant at 5% level (see Table 14).

$$\chi^2 \text{ O.asellus } = 7.347 \text{ (p < 0.01)}$$

$$\chi^2 \text{ P.scaber } = 36.817 \text{ (p < 0.001)}$$

Discussion

These choice chamber trials show that the intensity of the humidity response of woodlice is less in darkness than in light and that they move towards high humidity and away from light (Table 11b).

Both species were very much more mobile in low temperature and high humidity (p < 0.001) see Table 11b (iii) - (iv). Furthermore the data supports the hypothesis of there being significant association between the amount of movement and level of humidity (see Table 10).

Of the two species studied in these laboratory experiments P.scaber is proportionally slightly more active than O.asellus, yet is dramatically more mobile in the field (see Chapter 4). This is a criticism of trying to equate laboratory trials with field experiments. Although humidities and temperatures were similar to field micro-climates it is not possible to completely simulate field conditions. Furthermore, there is possibly much variability in the responses of individuals, related perhaps to their physiological state at the time.

These experiments were carried out over 24 hours, which has not been completed by any other researcher. In carrying out these experiments

over 24 hours it was anticipated that the animals' circadian rhythms would show more activity at night than during the day but this was not the case (see Figs 9-14). The results are similar for both species showing that the alternative hypotheses is acceptable in that there is a significant association between movement and temperature with more animals of O.asellus and P.scaber active at the lower temperature of 10°C which is the nearest to the mean temperature on Park Campus site.

It is worthy of note that there were significantly more O.asellus moving in both dry and humid conditions at 10°C than in either of the other two temperature regimes. This is the mean annual temperature for the Moulton Park site. There was less movement at 15°C and at 20°C than at 10°C which possibly indicates that the animals were more agitated at the higher temperature.

In contrast P.scaber showed little activity in humid conditions at all temperatures but were more active than O.asellus in a dry atmosphere.

Edney (1954) correlated species abundance with relative humidity and suggested the following optimum humidities: Trichoniscus pus ilus 84%; Philoscia muscorum 80%; Oniscus asellus 77%; Porcellio scaber 71%.

Until this study only Brereton (1957) has carried out night research on woodlice (his results will be discussed in the next chapter). P.scaber were often to be seen wandering in dry places at night, and during the day time were found regularly under logs, stones, and in litter; dark situations where environmental conditions are relatively constant. If nightfall involved only a reduction of the factors which normally operate to restrict them to their day time habitats, it seems unlikely that they would have any reason to leave them. An endogenous circadian rhythm would encourage movement at night-fall. Field observations by Brereton (op cit) on P.scaber have indicated a shortening in the activity period as days lengthen to midsummer and also lack of any clear relationship between activity and changes in temperature and humidity.

The decrease in the intensity of the humidity response at night enables woodlice to walk in dry places where they are never found active by day, and the increase photo-negative response after they have been conditioned to darkness ensures that they get under cover at daybreak and thus avoid predation and desiccation.

Light seems to be more important ecologically for O.asellus than P.scaber (see Tables 11b). The main response to light is photo-negative, unless the animals are in high temperatures or are dehydrated Warburg (1968), whereupon the response becomes photopositive. These two isopods living in woodland and grassland are more efficient at regulating water and can therefore revert to positive photoreaction.

These results confirm that isopods cope with environmental conditions in their habitat by adopting various patterns of activity in response to these conditions thus modifying their effects. Terrestrial isopods are cryptozoic animals and thus inhabit cool and humid microhabitats. This has been substantiated here in both laboratory and by field observations.

The response of an isopod to a single stimulus such as light, under laboratory conditions, appears here to be clear-cut and stereotyped, but as seen in the field population studies reported in Chapter 4, the strength and type of response to any one stimulus is influenced by the strength of other stimuli and by the physiological state of the animal. The results here should, therefore, be considered with caution as the behaviour of an isopod is very varied, corresponding precisely to external conditions and the needs of the body (Cloudsley-Thompson 1956).

In the present study a definite response to a dry atmosphere has been established (see Fig IX, XII, XIII and XIV, and Table 12). The characteristic response to humidity is a kinesis involving both speed of movement (orthokinesis) and a rate of random turning movements (klinokinesis). The intensity of the humidity response is less in darkness than in light. It was shown that excess activity in both species

in dry air brought the animal eventually to high humidities where the activity is reduced; in saturated air the animals are mainly motionless (see Fig IX-XIV and Table 12). Both mechanisms brought the animals to favourable humidities and caused them to remain there. This accounts for the activity patterns of isopods on the ha-ha wall at night (see Chapter 4). P.scaber is less prone to desiccation than O.asellus as it is more active in lower humidities (Edney 1954). This is possibly why P.scaber is found in large numbers on trees in summer whereas the greater number of O.asellus never leave the fallen wood and litter (Den Boer 1961; Brereton 1957). Wilkinson (1979) suggests that humidity has little effect on growth but that the major influences are temperature and day length. Of these two, temperature is more likely to be the determining influence. In the present studies populations peaked at the maximum length of daylight (16 hr) and at summer temperatures in excess of 11°C. Certainly activities at night on the ha-ha appeared to be 'triggered' by the photoperiod and this is confirmed by the behavioural studies reported here and elsewhere by other researchers (Gimta 1963; Cloudsley-Thompson 1961; Warburg 1984).

It must be emphasised that the distribution of isopods is affected by these environmental factors but the distribution of isopods at rest by day may be very different from their distribution at night.

By undertaking behavioural experiments over 24 hours it is anticipated that the animal, circadian rhythm of activity would manifest itself but this was not the case (see Fig 9-14). In the field, however, O.asellus were rarely seen in daylight except under logs, stones and beneath the bark of trees. Whereas P.scaber was seen during the summer active on the trunks during daylight (see Table 16).

Terrestrial isopods are essentially nocturnal animals. Restricted during the day to sheltered moist habitats, they emerge at night to crawl over the surface of stones, tree bark and bare ground. In a series of experimental studies confirmed here Cloudsley-Thompson (1952) demonstrated

a locomotory activity pattern in O.asellus which was a combination of an inherent rhythm and a direct response to environmental changes. These activities showed that movement was correlated with alternating light and dark periods, rather than with fluctuating temperature and humidity. The photonegative response of these animals increased during darkness, ensuring a return to sheltered conditions before daybreak. However, if drying conditions persisted, the woodlice became photopositive enabling them to move to other damper sites where they again became photonegative. The nocturnal activity which takes the woodlice to drier, more exposed sites than they would occupy during the day is not inhibited in animals by the lower humidity conditions, for these experiments also showed that humidity responses decreased in intensity during the night.

This is one reason why I attempted to reinforce the only other research undertaken at night (Brereton 1957). Davis et al (1977) found A.vulgare occurred at greater depth in litter than either P.scaber or P.muscorum by day, but all three were surface active at night. Sutton et al (1984) placed seven isopod species on a soil to surface-active continuum and it is worthy of note that work on resistance to desiccation (cf Edney 1954, 1968) much the same rank order is seen showing overall that these isopods show a set of co-adapted morphological and physiological traits which suit them to a particular way of life. The experiments reported here have shown a very significant correlation between the degree of humidity with more movement in dry conditions and also in lower temperatures (see Table 12).

In the order Isopoda, there are nine sub-orders. Of these only the Oniscoidea have colonised the land from the marine to the terrestrial environment. It is, therefore, reasonable to consider that aggregative behaviour is related to land adaptation. The correlation of aggregation both with temperature and humidity suggests that responses of isopods to each other are closely linked with responses to environmental stimuli (see Table 3).

The aggregation pheromone, discussed by Takeda (1984), therefore, may have been evolved by isopods at the time of migration to the land and have enabled them to adapt to life on land. Takeda (op cit) also gives evidence of body growth being accelerated as a secondary effect of aggregation.

In the foregoing study, the response of two species of isopods to the interaction of four environmental factors: temperature, humidity, light and aggregation, was analysed. The resultant behaviour is the main ecological factor keeping the animals in favourable micro-habitats which is related to the oscillations in populations discussed later.

The work reported in this Chapter shows the significance of behavioural studies to both ecology and evolution. As biologists thinking in terms of evolution through natural selection, they are aware that an understanding of the diversity in the animal kingdom requires that the behaviour of each species be seen in relation to the environmental context to which it has been adapted. Evolutionary trends are towards the colonisation of wider and therefore more exacting habitats. To this end P.scaber appears to be more advanced than O.asellus.

POPULATION STUDIES

POPULATION STUDIES

Introduction

As one aspect of an investigation into the part played by woodlice in eco systems, the population dynamics of species occurring together was examined. In Britain woodlice are often abundant in a wide variety of habitats as long as it is not disturbed, heavily grazed, waterlogged or too acid (Sutton 1968).

Previous population studies have been undertaken by a number of biologists including Heeley (1941), Brereton (1957), Cloudsley-Thompson (1952, 1958), Den Boar (1961), Paris & Pitelka (1962), Paris (1963), Sutton (1968) and Sunderland, Hassell and Sutton (1976).

Brereton (1957) studied variation in density of P.scaber during both the day and the night on both daily and seasonal time scales. Paris (1963) and Paris et al (1962), using capture-recapture techniques, related the population of Armadillidium vulgare to food availability, predators, and weather. They suggest that weather is the primary population regulating factor. Their views are similar to Andrewartha and Birch (1954) who state that weather is the primary population regulating factor. Sutton (1968) studied the population dynamics of Trichoniscus pusillus and Philoscia muscorum and Sunderland, et al (1976) continued the study of P.muscorum in a sand dune habitat. Both studies support Paris & Pitelka's suggestions. Growth, breeding and vertical migration in the soil were all affected by weather conditions.

Woodlice have been used for the study of the effect of light and humidity on behaviour (Allee 1926; Waloff 1941; Cloudsley-Thompson 1952). Allee (1926) found that when individuals were allowed to 'clump' they survived drying better than when they were kept separate. Waloff (op cit) showed that woodlice seek dark moist habitats but Cloudsley-Thompson (op cit) states that their behaviour cannot be wholly explained by these two responses. On the basis of

his experiments, Cloudsley-Thompson has suggested that an endogenous rhythm engenders movement away from the daytime retreats at nightfall. He also found that the photonegative response was heightened in darkness, and suggested that this accounts for the return to the daytime retreats as dawn approaches. Only Brereton (1957) has made detailed studies of the seasonal and diurnal-nocturnal changes in population ecology. Milne (1962) considered that intra-specific competition is the only perfectly regulating process, coming into action at high densities when the ultimate capacity of an environment is exceeded. Brereton (1957) favours intra-specific competition as a regulating factor rather than weather conditions.

In the present study an attempt was made to determine the population densities of woodlice in three different habitats between March 1978 and February 1980.

1. Detailed studies were made of isopod populations in Spinney Hill woods over two years.
2. Vertical migration of isopods and other invertebrates was studied on woodland trees over one year in the wood.
3. All night studies of isopods were made on the ha-ha wall over one year.

Field work was limited to two years, which is short in relation to the generation time, and consequently no reliable explanation of the long-term control of population density can be obtained. Therefore, attention is given to the description and analysis of short-term fluctuations of both O.asellus and P.scaber.

Materials and Methods

In Spinney Hill woods sampling was based on a grid system. An earlier study George (1970) had shown that placing 15 cm square wooden tiles in randomly selected positions in a grid, as described by Cole (1946), was ineffective as woodlice did not colonise. A sampling system using a 1/50m core borer was also tried but was discarded as being too small a sample as only very young woodlice, especially of Trichoniscus species were found. Therefore, a hand sampling method was undertaken selecting points on a grid system and selected at random. Ten 0.25m of litter was collected into a polythene bag and taken to the laboratory for sorting, every month, for two years.

During 1980-4 quarterly sampling as undertaken, both during the day and the night, of the major trees in the woodland to determine the distribution of isopods and the invertebrate animals associated with them. Samples were taken from the vegetation around the base of the trees, and from lichen, moss and beneath loose bark on tree trunks at 1.5m and at 4m heights. Sampling was undertaken on a time method as it is difficult to sample by area in such a habitat. Standardisation rests on the capacity of the observer to find animals in a unit of time. A thorough search was made for 10 min. in each part of the trees and on each tree studied. The drawbacks to this method are that the observer's concentration may vary with time and habitat and the results for different habitats are not direct indices of the abundance of animals in them. Complete and comparable counts in such diverse habitats are difficult.

Extraction

Samples were sorted by hand under strong illumination on a specially constructed white topped table. The animals were killed with ether and preserved in 70% alcohol and 5% glycerine.

In the two year study in Spinney Hill woods the following additional information was recorded:

- (i) Head widths of the animals were measured using a microscope with a micrometer eye piece. This measure was preferred to body length measurements because they can vary between wide limits depending on the contraction of the body at death (Sutton 1968) 1 micrometer unit = 0.5mm.
- (ii) The number of eggs in the brood pouches was counted by opening the brood pouch with dissecting needles.
- (iii) Animals were sexed by looking for male genitalia when animals were greater than 12mm. in length. Animals lacking male genitalia and with a length of more than 12mm. were considered to be female (Sutton 1972).
- (iv) The total catch of each species from the habitat were washed with distilled water, allowed to dry for 2 minutes on filter paper, and then weighed on a balance accurate to 0.01mg. Care was taken to avoid the transfer of moisture from the hands.

Results

Density.

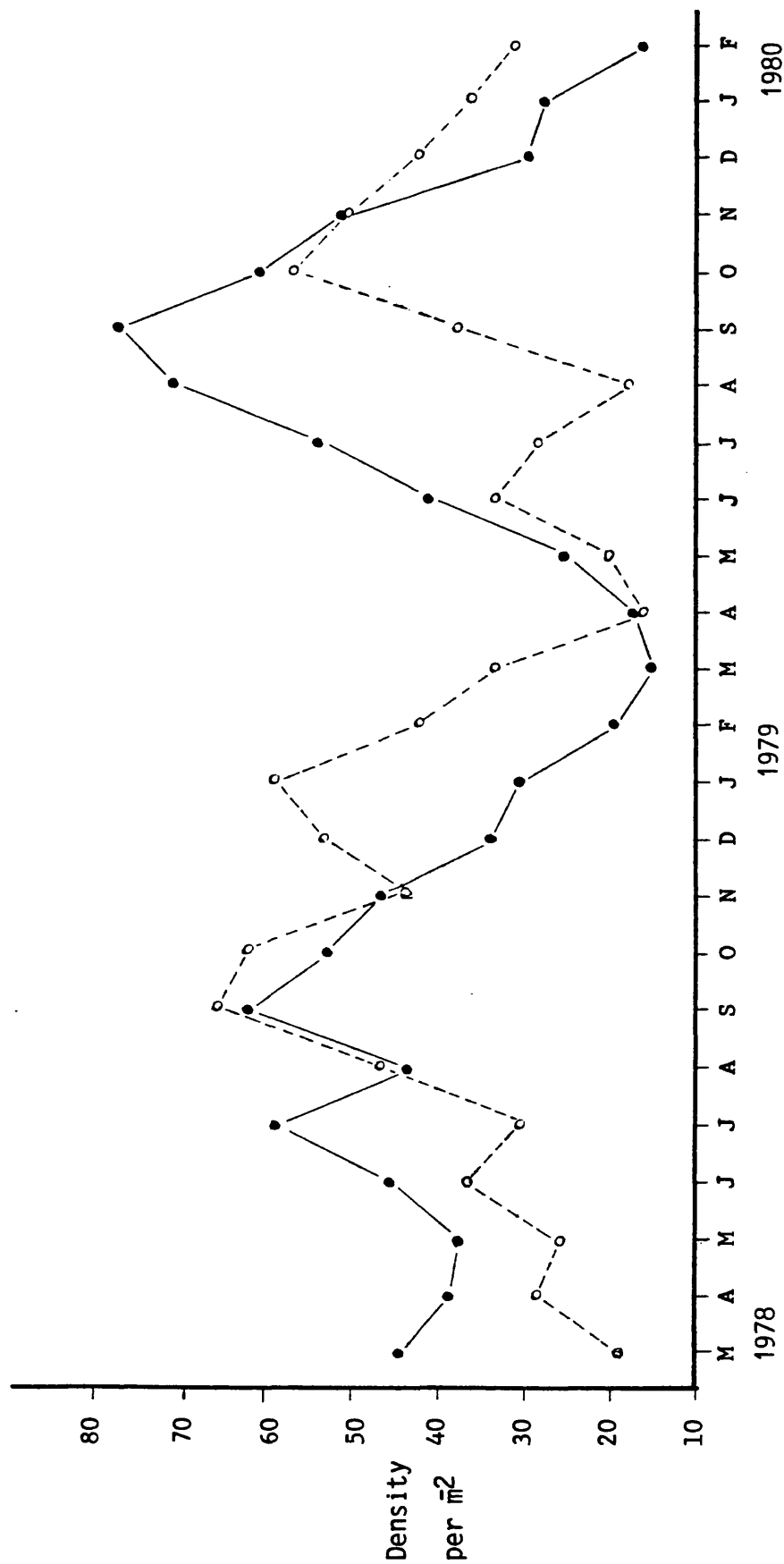
Mean densities per m^2 are shown in Fig.17. Neither species shows a particularly high density (O.asellus; 16-77 m^{-2} and P.scaber; 17-65 m^{-2}) as compared with Philsocia muscorum for which Sutton (1968) recorded densities ranging from 40-265 m^{-2} in grassland. They are comparable, however, with Al-Dabbagh & Block (1981) working on grass-heath where populations of Armadillidium vulgare ranged from 20-80 m^{-2} . Both these researchers, however, indicated that there are higher populations of isopods in grassland habitats

Fig. 17 Mean density m^2 for Oniscus asellus ·—·
and Porcellio scaber ·----· over two years

Fig. 17

Population Density

Oniscus asellus ·····
Porcellio scaber ·····



than woodlands. In the present study the woodland spinney had been frequently changed by man-made perturbations which may account for the low populations.

Population density was at its lowest in March-April 1979 and at its peak in September 1979 for O.asellus and in September 1978 for P.scaber. The numbers for both species showed a well defined pattern of change during the period of study (Fig.17) with the peaks coming in early autumn after the recruitment of the young during June-August. Numbers decreased gradually by March-April each year following the rigours of winter except for P.scaber which is high in January 1979.

The importance of water to the distribution, physiology and behaviour of terrestrial isopods is discussed in chapter 3 . An attempt was made during the study to measure the water available to isopods in the field and the relative humidity experienced by them in their microhabitat. The mean water content of the soil was only 28 % and this is probably due to low rainfall for most of the year and high winds. Both species show a considerable drop in density during the summer of 1978 and this could be due to low rainfall, high temperatures and low relative humidity (see Appendix A). A slowing and possibly some cessation of growth was probably due in the first instance to loss of food sources on the surface through drying of the litter rather than to movement away from food sources.

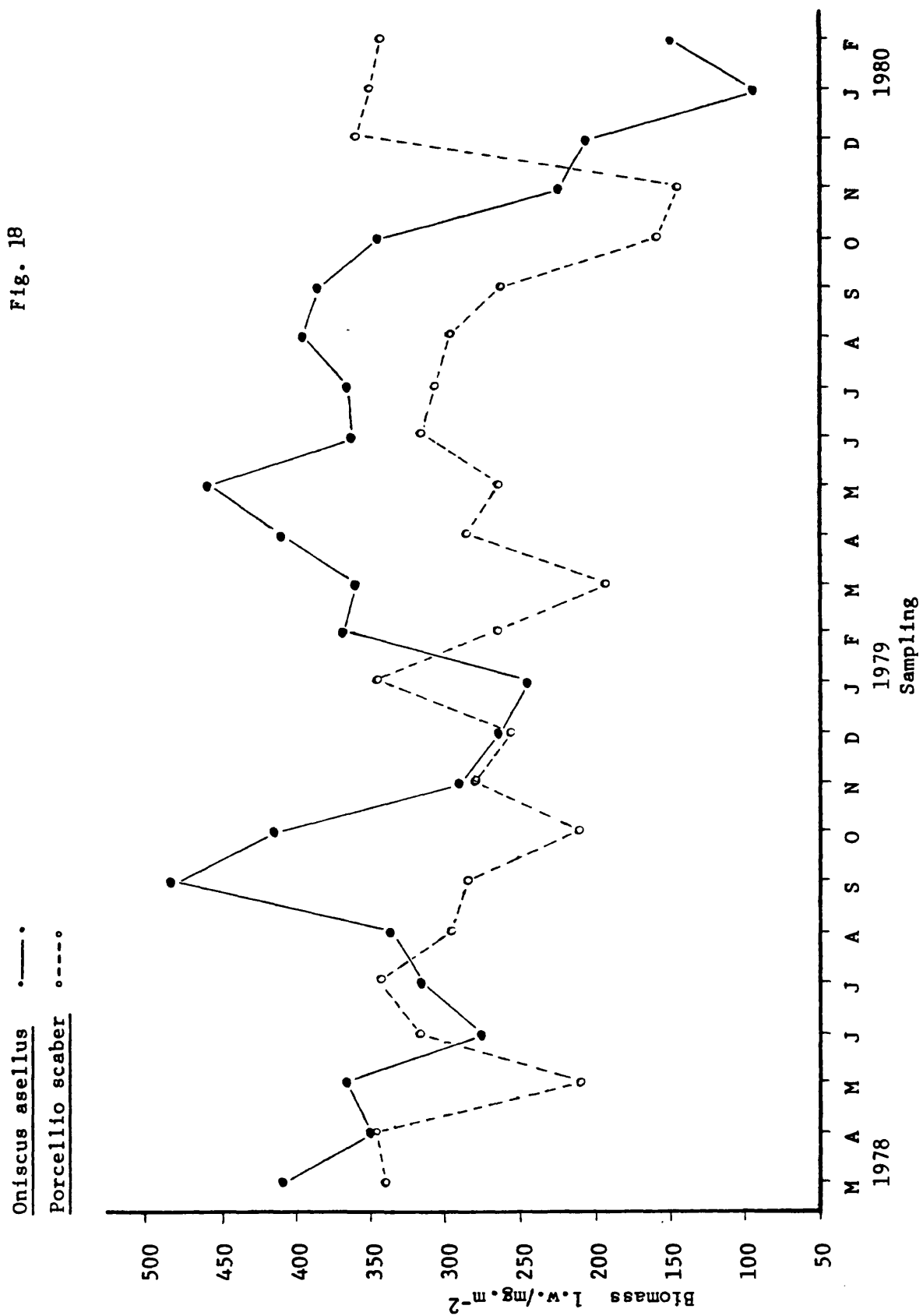
Generally the fluctuations in isopod numbers and the errors involved may have been the result of one or the combination of several of these factors including the sampling inefficiencies of the operator in field and laboratory.

Biomass.

Fig.18 show the actual live weight values of each species over two years. The difference in biomass between the two species is greater than that in population density partly because P.scaber is the smaller of the two species also because there was a greater number of young P.scaber caught in the samples.

Fig.18 Biomass l.w. (mg) for Oniscus asellus .—.
and Porcellio scaber o---o. over two years.

Fig. 18



Comparison of biomass and density figures for both species (Figs 17-18) show that the size structure of the population was changing since biomass and numbers did not rise and fall in step. The cause of this change is discussed in the next section. Both species showed a consistent pattern of abundance while there is a marked tendency for biomass to decline in the second year of study.

A general build up of population biomass was shown by both populations towards winter. This persisted throughout the winter and was followed by a decrease in the first half of each summer. This increase in biomass is attributable to the growth of the younger cohorts in the population. There is evidence, however, that P.scaber has two generations in both years as is seen by the two rises in the graph peaking in June and October compared to one per year in O.asellus. The growth rates exhibited by cohorts during separate growing seasons was another factor responsible for the change in population biomass. The mortality effect on the change in population biomass was obscured by these changes. The mortality effect can be seen in the early summer months due to the death of the other individuals.

Size structure.

(a) General

The monthly population structure of both species is shown in Figs 20-21 by frequency distribution of size, based on head width measurements for each sampling date. The number in each size class is shown as a proportion of the total number sampled on each occasion. The maximum frequency occurring was 19 (June 1978) and this is used as the unit of width of the bars which represents the data. All other data is scaled proportionally. A major assumption in the interpretation of these size distributions is that the upward progression of waves of animals through the size classes represents growth. Studies on the growth rates of animals kept in captivity under as near normal conditions as

Fig. 20 Size class distribution of Oniscus asellus in
each monthly sample from March 1978 - Feb 1980
Size classes are given by head-width in micrometer
units (1 unit = 0.5mm). The number in each size class is
shown as a proportion of the sample total.

Headwidth (micrometer units)

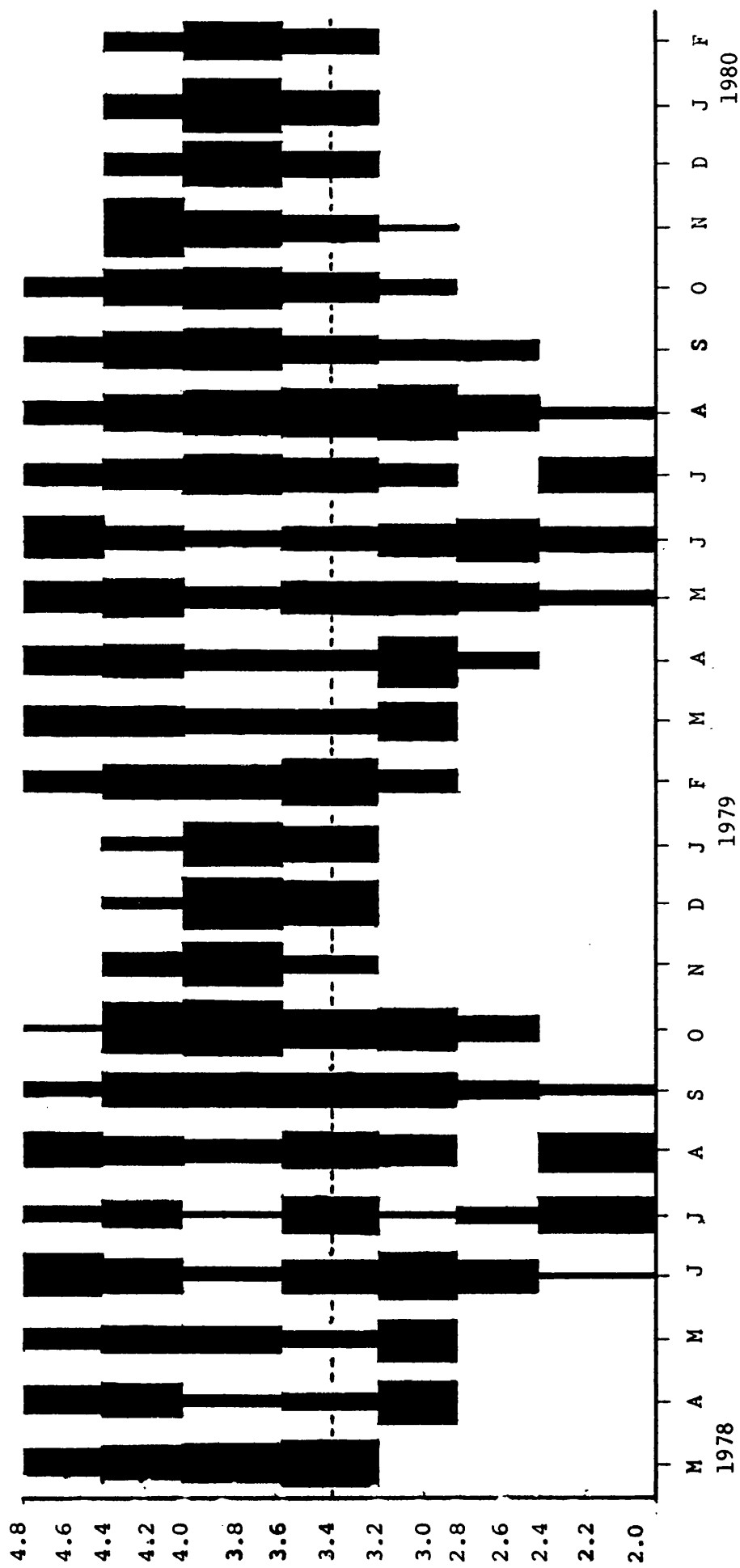


Fig. 20 *Oniscus asellus*

Fig. 21

Size class distribution of Porcellio scaber in
each monthly sample from March 1978 - Feb 1980

Size classes are given by head-width in micrometer
units (1 unit = 0.5mm). The number in each size class
is shown as a proportion of the sample total.

Headwidth (micrometer units)

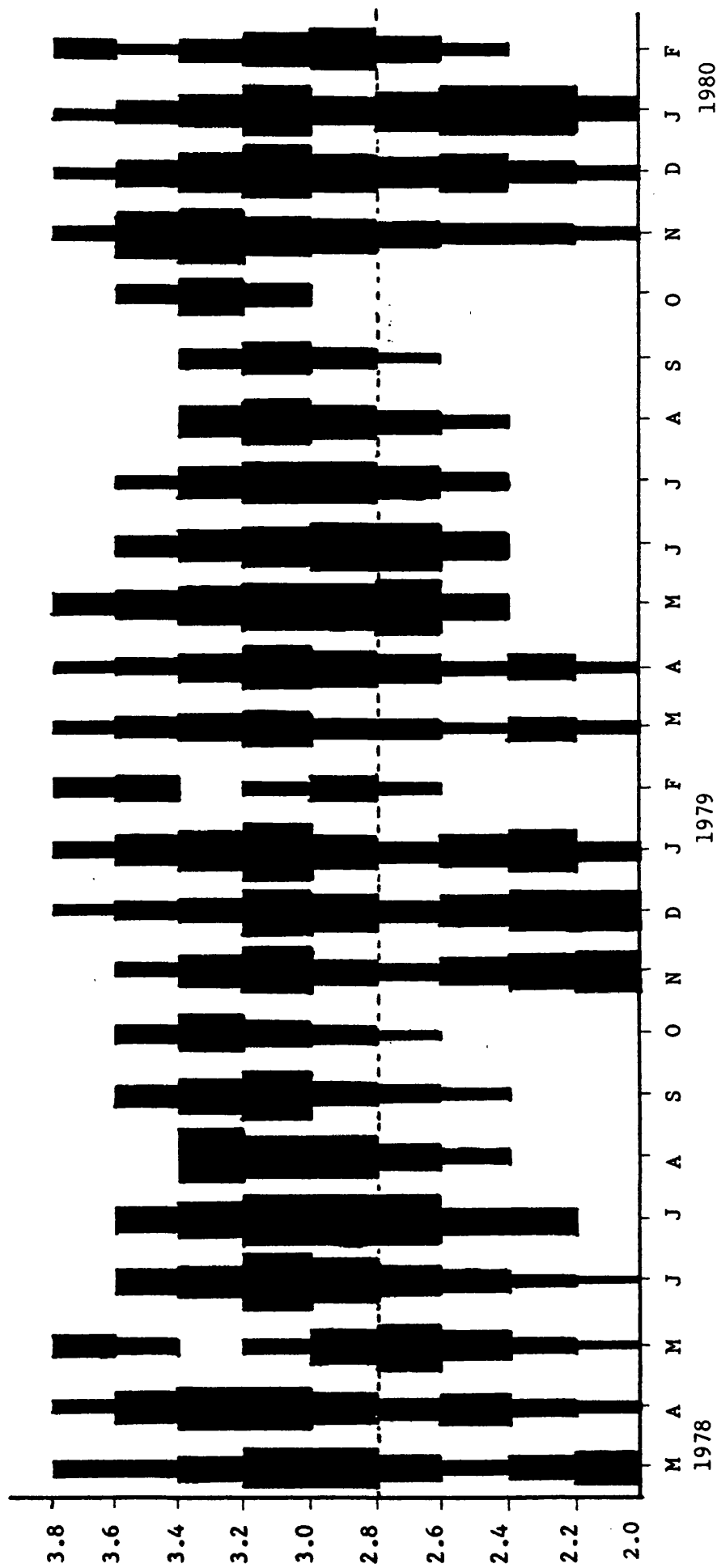
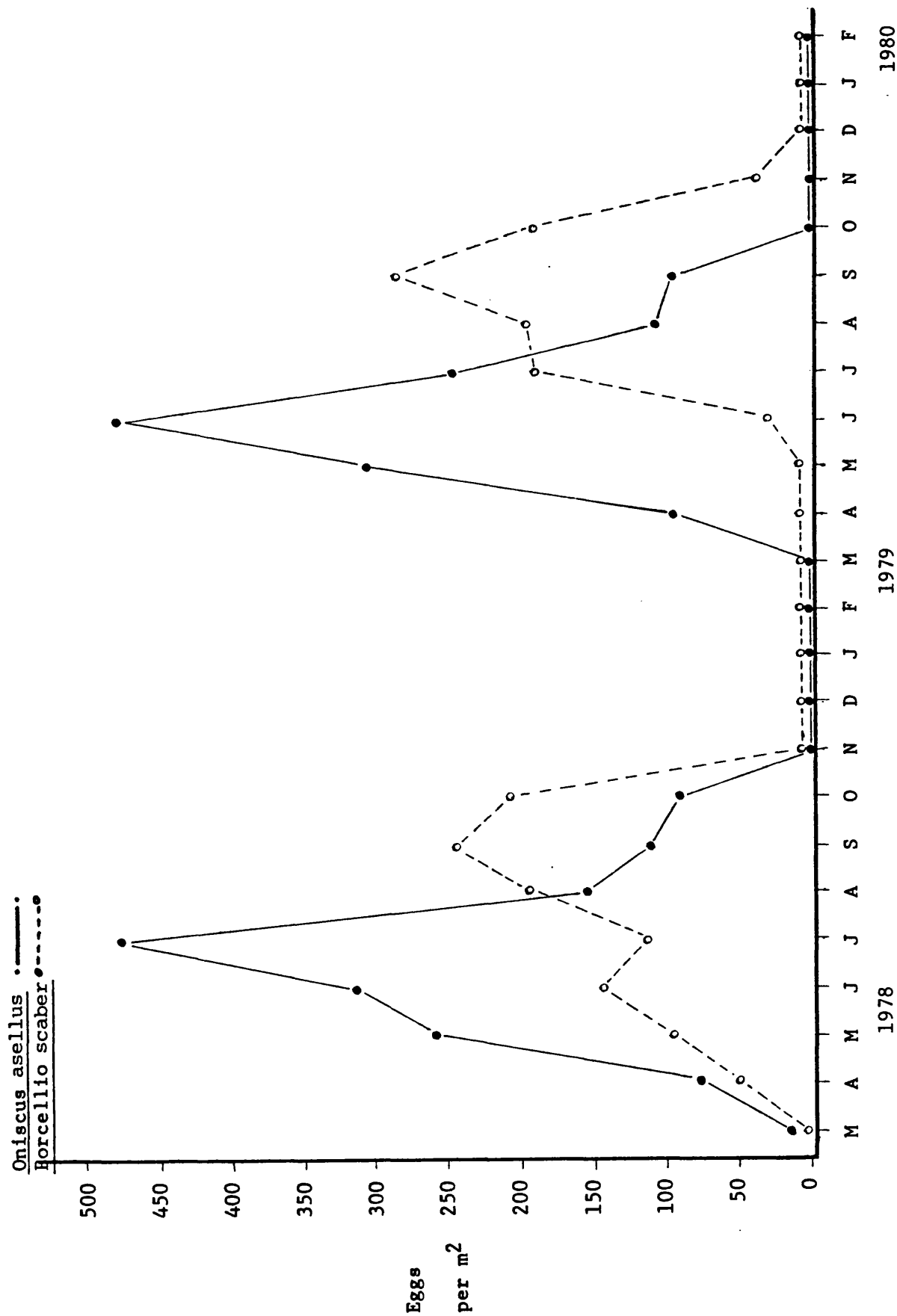


Fig. 21 Porcellio scaber

Fig 22 Egg standing crop for Oniscus asellus •—•
and Porcellio scaber •---• over two years

Fig. 22. Egg standing crop during 2 years sampling.



possible (see page 24) indicates that this assumption is valid, the growth increments of captive animals being similar to those which can be inferred from the size distribution. Captive animals show marked individual variation in growth rate which possibly accounts for the observed spread in size ranges of each cohort as it grows. A further point worthy of note is that the rate of growth decreases with age so that the cohorts are difficult to separate in later life. The dashed line in figs 20 & 21 represents the adult size level.

Growth of both species followed a distinctive pattern. Growth was seasonal and occurred during the months of April to October. Minimal growth took place during the winter period. This is clearly demonstrated when the monthly change in monthly head widths of each of the population cohorts during the 24 months of the study was examined. The equivalent values in weight (mg) are also very different with large individuals being present by the end of both growing seasons and in winter in the case of P.scaber.

(b) Oniscus asellus (Fig.20)

The contraction in the size range of O.asellus between March and May, 1978, November 1978 and January 1979 and November 1979 - February 1980 show the effect of differential growth rates of younger and older animals. There are only adults at these periods of the year and these are the larger animals that will survive the winter and reproduce.

The breeding season can also be correlated with climatic factors. March 1978 was an extremely cold month (see Appendix A) which possibly caused a delay in breeding.

This is not surprising as Warburg (1984) has shown that both the onset and duration of breeding, as well as the number of broods, at least to some extent depend on temperature and day length.

Eggs were present in brood pouches by April in both years (Fig. 22) and began to appear as free living young in June 1978 and May 1979. Again a

climatic factor may be responsible as mean temperatures were higher in 1979 than 1978 (see Appendix A). The numerical increase in juveniles meant the population density did not fall. The main recruitment came in July-August 1978 and June-July 1979 as indicated by the large numbers of animals at the bottom end of the size range and the declining number of gravid females. In the second half of the year the new recruits grew whilst remains of the adult group lingered on. Contrary to expectations, the release of the new brood did not cause a dramatic increase in numbers in either year. Apart from sampling error, this anomaly might be due to fairly high synchronised release between monthly sampling dates and to heavy mortality of the young. Brereton (1957) gives evidence for cannibalism of the young and observations in the present study confirms this. When moving in a dish in the laboratory adults will often pass over young, seemingly by accident. When this happens they sometimes seize them with their three front pairs of legs and whilst resting on the back four move the young forward into their mouths. Within 40 seconds the animal has disappeared. So far, however, there is no evidence of cannibalism in the field. In the field, an animal has freedom of movement and can isolate itself from the rest of the population when about to moult whereas in a laboratory culture with high densities this is not possible.

(c) Porcellio scaber (Fig. 21)

As with O.asellus, there is some contraction in size range of P.scaber in the winter months although less dramatically. P.scaber bred earlier in the spring of both 1978 and 1979. There were more adults available in the winter months than O.asellus which suggests that this may be a hardier animal. Further evidence for this is the fact that there were far more small P.scaber caught during the winter months of each year which implies greater survival capacity.

Another possible explanation is that there was a second wave of breeding which is a feature of Philoscia muscorum, Porcellio scaber and Ligia oceanica all of which are capable of iteroparity whereas Armadillidium vulgare and P. hoffmannseggii and O.asellus are semelparous (Sutton et al 1984).

In the second half of the year the new recruits grew while some remnants of the adult group remained. As with O.asellus the lowest numbers were in March-April 1979 which was a very cold spring with frosts and easterly winds. There is a sudden dip in populations during the summer of 1979 when precipitation was 393mm over three months; the wettest period recorded throughout this research. September was a dry month and the population rose dramatically whilst the numbers of O.asellus fell. Apart from sampling error, disease or predation this is the only explanation for this dramatic change as P.scaber shows a preference for a drier habitat than O.asellus. P.scaber were probably up the trees and O.asellus deep in the litter where they survived.

Breeding season

The breeding season which is defined here as the time from the first appearance of gravid females to the time of the last record of empty brood pouches in sample material is shown for both species in Fig 22. The highest proportion of gravid females was found in early summer and the pattern of breeding was similar in both years with the exception that O.asellus bred one month earlier in the second year in spite of the cold late spring (see Appendix A and Fig. 22).

This possibly indicates that photoperiod is the dominant 'trigger' for breeding and not necessarily temperature. P.scaber had two waves of breeding as shown earlier, namely in June and September each year. (Wieser, 1984)

Reproduction (Wieser 1963a) and sex determination (Becker-Cerus 1967) of terrestrial isopods are influenced by day length. The breeding periodicity of both species appeared to be highly synchronised and breeding commenced with both species at almost the same time in both years. Paris & Pitelka (1962)

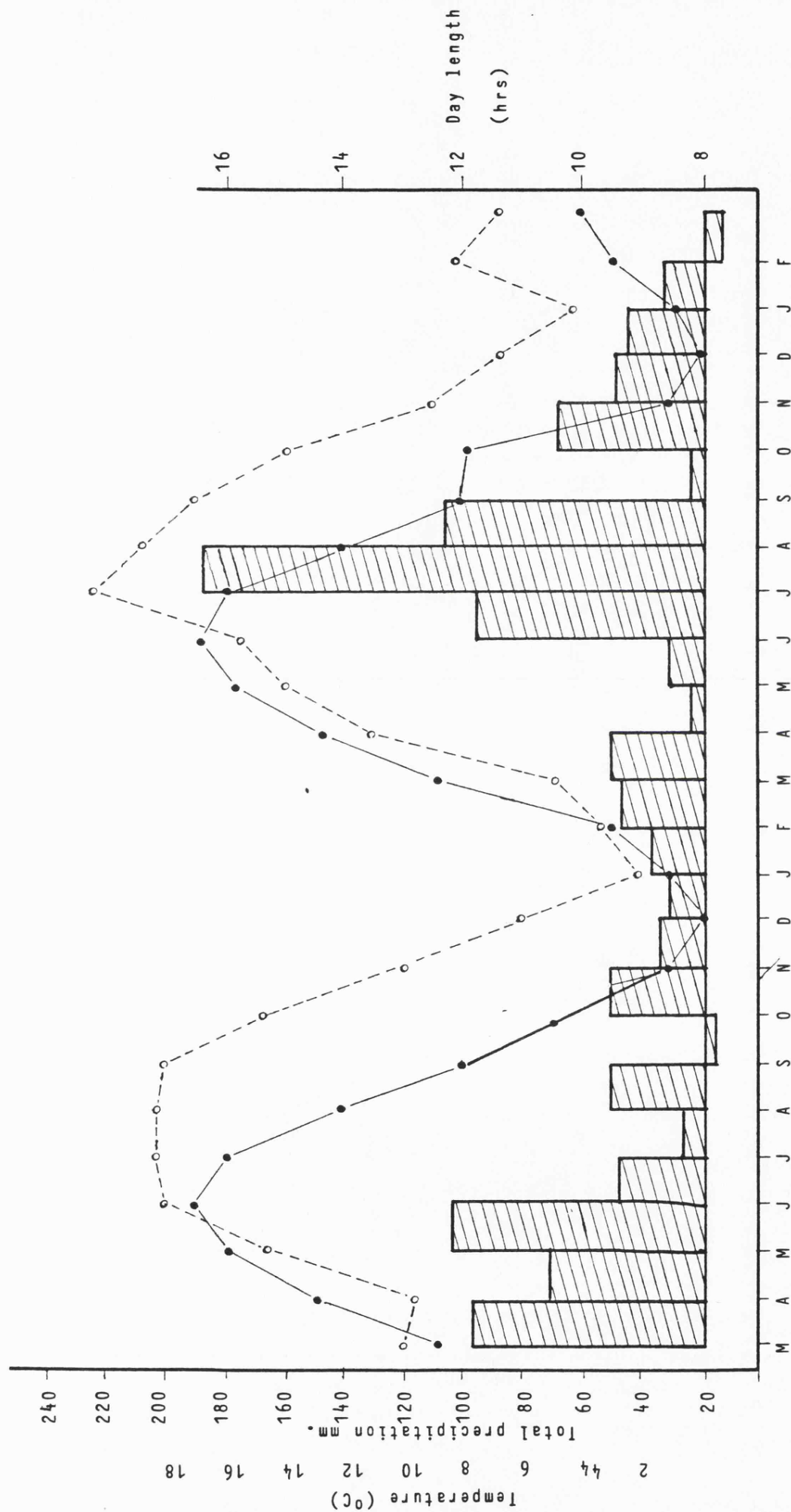
Fig. 23 Breeding periodicity of Oniscus asellus and
Porcellio scaber in relation to monthly rainfall
(histograms), monthly mean temperature ----° and day
length .— .



Oniscus
Porcellio



Fig. 23



related the onset of breeding to the photoperiod rather than other factors and suggested that breeding took place when the photoperiod was above 12 h of daylight. The same correlation was found for both species reported here (Fig 23) when breeding peaked at 15h daylight. It is evident, however that the peak of the breeding season was within the period when habitat temperatures were above 16°C. It may be that a more direct relationship of breeding to temperature is possible, especially as these isopods are known to have a photonegative reaction (see chapter 3) (Fig 16),

In addition the rate of energy metabolism is profoundly affected by season and it may be assumed, in agreement with other animal studies, that the decisive factor in this relationship is photoperiod (Weiser 1984) (see chapter 6).

Preliminary night activity studies

During the daylight surveys Porcellio scaber was only found in dark crevices and holes. It was noted as a casual observation, that these woodlice came out from the ha-ha wall to feed at night. Isopods are well known to have a nocturnal activity pattern (Cloudsley-Thompson 1952) and so it was not surprising to find these animals walking about or stationary on the wall at night. Night observations and sampling were carried out on 10th June throughout the night followed by twelve monthly samplings to establish the activity pattern and population density of the species on the wall.

Method

A quadrat 1m x 1m was marked on the wall with Stictite at a height of 1 m. above the ground in order to restrict the movements of animals in this area.

During the night observations, temperature and relative humidity were recorded every 45min. from 2200 hours - 0400 hours. A torch with a yellow filter was used for observational work and this did not appear to affect the animals.

Results preliminary night exercise.

Fig 24 shows the visible population within the 1m quadrat, time, temperature and relative humidity. By 22.30 h it was quite dark and the first isopods had appeared. The animals were mostly motionless and appeared to be grazing on a lichen Scoliciosporum chlorococcum. By 2400 h 108 isopods were recorded and this was the maximum observed during the night. This is contrary to Brereton (1957) who recorded the peak population for P.scaber at 2300 h. There was a rapid rise in humidity up to this time. By 0415 h there were no isopods to be seen and by now it was quite light. From these results it appears that lack of light 'triggers' the isopods to become active at night and seek shelter at dawn, although activity possibly increases with the rise in humidity (see chapter 3).

This exercise was repeated monthly over a year sampling on three consecutive nights, at midnight, in order to establish the total population and using the Lincoln Index method (Bailey 1952) (see Table 15 and Appendix C for the result). Animals were marked with quick drying cellulose paint with a different colour being used on each occasion.

Fig. 24 Nocturnal activity of isopods $\bullet\text{---}\bullet$ in lm^2
quadrat correlated with day length, temperature
and relative humidity $\circ\text{---}\circ$

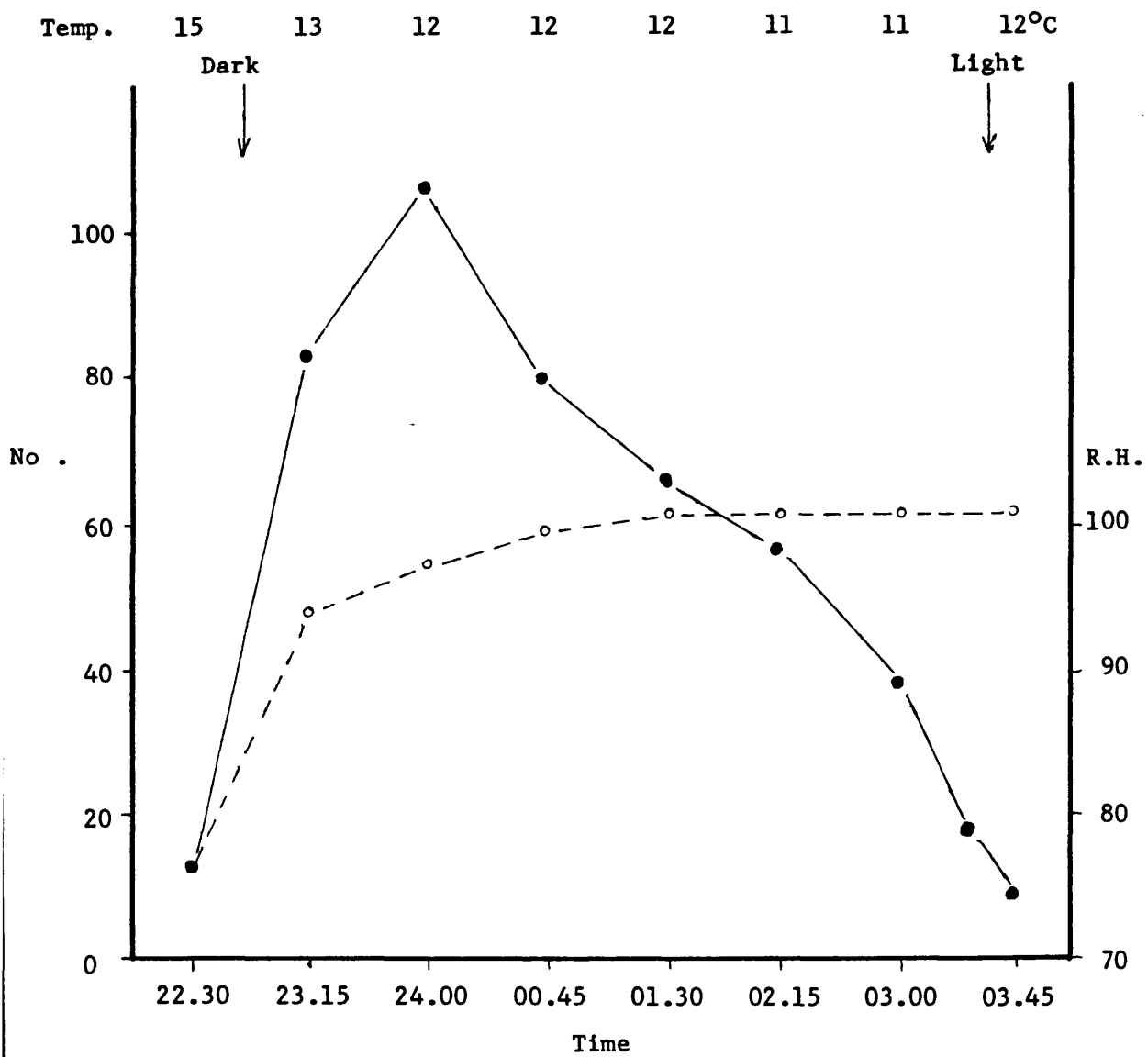


Fig. 24

Discussion

By using the Lincoln Index and the Bailey's Triple Index (1952) method of population estimate, the population densities can be estimated. The Bailey's triple index shows a very wide range of results from 0 to 888 (Density m^2). The results from the Lincoln index seen in Appendix C show an equally wide range of population numbers from 0 to 936 m^{-2} . Because of the small samples Bailey's (1952) correction formula was used. (see Appendix C).

The results show a response to more profound seasonal changes by the fact that in December and January species were scarce and tended to stay in crevices and holes in the brick wall.

The variable number points to the fact that isopods do not necessarily remain out all night but have waves of activity. It would be interesting to determine if different species have different times of feeding.

den Boer (1961) found that isopod night activity was caused by the need to shed water overload rather than motivated by the search for food and mates.

Observations made by Cloudsley-Thompson (1958) that woodlice are less active on windy nights could support this hypothesis. Heeley (1941) too noticed that woodlice became active as darkness increased, due to increasing humidity.

The number of woodlice captured in the present study and the estimated density by the Lincoln index are considerably different. This suggests that the animals do not come out onto the brick wall every night but have different activity patterns when climatic conditions are most suitable. It was noted that the lowest numbers tended to be found on cold breezy nights, particular low numbers occurring when the temperature fell well below freezing.

However, there seemed little correlation between humidity levels as has been suggested by den Boer (op cit). These results are in agreement with Cloudsley-Thompson (op cit), who found lowest numbers of isopods on cold, dry, windy nights. Results obtained on two still nights provided an interesting

contrast: on these nights temperatures exceeded 5.5°C , and large numbers of woodlice were found wandering on the wall.

On several evenings the wall was covered by a large number of O.asellus and P.scaber . By marking them and recapturing them it was realised that only a few were ever subsequently recovered. From this it was realised that the total number of isopods on the wall must have been high. The results from the Lincoln Index suggest that the population numbers do have a high variability with time. A possible reason for this variation in numbers is that there are inaccuracies in the estimates. For any capture-recapture population estimation the following assumptions have to be satisfied:

- (i) The marks are neither lost nor become indecipherable.
- (ii) The marked animals become completely mixed in the population.
- (iii) The probability of capturing an individual from the marked sub-population is taken as the same as that of the whole population.
- (iv) Sampling time is small in relation to total time.
- (v) There are no births, deaths, immigrations and emigrations in the period between sampling.

By recapturing twenty four hours later, using small spots of harmless paint, and painting them in the square it was possible to keep these factors to a minimum. However, a few isopods were killed by marking with paint or did not return to their crevices and mix back with the population. Similar principles apply to the Baileys Triple Index which was used to work out population densities for each individual month.

It is based on a deterministic model of survival and is somewhat inefficient at grouping data where large numbers are recaptured more than once. Again birth and death rates must be constant over a period of time, and intervals between sampling must allow for ample mixing of the marked individuals with the remainder of the population, and not so long that a large portion of marked

individuals have died. By using the conditions of recapture after 24 hours, marking and mixing factors were controlled. However, difficulties did arise: some isopods lost their marking when moulting occurred as it does frequently; some dropped off the wall when painted and were therefore disregarded from all counts. To avoid this they were removed, painted and replaced, but it was then difficult to redistribute them to their original positions.

Although inaccuracies are involved in using the Lincoln Index and Baileys Triple Index the overall activity of Porcellia scaber and Oniscus asellus can be seen. From the results it appears that temperature may be related to the behaviour response of woodlice and activity may increase with the rise in relative humidity. Chapter 4, shows from a laboratory experiment carried out in October 1979, that isopods remained active under most optimal conditions but preferred the higher relative humidity gradients wherever possible. It is interesting to note that in November and December the wind direction was predominantly south westerly rather than easterly although it is thought the direction had little direct influence on the wall as it lies in a small hollow.

The wall is covered with the green lichen S. chlorococcum and appeared to be a food source of the woodlice, in fact areas in the quadrat where dense patches occurred had the highest numbers of woodlice on them. Thus it may be suggested from the present study that the isopods on the wall did come out to feed, contrary to den Boer's (op cit) views. Similar evidence is given by Brereton (1957). In winter in the daytime the animals are found in crevices and on still humid evenings when the temperature has been around 7 - 10° C, some come out of the holes and feed, although none travel far. In the winter the numbers are low because the animals remain in their holes. This may be just the case in the present study. There is, however, a difficulty in explaining the results for January, when no isopods were found. Although temperatures fell below

freezing they also did in November, and a few isopods were captured. One possibility may have been due to physical disturbance of the niche over the Christmas holidays when children had been playing in the area as stones had been removed. Although these results are rather small and tentative they are original and most interesting. They point the way to further research.

Vertical migration of isopods and other invertebrates on four common trees on the College site.

Only Brereton (1957) has studied seasonal and day-night population changes in isopods. The previous studies on the ha-ha showed large populations active at night. The present study was to determine population changes in both species looking at five variables: time, 12 noon and midnight; tree species; species of isopod and other invertebrates; season and height on the tree. The surveys were undertaken quarterly during 1980.

Complete and comparable counts in such habitats as litter and tree trunks are difficult and laborious. After several preliminary investigations it was decided to use a sample unit of 15 min search rather than using an area basis, as there seemed no satisfactory way of determining what are comparable areas for sampling. In a searching-by-time method this difficulty is overcome and the standardisation rests on the capacity of the observer to find animals in a unit of time. The problems of this method are that the researcher's efficiency may vary with time and habitat, and the results for different habitats are not direct indices of the abundance of animals in them, e.g. if animals are rare but easily found in a certain habitat, they will appear relatively more abundant than they are. The isopods and other invertebrates recorded, however, were reasonably large and therefore this was not considered to be important.

The search was carried out for 15 min at ground level around the base of the trees, at chest height (1.5m) and at 4m. above the ground.

During this period a concentrated search was made at the given height on the same tree species quarterly. A strong knife was used to clear away loose moss, lichen and bark. Animals were collected in previously labelled plastic collecting tubes for later identification in the laboratory.

Results

The results of the daylight and night-time surveys are set out in Tables 16 and 17. A one way analysis of variance looking at mean values was undertaken and a two way analysis of variance in order to compare the possible ten pairings of variables. The conclusions are set out in Table 18 below. From these results it can be seen that of the individual variables the tree species, the species of isopod and the height above the ground are all highly significant ($p < 0.001$) whereas with the interactions between variables only tree species/isopod species and season/height are highly significant.

Quarterly daytime distribution of Porcellio scaber, Oniscus asellus and other invertebrates on different tree species over one year. 1980 (11 am - 1 pm)

Table 16

Table 16																						
	Porcellio scaber				Oniscus asellus				Diplopoda				Araneae				Others				Total	
	Feb.	May.	Aug.	Nov.	Feb.	May.	Aug.	Nov.	Feb.	May.	Aug.	Nov.	Feb.	May.	Aug.	Nov.	Feb.	May.	Aug.	Nov.		
Base of	Ash	55	8	5	108	39	31	19	42	7	19	13	6	6	7	9	4	5	15	19	6	423
	Beech	11	18	8	19	12	17	10	21	2	5	3	1	2	1	4	3	6	21	29	7	200
	Corsican Pine	3	14	20	4	4	11	12	2	1	3	2	3	18	5	4	15	4	17	22	5	169
	Dead Elm	78	19	13	64	22	115	116	18	14	7	8	10	19	31	40	15	77	28	36	10	580
	Total	147	59	46	195	77	174	157	83	24	34	24	20	45	44	57	37	32	81	106	28	1372
1.5m.ht.	Ash	2	25	30	7	0	6	4	0	1	3	1	1	3	2	7	4	11	18	13	19	176
	Beech	18	19	32	8	0	0	0	0	0	0	0	0	1	0	4	4	2	5	7	4	94
	Corsican Pine	0	0	0	0	0	0	0	0	0	0	0	0	3	7	8	4	11	16	26	14	89
	Dead Elm	48	62	70	29	0	10	6	0	0	7	8	4	14	18	31	5	14	18	19	10	383
	Total	68	106	132	44	0	16	10	0	1	10	9	5	21	29	50	17	38	57	65	47	747
4m.ht.	Ash	43	19	30	5	0	0	0	0	0	0	0	0	2	4	4	3	0	2	1	0	94
	Beech	0	8	15	12	0	0	0	0	0	0	0	0	0	0	0	0	0	8	12	0	55
	Corsican Pine	0	0	0	0	0	0	0	0	0	0	0	0	1	2	4	5	1	3	2	0	18
	Dead Elm	32	63	79	47	0	0	0	0	0	0	0	0	11	16	15	7	4	16	26	6	458
	Total	75	90	124	64	0	0	0	0	0	0	0	0	14	22	23	15	5	29	41	6	676

Quarterly night-time distribution of Porcellio scaber, Oniscus asellus and other invertebrates on different species over one year, 1980 (11 pm - 1 am)

Table 17

	Base of	Porcellio scaber				Oniscus asellus				Diplopoda				Araneae				Others				Total
		Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	
Trees	Ash	61	10	7	149	43	49	23	172	4	16	10	14	4	6	7	12	2	19	26	23	628
	Beech	18	21	11	30	10	16	28	47	1	4	3	10	2	4	9	16	6	29	30	11	306
	Corsican Pine	10	17	18	16	5	13	12	14	2	2	2	0	14	18	23	16	4	31	40	14	282
	Dead Elm	89	12	10	113	41	114	126	24	16	8	8	23	11	28	37	43	14	35	49	53	754
	Total	178	60	46	208	99	192	189	257	23	30	23	47	31	56	76	87	26	168	145	101	2079
1.5m.ht.	Ash	4	15	39	1	0	12	13	0	2	4	6	0	3	4	8	1	10	23	30	2	177
	Beech	21	34	26	0	0	0	0	0	0	0	0	0	2	6	11	0	2	11	18	0	131
	Corsican Pine	0	2	3	0	0	0	0	0	0	0	0	0	1	7	8	0	11	16	32	0	80
	Dead Elm	51	37	71	13	2	17	18	0	1	1	1	0	22	33	14	2	10	23	28	7	370
	Total	76	88	139	14	2	29	31	0	3	5	7	0	28	50	41	3	33	73	108	9	746
4m.ht.	Ash	3	27	42	0	0	0	0	0	0	0	0	0	2	4	2	0	0	3	9	0	92
	Beech	0	6	18	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	16	0	47
	Corsican Pine	0	0	0	0	0	0	0	0	0	0	0	0	2	11	4	0	2	7	11	0	37
	Dead Elm	31	73	92	2	0	0	0	0	0	0	0	0	15	23	20	3	2	6	41	0	311
	Total	34	106	152	2	0	0	0	0	0	0	0	0	19	38	26	3	5	22	77	0	497
		Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	Feb.	May	Aug.	Nov.	

Discussion

Daytime surveys over one year

The results of the daytime surveys are set out in Table 16. Three quite striking facts emerge from these results. The first is the predominance of woodlice over other animals of similar size; of the animals recorded 55% were isopods ($P = 0.001$). The second is the paucity of the fauna found on the Corsican pine and to a lesser extent on the Beech compared with Ash and dead Elm ($P = 0.001$). Thirdly the strong evidence that P.scaber moves on to trees in May and descends again in November ($P = 0.001$). The difference in distribution and the seasonal changes in distribution of the two species of woodlice are set out below.

Oniscus asellus

In winter O.asellus was most common under stones and decaying wood at the base of all four tree species. A few animals were found at 1.5 m on both Ash and Elm in Summer (May and August) but none at 4 m.

Porcellio scaber

In winter P.scaber was found in large numbers beneath stones, decaying wood and especially in the moss layer at the base of all four tree species. In Summer it was most common on trees with similar numbers found at both 1.5 m. and 4 m. with a descent in late Autumn.

There is a possible correlation between climatic conditions and population density. In February, there was a cold N.E. wind resulting in a very low temperature. As a result ice had accumulated on the trees killing the isopods. This would seem to account for the low numbers especially on Ash which was least sheltered. Brereton (1957) suggested that movement occurred in November and the present research would support this, although there were some animals found on two of the tree species on all sampling occasions. Another possible explanation is that some animals stay on the trees, breed and die there.

Night time surveys over one year

During the daylight surveys woodlice were only found in dark damp places and yet at night more animals were seen actually on the tree trunks which made sampling much easier. Quarterly surveys were carried out over the years between 2300 hrs. and 0100 hrs as the survey on the ha-ha had shown a maximum population at midnight. This is contrary to Brereton (op cit) who quotes 2300 hrs. as the peak of population. From the results on Table 17., it is clear that Porcellio scaber comes out from beneath bark, holes, moss and lichens in Summer to graze and possibly lose moisture (Vandel 1943; Cloudsley-Thompson 1952). Animals appeared to be grazing on the green lichen S.chlorococcum which was abundant on the three broad leaved trees but not on Corsican pine where there was no lichen growth. On the night of August 14th there was a very large number of Porcellio scaber at 4 m. in a stationary position for at least 15 minutes at a time, and this is thought to be due to the decrease in the intensity of the humidity response at night which enables these animals to dry out as discussed in chapter 4 of this research. The temperature on that evening was 8.8 °C and early that evening there had been a heavy shower of rain. On all other occasions woodlice were quite active which is contrary to Brereton (op cit) who had indicated a shortening in the activity pattern as days lengthen and also a lack of any clear relationship between activity and changes in micro climates. It is also clear from the results that contrary to Brereton (op cit) the Summer numbers did not fall because the animals had moved higher up the trees. The population densities were similar at night and day during the Summer months.

Distribution according to tree species at night

As in Table 16 there is quite clearly a difference in populations of isopods between the species of trees and the ranking is dead Elm, Ash, Copper Beech and Corsican Pine. This is in keeping with the results of the food trials in Chapter 5 although there was no evidence that the animals were

feeding on leaves. The reasons for the difference in distribution are probably mainly shelter, in that both ash and elm have crevices in the bark as compared to beech and both had a more abundant food supply. However, corsican pine disproves the first point in that it has a flakey bark with an abundance of shelter sites but does not have the algal food supply. In earlier food trials P.scaber grazed readily on the lichen S.chlorococcum but O.asellus did not (George (1970)).

Another factor from historical ecology is that the corsican pine is not an indigenous species being a recent import into this country (1759) and, therefore, has not been colonised by invertebrates until comparatively recently. There were, however, a reasonable number of animals at the base of this tree where there was an abundance of moss and woodland litter. (61).

Interaction of Porcellio scaber with Oniscus asellus

Sum over one year of the O. asellus, and P. scaber day/night populations

Derived from Tables 16 & 17

	Day		Night	
	<u>O.asellus</u>	<u>P.scaber</u>	<u>O.asellus</u>	<u>P.scaber</u>
Base of tree surrounds	491	447	737	592
1.5mht.	26	350	62	317
4m.ht.	0	353	0	294

From these results it appears there was some replacement of P.scaber by O.asellus around the base of the trees in summer. The exact cause of this relationship is difficult to surmise. Certainly more P.scaber moved up the trees in summer leaving more space possibly for O.asellus who moved onto the trees in smaller numbers. One possible cause of this shift was because of competition for space and food during the breeding season. Certainly woodlice were abundant on tree trunks during the summer (Table 16) However in winter both species appear to share the same ecological niche where there is

an abundance of food. The evidence suggests that O.asellus did not appear to drive P.scaber to the upper parts of the tree, nor did P.scaber exclude O.asellus from this zone. Further when autumn came O.asellus did not prevent P.scaber from re-entering the moss and litter at the base of the trees. Thus the available evidence suggests that the seasonal changes in the two populations of woodlice do not result from competition. It is suggested that P.scaber has a liking for S.chlorococcum as well as being able to stand dessication better than O.asellus (see Chapter 3).

General Discussion

These studies reveal that P.scaber spends a great deal of time on trees as was reported by Brereton (1955) but contrary to his findings a significant number of P.scaber also occur in the litter around the base of the trees in summer. In November the majority go into the moss and litter layer at the base of trees. In August the majority move to at least 4 m height up the trees and remain in crevices of bark during the day. During the night they are to be seen on the trunks of trees, presumably eating the lichen S.chlorococcum.

Biological interactions with other animals or members of its own kind would be most likely to be observed during periods of activity i.e. on summer nights. Predators, disease or climatic factors might cause the depletion or disposal of whole colonies, but if such adversity as this were common P.scaber would have little chance to survive, as growth in numbers of individuals is relatively slow and dispersal poor. If other animals regularly affect P.scaber numbers it is more likely to occur during the night when individuals leave the safety of their refuges.

A clear fact that emerges from these data is that the isopods differ with the species of tree ($P < 0.001$) but not between day and night ($P > 0.05$). (Table 1.8). It is possible that the latter is primarily due to sampling error as most animals were well concealed during the daylight hours.

Table 18

Conclusions

Individual Variables:

- | | |
|----------------------|-------------------------|
| 1. time | not significant |
| 2. tree species | very highly significant |
| 3. species of isopod | very highly significant |
| 4. season | not significant |
| 5. height | very highly significant |

Interactions

- | | |
|---------------------|-------------------------|
| 1. time x tree | not significant |
| 2. time x specimen | not significant |
| 3. time x season | not significant |
| 4. time x height | not significant |
| 5. tree x specimen | very highly significant |
| 6. tree x season | not significant |
| 7. tree x height | not significant |
| 8. species x season | not significant |
| 9. species x height | significant |
| 10. season x height | very highly significant |

No 3, 4 or 5 way analysis performed (likely that specimen v height v season
tree v specimen v height v season etc. will be significant)

> 5% (0.05) not significant

< 5% (0.05) significant

< 1% (0.01) highly significant

< 0.1% (0.001) very highly significant

The totals are markedly different with Ulmus procera being the most popular habitat for all taxa. In composition striking differences occur also with F.excelisior being the second most popular with all taxa and F.sylvatica ranked next at the 4m height but Pinus nigra being least popular at the base although there was an abundance of moss growing at the base.

There is reason to believe that P.scaber, O.asellus, Dermaptera, Araneae and slugs (molluscs) are permanent members of the tree fauna whereas Diplopoda especially Glomeris marginata and snails (molluscs) come to the tree trunks at night from the litter and some species of harvestmen (Opiliones) go from the trees to the litter layer. On the basis of his experiments, Cloudsley-Thompson (1952) has suggested that an endogenous rhythm engenders movement away from the daytime retreats of isopods at nightfall. He also found that the photonegative response was heightened in darkness, and suggested that this accounts for the return to the daytime retreats as dawn approaches. This is confirmed by the all night exercise on the ha-ha.

Out of all recordings made only on two occasions was P.scaber seen to be preyed on and this was by staphylinid beetles. It is important, however, to stress the fact that these observations on this limited predation overlook two possibilities. Firstly predation might occur under the bark and in crevices at other times, and secondly, the possibility of large scale predation by larger animals such as shrews (Soricidae), mice (Apodemus sylvaticus) and birds whose attack may never be seen, could be important. Brereton (op cit) experimented in the laboratory with small mammals and found that P.scaber was distasteful to the common shrew (Sorex araneus) and the pygmy shrew (Sorex minutus).

Many animals feed on isopods, however, mostly on non-conglobating forms, the main predators being arthropods, lower vertebrates and insectivorous mammals. The subject has been reviewed by Sutton (1970) and Sunderland & Sutton (1980).

The evidence produced in this study indicates that P.scaber has a preference for trees in the summer months. In the winter it can be found with other isopod species under logs and stones at the base of trees (O.asellus, A.vulgare, P.leavis) If all the species mentioned can shelter in the same place, their failure to do so on tree trunks must mean that they have a specific preference for certain habitats, which they occupy if available. There was no evidence of over-exploitation nor competition for food or predation. Evidence elsewhere in this research shows that isopods are not highly specific feeders and the need for a dark daytime refuge is common to them all.

Taking either of the two species, it can be said that it is common in the habitat which is most favourable to it, and less common in the ones which are less favourable. It could be exactly parallel with the performances of Tribolium confusum in the laboratory, where it has been shown that the population is higher under certain combinations of temperature and humidity than in others. Park (1940). One might assume that the greater the taxonomic distance between these ecologically similar animals, the less likely is the one to interfere with the other.

FEEDING TRIALS

Feeding Trials

Food Preference of Oniscus asellus and Porcellio scaber.

It is generally assumed that terrestrial isopods are detritus feeders (Paris, 1963, Raw 1967, Wieser 1986, Wallwork 1975), sometimes ingesting dead animals (Sutton 1972) and sometimes becoming coprophagous as a means of obtaining enough copper (Weiser 1966). Wieser (op cit) stated that P.scaber was unable to assimilate enough copper to optimise its level unless food contained about 1.2 μ g copper per milligram ash, or unless the copper supply was supplemented through coprophagy. There are some cases of cannibalism in laboratory cultures (Brereton 1957, George op cit) and others referred to by Paris (1963). Edney et al (1974) undertook laboratory studies which showed that isopods readily consumed several species of Drosophila.

Food of isopods may range from fresh plant material (Heeley, 1941; Paris & Sikora 1965) to dead litter and even decaying woody material (Paris 1963; Cromack 1967). Merriman (1976) showed that changes in food quality could cause changes in populations of Armadillidium vulgare

Terrestrial isopods are usually considered to be generalist decomposers.

Only Paris (op cit), Watson (1963), White (1968) and Rushton & Hassall (1983) have carried out studies to determine food preferences. Paris conducted laboratory experiments during daylight using common Californian grassland species of plants. Watson's work included exhaustive trials of woodland herb and tree species in Durham, England, both during the day and at night, and in both field and laboratory. For those foods most readily eaten he was able to list a table of preference by conducting laboratory experiments where the number of individuals feeding on each food was compared. Watson carried out feeding trials with the two species studied here and his results are therefore comparable. White (op cit) working with Trachoniscus rathkei, in Illinois found they had a strong preference for leaves of Asimina triloba, over two

species of Quercus and they maintained a positive copper balance by feeding on Asimina without resorting to coprophagy. Rushton & Hassell (1983) showed that A.vulgare had a marked preference for partly decomposed dicotyledonous plants from grassland heath over partly decomposed monocotyledonous plants.

In the present study food preference studies were carried out to determine which of the common potential foods available in and around the sampling site were preferred by O.asellus and P.scaber.

The investigations had three objectives which were to determine:

- 1) if the isopods settled differentially on the leaves of different species
- 2) the order of food preference of the two isopods in the laboratory under near natural conditions
- 3) the order of food preference between new and partly decomposed leaves.

Methods

O.asellus and P.scaber were collected in the vicinity of Spinney Hill woods and from under stones around the ha-ha brick wall, placed in containers and brought back to the laboratory. Approximately two hundred and fifty adults, all 14mm or more in length, of each species were used in feeding trials from July 1979 to January 1980.

All animals were fed on shredded carrot until orange faeces appeared. Shredded carrot was found to give bright orange faeces and was readily eaten. This was to ensure that there were faecal pellets produced of a different colour from those normally produced on a more normal diet. By first offering the marker food, then the natural food, followed by the marker again, all of the faeces produced from the supplied food could be easily recognised and collected.

In earlier trials (not reported here) the animals had been starved for 48 hours but Dunger (1958) criticised this method, previously used by van der Drift (1950) and Gere (1956), on the grounds that starvation could induce

feeding activity. Dunger's criticism may be valid as it is difficult to measure the parameters of consumption and rejection and thereby estimate assimilation if faecal material from ingested food is still being produced. Observations suggest that there was little increase in the rate of feeding in the first 24 hours after being placed on a food source. Further the feeding trials lasted seven days and initial voracity would be of little significance.

A series of crystalising dishes (15cm diameter x 7.5cm deep) were floored with damp glass fibre paper because woodlice will eat normal vegetable fibre filter paper (Watson 1963). The relative humidity in the chamber was maintained near to 100% using an inverted 5cm x 2cm tube filled with water standing in a small trough. Relative humidity was regularly monitored by examining pieces of cobalt thiocyanate paper taped to the side of each dish.

Freshly fallen leaves of all tree species that are common on the sampling sites were collected in early autumn, 1978, and placed in perforated fine mesh (64 μ m) nylon bags. They were returned to the litter, lightly covered with fallen leaves and left for one year. This was to ensure an ample supply of partially decomposed identified leaves in as near natural conditions as possible. A further supply of the same leaves was used immediately in the first food preference trial. The tree species used were Acer pseudoplatanus, Aesculus hippocastanum, Betula pendula, Fagus sylvatica, Fraxinus excelsior, Populus alba, Quercus robur, Salix chrysocoma and Ulmus procera.

Discs were cut from the leaves with a 2cm diameter cork borer, oven dried for 24 hours at 40°C and weighed on a micro balance. The leaf discs were then placed between filter papers and left immersed in distilled water for 24 hours to rehydrate to a more natural state. The leaf discs, one of each species, were set out at equal distances around the circumference of a circle in each dish. A small pill box was inverted in the centre of each dish to provide shelter. Shelters were considered necessary as George (1970) noted that without them P.scaber tended to remain feeding on the food all day, which is

contrary to their normal cryptic daytime habit of hiding.

Five adult specimens of one species were introduced into each container. Five replicates were used for each isopod species. All dishes were placed in an illuminated controlled environment room at 10°C and at 95% relative humidity which was considered to be as near natural conditions as possible. (11°C was the average temperature recorded for the year (Appendix A). A lighting regime of 10 hours darkness and 14 hours daylight, (Gro-lux lighting) was used to simulate field conditions.

The animals were allowed to settle in the choice chambers for three days. On the fourth day of the trial twelve hourly counts were made of the number of animals on each leaf species. The number of isopods settled on each food at each hourly observation was summed and divided by the number of replicates thus giving the mean number of isopod hours spent on each food.

The results are presented in Table 18.

Table 18

Results - Experiment 1. The number of isopods settled on each food species.

	O.asellus	Ranking	P.scaber	Ranking
Acer pseudoplanatus	3.75	4	4.56	3
Aesculus hippocastanum	12.25	9	12.12	9
Betula pendula	8.31	6	7.22	6
Fagus sylvatica	2.11	2	1.10	1
Fraxinus excelsior	3.62	3	4.43	4
Populus sp.	11.00	8	10.50	7
Quercus robur	1.46	1	2.11	2
Salix chrysocoma	7.50	5	6.25	5
Ulmus procera	10.00	7	11.75	8

Results Table 18

From these results it can be deduced that there is no significant difference in selection for settlement between the two species of woodlice as to tree species preferred. Both species of isopod settled more frequently on Aesculus hippocastanum, Populus alba and Ulmus procera whereas Quercus robur, Fagus sylvatica and Acer pseudoplatanus were least used. These results are confirmed by use of Spearman's Rank Correlation which has a value of 0.950 ($p < 0.001$).

Discussion

Some isopods counted on the food were not feeding but just appeared to be resting. Paris (1963) suggested that this should not affect results, for the animals should not settle more often on one potential food item than another if feeding is not taking place. Aggregation (see chapter 3) is, however, one of the most characteristic behaviour pattern of woodlice behaviour and has probably to some extent affected the results (Allee 1926, Gunn 1937, Waloff 1941, Cloudsley-Thompson 1956, Friedlander 1965, George 1970). Woodlice form large aggregations and these authors have carried out a number of behavioural studies concerned with this problem. For example Cloudsley-Thompson (op cit) showed experimentally that this behaviour results in a reduction of water loss and so may have survival value. More recently Takeda (1984) has shown that isopod faeces have an active aggregation pheromone which causes this gregarious behaviour. When isopods were desiccated, aggregation was usually intense. In optimum humidity, it was low. At still higher humidities it was unstable. Takeda further showed that resistance to desiccation was higher in the aggregated individuals in that, the lethal time was greater.

It is therefore suggested, that in the choice chambers where humidity is controlled, the results may be distorted by aggregation. A possible counter influence to aggregation is the disturbance caused by the combined effect of removing the feeding chamber lids every hour and the prolonged use of a torch

whilst counting, although a torch with a yellow filter was used and movement of the chambers were kept to a minimum.

The determination of the order of food preference of the two species.

At the end of seven days the discs from the last experiment were oven dried to obtain dry weight and the percentage of leaf discs eaten were obtained by subtracting this value from the initial weight. The results from each chamber were summed and divided by the number of replicates and expressed as the percentage of initial weight (fig 25 & 26).

Results

Fig 25 and 26 summarise these results.

Food preference can be deduced from these preliminary feeding trials. Preference was shown by both the species for Salix chrysocoma, Fraxinus excelsior and Acer pseudoplatanus whereas Fagus sylvatica and Quercus robur are virtually uneaten.

Both Q.robur and F.sylvatica were unpopular choices for eating and A.hippocastanum was ranked highest for settling and yet was one of the least eaten. The converse of this was Fraxinus excelsior which was minimally settled and yet was the second most popular as a food source. Watson (1967) recorded very similar results in his feeding trials.

Experiment 3. Determination of the food preference between fresh and partly decomposed leaves.

Choice chambers were set up as in Experiment 1 to determine if animals preferred fresh leaves or partly decomposed leaves, and to determine the amount eaten. Fresh and partly decomposed leaves from the same nine tree species were used in the trial. Freshly fallen tree leaves were used together with the leaves stored in nylon bags over the year. Leaf discs were cut and treated as

Fig. 25

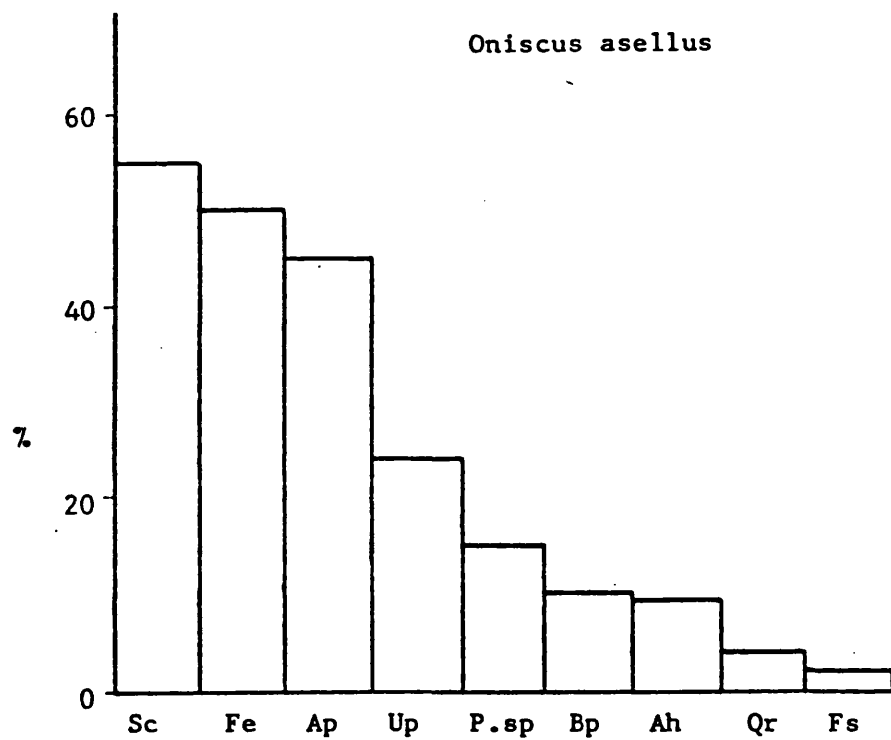
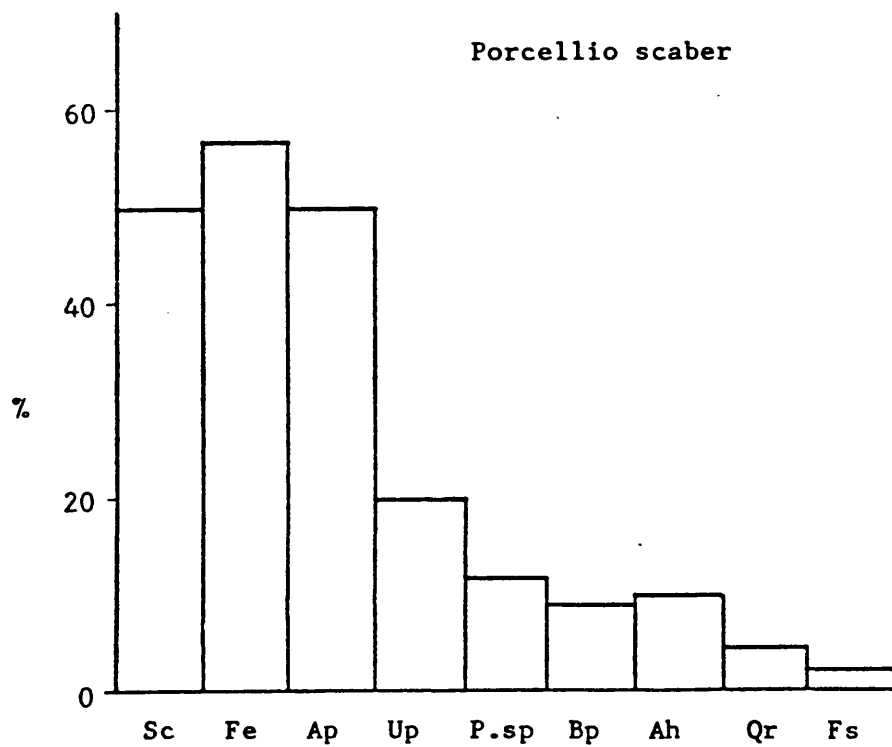


Fig. 26



Histograms show the mean % consumption by adults.

in experiment 1, weighed on a micro-balance and re-hydrated. The eighteen foods were randomly placed in a circle in the choice dishes. Five adults of one species of isopod were introduced into each chamber and five replicates were used for each species. Each day faecal pellets were removed from the choice chambers to avoid coprophagy. After seven days the leaves were removed, oven dried and re-weighed. The weight of leaves consumed was calculated for each dish, summed and divided by the five replicates to give the mean weight of each species consumed.

Results

Fig 26 and 27 show bar charts of the amount of fresh and partly decomposed food eaten by the two isopod species over a seven day period. This second food trial partially confirmed the previous experimental results but although the two species had similar preferences for food they consumed different quantities. Partly decomposed leaves of Fraxinus excelsior were much preferred to any other food source available with mean weights of 28mg and 25.3mg being consumed by O.asellus and P.scaber respectively. P.scaber has a preference for partly decomposed leaves whereas O.asellus has generally more equitable taste. The outstanding exception was Aesculus hippocastanum where partly decomposed leaves were greatly preferred whereas P.scaber ate this food the least. There were other minor variations in order of preference between the two species. O.asellus consumed freshly fallen leaves of Betula pendula whereas P.scaber showed a greater preference for Ulmus procera.

pH levels of the leaves of the nine tree species

In order to determine why certain leaves were preferred pH levels of the leaves of the nine tree species were calculated as this was considered to be a possible reason for isopod selection of foods.

OLD	NEW

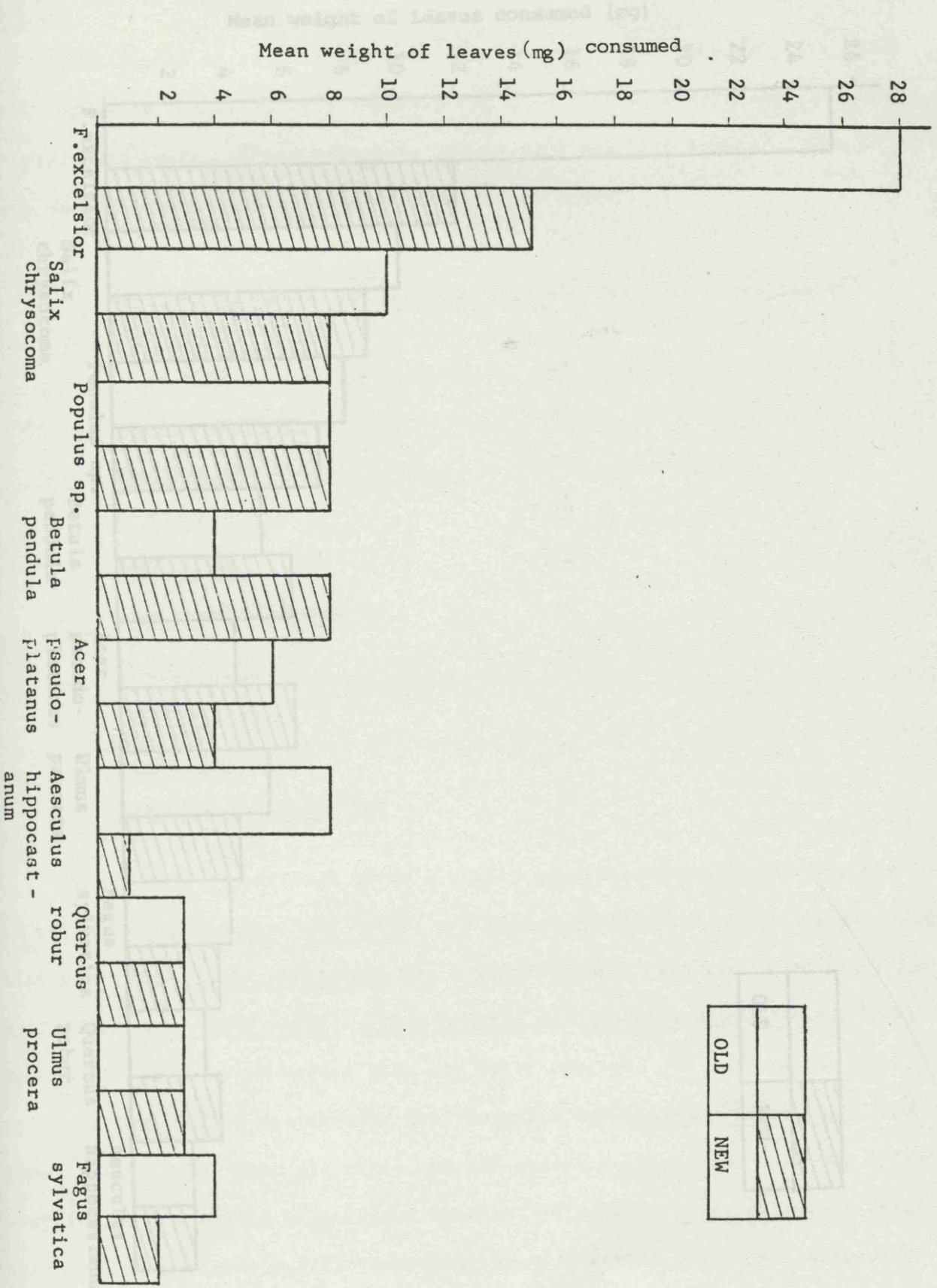
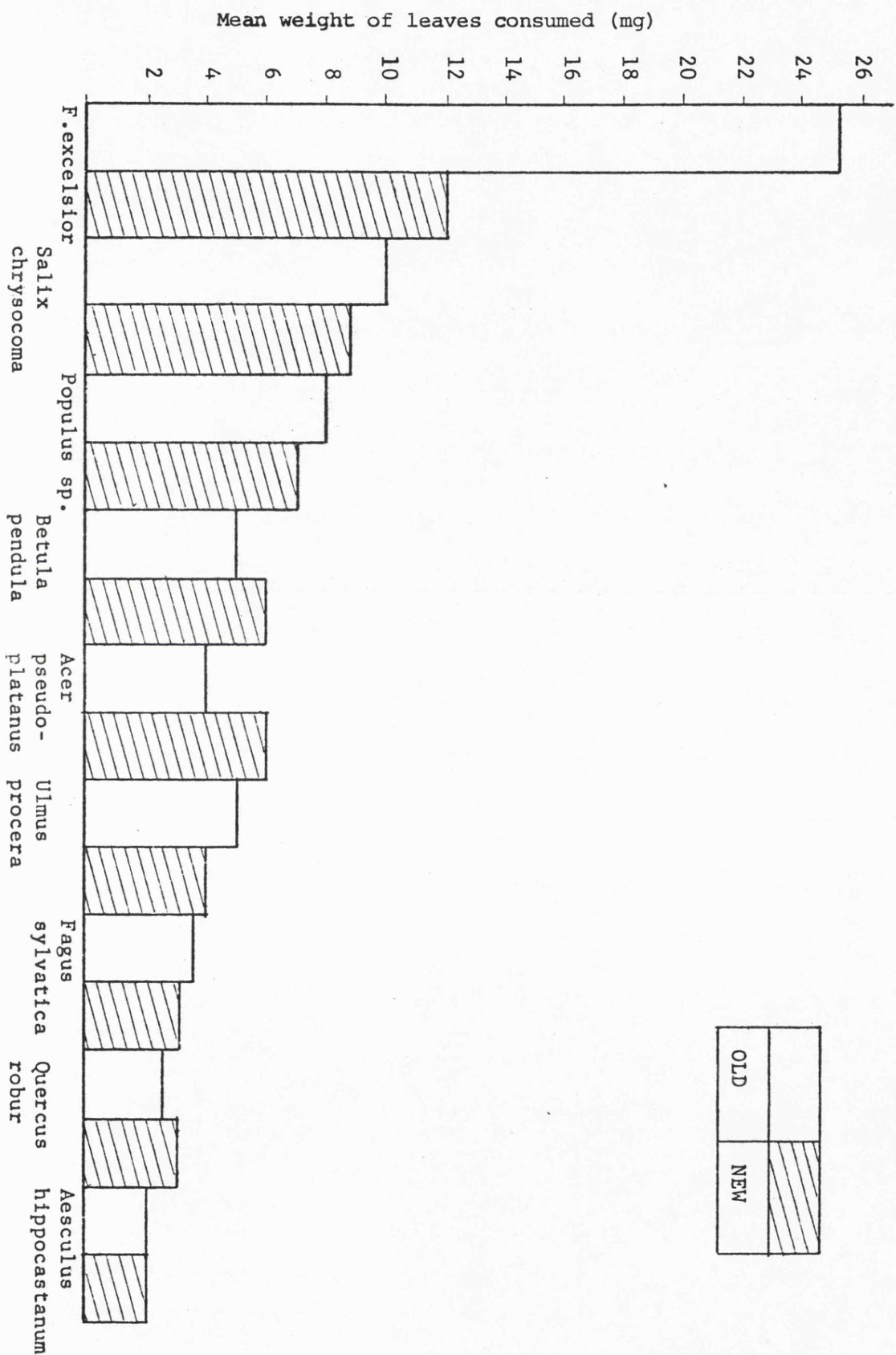


Fig. 27 Preferences of nine old and fresh leaves, October 1979 - *Oniscus ascellus*

Fig. 28

Preferences of nine old/fresh leaves - Porcellio scaber



OLD	NEW

Methods

Whole leaves of each of the nine tree species within the sampling sites were washed to remove surface deposits and then soaked in separate containers of distilled water. These were left for 14 days and then removed. The pH of each extract was measured using an electric pH meter.

Table 19 pH values of different leaves. (mean of 3 replicates)

<u>Leaf</u>	<u>pH</u>
<u>Salix chrysocoma</u>	6.96
<u>Fraxinus excelsior</u>	5.90
<u>Betula pendula</u>	5.79
<u>Populus sp.</u>	5.54
<u>Acer pseudoplatanus</u>	5.52
<u>Fagus sylvatica</u>	5.42
<u>Quercus robur</u>	4.77
<u>Ulmus procera</u>	4.75
<u>Aesculus hippocastanum</u>	4.74

An analysis of variance shows a highly significant difference between the pH values of the leaves. (F 45.06; $p < 0.001$). Application of a multiple range test shows that Salix chrysocoma has a significantly higher pH than all other species while Quercus robur, Ulmus procera and Aesculus hippocastanum had significantly lower pH values than any other species. To some extent this reflects the feeding preferences but the value for Fraxinus excelsior although numerically higher than all other species except S.chrysocoma does not differ significantly from the majority of species. Similarly Fagus sylvatica which is again not significantly different from the majority of other species proved amongst the three least popular species in the feeding trials.

Quercus robur and Fagus sylvatica have high tannin content as contrasted

with Fraxinus excelsior and Acer pseudoplatanus which will also make them unpalatable (Sutton 1972). Those with high tannin contents are often left by woodlice until after tannins have been removed by leaching (Sutton, op cit).

As well as moisture and temperature, the pH of the substrate and litter has a marked effect on the structure of animal communities (Mason 1976). Communities in mor humus with a low pH, are dominated by Acari and Collembola, with few insect larvae, while Oligochaeta and Isopoda are scarce. Insect larvae become important in transition moders while in mulls, with neutral or alkaline pH, Oligochaeta and Isopoda are abundant, with Acari and Collembola less important. Gastropods, with their high calcium requirements for shell formation, are only common in alkaline humus and soil. (Wallwork (1975).

Discussion

These results indicate that where F.excelsior is available both species utilize it as the principal food source but in its absence other leaves are accepted. This is confirmed by the work of Paris (1963) who showed that A.vulgare had distinct preferences for different foods especially dead leaves of the herb Picris echioides (Asteraceae) but could utilize a variety of foods.

The results from Experiment 3, show a marked preference in both species for partly decomposed leaves as compared with newly fallen leaves. Dunger (1958) reported a similar result, with seven of the nine leaf species he offered to Isopods being more acceptable in the partly decomposed state. This may reflect changes in chemical composition or the development of a microbial flora or both.

Hassell (1976) similarly found a preference for decayed leaves, in his study of P.muscorum, and concluded that the extent of decay probably had a greater influence on the order of preference than did inter-specific differences. Partly decomposed leaves were preferred to freshly

fallen ones which is also in agreement with Healey (1963) and Brereton (1956).

There is, however, abundant evidence that some terrestrial isopods are more catholic in their diet. A.vulgare is more omnivorous and has been reported to eat dead leaves, leaf mould, fungi and dead animals, Paris and Pitelka, 1962 (op cit) and Al Dabbagh (1976) also suggested that A.vulgare may be a grazing animal, as well as a scavenger, in grassland. This could certainly be the case with P.muscorum which were frequently found amongst grass tussocks (pers obs). Brereton (1956) suggested that P.scaber grazed on the lichen and thus avoided competition with its close relation O.asellus. Thus when dead plant material is present it seems to have been preferred but at least some species of isopods can adapt to feeding on fresh leaves, fungi algae and dead invertebrates including its own kind. George (1970) found that two species of Porcellio appeared to utilise what was available. On a limestone quarry the only apparent food was the lichen S.chlorococcum and bird faeces, both of which were readily eaten by P.spinicornis. On tree trunks P.scaber ate S.chlorococcum and the moss Mnium nordeum which was found at the base of trees.

Food preference can be related to morphological differences such as roughness and toughness of the leaves. Q.robur and F.sylvatica have much thicker cuticles compared to F.excelsior. U.procera leaves have a rough upper surface compared to S.chrysocoma and F.excelsior. A.hipocastanum has a round surface but a relatively thin cuticle and therefore decomposes more rapidly; this is possibly a reason why old leaves are preferred to fresh by O.asellus. Differences in palatability between leaves may depend on morphological characteristics, such as the hairiness or thickness of the epidermis. Chemical differences, particularly the polyphenols, are important (Mason 1979). Polyphenols gradually accumulate in leaves through the growing season. They cause precipitation of proteins in the leaves and

may also interfere with the functioning of digestive enzymes. Fagus and Quercus leaves have more polyphenols than the other species used in this study and this is a possible reason why they are eaten less readily by woodlice (Sutton 1972). Within the litter layer polyphenols are gradually leached out and are then degraded by micro-organisms, making the leaves more palatable. After the initial leaching period plant litter consists mainly of structured polysaccharides, which are difficult to break down, and many detritivores as a consequence have low assimilation efficiencies. Q.robur and F.sylvatica have high tannin content as contrasted with F.excelisior and A.pseudoplatanus which will also make them unfavourable, (Sutton op cit): Those with high tanin contents are often left by woodlice until after tannins have been removed by leaching. Wallwork (op cit)

It appears from these results that quantity is not a limiting factor in controlling population as food was abundant but quality of food is important to isopods and although food preferences occur they can eat a wide variety of fresh and partly decomposed materials and this adaptive ability probably contributes to their successful life on land.

PRODUCTION STUDIES

Production Studies

The present study attempts to look at the role of Oniscus asellus, and Porcellio scaber as decomposers in the detritus food chain. Petrusiewicz & Macfadyen (1970) proposed the following terminology for the components of energy budgets in whole ecosystems, species populations, and individuals.

$$\begin{array}{lcl}
 \begin{array}{c} \text{C} \\ \text{Energy of food} \\ \text{consumed} \end{array} & = & \begin{array}{c} \text{P} \\ \text{Energy of new} \\ \text{tissue produced} \end{array} + \begin{array}{c} \text{R} \\ \text{Energy of} \\ \text{respiration} \end{array} + \begin{array}{c} \text{FU} \\ \text{Energy of} \\ \text{rejecta} \end{array} \\
 \\
 \begin{array}{c} \text{A} \\ \text{Energy} \\ \text{assimilated} \end{array} & = & \begin{array}{c} \text{P} \\ \text{Energy of new} \\ \text{tissue produced} \end{array} + \begin{array}{c} \text{R} \\ \text{Energy of} \\ \text{respiration} \end{array}
 \end{array}$$

These recommended symbols are used throughout this account.

Quantification of these expressions in conjunction with biomass data permits the energy budget, in terms of energy flow per unit area of habitat per unit time, to be calculated.

Several attempts have been made to solve the equation for whole ecosystems e.g. (Odum & Odum 1955; Odum 1957) It is extremely difficult, however, to make all the measurements necessary for a whole system approach. Most researchers have restricted their study to the evaluation of the whole equation for single food webs, populations, or the study of one parameter of the whole equation in depth. The individual parameter most often studied is R, for terrestrial invertebrates, as it represents the greatest proportion of total energy flow. By these methods a synthesis of the total energy flow of an ecosystem can be made (Watson 1966; Hassall 1977).

The present study attempts to solve the whole equation for the two isopod species O. asellus and P. scaber. Due to lack of sophisticated equipment some components of the equation are determined more exactly than others, and to complete the equation, other workers' reports are quoted in places. For a complete energy flow study the rates of assimilation, respiration, body and reproductive growth together with the joules they represent must be determined.

Measurements of populations and biomass will enable the above data to be expressed in terms of energy per unit area of habitat per annum.

The data presented by Saito (1965) for the isopod Ligidium japonicum, Watson (1966) for Oniscus asellus and Porcellio scaber and Hassall (1976) for Philoscia muscorum are used to compare the results presented.

Respiratory studies

There is a very close link between respiration and transpiration, because the moist surface needed for oxygen uptake and carbon dioxide loss makes transpiration inevitable. In primitive isopods, 80 per cent of water loss occurs over the body surface and only 20 per cent across the pleopod gills. In higher forms, there is a progressive tendency for respiration to be concentrated in the gill region (Sutton 1972). These higher species lose far less water than the more primitive types and if, as seems reasonable, one assumes that oxygen consumption is just as great, it follows that these advanced forms in respect of water-loss, are more efficient at gas exchange. This efficiency is attributed to the presence of pseudotracheae, Sutton (op cit) with the implication that because these have a large enclosed surface with one small external opening, they lose less water than an open surface like a gill. As Edney (1968) has pointed out, a small exterior opening of itself will only slow up the rates of diffusion of oxygen and water, not alter them relative to each other. The point of a small external opening is that it can be closed or narrowed to cut down water-loss when oxygen requirements are not maximal, as for instance when the animal is at rest. There is an active oxygen gradient which will produce a constant income of oxygen to the animal. The evaporation of water is passive out-flow dependent on such factors as external R.H., so long as there is no respiratory activity. The efficiency of the insect tracheal system in conserving water rests with the spiracles which close in

such a situation. The problem with pseudotracheae is that no researcher has yet found any closing mechanism, although it is likely the air-flow over the pleopods is substantially reduced when the body is pressed close to the ground in plattened types like Oniscus, or when the animal is rolled up, as in Armadillidium.

Warburg (1984) discusses these eco-morphological strategies which are correlated to the climate of the test sites under consideration. Both species studied here are grouped as epigeon "clingers" which are slow moving flat and broad and these are adaptations for survival from both predators and drought. Whatever the mechanism, woodlice with pseudotracheae are much more efficient at oxygen uptake in dry air than those without, so clearly pseudotracheae are a valuable adaptation (Sutton 1972). It is therefore interesting to note that P.scaber has pseudotracheae but O.asellus does not. (see page 22)

Until recently it was thought that isopods, along with amphipods, had no respiratory pigment in the blood, but it is now known that haemocyanin is present. It has not been observed before as the quantities are too small to show colour and sensitive techniques were needed to detect it (Wieser 1965 b). The respiratory function of both fluid and pigment is more important in those advanced species where oxygen uptake is concentrated on the pleopods. These animals clearly place less reliance than primitive types on diffusion to the tissues from the body wall. Sutton (op cit) states that larger species have a more effective transport system than small species. The pattern of oxygen uptake is of some significance because it reflects the amount of energy used in general body metabolism as well as in various forms of activity such as locomotion, feeding and breeding. Wieser (op cit) found that locomotory activity doubled respiratory rates in P.scaber and A.vulgare, while the rates also increased sharply in spring with the onset of growth and gonadal development. Phillipson & Watson (1965) also found that breeding activity causes high oxygen consumption and that size is an important factor, juvenile

animals having higher respiration rates, relative to size, than others except breeding females.

Ecologists have used respiration studies for two major reasons. Firstly, respiration is measured in order to assess one of the parameters in the formation of an energy budget. Secondly, it has been used as a convenient measure of metabolic activity in order to assess or complete the role of populations in ecosystem processes (Petrusewicz 1970). The measurement of respiratory activity however, raises a number of practical problems.

In order to estimate the respiratory activity of a field population, it is necessary to know the respiratory rate of all the life stages or size classes in the population, and its relation to temperature and other environmental factors. In addition, detailed information of population density and size class structures is required. This clearly involves either a large number of determinations of respiratory activity or the acceptance of an overall population estimate in which a number of assumptions are made concerning the relationship between respiration rate and weight and respiration rate and temperature (Phillipson, 1967). While it is profitable to explore the latter approach, there are too few data at the present time on which to base an objective estimate of their reliability and it would be necessary to obtain more detailed estimates in order to make this assessment. It is possible, however, to build up most of the energy equation using Watson's 'best estimate method' (Phillipson 1962).

Another problem is to relate respiratory measurements to field conditions. There is no immediate answer to the problem of whether an animal respire in an enclosed vessel at the same rate as it does in the field. Problems concerned with the effect of change in temperatures on the rate of respiration can be overcome however by giving animals time to acclimate to laboratory conditions

or by running experiments at temperatures at which animals were collected in the field.

Methods

The isopods used for determination of oxygen consumption rates were collected from the field at Moulton Park and maintained in the laboratory under three different temperature regimes of 5°, 10° and 15°C. This was done in programmable temperature cabinets with 0.9m³ capacity. The cabinets had an operational range of -5°C to +40°C. The temperature control inside the cabinet was within $\pm 1^\circ\text{C}$.

The adults of both species (14mm) were kept in small perspex boxes with an abundant supply of leaf litter to a depth of 5cm for 48 hours in advance of the experiments being carried out.

Respirometry.

A Gilson differential respirometer was used (Anachem Ltd) which was operated in a constant temperature room. The main body of the respirometer consisted of 20 reaction vessels each of which was connected by Tygon tubes to its own manometer. The reaction vessels were submerged in a water bath which was maintained at a constant temperature ($\pm 0.02^\circ\text{C}$). The effect of the ambient temperature oscillations on the air volume in the exposed Tygon tubes, and hence on the observed respiration rates was reduced by operating the respirometer in a room maintained at the same temperature. Precautions were also taken to reduce the effect of heat produced by the respirometer stirring motor and refrigeration unit on the exposed Tygon tubes of the respiration vessels (Adcock 1975).

Gilson operating procedure.

1. An hour was allowed for the water bath to equilibrate at the desired temperature.
2. A total of 20 reaction vessels each of 7.5cm³ volume and with a centre well was used. A small piece of filter paper (Whatman No.1)moistened with 5% KOH solution were placed in the central well to absorb CO₂. An adult isopod was placed in each, and the reaction vessel connected to the system. A total of 14 isopods, 7 of each species, was measured in each run.
3. Six vessels were used as controls and they were positioned at the four corners of the bath with two in the centre. (i.e. vessels 1, 3, 10, 11, 19 and 20) each control vessel contained KOH moistened filter papers to absorb CO₂ but was without an animal.
4. The micrometers were set at the 100 μ l mark to allow for possible negative readings, and the system allowed to equilibrate for one hour before it was closed to the atmosphere and the measurement of oxygen uptake commenced. A reference flask was fitted to the apparatus when the respirometer was switched on one hour before the experimental flasks were connected. The reference flask was partially filled with a volume of distilled water at the ambient temperature, so that the remaining volume of air in the reference flask was equal to the total air in the reaction flasks.
5. Readings of volume change on the micrometers were made every 30 min . The oxygen consumption was measured over a 6 hour period.
6. At the end of the run, the animals were removed from the vessels and their live weight determined on a micro-balance, they were then oven dried for 24 hours and their dry weight measured.

Calculation of oxygen uptake rate.

The mean change in gas volume at each reading of the control flasks was used to correct the readings of gas volume change of the reaction vessels. The corrected volume change or oxygen uptake was then plotted against time for each animal. The oxygen uptake with time was linear and the slope of the fitted line calculated by regression analysis was used to calculate the rate of oxygen uptake in $\mu\text{l h}^{-1}$. The calculations were undertaken using a RML 380Z computer. Determinations of oxygen consumption of individual isopods were made at all the temperatures studied using oxycalorific equivalents of $20.197 \text{ J.ml}^{-1}\text{O}_2$.

Results

Respiration rate and live weight

Live weight of individuals of O.asellus and P.scaber were used to investigate respiration rate and metabolic rate. It was preferred to dry weight because the water content of the animals was considered to be important. However, dry weights were calculated using a micro-balance after the respirometry experiments and were found to be 31.0% and 29.2% respectively of wet weight. This compares well with Watson (1966) who found mean water contents for the two species of 68.99 and 67.85 respectively.

Correlation coefficients and regression lines for oxygen consumption against dry weight showed that O_2 consumption increased linearly with dry weight. Neither at 5°C or 15°C were regression coefficients significantly different from zero. and therefore these are presented as O_2 consumption per ml per hour based on the summation of all values determined. The values for 10°C are presented similarly but in both cases the correlation coefficients were significant.

As only 4 : 12 give a good fit for O_2 consumption being linear against dry weight no graph was drawn. More replicates are needed

in order to gauge this more accurately. Therefore, the mean temperature of 10° C was used for respiration of O.asellus as 0.2011 $\mu\text{l/h}$ per unit mg dry weight and 0.2606 $\mu\text{l/h}$ per unit mg dry weight for P.scaber (Table 20).

O₂ Uptake at three temperatures in both species

Table 20

	5°C	10°C	15°C
<u>O.asellus</u>	0.066 $\mu\text{l/mg/h}$	0.2011	0.4564
<u>P.scaber</u>	0.136 $\mu\text{l/mg/h}$	0.2606	0.4619

Both Watson (1966) and Al-Dabbagh (1976) found live weight was linearly related to dry weight over the complete size range. The prominent features of these researchers analyses were the increase in respiration rate with live weight and the decrease in metabolic rate with increasing size, both observed at all the temperatures studied. The sexes of individuals were not distinguished and therefore no differences were observed between male and female rates. Watson (op cit) showed gravid females did not give high rates of oxygen uptake when compared with non-gravid females of similar size. The present study shows a considerable rise in respiratory rate with temperature with P.scaber having a higher respiratory rate at all temperatures. This was to be expected as this isopod is the more active animal in both laboratory and field observations (see Chapter 4)(Edney and Spencer 1955 ; Wieser and Oberhauser 1984). Edney (1964) measured the weight-specific oxygen uptake in both A.vulgare and P.laevis for individuals acclimated to 10°, 20°, and 30°C . He found that isopods acclimated to 10°C and respired at the higher temperatures had a higher rate than animals acclimated to either 20°C or 30°C.

The dependence of respiration rate on body size is well established. Generally, respiration does not increase linearly with body weight,

but with a power of a fraction less than one. This is often attributed to the disproportionate increase in inert supporting tissues which occur with increasing size.

As the mean annual temperature for the sites studied was 11 °C the results from the respiration experiments at 10°C are taken as the best approximation. These are 0.2011 $\mu\text{l mg}^{-1}\text{h}^{-1}$ for O.asellus and 0.2606 $\mu\text{l mg}^{-1}\text{h}^{-1}$ for P.scaber and are used to calculate population metabolism. There were no significant differences in respiratory rate for animals in the dark or light in spite of the fact that woodlice have a nocturnal pattern of activity (see pages 69-74).

Rao & Bullock (1954) analysed data from various sources of arthropod research and concluded that the temperature coefficients (Q_{10}) commonly increases with increasing size in poikilotherms within physiologically normal temperature ranges. As in the present study, the experimental temperatures were within the field ranges normally encountered by the organisms concerned during the season when the respirometry measurements were made.

Rao et al (op cit) found that the temperature response indicated that small animals had larger increments in respiration rate with increasing temperature than larger animals over the temperature range 5° to 15°C. In most crustaceans, the respiration rate was directly proportional to two-thirds the power of their live weight.

This surface law was originally propounded by Sarrus and Rameaux (1939), (cited by Brady 1945) , who showed that Armadillidium vulgare had a metabolic rate proportional to its surface area. However, Raw (1967) gave a higher value for 15 species of forest floor arthropods including three isopods, A.vulgare, A.nasatum Budde-Lund, and Cydisticus convexus (De Geer).

In earlier studies undertaken (George 1970) respiratory rates of adult O.asellus and P.scaber were recorded once a month over one year. This is considered to be essential as populations, breeding, feeding and climate all vary with time.

Methods

Adults (14mm) of both species weighing 20mg or above were collected in the field, allowed to acclimate for 3 h, and then placed individually into the respirometer and were not fed in the laboratory or in the apparatus.

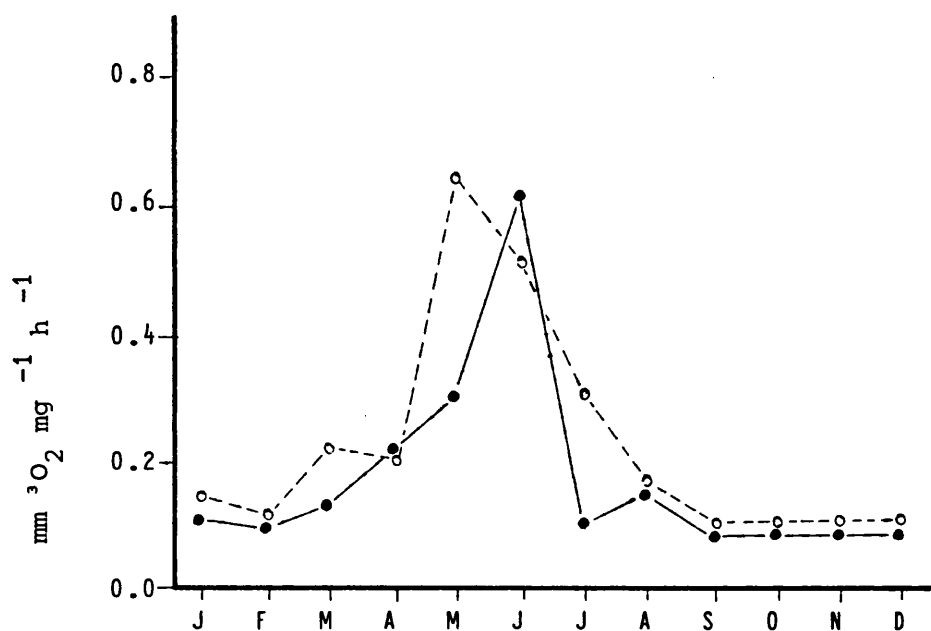
The respirometer used was the continuously recording one described by Phillipson (1962). Oxygen consumption rates were made at 15°C and the humidity of the metabolism chamber was kept above 90% RH by means of a strip of damp filter paper 3 x 1cm. The record for each individual was continuous over a period of 48h but the rates of oxygen consumption were calculated from the results obtained for the 24h period between 6 and 30 hours after the experiment began.

Results

Fig. 29 shows the monthly mean respiratory rate per unit weight between the two species of isopods studied over one year.

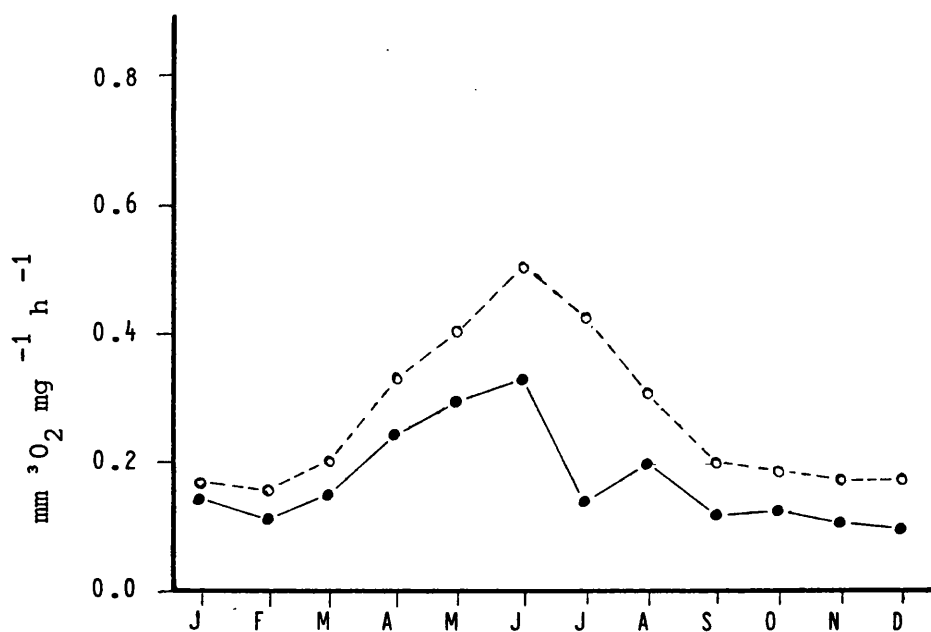
Consideration of the respiratory rates of adults as seen in Fig.29 shows that differences do occur from month to month and also between summer and winter. Much of the seasonal differences can be accounted for on the grounds of reproductive physiology because breeding itself is seasonal. The high rates for April females and May males in O.asellus and June females and males in P.scaber were probably due to a higher metabolic activity connected with gonad development. June and July saw a majority of early stage embryos in both species and these would be active metabolically and therefore, high respiratory rates would be expected. By September, young had been released from the brood

Fig. 29



Seasonal differences in the mean respiratory rate per unit weight of individuals of Oniscus asellus which exceeded 20 mg live weight,

Females ○---○ and Males .—.



Seasonal differences in the mean respiratory rate per unit weight of individuals of Porcellio scaber which exceeded 20 mg live weight,

Females ○---○ Males .—.

pouches and the respiratory rates had returned to that of January-February. These explanations of seasonal variations are in keeping with those of Phillipson (1965) with O.asellus.

One can criticise the above methodology in that animals should be acclimated to laboratory conditions before being placed in the respirometers and 15°C does not reflect the true field situation. Similarly, as discussed later, all stages of the life cycles of these animals should be measured in order to gain an accurate estimate of the annual respiratory metabolism of a species population.

Population respiration

From the foregoing data, an estimate of the total respiration of O.asellus and P.scaber for the year can be made. This can be done by detailed computation taking into account the average population density at each sampling time, changes in population size class structure with time, respiratory rate in relation to size, changes in this respiration rate caused by temperature and daily temperature changes in the field throughout the year.

This term was first used by Phillipson (1962) in reference to the mean energy expenditure of a species per unit weight per unit time, calculated from laboratory respiration data covering all life stages. Phillipson (op cit) further suggested that this best estimate could be used to estimate the annual energy loss due to respiration of a population by using the mean biomass of the population. However, as this part of the research did not include all these details, Phillipson's (1962) 'best estimate' methods were employed whereby the mean energy expenditure is calculated from laboratory respiration data covering all life stages. Phillipson (op cit) further suggested that this best estimate could be used to estimate the annual energy loss due to respiration of a population by using the mean biomass of the population. Phillipson and Watson (1965) estimated the annual respiratory metabolism of O.asellus by

calculating the weight specific oxygen consumption, at the mean field temperature, of an individual corresponding to the mean weight of the population at each sampling time. Thus the oxygen uptake per mg per unit time was known and by multiplying by the mean biomass per unit area, it could be converted to oxygen uptake per unit area per unit time. These are the methods employed here and Table 20 shows rates of respiration and the energy equivalents compared with other researchers. These data are used in Tables 32-33.

An alternative method of studying energy flow is the application of energy flow data obtained for individual size classes to populations where the individual size class composition is known.

This method was pursued by Saito (1965), Hassell (1976), and Al Dabbagh (1976) on Ligidium japonicum, Philoscia muscorum and Armadillidium vulgare respectively. All were able to distinguish age classes and the number of eggs produced by the population. Survivorship curves for the natural population, derived from the number of eggs produced, were drawn on the basis of population density and monthly age structure. These survivorship curves coincided with the Type II curve of Deevey (1947). Thus the mortality from one breeding season to the next was assumed to be constant. The mean growth rate of individual per unit time was calculated as the difference between consecutive mean weights for the year group in each sample. The decrease in numbers per unit time was calculated from the survivorship curves. Thus the researchers were able to measure population growth and estimate changes in population size. Measurement of respiration rate at field temperatures and the determination of calorific values of the species made possible the calculation of energy flow through the population in terms of $\text{K.cal m}^{-2} / \text{annum}$.

Discussion

Many factors are known to affect the respiration rate of individual animals, Petruszewicz (1970). One of the important factors certainly influencing isopod respiration is moulting. Wieser (1962) demonstrated a marked increase in isopod metabolism at the time of moulting, while Edney (1964), working with Porcellio laevis, showed that standard metabolic rate fluctuated irregularly from day to day before the posterior ecdysis, peaked during the intramoult period, and then it declined rather irregularly to the intermoult level. Generally, the moulting cycle is a continuous process, and oxygen uptake does not fall between moults to a constant low level, but rather follows a u-shaped curve however, in T.terricola, Workman (1978) showed that the respiration rate varied with the moulting cycle, and that the rate at moulting increased by 1.5 at 15 C. Therefore, individuals of the two isopods studied which were observed to be in ecdysis were not included in the data analysis since they exhibited a marked increase in respiration rate over non-moulting animals of similar adult size. However, the above needs to be noted in future holistic research of isopods. Gravid females were not considered although they also show higher respiratory rates in the presence of young (Phillipson & Watson 1965). This conflicts with Al-Dabbagh (1976) who found no differences.

Nutritional level is another factor affecting the respiration of land isopods, (Wieser 1963, 1972). The animals used in the present studies were cultured with excess food, as found in the habitats collected; thus it was assumed that starvation did not occur and consequently any effect on the respiration level would be minimal.

In recent work on P.scaber, Newall et al. (1974) showed a well defined time sequence in oxygen consumption: an active rate obtained in woodlice subjected to maximal disturbance of food presentation, handling and light; then a series of excited rates after initial exploratory activity had ceased;

followed by a standard rate which was achieved after 2 - 3 hours equilibration in the respirometer. No evidence of such changes in respiratory rate for the two isopods studied here was found, and no distinction could therefore be made. The measured rate was that normally occurring between 1 - 6 h after equilibration. The definition by Newell et al (op cit) of three levels of respiratory activity is accepted, the rates of oxygen consumption measured in this study were a mixture of the excited and standard rates, and may partly account for the variation obtained. Furthermore, the applicability of the mean respiration rates, obtained in these experiments, to field conditions becomes more realistic since they may not be strictly standard rates.

Table 20

Rates of oxygen consumption in terrestrial isopods.

Species	Rate of O ² consumption		Reference
	$\mu\text{l g}^{-1}\text{h}^{-1}$	$\text{Jg}^{-1}\text{d}^{-1}$	
P.scaber	151-347	72.48-166.56	Newell (1974)
P.scaber	134-260	64-125	Wieser & D.Ber Hauser (1984)
P.scaber	83-305	40-146	Wieser (1962)
P.scaber	200 \pm 7	96	Edney & Spencer (1955)
P.scaber	260	125	This study
O.asellus	115-684	55-328	Phillipson & Watson (1965)
O.asellus	197 \pm 8	95	Edney & Spencer (1955)
O.asellus	201	97	This study.

Data from the literature were converted to energy consumption on the basis of $1\text{ml O}_2 = 20\text{J}$. After Wieser (1984)

Table 21

Rates of energy assimilation in terrestrial isopods.

Species	Rate of assimilation		Food	Reference
	mg dw	$\text{g(fw)}^{-1} \text{d}^{-1}$ Joules		
<i>P.scaber</i>	12.6	233	Betula decayed	Hassall & Rushton (1982)
<i>P.scaber</i>	12.9	240	Betula freshly fallen	
<i>P.scaber</i>	9.0	165.7	Mixed decayed	This study
<i>P.laevis</i>	19-15.5	185-287	Betula over- wintered	Dallinger & Wieser (1977)
<i>O.asellus</i>	3.8	70	Larix	Debry & Lebrun (1979)
<i>O.asellus</i>	13.7	253.0	Mixed decayed	This study
<i>A.vulgare</i>	12.3	227	Astragalus danicus standing dead.	Rushton & Hassall (1983)

Data from the literature were converted to ash-free dry weight, assuming a ratio of ash-free dry weight to be 0.84 and to energy, taking lg ash-free dry weight = 22J (Allen et al., 1974) Furthermore, all data were extrapolated to 20°C assuming a Q_{10} of two. The values shown are either mean values of ranges representing twice standard deviations. After Wieser (1984).

Studies of the effects of temperature on oxygen consumption of invertebrates have taken three main experimental approaches (Newell et al 1974).

- a) The measurement of the rate of oxygen consumption of animals after minimal equilibration time at a variety of exposure temperatures directly after collection from their natural environment (acute measurement relating to natural conditions).
- b) The same type of measurement made on groups of animals acclimated under laboratory conditions to a series of different temperatures (acute measurements allowing the influence of thermal acclimation to be taken into account).
- c) Animals acclimated to a variety of temperatures and measurements made at these temperatures.

Using the second experimental approach, Newell et al (op cit) found no significant difference in metabolic rate of groups of P.scaber acclimated to four different regimes at any of the exposure temperatures. In the present study the experimental approach used is similar to type (b) since measurements were made at three different temperatures.

The 'best estimate' of respiration metabolism for O.asellus and P.scaber are $4.826 \mu\text{l O}_2 \text{ mg}^{-1} 24 \text{ h}^{-1}$ and $6.254 \mu\text{l O}_2 \text{ mg}^{-1} 24 \text{ h}^{-1}$ respectively are similar to Phillipson and Watson (1965) for O.asellus. Their value was $4.992 \mu\text{l O}_2 \text{ mg}^{-1} 24 \text{ h}^{-1}$ at a rather high annual mean temperatures of 16°C . However, Al Dabbagh (1976) recorded a much lower figure of 1.88 and $1.95 \mu\text{l mg}^{-1} 24 \text{ h}^{-1}$ at 11.17°C and 11.62°C for the two years at Weeting Heath working with A.vulgare and with all size classes as compared with the present study using adults only, which possibly account for the difference.

The 'best estimate' of respiratory metabolism for O.asellus and P.scaber was converted to energy units. (See Tables 20, 31 and 32)

Organisms have to achieve some kind of equilibrium between energy input and output. For 73 populations of non-insect invertebrates, Humphreys (1979) has calculated that of food energy assimilated (A) about 77% is used for maintenance (R), the rest being distributed amongst excreted energy (U) and production (P). Considering the range of assimilated energy as that summarised in Table 21 one would expect mean rates of respiratory energy of the order of $200 \text{ Jg(fw)}^{-1}\text{d}^{-1}$ with an approximate range from 70 to $300 \text{ Jg(fw)}^{-1}\text{d}^{-1}$. However, the data accumulated in Table 20 shows that respiratory rates measured in terrestrial isopods mostly fall short of this expectation.

The usual procedure in the determination of oxygen consumption is, first, to acclimate the animals to laboratory conditions and then to let them settle down in the respirometers until they have become quiescent. The resting rates in adult isopods varies between 100 and $150 \text{ ul O}_2 \text{ g}^{-1}\text{h}^{-1}$ which corresponds to $50 - 70 \text{ Jg}^{-1}\text{d}^{-1}$. But even active isopods Newell, Wieser and Pye (1974) consume only $140 - 170 \text{ Jg}^{-1}\text{d}^{-1}$, too little if the highest rates of energy uptake are taken into account. In only one paper have much higher rates of oxygen consumption, up to $320 \text{ Jg}^{-1}\text{d}^{-1}$, been recorded in a species of isopod. (Phillipson & Watson 1965). In this case specimens of Oniscus asellus were collected in the field and put into respirometers without a period of acclimation.

The conclusion one may draw is that the usual experimental procedure leads to an underestimation of the cost of maintenance of terrestrial isopods. The large range of variability in the rates of energy absorption must be matched by an equally large range of variability in the rates of energy dissipation. (Wieser 1984).

We may thus visualise the macro decomposers as feeding on a wide variety of organic materials, adjusting the rate of oxygen consumption to the rate of energy uptake. This complex series of adjustments may cause periods when animals are either hypo-or-hyper-phagous (see Wieser 1965a).

The rates of ingestion, egestion and assimilation for the two isopods O.asellus and P.scaber.

To obtain accurate information for the assimilation of food, discs of carrot were again used as a marker as described previously. By first offering the marker food, then the preferred food, followed by the marker again all of the faeces produced from the amount of preferred food consumed could be easily recognised and collected.

Methods

Adult individuals of both species were collected from the sampling sites as previously described and placed in feeding chambers and allowed to feed on carrot discs until orange faecal pellets were produced, when it was assumed that all faecal pellets from food consumed before capture had been voided. 40 further feeding chambers were set up with four most popular decomposed leaf disc samples as described earlier. Five replicates for each species and food source were considered sufficient to give accurate measurements of faeces production. For each food two 2cm discs taken from the same leaf were prepared. Only one disc of each pair was provided per chamber; the other was oven dried and weighed as a control. One adult of one species were placed as before in the chambers. The live weight of each individual animal was determined before each experiment. Black faecal pellets were collected every 6 hours over the week to ensure none were refected. At the end of the week remaining food was removed from each chamber and carrot discs introduced. The experiment was completed when the first orange faecal pellet had been produced. The food remains and all the black faeces from each chamber were oven dried separately and weighed. The live weight of each animal was determined. Assimilation efficiency was calculated as a percentage of the food ingested according to the formula:-

$$\frac{\text{Dry weight assimilated}}{\text{Dry weight ingested}} \times 100 = \% \text{ assimilation}$$

The dry weight of food ingested by each group of animal was calculated by the difference in dry weight between the control discs and food remains at the end of the experiment. The dry weight of food assimilated was calculated by the difference in dry weight of the food eaten and the faeces produced. (Appendix E) indicates a clear relationship between weight of faeces and weight of animal in both species ($p < 0.001$).

Results

Table 22

Mean dry weights and number of faecal pellets produced in 24 hr by adult

Oniscus asellus and Porcellio scaber. Ranges in brackets.

	Mean live wt. (mg.) of isopods	Mean No. of pellets	Mean dry wt. of pellets (mg.)
Adult <u>O.asellus</u>	441.0 (297.8-530.4)	77.7 (21.0-147.0)	10.71 (1.97-19.94)
Adult <u>P.scaber</u>	427.0 (304.6-558.4)	64.8 (18.3-141.1)	7.79 (3.764-11.228)

The food ingested and egested was 26% higher with woodlice feeding on Fraxinus excelsior and Salix chrysocoma than on Fagus sylvatica and Quercus robur. There was great variation in faeces production dry weight of animals and faecal pellets (Appendix E) between individuals of the same species. Preliminary experiments on the mean range of faeces production showed an increase with increasing weight which is in accord with Watson's results (1963). Watson also carried out both field experiments and laboratory experiments on faecal production and found laboratory experiments gave much higher rates than the field production. This emphasises the fact that experiments with isopods performed at laboratory temperatures do not reflect the field situation. His laboratory experiments, however, were conducted at 20° C which is considered too high and his results show 16% higher figures of production than the results reported here. 20° C is markedly higher temperature than animals are likely to encounter under field conditions. The mean annual temperature in Northampton is 11°C.

It is evident that experiments with these animals should be conducted under conditions as near natural as possible if the data are to have any relevance to field populations which in this research show highly significant results (see Appendix E).

To obtain accurate information for the assimilation of food by employment of the equation:-

Energy assimilation = Energy consumed - Energy of rejection.

All of the faeces produced from a known weight of food ingested must be accurately determined. Shredded carrot was again used as a marker food.

Methods

Adults of O.asellus and P.scaber were collected in the field, placed in feeding chambers in a controlled environment chamber at 10°C and allowed to feed on shredded carrot until orange faecal pellets were produced, when it was assumed that all field faecal pellets had been voided. The feeding chambers were prepared in the manner described in the last section. The possibility of C varying with the type of food consumed was mentioned earlier and to obviate possible errors from this source the four most preferred foods were offered as food. These were A.pseudoplatanus, F.excelsior, S.chrysocoma and Populus sp. The procedure adopted for the determination of food consumed for each animal was as follows.

Adult individuals of both species were introduced into 20 feeding chambers. The live weight of each animal was determined immediately before each experiment. For a given food, two 2cm discs similar in state of decomposition and texture were prepared. One was vacuum dried at 60°C and the other was offered as food to the animal. The dry weight of the vacuum dried disc was assumed to be the dry weight of the food offered. Each feeding chamber prepared was placed in the field and the animals allowed to feed for 24h. Black faecal pellets were collected every 6h to ensure none were relected or trampled into the filter paper. After 24h feeding the food was removed from

each chamber and shredded carrot introduced. The experiment was terminated when the first orange faecal pellet had been produced. The food remains and all the black faeces from each chamber were vacuum dried separately at 60°C and weighed.

Results

Assimilation.

Table 24 shows the mean percentage assimilation for all foods. The overall mean assimilation efficiency given by all the 20 experiments performed, 20.44% for O.asellus and 21.41% for P.scaber was assumed to be the best possible estimate of assimilation.

Rates of ingestion

Data on the food ingested were available from the above experimental results, where the amount of food ingested per 24h was determined as the dry weight of the food at the beginning of the experiment minus the dry weight of food remaining after 24h feeding.

Rates of egestion

Table 23 shows the mean egestion rate (mg.dry wt) 24h for O.asellus and P.scaber when fed on four different food items. Column 6 shows the mean rates of egestion obtained by the direct measurements of egestion rate made for the two species.

The experiments have shown that there was great variation in assimilation between adult individuals of the same size group feeding on separate foods, necessitating the employment of the mean percentage assimilation efficiency for each group.

Table 23 Mean egestion rate (mg. dry wt./24h) for O.asellus and P.scaber when fed on 4 different food items. (ranges in brackets.)

	Mean l.w.	A.pseudo-platanus	F.excelsior	S.Chryso-coma	Populus sp.	Mean
O.asellus	77.0	1.899 (0.20-5.84)	3.000 (0.196-1.16)	1.854 (0.33-3.18)	1.516 (0.50-2.51)	1.798
P.scaber	84.7	3.838 (1.70-5.95)	1.632 (0.26-2.76)	0.726 (0.18-1.30)	0.892 (0.23-2.26)	1.013

Table 24

Mean percentage assimilation for adult O.asellus and P.scaber when fed on four partly decomposed different food items.

	<u>A. pseudoplatanus</u>	<u>F.excelsior</u>	<u>S.chrysocoma</u>	<u>Populus sp.</u>
O.asellus	13.84 (9.3-35.1)	15.09 (13.3-60.1)	27.31 (1.6-66.6)	29.36 (0.9-96.2)
P.scaber	9.74 (0.2-38.7)	21.90 (9.4-34.3)	22.72 (15.5-89.7)	27.36 (13.6-79.0)

The ranges show that much variation in assimilation occurred between groups of animals and within plant species for all parameters. Because of this variation the mean percentage assimilation of all groups were calculated of O.asellus 20.44% and P.scaber 21.41%.

Mean %
assim.

20.44 \pm 24.39

21.41 \pm 23.97

Table 26

Mean ingestion rate (mg. dry wt/24h) for adult O.asellus and P.scaber when fed on 4 different food items. Ranges in brackets.

Mean l.wt. (mg)	A.pseudoplatanus mg/dry wt	F.excelisor	S.chrysocoma	Populus sp.	Mean rate all foods
77.0 (54.9-98.9)	2.449 (0.20-6.35)	3.624 (0.44-5.20)	2.486 (0.86-6.78)	2.193 (0.44-5.62)	2.393
84.7 (62.5-103.6)	4.479 (0.20-6.75)	1.017 (0.94-2.48)	1.972 (0.28-3.52)	1.333 (0.38-4.14)	1.436

The overall mean assimilation efficiency given by the experiments carried out was 20.44% for O.asellus and 21.41% for P.scaber.

If the food is taken as 100% then the faeces produced must be 79.56% and 78.59% respectively (Table 22). Knowing the dry weight of food ingested and of faeces produced, simple calculations determined the dry weight of food assimilated.

The mean dry weight of all foods eaten per 24h was 2.687mg. for O.asellus and 2.296mg for P.scaber. Table 26 shows the results obtained. Watson's (1963) investigations showed that the highest rates of ingestion were for females and that the rate of ingestion increases with the increasing weight of animals. Column 6 gives the mean dry weight of food eaten per 24h for all the foods used in the experiment. This mean was used to describe the mean rate of ingestion for all groups as there was such a large variation between the rate determined in each individual experiment.

The calculation of the 'best estimate' of A (assimilation) or energy entering the individual.

Because of the lack of detailed knowledge of the life stage composition of natural population of Oniscus asellus and Porcellio scaber it is not possible to calculate the energy assimilated by the populations per unit area of habitat per annum. Under these circumstances the employment of the 'best estimate' proposed by Phillipson (1962,1963) is permissible. 'Best estimates' for food

assimilation per gram live weight per 24hr were calculated from the data on ingestion, egestion and assimilation presented previously.

Methods

The methods used in determining the calorific values of biological material have been described by Watson (1964) who used a micro-bomb calorimeter which was capable of combusting samples of 5-100mg dry weight. This was the apparatus used here. The principle of the bomb calorimeter is to find the calorific value of materials by measuring the amount of energy given off when the substance is burnt in an excess of oxygen to ensure complete combustion.

For each species fresh samples were obtained of adult woodlice. Samples were vacuum dried at 60°C, finely ground with an agate pestle and mortar, pelleted and stored over a dessicant. Calorific values were obtained by burning pellets of approximately 10mg dry weight in a micro-bomb calorimeter which had previously been calibrated with thermochemical benzoic acid. All sample material was dried in a vacuum oven for 24h (60°C and 60nmHg) and stored in a dessicator. The materials were milled, pelleted and burned in the microbomb using samples of 35 - 195mg dry weight. At least three determinations were made on each sample.

Results

Calibration of the bomb.

The values of ten consecutive combustions of benzoic acid were determined. A mean value of 0.7573 ± 0.005 mV/100 cal was obtained. The calibration figure was used for calculation of the calorific value of all materials subsequently burned.

Calorific values of isopod bodies and faeces;

Table 27 show the results obtained

Table 27 Mean Calorific values obtained for body tissue of O.asellus and P.scaber based on 20 combinations (Ash free dry weights)

		Cal. Val. J/g.dry wt.	S.E.	%ash
Adults 11-14mm	<u>O.asellus</u>	15.006 \pm 0.087	0.043	34.85
	<u>P.scaber</u>	14.546 \pm 0.057	0.033	29.34

Calorific values of preferred foods:

Table 28 shows the results obtained. The mean calorific value of all foods used in the determination of A (assimilation) was 17.480 J./g.dry wt.

Calorific values of faeces.

- (a) O.asellus As there was a possibility that the calorific value of faeces produced would vary with the type of food eaten adults were fed separately with discs of each of the following foods Acer.
pseudoplatannus, Fraxinus excelsior, Salix chrysocoma and Populus sp.
The faeces produced by each adult from each food were pelleted and combusted Table 29 shows that considerable differences did occur, but not knowing the precise life-stage composition and the amounts of each food actually consumed by each life stage of a field population, the mean value for all faeces of 17.606 J/g.dry wt. was determined and assumed to represent the calorific value of faeces being produced by all individuals in the field.
- (b) P.scaber Adults were allowed to feed on the preferred foods as above. A mean calorific value of 16.339 J/g.dry wt. was obtained for faeces. All the mean values thus obtained for body tissue, foods and faeces

were later used to convert the 'best estimates' obtained for A and P into joules per gram live weight per unit time. (Table 31)

Table 28

The mean calorific values of foods.

Food material	No.	Cal.Val. J./g.dry wt.	S.E.	%ash
Acer pseudoplatanus	5	18.028	0.010	3.90
Fraxinus excelsior	5	19.324	0.023	3.53
Salix chrysocoma	5	17.639	0.025	9.64
Populus sp.	5	15.603	0.042	7.74
Mean all foods	20	17.648	0.073	5.91

The rates of egestion for the two isopods Oniscus asellus and Porcellio scaber.

To determine A (assimilation), data is required to satisfy the equation:-

$$\text{Food assimilation} = \text{Food ingested} - \text{Faeces egested.}$$

The following work presents data for faeces production under near natural conditions for both species.

Methods

10 crystalising dishes were lined with damp glass fibre filter paper and provided with a shelter as in previous experiments. 2cm old leaf discs of the four common foods available were placed in each dish. It is essential that absolute dry weights are utilised for the accurate determination of rates of assimilation, ingestion and egestion because the variation in water content of live food material may introduce errors into the experimental calculations.

Adult individuals of each species were collected in the field and one individual introduced into the appropriate dish. There were five replicates for each species. The dishes were placed in the cold room at 10°C and under normal lighting regimes for November, for one week. The faecal pellets were

removed every 6 hours to prevent them being relected. At the end of the 24h the live weight of each animal was determined. Faecal pellets were oven dried and weighed on an electrobalance.

Table 29

The mean calorific values obtained from faeces produced by adult O.asellus and P.scaber fed on four separate food items.

Faeces material	No	Cal.Val. J./g.dry wt.	S.E.	%ash	
Acer pseudoplatanus	5	17.812	0.007	3.32	<u>O.asellus</u>
	5	17.334	0.012	3.20	<u>P.scaber</u>
Fraxinus excelsior	5	17.125	0.035	6.29	
	5	17.794	0.023	4.43	
Salix chrysocoma	5	18.224	0.057	9.89	
	5	18.070	0.006	7.83	
Populus sp.	5	18.404	0.010	12.00	
	5	18.086	0.003	12.10	
Mean all faeces	40	17.606	0.040	8.89	

Wet weight/dry weight relationship of body tissue.

Because of the variation of live weight due to varying water content, Engelmann (1966) emphasised the need for weight determinations in energetics studies to be in terms of dry weight as was undertaken in this research.

The calculation of the 'best estimate' of A (assimilation) or energy entering the individual.

Because of the lack of detailed knowledge of the life stage composition of natural population of Oniscus asellus and Porcellio scaber it is not possible to calculate the energy assimilated by the populations per unit area of habitat per annum. Under these circumstances and where the researcher is attempting to study the whole ecology of a species, the employment of the 'best estimate' proposed by Phillipson (1962,1963) is permissible. 'Best estimates' for food assimilation per gram live weight per 24hr were calculated from the data on ingestion, egestion and assimilation presented in previous experiments.

Calorific values of the foods used and faeces produced were obtained by combusting pellet samples in a micro-bomb calorimeter.

The method employed to calculate the 'best estimate' of food assimilated, food ingestion and food egested per gram live weight per unit time for both species is shown below.

The data was obtained from Tables 22- 29

Tables 30 & 31 show the method employed to calculate the 'best estimate' of (assimilation)

1. The total of the mean weight of the adult groups for both species were determined and expressed in milligrams.
2. The total weights of food ingested and egested were converted to joules. The number of joules assimilated was calculated as Ingestion minus Egestion.
3. The results were then expressed as the 'best estimate' of joules assimilated per 24h by 1 gram live weight of isopods. The 'best estimates' are presented as mg/g. live weight of isopod/24h/ and joules/g. live weight of isopod/24h.

Table. 30

Calculation of the 'best estimate' of A (assimilation) for Oniscus asellus using the data obtained from laboratory experiments.

	Mean dry wt/mg.	Mean ingestion	Mean egestion (mg.dry weight per 24h)	Mean assimilation
(a)	69.975	2.393	1.798	0.595
Total mg is multiplied by mean cal. value of:-				
food:- (food = 4.186) faeces = 3.909 Kcal/g. to give				
(b)	Total calories	10.017	7.028	2.989cal.
(c)	Therefore lg. dry weight of <u>O.asellus</u> assimilates			
	$\frac{2.989 \times 1000}{69.975}$	cal./24h		
	I = 42.715 cal./g./dry wt./24h.			
	I = 178.549 joules/g./dry wt./24h.			

Table 31

Calculation of the 'best estimate' of A (assimilation) for P.scaber using the data obtained from laboratory experiments.

	Mean dry wt./mg.	Mean ingestion	Mean egestion (mg. dry weight per 24h)	Mean assimilation
(a)	65.85	1.436	1.013	0.423
Total mg. is multiplied by mean cal. value of:-				
food:- (food = 4.186) (faeces = 3.909) Kcal./g. to give				
(b)	Total calories	6.011	3.959	2.052 cal.
(c)	Therefore lg. live weight of <u>P.scaber</u> assimilates			
	$\frac{2.052 \times 1000}{65.85}$	cal.24hr.		
	I = 31.161 cal./g./dry wt./24h. or			
	I = 130.256 joules/g./dry wt./24h.			

These results compare favourably with Watson (1963). Watson (op cit) carried out an exhaustive number of tests as his whole thesis was on energetics of woodlice. The differences can be accounted for by the fact that he carried out research on all size classes of the two species and had access to more sophisticated equipment at the University of Durham. The present research tested adults of the two species only. Al Dabbagh (1976) working with A.vulgare found mean food consumption rates of 4.28 mg.dry wt./24h which is very high compared to these values and those isopods in the literature. (See Table 21).

The evaluation of the energy flow equation can now be partly constructed for O.asellus and P.scaber

$$C = P + R + Fu$$

$$A = P + R$$

The 'best estimate' given for each of the parameters A, R and Fu in the previous sections made possible the calculation of the energy budgets of O.asellus and P.scaber and should facilitate the calculation, from biomass data, of the amount of litter breakdown and energy flow per unit area of habitat per unit time by any population of O.asellus and P.scaber.

Energy budgets of O.asellus and P.scaber.

The 'best estimates' (J.g.live wt/24h) given in the previous sections were multiplied by 365 thus enabling the data to be presented in terms of J/g.live wt./annum. In addition the 'best estimates' of C, Fu and A were expressed as g.dry wt/g.live wt./annum, thus enabling the calculation of litter breakdown in terms of dry weight.

Results

The results can be seen in Tables 32 and 33. Consideration of the results obtained for litter breakdown and energy flow indicates that O.asellus has a higher consumption rate than P.scaber and a correspondingly higher excretion 76% whereas P.scaber has a twice as high respiration rate being the more active animal. Of the food ingested 25.5% (O.asellus) 24.3% (P.scaber) is assimilated and 60.5% O.asellus 48.8% (P.scaber) is returned to the ecosystem as faeces. These results are comparable to Watson (1965) who records 27.2% (O.asellus) 29.3% (P.scaber) is assimilated and 72.8% (O.asellus) 70.7% (P.scaber) is voided.

Discussion The equation is only partly completed as figures for growth and reproduction are not available. The quantification of other parts of the equation, however, provide a considerable body of information suitable for use with detailed population analysis, or by employment of the 'best estimates' with simple biomass data. Phillipson (1963) who devised this method emphasised that biological processes vary with age, physiological conditions and reasons. Clearly, if one is to approach an accurate measurement of the metabolic parameters involved in an energetics study, then measurements should be made as far as possible for all life stages at all seasons and under as near natural conditions as possible. Having taken a broad view of the total ecology of these two isopods this was not possible but nevertheless a great deal of data was accumulated and a variety of valuable field, laboratory and statistical techniques used.

The present study shows that if few animals are used in assimilation experiments, and if these are adults, it is possible that low assimilation efficiencies will result. For example Phillipson (1960b) and Watson (1965) showed that assimilation efficiency tends to decrease with size. Wieser (1965) has reported the assimilation efficiency of P.scaber over all life stages and

quotes an average assimilation efficiency of 25%. This figure is in close agreement with Watson (op cit) also gives 27.2% for O.asellus and 29.3% for P.scaber and for the present study of 25.5% and 24.3% respectively.

Generally, detritus feeders are considered as having a low assimilation efficiency and a high respiration:production ratio. Macfadyen (1967) discussed the three major trophic groupings of animals and concluded that carnivores are characterised by a high A : C efficiency, herbivores show an intermediate level and detritus feeders have the lowest efficiency. He added that herbivores have a high P : A ratio, which results in nearly as much or even more energy being channelled into production as into respiration. Detritus feeders, with their low assimilation rates correspondingly have a low P : A efficiency. Both species studied here fit into the detritus category with low A : C efficiency.

Table 32

The energy budget (best estimates) of lg. live weight of O.asellus
Joules per annum non bracket

Consumption C =
253149.78

Excretion Fu =
153243.33

Assimilation A =
64673.734

Respiration R =
35232.72

Model

Ingestion 100% = Egestion 60.5% + Respiration 13.9% + Assimilation 25.5%.

Table 33

The energy budget (best estimates) of lg. live weight of P.scaber
J/annum non bracket

Consumption C =
187931.62

Excretion Fu =
91746.28

Assimilation A =
50528.221

Respiration
45657.12

Model

Ingestion 100% = Egestion 48.8% + Assimilation 26.9% + Respiration 24.3%

The proportion of material which passes through the population is high 60.5% and 48.8% respectively but it is unlikely that such a high proportion of the mineral nutrients will pass through the population so rapidly. Hassell (1976) reports several examples of isopods assimilating minerals much more efficiently than organic matter and suggests that an assimilation efficiency of 20% in terms of energy is typical of the group as a whole.

Energy Budget

Given data for biomass, consumption, excretion, assimilation and respiration (Tables 32-33) for both P.Scaber and O.asellus and having deduced values of the numbers collected each month, over two years, from the graphs (Fig 17) representing densities per m^{-2} the following analysis was carried out;

(Tables 34-35)

regression equations of

consumption v mean biomass

rejecta v mean biomass

respiration v mean biomass

These produce correlation coefficients less than 1 but nevertheless values which are significant at the 5% level. The output provides predicted values of consumption, rejecta and respiration for each month using the mean biomass for that month and these are given in Tables 34 and 35. Included also are deduced values of the assimilation (= consumption - rejecta - respiration) and production (= assimilation - respiration).

The values for P.Scaber appear reasonably consistent and those for O.asellus seem to have a 'hump' around February-May of year 2 for both consumption and production. Those for O.asellus give production values some 6-7 times greater than those for P.Scaber and these are difficult to explain. There were larger animals collected in the Spring of 1979 with no juveniles (Fig 20) which may account for rise in production of O.asellus. Likewise O.asellus are larger than P.Scaber overall (Figs 20-21) with lower respiration rates (Table 20).

The difference between the consumption and production may be attributed to the fact that in June O.asellus attain puberty and their definitive sizes whereas P.Scaber produces less and reaches a higher peak of egg standing crop in September (Fig 22).

As has been stated earlier, isopods vary considerably in their various activities. To give one of the most clear cut examples for the inverse relationship between rate of ingestion and absorption efficiency is that of Porcellis laevis feeding on birch litter loaded with different amounts of copper (Dallinger and Wieser, 1977). The amount of organic material absorbed remained fairly constant although the rate of ingestion varied almost eight-fold.

The model given in Tables 34 and 35 are similar to the Hassell model (1977) working with Philoscia muscorum. Hassell's work is based on mean values and gives

$$\text{Consumption (100\%)} = \text{Production (2.11\%)} + \text{Respiration (16.16\%)} + \text{Rejecta (80.73\%)}$$

$$\text{Assimilation (19.27\%)} = \text{Production (3.11\%)} + \text{Respiration (16.16\%)}$$

i.e. Consumption (100%) Assimilation (25.5%) + Respiration and Rejecta (74.4%)

which are similar to each other and to the Hassell model.

The picture one obtains from Tables 21, 34 and 35) is that terrestrial isopods may maintain a certain constancy of absorption rate when feeding on one particular type of food under different environmental or nutritional conditions, but may also absorb different types of food at enormously varying rates. This is probably one reason why these generalists are so successful.

Although much of the energy ingested is rapidly defaecated again, it is unlikely that such a high proportion of the mineral nutrients will pass through the population so rapidly. Hubbell etal (1965) found that A vulgare assimilated strontium much more efficiently than organic matter.

If there is a similar uptake of other minerals such as calcium, by these terrestrial isopods then their high consumption rates coupled with low digestive and assimilation efficiencies for organic matter can be interpreted as an adoption for maintaining adequate mineral balance. This selective absorption would result in isopods concentrating the relatively low levels of nutrients available in dead plant material into animal biomass containing a relatively high proportion of mineral nutrients.

Table 34 - Energy Budgets for *O. asellus*

Month	Number collected	Biomass (mg/w)	Mean biomass (mg/w)	Predicted values for mean biomass of				Product ⁿ (j)	Recorded values of			
				Consum (j)	Rejecta (j)	Respir (j)	Assim (j)		Consum	Rejecta	Respir	Assim
M	111	410	3.69	6984	4227	973	1784	811	8651	5236	1205	2210
A	97	350	3.61	6954	4209	969	1776	807	7385	4470	1029	1886
M	94	370	3.94	7069	4278	985	1806	821	7807	4725	1088	1994
J	115	280	2.43	6545	3962	912	1671	759	5908	3576	823	1509
J	149	320	2.15	6445	3901	898	1646	748	6752	4086	941	1725
A	109	340	3.12	6784	4106	945	1733	788	7174	4342	1000	1832
S	156	480	3.08	6769	4097	943	1729	786	10128	6130	1411	2587
O	133	420	3.16	6797	4114	947	1736	789	8862	5363	1235	2264
N	117	300	2.56	6591	3989	918	1684	766	6330	3831	882	1617
D	85	270	3.18	6804	4118	948	1738	790	5697	3448	794	1455
J	76	250	3.29	6843	4142	954	1747	793	5275	3192	735	1348
F	50	370	7.40	8276	5009	1153	2114	961	7807	4725	1088	1994
M	39	360	9.23	8914	5395	1242	2277	1035	7596	4597	1058	1941
A	43	420	9.77	9101	5508	1268	2325	1057	8862	5363	1235	2264
M	64	460	7.19	8202	4964	1143	2095	952	9706	6874	1352	2480

Table 34 (cont'd)

Month	Number Collected	Biomass (mg/w)	Mean Biomass (mg/w)	Predicted values for mean biomass of				Recorded values of			
				Consum (j)	Rejecta (j)	Respir (j)	Assim (j)	Consum	Rejecta	Respir	Assim
J	104	370	3.56	6937	4198	967	1772	7807	4725	1088	1994
J	136	380	2.79	6671	4037	930	1704	8018	4853	1117	2048
A	178	400	2.25	6480	3922	903	1655	8440	5108	1176	2156
S	194	390	2.01	6398	3872	892	1634	8229	4980	1147	2102
O	153	350	2.29	6494	3930	905	1659	7385	4470	1029	1886
N	129	230	1.78	6318	3825	880	1614	7281	4218	479	1716
D	75	210	2.80	6673	4039	930	1704	6317	3816	818	1615
J	70	90	1.29	6145	3719	856	1570	5679	3414	810	1499
F	41	150	3.66	6972	4220	972	1780	6911	4099	940	1687
Total	2518	7970	90.23	168166	101799	23433	42953	153819	115653	21433	
P/annum	1259	3985	45.115	84083	50899.5	11716.5	21476.5	76909.5	57826.5	10716.5	1515

Figures for mean biomass are given correct to 2 decimal places.

Figures for rejecta and respiration are given correct to the nearest integer.

(and so, by implication, are figures for assimilation and production) where these figures are predicted from the regression equations.

Table 35 - Energy Budgets for P.scaber

Month	Number collected	Biomass (mg/w)	Mean Biomass (mg/w)	Predicted values for mean biomass of				Product ⁿ (j)	Recorded values of			
				Consum (j)	Rejecta (j)	Respir (j)	Assim (j)		Consum (j)	Rejecta (j)	Respir (j)	Assim (j)
M	48	340	7.08	5511	2692	1337	1482	145	5324	2601	1292	1431
A	71	350	4.93	4875	2382	1183	1310	127	5481	2678	1330	1473
M	65	210	3.23	4373	2136	1061	1176	115	3289	1607	798	884
J	91	320	3.52	4458	2178	1082	1198	116	5011	2448	1216	1347
J	76	350	4.61	4779	2335	1160	1284	124	5481	2678	1330	1473
A	117	300	2.56	4177	2040	1013	1124	111	4698	2295	1140	1263
S	165	280	1.70	3921	1915	951	1055	104	4385	2142	1064	1179
O	155	210	1.35	3819	1866	927	1026	99	3289	1606	798	885
N	110	280	2.55	4171	2038	1012	1121	109	4385	2142	11064	1179
D	134	260	1.94	3992	1950	969	1073	104	4072	1989	988	1095
J	149	350	2.35	4113	2009	998	1106	108	5481	2678	1329	1474
F	106	270	2.55	4172	2038	1012	1122	110	4228	2065	1026	1137
M	85	200	2.35	4114	2010	998	1106	108	3132	1530	760	842

Table 35 (cont'd)

Month	Number collected	Biomass (mg/w)	Mean Biomass (mg/w)	Predicted values for mean biomass of				Recorded values of				
				Consum (j)	Rejecta (j)	Respir (j)	Assim (j)	Product ⁿ (j)	Consum (j)	Rejecta (j)	Respir (j)	Assl (j)
A	40	290	7.25	5560	2716	1349	1495	146	4541	2218	1102	122
M	50	270	5.40	5014	2449	1217	1348	131	4228	2065	1026	113
J	85	320	3.76	4531	2214	1099	1218	119	5011	2448	1216	134
J	71	310	4.37	4709	2300	1143	1266	123	4855	2372	1178	130
A	45	300	6.67	5388	2632	1308	1448	140	4698	2295	1140	126
S	95	270	2.84	4259	2080	1033	1146	113	4228	2065	1026	113
O	143	160	1.12	3750	1832	910	1008	98	2506	1224	608	674
N	129	150	1.16	3763	1838	913	1012	99	2349	1148	570	631
D	106	360	3.40	4422	2160	1073	1189	116	5638	2754	1368	1516
J	91	350	3.85	4555	2225	1105	1225	120	5481	2678	1330	1473
F	79	340	4.30	4690	2291	1138	1261	123	5324	2601	1292	1431
Total	2306	6842	84.84	107116	52326	25991	28799		107115	52327	25991	28797
P/annum	1153	3420	42.42	53558	26163	12995.5	14399.5		53557.5	26163.5	12995.5	14398

Figures for mean biomass are given correct to 2 decimal places.

Figures for rejecta and respiration are given correct to the nearest integer (and so, by implication, are figures for assimilation and production), where these figures are predicted from the regression equations.

Thus it can be concluded that although invertebrate macrodecomposers may be directly responsible for dissipating only a very small proportion of the energy entering the soil system, their contribution to ecosystem functioning may be much more significant due to their capacity for rapid turnover of large amounts of organic material which together with selective absorption enables them to concentrate into animal biomass the small quantities of nutrients available in decaying plant litter.

GENERAL DISCUSSION

General Discussion

The main objective of this work was to study and compare the population and energy relationships of two species of terrestrial isopod, Oniscus asellus and Porcellio scaber, on Nene College sites. This structural and functional approach is in keeping with the definition of ecology as being "the study of the structure and function of ecosystems." (Odum 1962).

Most workers researching the ecology of isopods have studied one aspect only as it is difficult for one worker to measure accurately all of the required parameters in the time available. Hatchet (1947), Paris & Pitelka (1962), Saito (1965, 1969), Sutton (1968), Standen (1973), Al Dabbagh (1976), and Wilkins (1978) have all studied population ecology while Watson (1966, Hassall (1976), Al Dabbagh (1976), Wieser (1978) and Rushton & Hassall (1983) have undertaken bioenergetic studies.

One of the more recent developments in ecology, commended by Southwood (1971), has been a shift away from studying the distribution of organisms, towards understanding the dynamic ecological principles upon which these distributions are based. This study attempts this by studying the climatic, edaphic and behavioural aspects of population and production ecology of the two species and thus gain a holistic view of their ecology. By studying this general interdependence of this complex of factors no aspect has been investigated in such depth as achieved in the investigation^{cited} above.

The thesis is divided into discrete sections with discussion at the end of each chapter. This general discussion attempts an over-view.

Almost as many hypotheses regarding the controlling or regulatory mechanisms in isopod populations have been proposed, as there have been studies conducted. Each investigation seems to have prompted a different conclusion, but there are basically two contrasting viewpoints. Firstly, there is the idea that the population is stable as a result of density dependent.

processes, and secondly that it is held at a density level by factors independent of density, such as weather.

Weather conditions are held to be the major process determining population size in Porcellio spinicornis, by McQueen & Carnio (1974) and McQueen (1976a). In these studies, a model was built relating individual growth rates to temperature, which attempted to show how climatic fluctuations are capable of regulating population density. They showed that temperature strongly influenced demographic processes such as survival and reproduction in a population of P.spinicornis. However, a second study by McQueen (1976b) on Tracheoniscus rathkei on the same site, does not arrive at the same conclusion, and McQueen states that this is probably because P.spinicornis is close to the northern limit of its range, whilst T.rathkei is not and so is probably regulated by parasites or pathogens.

Hatchett (1947) also cites the weather as acting to control numbers in a population of Cylisticus convexus, as he observed individual growth rate to correlate closely with the amount of rainfall, and thus rainfall affected natality levels by affecting the individual size of parents. He does, however, concede that it may not be the sole limiting agent. Generally isopods are poorly adapted for terrestrial life (Edney 1954, 1960, 1968) and their ability to survive in extreme environments depends on their behavioural mechanisms as was witnessed on the ha-ha wall studies and in behavioural studies in the laboratory. (Chapters 3 and 4)

Most other studies show that climate, although important, does not absolutely control population density levels. Stachurski (1972) working on Ligidium hypnorum demonstrates a density dependent effect on natality through food availability, and Merriman (1976) found a correlation between food quality and natality in Armadillidium vulgare in the laboratory. He postulated that this could be a regulatory mechanism in this species in the field.

Other workers find that density dependence acts on mortality rather than natality, with mortality increasing as density rises. Paris (1963), working on A.vulgare in California suggest that competition for shelter sites could regulate his population and shelter site availability was affected by the weather.

The absolute density of isopods is difficult to establish owing to their vertical movements into the soil in times of drought or frosts or up into trees during the summer. In Arizona a total of 954 specimens of A.vulgare was counted under cover of 75 stones and logs in an area of 20 m^{-2} or 47.7 isopods m^{-2} (Warburg 1960). An average of 538 isopods m^{-2} was counted in California for the same species by Paris & Pitelka (1962). Al-Dabbagh (1976) counted 20 - 100 m^{-2} isopods of the same species in England. These are highly variable figures obtained for the same species which was the most abundant species of isopod in all three localities. There are several possible reasons for these variations in sizes of field populations. The mobility of these animals often precludes the use of reliable mark-recapture methods and direct counts are complicated by seasonal and diurnal vertical migrations of large segments of the population. Furthermore, direct counts suffer from the disadvantage that they may provide estimates of population activity rather than of population size. The nocturnalism of these animals also suggests that the micro-distribution pattern may vary during the 24-hour cycle, being strongly aggregated during the day and more dispersed at night when individuals emerge from their shelters to forage for food. For these reasons the present study was carried out over all seasons, day and night and both in litter and up to a height of 4m on trees. Thus it is suggested the population densities recorded in chapter 4 are the most thorough yet undertaken and where mean densities ranged over the year from 16 - 77 m^{-2} for O.asellus and 17 - 65 m^{-2} for P.scaber.

On the ha-ha wall no animals were visible by day but over 100 were recorded in a 1 m^{-2} quadrat soon after midnight. The research shows that these terrestrial isopods exhibit a strong circadian rhythm. (Fig 24)

In their activity patterns the two species studied here showed a responsive relationship to climatic factors especially in the more primitive O.asellus. Thus they responded to temperature and humidity of the air and moisture conditions of the soil. This was confirmed by behavioural studies carried out under laboratory conditions but these need to be supplemented by more field studies. 'Micro-habitats are selected as refuges by isopods according to the animals' moisture preferences and to some extent by the concentration of salts in the soil' (Warburg 1968).

Isopods adapt to environmental conditions in their habitat by adopting various behavioural patterns of activity in response to these conditions thus modifying their effects. In addition to the examples given above, which are supported by Brereton (1957), the activities on the trees and on the ha-ha wall indicate both the seasonal and diurnal pattern of activity. In attempting a synthesis of these behavioural observations two general considerations must be borne in mind. First, surface activity may subserve different functions in different species, and this may be reflected in Warburg's (1964) finding that the behavioural responses of different species varied under similar environmental conditions. Second, the response of an animal to a given situation may vary with its physiological state, particularly with its state of hydration; as Warburg also demonstrated that this state can change abruptly as water is lost or gained, and this may be followed by an equally abrupt behavioural change as was observed in the present research on the ha-ha wall and in laboratory behavioural studies.

Climatic factors affected the nocturnal emergence of both species and in addition Cloudsley-Thompson (1960) showed that activity pattern was correlated with wind speed. In a study on the vertical separation between three species, A.vulgare, P.scaber and P.muscorum, on dune grassland Davis; Hassall & Sutton (1977) have shown that three factors affected the burrowing pattern: temperature, relative humidity and the burrowing ability of the species and the highest correlation was with temperature. No correlation was found in the present study between activities and soil moisture as affected by monthly rainfall on the

Moulton Park site. This is confirmed by Al-Dabbagh & Block (1981) who showed wide variations in both precipitation and soil water content did not affect populations of A.vulgare. Nair (1984) however working in Delhi on Porcellio laevis found the breeding season coincided with the rainy season and high temperatures (28-33 °C).

Breeding reached its peak when day length was between 12 and 14 h. Longer day lengths appear to increase gonadal development but optimum temperature was also essential as a releaser. Weiser (1962) made similar observations in P.scaber and A.vulgare. The present research confirms these other workers' results. (Fig 23)

It is difficult to disentangle the various edaphic factors discussed in chapter 2. It has been known for some time that pH and nutrient content of soil influences the distribution of isopods (Wallwork 1975). Isopods are less numerous on acid than on neutral or alkaline soil. It is assumed that acid soils lack sufficient calcium (Sutton 1980). However, soil pH may also influence vegetation, i.e. food, as there was a strong correlation between pH and food preferences (see Chapter 5).

Ong (1980) found a highly significant correlation between 16 sample population sizes of four species of isopod and soil pH. Maximum population density occurred within a soil pH of 7 - 8. This could be attributed to metabolic requirements for calcium, the effect of pH on soil structure, nutrients and its consequent effects on the vegetation. For example, eating or sucking up of halophytic plants may compensate for insufficient saline concentration of the substratum. The results discussed in Chapter 2 indicate that populations are affected by soil pH.

The question of how and if natural populations are regulated has long been an area of controversy in population ecology, the two sides being that of density dependent regulation versus density independent limitation. The density dependent argument is exemplified by the views of Elton (1942), Haldane (1953) and Nicholson (1954), who maintain that the chief density dependent factors result from competition for resources and space. Andrewartha and Birch (1954) lead the argument for density independence, by attaching no importance to density. They

consider that since the supply of a resource is frequently independent of the numbers of animals searching for it, intra specific competition is not occurring. Dempster (1975) gives a very clear synthesis of the arguments for each case, and concludes that both types of limitation may occur in any population, but one or other will dominate depending on the predictability of the environment. It is extremely difficult to demonstrate competition in nature, where animals are more likely to disperse, than to remain in an environment to compete for a resource in short supply. Stachurski (1972) was able to show that competition for food was occurring in Ligidium hypnorum because his populations lived on "islands" in a swamp from which dispersal was difficult, and so semi-confined populations would be forced to compete for the available food.

The abundance of hypotheses concerning regulation or limitation in isopod populations typifies the confusion existing in this area. It does, however, illustrate that no single answer appears to suffice in all cases. Dempster's conclusions that both density dependent and independent processes occur, but that the dominance of one or the other depends on the situation of the population, seems to be a realistic assessment of the situation.

There are several ways in which the pattern of population changes could be explained. The differences in distribution show some degree of micro-geographical separation of the species, but there is considerable overlap especially at ground level in winter. At high densities competition for food might occur, causing a reduced rate of growth, and channelling more individuals into the slow cohort. There is no field evidence for this, however, as this present research indicates that food should always be abundant especially for litter feeding species. In addition both species have a wide range of foods available and the ability to consume a wide variety of the available litter and there was evidence of reasonable continuous growth throughout the summer months. However, it is conceivable that during dry periods the quality would be poor, and some of the available food would be unpalatable. This would be

similar to the findings of Stachurski (1972) and Merriman (1976): Food is probably only of limited importance as a factor in selecting a suitable habitat although nutritional values vary. (See pages 95 to 97)

Regulation could also be achieved at high densities by a closer coupling of predators to prey density as was suggested by Brereton (1957) who postulated tentatively from laboratory experiment that P.scaber was self regulated through cannibalism of the newly born young, and this occurred around an optimum density level. Continuous records over several years of predator density levels do not exist, making it difficult to assess the possible importance of this mechanism, but it is unlikely that polyphagous predators of this type can effectively regulate a population as very few predators were seen. (See Page 85)

The most likely explanation for the pattern of population change in levels in this study, is that of competition for shelter sites from extremes of humidity. Competition for this resource, which varies seasonally and annually with the weather, is the mechanism that Paris (1963) postulates for regulating Armadillidium vulgare. In this case, the results of competition affect mortality rates rather than natality (as in competition for food), those animals dying that do not succeed in finding refuges. Evidence for this hypothesis in the field is hard to find, as corpses are rapidly and efficiently removed by scavenging ants especially in the woodland site. (Fig 8)

This mechanism could operate to maintain stability at high densities, whilst other refuges protect individuals at low density levels, from the attacks of predators. These refuges mean that both at high and at low densities, the heterogeneity of the environment is important in maintaining the population. This aspect of population ecology has only recently attracted much attention. Free, Beddington and Lawton (1977) conclude from studies of interference between parasites (or predators) that spatial complexity and aggregation will often be dominant factors affecting predator/prey distributions, with areas of low prey density being considered as "refuges". There were ample "refuges" available on the Moulton Park sites.

Hassell and May (1974) arrive at similar conclusions regarding the importance of patchy distributions of both predators and prey, brought about by a heterogeneous environment.

This concept indicates the importance of the environment in isopod population demands; temperature controls growth, humidity affects food supplies and the abundance of refuges against desiccation, and the physical complexity of the habitat is important in interactions with predators. It highlights the possible reason why each study conducted arrives at different conclusions regarding the regulatory or limiting mechanisms, as these depend on the combination of environmental conditions acting at the time. Southwood (1971) discusses the importance of the habitat, and maintains that it is the crucial factor in determining the success of any population through the life history strategy it imposes. His own words summarise this idea best, "Habitat is the templet for biological success."

It can be said that population studies are aimed at answering three basic question questions;

- (1) what causes fluctuations in the numbers of a species in a habitat from year to year,
- (2) what determines the amplitude of these fluctuation,
- (3) what limits the distribution of the species.

In this study climate affected both the distribution and abundance of these isopods. Humidity and temperature of the air and moisture content of the soil affect their activity and distribution.

Micro habitats are selected as "refuges" by both species with O.asellus being most restricted whilst the more advanced P.scaber was active within a wider range of humidity, temperature and was active by day.

These findings are in keeping with Warburg (1984).

This study has attempted to provide some answers to these questions by studying population in three very variable sites which have been greatly influenced by man. The observations upon which the study is built are real; the conclusions drawn from them remain to be tested.

The two isopods chosen for this research have complex life histories in that they can reproduce more than once in a lifetime and show an overlap of generations. They provide, thereby, an excellent opportunity for the evaluation of methodological procedures, proven for animals with a more complex life history.

The quantification of the equation: Energy of food consumption = Energy of new tissue produced + Energy of respiration + Energy of faeces produced, provided a considerable body of information suitable for use with detailed population analyses, or by employment of the 'best estimates' with simple biomass data. (Tables 32 & 33)

Macfadyen (1963), Phillipson & Watson (1965), and Wieser (1984), amongst others, have emphasised that biological processes vary with age, physiological conditions and season. Clearly, if one is to approach a reasonably accurate measurement of all the metabolic parameters involved in a bioenergetic study then measurement should be as far as possible for all seasons, all life stages and under as near natural conditions as possible. This was not possible as the study was much broader than a study of bioenergetics so adult specimens only were used at one point in time.

The food preference experiments proved useful in that they made possible the preferring of foods most likely to be eaten in the field to animals in the assimilation experiments. The preliminary experiments showed that both species would attempt fresh plant material, as did A.vulgare, Paris (1963; Watson, 1965). The present study showed that O.asellus and P.scaber did not prefer fresh plant material, thus it seems that such foods constitute only an insignificant part of the diet of these two species as there is always an ample supply of partially decomposed food available. (see pages 95-97)

The present study showed that both species exhibit a marked preference for ingesting certain types of partly decomposed leaf litter over freshly fallen leaves. Experiments on the pH of leaves showed a significant preference for leaves with a neutral pH and those with less tannins. More recently, Hassall and Rushton (1984) show that preferences are related to anti-herbivore defences

adopted by plants and that microorganisms play an important role in weakening physical defences, so softening leaves; accelerating breakdown of complex chemicals, increasing the nutrient status of litter, and assisting in the digestive processes of the animals.

It must be emphasised that the results given in Figs 25-28 are rather crude calculations. At best they apply to a given site and to small groups of animals. The chemical properties of the food (for instance, its C : N ratio or its cellulose, lignin, tannin, and resin content), its state of decomposition affected by bacterial action and humidity, the seasonal fluctuation in animal food requirements, uneven growth rates and climatic influences are all variables which must be taken into account.

Nevertheless, the collection and comparison of these quantitative data represent a step forward in realising the importance of these isopods in the soil-biological chain and indicate the direction for further research.

The present study presents data for both species and it is evident that preference does not change with season as all of the preferred foods are available all the year round. There were large variations in the food consumed and assimilated. There is, therefore, a need for many replicate experiments to be undertaken at all life stages. An inverse relationship between rate of ingestion and efficiency of absorption has been reported by various authors, Dallinger & Wieser (1977), and Rushton & Hassall (1984). If this proves to be the rule then isopods have the ability to match the rates of energy absorption by an equally large range of variability of the rates of energy dissipation. This, coupled with the ability to use coprophagy in order to improve the nutritional value of primary food is advantageous as it would suggest a tendency to equalisation of the rates at which nutrients are absorbed Wieser (1984).

In nature, by switching from one type of food to another and by varying the rate at which digested food is absorbed across the gut these flexible generalists may achieve the optimal composition of nutrients and energy for maintenance,

growth and reproduction from foods of which each single one may be deficient in some respect. The effect of different kinds of food on growth and mortality of an isopod species has been analysed by Merriman (1976), and the ability to select food according to nutritional needs has been illustrated by an experiment performed by Dallinger (1977): Porcellio scaber of different copper status were given the choice between litter of various copper content. Copper rich animals preferred a low copper diet. The high-copper diet was neglected by both groups. This indicates that isopods have the ability to select food according to nutritional needs. (Wieser op cit)

The rate at which digested food passes across the gut wall is bound to be of paramount importance for the uptake of essential nutrients. Some of these nutrients may be less easily liberated than others from the bulk of food as it passes through the gut. Thus at high rates of ingestion and low absorption efficiencies some nutrients may leave the isopod's body in just the same state as they entered it with the food. They would only become available to the isopod at lower rates of ingestion. Conversely, scarce but easily liberated nutrients require a high rate of ingestion for a sufficient amount to pass from the food to the tissues. For these reasons the present research included micro-photographs of faecal pellets which showed that food had passed through the gut and part of the plants were readily identified. (See Appendix F)

Phillipson (1960) and Watson (1965) showed that assimilation efficiency tends to decrease with size. Wieser (1965) has reported the assimilation efficiency of P.scaber over all life stages as 25%. This figure is in close agreement with that of Watson (op cit) who gave 27% O.asellus and 29.3% for P.scaber and the present study gives 20.44% and 21.4% respectively.

The variation of respiratory rate with size, physiological conditions and season as shown by Watson (op cit) strengthens the argument raised by Macfadyen (1963) and others of the necessity of all the year round respirometric studies if one is to acquire an accurate estimate of the annual respiratory energy flow of a species population.

The peak breeding periods of both O.asellus and P.scaber in the present study agree with those given by Heeley (1941) and Wieser (1963) with P.scaber having a late second brood as suggested by Heeley (op cit) but not confirmed by Watson (op cit) who suggested that low temperatures in particular will suppress brood pouch formation. (See Fig 23)

Growth rates vary considerably as was pointed out by Paris and Pitelka (op cit) who notes fast growth in A.vulgare and Phillipson and Watson (op cit) in O.asellus. Some time ago a growth curve was constructed for P.scaber using published information (Wieser, 1965a, 1966b). In this species the rate of growth shows a distinct break at a body weight 3mg, with the rate of the smallest specimens corresponding to approximately $150\text{Jg}^{-1}\text{d}^{-1}$. It is significant that a similar break at about the same body weight has been observed for the rate of oxygen consumption (Wieser & Oberhauser 1984), and also for the rate of food assimilation (Wieser 1965a).

In view of the fact that much criticism has been levelled at respiratory studies at constant temperature, Phillipson & Watson (1965), Al Dabbagh (1976), it is interesting to note that the respiration results obtained at 10 °C, (the mean temperature of the habitat was 11 °C), fit well into the energy flow equation. Wieser (1965) has shown that P.scaber does not change its feeding regime until it has been subjected to laboratory conditions for a period of 3 days (See Table 14)

One wonders if metabolic measurements made on such animals, immediately after capture, at the annual mean environmental temperature, would reduce the need for micro-climatic studies. Indeed, the 'best estimates' calculated for the respiratory energy loss of O.asellus and P.scaber and O.asellus are very similar. The figure for the latter species having been calculated by Edney (1955) from respirometric measurements at field temperature of the habitat are justifiable. This is generally not accepted by most researchers, however, see Table 20 where highest oxygen consumption rates are those recorded by Phillipson & Watson (1965) where O.asellus was not given time to acclimate at all. Indeed, in all these energetic studies the problems associated with the extrapolation of consumption,

assimilation and respiratory rates of laboratory cultured isopods to the field are quite severe. This does not, however, imply a deficiency in the methodology, as it was based on a sound theoretical background, but merely to lack of knowledge of the feeding biology of O.asellus and P.scaber together with their micro-habitats.

Clearly, it is preferable to apply bioenergetic data to detailed population analysis together with measurements of leaf fall, bioenergetics of other key large decomposers such as Diplopoda and Lumbricidae as well as large populations of Acarina and Collembola in order to establish the importance of the Isopoda in promoting energy flow through the woodland ecosystems.

Calculations, therefore, of food consumption under field conditions for the individual energy budget were derived from the faecal production of individuals under assimilated field conditions in the laboratory. Whilst population food consumption was calculated from P and R and related to the assimilation: consumption efficiency obtained from the calculated individual energy budgets. It is hoped, however, that the problems involved in such extrapolation do not invalidate the results of the present study. To quote Nielson (1961) 'The best one can do because of the numerous variables in such studies is to present a fairly realistic picture which enables others to judge the order of magnitude involved'.

There are two main reasons for carrying out this study. The first is to allow an assessment of the role which the two species play within the ecosystem. The second is that energy studies allow the role of animals in different ecosystems and in different trophic levels to be compared.

Energy budget parameters allow direct comparison of different species in terms of their function within the ecosystem (see Table 21). Tables 32 & 33 indicate that both species play a larger role in breaking down leaf litter and producing food for other detritivores and necrophages than it does in passing material to carnivores.

The number of complete studies of energy budgets for field populations is still small (see page 131) whilst it has proved possible to produce an energy budget for both O.asellus and P.scaber in which some parameters are similar to

other workers, and which bear logical relationships to other studies, some reservations must be made. These will remain until either the consumption, assimilation or faeces production is measured in the field, and the large discrepancy between calculated and experimental food consumption figures is explained.

However, the study has provided data to assess the role of O.asellus and P.scaber in the woodland ecosystem. The animals are clearly of some importance in the breakdown of woodland litter and this has been quantified. Furthermore, by the production of faeces they provide food for other members of the community, and this appears to be more important, in terms of energy flow, than the energy passed to predators. The data gathered in this study will be of value in determining the functional importance of these animals in the woodland ecosystem but similar studies of woodland detritivores will be necessary before the importance of the detritus food chain, and of the individuals within it, can be fully assessed.

The two species have shown considerable differences between their behaviour and ecology with P.scaber being the more advanced of the two species. Both species have inherited features of the maritime past of isopods with P.scaber being the more flexible. The possession of pseudotracheae gives P.scaber an advantage over O.asellus by enabling it to be active by day as well as by night.

In conclusion, it seems that future work in ecology should depend primarily on measurements made under conditions as close as possible to the field. This is particularly important when there are no methods for direct measurement of the energetic parameters in the field. The use of simulated environmental regimes, representative of the actual physical conditions in the field is a promising development, and one which should be actively exploited. The evaluation of the effects of such regimes on the parameters of the individual energy budgets of invertebrate species is an important area for future work. These studies may partially solve some of the problems associated with extrapolation of data from laboratory to field. The development of a respirometer which incorporates a

fluctuating temperature regime similar to that of the field is another line of future investigation in the bioenergetics field. Workman (1978) constructed such an apparatus but, to date, it has not been fully evaluated.

Alternatively, when the kinetics of the elimination of radioisotopes from invertebrates are more fully understood, it may be possible to relate respiratory metabolism to the rate of elimination of a radioisotopically labelled substance from the animal's body, and thereby determine field respiration. Field techniques to measure individual feeding rates are probably the most urgently required, and this is true not only for O.asellus and P.scaber but for more terrestrial invertebrate species. These techniques must be based on a full understanding of the feeding biology of the animal concerned. In isopods the importance of soil and micro-organisms in altering the feeding rates of several species has been demonstrated. Therefore, carefully planned experimentation which will account for these variables will result in a more precise determination of food consumption and energy assimilation rates. It is in this area that much research effort is required to achieve a better insight into the bioenergetics of terrestrial isopods.

SUMMARY

Summary

- 1 The ecology of two common species of isopods, Oniscus asellus (Linnaeus) and Porcellio scaber (Latreille) was undertaken between 1978-85.
- 2 The morphology and biology of O.asellus and P.scaber were discussed. The species are two of the most widely distributed isopods in England.
- 3 Life histories of both species were studied in laboratory conditions for one year and the respective stages of breeding were constant for both species. P.scaber only liberated half the number of larvae compared with O.asellus.
- 4 Populations of the two isopods were sampled monthly over two years from Spinney Hill shelter belt woodlands and a ha-ha wall and surrounds at Nene College, Northampton.
- 5 The vegetation and soils were sampled for both sites. The woodland was dominated by coniferous and broadleaved trees whilst the ha-ha wall was surrounded by shrubs and herbaceous plants. The woodland site had a lower pH 5.1, higher organic C 26.9% but lower P and K. The soil surrounding the ha-ha wall had a pH of 6.3 with very high K. Average soil water content ranged from 28.0 on the woodland site to 18.5% at the ha-ha site.
- 6 Temperatures, relative humidities, prevailing wind and speed and number of frosts were taken on each sampling date. Monthly integrated temperatures and relative humidities were recorded and were more equitable on the woodland site than the ha-ha wall. The

mean temperature for the site was 11°C.

- 7 Behavioural studies were undertaken in the laboratory to determine how adaptations to life on land are connected with the physiology of these isopods. The analysis showed that high humidity 70% RH, dark conditions and low temperatures 10°C enabled the animals to be more active. P.scaber which possess pseudotrocheae were more flexible in their behaviour than O.asellus.
- 8 The population density in Spinney Hill woods ranged from 16-77 m⁻² O.asellus and 17-65 m⁻² P.scaber. Density for both species was at its lowest in March and peaked in September.
- 9 Population biomass for both species was highest in early winter and lowest in early spring, ranging from 104 mg m⁻² to 478 mg m⁻² for O.asellus and 164 mg m⁻² to 363 mg m⁻² for P.scaber. The changes were associated with population density and the growth of individual cohorts. Evidence is given that P.scaber had two generations in both years.
- 10 Growth of both species was seasonal and occurred between March and October with P.scaber breeding slightly earlier in both years. Breeding reached its peak when day length was between 12-14 hours. Size increments (head widths) were observed in the upward progression of size classes. Evidence is given for fluctuating results being correlated with climatic factors and a strong circadian rhythm.
- 11 Monthly night exercises over one year yielded evidence that isopods have a nocturnal activity pattern with light being the stimulus that creates the behavioural response to become active at night and to seek shelter at dawn. Densities over the year ranged from

0-958 m⁻² and are correlated with climatic factors.

- 12 Vertical migration population studies of invertebrates on four common tree species were recorded over four years both day and night and at different heights. 55% of all invertebrates were isopods. There was a paucity of animals on the Corsican pine and strong evidence that P.scaber (78%) ascends trees to at least 4 m in Spring and descends in Autumn (P = 0.001). O.asellus was mainly found under logs, stones and at the base of trees but a few ascended to 1.5 m. P.scaber is not in competition with O.asellus but feeds on the lichen S.chlorococcum and is better adapted for life on trees. Invertebrate populations differed with species of tree (P < 0.001) but not between day and night (P > 0.05).
- 13 Feeding trials using fresh and partly decomposed leaves from nine common tree species on site showed that given a choice both species preferred partly decomposed Fraxinus excelsior over all others but can utilise a wide variety of materials. There is a strong correlation between pH of leaves and food preferences. Food is only of limited importance as a factor in selecting a habitat.
- 14 Bioenergetic studies were made on both species to investigate all the parameters of the equation: $C = P + R + Fu$.
- 15 Data of individual respiration rates at three constant temperatures (5 . 10 . 15°C) were obtained using the Gilson respirometer using animals previously acclimated to these temperature regimes. The mean temperature of 10°C was used giving O.asellus as using 0.2011 μ l/h per unit dry wt mg and 0.206 μ l/h per unit dry wt mg for P.scaber.
- 16 The 'best estimate' for respiration metabolism for O.asellus and P.scaber were 0.2011 μ l O₂ mg⁻¹ 24 h⁻¹ and 0.2606 μ l O₂ mg⁻¹

respectively.

- 17 Consumption, assimilation and faecal production rates were measured for animals recently brought into the laboratory from the field. The mean dry weight of food eaten per 24h was 2.393 mg for O.asellus and 1.436 mg for P.scaber. Assimilation rates varied widely with 25.5% efficiency for O.asellus and 24.3% for P.scaber.
- 18 Energy budgets are given for both species in terms of 'best estimates' expressed as joules.g.dry wt of isopod per annum. O.asellus has a high consumption rate and higher excretion than P.scaber which was the most active animal with the higher rate of respiration. Of the food ingested 25.5% O.asellus, 24.9% P.scaber is assimilated and 60.5% O.asellus, 48.8% P.scaber is returned to the ecosystem as faeces.
- 19 Both species fit into the detritus category with low A:C efficiency which indicates that they play a large part in breaking down leaf litter and producing food for other detritivores.

ACKNOWLEDGEMENTS

Acknowledgement

I would like to warmly thank my supervisor Dr J Bullock for his excellent advice, encouragement and criticism throughout the course of this study. Thanks are also due to the Director of Nene College, Dr E Ogilvie, for allowing me to use College laboratory facilities.

My fees for this research period have been generously paid by the College and it is a pleasure to thank the Governors, Academic Board and my colleagues in the Faculty of Science who made the work possible.

Last, but no means least, to my wife for her patience, understanding and support throughout this long study period.

APPENDICES

APPENDIX A Monthly summaries

	°C Mean min.	°C Lowest min.	mm Total ppt.	FF Ground °C frost/ lowest	Wind Speed kts
March 1978	0.8	-1.9	98.5	18 (-6.0)	12
April	1.6	-1.9	71.2	9 (-4.5)	11
May	5.7	-1.8	103.8	5 (-4.0)	13
June	9.4	6.4	43.8	NONE	8
July	11.48	7.8	25.4	NONE	8
August	10.9	5.9	56.8	NONE	11
September	8.79	2.0	18.0	1 (-0.5)	10
October	7.24	1.0	56.6	2 (-1.8)	11
November	2.75	-4.0	37.1	12 (-4.6)	13
December	2.7	-3.0	35.1	15 (-7.6)	15
January '79	-0.7	-6.6	38.8	24 (-10.4)	12
February	1.97	-6.9	49.2	8 (-7.4)	9
March	1.27	-2.9	54.3	19 (-7.2)	11
April	3.6	-0.5	23.8	11 (-4.6)	11
May	5.4	0.0	35.5	6 (-4.6)	11
June	9.68	5.3	98.4	NONE	14
July	10.2	6.1	185.2	NONE	8
August	11.7	7.5	109.4	NONE	8
September	10.9	8.1	22.8	NONE	12
October	5.27	1.1	75.6	7 (-1.7))
November	3.4	-2.0	47.7	12 (-5.5))
December	2.0	-5.1	45.6	18 (-8.5))
January '80	1.54	-3.5	37.9	18 (-8.8))
February	-0.6	-5.5	36.9	22 (-9.5)	9
March	4.82	-1.1	91.0	7 (-4.4)	14

)
)
) No records -
) Anemometer blown
) down in gale
)

All figures from 4364 Moulton Park Climatological Station - reading at 0.900 GMT

APPENDIX B

Specific data for sampling dates

	overnight °C Air Temp min.	overnight °C Grass min.	R.H. % 0900 GMT	at 0900 Wind Speed Knots	at 0900 Direction	at 0900 cloud cover oktas	
<u>1978</u>							Read at 0900 hrs G.M.T. R.H. wind direction and cloud cover are the actual figures at the time of observation. Air min. and Grass min. are the lowest temperatures reached overnight.
March 4	3.0	1.1	75%	6	W	3	
April 5	-0.6	-4.1	95%	calm	calm	9	
May 6	1.0	5.2	80%	5	N	5	
June 5	12.7	12.7	95%	5	NW	7	
July 6	10.6	7.0	87%	2	NW	6	
Aug. 3	12.7	11.6	83%	2	NW	8	
Sept. 7	8.7	5.5	87%	5	SW	6	
Oct. 6	5.7	0.9	97%	5	SE	7	
Nov. 4	5.8	3.4	72%	5	W	2	
Dec. 3	6.1	3.5	90%	5	SW	4	
<u>1979</u>							
Jan. 4	-0.2	-0.5	91%	4	ESE	7	
Feb. 5	-1.1	-0.5	94%	4	NE	8	
March 6	-2.3	-2.0	95%	5	ESE	8	
April 7	-1.4	-3.7	75%	7	NW	0	
May 4	2.1	-0.3	44%	7	NE	1	
June 6	9.4	4.9	75%	5	NW	7	
July 5	9.4	7.4	68%	7	W	5	
Aug. 4	15.3	14.3	85%	8	SW	8	
Sept. 5	11.6	10.5	92%	4	SSW	8	
Oct. 6	8.5	7.9	85%	2	SW	7	
Nov. 4	-1.0	-4.0	87%	6	NE	8	
Dec. 3	1.0	-1.0	76%	4	NW	4	
<u>1980</u>							
Jan. 6	-1.6	-3.5	75%	3	NW	8	
Feb. 5	-0.1	-3.4	83%	3	SW	8	

Appendix C

Population statistics

1. Lincoln Index (Bailey 1952)

$$N = \frac{N1 \times N2}{r21}$$

N1	Total No captured on day 1
N2	Total No captured on day 2
r21	marked on day 1 and recaptured on day 2.

2. Bailey's Triple Index

a2 No. of newly marked animals released on day 2

n2 Total no. animals captured day 2.

r Recapture representing day of capture and second day of marking.

e.g. r21 total no. captured day 2 that were marked on day 1.

r31 No. captured day 3 marked on day 1.

r32 Total no. captured on day 3 that were marked on day 2.

$$\frac{a2 \times n2 \times r31}{r21 \times r32} = P$$

Table 15 Population statistics

Bailey Triple Index Small samples $P = \frac{a2 \times (N2 + 1) \times r31}{(r21 + 1) (r32 + 1)}$

Dates	N1	a2	r21	N2	r32	r31	Bailey Small
14-16 Mar.	17	22	4	26	2	1	39.6
16-19 Apl.	19	26	5	31	3	2	69.3
17-19 May	18	21	4	25	2	2	72.8
16-18 June	9	8	1	9	1	1	20.0
21-23 July	11	14	2	16	2	2	52.9
14-16 Aug.	14	16	2	18	1	1	50.7
18-20 Sept.	26	36	0	36	2	2	888.0
20-22 Oct.	62	39	5	44	9	7	204.8
18-20 Nov.	42	47	4	51	5	2	162.9
18-20 Dec.	10	11	2	13	1	0	51.3
14-16 Jan.							
18-20 Feb.	26	23	2	25	2	1	66.4

APPENDIX D

<u>O.asellus</u>		<u>P.scaber</u>	
l.w. (mg) isopods	Dry wt. pellets	l.w. (mg) isopods	Dry wt. pellets
297.8	1.97	304.6	3.76
316.5	2.46	310.2	4.14
341.7	3.88	317.5	4.42
358.8	3.90	336.2	4.80
361.7	5.63	356.5	5.18
377.9	6.30	360.3	5.51
384.2	7.09	374.5	5.89
401.6	8.21	410.6	6.45
417.2	9.37	421.7	6.83
431.4	9.67	431.5	7.41
459.7	9.83	442.8	7.79
467.3	10.25	451.9	8.17
478.4	10.53	462.7	8.45
489.7	13.04	468.4	8.73
492.6	13.83	473.7	9.21
507.5	16.82	491.3	9.59
518.7	18.09	503.5	9.97
523.4	18.63	520.5	10.35
528.6	19.84	543.7	10.73
530.4		558.4	11.23

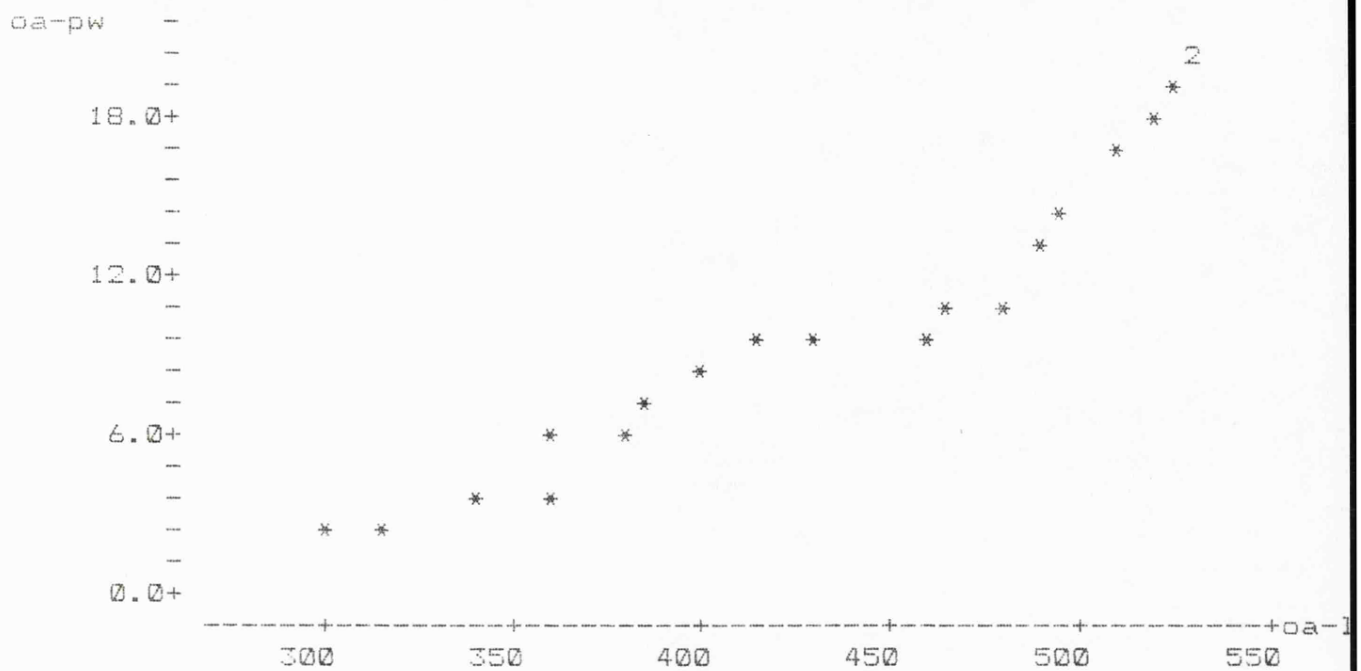
APPENDIX E

1

ROW	oa-lw	oa-pw	ps-lw	ps-pw
1	297.8	1.97	304.6	3.76
2	316.5	2.46	310.2	4.14
3	341.7	3.88	317.5	4.42
4	358.8	3.90	336.2	4.80
5	361.7	5.63	356.5	5.18
6	377.9	6.30	360.3	5.51
7	384.2	7.09	374.5	5.89
8	401.6	8.21	410.6	6.45
9	417.2	9.37	421.7	6.83
10	431.4	9.67	431.5	7.41
11	459.7	9.83	442.8	7.79
12	467.3	10.25	451.9	8.17
13	478.4	10.53	462.7	8.45
14	489.7	13.04	468.4	8.73
15	492.6	13.83	473.7	9.21
16	507.5	16.82	491.3	9.59
17	518.7	18.09	503.5	9.97
18	523.4	18.63	520.5	10.35
19	528.6	19.84	543.7	10.73
20	530.4	20.21	558.4	11.23

	N	MEAN	MEDIAN	TRMEAN	STDEV	SEMEAN
oa-lw	20	434.3	445.6	436.5	75.3	16.8
oa-pw	20	10.48	9.75	10.41	5.84	1.31
ps-lw	20	427.0	437.1	426.5	78.5	17.5
ps-pw	20	7.431	7.600	7.423	2.343	0.524

	MIN	MAX	Q1	Q3
oa-lw	297.8	530.4	365.8	503.8
oa-pw	1.97	20.21	5.80	16.07
ps-lw	304.6	558.4	357.5	486.9
ps-pw	3.760	11.230	5.262	9.495



Correlation of oa-pw and oa-lw = 0.961

The regression equation is
 $oa-pw = -21.9 + 0.0745 \text{ } oa-lw$

Predictor	Coef	Stdev	t-ratio
Constant	-21.879	2.228	-9.82
oa-lw	0.074510	0.005058	14.73

s = 1.661 R-sq = 92.3% R-sq(adj) = 91.9%

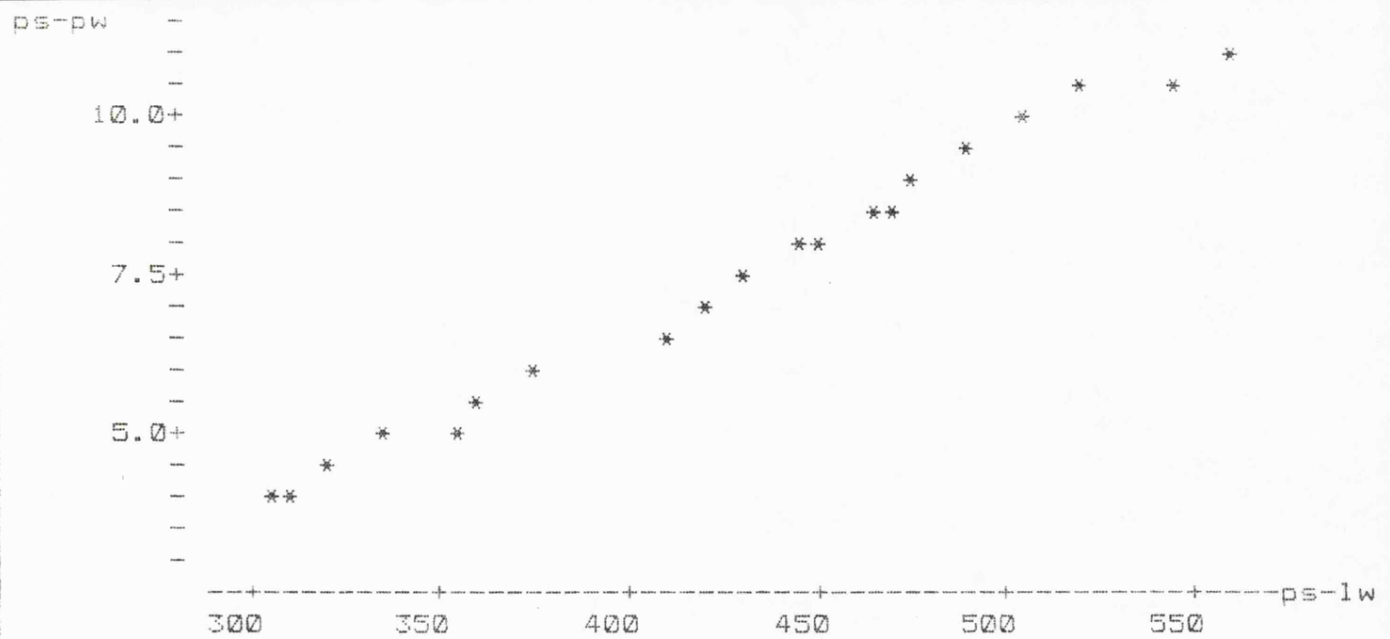
Analysis of Variance

SOURCE	DF	SS	MS
Regression	1	598.55	598.55
Error	18	49.65	2.76
Total	19	648.19	

Unusual Observations

Obs.	oa-lw	oa-pw	Fit	Stdev.Fit	Residual	St.Resid
13	478	10.530	13.767	0.433	-3.237	-2.02R

R denotes an obs. with a large st. resid.



Correlation of ps-pw and ps-lw = 0.995

The regression equation is
 $ps-pw = -5.26 + 0.0297 \text{ ps-lw}$

Predictor	Coef	Stdev	t-ratio
Constant	-5.2582	0.2919	-18.02
ps-lw	0.0297143	0.0006728	44.17

s = 0.2301 R-sq = 99.1% R-sq(adj) = 99.0%

Analysis of Variance

SOURCE	DF	SS	MS
Regression	1	103.31	103.31
Error	18	0.95	0.05
Total	19	104.26	

Unusual Observations

Obs.	ps-lw	ps-pw	Fit	Stdev.Fit	Residual	St.Resid
8	411	6.4500	6.9424	0.0526	-0.4924	-2.20R

R denotes an obs. with a large st. resid.

APPENDIX F

Identification of Cuticular Plant Remains in Faeces.

Of the food potentially available to an animal, only a small proportion is usually consumed. Highly selective consumers tend to achieve a high assimilation - consumption ratio because their food usually contains more nourishment and because they are better adapted to digest it. Non-selective feeders such as many detritus-consumers have much lower assimilation efficiency (Balogh, 1958).

A variety of approaches have been used in investigating the selection process by consumers such as direct observation in the field, gut content analysis, laboratory studies of food preference and the identification of cuticular plant remains in faeces. (Petrusewicz K. and Macfadyen, A. 1970). In addition to the laboratory studies of food preference described above some preliminary investigations were undertaken of the faecal pellets of woodlice which has not been attempted before. Work has been carried out on sheep by Martin (1964) who detected a regular yearly sequence of preferences in the species chosen. Healey (1965) worked with microarthropods. Similar methods have been widely used in the analysis of remains in the pellets rejected by carnivorous birds (Southern 1954). More recent work suggests the possibility of further improvements in the classification and identification of plant remains. In particular Stewart (1967) describes an improved technique for analysing plant epidermis in large herbivore faeces whilst the development of the scanning electron microscope, (Oatley (1966), provides an extremely rapid method of examining surface features at high resolutions. However, only materials which have survived the processes of digestion remain in the faeces and other rejecta and many of the more digestible foods do not leave traces.

Examination of faecal pellets confirmed what the animals were eating and showed how little this material was broken down. Micro-photographs were taken of parts of faecal pellets of woodlice (Plates 1-4) and these show quite clearly that woodlice alter the food that has passed through the gut very little. The food has not been subjected to digestive processes for long as part of the food is still green in the pellet, and nuclei, which are easily broken down, are clearly visible. It appears that woodlice feed on soft cellulose materials whilst the more woody materials such as tracheids and vegetable fibres are left.

The following plant remains are clearly visible and certain parts can be identified.

Plate 3 Leaf of moss, lateral root, tracheid, vascular tissues.

Plate 4 Leaf of moss showing thin cell walls with nuclei visible.

Plate 1 Algal spores and fungal lymphae.

Plate 2 Root tip or bud scales. Tracheid.

In plates 5, 7, 8 humus and grit are discernable. More work needs to be done on this subject and it should not be difficult to construct a key for faecal pellet analysis. Chemical tests would show if material was lignin, cutin or cellulose. Animals could be confined in dishes on one food type and their faeces analysed which would help to confirm analysis of pellets from the environment.

Plate 1 Micro-photograph of faecal pellet of
Porcellio scaber showing algal spores
and fungal hyphae.

Plate 2 Micro photograph of faecal pellet of
Porcellio scaber showing root tip or
bud scales and tracheid.

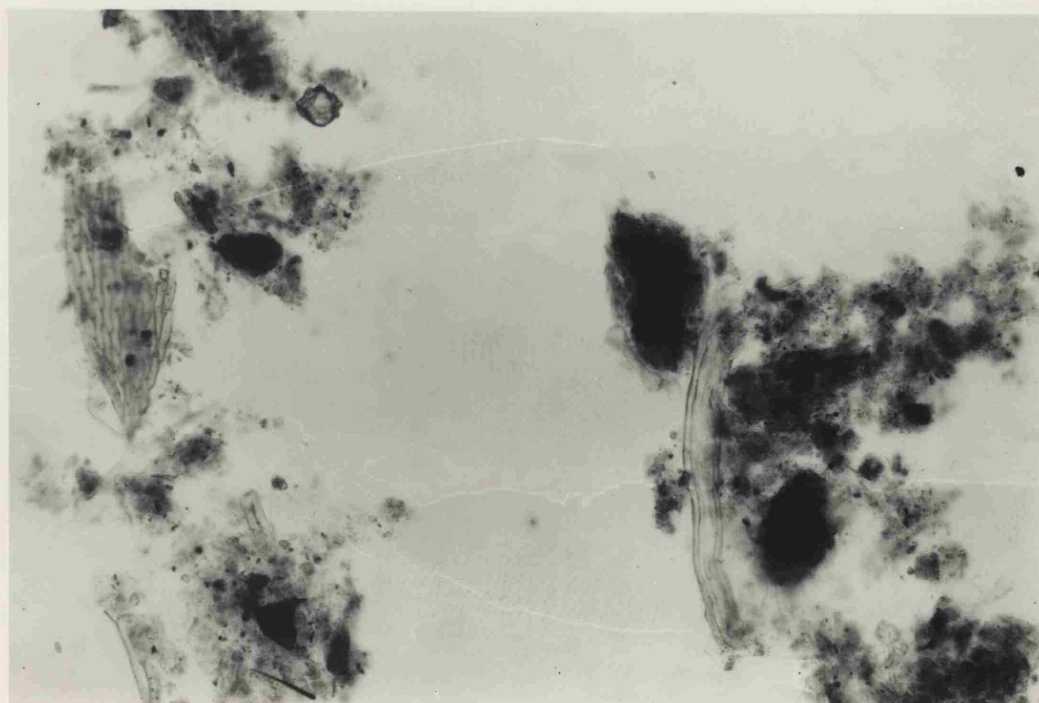
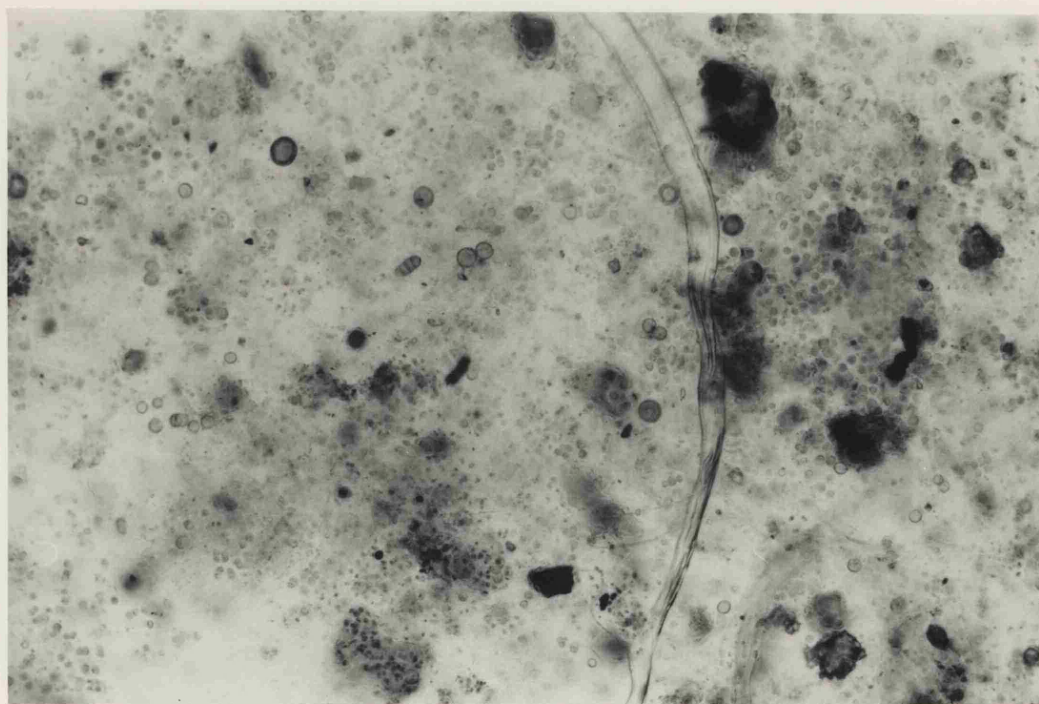
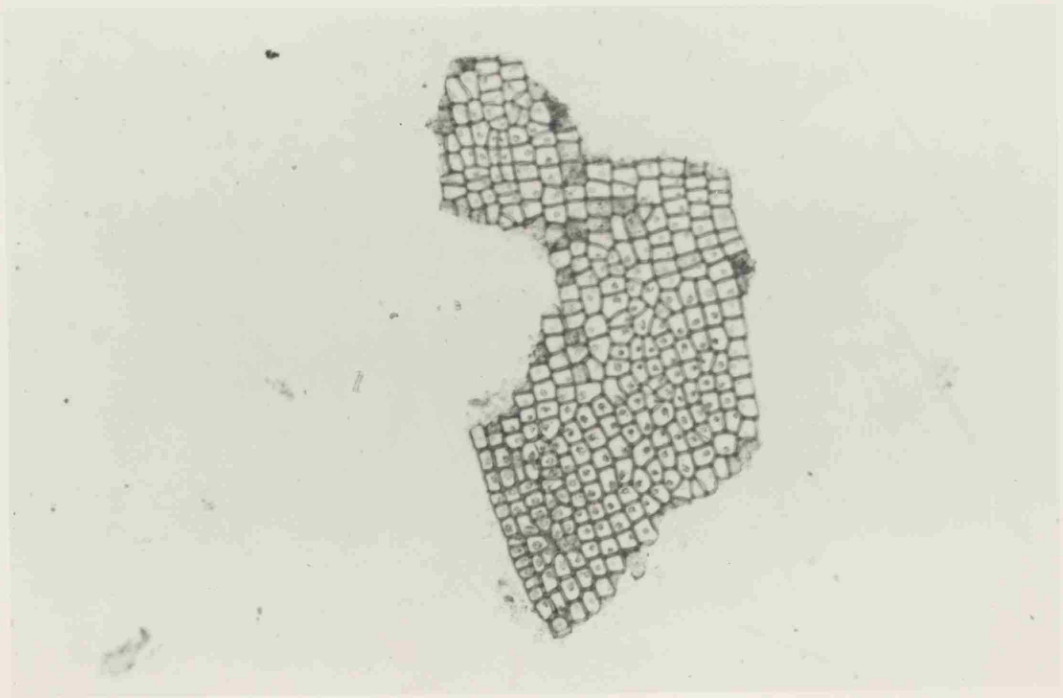
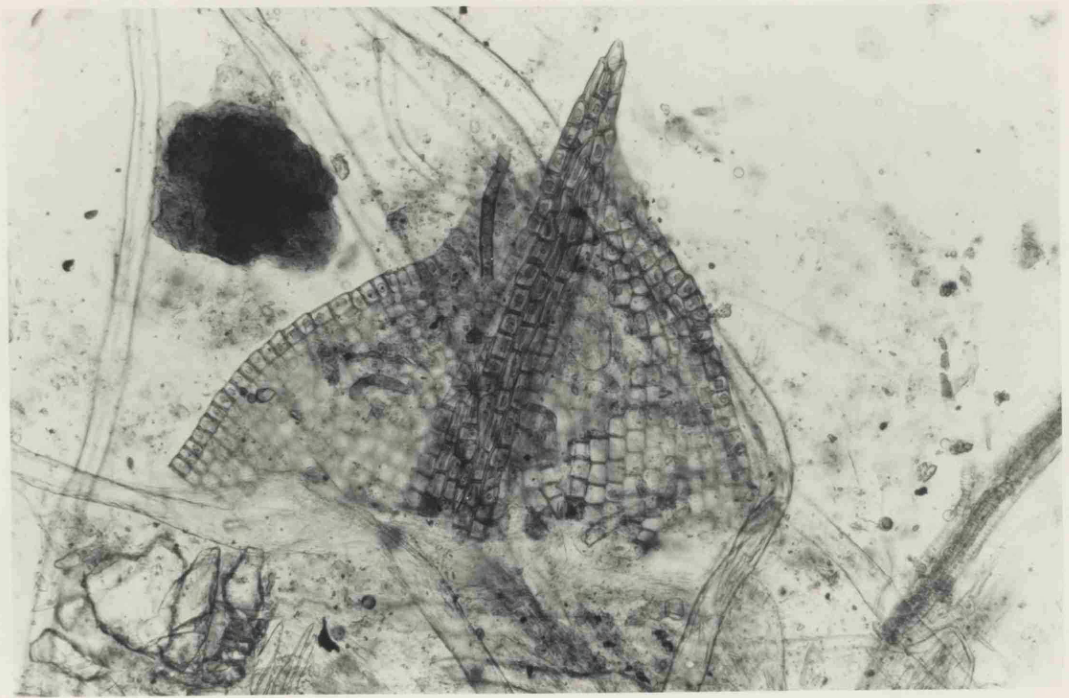


Plate 3 Micro photograph of faecal pellet of
Oniscus asellus showing leaf of moss,
lateral root, tracheid, vascular tissue.

Plate 4 Micro photograph of faecal pellet of
Oniscus asellus showing plant cell
walls with nuclei.



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