THE ECOLOGY OF ASELLUS AQUATICUS (LINNEUS) 1758
AND A. MERIDIANUS RACOVITZA 1919

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by

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TEXT CUT
OFF IN
ORIGINAL

The ecology of *Asellus aquaticus* (Linneus) 1758 and *A. meridianus* Racovitza 1919.

There are three species of the freshwater crustacean gen *Asellus* in Britain: *A. aquaticus*, *A. meridianus* and *A. cavati* The first two of these species are common and widely distribu, occurring in a variety of surface freshwater local the last is confined to subterrenean waters, and occurs only i southern England and Wales. Previous researches ha shown that *A. aquaticus* and *A. meridianus* may occur either together, or alone; and, furthermore, that apparently suita localities may contain neither species. No satisfactory hypothesis has hitherto been advanced to explain this differ distribution.

The primary aim of the present research was to provide such an explanation.

For this purpose, detailed studies were made of the geographical distribution, the life-cycle and the biotic potential of the species, and less detailed studies were made of the specific differences and similarities in food, microhabitat, vertical distribution and tolerance to dessication, low concentrations oxygen and high temperatures. Studies were also made of the distribution of the two species in the Merseyside area and in Lake Windermere, of the temporal change in the specific ratio at Llyn Llywenan, Anglesey, and at Hatchmere, Cheshire, and o the differences and similarities between localities containin both, only one, or neither of the species. Finally, a number of laboratoty experiments were undertaken, and these were designed to investigate whether the survival rate of either species differed when the species were reared separately and when they were reared together.

It is suggested that the following conclusion would appe to be the most likely one that can be drawn from the detailed results of the research:

A. meridianus was present in Britain before A. aquaticus and became widely distributed during the early post-glacial period. A. aquaticus arrived in Britain in comparatively re post-glacial time, and is now replacing A.meridianus, with wh therefore, it is in competition.

"Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world." (Charles Darwin, 1859, p.6.)

CONTENTS

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INTRODUCTION.

1. Interspecific competition.

One of the basic tenets of Darwin's theory of evolution is that 'competition' is of fundamental importance in nature: "A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its lifetime produces several seeds or eggs, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principal of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either, one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. "(1859 p.63). Crombie (1947) has summarized Darwin's definition of 'competition' (1859 p.62-3) as "the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply". However, Crombie seems to have interpreted Darwin too narrowly for on p.62 Darwin says, "I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny."

Darwin also concluded that the severity of competition would depend upon the degree of relationship between the competitors: the closer the relationship, the more severe the competition; conversely, the less the relationship the less severe the competition (1859 p.76). Darwin's conclusions concerning interspecific competition were extended by Lotka (1925) and Volterra (1926), who, independently, predicted on the basis of theoretical equations that where two or more species utilized the same resources only one could survive.

Grinnell (1904: quoted Udvardy 1959) had, by empirical methods, and somewhat earlier, arrived at virtually the same conclusion. He says (1904: p.375-6), "it is only by adaptation to different sorts of food, or modes of food getting, that more than one species can occupy the same locality. Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other". Unfortunately Grinnell's conclusions escaped the attention of contemporary biologists and it is only recently that Udvardy (1959) has redirected our attention to their fundamental nature.

An experimental confirmation of Lotka and Volterra's postulates was put forward by Gause in 1934. He was able to show that the results of experiments in which various species were cultured together could be interpreted in the light of Lotka and Volterra's equations. Gause himself does not appear to have formulated any general conclusions, based upon these results, but he was obviously aware of their implications, as he says (p.19), "as a result of competition two similar species scarcely ever occupy similar niches". However, the general hypothesis relating the existence of species and the extent of interspecific competition has become known as "Gause's hypothesis" or 'Gause's theorem', although recently other names have been proposed as being more appropriate: Hutchinson (1957) suggests 'the Volterra - Gause principle' and Udvardy (1959) suggests 'Grinnell's axiom'. For convenience it has been decided to retain here the name of 'Gause's hypothesis'.

Various statements of Gause's hypothesis have been put forward. At the Easter symposium of the British Ecological Society in 1944, Gause's hypothesis was read as 'two species with similar ecology cannot live together in the same place' (Anon. 1944). Lack (1945) says, "Gause contends that two species with similar ecology cannot live in the same area". Later (1947) he interprets Gause's hypothesis as; "two species with similar ecology cannot live in the same region"(page 62); "two animal species with the same ecology cannot live in the same region" (p.140); "two species with similar ecology cannot live together" (p.142).

Allee et al. (1949 p.660) interpret Gause's hypothesis as; "no two species in the same habitat have the same ecology". Hutchinson and Deevey (1949 p.342) state Gause's hypothesis as; "two species with the same niche requirements cannot form mixed steady state populations in the same region". Hutchinson (1957 p.417) suggests that Gause's hypothesis can be generalized and extended to the conclusion that, "two species when they co-occur, must in some sense be occupying different niches". Williamson (1957 p.422) notes; "Gause's hypothesis is often stated so as to imply that two species cannot remain in competition indefinitely".

All of these definitions have been criticized. Gilbert, Reynoldson and Hobart (1952), for example, criticizing the earlier ones, point out the subjective and arbitrary meaning of 'similar or same ecology'. The lack of emphasis on competition or of time are also important criticisms.

There is no doubt that a satisfactory definition is fraught with difficulties, but Hutchinson (1957) has presented a formal abstraction which appears to have circumvented many of these. He equates the species niche (a term which itself has been the subject of much teleological controversy (see Udvardy (1959)) to an 'n-dimensional hypervolume' in which each dimension corresponds to an environmental parameter.

He calls this hypervolume 'the fundamental niche'. Where the fundamental niches of two species intersect competition will occur in the volume of intersection, and here only one species is favoured.

There are a number of theoretical cases where it would be expected that Gause's hypothesis would not apply. Skellam (1951) has shown that where one species replaces another in competition but is inferior to its competitor in ability to disperse, and that more than enough positions are available for colonization, then both may survive. The same situation had, independently, been envisaged by Hutchinson (1951) who called the species which was inferior during actual competition a 'fugitive species'. Species would also be expected to co-exist if their numbers were regulated primarily by density independent factors for, logically, if the presence of an individual of the same species has no affect upon the population density then the presence of a similar species is also unlikely to have any affect. Co-existence would also be expected if no resource was in short supply or where changes in the environment occurred such that the first one species was favoured and then another. Hutchinson (1949) suggested that this might be the explanation of why no single planktonic species becomes dominant in the epilimnion of lakes. It is suggested that even a difference in size itself may allow related species to co-exist (Huxley 1942, Brooks 1950, Hutchinson 1951). Williamson (1957) has presented a number of mathematical cases where competing species could co-exist. He noted that his conclusions could be generalized to the proposition that it is possible to have as many species as controlling factors. He noted also that two competing species could co-exist even if there were only a single controlling factor, providing this exhibited a 'preference'. The example quoted by Williamson was two species of snail controlled by a bird which preferred whichever snail was the most common.

Two approaches have been made to test the validity of Gause's hypothesis; the experimental approach and the observational approach.

Most of the experimental work has been carried out with graminivorous beetles but Drosophila, Daphnia and other animals have also been used. The results gained by Birch (1953, a,b,c), Birch, Park and Frank (1951), Crombie (1943, 1944, 1945), Park (1948 etc.), and many others, indicate that where two or more species utilize the same limited resource, only one survives. Nevertheless, as Park's experiments in particular have indicated, the results of interspecific competition, even under identical conditions, may be the result of only statistical probability: even the slightest variation in the experimental conditions such as a change in the humidity, or an alteration in the initial ratios of the competitors, may reverse the outcome of competition. Re-examination of experiments in which it at first appeared that competitors could co-exist has always revealed the presence of more than one available niche. L'Heritier and Tessier (1935), for example, reported the co-existence of equilibrium populations of *Drosophila funebris* and *D. melanogaster*. But Merrell (1951) repeated this experiment and demonstrated that the *Drosophila* occupied two slightly different niches.

However, the environmental factors in nature are not only extremely numerous but also undergo wide variations, and, therefore, the experimental conclusions in no way prove the validity of Gause's hypothesis in nature. As Hutchinson (1957 p.418) so succintly puts it, "it would of course be most disturbing if confirmatory models could not be made from actual populations when considerable trouble is taken to conform to the postulates of the deductive theory".

In the observational approach the delimitation of specific niches of congeneric sympatric species has been of especial interest. The results, however, are some what contradictory. The work, for example, of Lack (1944, 1946, 1947) on various species of birds, of Hartley (1953) and Betts (1955) on titmice, of MacArthur (1958) on warblers, of Kohn (1959) on *Conus*, of

Dobzhansky et al. (1956) and da Cunha et al. (1957) on Drosophila, and of Hartman (1957) on Clionidae indicates that where two or more closely related species co-exist, there is a difference in the niche occupied by each.

On the other hand the work, for example, of Ross (1957) on aphids, or Eltringham and Hockley (1958) on Limnoria, of Diver (1940) on Syrphus and Sphaerophoria, and of Fryer (1957, 1959) on certain copepods and cichlid fishes indicates that Gause's hypothesis may not always apply in nature. It seems, in fact, that under certain circumstances congeneric species may exist sympatrically.

Two rather different empirical approaches have been made by Elton (1946) and MacArthur (1957). Elton (1946) analysed the data from a number of ecological surveys and concluded that the average number of species per genus in small communities was less than the same ratio in larger communities. He explained this difference on the grounds of interspecific competition between related species. Elton did not, however, allow for the random distribution of species in differently sized samples, and his data, on re-analysis by Williams (1947) in fact showed exactly the opposite; there were rather more species per genus in small communities than were expected.

For groups of sympatric species MacArthur (1957) plotted the mathematically derived curve relating the species abundance to the species rank (that is to say its position in the scale of commonness and rareness) if niches are either overlapping or non-overlapping. He found that the data from many bird censuses fitted more closely the curve for non-overlapping niches than the curve for overlapping niches. Kohn (1959) has applied data collected from multispecific associations of Conus and also finds that in certain cases there is a close correlation between the mathematically derived curve of non-overlapping niches and his empirical curve.

One may only conclude from the available evidence that Gause's hypothesis, as a wide generalization, seems to be true; that where related species co-exist there is usually a difference in the niche occupied by each. Those species which do not conform to Gause's hypothesis have been termed 'opportunistic species' by MacArthur (1960).

Most animal populations, therefore, appear as if inter-specific competition[1] is regulating their structure. But most

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[1] Footnote 1. In order that no confusion may arise, it is important to note here that the term interspecific competition is used in Birch's sense 1 (1957 p.6), i.e. competition is the process that "occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process".

of the evidence supporting this fact is entirely circumstantial, and it is only by inference that interspecific competition is assumed to be an important factor. In fact, as Andrewartha and Birch (1954) point out, the empirical evidence may be construed to indicate exactly the opposite; that niche differentiation usually results in interspecific competition being non-existent. Moreover, much of the evidence is concerned with situations in which competition would seem to have occurred, if at all, at some past time, and not with situations in which competition is a current process.
The significance, therefore, of interspecific competition as an actual and extant process in natural populations is still largely unresolved.

Several authors have attempted to indicate for various groups the significance of interspecific competition. For example, Udvardy (1951) concludes that for European birds interspecific competition is of no importance. On the other hand, Larkin (1956 p.335) concludes that while the demonstration of actual competition in fish populations is extremely difficult, "it seems certain that competition does occur as measured by its end product". Hynes (1955) concludes that the present distribution of British fresh-water shrimps may be explained in terms of zoogeography and interspecific competion. Zimmerman

(1960 p.151), however, concludes that in <u>Laccophilus</u> "if competition does exist it is present for only four or five days in the year".

The number of cases in which competition is a demonstrated fact are extremely few. Amongst these must be mentioned Brian's (1952) study of four ant species and Pitelka's (1951) study of humming birds. In both of these studies the aggressiveness of one species to another was shown to be a factor of importance.

It is as a contribution to this gap in our knowledge of examples in which interspecific competition is an <u>actual and extant</u> process that the present research is primarily intended.

2. The problem of the ecology of Asellus aquaticus (Linneus) 1758 and A. meridianus Racovitza 1919.

The existence of localities which contain both *Asellus aquaticus* and *A. meridianus*, as well as localities which contain only one or the other of these species, has been known from the earliest times following the taxonomic separation of the two species in 1919. Dudich (1925), for example, noted that Unwin's (1920) study of the reproduction of '*A. aquaticus*' had been carried out on a mixed population of *A. aquaticus* and *A. meridanus*, and Maury (1927) noted the presence in northwestern France of localities which contained both or either species of *Asellus*. Stammer (1932), also, noted that in the lower Rhine area both species were nearly always found together but that in the upper waters of the rivers of this area *A. aquaticus* usually predominated.

Needham (1942) clearly stated the problem when he wrote (p.73), "researches have shown that in England the areas of distribution of the two species overlap considerably and that in such districts they may be found living together or either may occur alone".

Nobody has hitherto presented a satisfactory explanation of this distribution. But, several suggestions have been advanced. Needham (1942) suggested that one species might possess an advantage in another sort of habitat, or, alternatively, the distribution might be entirely fortuitous. Maury (1927) concluded that it was the conditions in each habitat which determined whether one or the other or both species would be present. He says (p.58), "il y a donc des conditions du milieu qui déterminent l'absence de l'une on l'autre espèce, suivant le cas". The principle environmental factor was thought by Maury to be the temperature. At the British Ecological Society's Easter symposium in 1944 it was suggested that Asellus provided an example of two species with similar ecology which co-exist, constituting, therefore, an exception to Gause's hypothesis (Anon. 1944).

But, in spite of the indirect interest shown in the problem, no detailed ecological work on either species has yet been done. Macan (1954 p.138), referring to a survey of Irish fresh-water loughs, has recently emphasized this gap in our knowledge: "the ecology of Asellus is, as usual, obscure. Its presences and absences could not be explained, and the two places where A. meridianus was found were as unlike as any visited".

It is not intended to review here, in detail, previous research on the genus Asellus. Pertinent work will be referred to as it becomes relevant in the text of the thesis. Briefly, however, previous research has tended to be concentrated along two rather broad lines; the morpho-taxonomical and the physiological. Nevertheless, there is some previous ecological work. The work, for example, of Kaulberz (1913), Unwin (1920), Janke (1926), van Emden (1922), Maercks (1930) and Birstein (1951) is especially worthy of mention. There is also a large number of ecological facts which lie scattered throughout the literature. However, apart from the work of Unwin (1920) who, unknowingly, was probably dealing with A. meridianus as well as perhaps A. aquaticus, most of this previous ecological work is concerned with only A. aquaticus; our knowledge, therefore, of the ecology of A. meridianus is even more limited than it is for A. aquaticus.

Our lack of knowledge of the ecology of A. aquaticus and A. meridianus is surprizing when the commoness in nature of both species is considered. Not only may huge populations of either species be maintained in certain places, but both species (in Great Britain at least) are widespread geographically and both may occur in a wide variety of fresh-water habitats. Although both species seem to prefer still waters both may be found in moving waters. Berg. (1948), for example, recorded A. aquaticus from a part of the R.Susaa in Denmark in which the current was above 50 cm/sec.

Typically, both species are found in normal fresh-waters, but both have been recorded from very soft waters and from brackish waters. Warwick (1959), Redeke (1937) and Holthuis (1954), for example, have recorded *A. meridianus* from brackish habitats. It has also been collected from Loch Ken in Scotland which contained only 0.15 meq/l. of calcium in June 1959. *A. aquaticus* has perhaps an even wider tolerance. Thus, although Thienemann (1913 quoted in Lockwood 1959) recorded *A. aquaticus* from Westaphalian brine pools which contained 434 mM./l. NaCl and Välikangas (1933 quoted in Lockwood 1959) recorded it from a part of the Baltic which contained 103 mM./l. NaCl, it has also been collected from Loch Oich in Scotland in which only 0.12 meq/l of calcium were recorded in June 1959.

In spite of the fact that *A. meridianus* appears never to have been recorded from an organically polluted river, *A. aquaticus* is often one of the commonest animals in such habitats (Hynes 1960), and both species have been collected from polluted still waters.

Not only is our lack of ecological knowledge surprizing when the commonness in nature of both species is considered; it is the more surprizing when one considers also the ease with which both species may be cultured in the laboratory, collected in the field, and quickly and reliably indentified.

The aims of the present research, therefore, are fourfold:

(a) to summarize the scattered literature on the ecology of A. aquaticus and A. meridianus;

(b) to present new data on their ecology;

(c) to attempt to interrelate their ecology in order to explain their distribution in nature;

(d) and to correlate this inter-relationship with contemporary biological thought concerning the significance of inter-specific competition in closely related species.

TAXONOMY

Within the order ISOPODA the loss of a single pair of pleopods in the female is considered to be diagnostic of the sub-order Asellota (Hansen 1904 p.311; Needham 1938 p.127). On comparative morphological grounds, Hansen (1904 p.312) concluded that it is the second pair of pleopods that is absent. However, Racovitza (1919b. p.109) by direct examination of a normal female of A. meridianus, and also by examination of two irregular females of Stenasellus Virei Dollf., indicated that Hansen was incorrect; it is the first pair of pleopods that is absent. Maercks (1930) from a study of intersexes in A. aquaticus, and Needham (1938) from a study of the development of the first and second pleopods of A. aquaticus, likewise concluded that it is the first pair of pleopods that is absent.

Further evidence in support of the views of Racovitza, Maercks and Needham is given by the discovery during the present research of two peculiarly modified intersexes of Asellus, and a number of females of A. aquaticus in which the anatomically first pair of pleopods is intermediate in form between the anatomically first pair of normal female pleopods and the second pair of male pleopods. The two intersexes differ from those studied by Maercks in that the left and right sexual pleopods are dissimilar.

A brief description of the two intersexes is given below:

Inter-sex 1.

A. aquaticus; collected from Buckley Lake, Flintshire, 27th May 1958; length = 8.5 mm.; ovigerous (both left and right oöstegites present); left and right penes present; "first"[1] left pleopod similar in construction to the second pleopod of normal males; "first" right pleopod similar in construction to the "first" right pleopod of normal females.

Inter-sex 2.

A. meridianus; collected from Padeswood, Flintshire, 25th April 1958, length = 9.5 mm.; small oöstegites present on both left and right sides; left and right penes present; "first" left pleopod similar in construction to the second pleopod of normal males; "first" right pleopod similar in construction to the "first" right pleopod of normal females.

Since it would seem more reasonable to assume that in these intersexes each pair of left and right pleopods has developed from the same abdominal segment, rather than from a different one, it must be concluded that the "first" pair of pleopods in the female is the morphological homologue of the second pair of male pleopods.

Figure 1 pp3 shows the form of the "first" pleopod in a number of specimens of A. aquaticus. The specimens are regarded as females as in all of them penes were absent and brood pouches or regressed oöstegites were present.

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[1] Footnote 1. The inverted commas indicate that the pleopod is anatomically the first.

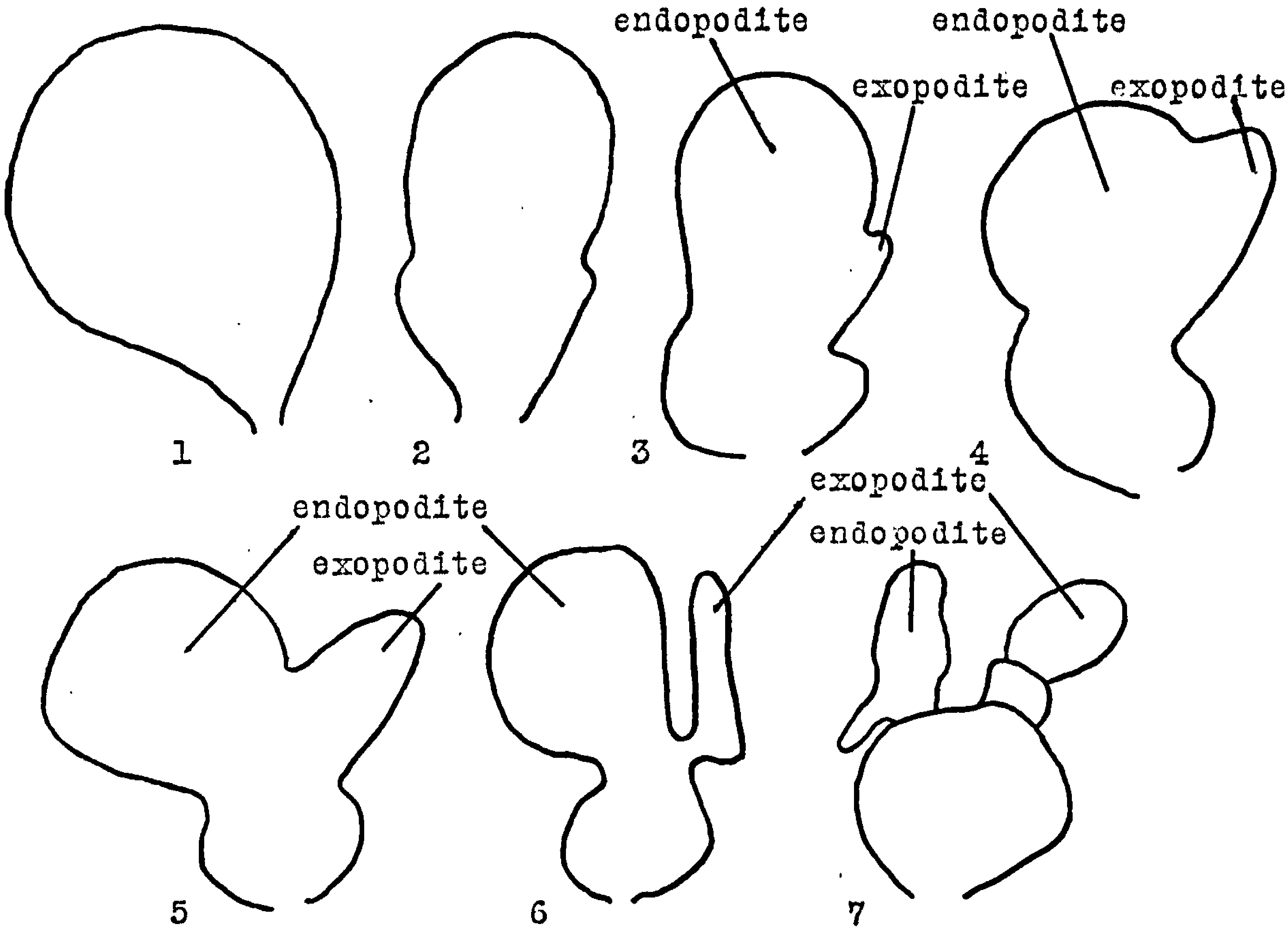


Fig. 1. Diagram illustrating the form in A. aquaticus of the "first" left pleopod in a normal female, and in several abnormal females; and the form of the second left pleopod in a normal male.

(drawings are not to the same scale)

Explanation of figure:

1. The "first" left pleopod in a normal female.
2-6. The "first" left pleopods of females collected from the following places on the date indicated.
2. Reading (Berkshire); 9th Dec. 1958.
3. Hatchmere (Cheshire); 13th Aug. 1959.
4. Hatchmere (Cheshire); 16th Nov. 1959.
5. Hatchmere (Cheshire); 30th Nov. 1959.
6. Hatchmere (Cheshire); 16th June 1959.
7. The second left pleopod of a normal male.

It can be seen from figure 1 that pleopods 2-6 show a continuious series of intermediates between the "first" pleopod of normal females and the second pleopod of males. The occurrence of these intermediates indicates, a posteriori, that the "first" pair of female pleopods and the second pair of male pleopods is homologous.

Racovitza (1919b. p.112) regarded the second female pleopod (i.e. the "first" female pleopod) as the fusion of a protopodite and an exopodite. Maercks (1930), however, concluded that the distal portion of the pleopod is principally derived from an endopodite. A study of Needham's (1938, p.131-136) drawings of the developing male second pleopod of A. aquaticus, and a study of the series of pleopods intermediate in form between the female "first" pleopod and the male second pleopod (figure 1, 2-6) are clearly in support of Maercks views; the distal portion of the female "first" pleopod is principally derived from an endopodite.

The sub-order Asellota has recently been estimated (Waterman 1960) to contain over 500 species. These comprize both marine and fresh-water forms, but within the family Asellidae only fresh-water species are encountered. According to Birstein (1951), the exact time of origin in freshwater of the family is completely uncertain, as there is a total lack of paleaontological data and of intermediate forms linking the Asellidae with the related marine Parasellidae.

The family Asellidae is divided by Birstein (1951) into five genera: Stenasellus, Synasellus, Johanella, Lirceus and Asellus. The genus Asellus was created by Geoffroy Saint-Hilaire (1764 p.672; quoted by Racovitza 1919), but the type species had earlier been summarily described by Linneus (1758) under the name Oniscus aquaticus. Despite subsequent controversy, the type species became referred to as Asellus aquaticus (Linneus) 1758.

Up to the year 1919 all specimens of Asellus were ascribed to only two species: A. aquaticus and A. cavaticus Schiödte. But, in 1919 the species "A. aquaticus" was re-examined by Racovitza who concluded that more than one species had been confused under this name: "Asellus aquaticus auctorum est un grave erreur taxonomique et non une espèce. Sous ce nom consacré par de nombreux lustres, se cache un mélange de formes disparates, d'origine diverse et de valeur taxonomique multiple" (p.33). Racovitza regarded those species which had formerly been ascribed to "A. aquaticus" as being divisible into two quite distinct lines. The type species of the two lines were carefully described by him and designated A. aquaticus L. (sic) and A. meridianus nov. sp. The most salient differences between these species were shown to be in the 1st and 4th male peraeopods, the 1st and 2nd pleopods, the "first" (see footnote 1. p 2.2) female pleopod, and the number of plumose setae on the inner lobe of the 1st maxilla of both sexes.

The difference between the two species were clearly regarded by Racovitza (1919 p.34) as being at least subgeneric value. However, the actual elevation of the two lines to the status of subgenera was undertaken by Dudich (1925). For the line of which *A. aquaticus* was the type species he created the subgenus *Asellus sensu stricto*; for the line of which *A. meridianus* was the type species he created the subgenus *Proasellus*. *A. cavaticus* was regarded by Dudich as belonging to the subgenus *Proasellus*.

Further new subgenera have been created by Stammer (1932; *Baicalasellus* and *Conasellus*), Birstein (1951; *Mesoasellus*), and Karaman (1952; quoted in Chappuis 1953; *Subasellus*, *Arcasellus*, and *Coxasellus*).

The taxonomic validity of these subgenera has been questioned by Chappuis (1953, 1955). He was especially critical of the characters used by Karaman in erecting the subgenera *Subasellus*, *Arcasellus*, and *Coxasellus*: "Il me faut protester énergiquement contre ce mode de procéder. Faire une révision du genre basée sur les nouveaux caracteres choisis par Karaman est chose impossible" (1953 p.68). Chappuis (1953) concluded that the most reasonable taxonomic procedure seemed to be to disregard all subgenera, and merely to divide the genus into groups of species. Bresson (1955) agreed with Chappuis in that she refused to accept the subgenera Subasellus, Arcasellus and Coxasellus, but she thought that it was necessary to retain the subgenera Asellus s.s., Proasellus, and Baicalasellus. Of the remaining two subgenera, she made no reference at all to one, Mesoasellus, and the other, Conasellus, she regarded as synonymous with Proasellus.

Since Racovitza's (1919) revision of the genus, very many new species and subspecies have been described. Most of these have been referred to the subgenus Proasellus, but it is difficult at present to draw satisfactory conclusions as to the validity of many of them, and to the value of the criteria which have been used in the delimitation of subgenera. Little is known, for example, of the extent of individual variation, or of the extent of genetical isolation. However, our limited knowledge of individual variation does perhaps indicate that taxonomic categories have been interpreted too narrowly. Thus, Roubault (1954), by altering the salinity of the water, was able to transform specimens of A. banyulensis Rac. into specimens which were almost indistinguishable from those of A. coxalis Dollf. Moreover, brief studies undertaken during the present research revealed that phenotypic variation could, to some extent, account for the difference between A. meridianus and its subspecies A. meridianus belgicus Arcangeli, and between A. aquaticus and A. aquaticus forma cavernicola Rac.

A. meridianus belgicus is separated from the typical form of A. meridianus by differences in the chaetotaxy of the 1st and 2nd male pleopods and by other minor differences.Table 1. p.2.9 shows the number of setae on the 1st and 2nd male pleopods of specimens of A. meridianus from Padeswood (Flintshire), and on the 1st and 2nd male pleopods of the type species of A. meridianus described by Racovitza (1919), and the type species of A. meridianus belgicus described by Arcangeli (1935). The data on A. meridianus from Padeswood were obtained from specimens collected on the 27th March 1958, and ranging in size from 4.5 mm. to 9.5 mm. in length, and from adult specimens collected on the 25th July 1958, the 29th September 1958, the 28th November 1957, and the 29th January 1958. Specimens of different size, and collected at different seasons were used in order to give an as wide as possible indication of phenotypic variation.

The small size of the specimens (length = 5mm.) from which Arcangeli described A. meridianus belgicus may also account for

TAXONOMIC CHARACTER	A	B	C
Number of pegs on the basipodite of the 1st male pleopod.	1-2	1	1
Number of setae on the outer-edge of the distal segment of the 1st male pleopod.	13-25	20-22[1]	5[2]
Number of feathered setae on the inner edge of the basipodite of the 2nd male pleopod.	1-6	3	2
Number of feathered setae on the distal edge of the exopodite of the 2nd male pleopod.	7-20	14	8-9

Table1. The number of setae on the 1st and 2nd male pleopods in A. meridianus from Padeswood (Flintshire), of the type species of A. meridianus, and of the type species of A. meridianus belgicus.

Explanation of Table:

A = number recorded for A. meridianus collected from Padeswood (Flintshire).

B = number recorded for the type species of A. meridianus by Racovitza (1919).

C = number recorded for the type species of A. meridianus belgicus by Arcangeli (1935).

1 Racovitza quoted the number of setae as 20-22 but drew 26 (p.40 fig.10,1919).

2 Although two of these setae were feathered, and feathered setae were neither found in Padeswood specimens of A. meridianus nor drawn by Racovitza for A. meridianus, Needham (p.64 1942) noted that feathered setae could occur here in A. meridianus.

some of the differences between the chaetotaxy of A. meridianus belgicus and A. meridianus, for a study of the development of the male pleopods of A. meridianus (Needham 1942) indicates that small specimens possess fewer setae than larger ones.

A. aquaticus differs from A. aquaticus forma cavernicola in the absence of eyes and body pigment. However, in a sample from a cave in Burgenland (Austria) sent to me by Dr. H.Löffler, every gradation existed; some specimens possessed both eyes and pigment; other possessed eyes but lacked pigment; and yet others lacked both eyes and body pigment.

Variation in taxonomic characters has been recorded also by other authors. Cooper (1925), for example, dealing with A. aquaticus, referred to variation in the number of plumose setae on the inner lobe of the 1st maxilla, and noted that the triangular apophysis on the 1st peraeopod of males "is not of great value as it varies greatly with age". Yet both of these characters were used by Dudich (1925) in the delimitation of the subgenus Asellus s.s.

The most stable and reliable taxonomic character would appear to be the conformation of the tip of the endopodite of the 2nd male pleopod. Both Braga (1948) and Chappuis (1949, 1953) have indicated that it is upon this character that most emphasis should be placed, and it was mainly upon the basis of this character that Chappuis (1949) subdivided the subgenus Proasellus into four groups of species.

A few authors have carried out experiments concerning the extent of genetic isolation between species. Vandel (1926) attempted to cross A. meridianus, A. aquaticus and A. banyulensis, and Haemmerli - Boveri (1926) attempted to cross A. aquaticus and A. cavaticus. Both authors failed to obtain any hybrids, although interspecific precopulation was frequently observed. On the other hand, Needham (1942), in order to explain the intersex recorded by Unwin (1920), suggested that A. aquaticus and A. meridianus occasionally interbreed: "The intersex might then be due to interbreeding, which though rare may occasionally occur" (p.76).

A knowledge of the extent to which A. aquaticus and A. meridianus are genetically isolated is especially relevant within the ecological context of the present work. For this reason therefore, attempts were made to cross A. aquaticus and A. meridianus.

On the 15th March 1960 the males and females of five precopulating pairs of A. aquaticus, and five precopulating pairs of A. meridianus, were separated. Each male thus obtained was placed in a petri-dish, together with a little water and an elm leaf. To each petri-dish containing a male *A. aquaticus* was added one of the separated *A. meridianus* females, and to each petri-dish containing a male *A. meridianus* was added one of the separated *A. aquaticus* females. All females were smaller than the male with which they were placed.

The petri-dishes were kept at room temperature (18-22°C). Each interspecific pair was observed at approximately daily intervals, and the sexual condition of the female noted. The daily observations are summarized in diagrammatic form in figure 2. p.2.13.

It can be seen from this figure that interspecific precopulation was observed in two pairs, *A. meridianus* ♂ X *A. aquaticus* ♀, and *A. aquaticus* ♂ X *A. meridianus* ♀. It can also be seen that all females became ovigerous, although the time at which they did varied from 1-14 days after the beginning of the experiment. Three of the ovigerous *A. meridianus* females, and one of the ovigerous *A. aquaticus* females, died whilst still ovigerous. Examination of the eggs contained with the brood pouches of these females revealed that they had undergone no embryonic development. It must, therefore, be concluded that the eggs were infertile; normal eggs, incubated for a similar period of time and at the same temperature would

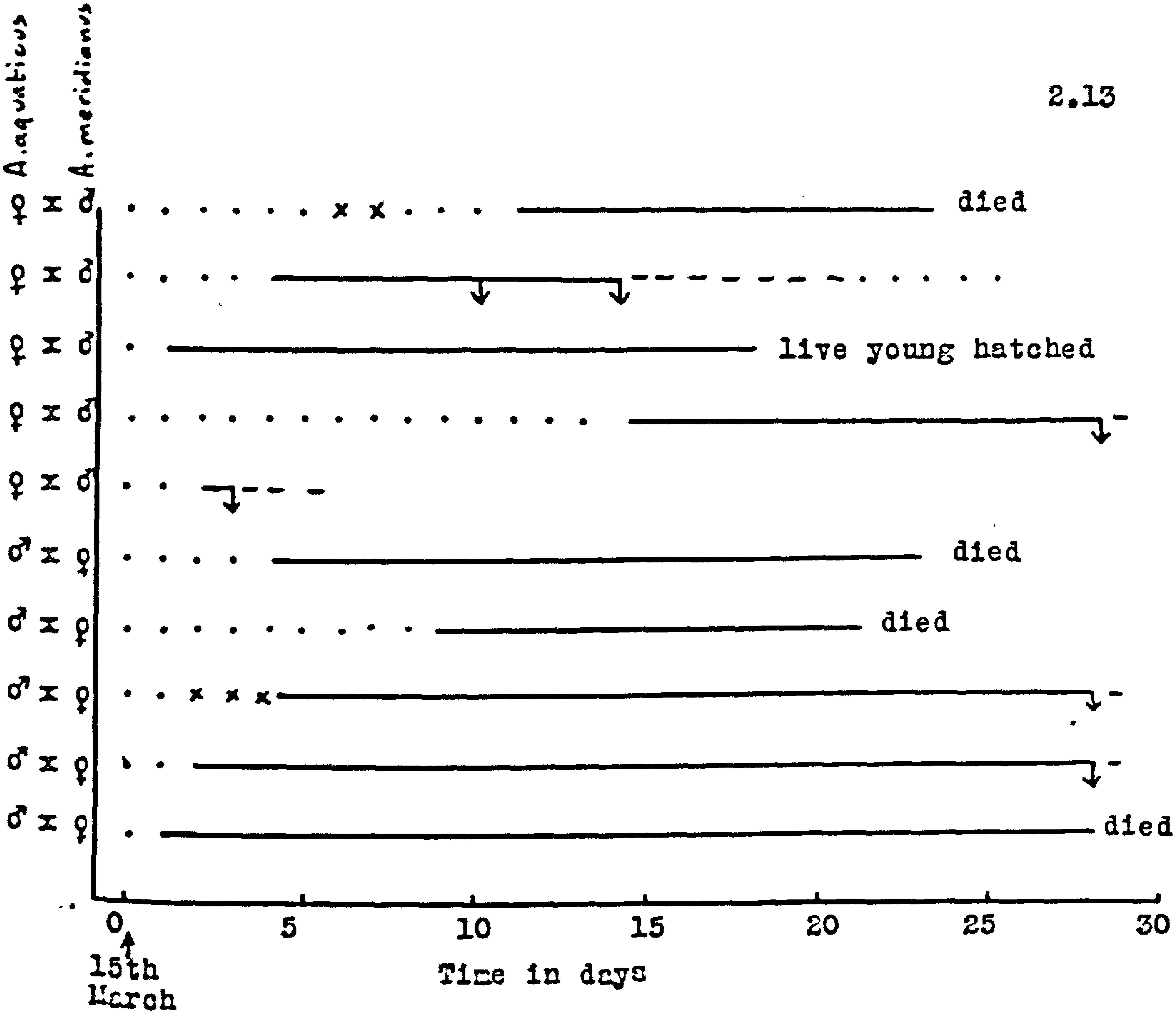


Figure 2. Diagram showing the results of the interspecific crossing experiment.

Explanation of figure.

• • • ♀ with small oöstegites; not in precopulation.

× × × ♀ and ♂ in precopulation.

——— ♀ ovigerous.

— — — ♀ with empty brood pouch.

↴ ♀ dropped all or some eggs.

have clearly shown embryonic development. Three of the ovigerous A. aquaticus females, and the remaining two ovigerous A. meridianus females dropped all their eggs in an undeveloped condition after a varying period of incubation. It must be presumed that these eggs, also, were infertile, for even those that had been incubated for 26 days showed no embryonic development. The remaining ovigerous A. aquaticus female released live young after an incubation period of 17 days. This brood was separated from the female and kept under observation, but, unfortunately, only one specimen survived to an age at which the sexual pleopods were well developed. The sexual pleopods of this survivor proved to be those of a typical A. aquaticus female.

In only one instance, therefore, did any of the females in the interspecific pairs produce a live brood. The eggs of this female must have been fertilized, for the results of Haemmerli-Boveri (1926), and results from the present experiment indicate that unfertilized eggs do not develop. A number of facts suggests that this fertilization was effected by the A. aquaticus male from which the female had been separated, and not by the A. meridianus male with which she then was placed.

It is known from observations during the present research, and also from the work of Unwin (1920) and others, that before copulation and oviposition can occur in Asellus, the female must moult. This moult, the "Parturial - haütung" (Emden 1922), consists of two phases. During the first phase the posterior part of the old cuticle is cast, revealing the open vaginae; during the second phase the anterior part of the old cuticle is cast, releasing the large oöstegites. Introduction of male sperm into the vaginae occurs in the first phase, whilst ovi-position occurs in the second phase. An interval of up to 24 hours between the completion of the two phases has been recorded by Unwin (1920), and an interval of up to four days by Haemmerli-Boveri (1926). However, in a number of precopulating pairs of A. aquaticus and of A. meridianus observed at daily intervals in March 1959, this interval was never more than one day. It can be seen from figure 2 that the female which produced the live young was ovigerous from the very first observation after her separation from the A. aquaticus male, and it is possible, therefore, that this female had cast the posterior part of her old cuticle and copulated with the A. aquaticus male before separation. The lack of live broods from females for which there is no doubt that fertilization did not occur before separation, and the form of the sexual pleopods in the sole survivor of the live brood, also indicate that fertilization of the female which produced the live brood was effected by the A. aquaticus male.

It may be concluded from the experimental results that there is no evidence that *A. aquaticus* and *A. meridianus* interbreed. This conclusion is further supported by information obtained from the field. Thus, although over 9,000 specimens of *A. aquaticus* and *A. meridianus* from two localities where both species occurred were examined in the course of investigations into their life - histories (see chapter 4), none of these specimens, nor the many specimens collected from other localities where both species occurred, ever had intermediate taxonomic characters. Even interspecific precopulation appears to be negligible in the field, for no interspecific pairs were collected during the present research, and there is only a single record in the literature (Vandel 1926) of such a pair. Needham's (1942) suggestion that intersexes in *Asellus* are due to interbreeding must be regarded as incorrect; an examination of all the intersexes discovered during the present research revealed that none of these possessed any indication of intermediate taxonomic characters.

The British species of Asellus.

A. aquaticus and A. meridianus were recorded from Britain by Racovitza (1919) when he first described these species, and soon afterwards were also recorded from Britain by other workers (Tattersall (1920), Chilton (1920), Cooper (1925)). A.cavaticus was first recorded from Britain by Tattersall (1930). Up to 1944 these three species were the only species of Asellus recorded from Britain, but in that year, and in 1945 and 1946, Collinge (1944 a,b, 1945 a,b, 1946 a,b,c.) described four new species of Asellus, and numerous varieties of A. aquaticus. The four new species of Asellus were named A. crypticus, A. hazeltoni, A. patoni, and A. quicki. These new species and the varieties of A. aquaticus described by Collinge cannot be accepted; Birstein (1951), although recognizing A. hazeltoni (= A. collingei Birstein), pointed out that A. crypticus and A. quicki were insufficiently described, and Moon (1953), after a re-examination of Collinge's specimens, concluded that all could be referred to either A. meridianus or to the typical form of A. aquaticus.

Only three species of Asellus, therefore, are known from Britain: A. aquaticus, A. meridianus and A. cavaticus. This statement is supported by a careful morphological study of all specimens of Asellus which were collected from throughout Britain during the investigation into the geographical distributions of *A. aquaticus* and *A. meridianus* (see chapter 3). In this study particular attention was paid to the structure of the 1st and 2nd male pleopods, and these were examined under the low and high powers of the microscope. The study revealed that the few specimens of *A. cavaticus* at my disposal did not differ significantly from those described by Tattersall (1930), and that all specimens of *A. aquaticus* and *A. meridianus* were similar to the type species described by Racovitza (1919).

The lack of any geographical variation in *A. aquaticus* in Britain is not surprizing when the recent origin and post-glacial immigration to Britain of this species is considered. On the other hand, the discovery of some geographical variation in *A. meridianus* would not have been altogether unexpected. Braga (1956), for example, has suggested that a close examination of *A. meridianus* in western Europe will reveal that it is comprized of several forms: "La large distribution atribuée à l'*A. meridianus* dans l'Europe occidentale nous fait soupçonner, vue la diagnose très étroite de cette espèce, qu'il y aura probablement d'autre formes qui ont été confondues avec le type de Racovitza. Ces formes doivent peut-être se traduire en systématique par des coupures de catégorie plus élevée que celle de simples biotypes locaux. Le group d'*A. meridianus* doit être revisé". (p.2).

Some geographical variation in *A. meridianus* has, in fact, been reported by Needham (1942 p.64). He stated that specimens of *A. meridianus* from the north of England differed from the type species in that they possessed feathered setae on the distal segment of the 1st male pleopod. However, Needham's statement is incorrect; such setae are not found in *A. meridianus* from northern England.

Although there are no significant morphological differences between specimens of *A. meridianus* from Britain and from the continent, there may be some chromosomal differences. Thus, Vandel (1937) found that in *A. meridianus* from the continent 2n = 14, and later (1947; quoted by Muldal 1951) that 2n = 16, whereas Muldal (1951) found that in *A. meridianus* from Britain 2n = 10.

A brief key for the separation of the British species of *Asellus* has been recently published (Hynes, Macan and Williams 1960). The species are separated in this key on the basis of their differences in head pigmentation, 1st male peraeopods, 1st and 2nd male pleopods and "first" female pleopods, and on the presence or absence of eyes and pigment. The difference in the pattern of pigmentation on the head of *A. aquaticus* and *A. meridianus* was first observed by Scourfield (1940). This difference is evident in even the smallest specimens, and is especially useful as it allows of specific indentification in the field. Although care is required in its use, it has been found to be over 99% accurate.

Apart from the morphological differences between _A. aquaticus_ and _A. meridianus_ outlined by Racovitza (1919) and Scourfield (1940), there are a number of more subtle differences which distinguish the two. But, none of these is determinative when used alone, and it is only with practice that they are of use. Perhaps the two most evident are head-shape and colour. In general, in _A. meridianus_ the head tends to be smaller in proportion to the rest of the body than does the head of _A. aquaticus_, this difference being especially visible in larger specimens. Furthermore, the front of the head of _A. meridianus_ usually presents a more rounded appearance than does that of _A. aquaticus_. In colour _A. meridianus_ is usually darker than _A. aquaticus_, although Cooper (1925) and Warwick (1959) regarded the opposite to be the case.

GEOGRAPHICAL DISTRIBUTION.

A knowledge of the geographical distribution of closely related species has often proved useful in the elucidation of their ecological inter-relationships. Thus Hynes (1954), for example, infers mainly from zoogeographical evidence that *Gammarus duebeni* Lillj. is excluded from most fresh-waters in England, Scotland and Wales by the presence there of *G. pulex*(L.), for in Ireland, where indigenous *G. pulex* is absent, *G. duebeni* is widespread in fresh-waters. Similarly, Reynoldson (1958a) suggests that *Dendrocoelum lacteum* (Müll.) may be excluded from certain habitats in Britain by the presence of *Polycelis nigra* (Müll.), for in Sweden, where *P. nigra* is absent, *D. lacteum* is found in habitats which in Britain typically contain *P. nigra*. However, Reynoldson (pers. comm.) has not so far been able to demonstrate any actual competition between these two species. Our deductions concerning the interspecific relationships in Britain of the Blue, Irish and Brown hares (Harrison - Mathews 1952), and of the various species of field mice, are also based largely on zoogeographical evidence (Beirne (1952)).

But, whether a knowledge of the geographical distribution of related species is of any deductive value or not, no ecological study can be considered complete without such knowledge.

1. The Distribution of *A. aquaticus* and *A. meridianus* outside Britain.

The geographical extent of *A. aquaticus* outside Britain is indicated in fig. 8, p.3.42, and the details of its distribution in Denmark, western Germany, France and the Low countries in fig. 3a, p.3.37. The geographical extent of *A. meridianus* outside Britain is indicated in fig. 3b, p.3.37. In these maps the distributions of *A. aquaticus* and *A. meridianus* have been plotted in France on a departmental basis and in Denmark, western Germany, and the Low countries on a provincial basis. Where a department or province is completely blacked in this indicates that a definite locality record exists; where it is only vertically hatched this indicates that I am unaware of any definite locality records, but that the species concerned has been recorded from the general area. The maps have been compiled using information obtained from three sources; from a number of collections made in France during the present research; from collections made for me or records sent to me by several foreign and British zoologists; and from records in the literature.

The collections in France were made during August and September 1959, when 105 localities were visited. These localities were mainly distributed along the western coast of

France from Dieppe in the north to Banyuls - sur - Mer in the south. The majority of localities were sluggish streams, but collections were made also from lakes, ponds and rivers. At each locality a stramin hand - net was vigorously pushed to and fro amongst the debris and vegetation present, and the debris thus loosened collected in the net. When it was judged that sufficient debris had been collected it was transferred to a flat enamel dish containing a little water, and carefully searched for specimens of *Asellus*. If *Asellus* was not found in the first collection, two or three collections were made before *Asellus* was presumed absent. Specimens were transferred to a small tube containing 70% alcohol and were identified on arrival back at Liverpool. Of the 105 localities investigated 24 contained only *A. meridianus*; 3 contained only *A. aquaticus*; 2 contained both *A. aquaticus* and *A. meridianus*; 1 contained both *A. aquaticus* and *A. coxalis* (sens. lat.); 3 contained only *A. coxalis* (sens. lat.); and 72 contained no *Asellus*.

Collections of *A. aquaticus* from Germany were made by Dr. H.B.N. Hynes (near Mainz); from Austria by Drs. T.B. Reynoldson (Mondsee) and H. Löffler (Burgenland); and from France by Dr. H.B.N. Hynes (department of Meuse), Prof. J. Legrand (department of Aisne), and Madame Balesdent - Marquet (department of Meurthe-et-Moselle). Collections of *A. merid-*

-ianus from France were made by Dr. H.B.N. Hynes (department of Finistère), Prof. J. Legrand (department of Vienne) and Mons. L. Berner (department of Allier and Ain). Records of the presence of A. aquaticus in Holland have been sent by Dr. L.B. Holthuis, and in France by Prof. J. Wautier (department of Rhône), Dr. P. Aguesse (department of Bouches-du-Rhône) and Mons. A. Roubault (department of Seine-et-Marne). In addition, Dr. Per Brink (Hynes pers. comm.) records A. aquaticus from northern Sweden (Jokkmokk, R. Lule). Records of the presence of A. meridianus in Holland have been sent by Dr. L.B. Holthuis, and in France by Prof. P.A. Remy (departments of Moselle and Lorraine), Prof. P.A. Chappuis (department of Haute-Garonne), Mons. A. Roubault (departments of Seine-et-Marne), and Madame Balesdent - Marquet (department of Meurthe-et-Moselle).

All collections of Asellus from outside Britain have been deposited at the British Museum, London.

Distributional records of Asellus are scattered throughout a wide field of literature, and many records appear as only incidental facts in papers which are not primarily concerned with Asellus. Moreover, many of the earlier records are of dubious validity. The following account of published geographical records of Asellus is not therefore claimed to be an exhaustive one.

A. aquaticus has been recorded from FRANCE by Racovitza (1919), Maury (1925,27), Vandel (1926), Chappuis (1949) and Birstein (1951); from GERMANY by van Kaulberz (1913), Emden (1922), Janke (1926), Maury (1927), Maercks (1930), Stammer (1932), Chappuis (1949), Birstein (1951) and Seitz (1954); from HOLLAND by Redeke (1937), Chappuis (1949), and Holthuis (1954,56) and Smissaert (1959); from BELGIUM by Arcangeli (1938 quoted in Remy 1940) and Chappuis (1949); from DENMARK by Stammer (1932), Berg (1938,48,56), Stephenson (1944) and Dunn (1954); from SWITZERLAND by Carl (1908 quoted by Racovitza 1919), Stammer (1932) and Chappuis (1949); from SWEDEN by Stammer (1932), Brundin (1949) and Chappuis (1949); from NORWAY by Sars (1899), Maury (1927), Stammer (1932) and Chappuis (1949); from AUSTRIA by Birstein (1951); from ITALY by Dudich (1925 synonym *A. arthrobranchialis*), Stammer (1932) and Chappuis (1949); from YUGOSLAVIA by Racovitza (1919), Dudich (1925), Remy (1940), C. and L. Kosswig (1940), Chappuis (1949) and Birstein (1951); from ALBANIA by Monod (1932 quoted in Remy 1940); from POLAND by Dudich (1925a), Stammer (1932) and Urbanski (1947); from ROUMANIA by Chappuis (1949); from HUNGARY by Dudich (1925a), Stammer (1932), Chappuis (1949) and Birstein (1951); from CRETE by Chappuis (1949); from GREECE by Remy (1940), Stephanides (1948) and Chappuis (1949);

from TURKEY by Remy (1940), C. and L. Kosswig (1940), Bresson (1955) and Chappuis (1949); from PERSIA by Remy (1940), Bresson (1955) and Birstein (1951); from the CAUCASUS and MANGISTAN by Birstein (1951); and from European RUSSIA by Tschetwerikoff (1911), Stammer (1932) and Birstein (1951).

A. aquaticus has been recorded also from SIBERIA by Chappuis (1949) and Remy (1940); from CHINA by Shen (1936) and Remy (1940); from LABRADOR by Packard (1867; quoted by Richardson (1905)); and from GREENLAND by Fabricius (1780), Krøyer (1838), Packard (1867), Richardson (1905) and Stephensen (1913). The records of Fabricius, Krøyer and Packard have been quoted from Richardson (1905). As Birstein (1951) points out, however, the east Asian species of _Asellus_ are not _A. aquaticus_ and, although the eastern limit of _A. aquaticus_ has not yet been accurately determined, it is absent from the Urals and is probably not present further east. Similarly, Johansen (1926) has shown that _A. aquaticus_ is not present in Labrador: the record of its presence there is the result of a misidentification. Since _A. aquaticus_ was recorded from neither Iceland nor the Faröes by Poulsen (1937, 1939), the record of _A. aquaticus_ in Greenland seemed inexplicable. Chappuis (1949) and Birstein (1951), both of whom have given recent synopses of the distribution of _A. aquaticus_ have nevertheless perpetuated the early records of its presence there. Birstein (1951) does suggest, however, that it might be a mistake. Because of the interest of this matter I wrote to Dr. Røen who has collected extensively in Greenland. His important reply (1st March 1960) is given in full below:

"The appearance of <u>Asellus aquaticus</u> in Greenland is very doubtful. All statements about finding of the species are from last century, and in fact, these do not seem reliable. I myself never saw the species in Greenland, even though I have examined ab. 250 freshwater localities. I have also contacted the Greenland Fishery Examinations Department; here the stomach contents from a great number of sea trouts has been examined also stocks of trouts wich have never been in salt-water - but traces of <u>Asellus</u> were never found in these stomachs."

"In "Meddelelser om Grønland", vol.22, no.1, pp.239-240 Stephensen gives a summary of the old finding and only in one case there is an indication of place. viz. from the fish cape in S.W. - Greenland. This is one of the places where in the old days sailing ships went to have the water tanks filled up. One might imagine that the water tanks were polluted and therefore had to be cleaned. If <u>Asellus</u> from Denmark were in the water tanks the species might have been thrown out, and later on somebody collected them thinking it was real Greenland species. The mistake can be explained the way that most of the old statements rely on collections made by different people who liked to do the Zoological Museum in Copenhagen a favour. I may add that from the same period a great number of Entomostraca has been stated from Greenland, and these have never been found since".

"Stephensen does give a Greenland name for the species, but the spelling is mistreated in such a way that none of the Greenlander living here in Denmark, whom I have asked the question, was able to tell what it meant. The name may rely on a mistake, which is the case with several Greenland names stated by Stephensen".

It would thus appear that A. aquaticus is probably absent from Greenland.

Birstein (1951) emphasizes the absence of A. aquaticus from the Arctic and especially from the Arctic islands. It has also never been recorded from Africa. In Europe it has never been recorded from the Iberian peninsula, and it was recorded from neither the Balaeric Isles by Margalef (1952) nor from Corsica by Angelier (1957).

Outside Britain A. meridianus has previously been recorded from only France, Germany, Holland and Belgium. From FRANCE it has been recorded by Racovitza (1919), Hubault (1931,34), Poisson (1932), Stammer (1932), Remy (1932), Chappuis (1949) and Hynes (1959); from GERMANY by Stammer (1932); from HOLLAND by Redeke (1937), Holthuis (1954,56) and Smissaert (1959); and from BELGIUM by Arcangeli (1935 subsp. *A. meridianus belgicus*) and Chappuis (1949).

The distribution of *A. aquaticus* and *A. meridianus* in northwestern France is of especial interest because of the relative isolation of parts of this area. Fig.4 p.3.38 shows in diagrammatic form the proportion of the two species in each department of this area. This figure is based mainly upon the records of Maury (1927) and Hynes (1959), and upon collections made during August 1959. Although Maury's records are not strictly comparable with later ones because of the difference in time of collection, the figure does indicate in a general manner that in the peninsulas of Brittany and Normandy and on Sark and Guernsey (Channel Isles) *A. meridianus* is the more common if not the only species of *Asellus* present. A full explanation of the figure and a table indicating the details of the records on which it is based are given on the page facing the figure.

2. The Distribution of *A. aquaticus* and *A. meridianus* in Britain.

Figs. 5 and 6, pages 3.39 and 3.40, show the distribution in Britain of *A. aquaticus* and *A. meridianus*. These figures have been plotted on a vice-county basis. The small arrows at various points along the coastal line indicate that there is a record from an island at that point. Although there exist a number of published distributional records of *Asellus* in Britain, the maps have been compiled almost entirely from recent records. Table 1, appendix A, pages 10.1-10.5, indicates the number of records for each vice-county. Records obtained before June 1960 have been published in map form (Hynes, Macan and Williams 1960). Records have been obtained from four principal sources: from collections made during the present research; from collections made for me and specimens sent to me by numerous amateur and professional zoologists; from collections in the possession of Prof. H.P. Moon; and from collections made by Mr. T. Warwick.[1] A few additional records from collections in the British Museum and from the literature have also been used. In all cases in which specimens were not examined by myself a record was accepted as valid only if it was certain that the person who identified the specimens was clearly aware of the specific criteria.

Footnote 1. Warwick has subsequently published his records (Warwick, 1959).

Collections from various vice-counties were made during the present research as opportunities presented themselves. All collections were made in the manner described on page 3.3. In May 1959 a special expedition to Scotland was undertaken, and during this a total of 69 localities were investigated in 22 vice-counties extending as far north as E. Ross. In addition much valuable information was obtained on the northern occurrence of Asellus from Mr. N.C. Morgan (Fresh-water Fisheries Research Laboratory, Pitlochry), Dr. G. Richter (Gordonstoun) and Mr. T. Warwick, (Edinburgh).

During February 1960 a circular letter requesting the coöperation of amateur naturalists in obtaining vice-county records was sent to the secretaries of all natural history and related societies in vice-counties for which no records were available. These societies are listed in the "Directory of Natural History and other Field Study Societies in Great Britain" (1959). In all 161 letters were mailed. Type specimens were sent when requested.

Many professional zoologists also have coöperated by collecting specimens of Asellus and/or sending information about its absence in particular areas. Their names are included in the acknowledgements.

My entire collection of Asellus from Britain has been deposited at the British Museum, London.

In the literature both A. aquaticus and A. meridianus have been recorded in Britain many times. Amongst those who have recorded A. aquaticus are Racovitza (1919), Tattersall (1920), Chilton (1920), Cooper (1925), Maury (1927), Palmer (1934), Scourfield (1940), Munro (1953), Moon (1953), Macan and Lund (1954), Fryer (1955), Weerekoun (1956), Moon (1957a,b), Tucker (1958), and Lockwood (1959). Amongst those who have recorded A. meridianus are Racovitza (1919), Tattersall (1920), Chilton (1920), Cooper (1925), Maury (1927), Palmer (1934), Humphries (1936), Pyefinch (1937), Scourfield (1940), Dunn (1952), Moon (1953), Galliford (1953), Macan and Lund (1954), Fryer (1955), Davis (1956), Moon (1957a,b), and Tucker (1958). The check - list of Asellus species in Britain produced by W.E. Collinge (Collinge 1946a) has been ignored; Moon (1953) has shown that Collinge's identifications are invalid.

Many of the vice-counties in figures 5 and 6 are blank simply because no collections have been made, and not because Asellus is presumed absent. However, in certain areas in the north of Scotland and on some of the Scottish islands careful searches for Asellus have been made without success. Dr. J.D. Hamilton (pers. comm.) did not find it on St. Kilda, and Mrs.

P.E. Davis (pers. comm.) and Mr. I. Efford (quoted from Reynoldson pers. comm.) have been unable to find it on Fair-Isle. In the Outer Hebrides it was recorded from neither the Isle of Lewis by Elton (1936) nor from Barra by Forest et al. (1936), and Bertram (1939) did not record it from Canna or Sanday in the Inner Hebrides. Furthermore, Reynoldson (pers. comm.) did not find any on Islay, despite a careful search of 20 lakes, and members of the Buteshire Natural History Society were unable to find any on Bute.

On the Scottish mainland Mr. N.C. Morgan (pers. comm.) has made collections from over 30 lochs in western Sutherland without finding Asellus. These lochs included many of the calcareous lochs in the Durness district. Moreover, he was unable to find Asellus in the Strathpeffer and Bonar Bridge area of E. Ross, the Ardnamurchan peninsular of Westerness, in Loch Garry in Easterness, and in eastern Sutherland. Dr. Hynes (pers. comm.) notes the absence of Asellus from the Stoer area of western Sutherland and Mr. T. Warwick (pers. comm.) did not find it in the Arisaig area of Westerness. In addition Dr. Hynes informs me that the late Mr. D.M. Reid was never able to find Asellus in Sutherland despite careful searches.

It would appear, therefore, that Asellus is probably absent from many of the Scottish islands and from most of the

Scottish mainland north of the Great Fault. North of the Great Fault *Asellus* has been recorded from only two localities. Both of these are situated in the lowland area of Caithness and contained *A. aquaticus.*

The number of localities in Ireland from which *Asellus* has been recorded are few; it seems, however, that both species are wide-spread there.

Although it can be seen from the maps (figs. 5 and 6) that the distribution of *A. aquaticus* and of *A. meridianus* in Britain is essentially similar, the maps reveal also that there are a few important points of difference between the distributions of the two species. Thus, on all the western peninsulas of Britain for which positive records of *Asellus* exist, *A. meridianus* would appear to be the predominant if not the only species of *Asellus* present. This is perhaps shown more clearly by the table below, in which all the records of *Asellus* from western peninsulas have been collected together.

Vice-county	Number of positive records:	
	A. meridianus	*A. aquaticus*
Clare	1	1
Galway, W.	1	0
W. Mayo	2	0
Westerness	0	1
Ayr	1	1
Kirkcudbright	3	0
Wigtown	1	0
Carnarvon	4	0
Pembroke	1	0
W. Cornwall	2	0
E. Cornwall	1	0

Similarly all but one of the records of *Asellus* from the offshore islands of Britain are of *A. meridianus*. It is thus the only species recorded from the Isle of Man, Bardsey,Island, Skokholm, Lundy, the Scilly Isles, the Isle of Wight, Guernsey and Sark. Pyefinch (1937), Galliford (1953)and Davis (1956) also note that it is the only species recorded by them from, respectively, Bardsey, Lundy and Skokholm.

Both A. aquaticus and A. meridianus are present on the offshore island of Anglesey. Because of the geographical isolation of this island, the relative distribution of the two species is of interest. The distribution is shown in figure 7, p.3.41. The map has been compiled from records collected by Dr. Hynes in 1950 and identified by Prof. Moon (Moon 1960, pers. comm.); from records collected by Dr. Reynoldson in 1958 (Reynoldson 1959, pers. comm.); and from records collected in 1959 during the present research. Since these records were collected at different times the map is to be considered, therefore, as only a general indication of the distribution over a 10 year period. The details of the change in the numerical ratio of the two species at L. Llywenan is discussed in chapter VII.

Of the 40 localities (comprising ponds, lakes and streams) where Asellus was collected, 35 contained only A. meridianus; 1 contained only A. aquaticus; and 4 contained both species. L. Penrhyn has been included as a locality containing both species although Reynoldson recorded only A. aquaticus from here in 1958. However, both species were collected in April 1959, and since Reynoldson collected only a few specimens it seems likely that both were present in 1958.

It is thus evident that the predominant species of *Asellus* in Anglesey is *A. meridianus*. The localities where *A. aquaticus* is present are restricted to Holy Isle and that part of Anglesey close to Holy Isle.

3. The Distribution of the subgenera Asellus sensu stricto and Proasellus.

The causal zoögeography of *A. aquaticus* and *A. meridianus* cannot be fully understood without a knowledge of the distribution of species related to them. Although, as noted in chapter 11, the taxonomy of *Asellus* is still a subject for argument, most authorities agree that *A. aquaticus* and *A. meridianus* belong to two clearly demarcated species - groups. For convenience, and following Dudich (1925), these groups will be referred to as subgenera.

The most recent review of the two subgenera is that of Birstein (1951). Under the subgenus *Asellus* s.s. he lists 5 species and 7 subspecies, and under the subgenus *Proasellus* he lists 22 species and 22 subspecies. *A. collingei* must be deducted from Birstein's list as it has since been proven invalid (Moon 1953). Many species and subspecies of *Asellus* s.s. and *Proasellus*, however, have been described since Birstein's review. Those which must be regarded as belonging to *Asellus* s.s include A. aquaticus Berczliki Ponyi described from Hungary by Ponyi (1956), and the forms and subspecies of A. aquaticus in eastern Europe described by Karaman (see Chappuis 1953). The entire distribution of Asellus s.s. is indicated in fig. 8, p. 3.42. Those species and subspecies of Proasellus of which Birstein was unaware, or which have been described since 1951 include A. arthrodrilus Braga (1945), A. coxalis ibericus Braga (1946), A. conimbricencis Braga (1946), A. peyerimhoffi bougiensis Braga (1948), A. slavus Remy (1948), A. coxalis gabriellae Margalef (1950), A. Xavieri Braga (1956), A. Heilyi Legrand (1956), A. slavus salisburgensis Strouhal (1958), and possibly also A. pauloae Braga (1958). The entire distribution of Proasellus is also indicated in Fig. 8, p. 3.42.

The species of 'Proasellus' described from America by Bresson (1955) have been omitted from figure 8. It is felt that the taxonomic characters which constrained Mme. Bresson to put these species in the subgenus Proasellus are due to convergent evolution, and not to a close phylogenetic relationship. Her equation of the north American subgenus Conasellus with Proasellus is also regarded in the same light.

From figure 8 it can be seen that the subgenus Asellus s.s. is widespread in Europe but is absent from the Iberian peninsula and perhaps from the extreme north. In Asia it is widely spread in the west, but for vast areas of central Asia it is not encountered except in the Ob' and Irtysh basins, in L. Baikal, and in the delta of the rive Lena. This absence is apparently actual, and not due only to the absence of collections (Birstein 1951). In eastern Asia it is once more widespread and is present in Khabarovsk (U.S.S.R.), China, Japan, and Korea. In Europe and western Asia the area of distribution of *Asellus* s.s. is almost synomynous with that of *A. aquaticus*; elsewhere, species other than *A. aquaticus* are encountered.

The distribution of *Proasellus* is far more restricted and it is almost entirely limited to western Europe and the circum - Mediterrenean region. Many of the species and subspecies of the genus are known only from the region from which they were first described, but four species, *A. meridianus*, *A. cavaticus*, *A. coxalis*, and *A. anophthalmus* Karaman have a wider distribution. The distribution of *A. meridianus* has already been described. Dr. E.M. Sheppard (pers. comm.) records *A. cavaticus* from south Wales, and it has previously been recorded from southern England (Tattersall 1930), France, Switzerland, Germany, and Austria. Records of its presence elsewhere in Europe are probably incorrect (see Chappuis 1949).

A. coxalis and its subspecies are widely distributed along the periphery of the Mediterranean, and A. anophthalmus and its subspecies are found in the Balkans.

4. Discussion.

A discussion of the causal zoögeography of A. aquaticus and A. meridianus may conveniently be divided into two parts; one part dealing principally with the origins and subsequent distributions of the two species; another part dealing principally with the significance of their present distributions.

When Racovitza (1919) first demarcated A. aquaticus and A. meridianus (but see chapter 11) his knowledge of their relative distributions was extremely limited. Nevertheless, he concluded from the data available that A. aquaticus was of northern origin and was spreading southwards. Dudich (1925) presented some apparently contradictory evidence when he described A. arthrobranchialis from Italy. This species was considered by Dudich to be more primitive than A. aquaticus. However A. arthrobranchialis Dudich has subsequently been synonymized with A. aquaticus by Chappuis (1949). Arcangeli (1935) emphasized an origin of A. aquaticus in northern and central Europe, and, in opposition to Racovitza, was of the opinion that its presence in southern Europe was not due to immigration southwards from more northerly regions; it was merely the remnants of populations which had been forced south by the advancing ice during the Ice-age. After the retreat of the ice, A. aquaticus once more, according to Arcangeli, returned to the north. Chappuis (1927; quoted by Birstein 1951) shared Racovitza's views and assumed that A. aquaticus was of northern origin.

Birstein (1951) suggested, on the basis of the disjunct distributions of Asellus s.s. in Asia, that A. aquaticus originated in Siberia as a result of isolation during the Ice-Age. After the retreat of the ice A. aquaticus subsequently spread to north eastern Europe. The distributions of species of Asellus s.s. other than A. aquaticus support this theory in that all are recorded from regions which it has been suggested remained free of ice during the Ice-age, or at least were not completely frozen. Thus, it is thought by Soviet biogeographers (Birstein 1951; compare also Thienemann 1950, and Segestråle 1957) that during the Ice-age the Ob' and Irtysh rivers, which contain A. latifrons Birstein, flowed along the periphery of the ice, and that the river Lena, which contains A. epimeralis Birstein, was never frozen solid. Birstein adds that previous hypotheses on the origin of A. aquaticus were based upon too little knowledge of the Asiatic distribution of this species and of the subgenus Asellus s.s.

Birstein's hypothesis would certainly seem to fit best the known facts. His emphasis upon the Ice-age and geographical isolation as salient factors is especially significant, as these are the two factors which are known to have been of importance in the distribution and evolution of many animals. Thienemann (1950), for example, has recently demonstrated the importance of the Ice-age in the distribution of much of the European fresh-water fauna, and Mayr (1942) in particular has pointed out the importance of geographical isolation in speciation, and noted that in Asia isolation has given rise to many new forms.

Birstein's conclusions concerning the post-glacial immigration to Europe of A. aquaticus are supported by the extreme paucity of subspecific variation of this species in Europe despite its wide area of distribution. Birstein regarded the immigration as having occurred quite early in post-glacial times; the presence of A. aquaticus in Britain seemed to him to indicate that A. aquaticus had reached Britain before the connection between Britain and France had been broken. Chappuis (1949), likewise, regarded the presence of A. aquaticus in Britain as an indication of an early post-glacial immigration. Moreover, Chappuis (1949) suggested that the presence of

A. aquaticus in Greenland and in Crete perhaps indicated an even earlier immigration. Contempory evidence however, does not support this latter suggestion: A. aquaticus is not present in Greenland (see p. 3.8.), and Chappuis (1953) in a later paper suggests that the presence of A. aquaticus in Crete may be due to its introduction there by Man in historical time.

No one appears to have considered that the rate of immigration of A. aquaticus may have undergone fluctuations. Although the absence of any resistant resting stages has meant that at all times the colonization of disjunct areas has been a slow process, it is nevertheless to be expected that immediately after the retreat of the ice, when large numbers of fresh-water lakes, pools, etc., were present as a result of the melting of the ice, the spread of A. aquaticus was perhaps more rapid than in later periods, when much of Europe was forested and formed of 'closed-communities'. The close proximity of the ice-sheet need not necessarily have meant that a temperate fresh-water fauna was absent. Indeed, the temperature of the water formed from the melting ice-sheet may have been quite high (Segestråle 1954). Charlesworth (1957) noted that aquatic animals and plants in particular may have rapidly colonized fresh areas soon after the retreat of the ice. He says (p. 1428): "Aquatic animals and plants as well as mosses probably pioneered fairly quickly; waterlogged tracts, areas of defective drainage, and lakes and pools which abounded in the ice-free zone in hollows of the rocks and drifts (eshers, drumlins, moraines, till) were early restocked". The invasion of Scandanavia by _Gammarus pulex_ (Segestråle 1954), the distribution of _Pallasea_ and other glacial relicts in Europe (Segestråle 1957), and the distribution of _Mysis relicta_ Loven and _Pontoporeia affinis_ Lindstr. in North America (Ricker 1959), have all been explained on the basis of an early post-glacial spread via the ice-lakes near the margin of the retreating ice sheet.

A second period of rapid spread has perhaps taken place within historical time. Within this period the clearing of much of the forested area of Europe for agricultural purposes, the construction of canals and the artifical transfer of fish are all factors which may have accelerated the spread of _A. aquaticus_. Moon (1957a) also considers that the activities of Man may have increased the dispersal rate of _Asellus_.

An incomplete post-glacial distribution for many immigrant groups of animals and plants has been postulated. Godwin (1956), for example, has noted the incomplete distribution of many post-glacial immigrant plants, and Thienemann (1950) has noted the same phenomenon for many aquatic animals. Our knowledge of the distribution of A. aquaticus suggests that this species also has not yet reached its maximum possible distribution in Europe. Its absence or rarity in the more isolated parts of France (eg. Normandy and Brittany), the very disjunct nature of its distribution in France (see fig.3, p.), its absence from the Isle of Man and most offshore British islands, and its scarcity in the western peninsulas of Britain, in most of northern Scotland and in Anglesey are all facts which suggest that the maximum possible distribution of A. aquaticus in Europe has not yet been attained.

As previously noted, Racovitza (1919) regarded the spread of A. aquaticus as taking place in a southerly direction. Birstein (1951) regarded the spread as taking place from north-eastern Europe. However, if it is assumed that A. aquaticus immigrated to Europe from Siberia via the water logged areas left behind by the retreating ice, it would then appear more reasonable to suppose that the post-glacial spread of A. aquaticus has been principally in a westward direction along a broad front. Furthermore, a similar direction of post-glacial advance has been indicated by Segestråle (1957, see especially his map fig.37, p.95) for many glacial 'relicts'.

The geography of the regions to which *A. aquaticus* spread would of course have altered the direction of advance to some extent. Thus, the entry of *A. aquaticus* to Sweden and Norway may have occurred via two routes: a northerly one through Finland; and a southerly one across the Danish islands, which at various times during the post-glacial connected Jutland with southern Sweden (Segestråle 1954). The fresh-water condition of the Baltic (as the Ancylus Lake) during the early post-glacial (see Segestråle 1957) may also have aided this dispersal. In Britain the main direction of advance has probably been northwards. Chappuis (1959 pers. comm.) regards the direction of advance of *A. aquaticus* in France as a westward one. He says: "In France we have in general *A. aquaticus* and *A. meridianus*; the first species advancing from the east by the canals".

Whereas the origin of *A. aquaticus* has usually been discussed without reference to the subgenus *Asellus* s.s., the origin of *A. meridianus* has always been discussed with close reference to the origins of the subgenus *Proasellus*. A study of the comparative morphology of *A. coxalis* from Syria, *A. coxalis peyerimhoffi* Rac. from Algeria, and *A. banylensis* and *A. meridianus* from France led Racovitza (1919a), to suggest that the subgenus *Proasellus* had originated in Asia Minor, from whence it spread along the southern shores of the Mediterranean and reached Europe via the Iberian peninsula. But the discovery of numerous species of <u>Proasellus</u> in southern Europe, the Balkans, and the Aegean islands led Remy (1932), to reconsider Racovitza's views. Remy agreed with Racovitza on an origin in Asia minor for <u>Proasellus</u> but suggested that the subsequent migration to Europe occurred through regions bordering both the northern and southern shores of the Mediterranean. Arcangeli (1935) agreed with neither Racovitza (1919a) nor Remy (1932). He believed it unneccessary to postulate a migration of <u>Proasellus</u> species from Asia minor simply because <u>A. coxalis</u> was the most primitive species of <u>Proasellus</u> and was found there; the various species of <u>Proasellus</u> were thought by him as having arisen <u>in situ</u>. The problem was regarded by Braga (1946 p.1) as extremely complicated: "La répartition actuelle des espèces d'<u>Asellus</u> sur le périmètre de la Méditerranée est un fait biogéographique non expliqué encore d'une façon satisfaisante. L'étroite parenté qui lie un grand nombre de formes que colonisent les deux rivages méditerranéens, de l'Asie Mineure à la Péninsule ibérique, et, aussi, l'aselle de Madère, soulève nombre de complications". Birstein (1951) concluded that the subgenus <u>Proasellus</u> was extremely ancient and native to the circum-mediterranean countries. He pointed out, furthermore, that before the Pliocene the eastern part of the Mediterranean was dry land and this fact could easily explain the disjunct distribution of many related forms in eastern Europe, the Aegean islands and Asia minor.

There can be little doubt that the high endemism and multiplicity of species and subspecies of Proasellus are strong evidence in support of the view that the species and subspecies originated in situ, and that the subgenus is extremely ancient. Moreover this view is supported by the geological evidence. Thus, the island of Madeira, where occurs A. italicus perarmatus Remy, has been separate from the main Afro-European land-mass since the Miocene, and L. Ohrid, containing several endemic forms, has been isolated since the late Tertiary (Stanković 1955). Birstein's (1951) explanation of the disjunct distribution of related forms in the eastern Mediterranean likewise indicates the great age of the subgenus.

Many of the species and subspecies of Proasellus may have arisen during the Ice-age, for at that time the Mediterranean area and the Balkans were Europe's forested regions (Charlesworth 1957), and thus provided favourable conditions for the production of the endemic species of freshwater animals.

Whether Proasellus extended over a wider area preglacially than it does at present is uncertain. Birstein (1951) suggested that it at least extended further north, and he quoted Arcangeli (1935) as supporting this suggestion. However, Birstein appears to have misquoted Arcangeli for Arcangeli did not indicate this; he emphasized in fact that any extension northwards of Proasellus took place after the Ice-age[1] Stammer (1932) noted that in Germany A. cavaticus is found in areas which have no surface forms of Proasellus, and he concluded from this that Proasellus had had a wider distribution prior to the Ice-age; he regarded A. cavaticus as a relict species which had been able to survive at the edge of the ice sheet only by becoming cavernicolous. The presence of A. cavaticus in formerly glaciated parts of Switzerland is similar evidence in support of Stammer's views.

A post-glacial northern advance of A. meridianus has been indicated by Racovitza (1919), Arcangeli (1935), Chappuis (1949) and Thienemann (1950), but this species is the only Proasellus species for which such an extension has been postulated. Theinemann (1950, p.694) regarded this post-glacial advance as of very recent occurrence.

Racovitza (1919) suggested that the distribution of

Footnote 1. Birstein's paper was translated for me by Mr. Henry (Dept. of Russian, University of Liverpool), and Arcangeli's paper by S. Giovanni (University of Bari, southern Italy).

A. meridianus was directly related to that of A. aquaticus; he regarded A. meridianus as being driven("refouler") south-wards by A. aquaticus. Birstein (1951 p.82) likewise suggested that there was a correlation between the distribution of A. meridianus and A. aquaticus. But previous hypotheses concerning the northwards spread of A. meridianus and its distributional relationships with A. aquaticus have been based upon few data and especially upon less detailed inform-ation of the distributions of the two species in Britain and in western Europe than are now available.

Examination of figures 3a and 3b, and 5, 6 and 8 indicates that only in Britain has A. meridianus extended far to the north of the maximum southern limit of the ice sheet; else-where in western Europe A. meridianus extends north of this limit only in northern Holland. This lack of a northward advance of A. meridianus on the continent is surprizing when is considered not only the present similarities in climate between western Europe and Britain, but also the distributions of species which are considered to have had a similar post-glacial distributional history. Polycelis felina (Dalyell), and the mite Feltria romijni (Bessel.), for example, are species which have extended north of the maximum southern limit of the ice sheet during the post-glacial, not only in Britain, but also on the continent; P. felina is found in Denmark (Dahm 1956, 1958), and *F. romijni* reaches the southern border of Denmark (Efford pers. comm.). The distribution of *Dugesia gonocephala* Dugès is also of interest in this connection as although absent in Britain it has spread northwards post-glacially as far as Denmark (Dahm 1958). Furthermore, although the climate of western Europe is known to have differed from that of central Europe during the Post-glacial in that it became warmer more rapidly, it has been similar to that of Britain throughout the Post-glacial (c.f. Thienemann's (1950 p. 627-628) "Theorie der schiefen Front").

It is suggested that the most reasonable explantion of the distribution of *A. meridianus* is to be sought in the light of two facts: the severance during the early post-glacial of Britain from France (c. 6,000 years ago; Trusheim 1943, quoted by Hynes 1954); and the post-glacial arrival of *A. aquaticus* in north western Europe.

It may be presumed that as the ice retreated *A. meridianus* began at the same time to spread northwards. However, with the regression of the ice came the westward invasion of *A. aquaticus*, and this invasion was probably especially rapid in north western Europe near the edge of the ice-sheet (see p. 3.23). Whether *A. meridianus* extended further north in western Europe prior to the arrival there of *A. aquaticus* is not known, but it is suggested that the distribution of A. meridianus in this region has been and is limited by A. aquaticus. By the time A. aquaticus had reached north western France the land connection between this region and Britain had been severed, and the spread of A. aquaticus to Britain was therefore hindered. In this case, suggestions that A. aquaticus reached Britain before the connection between Britain and France had been broken (Birstein 1951; Chappuis 1949) must be regarded as probably incorrect. In Britain, in the absence of A. aquaticus, A. meridianus was able to extend far to the north, and this extension, as in the case of A. aquaticus on the continent, was perhaps most rapid in the Pre-boreal period of "open-communities" (see p. 3.23). It is not unlikely that during the Ice-age A. meridianus was able to survive in southern England (and possibly also in the extreme south of Ireland), for survival here has been postulated for other fresh-water species (e.g. Gammarus lacustris G.O. Sars; see Segestråle 1954 p. 56), and this would mean of course, that A. meridianus could begin to extend northwards as soon as conditions were suitable. Nevertheless the absence of A. meridianus from ecologically suitable areas of northern Scotland and the Scottish islands does indicate that even the length of time which has elapsed since the regression of the ice to the present has been insufficient to allow for the colonization of all possible areas by _A. meridianus_. A similar explantion has been postulated for the absence of certain other fresh-water species from suitable habitats in northern Scotland (see, for example, Hunter in Slack 1957 p.85).

The time at which _A. aquaticus_ reached Britain is uncertain, but the widespread distribution in Britain of _A. meridianus_, and in particular the presence of _A. meridianus_ in Scotland, perhaps indicates that this time was considerably delayed. At all events the forested nature of Britain during the Boreal and later periods (Tansley 1951) would presumably have prevented any rapid spread of _A. aquaticus_ after the Pre-boreal; the most rapid advance of _A. aquaticus_ in Britain may therefore have taken place within historical times (see p. 3.24). The presence of _A. aquaticus_ in almost all canals from which collections have been made would undoubtedly seem to support this suggestion. Moreover, the fact that _A. meridianus_ has never been recorded from a canal (total number of records of _A. aquaticus_ from canals = 15) is perhaps further evidence that its spread is limited by _A. aquaticus_.

The presence of only _A. meridianus_ in the western peninsulas of Britain, on the Isle of Man, and on all but one of the offshore islands of Britain from which Asellus has been recorded, as well as its predominance in Anglesey, would certainly seem to indicate that the spread of A. meridianus took place prior to that of A. aquaticus. On the other hand the apparently widespread distribution of A. aquaticus in Ireland is anomolous, for Ireland has been separated from the rest of the British Isles since the early post-glacial (Godwin 1956). The occurrence of A. aquaticus here may possibly be due to its accidental introduction by Man; it is known, for instance, that extensive fish management projects and similar activities are carried on in Eire (see for example, the secretary's reports of the "Inland Fisheries Trust Incorporated"). Moon (1957b p.407) is certainly strongly in favour of the view that Man has greatly aided the distribution of A. aquaticus. However, if an artifical introduction of A. aquaticus to Ireland is accepted, the absence there of the analogous species Gammarus pulex must be explained. Hynes (pers. comm.) suggests that the absence may possibly be the result of a more limited ability of G. pulex to withstand unfavourable conditions during transport. The presence of A. meridianus in Ireland presents no difficulties; it may either have survived the Ice-age in the extreme south of Ireland, or spread over-land post-glacially via the land-bridges, which are known to have existed in Pre-Boreal times, and which connected Ireland to the Galloway peninsula and North Wales (Charlesworth 1957). The occurrence of A. meridianus on the offshore islands of Britain also presents no difficulties of explanation, for many of these were joined to the mainland in the early post-glacial (Beirne 1952). If, however, the contention of many geologists that the Isle of Man was never joined to Britain post-glacially is accepted, then an explanation of the presence here of A. meridianus is more difficult. On the other hand, if the recent contention by Mitchell (1960) that one of the three post-glacial land-bridges connecting Britain and Ireland incorporated the Isle of Man is accepted, then no difficulty is encountered.

The above suggested explanation of the differences in distribution in Britain and western Europe of A. meridianus and A. aquaticus is necessarily highly speculative, and it is by no means looked upon as being conclusive. But, on the basis of the available zoögeographical data, it is thought to be not unreasonable. Indeed, the idea of successive post-glacial invasions has been used to explain the distributions of other closely allied species; the distributions of Gammarus pulex and G. duebeni (Hynes 1954), of the blue, Irish and brown hares (Harrison - Matthews 1952), and of the various species of

Apodemus (see Beirne 1952) have all been explained in this way.

Logically inherent in this explanation of the distribution of A. aquaticus and A. meridianus is the idea that inter-specific competition is occurring. Zoögeographical data can of course supply only indirect evidence of such a process; it remains to be seen, therefore, whether the explanation requires modification in the light of more direct evidence from other fields of investigation.

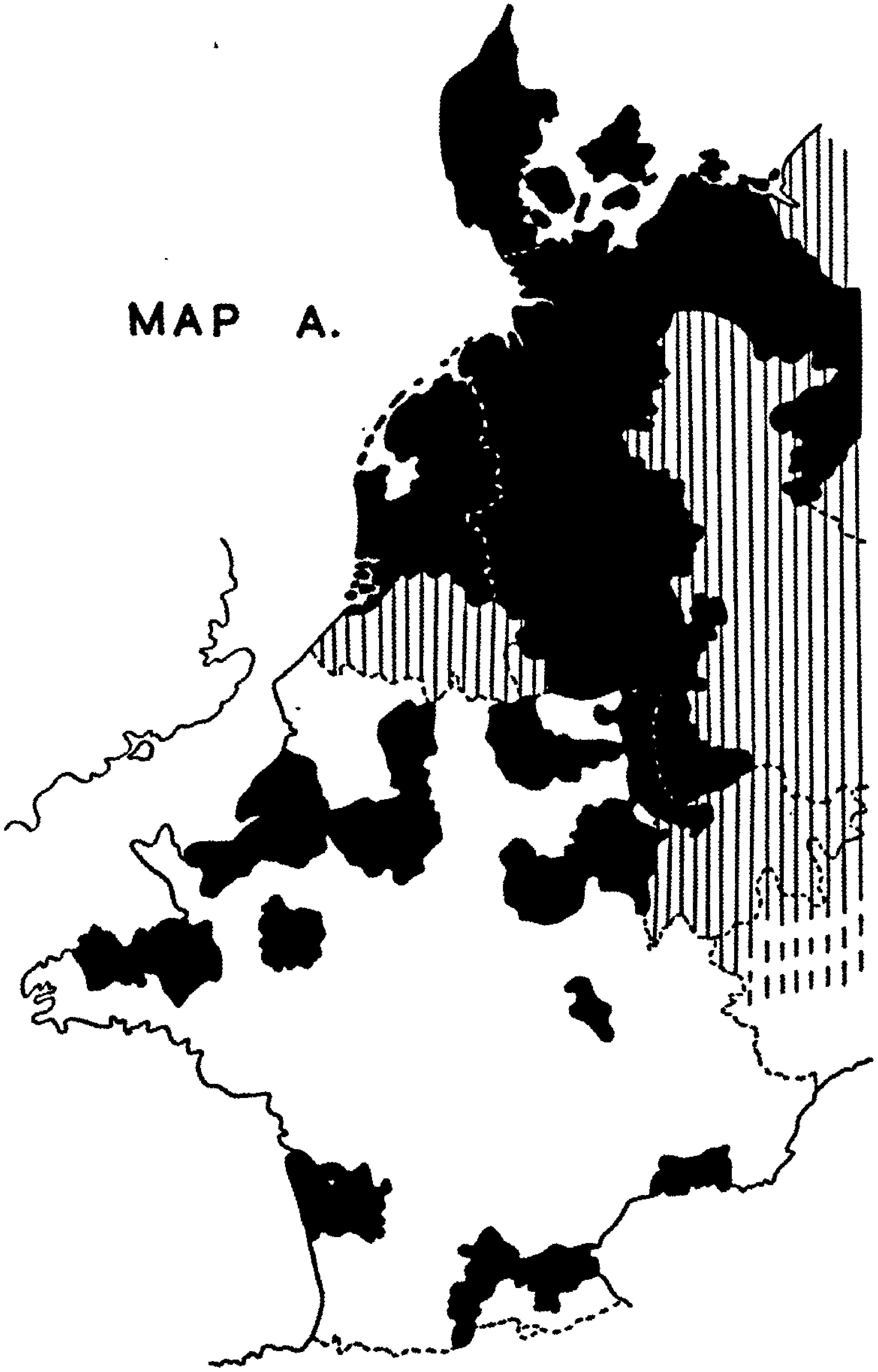
Figure 3a (Map A)

The Distribution of A. aquaticus in Denmark, western Germany, the Low Countries, Switzerland and France.

Figure 3b (Map B)

The Distribution of A. meridianus outside Britain.

MAP A.



MAP B.

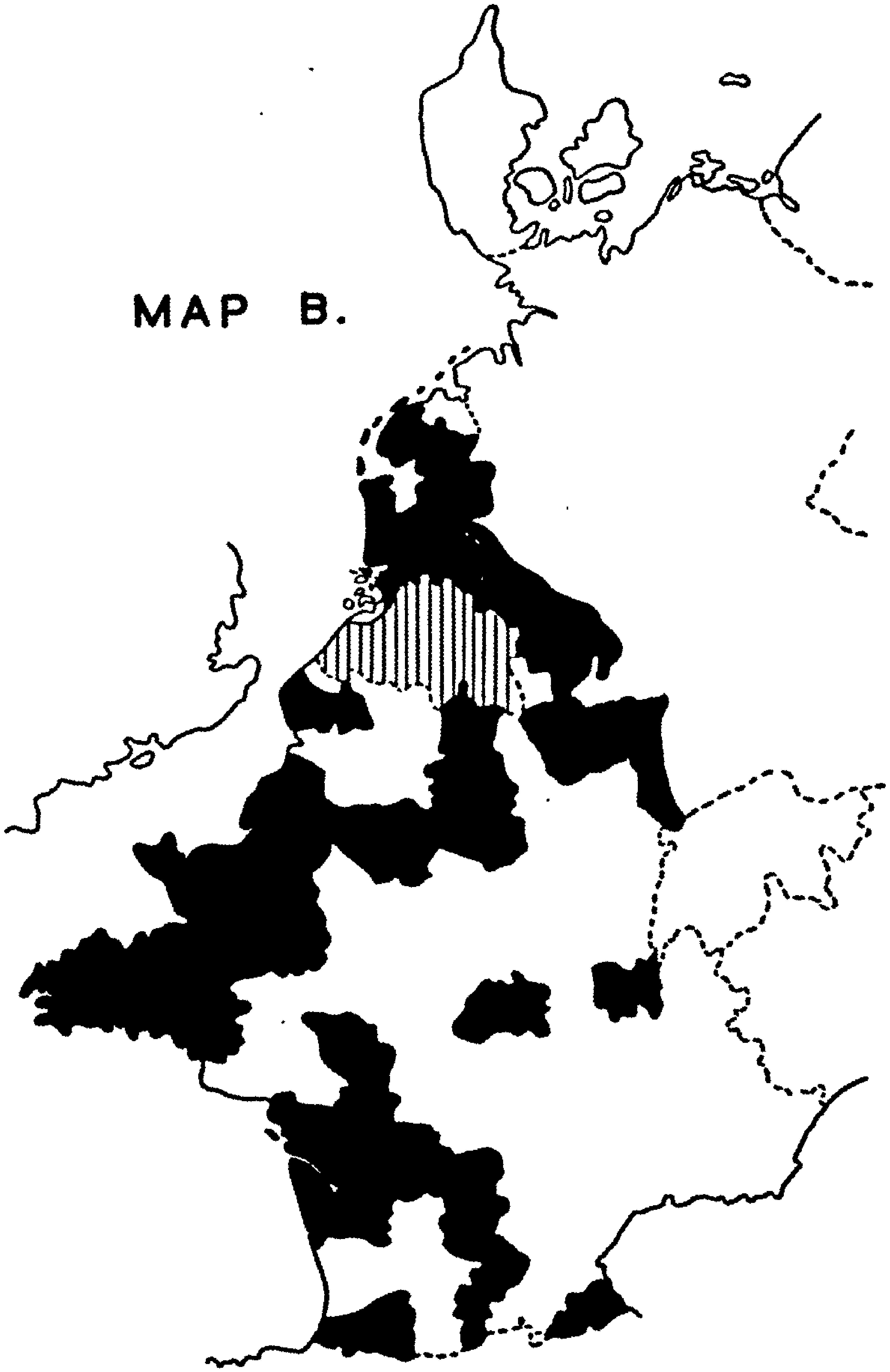


Fig. 4 Map showing in diagrammatic fashion the proportions of A. aquaticus and A. meridianus in northwestern France.

Explanation of map: ■ = A. aquaticus; ▨ = A. meridianus
The proportion of the areas shown black or dotted in the circle in each Department indicates the ratio of the number of records of A. aquaticus to those of A. meridianus. Where only a single record exists this is shown as a small circle with (1) at the side. Records from the adjacent Channel Isles have been included.

Department	Total no. of records	The no. and date or source of the records A. meridianus	: A. aquaticus
Seine inférieure	4	2, August 1959	2, August 1959
Eure	3	1, (Maury, 1927)	2, (Maury, 1927)
Calvados	18	2, August 1959 11, (Maury, 1927)	5, (Maury, 1927)
Manche	9	6, August 1959 3, (Maury, 1927)	0
Orne	5	5, (Maury, 1927)	0
Sarthe	19	18, (Maury, 1927)	1, (Maury, 1927)
Mayenne	4	4, (Maury, 1927)	0
Ille-et-Vilaine	1	0	1 August 1959
Côtes-du-Nord	4	3, August 1959	1 August 1959
Finistère	8	8, (Hynes, 1959)	0
Morbihan	2	2, August 1959	0
Guernsey	1	1, October 1958	0
Sark	1	1, (Moon, pers. comm.)	0

Table showing the details of the records upon which the map opposite is based.

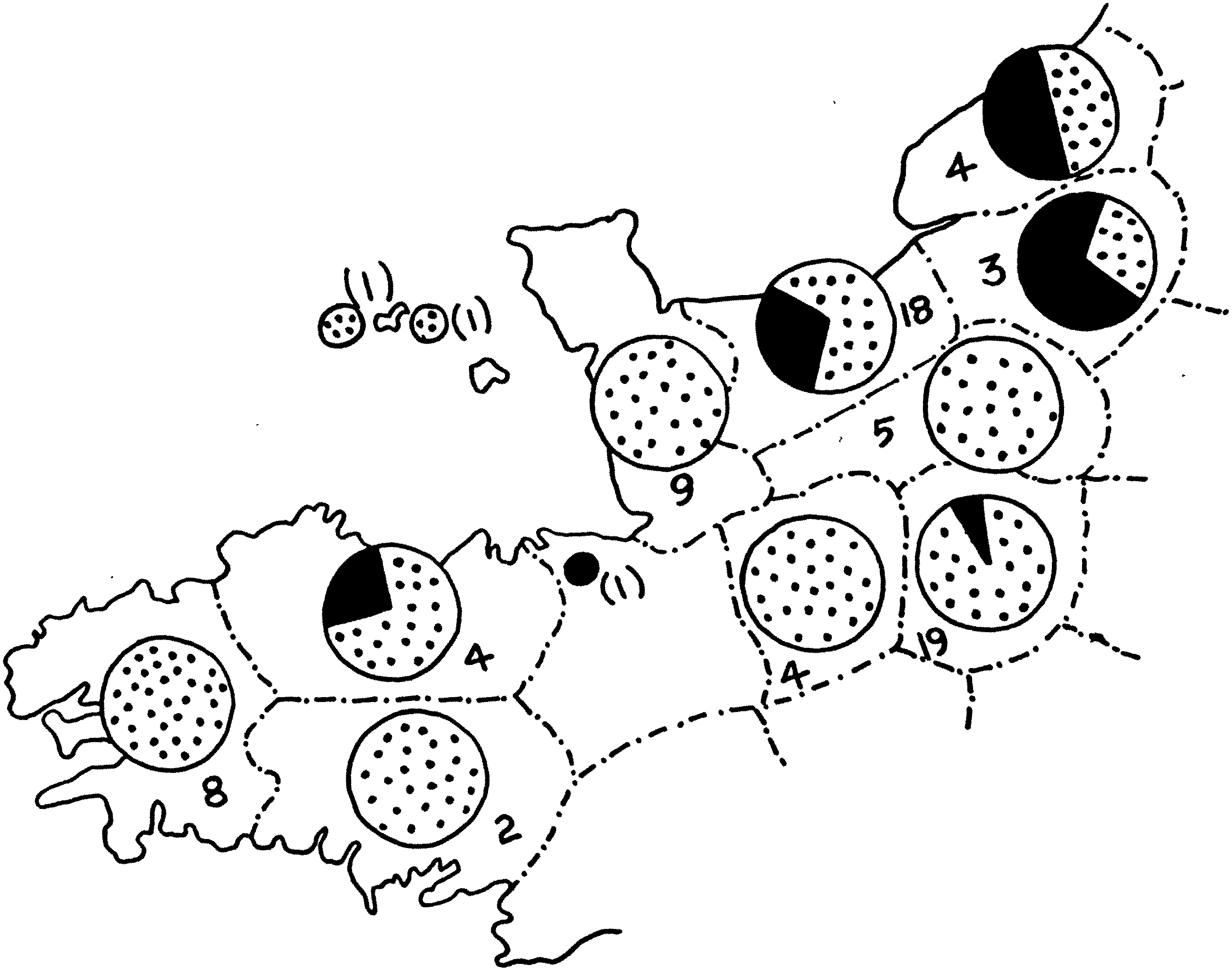

4
3
18
(1)
(1)
5
9
(1)
4
19
4
8
2

Figure 5.

The Distribution of A. aquaticus in Britain.

Figure 6.

The Distribution of A. meridianus in Britain.

Figure 7.

The Distribution of *A. aquaticus* and *A. meridianus* in Anglesey.

Key to Map:

●	*A. aquaticus* only
+	*A. meridianus* only
✦	*A. aquaticus* and *A. meridianus*

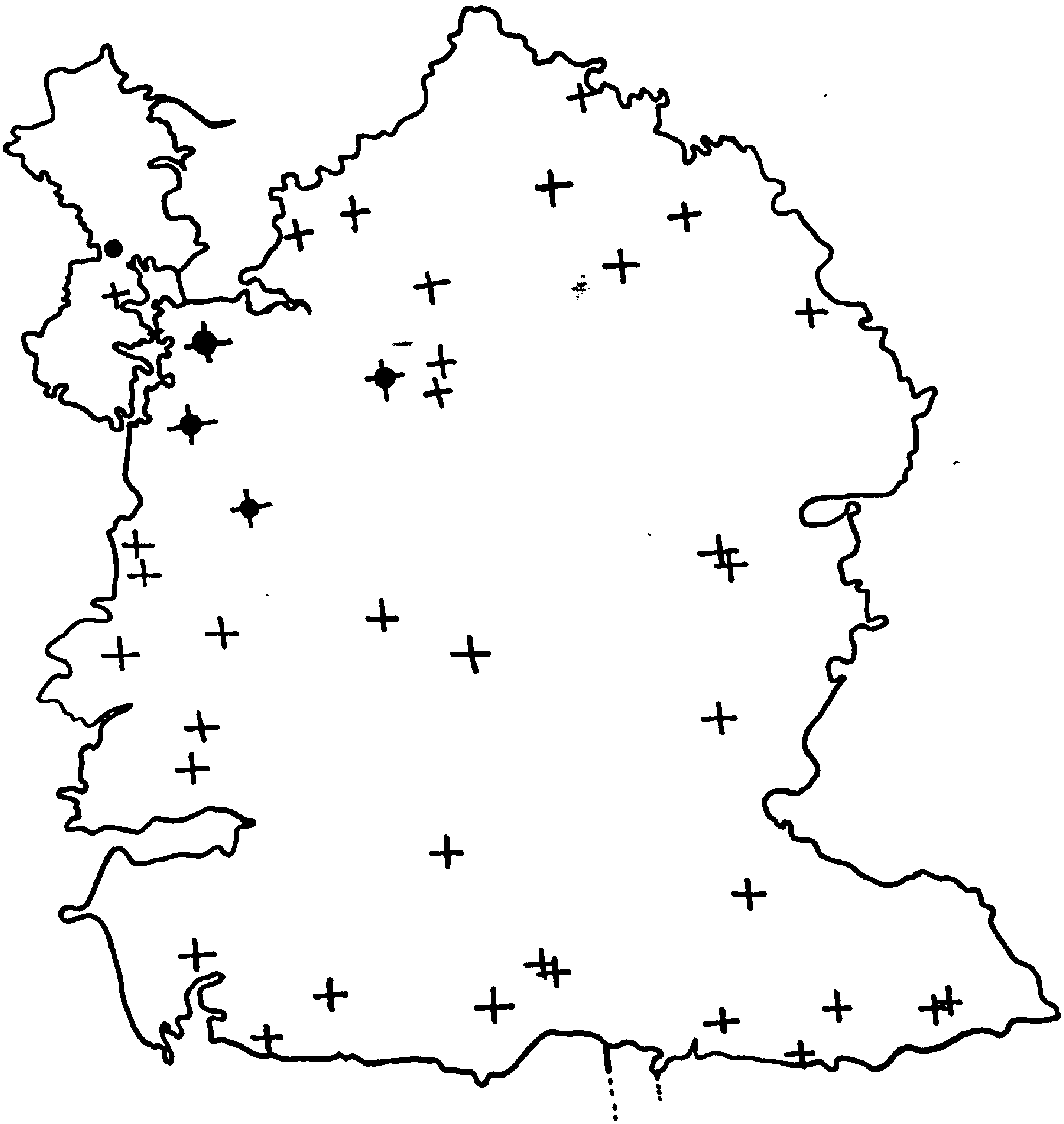


Figure 8.

The Distribution of the subgenus *Asellus sensu stricto* and of the subgenus *Proasellus*.

Key to Map:

— — — Maximum southern limit of the ice-sheet during the Ice - age.

⁙ *Asellus* s.s.

|||| *Proasellus*

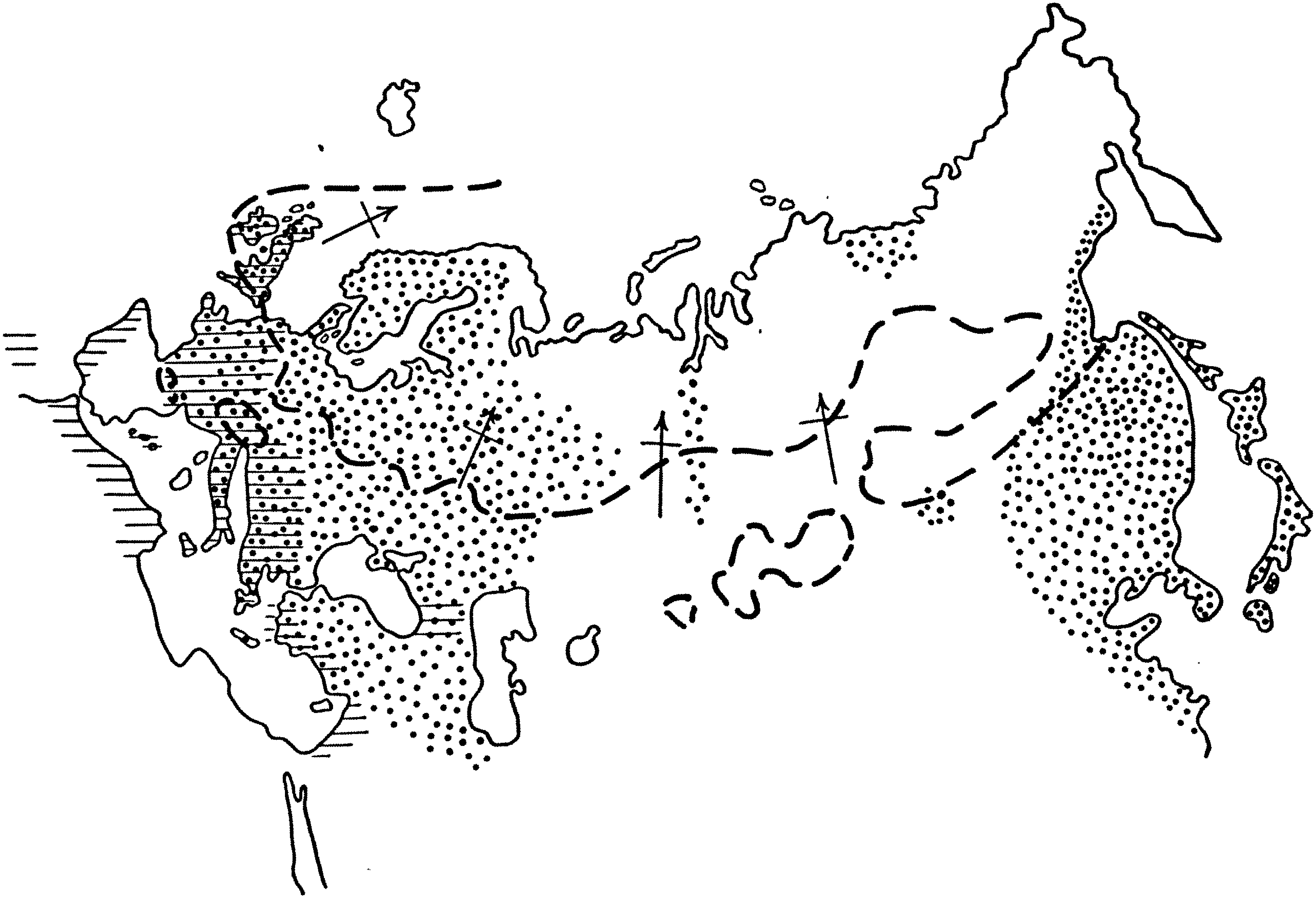
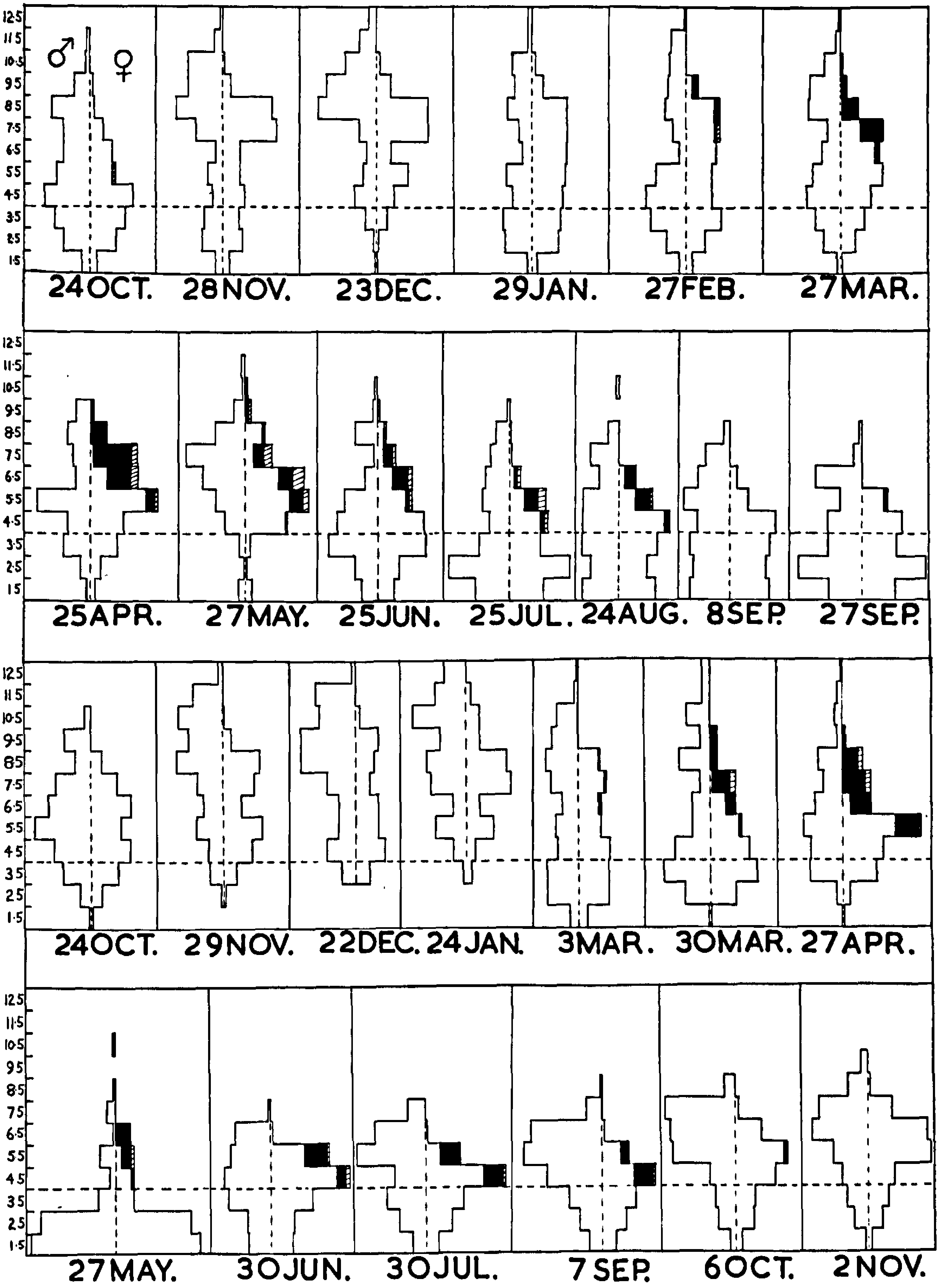


Fig. 9 Histograms showing the population structure of the samples collected from Buckley Lake, Flintshire, from the 24th October 1957 until the 2nd November 1959.

Key:

The vertical scale (in mm.) indicates the length of the animals, and the horizontal scale the number of animals in each size-group as a percentage of the total number in the sample (horizontal scale:7mm.=10%). The horizontal dotted line in the lower part of each histogram indicates the size below which separation of the sexes proved impracticable; above this line males are shown on the left, and females on the right of the vertical dotted line. Completely black areas on the right of the vertical dotted line represent ovigerous females; cross-hatched areas represent females with empty brood pouches.

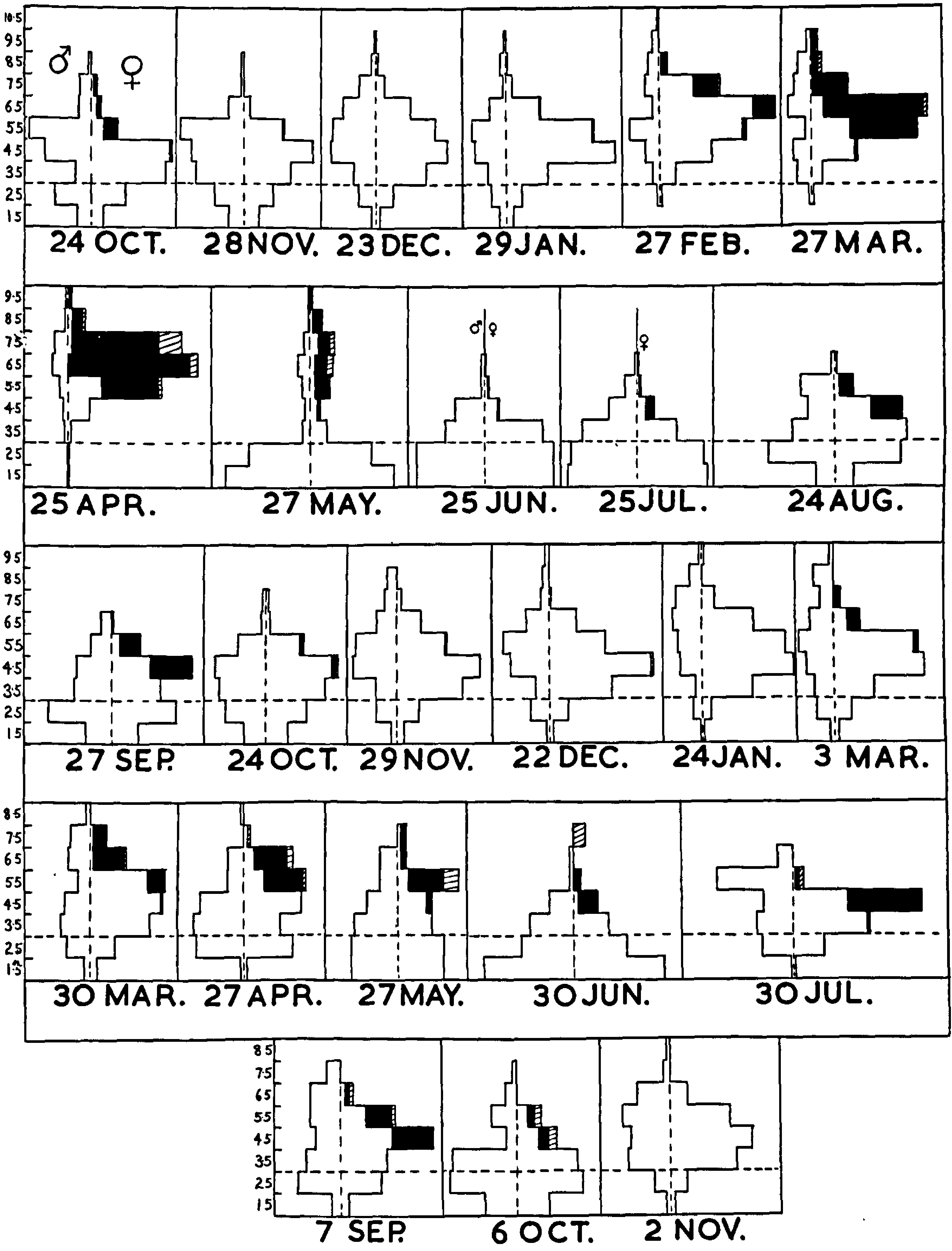

12·5
11·5
10·5
9·5
8·5
7·5
6·5
5·5
4·5
3·5
2·5
1·5
♂
♀
24OCT.
28NOV.
23DEC.
29JAN.
27FEB.
27MAR.
25APR.
27MAY.
25JUN.
25JUL.
24AUG.
8SEP.
27SEP.
24OCT.
29NOV.
22DEC.
24JAN.
3MAR.
30MAR.
27APR.
27MAY.
30JUN.
30JUL.
7SEP.
6OCT.
2NOV.

A. AQUATICUS

T.2

Fig. 10 Histograms showing the population structure of the samples collected from Padeswood Lake, Flintshire, from the 24th October 1957 until the 2nd November 1959.

Arranged as in fig.9

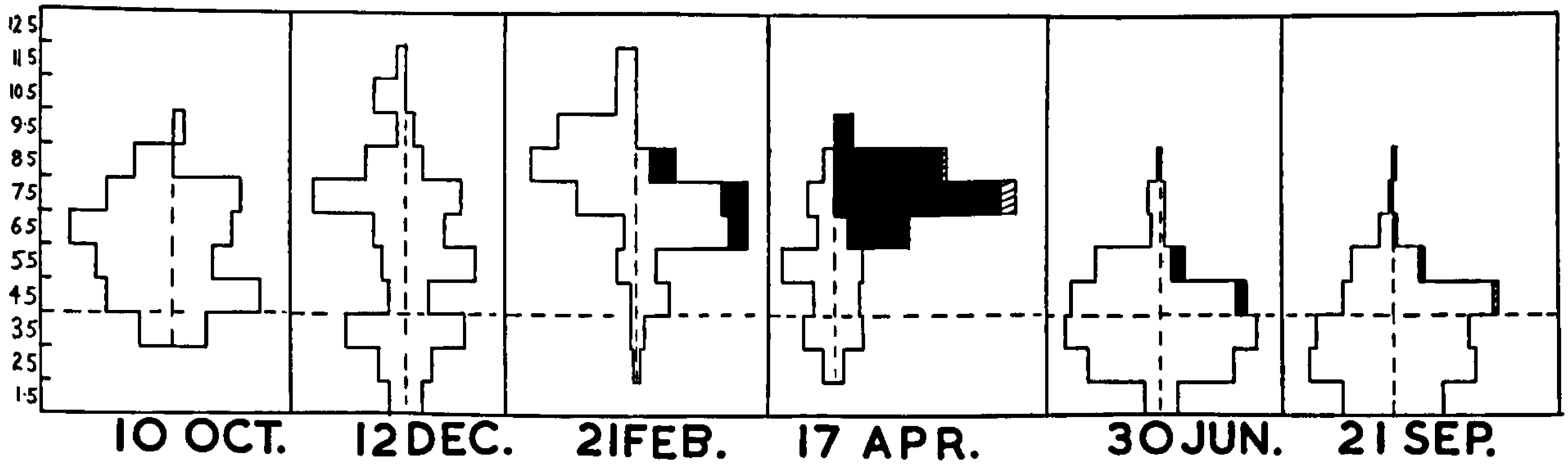


A. MERIDIANUS

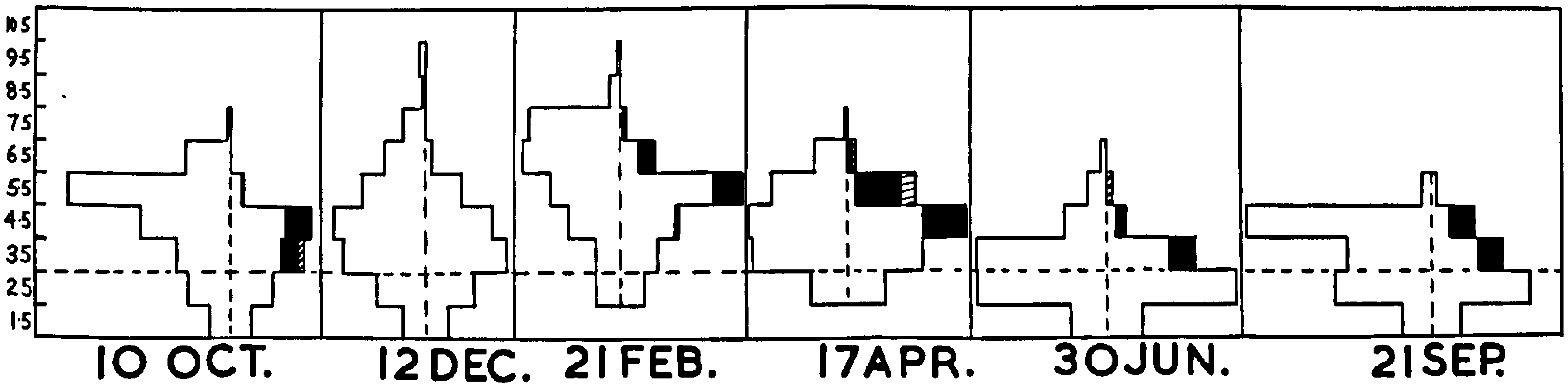
4.3

Fig. 11 Histograms showing the population structure of the samples collected from Llyn Llywenan, Anglesey, from the 10th October 1957 until the 21st September 1958.

Arranged as in fig.9



A. AQUATICUS

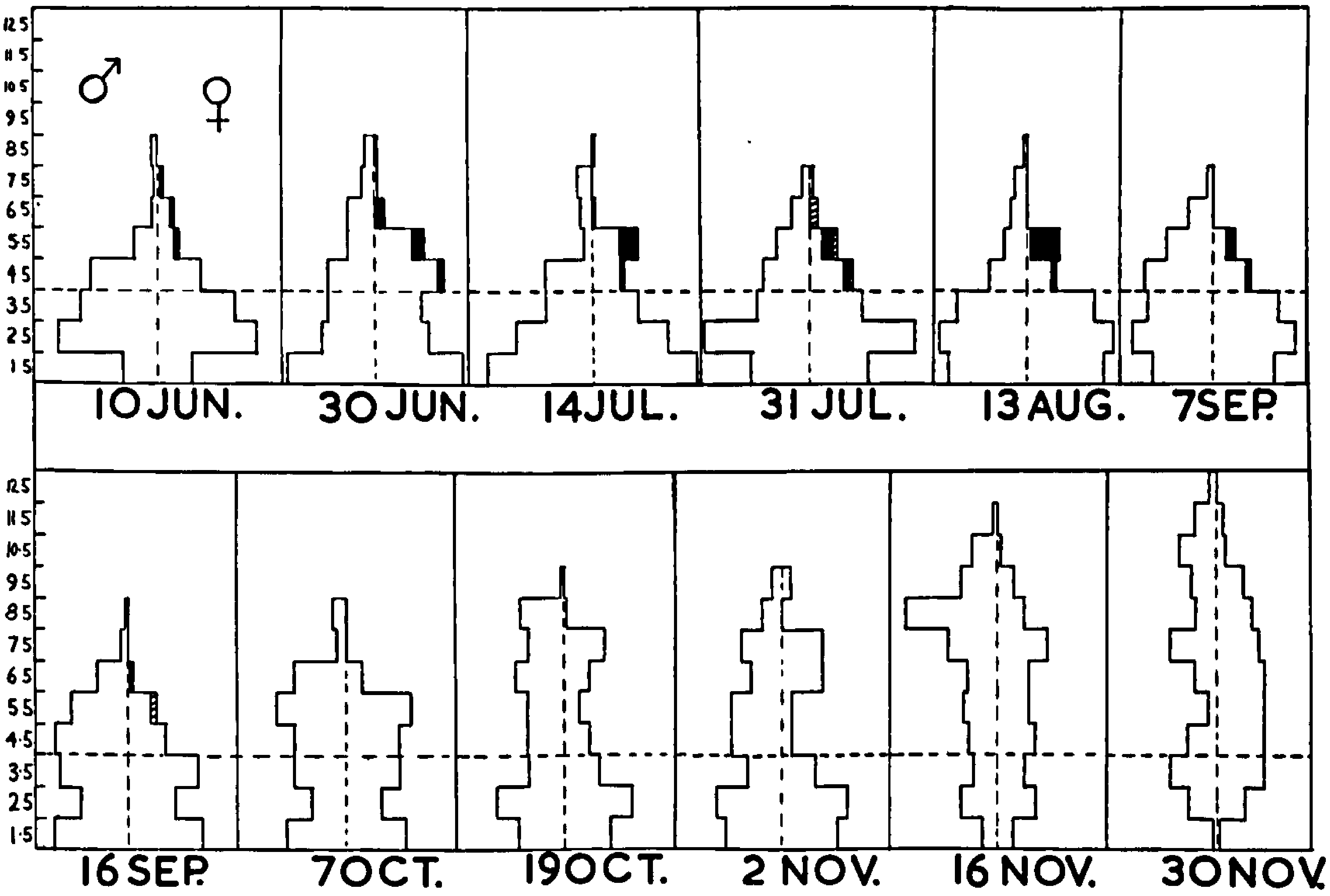


A. MERIDIANUS

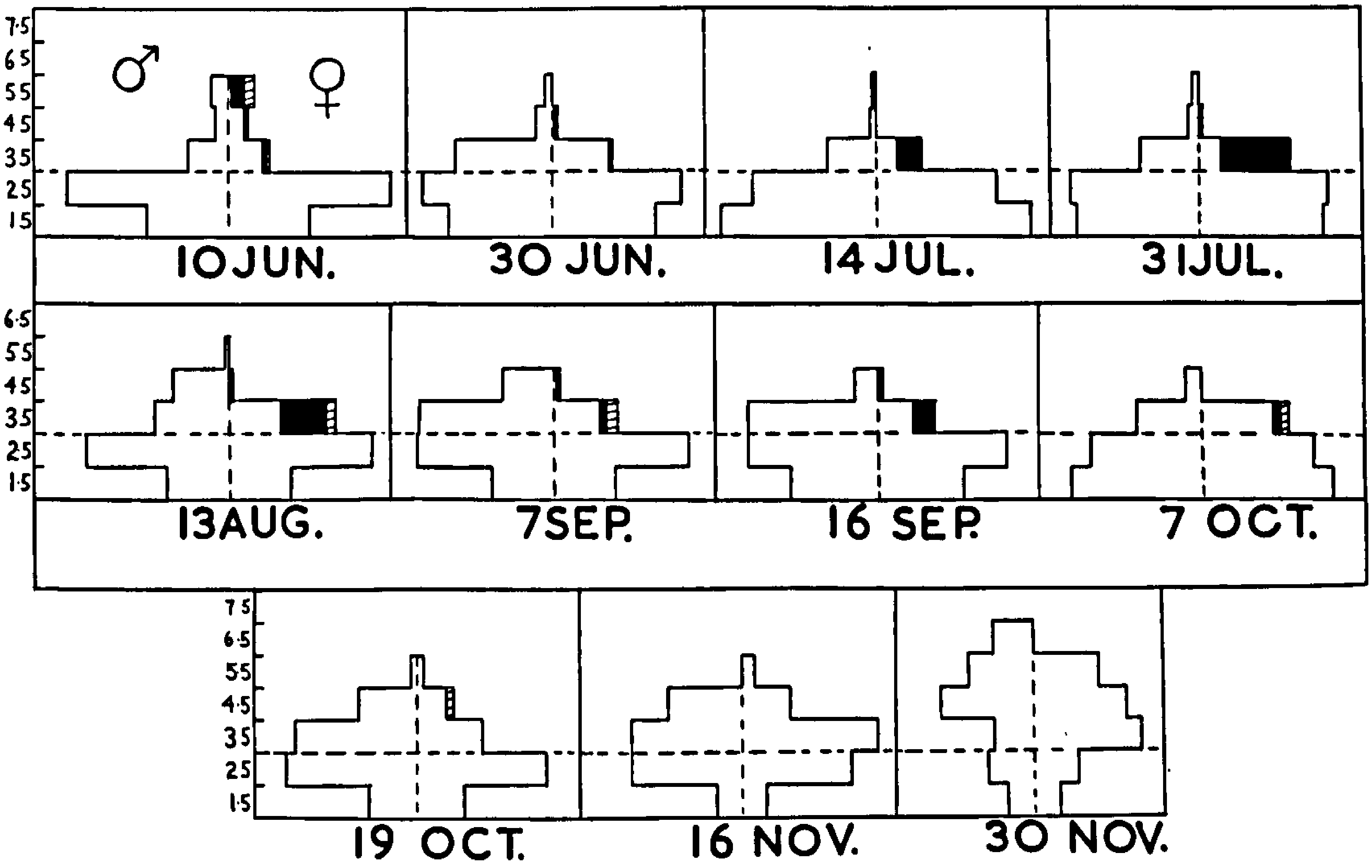
4.4

Fig. 12 Histograms showing the population structure of the samples collected from Hatchmere, Cheshire, from the 10th June 1959 until the 30th November 1959.

Arranged as in fig.9



A. AQUATICUS



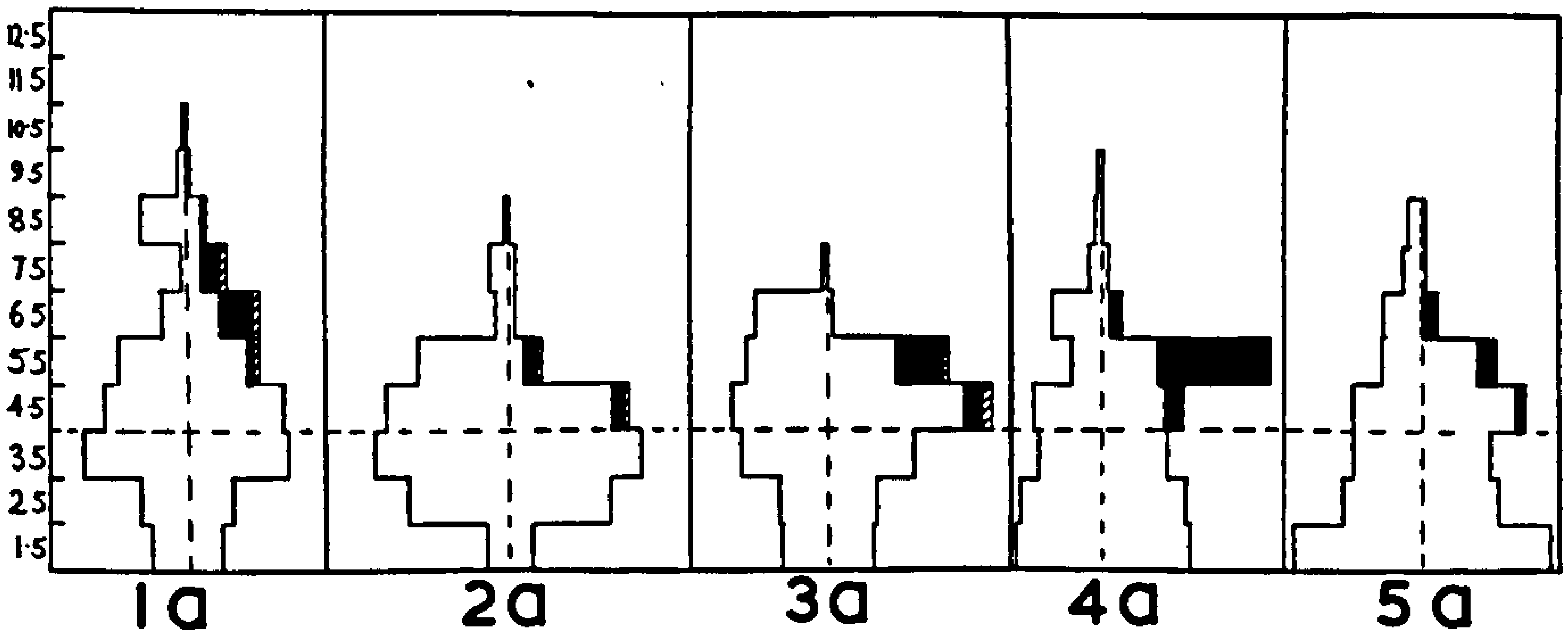
A. MERIDIANUS

4.5

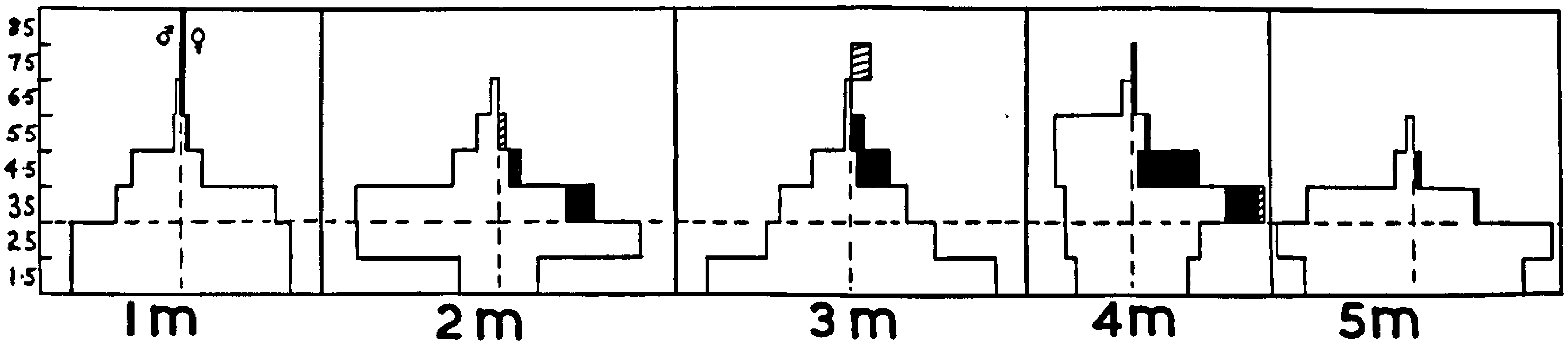
Fig. 13 The population structure of all samples collected in June

Arranged as in fig.9

1a Buckley Lake,25th June 1958	1m Padeswood Lake,25th June 1958
2a L. Llywenan,30th June 1958	2m L. Llywenan, 30th June 1958
3a Buckley Lake,30th June 1959	3m Padeswood Lake,30th June 1959
4a Pond nr. Bidston,30th June 1959	4m Pond nr.Storeton,30th June 1959
5a Hatchmere,30th June 1959	5m Hatchmere,30th June 1959



A. AQUATICUS



A MERIDIANUS

4.6

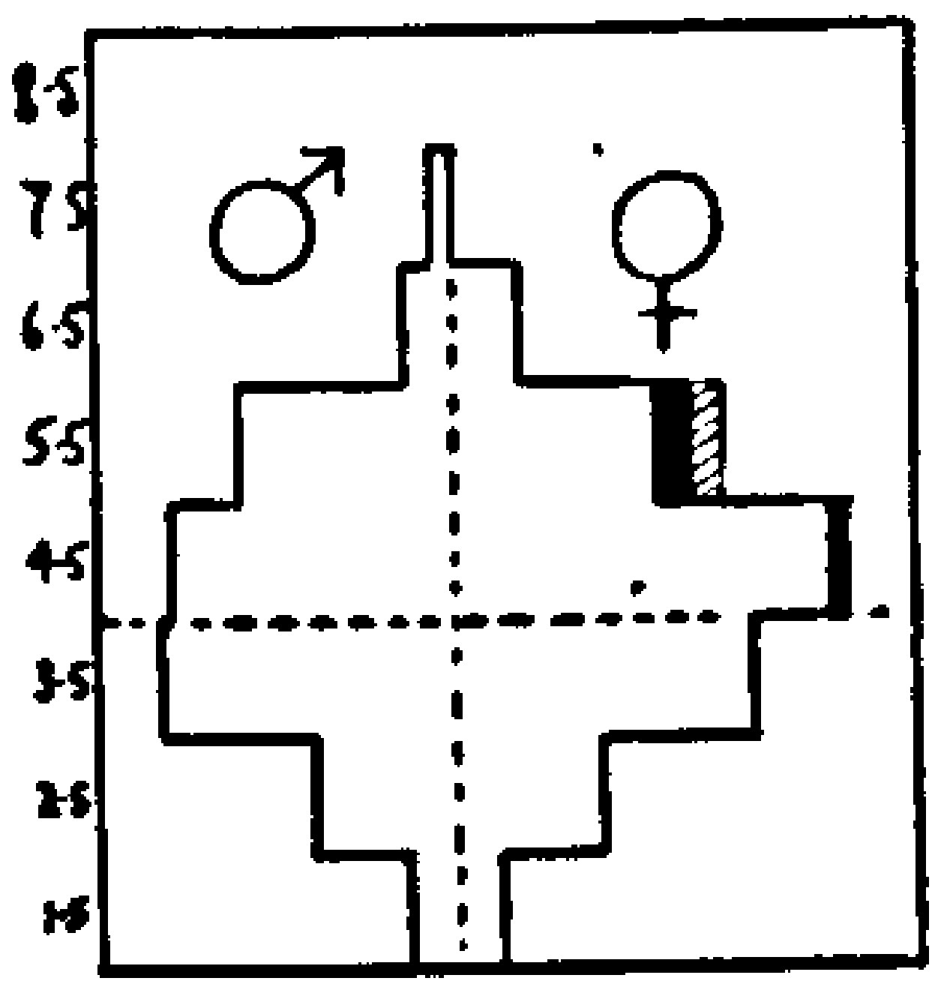
Fig. 14a Histograms showing the population structure of two separate samples of *A. meridianus* collected from Padeswood Lake, Flintshire, on the 27th October 1958.

Fig. 14b Histograms showing the population structure of four samples of Asellus obtained using the sieve-method; and the population structure of these samples when specimens hand-sorted from the debris on the wire-mesh have been included.

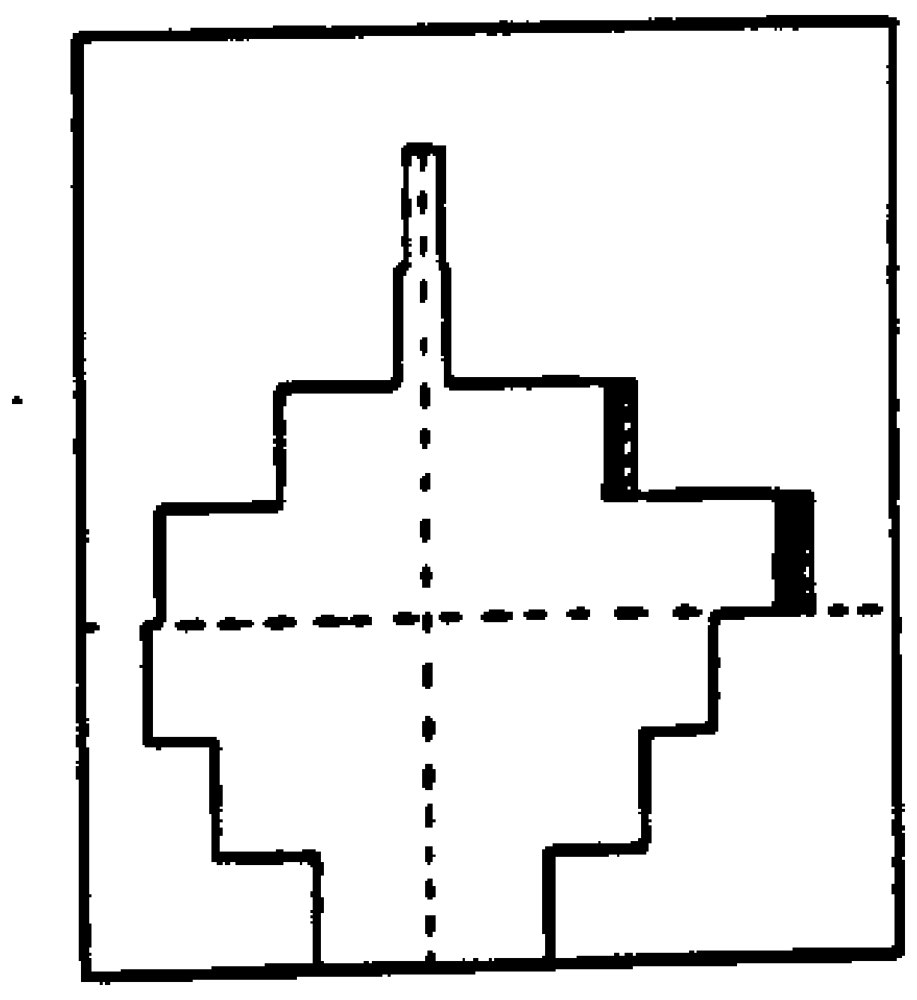
In each separate compartment, the histogram drawn on the left represents the sample obtained using the sieve-method; and the histogram drawn on the right represents the sample when specimens from the debris on the wire-mesh have been added.

1a *A. aquaticus* from Buckley Lake, Flintshire.
2a *A. aquaticus* from Hatchmere, Cheshire.
1m *A. meridianus* from Padeswood Lake, Flintshire.
2m *A. meridianus* from Hatchmere, Cheshire.

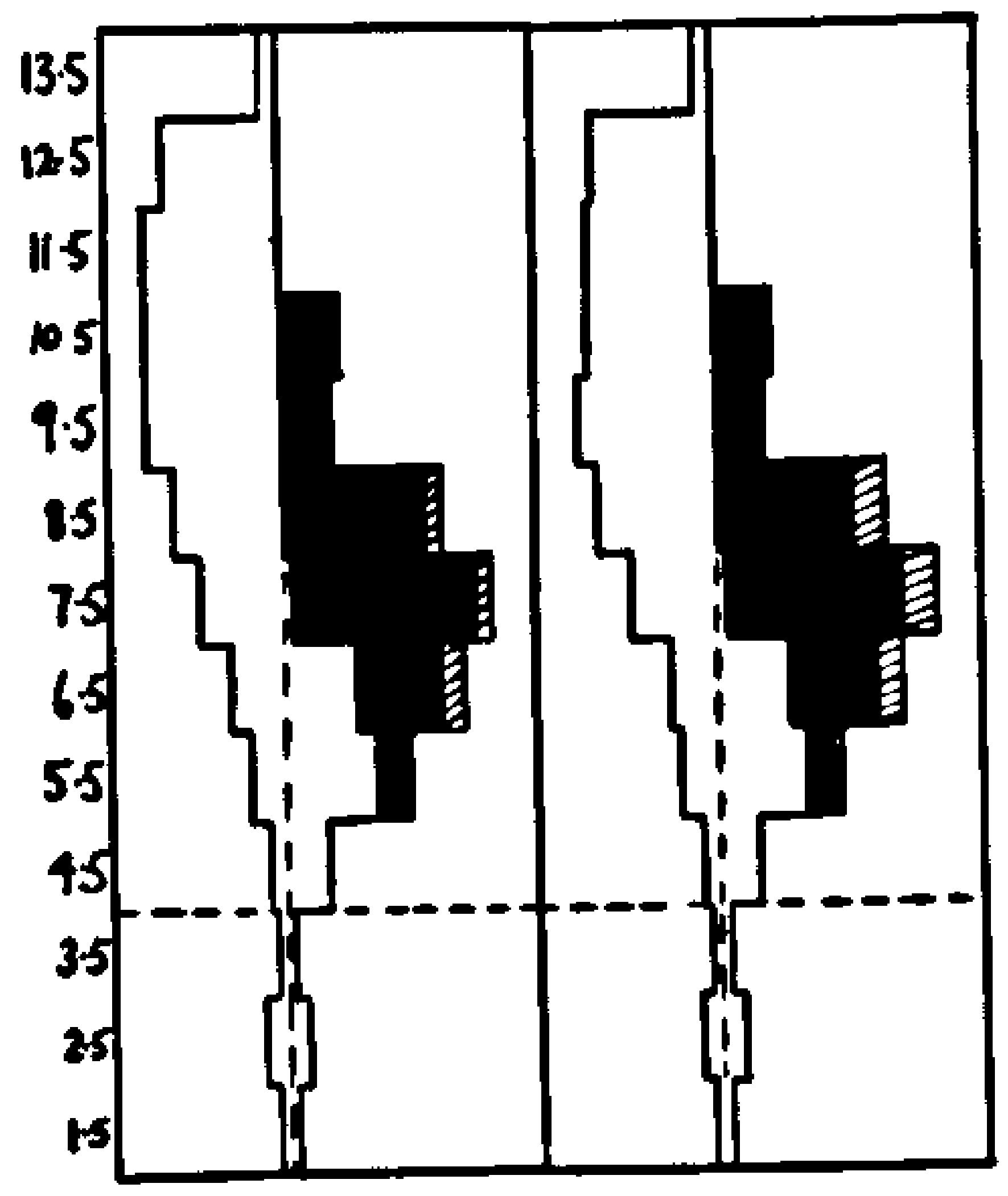
Fig. 14a & b are arranged as in fig.9


8·5
7·5
6·5
5·5
4·5
3·5
2·5
1·5
♂
♀

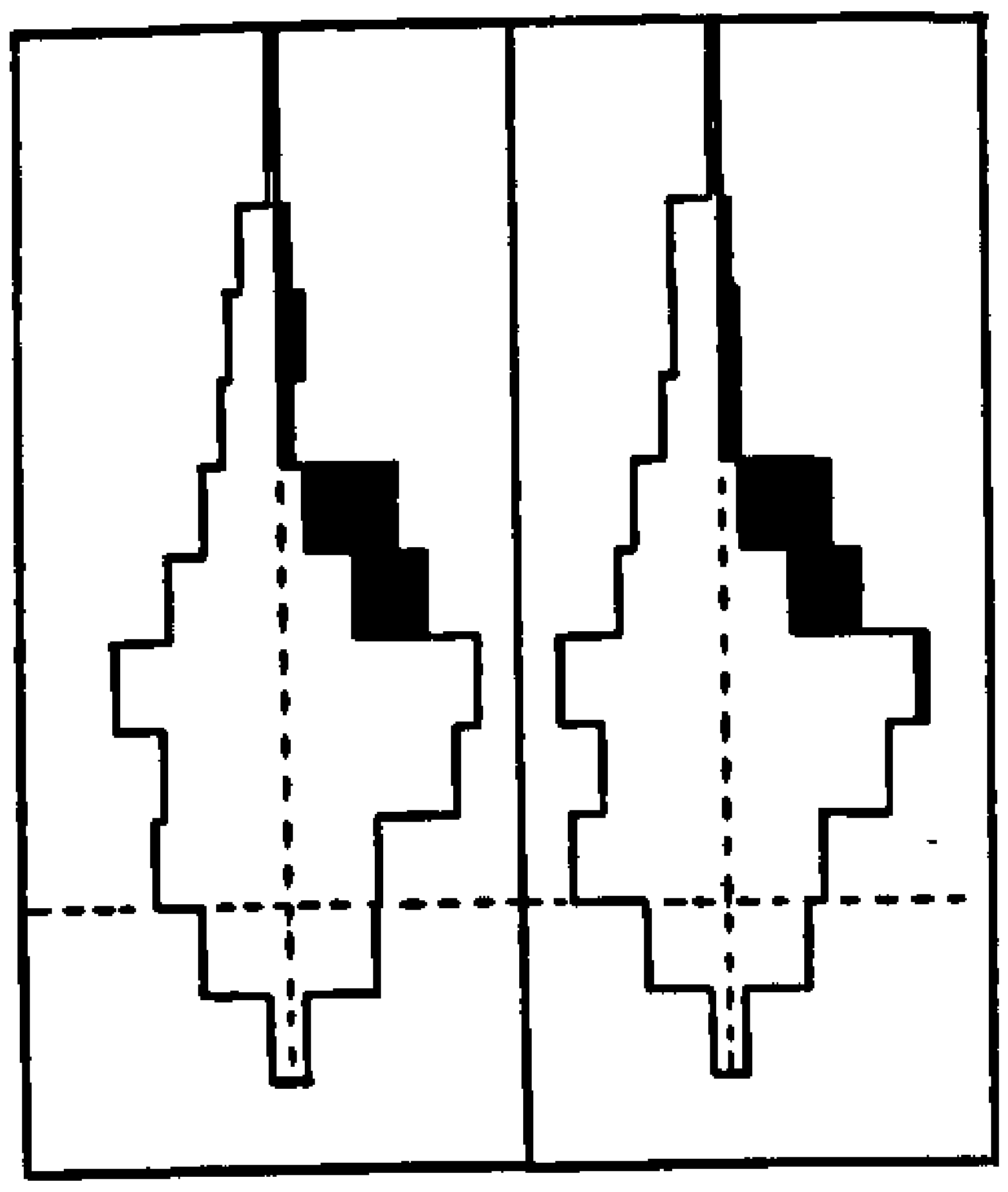
1.



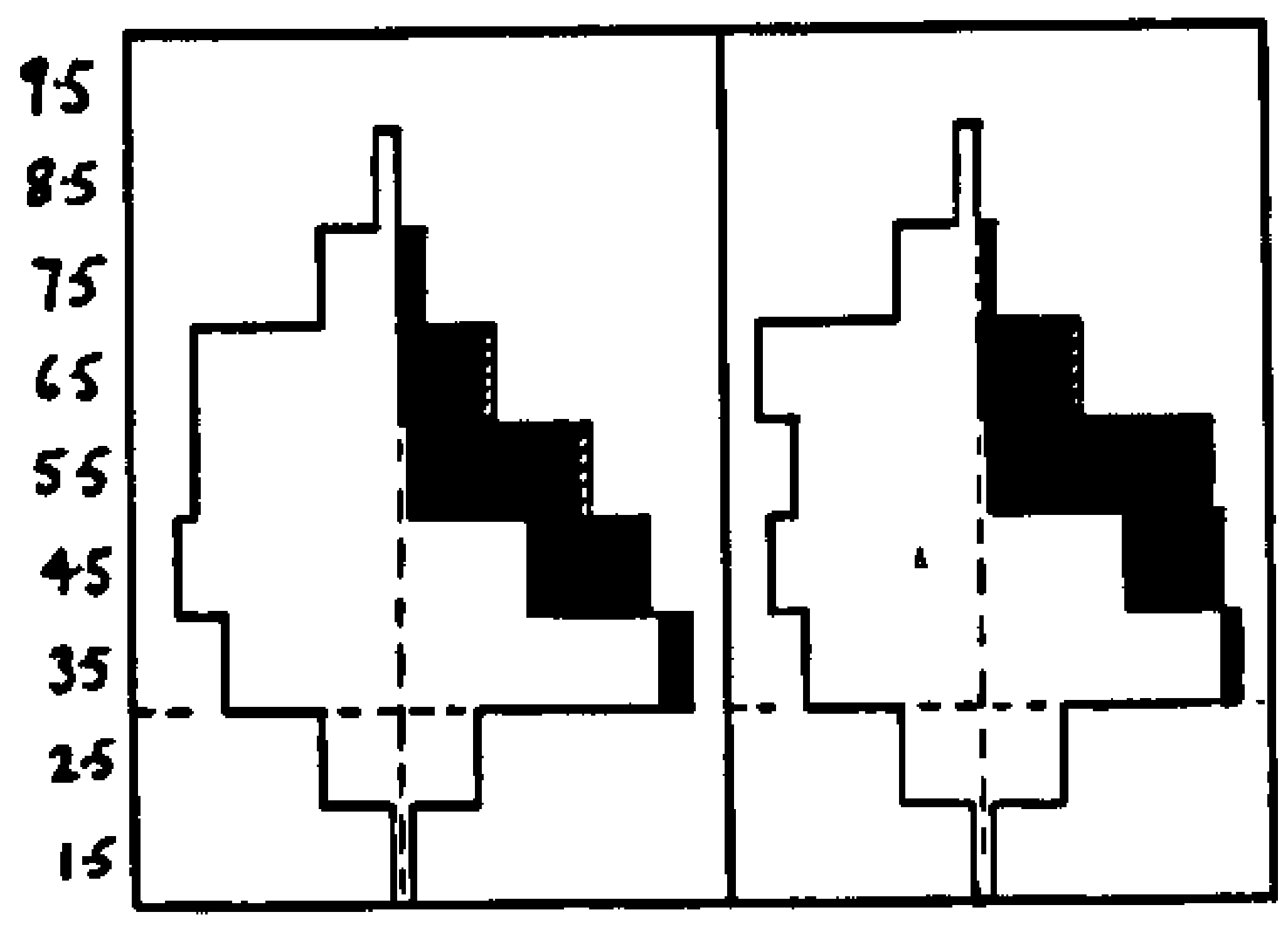
2.


13·5
12·5
11·5
10·5
9·5
8·5
7·5
6·5
5·5
4·5
3·5
2·5
1·5

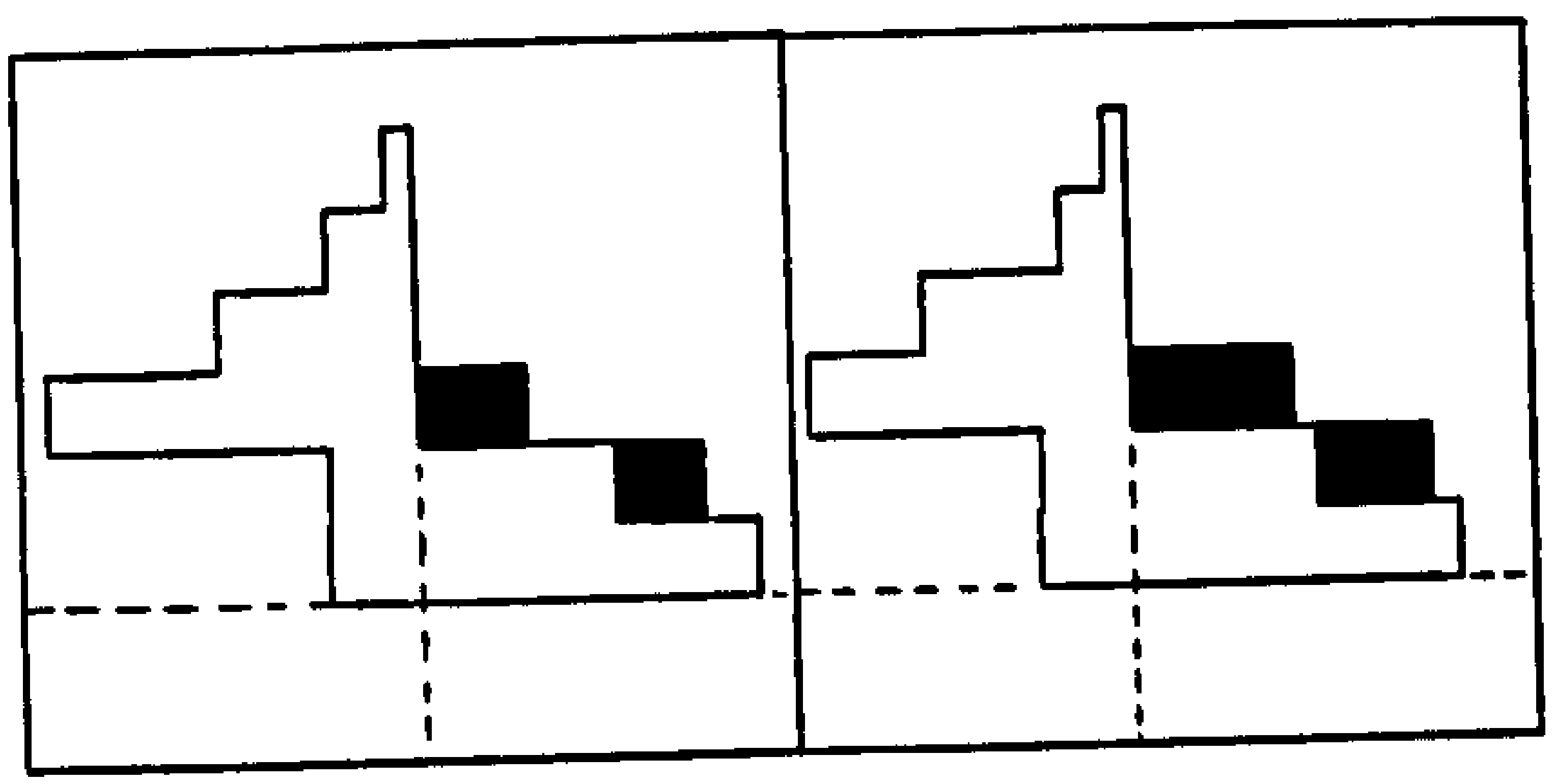
1a



2a


9·5
8·5
7·5
6·5
5·5
4·5
3·5
2·5
1·5

1m



2m

THE LIFE CYCLE

Interaction between closely allied species may be restricted to only one part of, or occur throughout, their life-cycles. For this reason, a detailed knowledge of the life-cycles of closely allied species is essential if a satisfactory evaluation of their ecological interaction is to be attempted; "the superiority of one species over another must be estimated in terms of the whole life-cycle" (Crombie 1947, p.48).

A number of investigations of the life-cycles of marine, brackish-water and fresh-water crustaceans exist, and it is upon these that the present work on the life-cycle of A. aquaticus and of A. meridianus has been modelled. The investigations of Markus (1930) on Mancasellus macrourus Garman, Howes (1939) on Idotea viridis (Slabber), Hiatt (1948) on Pachygrapsus crassipes Randall, Clemens (1950) on Gammarus fasciatus Say, Kinne (1952) on G. duebeni Lillj., Daum (1954) on Caecosphaeroma (Vireia) burgundum Dollfus, Naylor (1955) on Idotea emarginata (Fabricius), Hynes (1955) on several species of Gammaridae, and Jefferies (1958) on Palaemonetes varians (Leach) have been especially useful.

The details of the sequence of events involved in reproduction in Asellus are well known, and have been described for *A. meridianus* by Unwin (1920), and for *A. aquaticus* by Emden (1922), Maercks (1930) and others. There would appear to be no fundamental difference between *A. aquaticus* and *A. meridianus* in these details. Briefly, the sequence of events is as follows:-

Some time before the female is ready to oviposit she is seized by the male who, using his first and fourth peraeopods, places her, dorsal side uppermost, between his legs. The female is kept in this position by the male's fourth pair of peraeopods. This association of male and female is known as precopulation and it may last for less than a day to more than a week, depending on the temperature, the nearness of the female to oviposition, and other factors. Before oviposition the female must moult, and, as described on p. 2.14 - 2.15, this takes place in two phases. During the first phase the posterior part of the old cuticle is cast revealing the open vaginae situated ventro-laterally on the fifth thoracic segment. Copulation may occur as soon as this phase has been completed, and is effected principally by the endopodites of the second pleopods of the male. In copulation the male extends either its left or right endopodite downwards and forwards into the gap between the respectively left or right fourth and fifth female peraeopods, and introduces sperm into the vagina of that side. As soon as the endopodite has discharged all its sperm, it is withdrawn, and the process repeated by the endopodite of the other side. The whole process may occur several times, but between each discharge there is a pause whilst the sperm sacs of the endopodites are refilled by the penes. When copulation has completely finished, the male and female separate[1], and the female undergoes the second phase of her moult. In this phase the anterior part of the old cuticle is cast releasing the large oöstegites which form a brood pouch beneath the anterior part of the thorax. The oöstegites arise from the bases of the first four pairs of peraeopods, but very rarely, as in one specimen of <u>A. aquaticus</u> from Buckley Lake, Flintshire, collected on the 11th March 1960, only the first three pairs of peraeopods may possess oöstegites. Fertilization is internal. The eggs are released into the brood-pouch shortly after the second phase of the female moult has been completed, and are incubated for a varying period of time. Females which are incubating eggs are said to be ovigerous. The eggs develop within the brood-pouch into juveniles which are released when they are approximately 1mm. long. After the

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Footnote 1. Muldal's (1951) statement that the male and female remain together "even when the embryos are well advanced in development" (p.1128) is incorrect.

release of the juveniles the female undergoes a further moult whereby she loses her brood-pouch, her oöstegites being reduced once more to small club-shaped lamellae. The moult preceding oviposition has been termed the "Parturialhäutung" by Emden (1922); the moult following the release of the juveniles has been termed the "Zwischenhäutung" by Haemmerli-Boveri (1926). In the breeding season these moults are normally consecutive, whilst in the non-breeding season successive moults occur without the production of a brood pouch.

In contrast to our detailed knowledge of the sequence of events involved in the reproduction of A. aquaticus and A. meridianus, our knowledge of their life-cycles in the field is more restricted. As far as I am aware the only information available upon the life-cycle of A. meridianus is limited to the papers of Unwin (1920) and Dunn (1952). These authors largely confined themselves to a few notes upon the times at which ovigerous females could be found and were most abundant. Rather more information upon the life-cycle of A. aquaticus exists, for, apart from those papers in which the reproduction of A. aquaticus is the principal theme (e.g.'Kaulberz (1913), Emden (1922), Janke (1926), Maercks (1930), a large number of isolated facts exist in other papers (e.g. Vandel (1926), Berg (1938), Berg (1948), Needham (1949), Balesdent - Marquet (1955), Berner (1956), Weerekoon (1956)). In addition, Birstein (1951) has quoted some so far unpublished data obtained by M.V. Zheltenova. But, although it is possible, by combining information from all these sources, to gain a fairly complete general picture of the life-cycle of *A. aquaticus*, the details of this picture are by no means clear. It was to clarify this picture, and to provide a similar picture for *A. meridianus*, that the following research was undertaken.

Both field and laboratory investigations were made during the study of the life-cycle of *A. aquaticus* and of *A. meridianus*. The field investigations consisted of the collection of regular samples from a number of localities, and the subsequent analysis of these samples; the laboratory investigations consisted of a breeding programme undertaken on the roof of the laboratory, and some brief investigations of the length of time of incubation at various temperatures.

(a). Field Investigations

1. Methods.

Regular samples of *Asellus* were collected from four localities, of which one contained only *A. aquaticus* (Buckley Lake, Flintshire), one only *A. meridianus* (Padeswood Lake, Flintshire), and two both *A. aquaticus* and *A. meridianus* (Llyn Llywenan, Anglesey; Hatchmere, Cheshire). These localities are described below.

Buckley Lake.

Buckley Lake, M.R.109/279650, is situated amongst semi-rural environs about 2½ miles east of Mold in Flintshire, North Wales. Surrounded by rough pasture and a few houses, it is approximately 100 yds. long and 25 yds. wide, and has been formed from a quarry. There are no apparent inflowing or outflowing streams. Fish-stocking takes place periodically, and the fishing-rights are possessed by a local angling club. The banks are mostly steep but give rise to a shallow shore terrace which is not very wide and ends abruptly. The substratum consists mainly of gravel and muddy silt, although some domestic refuse is also present. There is scarcely any emergent vegetation apart from a few isolated clumps of *Juncus inflexus* L.,, but, near the margins of the lake, submerged vegetation is abundant. This consists mainly of *Potamogeton crispus* L., and *Myriophyllum alterniflorum* DC. During the summer months there is a dense mat of the alga *Rhizoclonium* sp. on the surface at the edges of the lake. The fauna is abundant, and, apart from *A. aquaticus*, includes oligochaetes, *Haemopis sanguisuga* (L), *Planorbis albus* Müll., *Limnaea pereger* (Müll.), *Gammarus lacustris* G.O. Sars, ? *G. pulex* (L.), Hydracarina, *Caenis* sp., *Chloeon* sp., *Ischnura elegans* (van der Linden), *Corixa dorsalis* Leach, *C. falleni* (Fieb.), *C. fossarum* (Leach), *Sialis lutaria* (L.), Limnophilidae, Polycentropidae, Phryganeidae, Chironominae, Tabanidae, Tipulidae, *Haliplus* sp., *Hydroporus* sp., *Ilybius* sp., and *Gasterosteus aculeatus* L.

The results of an analysis of a water sample collected on the 25th March 1960 are indicated in the table on p. 4.20. The analysis was carried out by Mr. J. Heron of the Freshwater Biological Association.

The regular samples of *A. aquaticus* were collected from a small area at the northeastern end of the lake.

Padeswood Lake.

Padeswood Lake, M.R. 109/278620, is situated amongst agricultural environs about 3 miles south-east of Mold in

Flintshire, North Wales. Surrounded by low-lying grazing land, it is approximately oval in shape, and is about 300 yds. long and 200 yds. wide. There is a single large outflowing stream and numerous small inflowing streams. The lake is almost completely surrounded by a wide belt of reedswamp, but open water reaches a well-defined bank at the southern tip. At the water's edge this bank is gently sloping and gives rise to a similar shore terrace. The substratum here consists mostly of mud and finely divided vegetable debris. At the southern end of the lake some sort of organic pollution is occurring from one of the inflowing streams. The most obvious effect that this pollution has so far had has been a reduction in the numbers of A. meridianus in this region; in July 1958, for example, one dip of a pond-net produced hundreds of specimens, whereas in July 1960 a similar dip produced only a few specimens. At present the pollution appears to be restricted to the southern end of the Lake. The reedswamp consists almost entirely of Typha latifolia L. and Carex riparia Curt., but also present on the landward side of the reedswamp are C. otrubae Podp., Phalaris arundinacea L. Filipendula ulmaria (L.) Maxim., Mentha aquatica L., and Myosotis sp. There is no floating vegetation and very little submerged macrophytic vegetation apart from some sparse Callitriche. Algae present near the source of pollution include Spirogyra sp., and

Hormidium sp., and Tribonema sp. During the past two years there has been a gradual decrease in the abundance and diversity of the fauna at the southern end of the lake, but still present elsewhere are Polycelis sp., Stylaria lacustris(L.) and other oligochaetes, Glossosiphonia complanata (L.) Planorbis albus, Physa fontinalis (L.), Hydrobia jenkinsi, Ostracoda, Cyclops sp., Gammarus pulex, Hydracarina, Argyroneta aquatica Cl., Caenis sp., Chloeon sp., Nemurella picteti Klapalek, Ischnura elegans, Nepa cinerea L., Corixa praeusta (Fieb.), C. falleni, Sialis lutaria, Limnophilidae, Polycentropidae, Sericostomatidae, Chironominae, Anopheles sp., Helodidae, Laccophilus sp., Nymphula sp., and Gasterosteus aculeatus.

The results of an analysis of a water sample collected on the 25th March 1960 are indicated in the table on p.4.20. As before, the analysis was carried out by Mr. J. Heron of the Freshwater Biological Association.

The regular samples of A. meridianus were collected from a fairly wide area at the southern end of the lake.

Llyn Llywenan

Llyn Llywenan, M.R. 106/348816, is a large shallow lake situated amongst agricultural environs about 3 miles north-east of Valley, Anglesey. It is surronded by rough pasture and grazing land, and there is a single large outflowing stream and several smaller inflowing streams. Although in size it is approximately ¾ mile long and ¼ mile wide, in depth it does not exceed about 6 feet. Reedswamp occurs around most of the lake, but the shore-line is exposed at several points at the northern end. *Phalaris arundinacea* is the dominant reedswamp species but also present here are *Typha latifolia* and *Iris* sp. On the landward side of the reedswamp there is a rich marsh flora in which the more common species are *Menyanthes trifoliata* L., *Alisma plantago-aquatica* L., *Mentha aquatica*, *Juncus articulatus* L., *Myosotis* sp., *Galium palustre* L., *Veronica beccabunga* L., *V. scutellata* L., *Glyceria fluitans* (L.), and *Salix* sp. Floating vegetation occurs in sheltered parts of the lake and includes *Lemna minor* L., *L. trisulca* L., and *Ranunculus* sp. Submerged vegetation includes *Fontinalis* sp., *Potamogeton obtusifolius* Mert. & Koch, *Littorella uniflora* (L.), *Elodea canadensis* Niche., *Myriophyllum* sp., and *Callitriche stagnalis* Scop. Hynes has already published a short description of this lake (Hynes 1955). He noted that the fauna is rich and abundant, and, apart from *A. aquaticus* and *A. meridianus*, includes *Polycelis* sp., *Stylaria lacustris* and other oligochaetes, *Glossosiphonia* sp., *Erpobdella* sp., *Piscicola geometra* (L.), *Daphnia* sp., *Gammarus lacustris*, Hydracarina, *Argyroneta aquatica*, *Caenis* sp., *Ischnura elegans*, *Plea leachi* McGreg. & Kirk., *Corixa* spp., *Phryganea* sp., *Traienodes* sp., Leptoceridae, Polycentropidae, *Limnius tuberculatus* Müller, *Deronectes depressus* Fabr., *Haliplus* sp., *Sphaerium corneum* L., *Physa fontinalis*, *Planorbis* spp., *Limnaea* spp., *Gasterosteus aculeatus*, *Pygosteus pungitius* (L.), *Anguilla vulgaris* L., and *Salmo trutta* L. *Theromyzon tessulatum* (Müll.), *Eurycerous lamellatus* (Müll.), *Coenagrion* sp., *Valvata piscinalis* (Müll.), and *Notonecta glauca* L. have also been noted.

The results of an analysis of a water sample collected on the 31st March 1959 are indicated on the table on p.420 . These results are similar to those obtained by Hynes in 1955 (Hynes 1955), and by Reynoldson in 1951 and 1952 (Reynoldson 1958). For comparative purposes Hynes' and Reynoldson's results (converted to m.equiv/L) are also indicated in the table. The methods used for the analysis of the 1959 water sample are described in chapter VI.

The regular samples of *Asellus* were collected at the northern tip of the lake, where the substratum is mainly small stones and gravel.

Hatchmere.

Hatchmere, M.R. 109/553722, is a large lake situated about 4 miles south-east of Frodsham, Cheshire. It is surrounded by pasture and low wooded hills, and near one corner there is a small caravan site and a few houses. It is approximately 400 yds. long and 300 yds. wide, and there is a single outflowing stream and a few smaller inflowing streams. At one end of the lake there is an extensive carr, and a wide reedswamp extends almost completely around the shoreline. At one point there is a well-defined bank which leads to a shallow and rather exposed shore terrace of sand. Elsewhere, the substratum consists mainly of a thick layer of vegetable debris overlying silt and mud. Phragmites commonis Trin. and Typha latifolia are the dominant species of the reedswamp, but also present on the landward side are Glyceria sp., Juncus effusus L., J. articulatus L., Sparganium sp., Carex acutiformis Ehrh., Iris pseudacorus L., Polygonum amphibium L., Apium nodiflorum (L.) Lag., Galium palustre, Potentilla palustris (L.) Scop., Filipendula ulmaria, Ranunculus lingua L., R. lutarius (Revel), Mentha aquatica and Viola palustris L. Salix sp., Myrica gale L., Alnus glutinosa (L.), Quercus robur L., Sorbus aucuparia L., Rubus sp. and Betula sp. are the main species within the carr. At the edges in the more sheltered parts of the lake there is a little floating vegetation composed of Nuphar lutea (L.) Sm.

and *Lemna trisulca*, but there is no completely submerged vegetation. Apart from *A. aquaticus* and *A. meridianus* the fauna includes *Polycelis* sp., oligochaetes, *Erpobdella* sp., *Glossosiphonia complanata*, *Bithynia tentaculata* (L.), *Planorbis carinatus* Müll., *Sphaerium* sp., Ostracoda, *Gammarus lacustris*, *G. pulex*, Hydracarina, *Argyroneta aquatica*, *Leptophlebia* sp., *Nepa cinerea*, *Corixa falleni*, *C. punctata* (Illig.), *C. moesta* (Fieb.), *Sialis lutaria*, Limnophilidae, Polycentropidae, *Molanna* sp., Chironominae, Tanypodinae, Tipulidae, *Gyrinus* sp., *Noterus* sp., and *Cyprinus* sp. During the summer months there is a dense plankton.

The results of the analyses of water samples collected during October 1954 and 1955 have been published by Gorham (Gorham 1957a). These results are indicated in the table on p4.20.

The regular samples of *Asellus* were collected from amongst the phragmitetum bordering the carr at the northen end of the lake.

The samples from Buckley and Padeswood Lakes were collected at monthly intervals over a two year period extending from October 1957 until November 1959. The samples from Llyn Llywenan were collected at approximately bimonthly intervals

	Total salts m.equiv/L.	Ca	Mg	Na	K	HCO_3	Cl	SO_4	NO_3-N
BUCKLEY	10.60	2.113	5.430	2.170	0.7445	5.880	2.160	2.545	0.015
PADESWOOD	8.540	5.750	1.200	1.218	0.2415	5.220	0.980	2.232	0.108
LLYWENAN	1.55	0.60	0.28	0.61	0.06				
(Hynes,1955)	2.57	0.75	0.82	0.96	0.04		1.31		
(Reynoldson,1958)		0.44-0.66	0.56-1.05				0.85-0.97		
HATCHMERE (Gorham,1957a)	3.22	1.67	0.97	0.48	0.10	1.65	0.62	0.94	0.17

<u>Table.</u> <u>The ionic composition of the localities from which the regular samples of Asellus were collected.</u>

(all figures in milliequiv./L.)

over a period extending from October 1957 to September 1958, and those from Hatchmere at approximately biweekly intervals over a period extending from the 10th June until the 30th November 1959. The samples collected from Buckley and Padeswood Lakes before July 1958, and all the samples from Llyn Llywenan, were obtained by Dr. H.B.N. Hynes. Those collected from Buckley and Padeswood Lakes on the 7th September 1959, and from Hatchmere on the 7th and 16th September 1959, were obtained by Miss J. Venn.

Two further samples of Asellus were collected as part of the field investigation of the life-cycles: one of A. aquaticus from a small pond, M.R.100/273903, near Bidston, Cheshire; and one of A. meridianus from a small pond, M.R.100/302843, near Storeton, Cheshire. They were collected on the 30th June 1959.

Each sample of Asellus was collected by vigorously working a stramin hand-net to and fro amongst the vegetable debris, stones, etc. comprizing the substratum at each locality. The contents of the net were transferred at intervals to a large jar containing a little water. Collection was continued until it was judged that about 200 specimens of each species had been obtained. To determine if each sample collected in this manner was a truly random sample of the population, two samples of A. meridianus were collected from Padeswood Lake on the

27th October 1958. These samples were analysed separately but in an identical manner. The analysis took a similar form as that to which the regular samples were subjected, as described in detail on p.4.24. Briefly, the specimens were divided into 1 mm. (length) size groups, and each size group above 3.5 mm. then divided into males, females with small brood lamellae, ovigerous females, and females with empty brood pouches. The results are indicated in table 1, appendix B, p.10.6, and are shown in diagrammatic form in fig.14a, p.4.6. It can be seen from this figure that there is no marked difference in the population structure of the two samples, and this would seem to indicate, therefore, that samples collected in the described manner are indeed random.

In the samples collected from Buckley and Padeswood Lakes before July 1958, and in all the Llyn Llywenan samples, the specimens of Asellus were separated from the vegetable debris, mud, etc. also present in the jar, by hand-sorting. However, this method of separation was extremely tedious and slow, and in all other samples specimens of Asellus were obtained by another, more rapid, method. This method made use of the fact that specimens of Asellus, when disturbed, become restless and move about. Briefly, the technique was to place small amounts of debris containing the Asellus on to a wire frame of $\frac{1}{4}$ in. mesh which was suspended just below the surface of water contained in a large, flat dish. The Asellus, thus disturbed, almost immediately became restless, and moved from out of the debris on to the wire mesh through which they then passed into the water below. Not all the debris was retained, of course, but separation of the Asellus from the finer material which passed through the wire mesh was easily achieved by using a very fine sieve, and from the less fine material by hand-sorting.

In terms of the percentage of specimens removed from a sample, the efficiency of the method (henceforth referred to as the sieve-method) was high for both species: in a sample from Buckley Lake, 207 out of 218 specimens of A. aquaticus were obtained (=95% efficient); in a sample from Padeswood Lake, 374 out of 494 specimens of A. meridianus were obtained (= 76% efficient); and in a sample from Hatchmere, 173 out of 183 specimens of A. aquaticus (=95% efficient), and 56 out of 69 specimens of A. meridianus (= 81% efficient) were obtained. It appeared that the efficiency mainly depended upon the type of debris in the sample.

There was no apparent difference in the population structure of samples obtained using the sieve-method, and those obtained by hand-sorting. This is indicated by fig.14b p.4.6 which compares the population structure of four samples obtained using the sieve-method, with the population structure of these samples when specimens hand-sorted from the debris remaining on the wire mesh were added to them. Two of the samples were of A. aquaticus from Buckley Lake and Hatchmere; two of the samples were of A. meridianus from Padeswood Lake and Hatchmere. The analysis took a similar form as that to which the regular samples were subjected, and the detailed results are presented in tables 2-5, appendix 6, pp. 10.7 – 10.10.

All specimens of Asellus were killed by immersion in 70% alcohol, and samples were also preserved in this until analysed. In the analysis of a sample, each specimen was measured and placed in a size group, and then, where possible, each size group divided into males, females with small brood lamellae, ovigerous females, and females with empty brood pouches. In samples which contained both species of Asellus, specific separation was carried out after measurement, during the sub-division of the size groups, and was based upon the morphology of the sexual pleopods.

In conformity with most other workers on the Crustacea, overall length was chosen as the index of size. Needham (1949) used abdomen width as an index of size in Asellus, but also showed (Needham, 1937) that there is an almost direct relationship between abdomen width and overall length in Asellus.

The length was regarded as the distance from the anterior border of the head to the posterior border of the abdomen. In practice, individual specimens shorter than 9.5 mm. were not actually measured, but each was matched against a row of eight specimens whose lengths were 1.5, 2.5, 3.5, 4.5, 5.5, 6.5, 7.5 and 8.5 mm. Specimens longer than 9.5 mm. were directly measured against a scale. Using these methods it was possible to rapidly divide a sample into 1 mm. size groups, and to avoid, to some extent, Needham's (1937) difficulty in measuring dead, bent specimens. To check that there was no personal bias towards particular size groups, a single sample was twice divided into size groups; once by myself, and once by another person, Mr. A.L. Rice. The numbers of specimens which were placed in each size group during the two divisions are shown in the table below;

SIZE - GROUP mm.

	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5
Author	3	7	19	20	39	25	18	14	7	3
A.L.Rice	2	7	19	20	43	21	21	13	8	1

These figures were subjected to a Chi-squared test which revealed that there was no significant difference between the two sets of figures.

The division of size groups into males, females with small brood lamellae and ovigerous females with empty broodpouches was carried out by examining the ventral surface of specimens beneath a binocular microscope. Sexual differentiation was based on the morphology of the sexual pleopods. Although in many cases it proved possible to distinguish between males and females of A. aquaticus which were 3.5 mm. or less in length, and between males and females of A. meridianus which were 2.5 mm. or less in length, it was found practicable to limit sexual differentiation to size groups above 3.5 mm. in A. aquaticus, and to those above 2.5 mm. in A. meridianus. The sexual condition of females was easily discernible when the anterior, ventral part of the thorax was examined. Specific separation of specimens smaller than 2.5 or 3.5 mm. in samples containing both A. aquaticus and A. meridianus was achieved by examining the pattern of pigmentation on the dorsal surface of the head (but see page 2.16)

2. The Life - Cycle of A. aquaticus and of A. meridianus as indicated by the Field Investigations.

The detailed results of the analyses of the regular samples of A. aquaticus and of A. meridianus are presented in tables 1,2,3, and 4. Appendix C, pages 10.11-10.44, and are shown in diagrammatic form as histograms in figs. 9,10,11, and 12, pages 4.1-4.4.

The breeding season may be regarded as that period during which ovigerous females or females with empty brood pouches occur. Fig. 9 shows that the breeding season of A. aquaticus at Buckley began in 1958 during February, and the sample collected in early March 1959 indicates that breeding at Buckley also began during February in 1959. Breeding continued at Buckley in 1957 and 1959 until October, and in 1958 until September. The maximum extent of the breeding season of A. aquaticus at Buckley may, therefore, be regarded as having been from February until October. Fig. 10 shows that the breeding season of A. meridianus at Padeswood began in 1958 during January, and in 1959 probably during February. Breeding continued at Padeswood in 1957 until November, in 1958 until December, and in 1959 until October. Thus, at one time or another, breeding females of A. meridianus were collected from Padeswood in all months of the year. The main period of breeding, however, may be regarded as having been between February and October.

Since it is known that for both species the time of incubation of each brood is short (see p.4.61), it is to be expected that both produced several broods during their extensive breeding seasons. The wide range of size-groups that occurred in all samples from Buckley and Padeswood indicates that there were no well-defined temporal divisions between these broods.

It can be seen from an examination of the histograms (figs. 9 and 10) that the breeding of A. aquaticus and of A. meridianus was not of equal intensity throughout their breeding season; apart from the gradual increase and decrease in the number of breeding females at the beginning and end of the breeding season, two maxima in the breeding intensity occurred. These maxima are indicated more clearly by fig.15, p. 4.69, which shows (a) the number of breeding females as a percentage of the total number of females above 3.5 mm (in the case of A. aquaticus) or 2.5 mm (in the case of A. meridianus) present each month, and (b) the number of breeding females as a percentage of the total population present each month. In the compilation of these percentages, the data for the same months each year have been pooled. It can be seen that for both species the first and greater maximum occurred in spring, the actual maximum being in April, and the second and lesser maximum during the late summer, and early autumn. The second maximum occurred later and was more pronounced at

Padeswood than at Buckley.

The variation in the intensity of breeding was reflected, to some extent, by the variation in the number of juveniles. Individuals were regarded as juveniles if they were less than 4.5 mm. in the case of A. aquaticus, or less than 3.5 mm. in the case of A. meridianus. The variation is illustrated by fig. 16, p. 4.70, in which the number of juveniles of both species present each month has been plotted as a percentage of the total population. In the compilation of the percentages, the data for the same months each year have been pooled. The figure shows that, as expected, large numbers of juveniles occurred from about 3 months after the commencement of the breeding season until about one month after the end of the breeding season. The rapid rise in the percentage of juveniles of both species in early spring can clearly be correlated with the spring maxima in the intensity of breeding, but the small rise in the percentage of juveniles of A. aquaticus in the early spring would appear not to have been directly correlated with any variation in breeding intensity. A complete explanation of this latter increase cannot at present be given, but it is of interest to note that Jefferies (1958) observed a similar phenomenon in Palaemonetes varians, and suggested that it was due to the re-appearance of juveniles which had spent the winter months in deeper water out of reach of the collecting net. The gradual decrease in the percentage of juveniles of A. aquaticus during March and April may be satisfactorily explained as due to their growth to a length greater than 3.5 mm.

It is evident from an examination of the histograms (figs. 9, and 10) that in both A. aquaticus and A. meridianus the spring maximum in the intensity of breeding was due to the breeding of overwintered females. The samples collected on the 27th February 1958 suggest that in A. aquaticus the first of these females to become ovigerous were confined to the larger size-groups, whereas in A. meridianus the first of these females to become ovigerous occurred over a wide range of size. Towards the end of spring the larger males and females decreased in frequency at both Buckley and Padeswood, and this decrease was presumably due to the death of these individuals. The decrease is shown more clearly at Buckley by the samples collected in March, April and May 1959, than by those collected in the spring of 1958, and more clearly at Padeswood by the samples collected in April, May and June 1958, than by those collected in the spring of 1959. It is not clear from the histograms exactly when the smaller overwintered males and females at both localities died, but it seems probable that their death was at some time in the early summer. If this was so then in A. aquaticus there would appear to have been a progressive relationship between the time at which breeding began and the time of death. Thus, the largest overwintered females became ovigerous first and died first, and the smallest overwintered females became ovigerous last and died last. The histograms do not reveal any marked difference in either species between the sexes in the time of death.

The death of the overwintered adults of both species towards the end of spring and in the early summer is also indicated by the marked fall in the average size of the sexes at this time of year. This is shown in fig.17,p.4.71. In the compilation of this figure the data for the same months each year have been pooled, and it has been assumed that the sex-ratio of specimens smaller than 4.5 mm. (in the case of <u>A. aquaticus</u>) or 3.5 mm. (in the case of <u>A. meridianus</u>) is approximately 1:1.

The juveniles released by the overwintered females first appeared in large numbers at Buckley during June in 1958 and during May in 1959, and at Padeswood during May in both 1958 and 1959. In both species, therefore, incubation during the spring months would appear to have lasted for a relatively long period of time. Since this fact is supported by further evidence (see p.4.41), it would seem that those females of <u>A. aquaticus</u> and of <u>A. meridianus</u> possessing empty brood pouches at the beginning of the breeding season had lost their eggs by some cause other than the release of juveniles.

The subsequent growth of the juveniles produced by the overwintered females can be followed more clearly at Buckley in the samples collected during 1959 than in those collected during 1958, and more clearly at Padeswood in the samples collected during 1959. It can be seen (fig.9)that by June in 1959 most of the juveniles of A. aquaticus liberated the previous month had grown several mm. in length, and that a sexual difference in size had already become apparent. Furthermore, it can be seen that many of the females of A. aquaticus liberated the previous month were ovigerous, and it would, therefore, appear that the time taken to reach maturity by these females was about one month. The smallest ovigerous female collected from Buckley at this time was just over 4.0 mm. A similar sequence of events would seem to have taken place at Padeswood. Here, however, although it can be seen (fig.10) that by June in 1958 many of the juveniles of A. meridianus liberated the previous month had grown 2-3 mm., substantial numbers of ovigerous females did not occur until July and August; it would appear that the time taken to reach maturity by these females was between two and three months. The smallest ovigerous female collected at Padeswood in the summer of 1958 was just over 4.0 mm., and in the summer of 1959 3.5 mm.

At both Buckley and Padeswood, the breeding of the individuals produced in late spring accounted for the second maximum in the intensity of breeding. The histograms do not reveal whether any of the individuals produced during this second maximum were, themselves, able to breed.

The histograms indicate that the individuals produced by overwintered females eventually comprized the large size-groups in the winter samples of both *A. aquaticus* and *A. meridianus*. Thus, winter samples of both species would seem to have consisted entirely of individuals which had been produced in the *preceding* breeding season. Of the females in the winter samples, some had bred from mid-summer until autumn, others had bred only in autumn, and others had not bred at all. Since it has already been indicated that all the females in the winter samples bred after overwintering and then died, it is evident that individuals of *A. aquaticus* and *A. meridianus* took part in *either one or two breeding seasons*; individuals produced in the early part of the breeding season took part in two seasons; individuals produced in the late part of the breeding season took part in only one season. In contrast to the short time taken to reach maturity by the former individuals, the time taken to reach maturity by the latter individuals was probably of the order of six months.

To summarize briefly, the life-cycle of *A. aquaticus* and of *A. meridianus* as indicated by the regular samples from Buckley and Padeswood Lakes would thus appear to be as follows:

The length of life of all individuals is approximately one year. The breeding season extends from February until October, and during this period many broods are produced between which there are no sharp temporal divisions. Two maxima in the intensity of breeding occur. The first of these maxima occurs in spring and results from the breeding of overwintered individuals. Shortly after the spring maximum most of the overwintered individuals die. The second maximum in the intensity of breeding results from the breeding of individuals produced during the first maximum. During the summer months A. aquaticus takes about one month to mature, and A. meridianus between two and three months. The smallest ovigerous females of A. aquaticus at this time are just over 4.0 mm. in length, and the smallest ovigerous females of A. meridianus about 3.5 mm. in length. Many adults and juveniles overwinter. The largest overwintering individuals are produced in the early part of the preceding breeding season and breed before overwintering; the smallest overwintering individuals are produced in the late part of the preceding breeding season and do not breed before overwintering. There is a complete range of intermediates between the largest and smallest of these overwintering individuals. All the overwintered individuals breed in spring and then die. Individuals may thus take part in either one or two breeding seasons.

It is evident from the above summary that the regular samples from Buckley and Padeswood indicate the essential similarity between the life-cycle of A. aquaticus and A. meridianus. They indicate also, however, a few points of difference. Thus, it would appear that A. meridianus differs from A. aquaticus in having a rather more extensive breeding season, and a later and more pronounced second maximum in the intensity of breeding. Furthermore, the juveniles of A. meridianus show no indication of an increase in early spring, as do those of A. aquaticus, and the individuals produced by the overwintered females of A. meridianus take rather longer to mature than do those of A. aquaticus. It seems reasonable to suppose that the longer time taken by juveniles of A. meridianus to mature during the summer is correlated with the later and more pronounced autumnal breeding maximum of this species.

The regular samples from Llyn Llywenan and Hatchmere were collected in order to check whether the life-cycle of A. aquaticus and of A. meridianus in localities where A. aquaticus and A. meridianus co-exist was similar to that in localities where only A. aquaticus or only A. meridianus exists, as indicated by the samples from Buckley and Padeswood.

The detailed results of the analyses of the regular samples from Llyn Llywenan and from Hatchmere are presented in Append-

-ix C, tables 3 and 4, pages 10.32-10.44; and are shown in diagrammatic form in figs. 11 and 12, pages 4.3 and 4.4.

The samples from Llyn Llywenan show (fig. 11, p. 4.3) that the breeding season of both A. aquaticus and A. meridianus at Llyn Llywenan extended in 1958 at least from February until September. The sample collected on the 10th October 1957 shows that in 1957 A. aquaticus had ceased to breed by October, whereas A. meridianus was still breeding in that month. Only a single maximum in the intensity of breeding of A. aquaticus is indicated, but there is an indication of two maxima in the breeding intensity of A. meridianus. Very large numbers of juveniles of both species occurred in only the June and September samples, although many juveniles of A. meridianus were present in the October and December samples, and many juveniles of A. aquaticus in the December sample. The presence of many juveniles of A. aquaticus in the December sample is in contrast to their absence from the December samples from Buckley, and may have been related, in some way, to the very shallow nature of Llyn Llywenan. The histograms show that the large number of females of both species breeding in the spring had overwintered. The majority of these females probably died about May, for most were absent from the June sample. It is to be presumed that the many small individuals of A. aquaticus and of A. meridianus comprising the June sample were produced by these overwintered females. Some small individuals of both species were breeding in June, and both species, therefore, must have taken less than two months to mature. The smallest ovigerous female of A. aquaticus in the June sample was just over 4.0 mm., and the smallest ovigerous female of A. meridianus was just over 3.0 mm.

It can thus be seen that, although the details of the life-cycles are less clear, the life-cycle of A. aquaticus and of A. meridianus at Llyn Llywenan appears to have been similar to that at Buckley and Padeswood. The only major difference was the smaller size, and perhaps shorter time, at which A. meridianus matured in the summer at Llyn Llywenan.

Since samples were collected from Hatchmere during only the latter half of 1959, the full life-cycle of A. aquaticus and of A. meridianus at Hatchmere cannot, of course, be determined from these. Nevertheless, the essential similarity of these samples (fig. 12, p. 4.4) to samples collected during the same period in 1958 and 1959 from Buckley and Padeswood suggests that the life-cycle of A. aquaticus at Hatchmere did not differ fundamentally from that at Buckley, and that the life-cycle of A. meridianus at Hatchmere did not differ fundamentally from that at Padeswood; as at Llyn Llywenan, the only major difference at Hatchmere appears to have been the smaller size at which

A. meridianus matured in the summer. Furthermore, in contrast to the samples from Llyn Llywenan, the samples from Hatchmere clearly show the differences between A. aquaticus and A. meridianus in the extent and time of the second maximum in the intensity of breeding. These differences are indicated by fig. 15, p. 4.72. It can be seen from the figure that the second maximum in the intensity of breeding of A. meridianus at Hatchmere was more pronounced and continued rather longer than that of A. aquaticus.

It is evident from the foregoing remarks concerning the samples from Llyn Llywenan and Hatchmere that there appear to be no fundamental differences in the life-cycle of A. aquaticus and of A. meridianus in localities where A. aquaticus and A. meridianus co-exist, or where only A. aquaticus or only A. meridianus occurs. The only major difference indicated by the samples would seem to have been that A. meridianus matured in the summer at Llyn Llywenan and Hatchmere at a length shorter than at Padeswood. This difference, however, was apparently the result of some cause other than the presence of A. aquaticus, for a sample collected on the 30th June 1959 from a pond near Storeton (Cheshire), where only A. meridianus occurs, contained large numbers of ovigerous females of length 3.5 mm. By reference to other June samples, it is to be presumed that these small females had probably been produced by overwintered females. The details of the analysis of the sample from Storeton are presented in table *5*, Appendix *C*, p.*10.45*, and are shown diagrammatically in fig.*13*, *p.4.5 (4~)*.

Although the comparison of the samples from Buckley, Llyn Llywenan and Hatchmere indicates that there was no fundamental difference in the life-cycle of <u>A. aquaticus</u> and <u>A. meridianus</u> at these three localities, the comparison indicates also that the exact timing of the life-cycles varied from place to place and from year to year. This variation is perhaps indicated most clearly by the differences between the June samples. For convenience, the histograms of all the June samples have been collected into one figure (fig. *13*), and this figure shows also the structure of two additional June samples collected from Bidston (<u>A. aquaticus</u>) and Storeton (<u>A. meridianus</u>). It can be seen from fig. *13* that at Buckley in June 1958 many of the large overwintered individuals of <u>A. aquaticus</u> were still present and that there were, in addition, many small non-breeding individuals. On the other hand, at Buckley in June 1959, and at Llyn Llywenan in June 1958, none or few overwintered individuals would appear to have been present, and many of the individuals produced by the overwintered females had begun to breed. Similarly, the minor difference of structure between all three

1959 June samples of A. aquaticus would seem to have resulted from slight alterations in the timing of the life-cycle at the three localities. Fig. 13 illustrates the similar differences that occurred in the timing of the life-cycle of A. meridianus. It can be seen that at Padeswood in June 1959 there were few over--wintered individuals of A. meridianus present, but large numbers of small individuals of which none had reached maturity. On the other hand, at Llyn Llywenan in June 1958, although there were again few overwintered individuals present, many of the small individuals present had matured. At Padeswood in June 1959 rather more overwintered individuals would appear to have survived until June than in 1958, yet at Hatchmere in 1959 no overwintered individuals survived until June. Large numbers of mature individuals produced by overwintered females occurred in June 1959 only at Storeton.

Previous work on the life-cycle of A. aquaticus indicates that its life-cycle, as indicated by the field investigations of the present research, is not the same throughout Europe. The life-cycle, in fact, seems to exhibit a geographical variation, and this variation is apparently correlated with the climate. Thus, in the severe climate of Moscow, the breeding season lasts for only five months, from April until August (Zheltenova; quoted by Birstein, 1951). In less severe climates the breeding season is a little more extensive; a breeding season lasting from

April until September has been observed at Königsberg (= Kalingrad) by Leichman (1891; quoted by Maercks, 1930), at Loch Lomond by Weerekoon (1956), and at Warsaw by Rosenstadt (1888; quoted by Maercks, 1930). Maercks (1930) noted that the breeding season at Berlin usually extends from March or April until September, and in Denmark Berg (1948) noted that ovigerous females are present in spring, summer and autumn. In the temperate climate of Lorraine, ovigerous females were found by Balesdent-Marquet (1955) in all months except November, and Kaulbersz (1913) found precopulating pairs in all months in the vicinity of Munich. In Central and southern France the greatest intensity of breeding seems to occur in the winter months; Berner (1956) observed that the breeding season at Limogne usually lasts from autumn until spring, and Vandel (1926) observed that breeding in the vicinity of Toulouse is greatest during December and January. However, breeding would appear not to be completely absent during the summer and autumn in southern France, for I was able to find an ovigerous female at Toulouse on the 30th August 1959.

It would thus seem that in northern Europe the breeding season of A. aquaticus is short, and is limited to the spring and summer. In more temperate regions the breeding season lengthens, beginning earlier and ending later. Finally, in the most temperate part of the European range of A. aquaticus, although there would still appear to be a maximum in the intensity of breeding, breeding occurs in almost all months. The breeding season of A. aquaticus indicated by the present field investigations occupies an intermediate position in this scheme; the winter is sufficiently severe to inhibit breeding, but the inhibition lasts during only November, December and January.

The most detailed of the previous observations on the life-cycle of A. aquaticus in the field are contained in the papers of Emden (1922), Meercks (1930) and Zheltenova (Birstein, 1951). Less detailed previous observations are contained in the papers of Berg (1948) and Needham (1949), and, in addition, various relevant facts exist in a number of other papers (eg. Janke (1926) Balesdent-Marquet (1955), Weerekoon (1956)). Most of these previous observations are comparable with those of the present research in that they were made in regions where spring and summer form the main breeding season, and winter the non-breeding season of A. aquaticus. In general, the observations are in broad agreement with my own field investigations.

Emden (1922), working at Leipzig, noted the "seasonal dimorphism" in the average size of mature males and females; he observed that the average size is much greater in spring than in summer and autumn. Emden emphasized that this phenomenon is not due to the breeding of two separate genera-

-tions, as had been proposed for Idothea tricuspidata by Gadzikiewicz (1907); quoted by Emden, (1922)), but is due to the fact the "die geschlechtsreifen Sommer-und Herbsttiere im selben Jahre geboren worden sind, einiger Bruten zur Welt bringen, und im Frühjahr des nächsten Jahres einer letzten Brunstperiode absterben" (p. 97). Janke (1926) disagreed with Emden's views; he thought that individuals are not able to reproduce in the year of their birth.

Maercks (1930), working at Berlin, also noted the "seasonal dimorphism" in the average size of adult males and females, and completely agreed with Emden (1922) in the explanation of it. Maercks, too, emphasized that it was not due to the breeding of two separate generations. However, as additional proof, he stated that if one accepts that the "seasonal dimorphism" is due to the breeding of two separate generations, then: "auch müßte man dann wohl einen zweiten Höhepunkt der Geschlechtstätigkeit im Spätsommer und Herbst annehmen, tätsachlich läßt sich aber nur ein Höhepunkt feststellen, der von Frühjahr bis Frühsommer andavert". The logic of this statement cannot be accepted; although the present research shows that there is, in fact, a second maximum, this by no means implies that the "seasonal dimorphism" in size is due to the breeding of two separate generations. The smallest ovigerous females seen by Maercks were 4.5 mm. in length, and the smallest mating males 7.0 mm. in length. The length of life was regarded by Maercks as being about one year.

Zheltenova made her observations in the vicinity of Moscow, and her results are quoted by Birstein (1951 p.41). She noted that at the beginning of the breeding season only the larger males and females reproduce, and that these then die and are replaced by smaller breeding males and females. She observed that the average size of the larger males and females is, respectively, 10.4 mm. and 8.8 mm., and that the average size of the smaller males and females is, respectively, 4.7 mm. and 4.3 mm. According to her, only females which are fertilized before June will produce offspring which will breed in the year of their birth. The length of life was regarded by Zheltenova as probably not exceeding two years.

Berg (1948) paid particular attention to the annual variation in the average size of A. aquaticus in the R. Susaa (Denmark), and noted that it was greatest during winter and spring, and least during summer and autumn. He explained this variation as due to an annual life-cycle: "the large individuals in the spring are the generation (or generations) of the year before which have overwintered. They die off in the late spring and are succeeded by the generation or generations of the present year, which have a small size in the summer but grow larger in the autumn and winter". (p. 77). Berg noted also that the greatest percentage of ovigerous females occurred during spring and summer.

Needham (1949) regarded the length of life as just over one year. He noted that the two year groups overlapped in early summer, at which time they were approximately separable into "seniors" and "juniors".

Previous observations on the life-cycle of A. meridianus, as already indicated, are, as far as I am aware, confined to the works of Unwin (1920) and Dunn (1952). Their brief observations are compatible with those of the present research.

Most of Unwin's (1920)[1] observations were concerned with the actual sequence of events involved in reproduction and not with the life-cycle as such. He noted that the earliest date on which he had found an ovigerous female was the 24th January, and that in a mild autumn ovigerous females could be found as late as the end of November. He noted also that precopulating pairs were commonest in spring.

Dunn (1952) found precopulating pairs and ovigerous females of A. meridianus between February and November, and observed that "breeding appeared to be speeded up during the summer months". (p.28). She observed also that the average size was greater in

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[1] Footnote 1. Unwin (1920) made his observations on "A.aquaticus" before this species was accurately redescribed by Racovitza(1919) (see p.2.5). It is clear from Unwin's drawings that he was, in fact, dealing with A. meridianus.

the non-breeding season than in the breeding season; in December and January the average size was 6.0 mm.; in June and July the average size was 4.0 mm.

(b) Laboratory Investigations.

The field investigations, although indicating the general pattern of the life-cycle of *A. aquaticus* and of *A. meridianus*, do not reveal the details of the life-cycles. They do not, for instance, accurately reveal the number of broods produced by each female, nor the seasonal variation in the time taken to incubate eggs or reach maturity. Such detailed information, however, is essential for a complete comparison of the life-cycles and in the calculation of biotic potentials. It was to provide this and similar information that the laboratory investigations were undertaken.

1. Breeding programme.

Briefly, the aim of the laboratory breeding programme was to keep under continued observation individuals released at varying periods throughout the breeding season, and to note the changes in the sexual condition of these individuals up to the time of their death. Much more attention was paid to females than to males, and particular attention was paid to the number of broods produced by each female.

Throughout the breeding programme individuals were cultured in a variety of small jars and dishes kept in the shade on the roof of the laboratory; in this position it was hoped that they would be subjected to an approximately similar temperature regime as occurred in the field. The animals were fed on elm leaves which had been soaked in water for three to four days before their addition to the breeding dishes. The leaves were collected in the autumn of 1957 and had been naturally shed. Elm leaves had originally been chosen as the food material since both Hynes (1954, 1955) and Sexton (1928) had found them eminently suitable for feeding Gammarus. In the present investigations also elm leaves proved a satisfactory diet for both A. aquaticus and A. meridianus (but see p.6.6). All the individuals were reared in Liverpool tap-water. The results of an analysis of a sample of this water collected on the 25th March 1960 are shown in the table below;

Total salts m/equiv./L.	Ca	Mg	Na	K	HCO_3	Cl	SO_4	NO_3-N.
2.120	1.030	0.625	0.447	0.031	0.920	0.472	0.572	0.156

All the results are expressed as m/equiv./L. The analysis was carried out by Mr. J. Heron of the Fresh-water Biological Association. The chemical composition of Liverpool tap-water, however, would not appear to be constant; in March 1959 an analysis of the calcium and magnesium contents gave, respectively, 0.335 and 0.03 m/equiv./L. The frequency at which the breeding dishes were observed varied according to the season; in the warmer months the dishes were observed at weekly intervals or less; in the colder months the dishes were observed at intervals of two or three weeks. At each observation notes were made of (a) the survival of individuals, (b) the presence or absence of precopulating pairs, (c) the presence or absence of recently released juveniles, (d) the sexual condition of the females, i.e. whether they were non-ovigerous, ovigerous or possessed empty brood pouches, and (e) the temperature. Recently released juveniles were always removed from their parents and placed in separate breeding dishes. If, during the early part of the breeding programme, the male specimen of a pair of breeding individuals died it was replaced, but later, when it became apparent that the presence or absence of a male had no affect upon the sexual condition of a female (see also Haemmerli - Boveri, 1926), dead males were not always replaced. At intervals of about a month the approximate length of all individuals was measured by comparing them against 1 mm. squared graph paper. When necessary, the water in the breeding dishes was changed and fresh elm leaves were added.

The breeding programme began in early March 1959 with the collection from the field of 7 pairs of large precopulating males and females of <u>A. aquaticus</u>, and of 8 pairs of large precopulating males and females of <u>A. meridianus</u>. As far as possible, these pairs, the broods produced by them, and the offspring of the broods produced by them were kept under continued observation. In addition, in late February 1960 30 females of <u>A. aquaticus</u> and 25 females of <u>A. meridianus</u> were collected from the field and isolated. The size of these females ranged from 9.5 to 3.5 mm. in the case of <u>A. aquaticus</u>, and from 6.5 to 2.5 mm. in the case of <u>A. meridianus</u>. Many of these females were ovigerous but to each of those that were not was added a slightly larger males of the same species. These females or pairs were likewise kept under continued observation. In all, and for varying periods of time, over 150 breeding dishes were kept under observation.

Despite the care paid ensuring that the initial conditions within each breeding dish were similar, there was a great deal of variation in the growth-rates and life-cycles of individuals of both species throughout the breeding programme. This variation was confined not only to a variation between individuals contained in different breeding dishes; it occurred also between individuals contained in the same dish. It is difficult at the moment to give a complete explanation of this variation, but it is of interest to note that Hynes (pers. comm.) observed a similar phenonemon in breeding experiments with *Crangonyx sp.* At all events, although it is known that differences in the diet of *Gammarus* can produce a similar variation (O'Brien and Yarnold 1937), gross differences in the diet of the *Asellus* would seem not to have been the cause of the variation.

The results of the breeding programme can be summarized as follows:

Breeding females of *A. aquaticus* occurred from February until September, and breeding females of *A. meridianus* from February until October. In both species the first females to become ovigerous at the commencement of the breeding season were confined to the larger size-groups, and the last females to become ovigerous occurred in the smallest size-groups. The breeding programme revealed, therefore, a progressive relationship in both species between the time at which breeding began and the size of the breeding female. The larger overwintered females of *A. aquaticus* (8.5-9.5 mm.) and of *A. meridianus* (5.5-6.5 mm.) produced 1-3 broods before their death. Incubation of the first brood of these females began in both species in late February or early March, and the juveniles were released about the end of April or beginning of May. Where a second brood was borne, incubation of this began in both species about the middle of May and incubation continued for about one month until the middle of June. Where yet a third brood was borne, incubation of this began in both species about the middle of July and continued for about three weeks until the end of July. No large overwintered females of each species were recorded as having produced more than three broods after overwintering, although one such females of *A. aquaticus* survived until December, and two such females of *A. meridianus* survived until October. There was a clear indication that large overwintered males of both species died before the large overwintered females. As already indicated, smaller overwintered females of the two species commenced breeding at a somewhat later time than the larger over-wintered females. None of these smaller females, also, was recorded as having produced more than three broods after over-wintering, although many survived for the whole of the breeding season. The medium-sized overwintered females of *A. aquaticus* (c. 7.5 mm.) and of *A. meridianus* (c. 4.5 mm.) first became ovigerous about the middle of March. In these females the incubation times of the first and successive broods and the intervals between broods corresponded in general to those of the larger overwintered females, but differed by a delay in timing of about two weeks. Similarly, the smallest overwintered females of *A. aquaticus* (c. 3.5 to 6.5 mm.) and of *A. meridianus* (c. 2.5 to 3.5 mm.) first became ovigerous about the end of March and then exhibited the same sequence of events as the largest overwintered females, although differing from these by a delay in timing of about one month. Most of the medium-sized and smallest over-wintered females of both species died at various times during the breeding season, but many survived until November, and a few survived even longer. As in the larger size-groups, there was an indication that the males died before the females.

Because of the wide range in the size of overwintered females of both species and the consequent differences in the timing of broods produced by these females, there was a continual liberation of juveniles by them from about the end of April until the late summer. The time taken to reach maturity by these juveniles varied according to the time at which they were released. The shortest time taken to reach maturity by females of either species released about the end of April was approximately $1\frac{1}{2}$ months. It would seem that males of either species released about the end of April also took approximately $1\frac{1}{2}$ months to mature, for these males were responsible for the successful fertilization of the matured females. Females of both species released after the end of April usually took a little longer to mature, but all those released before mid-June reached maturity the same breeding season, whereas females of the two species released after mid-June did not breed until the following breeding season. In both species the average time taken to reach maturity by females which matured in the year of their birth was 2.3 months, and the average size at which maturity was attained by these females was 4.8 mm. (A. aquaticus) and 4.4 mm. (A. meridianus). In general, it would appear that in both species the average size at which maturity was attained by males which matured in the year of their birth was 5.5-6.0 mm. (A. aquaticus) and 5.0-5.5 mm. (A. meridianus). The average size at which maturity was attained by females which overwintered before reaching maturity was 5.7 mm. in both species, and the average time taken to reach maturity by these females was 9.6 months (A. aquaticus) and 8.1 months (A. meridianus). The females of A. aquaticus and A. meridianus which had been produced by overwintered females, and which had matured the same breeding season, first began to release juveniles in early July. The release of juveniles by these females continued until the end of the breeding season. It is thus evident that during the breeding programme juveniles of both species were liberated throughout the breeding season; from the end of April until the late summer juveniles were released by overwintered females; from the beginning of July until the end of the breeding season juveniles were released by females which had matured in their year of birth. All the females released from females which had matured in their year of birth overwintered before breeding.

The number of broods produced by each females of A. aquaticus and of A. meridianus depended upon the time at which the female had been released; females released at the beginning of the breeding season produced the maximum number of broods, and females released at the end of the breeding season apparently produced the minimum. Thus, females of A. aquaticus released between the end of April and mid-May produced 3 broods before overwintering; those released between mid-May and mid-June produced 1 or 2 broods before overwintering; and those released after mid-June produced no broods before overwintering. As has already been indicated (p.4.51,52), all overwintered females of A. aquaticus were capable of producing a maximum of 3 broods in the spring before their death, and it is evident, therefore, that during the breeding programme females of this species produced either 3,4,5 or 6 broods during their life. A similar pattern of events was shown by females of A. meridianus. Females of A. meridianus released between the end of April and mid-May produced a maximum of 4 broods before overwintering; those released between mid-May and mid-June produced 1,2 or 3 broods before overwintering; and those released after mid-June produced no broods before overwintering. Since it has already been indicated that in A. meridianus also all overwintered females were capable of producing a maximum of 3 broods in the spring before their death (p.4.51,52), it is evident that during the breeding programme females of A. meridianus produced either 3,4,5,6 or 7 broods during their life.

The breeding programme did not reveal any difference between A. aquaticus and A. meridianus in the time for which females incubated their eggs. The breeding programme did reveal, however, that in both species there was a seasonal difference in this length of time; during spring incubation lasted for about 6 weeks, but later, as the temperature rose, the time shortened, and from June until the end of the breeding season incubation lasted for between 2½ and 3 weeks.

Apart from the variation in the length of time of incubation, the breeding programme revealed also a variation in the time-interval between broods. The shortest interval between broods in A. aquaticus was 8 days, and in A. meridianus 4 days. Both of these intervals occurred between the first and second broods of females which had matured in their year of birth. The interval between the later summer and autumn broods of these females was rather longer, and in both species intervals of up to 3 weeks were recorded. However, for both species the average interval at this time would appear to have been about 1½-2 weeks. After overwintering there was a great deal of variation between individuals, but during spring the shortest interval recorded for both species was 2 weeks. The interval between broods in overwintered females was investigated also at laboratory temperatures (18-21°C) during June 1959. In this investigation only large overwintered females were used. Briefly, it was found that in 14 females of A. aquaticus the interval between broods varied from 8 to 32 days, the average being 17.7 days, and in 8 females of A. meridianus the interval between broods varied from 14 to 29 days, the average being 18.6 days. Thus, in contrast to the limited amount of variation shown by the two species in length of incubation at an approximately constant temperature (see p.4.63), the time-interval between broods in the two species in a limited temperature regime appears to show much more variation. This would seem to indicate, as indeed one would expect, that apart from temperature other factors are of importance in the determination of the length of this interval.

Because of the inconstancy of the observations during the breeding programme it is not possible to provide detailed information upon the length of time of precopulation in A. aquaticus and A. meridianus. However, in both species precopulation during the spring lasted for a much longer time than later in the year; many pairs of both species during spring precopulated for more than one week, and precopulation at this time would seem to have been always longer than one day, whilst on the other hand many pairs of both species during the summer and autumn precopulated for less than a day, and precopulation at this time was never longer than one week. During the breeding programme several pairs of both species exibited only intermittent precopulation.

Although no previous relevant laboratory investigations on <u>A. meridianus</u> have been made, a few such investigations of <u>A. acuaticus</u> exist.

The most extensive of these investigations would appear to be those of Zheltenova (Birstein, 1951) (it is to be presumed that her investigations were carried out under laboratory conditions, although this, in fact, is not stated). Her pertinent observations may be summarized briefly as follows:
A period of only 5-6 days separates broods. During the summer, the maximum number of broods produced by a female is 2, but the total number of broods produced by a female during her life is 4-5. Only those females fertilized before mid-June will reproduce in their year of birth. At first the females parallel the males in the frequency of moulting, but later the intervals become longer in the female. 13-15 moults occur before maturity, and at this time the females are 3.4-4.0 mm. in length. On average, females are mature after 50-55 days. Moulting in the male is not closely associated with the sexual cycle as in the female, and generally occurs at intervals of 13-20 days. Growth and moulting in both sexes cease in the winter.

Less extensive relevant laboratory investigations on

A. aquaticus have been made by Wege (1911; quoted by Unwin, 1920), Kaulberz (1913), Haemmerli-Boveri(1926), Maercks (1930), Needham (1949) and Balesdent-Marquet (1956).

Wege (op. cit.) recorded from 8-30 days between moults. Kaulberz (1913) also recorded the interval between moults and observed that age, sexual condition, temperature and feeding were the main factors affecting this interval. He recorded an average of 24 days between moults under poor food conditions. Haemmerli-Boveri (1926) was concerned with the interval between moults only in breeding females. At laboratory temperatures (18-22°C) she noted that the interval between Zwischenhaütung and Parturial-haütung varied between 5 and 10 days, although she noted that sometimes this interval was longer. Maercks (1930) reared the progeny of 6 females at room temperatures (19-20°C). He found that sexual maturity was attained after 3 months at an average size of 6 mm. (females) and 7 mm. (males). The individuals lived for approximately one year. Maercks reared a number of individuals at 5-10°C also. He found that at this temperature females did not mature until the 13th month. Needham (1949) noted the mean eclosion time at various abdomen widths in both sexes of A. aquaticus at room temperature. According to Needham (1949) the eclosion time is the interval between the time at which an amputation occurs and the time at which the part amputated first appears following an ecdysis. Since the first appearance of the amputated part occurs after the next ecdysis if the amputation occurred before the middle of a stadium, but after the next but one ecdysis if the amputation occurred after the middle of a stadium, it is evident that "the mean eclosion time is virtually equal to the duration of one stadium, though its variance is much greater " (Needham 1949, p.50). In an earlier paper (1937) Needham had noted the relationship between abdomen width and body length in males and females, and it is possible, therefore, by rearranging and combining his data to provide information on the average intermoult interval at various body lengths of males and females. Thus, at a mean body length of 3.0 mm. the average intermoult interval in males and females was 10 days, at 4.0 mm. was 10 days, at 5.0 mm. was 11 days, at 6.0 mm. was 15 days and at 7.0 mm. and above was approximately 20 days. Needham's data do not reveal any significant difference between males and females in the average intermoult interval. Balesdent-Marquet (1955) noted simply that the length of the intermoult interval is inconstant except for the Parturial--haütung - Zwischenhaütung interval, and that the intermoult interval decreased with increase of temperature.

It can be seen from the above summary of the previous relevant investigations on A. aquaticus that there would appear to be several points of difference between these and the results obtained from the breeding programme of the present research. However, it is possible to provide reasonable explanations for these differences. Thus, the difference between the shortest interbrood interval (5 days) recorded by Zheltenova (Birstein, 1951) and Haemmerli-Boveri (1926), and the shortest interbrood interval (8 days) recorded during the breeding programme may be explained as due to a difference in the definition of the interbrood interval; Haemmerli-Boveri and presumably Zheltenova regarded the interbrood interval as the interval between Zwischenhaütung and Parturialhaütung, whereas during the breeding programme the interbrood interval was regarded as the interval between the release of the juveniles and the Parturialhaütung. The smaller number of broods recorded by Zheltenova may perhaps be explained as due to the climatic differences between Moscow and England (but see p.4.40). If these explanations are accepted, it would seem that the results of the previous investigations and the results obtained from the breeding programme are in general in agreement with each other.

2. The length of time taken to incubate eggs.

Laboratory investigations were made of the relationship in A. aquaticus and in A. meridianus between the length of time taken to incubate eggs and the temperature. These investigations were undertaken in order to determine more clearly the seasonal variation in the length of time of incubation.

Freshly ovigerous females of both species were obtained by observing precopulating males and females at daily intervals, and by removing the females as soon as they became ovigerous. Each female thus obtained was isolated in a petri-dish containing a little water and an elm leaf, and the petri-dish was then placed in the appropriate temperature regime. Observations were continued at daily intervals until the female had released all the juveniles in her brood pouch. The date by which all the juveniles had been released was noted. At high temperatures these two dates were usually contemporaneous, but atlow temperatures there was a tendency for juveniles to be released over a period lasting from less than a day to several days. In the present investigation, incubation was regarded as having finished when the first of the juveniles were released. Constant temperature apparatus was not available, and the results, therefore, are to be regarded as only approximate. The detailed results are shown in appendix D p.10.46-47, but a summary of the results is presented in the following table:

Mean temperature °C	The average length of time (in days) taken to incubate eggs, and, in brackets, the number of specimens upon which this average is based.			
	A. aquaticus		A. meridianus	
23.5	12.5	(6)	13.0	(2)
21	15.2	(11)	14.8	(4)
20	18.1	(8)	18.5	(4)
19	19.0	(2)	18.8	(4)
18	19.4	(5)	20.7	(8)
10	45.3	(3)	42.5	(2)

In addition, at a mean temperature of 8.5°C five females of A. aquaticus took over 49 days to incubate their eggs, and four females of A. meridianus took over 46 days to incubate their eggs.

It can be seen from the table that in both A. aquaticus and A. meridianus there is an inverse relationship between the length of incubation and the temperature. The table shows also that there is apparently little specific difference in this relationship. Apart from indicating a general relationship between the length of incubation and the temperature, the results suggest also that temperature is, in fact, the principal factor controlling the length of incubation; despite the fact that the incubations occurred at different times of the year, and that females of different sizes and at different stages of their life-cycle were used, there was nevertheless only slight variations in the length of incubation at any one temperature.

In general, the results are in agreement with those of Unwin (1920), Haemmerli-Boveri (1926), and Janke (1926) and Balesdent-Marquet (1955). Unwin (1920) noted that in spring three females of <u>A. meridianus</u> took 31, 32 and 35 days to incubate their eggs. Haemmerli-Boveri (1926) observed that females of <u>A. aquaticus</u> took 14-17 days to incubate their eggs in the laboratory (18-22°C). Janke (1926) found that in spring in an aquarium maintained at the same temperature as the field, females took 6-7 weeks to incubate their eggs. Balesdent-Marquet (1955) did not directly measure the length of incubation in <u>A. aquaticus</u>, but measured instead the interval between Parturialhaütung and Zwischenhaütung. At 20-23°C she recorded this interval as 10-15 days, at 13°C as 28-32 days, and at 9-10°C as 45-50 days.

c). <u>Discussion</u>.

The data from the laboratory investigations on <u>A. aquaticus</u> and <u>A. meridianus</u>, although providing detailed information, do not of course accurately reveal the life-cycle of the two species as it occurs in the field; it is to be expected that during these investigations the constant diet of elm leaves, the lack of predators, the smaller "Lebensraum", etc. will have had some affect. On the other hand, as already noted, the data from the field investigations provide only a general picture of the life-cycle of the two species as it occurs in the field. By combining the data from the laboratory and field investigations, however, it is possible to arrive at a fairly detailed theoretical picture of the natural life-cycle. This theoretical picture would seem to be as follows:

The breeding season of A. aquaticus extends typically from February until early October, and that of A. meridianus from February until late October. During the breeding season both species show two maxima in the intensity of breeding; the first occurs in spring, and the second during the late summer and early autumn. The second maximum occurs later and is more pronounced in A. meridianus than in A. aquaticus. In both species the first maximum results from the breeding of over-wintered individuals. During this maximum there is a progressive relationship in both species between the time at which breeding begins and the size of the breeding female; the largest overwintered females are the first to begin breeding, and the smallest overwintered females are the last to begin breeding. It would seem that under natural conditions over-wintered females of both species produce fewer broods than are produced by such females under artificial conditions. This phenomenon is the result of the much later death of overwintered females under artificial conditions, the effect perhaps of the lack of predators. Thus, under natural conditions, most of the largest overwintered females of both species produce only one brood before their death at the end of spring. In both species incubation of this brood lasts for approximately 2 months. Under natural conditions most of the smaller over-wintered females of A. aquaticus and A. meridianus also produce only one brood before their death in the early summer, although some of these females (and especially the smallest ones), as well as a few of the largest overwintered females of both species, survive long enough to produce a second brood. In both species the length of time for which these broods are incubated varies according to the time at wich incubation begins; when incubation begins during March, it lasts for approximately 1½ months. when incubation begins during April, it lasts for approximately 1 month; and when incubation begins during May it lasts for slightly less than 1 month. The death of the largest overwintered males of the two species occurs towards the end of spring; the death of the smaller overwintered males of the two species occurs during the early summer.

Because of the wide range of size of overwintered females, and the consequent difference in the timing of the broods produced by these females, there is a continual release of juveniles by overwintered females of the two species from about the end of June. In both species most of these juveniles attain sexual maturity after approximately $1\frac{1}{2}$ to 2 months, and the second maximum in the intensity of breeding in the two species results from the breeding of these individuals. The smallest size at which maturity is attained by females during this second maximum is 4.0 mm. (A. aquaticus) and 3.0 mm. (A. meridianus). In neither species do any of the juveniles produced during the second maximum reach maturity before overwintering.

The number of broods borne before overwintering by females which mature in their year of birth depends upon the time at which females were released; those females of A. aquaticus which are amongst the first juveniles to be released by overwintered females produce a maximum of 3 broods before overwintering, whilst those females of A. aquaticus released a little later produce only 1 or 2 broods before overwintering; those females of A. meridianus which are amongst the first juveniles to be released by overwintered females produce a maximum of 4 broods before overwintering, whilst those females of A. meridianus released a little later produce 1,2 or 3 broods before overwintering. In both species the length of time taken to incubate all broods produced by females which subsequently overwinter is approximately $2\frac{1}{2}$-3 weeks, and the interval between the broods varies from approximately one to two weeks.

The number of broods produced by all overwintered females of both species has already been indicated (see p. 66) and it is evident, therefore, that the maximum number of broods that are produced by females of <u>A. aquaticus</u> and <u>A. meridianus</u> is, respectively, 5 and 6. In both species the females that produce the maximum number of broods are released at the very beginning of a breeding season, produce 3(<u>A. aquaticus</u>) or 4(<u>A.meridianus</u>) broods before overwintering, and produce 2 broods after over-wintering. The length of life of these females is just over 1 year. In both species the minimum number of broods is produced by females which are released at the very end of a breeding season, and which consequently produce no broods before overwintering. In both species, these females live for less than 1 year. In general, it would appear that during their entire life the usual number of broods produced by females of <u>A. aquaticus</u> is 3 or 4, and by females of <u>A. meridianus</u> is 3, 4 or 5.

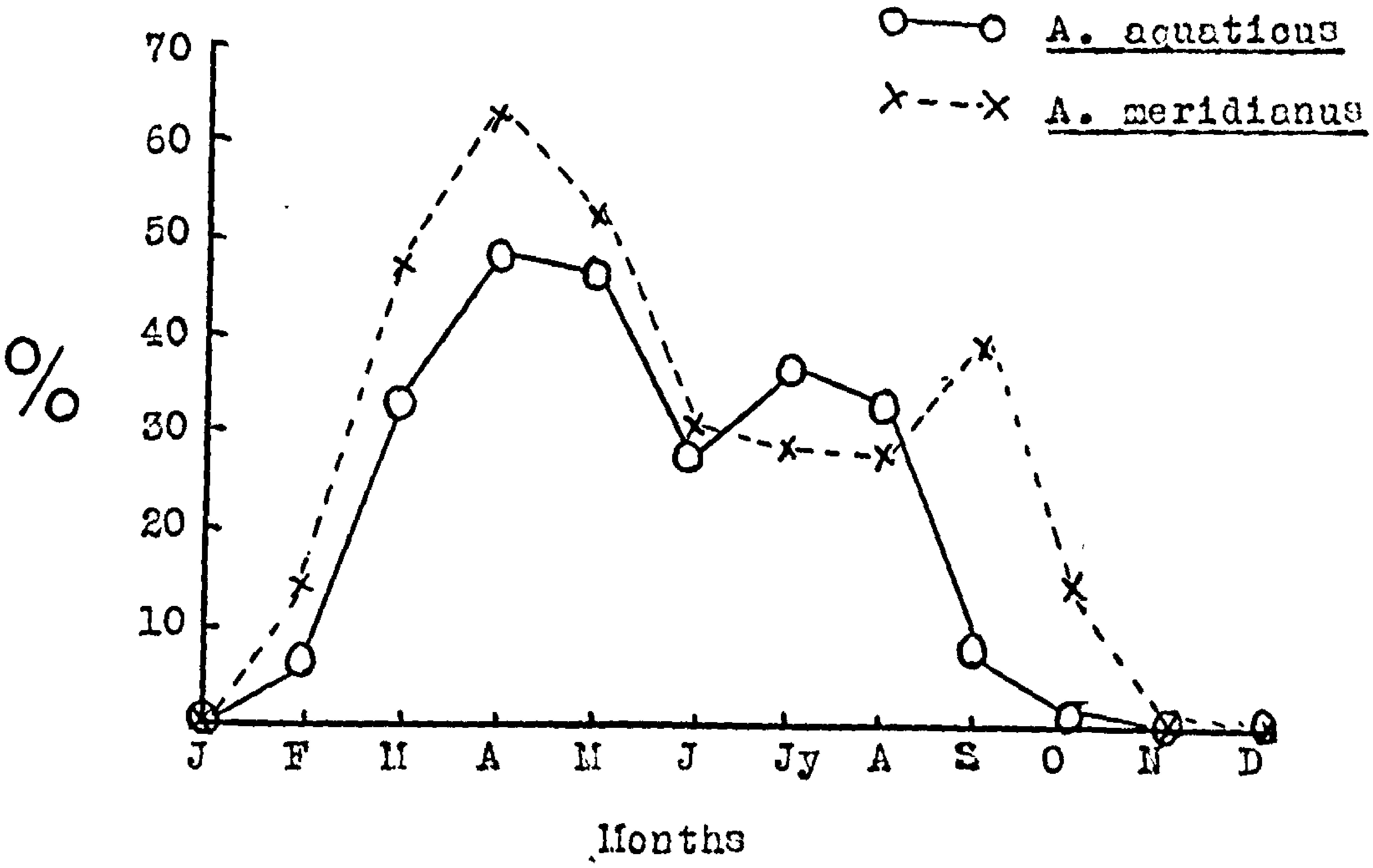

Fig. 15a Graph showing the number of breeding females at Buckley and Padeswood Lakes as a percentage of the total number of females above 3.5mm. (A. aquaticus) or 2.5mm. (A. meridianus) present.

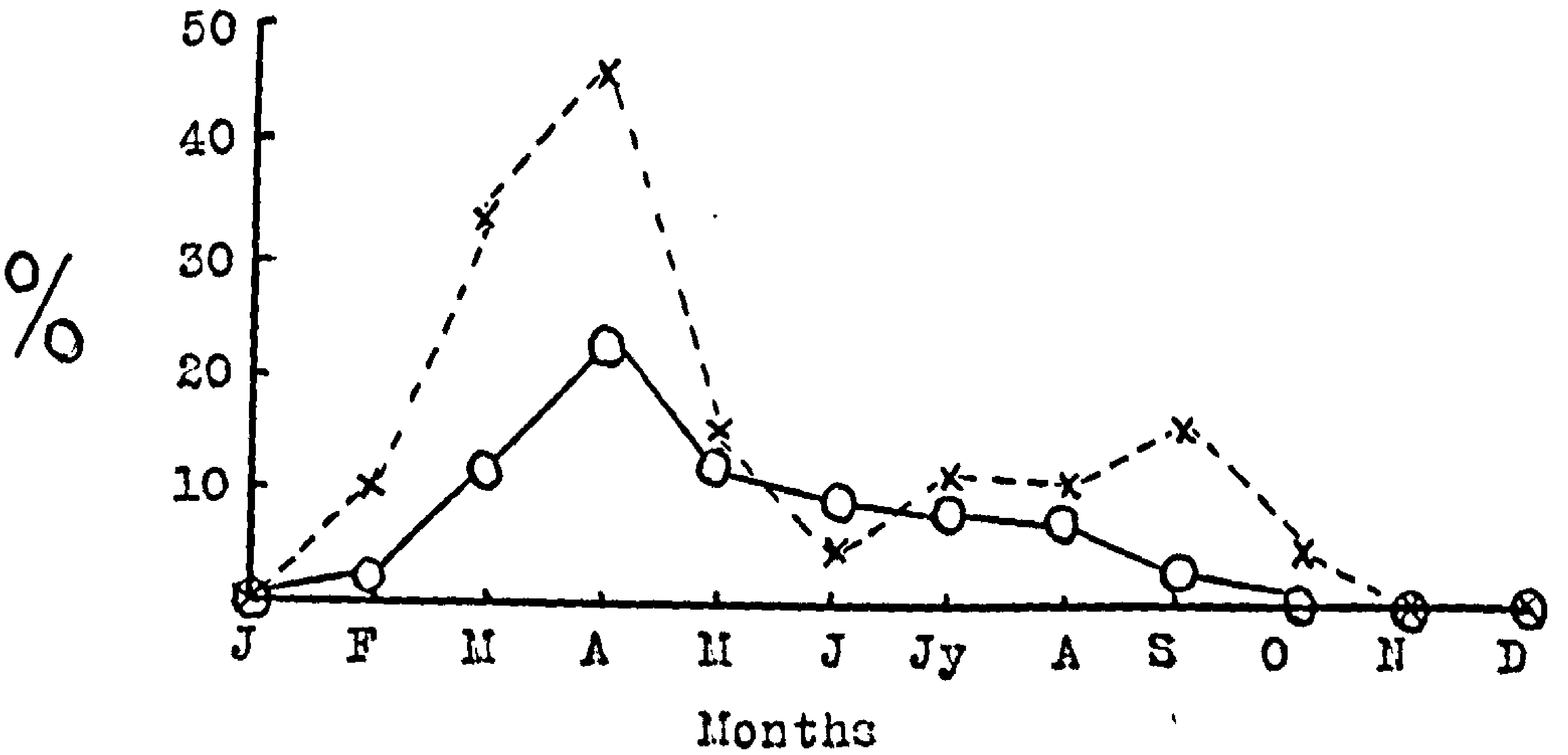

Fig. 15b Graph showing the number of breeding females at Buckley and Padeswood Lakes as a percentage of the total population present.

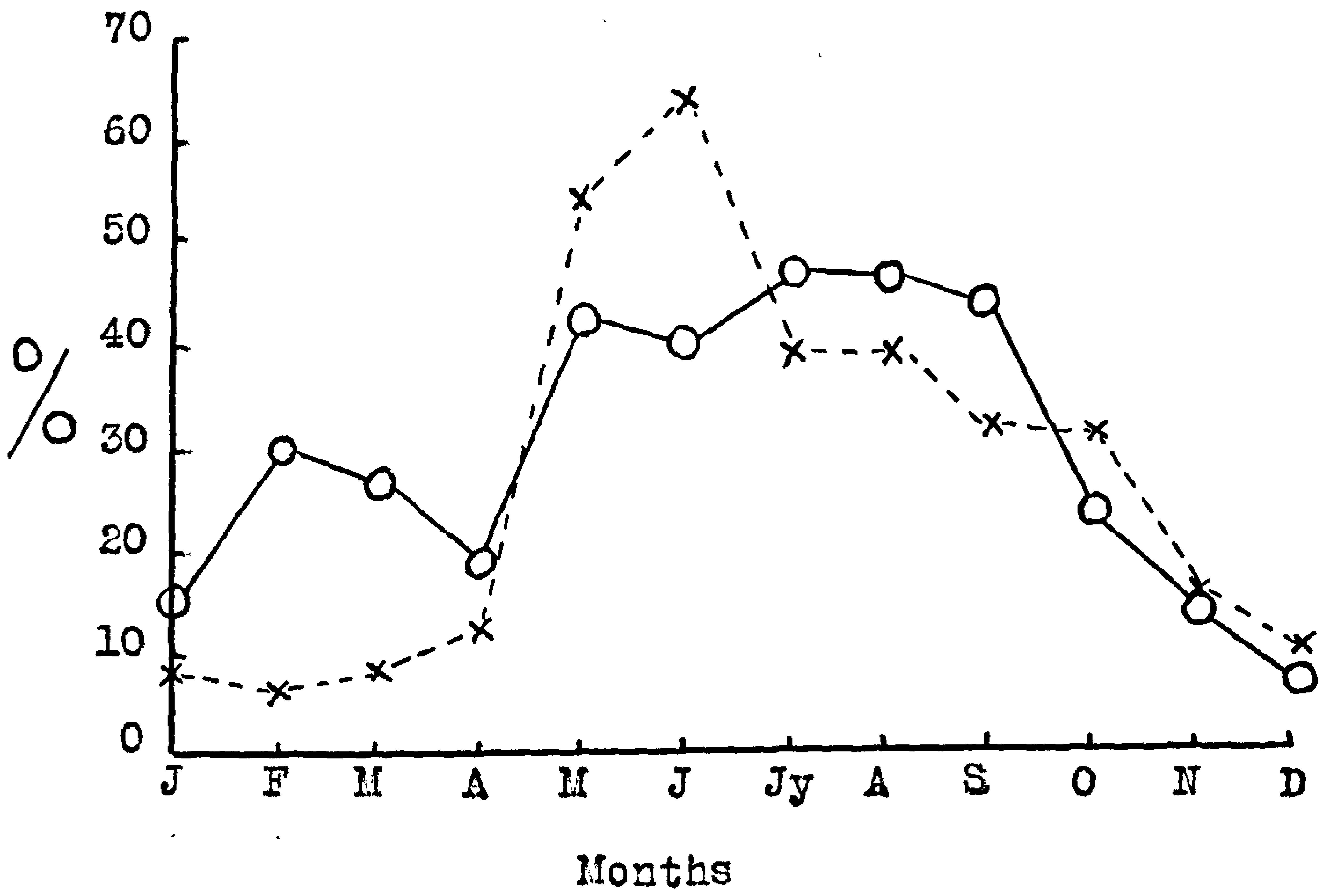

Fig. 16 Graph showing the number of juveniles as a percentage of the total population present each month.

o——o = *A. aquaticus* (Buckley lake)
x---x = *A. meridianus* (Padeswood l.)

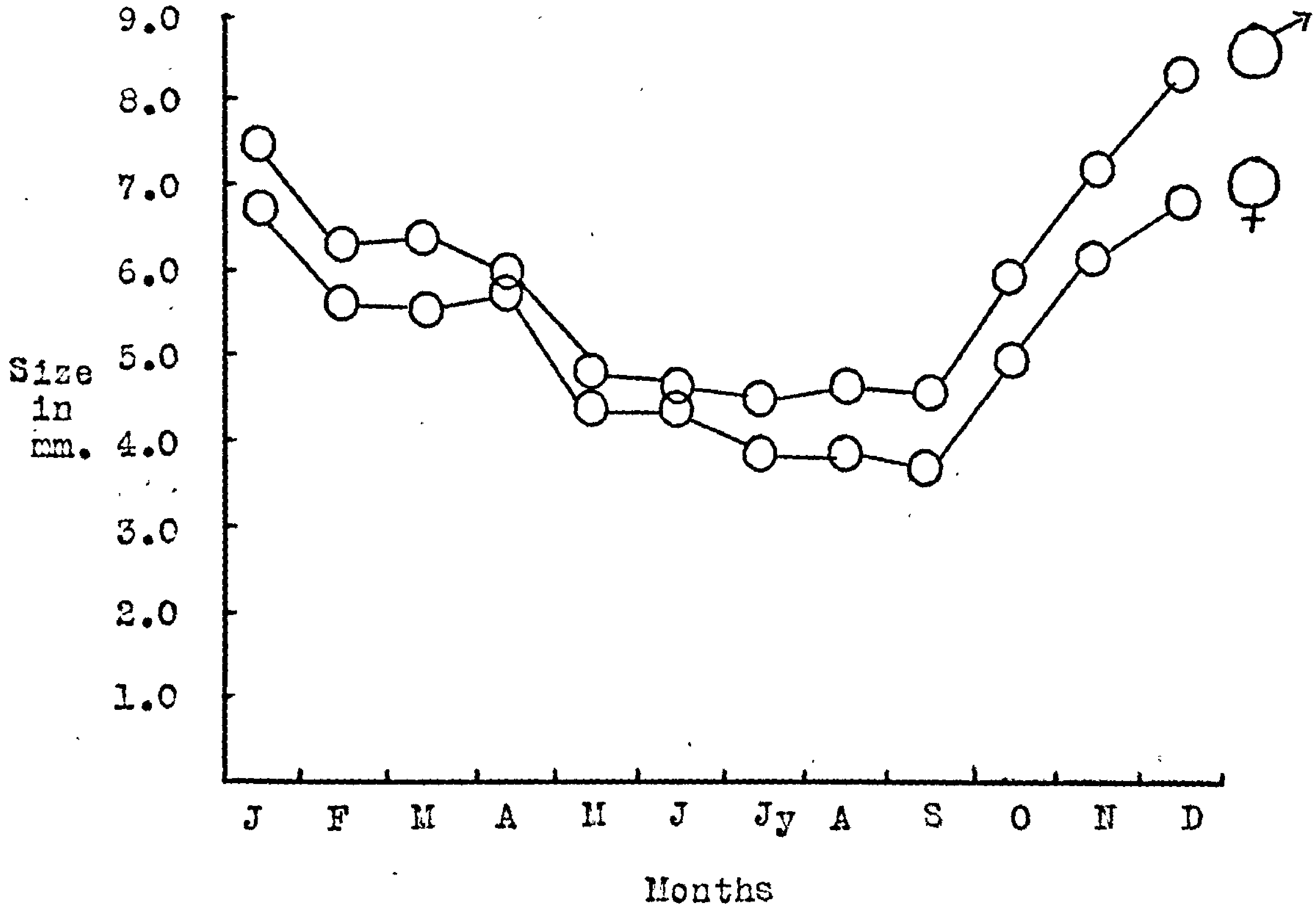

Fig. 17a Graph showing the average monthly size of males and females of A. aquaticus at Buckley Lake.

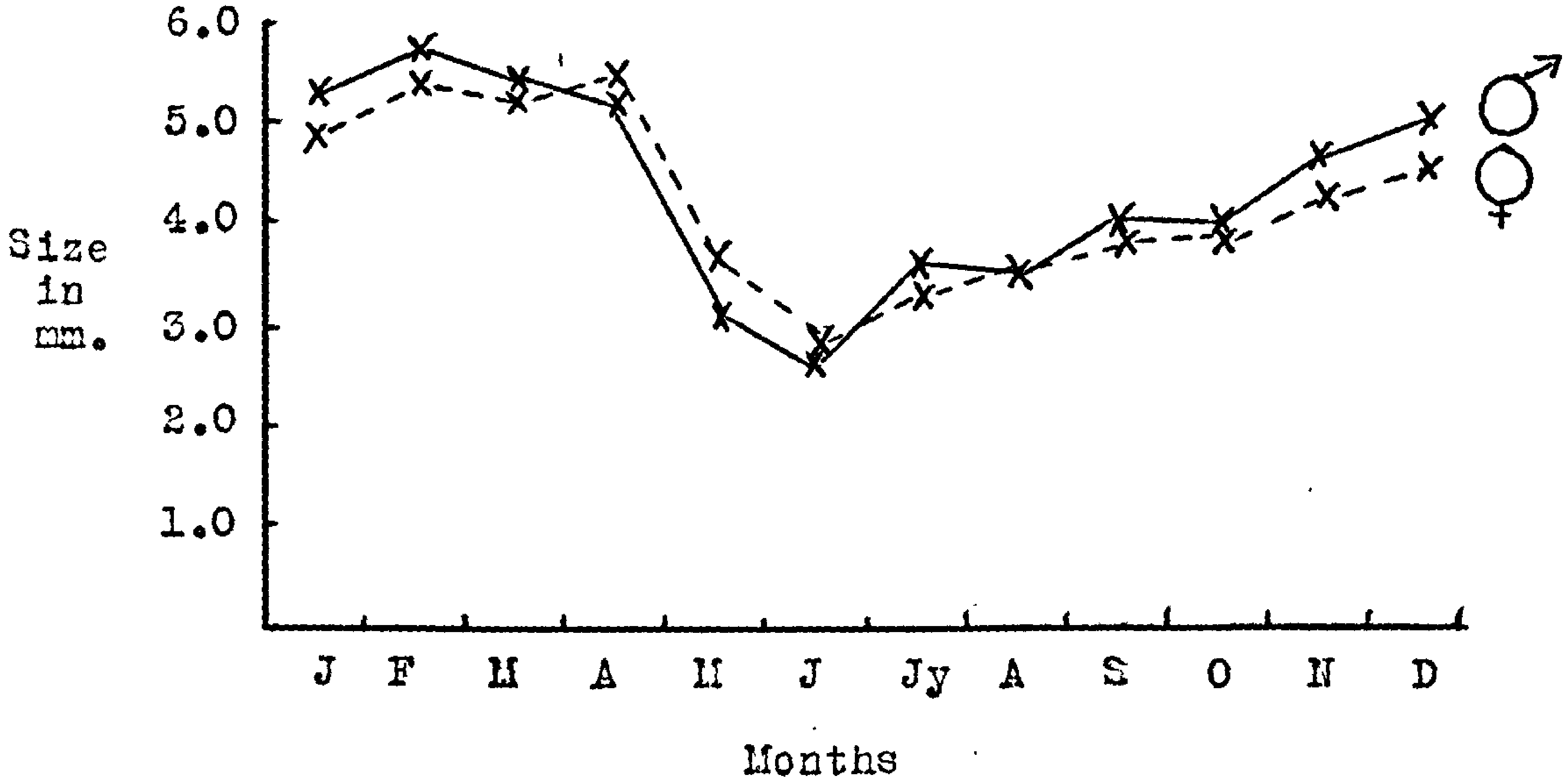

Fig. 17b Graph showing the average monthly size of males and females of A. meridianus at Padeswood Lake.

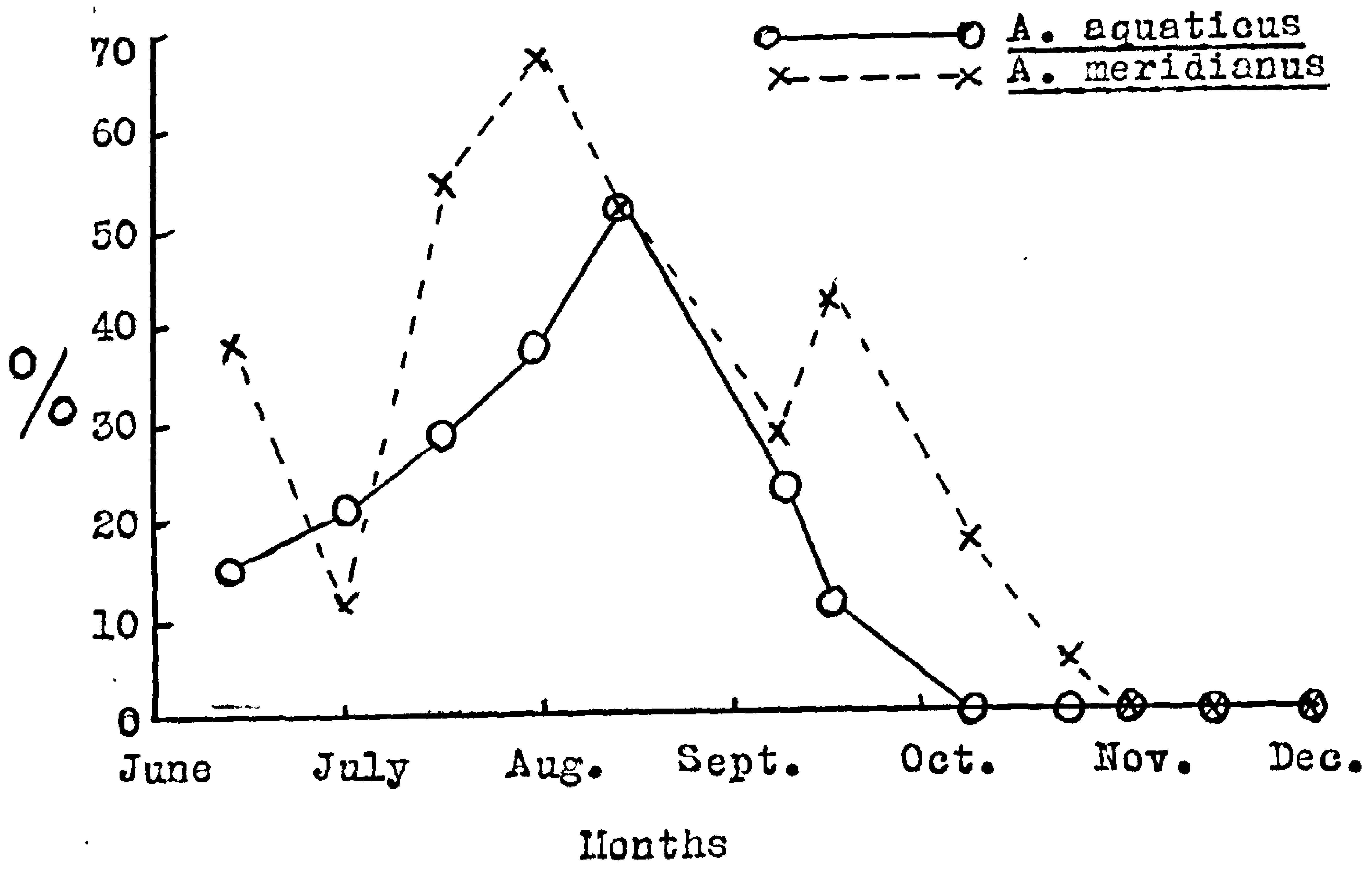

Fig. 18a Graph showing the number of breeding females at Hatchmere (June-November 1959) as a percentage of the total number of females above 3.5mm. (A. aquaticus) or 2.5mm. (A. meridianus).

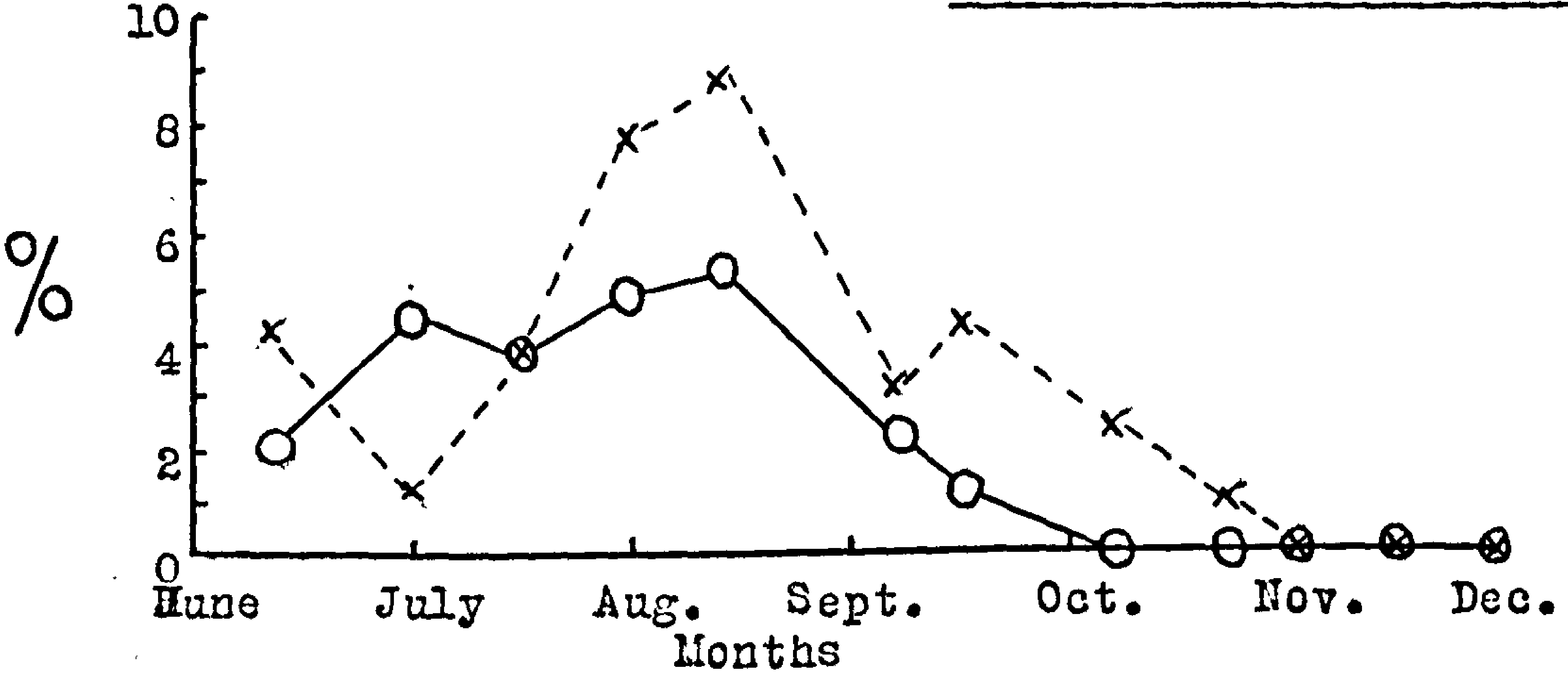

Fig. 18b Graph showing the number of breeding females at Hatchmere (June-November 1959) as a percentage of the total population present.

BIOTIC POTENTIAL.

One of the differences of great ecological significance between closely allied species may be a difference of reproductive rate. Such a difference may have profound consequences. In the theoretical case, for example, of two competing species which have identical needs and habits, but which differ in reproductive rate, one or other of the two species will ultimately become extinct. Which of the two species to become extinct will depend not only upon the reproductive rate of both species, but also upon the initial numerical ratio of the species; normally, the species possessing the inferior reproductive rate will become extinct, but if this species has an initial numerical superiority above a certain critical value, then it will be the other species (Crombie 1947). An empirical example in which a difference in reproductive rate would seem to have important consequences is provided by certain British species of _Gammarus_ (Hynes 1955); Hynes suggests that in Britain the ecological dominance of _G. pulex_ over _G. duebeni_ and _G. lacustris_ is largely due to the greater reproductive rate of _G. pulex_ as compared with the other species.

Various concepts and definitions aimed at clarifying what is implied by the term 'reproductive rate' have been advanced, and the most important of these have been those concerned with the maximum reproductive rate. Perhaps the three most important are the concepts of biotic potential, of the intrinsic rate of natural increase (r_i), and of the innate capacity for increase (r_m). The first of these concepts, although the least specific, has been widely employed and proven extremely useful. It will be used in the present chapter, the final aim of which will be to compare the biotic potentials of *A. aquaticus* and *A. meridianus*.

Chapman (1928) was the first to use the term biotic potential. He defined it in such general terms, however, that his original definition has given rise to a variety of inter-pretations (see Odum 1959). In the present work the biotic potential is regarded as "the ability of a species to multiply in a given time when freed from all environmental resistance[1]" (Imms 1944, p,128). Defined as such, the factors upon which the biotic potential depends are the sex-ratio, the number of broods borne by females time, the number of progeny produced from each brood and the length of the developmental cycle. The second and fourth of thse factors have been discussed in chapter 1V; the first and third will be discussed here.

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[1] Footnote 1. The environmental resistance is regarded as the sum of the effect of all environmental factors which are responsible for the difference between the maximum potential population and the actual population.

The Sex - Ratio.

A great deal of information concerning the sex-ratio of A. aquaticus and A. meridianus was gathered during the field investigations on the life-cycle of these species. This information is summarized in figs 19 and 20 . Fig 19 indicates the sex-ratio of A. aquaticus and of A. meridianus in each sample collected from, respectively, Buckley Lake and Padeswood Lake during the period October 1957 - November 1959; fig 20 indicates the mean monthly sex-ratios of the two species as calculated by combining all the data from the regular samples collected from Padeswood and Buckley Lakes, Hatchmere and Llyn Llywenan. The mean monthly sex-ratio of the two species is indicated also in the table on p. 5.6 , and this table shows in addition the number of specimens upon which each monthly mean is based.

The sex-ratios presented in the figures and in the table are based only upon specimens of A. aquaticus which were greater than 3.5 mm. in length, and upon specimens of A. meridianus which were greater than 2.5 mm. in length; as previously noted in chapter 1V, it was found practicable to limit sexual differentiation to size-groups above these lengths. The details of the methods used in the collection and subsequent analysis of samples are described in chapter 1V.

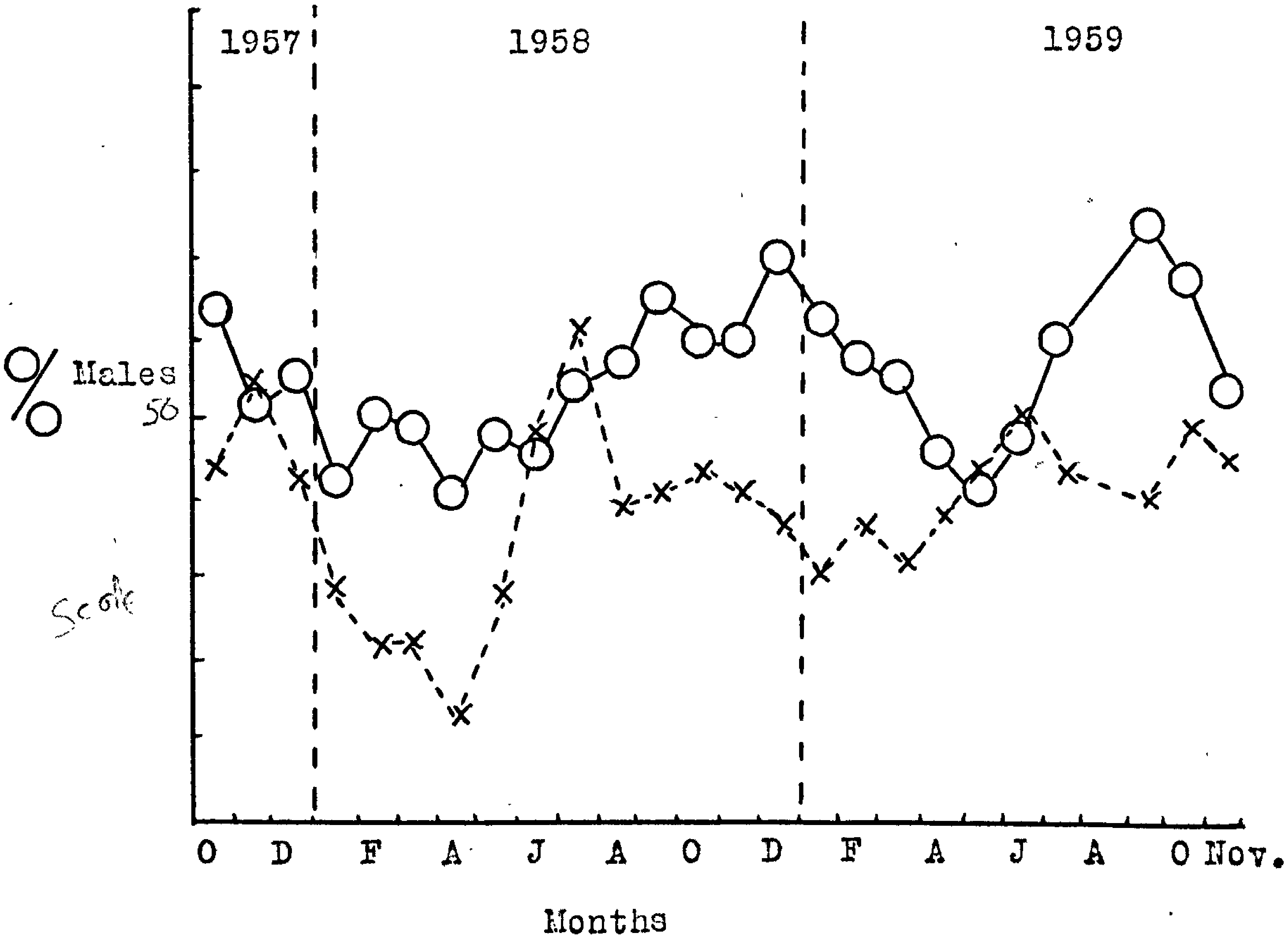

Fig. 19 Graph showing the sex-ratio (shown as % males) of A. aquaticus at Buckley Lake and of A. meridianus at Padeswood Lake (Oct. 1957 - Nov. 1959).

○——○ A. aquaticus

×- - - - -× A. meridianus

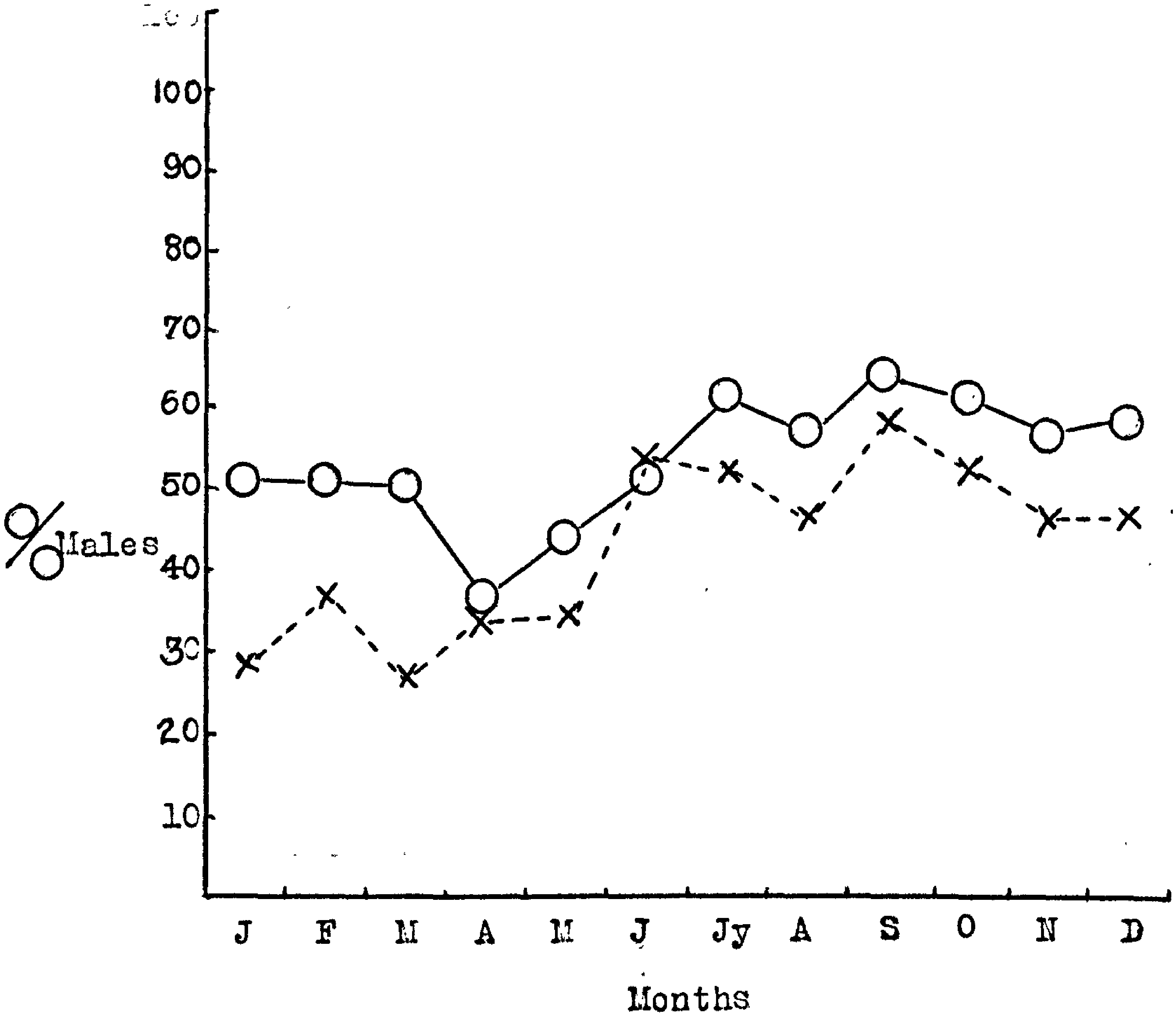

Fig. 2o Graph showing the mean monthly sex-ratio of A. aquaticus and A. meridianus (shown as % males) as calculated from all the regular samples.

O——O A. aquaticus

X- - - -X A. meridianus

	A. aquaticus		A. meridianus	
Month.	Mean % of males	Total no. of specimens upon which mean is based	Mean % of males	Total no. of specimens upon which mean is based
January	52	376	29	578
February	52	590	37	676
March	51	383	27	476
April	36	383	34	617
May	44	260	35	302
June	52	757	53	762
July	62	487	52	584
August	58	141	47	356
September	65	638	59	494
October	62	801	53	758
November	57	1,011	47	634
December	59	454	47	552

Table showing the mean monthly sex - ratio of A. aquaticus and A. meridianus as calculated from all the regular samples.

It can be seen from figs. 19 and 20 that the sex-ratio of both *A. aquaticus* and *A. meridianus* varies throughout the year, and, furthermore, that the pattern of this variation is essentially similar in the two species. Thus, in both, the percentage of males is least during the spring, rapidly rises during the early summer, and is greatest during the summer and autumn. The figures show also, however, that there is a constant difference between the two species in that the percentage of males of *A. aquaticus* is greater than that of *A. meridianus* in nearly all months. This constant difference is clearly revealed by the calculation of the mean annual sex-ratio of the two species: the mean annual percentage of males of *A. aquaticus* based upon 6,281 specimens from four localities, is 54.%; the mean annual percentage of males of *A. meridianus*, based upon 6, 789 specimens from four localities, is 43.3%.

The monthly variation in the sex-ratios of the two species can to some extent be correlated with the sexual dimorphism in size. Thus, the rapid rise in the percentage of males of the two species during the early summer would seem quite certainly to be due to the fact that the males released by overwintered females during the spring reach the limits of sexual differentiation before the females released at the same time. Not all the variationsin the sex-ratios of the two species can, however, be explained in this manner, and it would seem that at least some of the variation is due to a difference in the sex-ratio of broods produced at different times of the year, and to a difference in the survival of the two sexes. Because of the lack of sharply defined temporal divisions between broods in both species, it is not possible to evaluate accurately the influence of these latter factors, but, at all events, it would appear that the decline in the percentage of males of the two species during the winter is due to the death of overwintering males before that of overwintering females.

In order to appreciate correctly the ecological significanc of the difference between the sex-ratios of *A. aquaticus* and *A. meridianus*, it is necessary to have information concerning three points: (a) the necessity or otherwise of males in reproduction, (b) the "availability" of males, and (c) the effectiveness of fertilization.

Information concerning the necessity or otherwise of males in the reproduction of *A. aquaticus* and *A. meridianus* is provided by the work of Haemmerli - Boveri (1926) on *A. aquaticus*, and by the results of the experiment in which inter-specific crossing between the two species was attempted (see p. 2.14). The only conclusion that may be reached from this information is that in the reproduction of both species males are absolutely essential; unfertilized females of either species never produce live young.

Information concerning the "availability" of males of _A. aquaticus_ and _A. meridianus_ (i.e. the proportion at any one time of males which can successfully fertilize females) is provided by both laboratory and field evidence obtained during the present research. The laboratory evidence is derived from a brief experiment in which a male of either species of _Asellus_, after fertilizing one female of the same species, was immediately placed with another such female which was about to oviposit. The interval between each oviposition was noted, and every female was observed until the subsequent Zwischenhäutung. Due to the death of both males, the results of this experiment are unfortunately incomplete. The results indicate, however, that the interval between successful and consecutive fertilizations in males of both species need not be long, and, at all events, can be very much shorter than the interval between consecutive fertilizations in females of the two species. In the experiment, the _A. aquaticus_ male fertilized three females which oviposited on the 22nd February, the 26th February and the 1st March, and the _A. meridianus_ male fertilized two females which oviposited on the 26th February and 1st March. All five females subsequently released live young after an incubation period of about 3 weeks.

The field evidence concerning the "availability" of males in both species is derived from the field investigations of the life-cycles of the species (chapter lV). During these investigations <u>every</u> sample collected always contained non-precopulating males of <u>A. aquaticus</u> and/or <u>A. meridianus</u>. The laboratory and field evidence concerning the "availability" of males would appear to suggest, therefore, that in field populations of the two species there is never at any time a shortage of mature males capable of effecting successful fertilizations.

For both <u>A. aquaticus</u> and <u>A. meridianus</u>, information concerning the effectiveness of fertilization under natural conditions is perhaps provided by the investigation of the number of eggs or embryos borne by females of these species. This investigation is to be discussed in detail shortly, and it is pertinent, therefore, to note here only that during the investigations records were made of the number and the stage of development of eggs or embryos within the brood pouches of several hundred ovigerous females of both species. The investigation revealed that in <u>every</u> ovigerous female of <u>A. aquaticus</u> examined the eggs or embryos within the brood pouch were at the same stage of development, but that in approximately 1% of the ovigerous females of <u>A. meridianus</u> examined the eggs or embryos were at two different stages of development, one of these stages always being that of recently oviposited eggs. The most reasonable explanation of this phenomenon would seem to be that in A. aquaticus fertilization was so effective that there were never any unfertilized eggs, but that in A. meridianus fertilization was slightly less effective so that in about 1% of cases a number of eggs remained unfertilized and consequently failed to develop. The investigation revealed, therefore, that in both species fertilization would appear to be very effective, but that it would appear to be slightly less so in A. meridianus.

The three points of information which are necessary for a correct appreciation of the ecological significance of the difference between the sex-ratios of A. aquaticus and A. meridianus, and which have been discussed in the foregoing paragraphs, may be briefly summarized as follows: reproduction in both species is completely sexual, and the presence of males, therefore, is essential; in field populations of both species there would never appear at any time to be a shortage of males capable of effecting fertilization; and, under field conditions, fertilizations by males of both species would appear to be very effective, although perhaps slightly more so in A. aquaticus than in A. meridianus. From a consideration of this summary, it must be concluded that the difference between the sex-ratios of the two species will have a significant effect upon their biotic potentials; manipulation of the data on the sex-ratios indicates that during the entire year there are on average

23% more females of A. meridianus than of A. aquaticus. It is to be expected therefore, that breeding will be more intense in A. meridianus than in A. aquaticus, and this expectation is amply borne out by an examination of fig.15b p.4.69, which shows the number of breeding females of the two species at Buckley and Padeswood Lakes as a percentage of the total population present each month. It can be seen from the figure that in nearly all months the number of breeding females of A. meridianus was greater than that of A. aquaticus. Thus, with regard to the biotic potential of the two species, it is evident that the differences between their sex-ratios are more advantageous to A. meridianus than to A. aquaticus. The difference between the effectiveness of fertilization in the two species is so slight that it is regarded as being of no significance.

No previous work on the sex-ratio of A. meridianus exists, but Seitz (1954,1953) has presented some detailed information concerning the sex-ratio of A. aquaticus. The results presented in his 1954 paper, although based only upon specimens collected during 9 months of one year and 5-6 mm. or greater in length, are in very close agreement with the results of the present research. Thus, Seitz also found that the percentage of males in field populations of A. aquaticus was least during the spring, rose rapidly during June, and was greatest during the summer and early autumn. In his earlier paper (1953), Seitz was mainly concerned with the analysis of the sex-ratio within each brood. He found that broods could consist of either sex alone, but that most consisted of a mixture of the sexes with a preponderance towards one or the other. The factors which control the intra-brood sex-ratio in A. aquaticus are at present unknown, but it is of interest to note that Collinge (1947) regarded high temperatures and a highly nutritive diet as favouring the production of females in certain species of land isopods, and that Kinne (1952a) found that in Gammarus duebeni the main factor controlling the intra-brood sex-ratio was the temperature at which the female had been kept shortly before oviposition.

The number of progeny in each brood.

All the ovigerous females of A. aquaticus and A. meridianus collected during the field investigations on the life-cycle of these species were carefully preserved. A certain number of these females were subsequently examined in order to obtain data on the number of progeny in each brood. The females subsequently examined comprized all the ovigerous females of A. aquaticus collected from Buckley Lake, Llyn Llywenan and Hatchmere, all the ovigerous females of A. meridianus collected from Padeswood Lake, and all the ovigerous females of A. meridianus in the 3.5 mm. size-group collected from Llyn Llywenan and Hatchmere. In all, 266 ovigerous females of A. aquaticus and 568 ovigerous females of A. meridianus were examined. In the examination of each female, the eggs or embryos were removed from the brood pouch under a binocular microscope, and a note was then made of their number and stage of development. Four stages of development were arbitrarily demarcated:

stage (a) spherical eggs, either translucent and yellow, or opaque and white,

stage (b) comma-shaped eggs showing little or no development of appendages,

stage (c) embryos with well-developed appendages, but still contained within the egg-skin,

stage (d) embryos with well-developed appendages, and not contained within the egg-skin.

These developmental stages are approximately equivalent to the four recognized by Janke (1926) for A. aquaticus.

Before the number of eggs or embryos in each brood pouch can be regarded as a valid estimation of the actual number of progeny released at the end of incubation, it is necessary to reinvestigate the hypothesis that there is a progressive and intensive reduction in the number of eggs and embryos during incubation. This hypothesis was first advanced by Janke (1926) for A. aquaticus, and has since been reiterated by several other authors (e.g. Berg 1938, 1948; Birstein 1951). Janke based his hypothesis upon three facts: firstly, upon the fact that he noted a great increase in the volume of the embryos during incubation without a corresponding increase in the volume of the brood pouch; secondly, upon the fact that oviger--ous females which he maintained on a sieve always dropped eggs through the mesh; and thirdly, upon the fact that when he counted the number of embryos in a "large number" of females he found an average of 150 for embryos which had not left the egg-skin, an average of 100 for embryos just about to undergo the first larval moult, and an average of 80 for fully developed embryos. There are, however, several points of criticism that may be raised against Janke's evidence. He did not indicate, for instance, exactly how many ovigerous females he used in calculating the number of embryos in the various stages of development, and nor did he indicate how large the females were or at what time of the year they were collected. As will be shown presently, such information is extremely relevant, for not only is there a variation in the number of embryos with the size of the parent, but there is also a seasonal variation in this number. Furthermore, Janke noted that the eggs dropped by the females maintained on the sieve were abnormal: "an den ausgestoßenen Eiern waren irgendwelche Abnormitäten oder besondere Krankheitserscheinungen nicht festzustellen" (1926, p.685). It is quite possible, therefore, that these eggs were dropped only because they were abnormal, an explanation supported by the fact that unfertilized females tend to drop their eggs (see p. 2.13). The presence of the sieve may also have had some affect, for during the present research a perfectly normal ovigerous female of A. aquaticus maintained on a sieve at room temperatures discarded all her eggs within one week. In this instance, it appeared that in some way the surface of the sieve was extremely irritating to the female, and this may have caused the loss of her eggs.

The present evidence upon which the re-investigation of Janke's hypothesis is based has been derived from three sources: evidence has been derived from the investigation of the relationship between the length of time of incubation and the temperature, from the examination of the number of eggs or embryos in the four developmental stages in females collected from the field, and from an investigation of the actual number of juveniles released by ovigerous females.

All three sources provide evidence which is applicable to both A. aquaticus and A. meridianus.

1) Evidence derived from the investigation of the relationship between the length of time of incubation and the temperature: (see p.4.61).

During this investigation, all incubating females were observed at daily intervals. The observations revealed that most of the females of either species lost a few eggs or embryos from their brood pouches in the course of incubation, and that a few lost many and some lost none. The observations did not reveal any conclusive difference between the two species in the number of eggs or embryos lost.

2) Evidence derived from the examination of the number of eggs or embryos in the four developmental stages in females collected from the field:

The reason why Janke's evidence based upon the number of embryos at different stages of development cannot be accepted has already been intimated. It is possible, however, to use the fundamental idea upon which his evidence is based to provide acceptable evidence. Thus, in the table shown on the following page is presented various averages of the number of eggs or embryos in the four developmental stages in females collected from the field. But, in this table each set of averages has been obtained from females which were of the same size, and which had been collected at the same time. The data shown in the table have been selected from a great deal of similar data, but the *only* criterion of selection has been the number of specimens upon which each average is based; all those sets of averages based upon reasonably large numbers of specimens are shown.

It can be seen from the table that for neither species is there conclusive evidence of a significant reduction in the number of eggs or embryos during incubation, although the data referring to *A. meridianus* indicate that such a phenomenon may occur in this species.

3) Evidence derived from an investigation of the actual number of juveniles released.

Fig.21 and 22,pp.5.34,5.35,show for,respectively,*A.aqauticus* and *A. meridianus* the average number of eggs or embryos in females of different sizes and at different times of the breeding season. The figures are to be discussed in more detail shortly, but it

Date of collection	Size of female	Average no. of eggs in each developmental stage.			
		stage(a)	stage(b)	stage(c)	stage(d)
A. aquaticus					
17th May	8.5mm.	86 (2)	91 (7)	115 (4)	117 (6)
17th May	7.5	106 (9)	93 (10)	84 (3)	86 (9)
A. meridianus					
27th March	6.5	56 (41)	52 (19)	52 (4)	47 (7)
25th April	7.5	60 (7)	60 (8)	59 (5)	50 (28)
25th April	6.5	43 (21)	48 (23)	42 (4)	41 (19)
25th April	5.5	36 (18)	44 (5)	37 (2)	27 (9)
24th April	4.5	18 (16)	16 (6)	18 (3)	16 (7)

The number shown in brackets after each average indicates the number of females upon which the average is based.

must be noted here that the averages are based only upon females containing eggs or embryos in developmental stages (a) to (c). By interpolation of these figures, it is possible, therefore, to estimate the average number of eggs or embryos (developmental stages (a) to (c)) in any female of either species collected from the field. Then, by comparing this estimated number with the actual number of juveniles released by the female, an approximate indication of the number of embryos lost during at least developmental stage (d) may be obtained. This procedure has been carried out on 17 females of A. aquaticus and 13 females of A. meridianus. The detailed results are shown in the table overleaf. It can be seen from the table that most of the females investigated would appear to have lost some of their embryos during incubation, the estimated maximum loss being 78% in A. aquaticus and 66% in A. meridianus. But, it can also be seen that several females of both species would appear not to have lost any of their brood.

From a consideration of all three sources of evidence outlined in the preceding paragraphs, the most probable conclusion would seem to be that in both A. aquaticus and A. meridianus most ovigerous females lose some eggs or embryos during incubation. The extent of the loss, however, is extremely variable; some females of both species lose almost

Date of liberation of juveniles	Size of female (mm.)	Number of juveniles released	Estimated number of eggs and embryos (stages - (a) to(c))	Percentage reduction
<u>A. aquaticus</u>				
15th March	8.0	92	85	-4
18th March	6.5	53	53	0
29th March	8.5	100	100	0
12th March	8.0	82	85	4
14th March	8.0	82	85	4
8th March	8.0	61	85	8
2nd April	8.5	90	100	10
27th March	7.5	63	73	14
14th March	8.0	70	85	18
14th March	7.5	50	63	20
30th March	7.0	48	70	31
6th April	7.0	52	75	31
16th March	8.0	45	85	47
30th March	9.0	49	120	59
5th April	7.5	29	75	61
30th March	7.5	21	77	73
2nd April	7.5	19	87	78
<u>A. meridianus</u>				
2nd April	4.5	44	35	-26
31st.March	5.5	51	43	-19
2nd April	4.0	21	35	4
11th March	5.0	28	30	7
16th March	5.0	25	30	13
2nd April	4.5	29	35	17
1st April	5.0	33	40	17
14th March	5.0	25	30	17
15th March	5.0	23	30	23
31st March	5.5	31	43	28
14th March	6.0	31	44	30
2nd April	4.0	22	35	37
6th April	4.5	12	35	66

their entire brood, whilst a few females of both species lose none of their brood. At all events, it would seem that in both species the usual extent of the loss is far less than that envisaged by Janke (viz. 47%); because of the very approximate nature of the evidence, it is not possible to give an exact estimate of the average percentage loss, but for both species a figure of 20% is not without foundation and would not appear to be unreasonable. The factors responsible for the loss are at present unknown, but it seems likely that they include the action of walking, the constant movements of the brood pouch lamellae, the continual current of water passing through the pouch and the movements of the eggs or embryos themselves. If indeed most of the loss is due to these causes, then the loss must be regarded as a purely accidental one and not as purposive.

It is of interest to note at this point that a similar reduction in the number of embryos during incubation would seem to occur in Caecosphaeroma (Vireia) burgundum; Daum (1954) noted that in 7 females of this species the average number of eggs in the brood pouch was 8, but that the average number of juveniles released by these females was only 6. Similarly, Kinne (1953) noted that, even under the optimum conditions of salinity and temperature, never more than 95% of the brood of Gammarus duebeni survived. On the other hand, Hynes (1955) and Jefferies (1958) stated that there was no intra-brood mortality in, respectively, *Gammarus pulex* and *G. lacustris*, and *Palaemonetes varians*.

Because it would seem that most ovigerous females of *A. aquaticus* and *A. meridianus* lose some eggs or embryos during incubation, it is evident therefore that the number of eggs or embryos within the brood pouch cannot be regarded as a direct valid estimate of the actual number of progeny released at the end of incubation. Furthermore, there is the additional point that the number of embryos in developmental stage (d) provides an even less reliable estimate than is provided by the number of eggs or embryos in developmental stages (a), (b) and (c), for in both species there is the tendency for juveniles to be released over an extended period of time (but see p.4.62). However, by using only those ovigerous females possessing eggs or embryos in developmental stages (a), (b), or (c), and by allowing for the reduction in the number of eggs or embryos during incubation, it is possible to obtain from the examination of the ovigerous females of the two species an indication of the variation in the number of juveniles released.

The results of the examination are partly shown in graphical form in fig. 21 and 22 , pages 5.34 and 5.35 . These figures are based upon only those specimens possessing eggs or embryos in developmental stages (a), (b) or (c). More detailed results are contained in appendix E, p.10.48. Strictly speaking, the figures show only the variation in the number of eggs or embryos of the two species, but, by reducing each value shown by approximately 20%, an indication is also given of the variation in the actual number of juveniles released.

It can be seen from the figures that in both A. aquaticus and A. meridianus there is a clear relationship between the size of the ovigerous females and the number of eggs or embryos borne by them, and, furthermore, that there is a seasonal variation in this relationship. The seasonal pattern of variation is similar in both species; in both the maximum number of eggs or embryos is borne during the spring, the minimum during the early summer. The correlation between the size of ovigerous females and the number of eggs or embryos is shown also by figure 23, p.5.36. Here, the monthly data have been combined to produce an annual average number of eggs or embryos (developmental stages (a), (b) and (c) only) for each size group of ovigerous females. The figure compares each such average in the two species. Comparing the averages, it can be seen that in the smaller size groups the averages are very similar in the two species, but that in the larger size groups more eggs or embryos are borne by females of A. aquaticus.

Only Unwin (1920) has hitherto presented data on the number of eggs or embryos borne by females of *A. meridianus* His observations, however, are extremely brief; he noted only that the number varied from 39 to 62, and that "the average of many specimens is 46" (p.340). Rather more data have been presented concerning the number of eggs or embryos borne by females of *A. aquaticus*. Kaulberz (1913) recorded 50 - 60; Janke (1926), as already noted, recorded from 80 to 150; and Weerekoon (1956) recorded an average of 22 from 16 females in Loch Lomond. But, none of these authors realized that the number of eggs or embryos was dependent upon, amongst other things, the size of the ovigerous female. Their figures, therefore, are of little use for comparative purposes. Berg (1938; 1948), on the other hand, was clearly aware of the correlation between the number of eggs or embryos and the size of the ovigerous female. In the earlier paper, based upon his work at Esrom lake, he recorded from 12 to 52 eggs or embryos in females of *A. aquaticus* ranging in size from 3.9 mm. to 7.0 mm.; in the later paper, based upon collections made from the R. Susaa, he noted in detail not only the increase in the number of eggs or embryos with increase in size of the females bearing them, but also a seasonal difference in the average number of eggs or embryos borne. This seasonal difference, however, he explained entirely in terms of a seasonal difference in the average size of females. His figures for the average number of eggs or embryos/female in each season of the breeding period were 94.2 for the spring, 29.7 for the summer and 23.7 for the autumn; his figures for the average number of eggs or embryos borne by females of sizes 5.0, 6.0, 7.0, 8.0, 9.0, 10.0 and 11.0 mm. were, respectively, 24.9, 28.3, 36.8, 83.5, 105.2, 120.8 and 152.3. These latter data are in close agreement with the data of the present research (c.f. Berg's data and fig.23).

The sort of variation in the number of eggs or embryos in A. aquaticus and A. meridianus recorded in the present research is paralled by the work of many authors on other crustacean species. Clemens (1950), Kinne (1952), Hynes (1954,1955), and Jefferies (1958), for instance, recorded for various species a clear correlation between the number of eggs or embryos borne and the size of the female, and Kinne (1952) recorded also for Gammarus duebeni a seasonal variation in the number of eggs or embryos borne by females of the same size.

Discussion.

Using the data outlined in the preceding sections of this chapter, and the data concerning the number of broods borne by females and the length of the developmental cycle outlined in chapter lV, it is now possible to calculate the approximate biotic potential of *A. aquaticus* and of *A. meridianus*.

For ease of comparison it is convenient to consider for each species the biotic potential of a single female which is released at the very beginning of a breeding season, and which survives for its normal length of life. Thus, for either species will be considered the biotic potential of a female which begins its extra-marsupial life about the end of April, which breeds before and after overwintering, and which dies at the end of spring.

The *A. aquaticus* female will reach maturity after 1½ months, and her first brood will be incubated during the latter half of June. The approximate size of the female at this time will be 4.5 mm., and she will, therefore, bear about 10 eggs or embryos. Following the reduction in this number during incubation, about 8 juveniles will eventually be released. Two further broods will be produced by the female before the winter, and these will be released during July and August/

/September. Referring to figs. 9 and 12, pages 4.1 and 4.4, it would seem that the approximate size of the female at these times will be 5.5 and 6.0 mm. The broods, therefore, will consist of 25 and 36 eggs or embryos, respectively, and followin the reduction in these numbers during incubation, about 20 and 29 juveniles will be released. The approximate size of the female after overwintering will be 9.0 mm. (fig.9 p.4.1), and she will produce only one further brood before her death at the end of spring. This brood will consist of about 125 eggs or embryos, and following the reduction in this number during incubation, about 100 juveniles will be released. The approximate total number of juveniles released by the female during her life, therefore, will be 149. This number, however, is not the biotic potential, for, before the death of the female, most of her offspring produced before overwintering will themselves produce a brood. In order to calculate the number of progeny produced by the offspring, it is necessary to consider the sex-ratio of the various broods produced before overwinterin by the original female. It is quite likely that this sex-ratio varies (see p. 5.8), but because of the lack of sharply defined temporal divisions between broods it is not possible to determin exactly this variation. In the absence, therefore, of an exact estimation, it seems not unreasonable to regard the average sex-ratio during the period June-December as providing a fairly accurate approximation[1]. In A. aquaticus this average is 8 0.6:0.4:1:0:0. The number of females in each of the broods produced by the original female before overwintering will be, therefore, respectively, 3.2, 8 and 11.6. All of these females will mature only after overwintering, and will begin incubating in March or April. By reference to fig. 9 p.4.1, it would seem that at this time the approximate size of these females will be, respectively, 7.5, 6.5, and 5.5 mm. Each female of the first brood will bear, therefore, about 82 eggs or embryos, and each female of the second and third brood, about 65 and 40 eggs or embryos, respectively. Following the reduction in these numbers during incubation, each female of the 1st, 2nd and 3rd brood will eventually release about 66, 52 and 32 juveniles, respectively. Multiplication of these numbers of juveniles by the number of females producing them will give the total progeny of the offspring of the original female. Thus, the females in the first brood of the original female will produce a total of 211 progeny, and similarly, the females of the 2nd and 3rd broods, totals of 416 and 371 progeny, respectively. Adding these figures, it can be seen that the total progeny of the offspring of the original female will be 998. The approximate biotic potential of the A. aquaticus female is, therefore, 998 + 149, i.e. 1,147.

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[1] Footnote 1. The sex-ratio of this period is regarded as a more reliable a figure than the annual average sex-ratio, for it seems likely that the sex-ratio during the period December-May is greatly influenced by a differential survival of the sexes.

The approximate biotic potential of the *A. meridianus* female is calculated in a similar manner:

The *A. meridianus* female will reach maturity after 1½ months, and her first brood will be incubated during the latter half of June. The approximate size of the female at this time will be 3.5 mm., and she will, therefore, bear about 10 eggs or embryos. Following the reduction in this number during incubation, about 8 juveniles will eventually be released. Three further broods will be produced by the female before the winter, and these will be released during July, August and September/October. Referring to fig. 10 , p.4.2 , it would seem that the approximate size of the female at these times will be 4.0, 5.0 and 5.5 mm. The broods, therefore, will consist of about 18, 22 and 31 eggs or embryos respectively, and, following the reduction in these numbers during incubation, about 15, 18 and 24 juveniles will be released. The approximate size of the female after overwintering will be 7.5 mm. (fig. 10 p.4.2), and she will produce only one further brood before her death at the end of spring. This brood will consist of about 60 eggs or embryos, and, following the reduction in this number during incubation, about 48 juveniles will be released. The approximate total number of juveniles released by the female during her life, therefore, will be 113. This number, however, as in the case of the A. aquaticus female, is not the biotic potential, for, before the death of the A. meridianus female, most of her offspring produced before overwintering will themselves produce a brood. As before, in order to calculate the number of progeny produced by the offspring, it is necessary to consider the sex-ratio of the various broods produced before overwintering by the original female. For the same reasons as have been advanced for the A. aquaticus female (p.5.29), the average sex-ratio of A. meridianus during the period June--December must be regarded as indicating this sex-ratio. The approximate sex-ratio of the broods produced before overwintering by the original female is, therefore, 0.5. Thus, the number of females in each of the four broods produced before overwintering by the original female will be, respectively, 4,7.5, 9 and 12. All of these females will mature only after overwintering, and will begin incubating during March or April. By reference to figure 10 ,p.4.2 , it would seem that at this time the approximate size of these females will be, respectively, 7.0, 6.5, 6.0 and 5.5 mm. Each female of the first brood will bear, therefore, about 57 eggs or embryos, and each female of the 2nd, 3rd and 4th brood, 55, 50 or 45 eggs or embryos, respectively. Following the reduction in these numbers during incubation, each female in the 1st, 2nd, 3rd and 4th brood will eventually release about 46, 44, 40 or 30 juveniles, respectively. Multiplication of these numbers of juveniles by the number of females producing them will, as before, give the total progeny of the offspring of the original female. Thus, the females in the first brood of the original female will produce a total of 184 progeny, and, similarly, the females of the 2nd, 3rd and 4th broods, totals of 330, 360 and 430 progeny, respectively. Adding these figures, it can be seen that the total progeny of the offspring of the original female is 1,306. The approximate biotic potential of the *A. meridianus* female is, therefore, 1,306 + 113, i.e. 1,419.

The estimations of the biotic potentials of *A. aquaticus* and *A. meridianus* given above must be regarded as only very general approximations; both sets of calculations, for instance, are based upon a highly theoretical picture of the two life-cycles and of the sizes of females at various points of time. Nevertheless, both estimations probably have a certain validity, although it is doubtful if this extends to the indicated difference between the two; the most reasonable conclusion, in fact, would seem to be that the biotic potentials of *A. aquaticus* and *A. meridianus* are of approximately the same order. This similarity between the two biotic potentials would seem to be the result of a balance between three points of difference, namely, the difference in the length of the breeding season, the difference in the size of ovigerous females; it would appear that in A. meridianus the bias towards the production of females and the slightly longer breeding season compensate for the smaller average size of females and the consequent smaller number of juveniles released by each female. However, it must be noted here that several factors of the external environment (and especially food and temperature) can greatly affect the life-cycle of the two species. The extent of this affect is apparently not always the same in the two species, and, therefore, it is to be expected that marked changes will occur between the biotic potentials of the two from year to year and from place to place.

Zheltenova (Birstein 1951) has previously presented an estimate of the biotic potential of A. aquaticus. Her estimate is almost three times higher than the one presented here, but since no details of the calculations are given it is not possible to discuss it further.

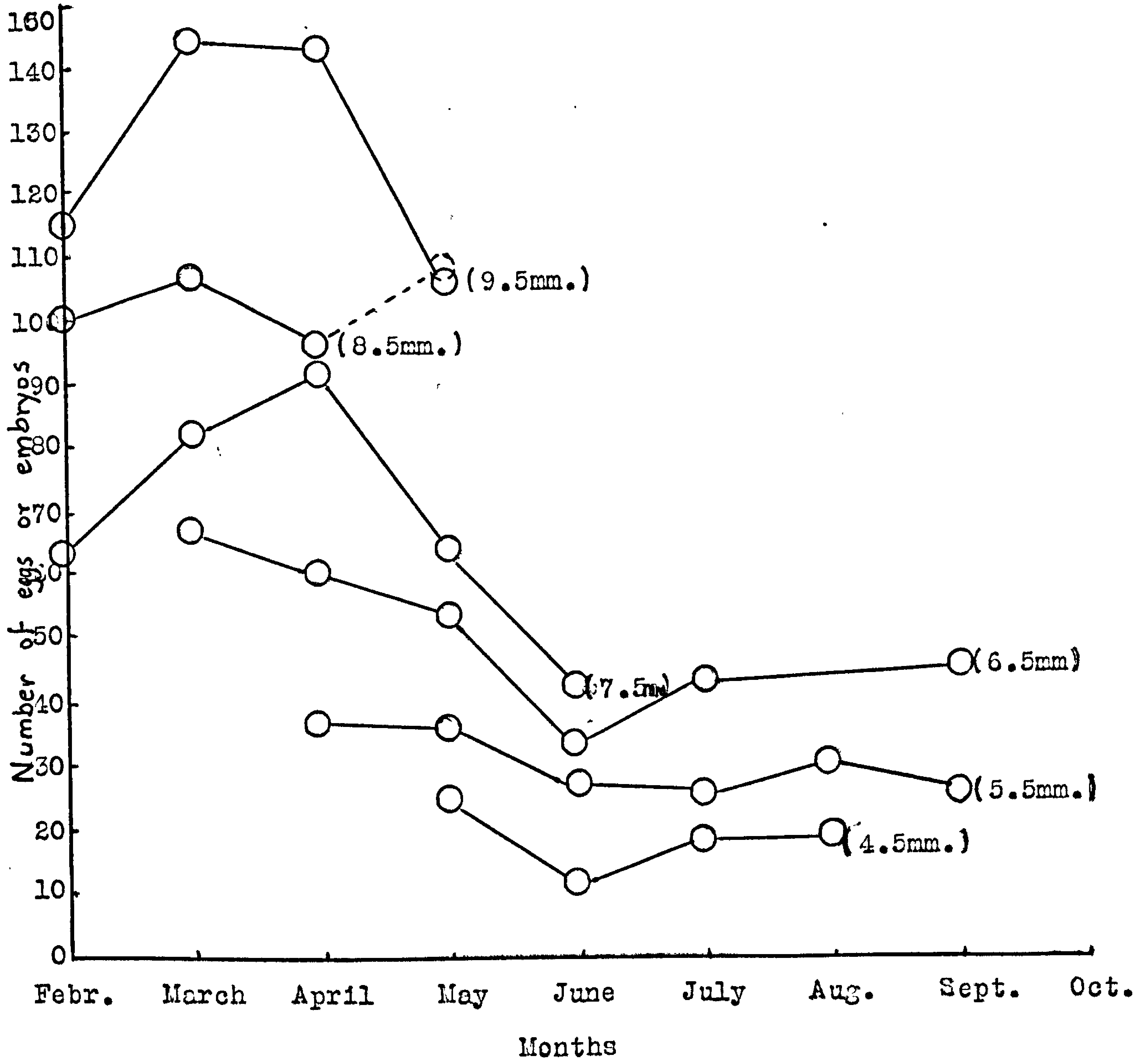

Fig. 21 Graph showing the mean number of eggs or embryos borne by females of A. aquaticus in each 1 mm. size-group in each month of the breeding season.

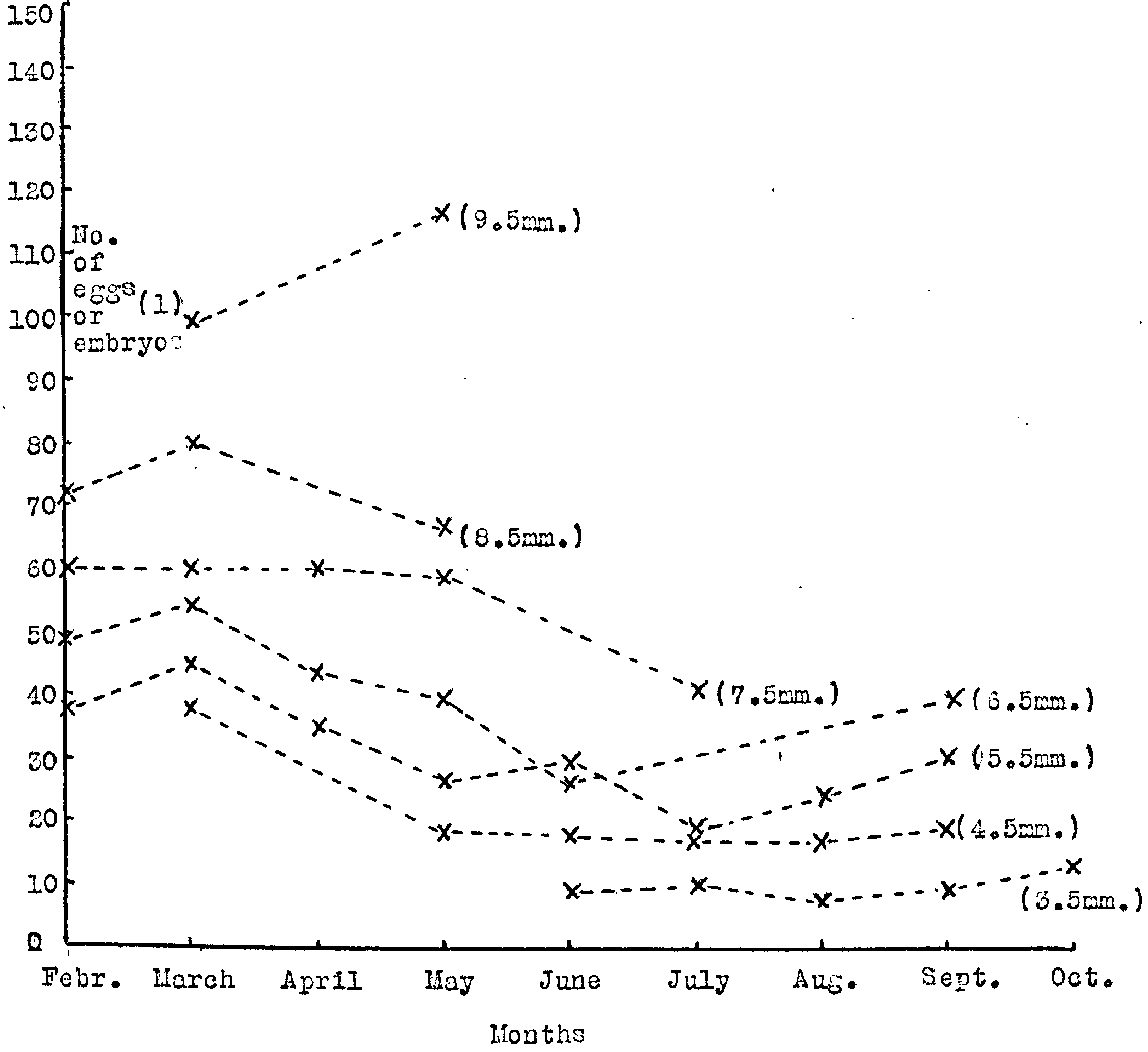

Fig. 22 Graph showing the mean number of eggs or embryos borne by females of A. meridianus in each 1 mm. size-group in each month of the breeding season.

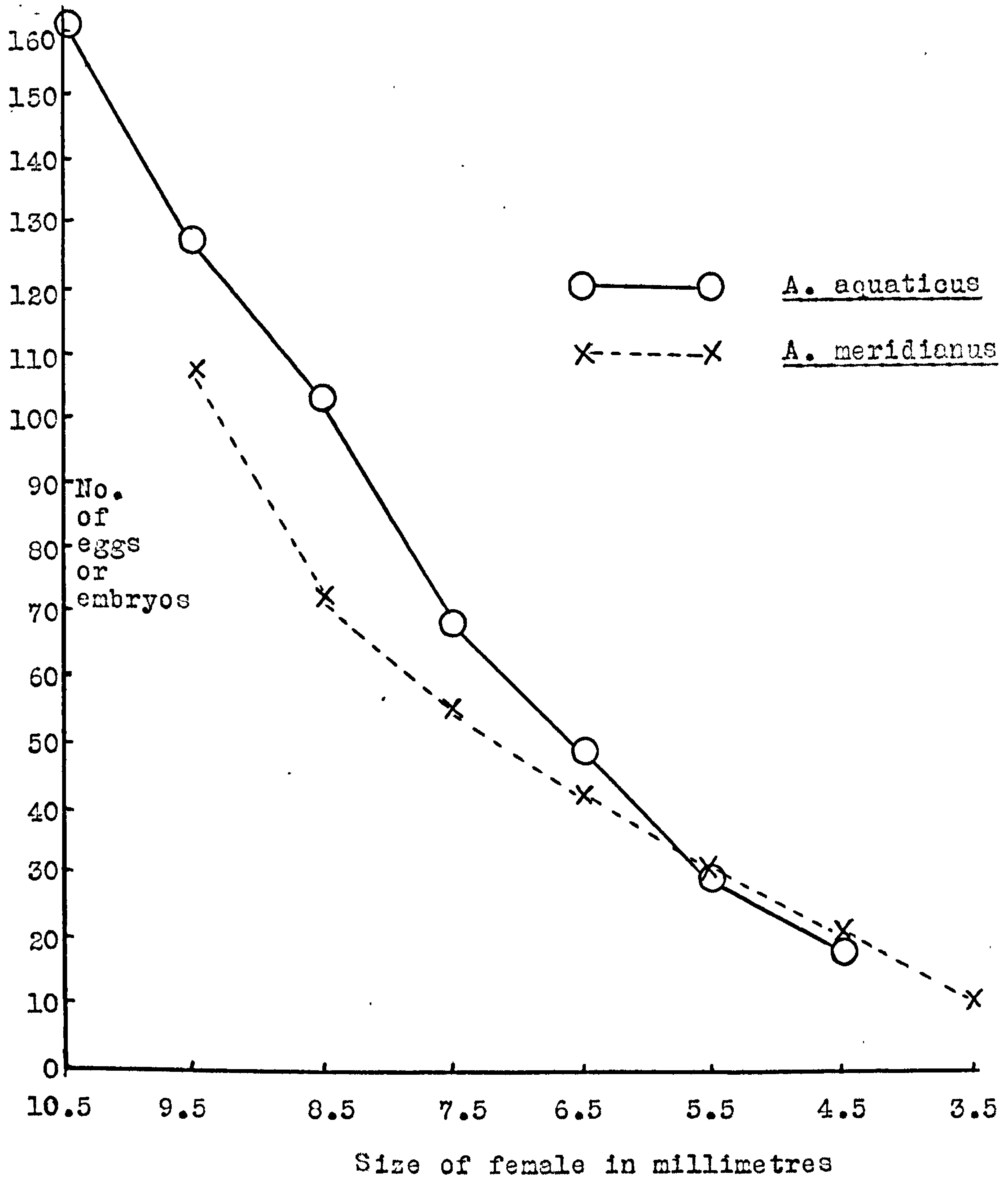

Fig. 23 Graph showing the relationship between the annual average number of eggs or embryos and the size of females of A. aquaticus and A. meridianus.

THE DEGREE OF ECOLOGICAL SIMILARITY

a) Food.

Numerous workers have demonstrated specific differences in food and feeding habits in many groups of sympatric and closely related species (e.g. Lack (1944,1946,1947), Hartley (1953), Betts (1955), Dobzhansky et al (1956), de Cunha et al. (1957), Hartman (1957), MacArthur (1958), Kohn (1959). Proponents of Gause's hypothesis have regarded such differences as strong indirect proof of the validity in nature of the hypothesis, and as having resulted from interspecific competition. Such differences, in fact, are looked upon as being the principal means whereby related and sympatric species can co-exist. On the other hand, however, Andrewartha and Birch (1954) contended that for many animal populations food is not a limiting factor, and, therefore, food differences could hardly have arisen as the result of interspecific competition. Furthermore, there have recently been advanced several examples of groups of sympatric and related species within which there seems to be no specific food differences (e.g. see Dumas (1956), Fryer (1957, 1959)).

During the present research, comparative information concerning the food and feeding habits of A. aquaticus and A. meridianus has been obtained from three principal sources;

information has been obtained from a study of the mouth parts, from an analysis of the contents of the fore-guts, and from observation of the feeding habits of captive specimens.

Sars (1867), Tschetwerikoff (1911), Birstein (1951) and others have figured the complete mouthparts of *A. aquaticus*. As far as I am aware, however, no author has hitherto figured the complete mouthparts of *A. meridianus*, although Racovitza (1919) must obviously have made a close study of them, as he concluded that they differ from *A. aquaticus* only in the number of spines on the inner lobe of the first maxilla. Nonetheless, in order to be quite certain of Racovitza's implied conclusions, drawings of the mouthparts of both species were made and compared. These drawings are shown in figs. 24 and 25, p.6.3 and 6.4. The drawings show the appendages of the left side, and were based upon large male specimens.[1] A camera lucida was used in their preparation. It can be seen from the figures that the mouth-parts are extremely similar in the two species; the only salient differences would seem to be in the number of spines on the inner lobe of the 1st maxilla (*4 in A. aquaticus*; 5 in *A. meridianus*), and in the larger number of spines on the anterior portion of the terminal basal part of the maxilliped in

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[1] Footnote 1. Apart from the coxopodite of the maxilliped, there would appear to be no differences between males and females in either species. The maxillipeds are similar in females of both species.

6.3

__Fig__. 24 __The mouthparts of A. aquaticus and A. meridianus__

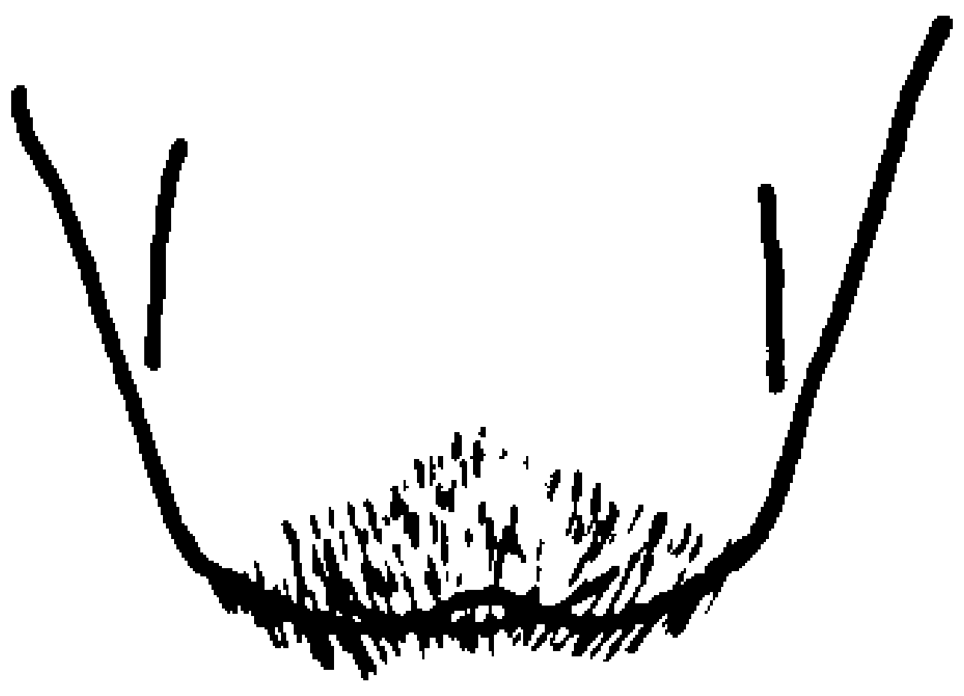
(I)

(The appendages are from the left side)

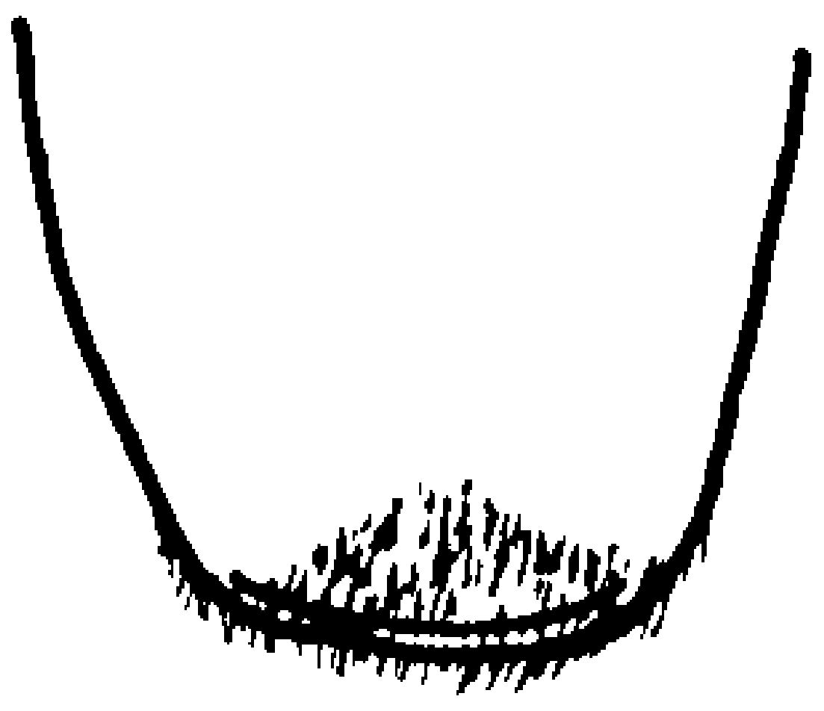
a. __A. aquaticus__

m. __A. meridianus__

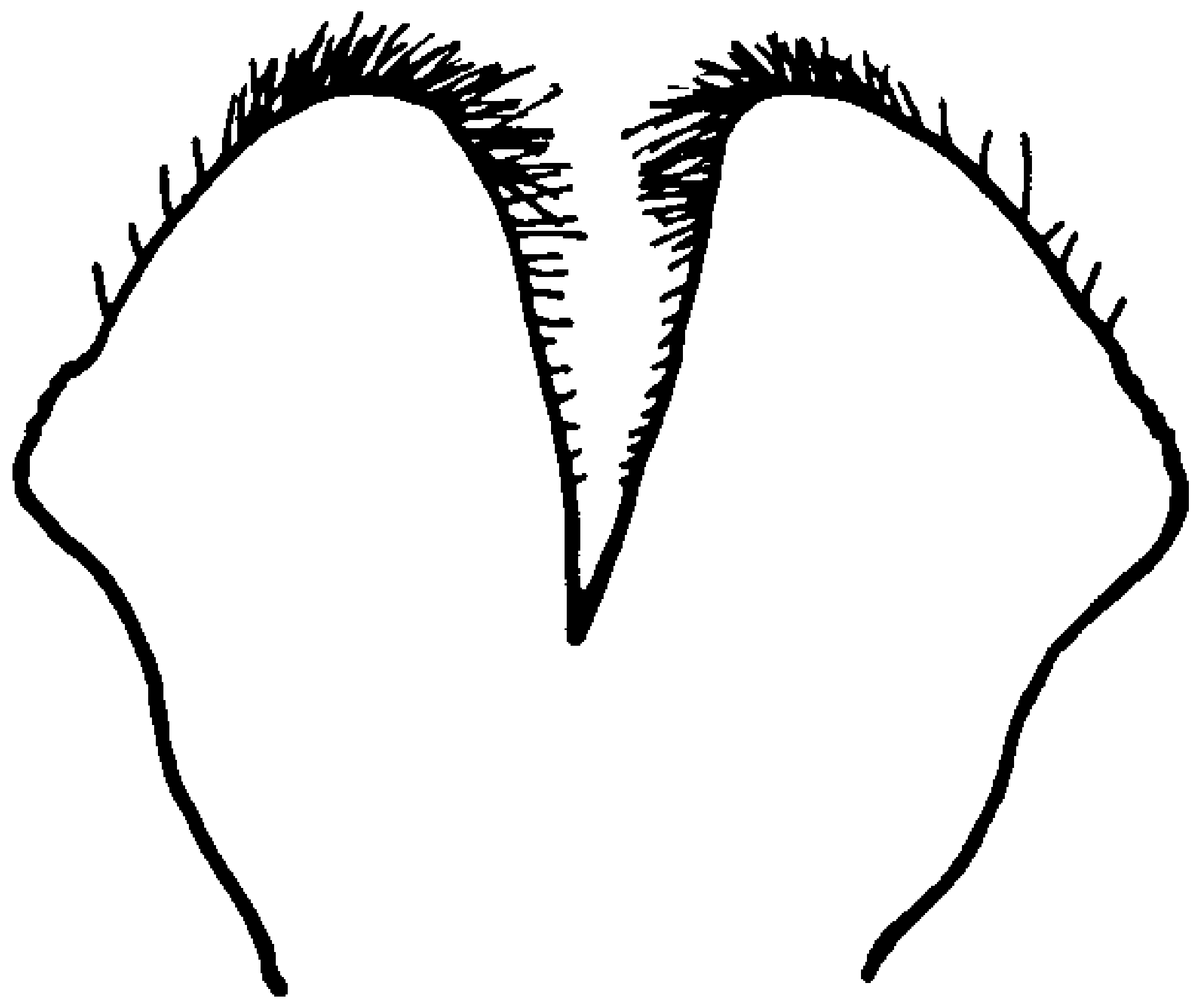
1. Upper lip or labrum
2. Lower lip or paragnath
3. Mandibles



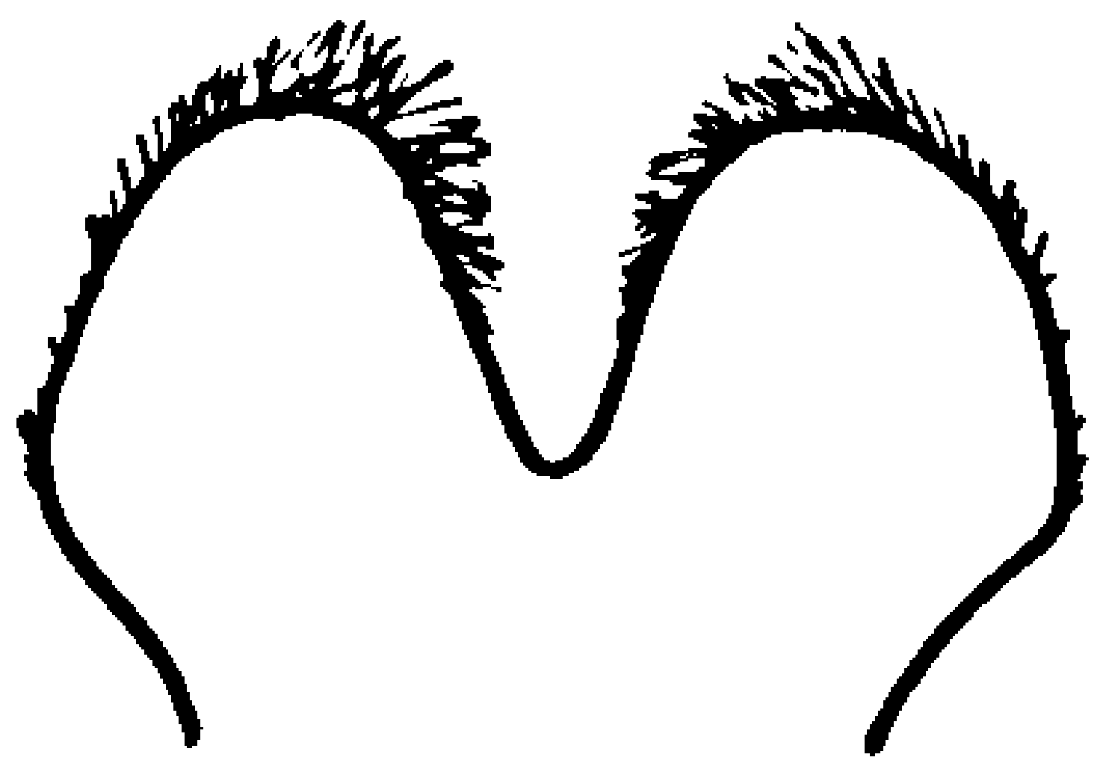
1a



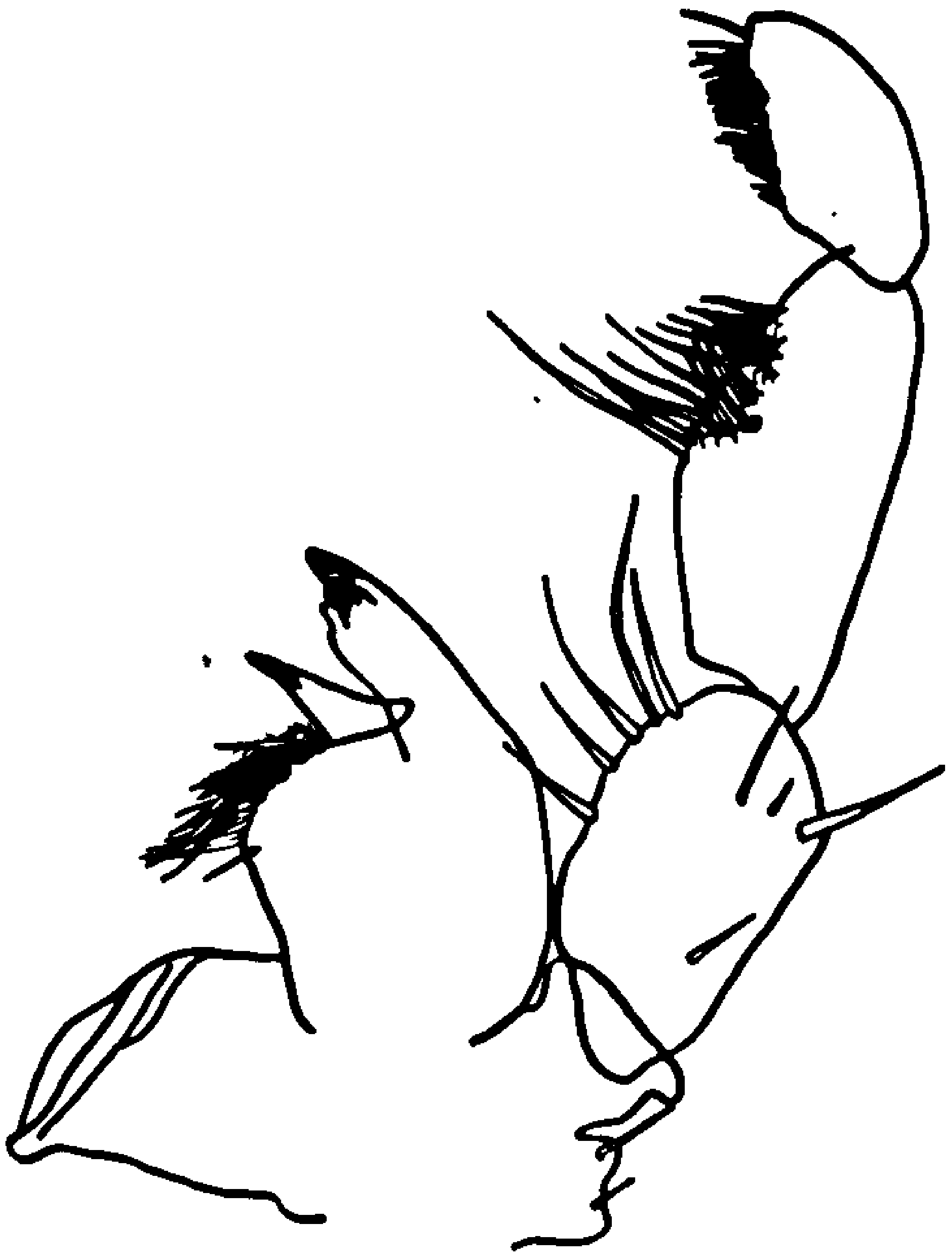
1m



2a



2m



3a

3m

0·5mm.

6.4

Fig. 25 The mouthparts of A. aquaticus and A. meridianus

(II)

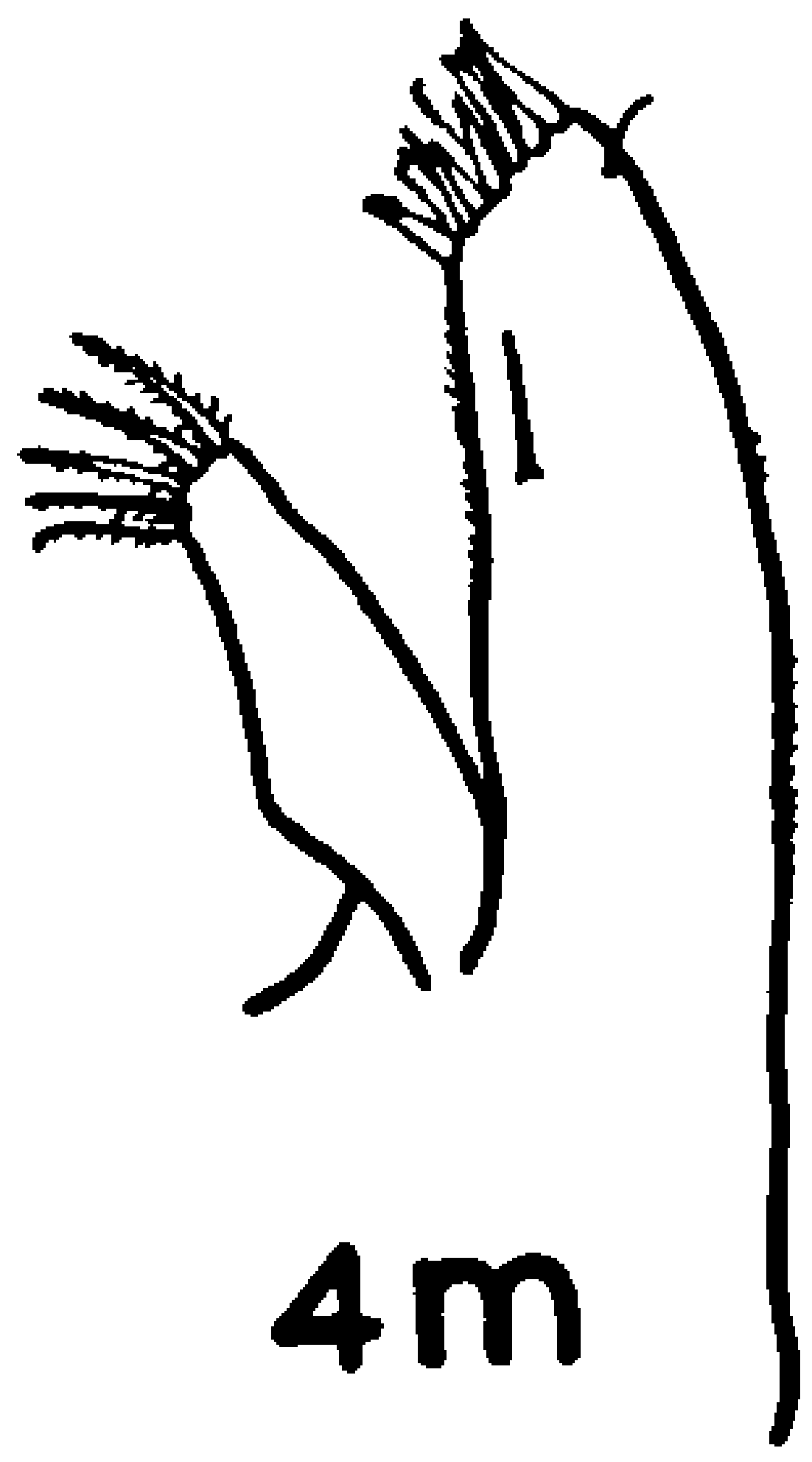
(The appendages are from the left side)

a. A. aquaticus

m. A. meridianus

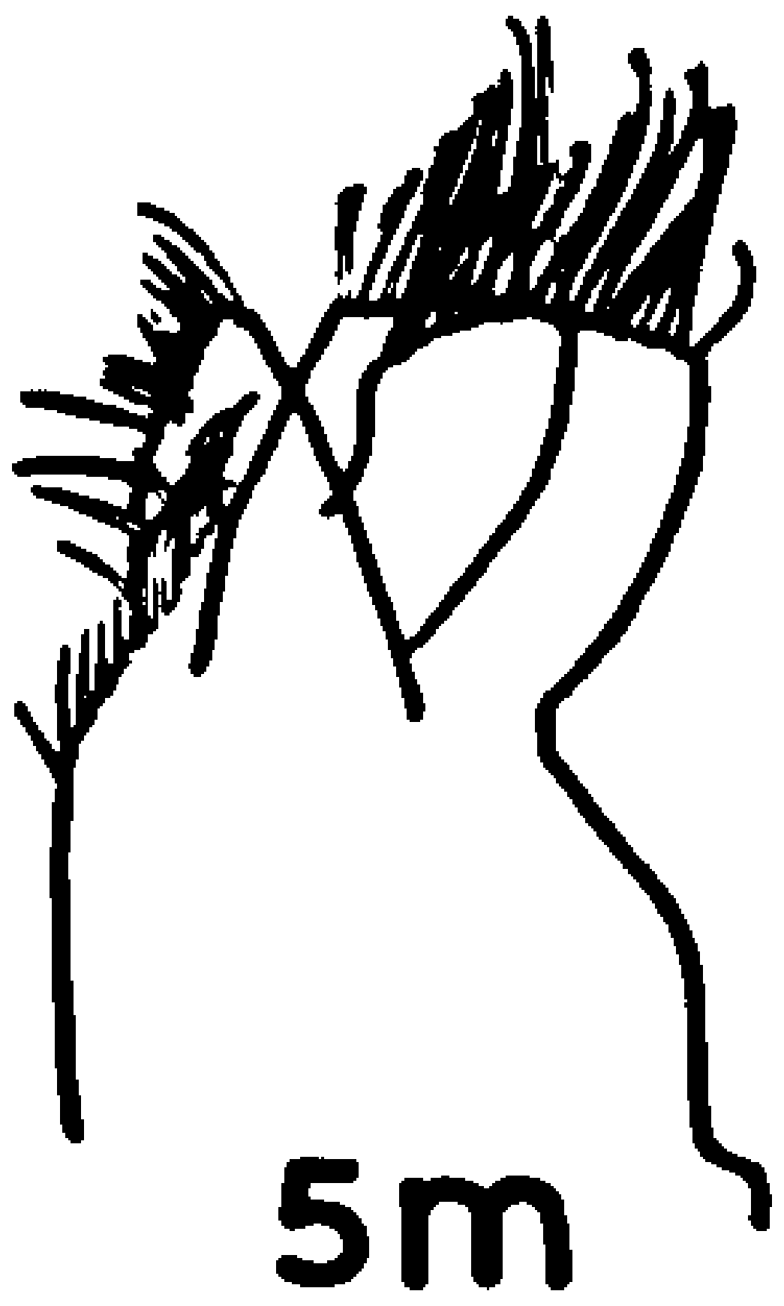
4. Maxillules (first maxillae)
5. Maxillae (second maxillae)
6. Maxillipedes

4a



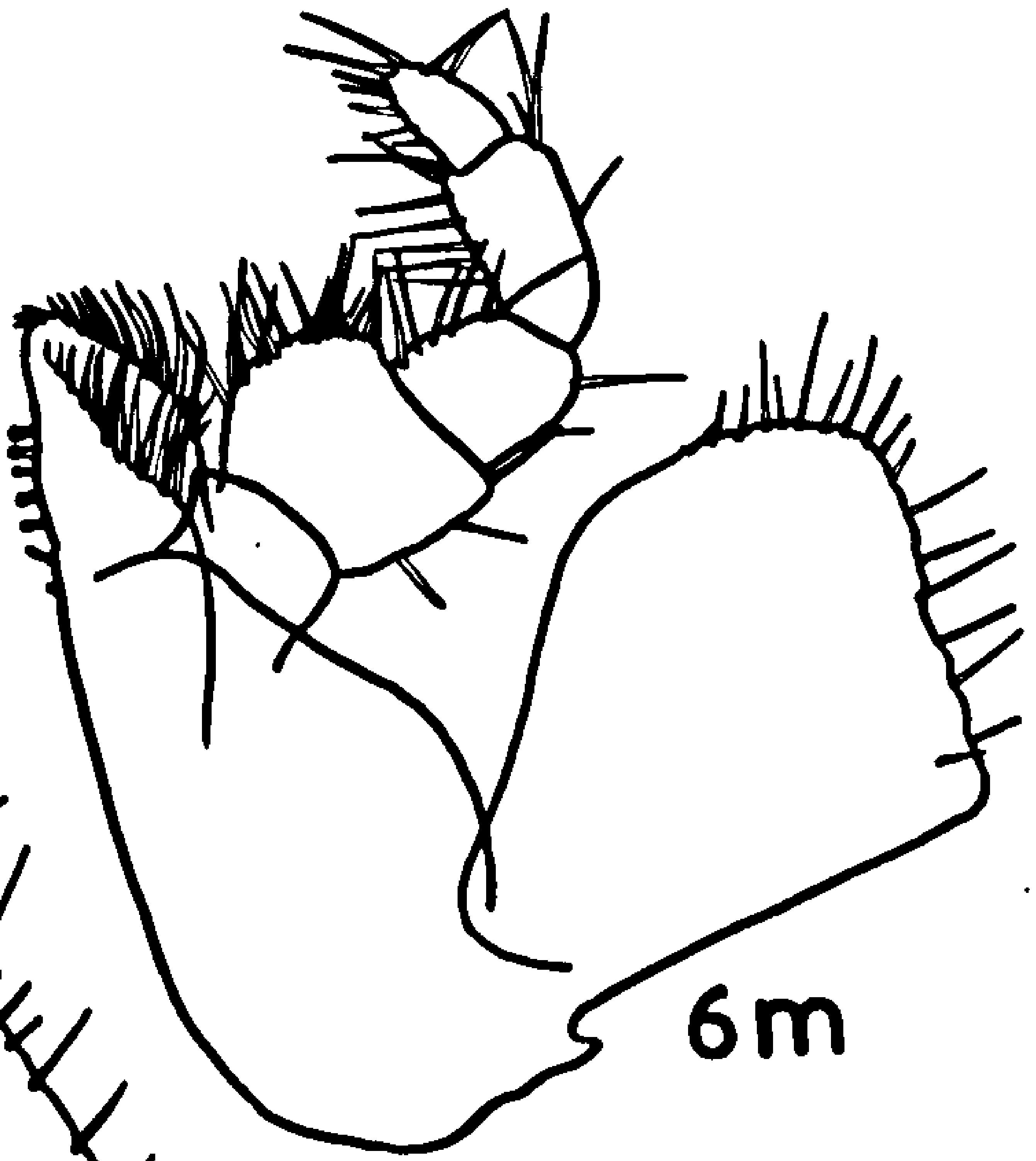
4m

5a



5m

6a



6m

0·5mm.

A. aquaticus. It is difficult to see how these minor differences in chaetotaxy could account for any gross specific food differences, and it must be concluded, therefore, that the study of the mouthparts does not indicate any major difference between the food of the two species. The similarity between the mouthparts of the two species and the mouthparts of *Idotea* (see Naylor, 1955b), suggests that the mechanism of feeding is probably the same in the two genera. The mechanism has been fully described for *Idotea* by Naylor (1955a). Thus, it may be presumed that the mechanism of feeding in *A. aquaticus* and *A. meridianus* consists essentially of six operations, namely, biting, scraping, pushing, combing, brushing and trituration. Sieving and further trituration occurs in the fore-gut (Rehorst, 1914).

Fig. 26 p. 6.7 , shows the percentage occurrence of various constituents in the fore-gut of *A. aquaticus* and *A. meridianus*, and is based upon an examination of the foreguts of 25 large adult specimens of each species. These specimens had been collected from Llyn Llywenan, and preserved in 70% alcohol. In the examination, the fore-gut of each specimen was first removed by dissection under a binocular microscope, and was then macerated on a microscope slide and examined under the low and high powers of the microscope. As was to have been expected from the study of the mouthparts, the determination of the contents comprized grit and indeterminate "mush", the other constituents forming only a very small fraction of the total volume.[1] Nevertheless, some differences between the species would seem to be indicated; as can be seen from the figure, the percentage occurrence of all constituents other than grit amd finely divided "mush" was higher in <u>A. aquaticus</u>. It is not clear whether this difference is the result of a less efficient trituration in <u>A. aquaticus</u>, or is due to the rather wider variety of material ingested by this species, but it seems not unreasonable to suppose that the latter explanation is the more probable. In both species the arthropod remains consisted almost entirely of small setae, and no diatoms were seen. Rehorst (1914) also noted the constant presence of grit in the fore-gut of <u>A. aquaticus</u>.

During the present research, both species were successfully reared through at least two generations using dead elm leaves as a food source. The leaves themselves, however, may not have been the actual food material; although both species skeletonized the leaves (<u>A. aquaticus</u> more readily than <u>A. meridianus</u>), it seems quite possible that the actual food was the film of bacteria, protozoa, rotifera, etc., associated with the surface of each leaf. Such food items, being soft bodied, would not of course have been revealed by the analysis of the gut

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<u>Footnote 1</u>. It is of interest here to note that Dr. T.B. Reynoldson (pers.comm.), has observed the presence of fungus in the foregut of Asellus.

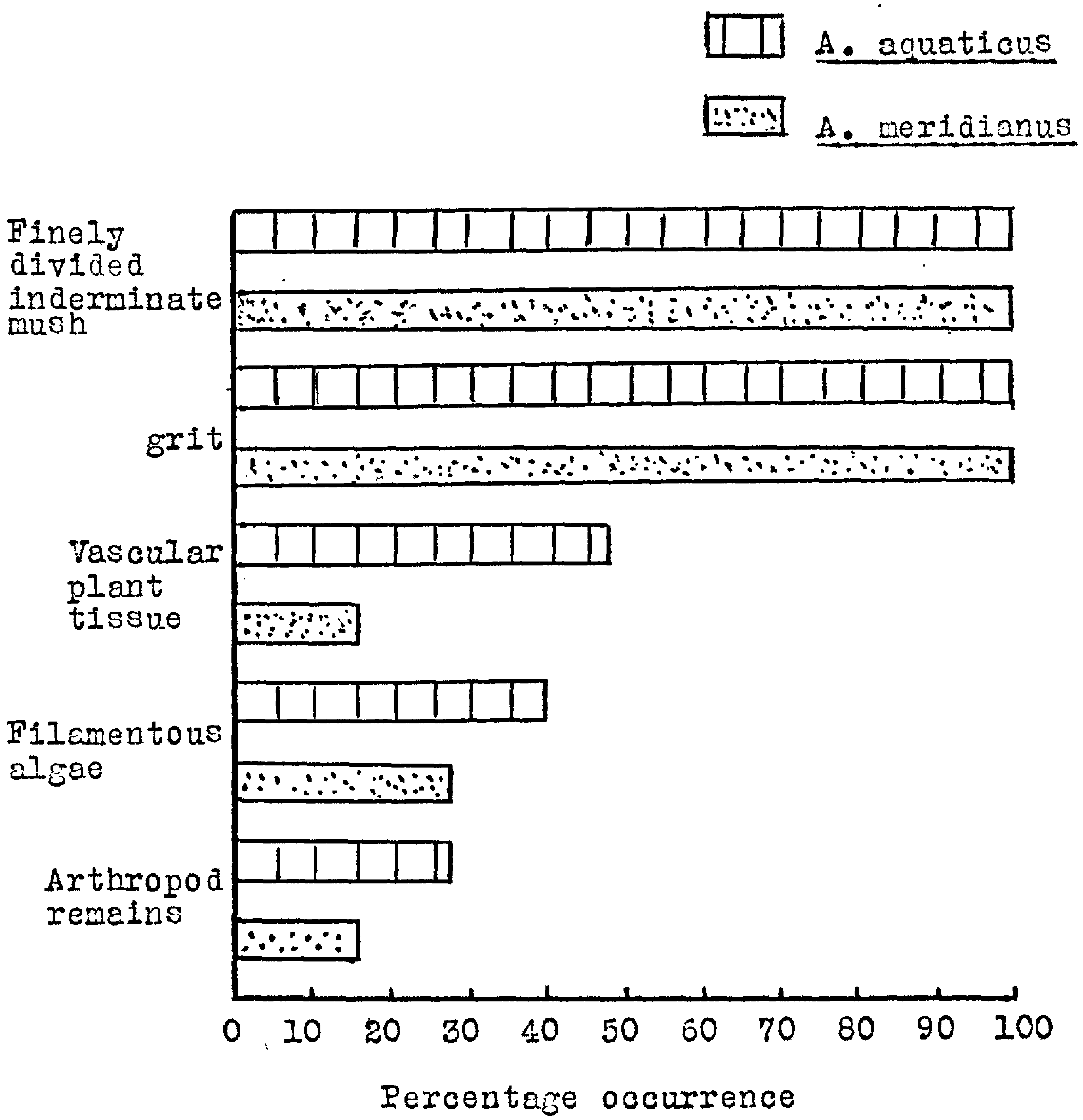

Fig. 26 Diagram comparing the contents of the foregut of A. aquaticus and of A. meridianus.

contents. Several facts support the suggestion that the two species feed on microörganisms; several specimens of both species lived for a period of at least 3 months in large jars which originally contained only water and washed sand; freshly released juveniles of both species did not usually survive when placed with an elm leaf which had not previously been in contact with an adult specimen of Asellus for a short period of time, and which, therefore, had presumably not developed the associated fauna and flora of microörganisms; and finally, Moon (Holland, 1956), referring to specimens of Asellus collected from a water mains system, noted than "any material in the mains which is a substratum for bacteria appears to be readily consumed". But, whether or not microörganisms form the food material, it is certain that both species ingest a wide variety of material; living specimens of Asellus, exuviae, decaying leaves of Elodea and Callitriche, for example, have been recorded during the present research as having been ingested by specimens of both species.

The only reasonable conclusions that can be deduced from the information outlined in the preceding three paragraphs would seem to be that no gross differences in food occur between A. aquaticus and A. meridianus, that both species perhaps feed on microörganisms although both ingest a wide variety of materials, and that A. aquaticus would appear to be slightly more omnivorous.

Most previous authors (e.g. Cooper, 1925; Collinge, 1946d; Weerekoon, 1956) have regarded the food of Asellus as decaying vegetable matter, a conclusion no doubt resulting from the observation that Asellus is most frequently associated with such material. A somewhat different viewpoint would seem to be held by Moon. He, in addition to noting that bacteria appears to form the diet of Asellus in water mains (see p.6.8), noted that in L. Windermere "both species feed on the silt, fine debris and bacteria covering the stones and leaves" (p. 120,1957a).

b) Microhabitat.

Two investigations were undertaken in order to determine whether there are any differences between A. aquaticus and A. meridianus in their preference for various microhabitats. The first of these investigations involved the close observation, over a short period of time, of specimens of both species kept together in an aquarium in which there were several microhabitats. This did not reveal any difference between the species in the extent to which they preferred any particular microhabitat. The second of the investigations involved the collection of small samples from various microhabitats in two localities containing both species. These localities were Llyn Llywenan, Anglesey, and Hatchmere, Cheshire. The samples from Llyn Llywenan were collected on the 30th March 1959; those from Hatchmere were collected on the 19th October 1959. Two additional samples were collected from Llyn Llywenan on the 7th May 1960. The results are shown in the table on p. 6.11. It can be seen from this table that, although there are variations in the ratio of the two species from microhabitat to microhabitat, there would appear to have been no microhabitat which was exclusively dominated by either species. It must be concluded, therefore, that both the observations of the two species in the aquarium and the collection of samples from microhabitats in the field indicate that there are no marked differences in the microhabitats of the two species. This conclusion is also supported by the fact that there was never any subjective indication of a specific difference in microhabitat in any of the several hundred localities from which collections were made during the present research.

The work of Brundin (1949), Dunn(1952) and Moon (1957a) also would appear to indicate that there are no gross specific differences in microhabitat. Brundin collected a number of samples from various microhabitats in Lake Stråken, Sweden, and in all of these except those from the profundal *A. aquaticus* was extremely abundant. Similarly, Dunn (1952) noted that *A. meridianus* at Bala Lake occurred in all types of shore and could be collected throughout the year from under stones,

Microhabitat	Number of collections	No. of specimens in each collections	
		A.aquaticus	A. meridianus.
Llyn Llywenan			
Small stones and gravel beneath large boulders; exposed shore.	4	10	14
		10	0
		31	2
		8	6
Gravel and small stones; no vegetation.	5	21	8
		2	1
		12	5
		14	3
		23	9
Littorella sward on small stones and gravel.	4	22	43
		13	30
		135	116
		200	25[1]
Base of Phalaris stems.	4	19	38
		17	43
		90	56
		230	63[1]
Roots of Typha.	1	18	8
Rotting vegetable debris amongst reed-bed.	1	20	2
Mud.	2	8	4
		12	2
Hatchmere			
Vegetable debris overlying sand; slightly exposed.	1	23	1
Amongst reed-bed.	3	9	3
		30	4
		166	111
Finely divided vegetable debris in sheltered region; no live vegetation.	3	7	1
		35	0
		26	4

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[1] Footnote 1. These samples were collected on the 7th May 1960.

detritus, plants and in mud. Moon (1957a) concluded that there was no physical factor which differentiated the several hundred localities from which he collected either species in L. Windermere.

c) Vertical Distribution.

Detailed observations on the vertical distribution of *A. aquaticus* and *A. meridianus* have not been made during the prsent research; the purpose of the present section is merely to bring together the rather scattered information already in existence concerning this topic, and to place on record the brief observations of the present research.

Information concerning the vertical distribution of *A. aquaticus* has hitherto been presented by Wesenberg-Lund (1917), Berg (1938, 1956), Brundin (1949), Weerekoon (1956) and Moon (1957a); information concerning the vertical distribution of *A. meridianus* has been presented by Humphries (1936), Dunn (1952) and Moon (1957a). Only Moon has considered the vertical distribution of the two species when they occur together.

Wesenberg-Lund (1917) found that in Fure Lake *A. aquaticus* was most abundant at depths of 4-5 metres, Berg(1938,1956) noted that whereas in Esrom Lake *A. aquaticus* extended from 0-17m., exhibiting two maxima, at depths of 2m. and 9m., in Lake Gribsø it was restricted to the first two metres of the lake bottom.

Brundin (1949) found that in Lake Innaren *A. aquaticus* extended from 0-18 m., but that most individuals were confined to depths of 0-3.5 m. He noted a single maximum occurring at about 1.5 m. Weerekoon (1956) noted that in Loch Lomond *A. aquaticus* occurred mainly from 0-4.0 m., the maximum numbers occurring between 0.7 and 2.4 m.

Humphries (1936) noted that in Lake Windermere *A. meridianus* extended down to 3 m.[1] A similar result was recorded from Bala Lake by Dunn (1952); she noted that there, also, *A. meridianus* extended down to only 3 m. Dunn noted in addition that the maximum numbers occurred at 2 m.

Although from a consideration of the literature summarized above it would appear reasonable to conclude that both species are essentially littoral,[2] it is not possible to conclude that there is a clear specific difference in vertical distribution. Moon's work (1957a), however, indicates that when the two species occur together there is a specific difference in vertical distribution. He dealt with the vertical distribution of the two species in Lake Windermere, and concluded that within this lake although either species may dominate the shore above 2 m., *A. meridianus* appears to dominate the region below 2 m. He based

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Footnote 1; She did not record *A. aquaticus* from the lake.

Footnote 2. The term littoral is used here *sensu* Odum (1959); viz., the shallow water region with light penetration to the bottom, and typically occupied by rooted plants.

this conclusion upon the results of a number of dredgings below 2 m., and upon a series of Ekman grabs made in a small sheltered bay, Ash Landing. At Ash Landing he found that *A. aquaticus* was the only species at a depth of 0-0.25 m. and was also most abundant at this depth, but that at depths of about 2 m. *A. meridianus* was the most abundant species. He found that the lower limit for both species in this part of the lake was about 4 m. Moon (1957a) explained the specific difference in vertical distribution as the result of interspecific competition; "the suggestion is made that *meridianus* is more sublittoral than littoral, and unable to compete with *aquaticus* in the littoral region" (p. 123).

Because of the great interest of Moon's findings, an attempt was made in April 1960 to verify them, and for this purpose a series of Ekman grabs were made at Mitchell Wyke, Windermere, and once more at Ash Landing, Windermere. Mitchell Wyke was selected since there Moon had previously recorded both species from the littoral region. The number of specimens of both species in each grab and the depths at which the grabs were made are shown in the tables on p. 6.15. The tables show that at both positions the results differed markedly from the expected; not only would it appear that *A. meridianus* has almost completely disappeared at both positions, but it would appear also that *A. aquaticus* now has the same pattern of vertical distribution as that formerly exhibited by *A. meridianus*, viz. a maximum at about 2 m. Thus, although of great interest in another respect (see p. 7·4), the results, unfortunately, provide no evidence concerning the validity of Moon's conclusion.

A. = *A. aquaticus*
M. = *A. meridianus*

Results of Ekman grabs at Ash Landing, April 1960.

Depth in metres.		0.0	1.5	1.9	2.2	2.9	3.0	4.0
No. of specimens	A.	1	9	10	22	6	10	0
	M	0	0	0	0	0	0	0

Results of Ekman grabs at Mitchell Wyke, April 1960.

Depth in metres.		0.0	1.5	2.0	2.5	3.0	3.5	4.0
Series 1.	A	1	6	8	12	5	7	2
	M	0	0	0	0	0	0	0
Series 2.	A	1	14	17	0	-	0	0
	M	0	1	0	0	-	0	0
Series 3.	A	7	35	-	10	5	1	0
	M	0	2	-	0	0	0	0

d) Tolerances.

For groups of related and sympatric species whose populations inhabit discrete and relatively small localities, it is evident that the ability of each species to tolerate the environmental stresses will be of great significance. This significance, moreover, relates not only to the environmental stresses within each locality, but also to those undergone during the actual dispersion; as both Skellam (1951) and Hutchinson (1951) have pointed out, the superiority in actual competition of one species over another may be completely counterbalanced by the inferiority in ability to disperse (but see p. 1.5).

With regard to *A. aquaticus* and *A. meridianus* in particular, it would seem that the most important environmental stresses are likely to be low oxygen concentrations, high temperatures and dessication: it is felt that a low oxygen concentration is probably a limiting factor in many organically polluted localities, and, in conjunction with high temperatures, in many other localities during the summer; dessication is regarded as an important environmental stress undergone during dispersal.

1. Tolerance to high temperatures.

A few authors have hitherto presented information concerning the ability of various species of *Asellus* to tolerate high temperatures. Birstein (1951) noted that the upper temperature limit for A. aquaticus is about 28°C, and Holland (1956), also referring to this species, stated that it could be maintained in aquaria with temperatures of up to 28°C. Berner (1956), presumably referring to A. banyulensis, noted that temperatures of up to 28°C or even more were tolerated. Extremely detailed observations on the tolerance of A. intermedius to high temper--atures have been presented by Sprague (pers. comm.; 1959). He showed for this species that there was no indication of a persistent seasonal variation in the resistance to high temper--ature, and that acclimatization only slightly increased the upper temperature limit. He recorded 34.6°C as the highest temperature at which, following acclimatization, only 50% mortality occured over a 24 hour period of exposure. Nobody, however, has so far presented information concerning the tolerance of A. meridianus to high temperatures, and, therefore, to provide such information for this species, as well as for A. aquaticus, the following experiment was undertaken during May 1960.

Ten large specimens of both A. aquaticus and A. meridianus were put in each of eleven large jars containing tap-water, a few elm leaves, a heater, a thermostat, a thermometer and an aerator. The water in each jar had been equilibrated to a certain constant temperature before the addition of the Asellus, and this constant temperature was maintained for the duration of the experiment. The specimens added were selected regardless of their sex,[1] and had been acclimatized to laboratory temperatures (18-21°C) for at least one week before the commencement of the experiment. They were allowed to remain in the jars for five days. After this interval the jars were emptied, and the number of survivors of both species was counted. The complete results are indicated in the table on p.619.

It can be seen from the table that under the conditions of the experiment there would appear to be no marked differences in tolerance to temperatures up to 28°C, but that at 30°C A. aquaticus is slightly more tolerant than is A. meridianus. Both species are completely intolerant of a temperature of 32°C. Several criticisms can of course be raised against the extrapolation of these results to natural conditions, but, nevertheless, it seems not unreasonable to regard them as providing an indication of the range of temperatures that can be tolerated for short periods under natural conditions by both species.

2. Tolerance to low concentrations of oxygen.

Data within the papers of several authors indicate that A. aquaticus can exist in waters containing only relatively

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[1] Footnote 1. From a consideration of Sprague's work it seems likely that in Asellus the resistance to high temperatures is the same in both sexes.

A = *A. aquaticus*.

M = *A. meridianus*.

Temperature		24°C	26°C	28°C	30°C	32°C
Series 1.	A	10	6	7	2	0
	M	10	8	10	0	0
Series 2.	A	-	8	6	8	-
	M	-	7	6	3	-
Series 3.	A	-	7	6	5	-
	M	-	6	5	2	-

Table showing the number of survivors (out of 10 specimens of each species) after exposure to various temperatures for five days.

low concentrations of oxygen. Thus, Levanidov (1949; quoted in Birstein, 1951), citing Mudretsovoi, noted that A. aquaticus can survive for 22-48 hrs. without any oxygen at 16-20°C. Levanidov himself found that under natural conditions an oxygen concentration of 0.4 - 0.5 mg/L seems to be the lowest concentration at which A. aquaticus occurs. Berg (1948) collected A. aquaticus from parts of the River Susaa which contained only 2.7cc./L, 2.3cc/L and 2.4cc/L, and noted that these figures were equivalent to, respectively, 44%, 37% and 45% oxygen saturation. He did not, however, find any A. aquaticus in parts where the concentration of oxygen was 0.07 - 1.3cc/L. Holland (1956), measuring the length of survival of A. aquaticus in sealed bottles which had various initial concentrations of oxygen, found that in bottles which originally contained 89%, 23%, and 0.2% oxygen A. aquaticus survived for, respectively, 7 days, 5 days and 24 hrs.

Edwards (pers. comm.; in press) also has presented data which indicate that A. aquaticus can tolerate low concentrations of oxygen, and, moreover, he investigated not only the tolerance of this species, but also the tolerance of A. meridianus. Briefly, he found that both species behave in a similar manner in low concentrations of oxygen, and that the oxygen consumption of both remains at approximately the same level in varying concentrations of oxygen (i.e. both species possess what has been termed a "regulatory" or "independant" type of respiration). Both species, he observed, maintain their independent respiration down to oxygen concentrations of 1.5p.p.m. His findings, there--fore, provide no support for the suggestion that the apparent absence of <u>A. meridianus</u> from organically polluted lotic habitats (see p. 1.15) is the result of its lower tolerance to low concentrations of oxygen, although, as Edwards points out, the effect of oxygen concentration on activity, growth, reproduction, etc. will need to be studied before any reliable ecological generalization concerning the influence of oxygen concentration can be made. At all events, in lentic habitats of fairly low oxygen concentrations there would appear to be no specific difference in distribution. This fact was revealed by a brief investigation of 8 Merseyside localities undertaken during March, 1959. In this investigation, the concentration of oxygen was measured using a modification of Winkler's method (Mackereth, 1957). The results of the investigation are shown below:

Position of locality	Species of Asellus	% saturation of oxygen
273903	A. aquaticus	16.0
233890	A. aquaticus	15.0
242885	A. aquaticus	12.7
313853	A. aquaticus	24.0
260861	A. meridianus	11.9
276854	A. meridianus	13.0
302843	A. meridianus	13.3
307850	A. aquaticus & A. meridianus	13.0

It is of interest at this point to compare Edward's observations with the somewhat parallel observations of Berg. (1953) on *Ancylus fluviatilis* (Müll.) and *Acroloxus lacustris* (L.). These species occupy usually distinct habitats, and these habitats differ markedly in their oxygen concentrations; *A. fluviatilis* occupies well aerated streams, and *A. lacustris* stagnant waters. It had been suggested (see Berg, 1953) that this ecological distribution was the result of a difference in specific tolerances to low concentrations of oxygen. Berg, however, showed that both species are extremely similar in their oxygen requirements, and, therefore, such an explanation cannot be unreservedly accepted; as in the case of *A. aquaticus* and *A. meridianus* it appears that factors other than a simple difference in tolerance to low concentrations of oxygen are responsible for the ecological distribution.

3. Tolerance to dessication.

Since the dispersal of *A. aquaticus* and *A. meridianus* from one locality to another will normally involve the removal of specimens from water for varying periods of time, it is evident that any marked specific difference in the extent to which dessication is tolerated will have a significant affect upon the specific dispersal ability. In order to determine, therefore, whether there is any such specific difference in tolerance, the following experiment was carried out during September 1960.

Into each of 280 small plastic dishes was placed a filter paper which completely covered the bottom of the dish. The dishes were then divided into groups of ten, and into each dish of the first 14 groups was placed a large unsexed specimen of *A. aquaticus*, and, similarly, into each dish of the second 14 groups a large unsexed specimen of *A. meridianus*. These specimens had been acclimatized to laboratory temperatures (18-21°C) for at least one week before the commencement of the experiment. They were added to the dishes using a bulb pipette and the minimum amount of water, and the exact time at which each specimen was added was noted. The small amount of water used in the transference of the specimens was soon absorbed by the filter paper in each dish, and very quickly evaporated leaving dry the filter paper and the specimen of *Asellus*. After a certain interval of time each group of ten dishes was filled with water, and the number of specimens which then recovered noted. The interval of time for which each group of dishes was left dry, and the number of specimens which did not recover are indicated in the table on p.624.

It can be seen from the table that, although there would appear to be some specific differences in tolerance, these are not so marked as to suggest that there is a gross specific difference in the ability to survive dessication.

A = *A. aquaticus*

M = *A. meridianus*

Number of hours each group of dishes remained dry.		1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8
Number of dead specimens in each group of 10 dishes.	A	0	0	0	0	1	0	1	0	2	2	6	9	9	10
	M	1	1	0	1	2	1	2	5	4	7	9	7	7	8

Table showing the number of dead specimens (out of 10) of both species after being out of water for various periods of time.

e) Investigations of localities containing both, one, or no species of Asellus.

A number of investigations were undertaken in order to determine whether there are any differences between localities which contain both *A. aquaticus* and *A. meridianus*, only *A. aquaticus*, only *A. meridianus*, or neither species. These investigations dealt with the differences in the main physical characteristics, the associated flora and fauna, and the concentrations of certain chemical solutes.

1. Main physical characteristics.

Throughout the present research notes were made of the size, substratum, estimated depth and the rate of water flow (if any) at all of the several hundred localities from which collections were made. The vast majority of these localities comprized ponds, lakes or localities where the water was only slowly flowing. The only conclusion that can be reached from a study of the notes is that there would never appear to be any correlation between the main physical characteristics of a locality and the absence or presence of each species of *Asellus*; both species occur indiscriminately in localities ranging from small ponds with a substratum of thick mud to large lakes with a substratum of stones and boulders

This conclusion is supported by a consideration of the papers of Dunn (1952), Weerekoon (1956), Moon (1957b) and Tucker (1958). Thus, whereas Dunn (1952) recorded *A. meridianus from the large* oligotrophic lake, Llyn Tegid, Weerekoon (1956) recorded *A. aquaticus* from the physically similar lake, Loch Lomond. Moon (1957b), after an investigation of 102 localities in the Lake District, concluded that "the occurrences of *A. aquaticus* and *A. meridianus* are sparse, and show no apparent correlation with any known physical or chemical factor of the environment" (p. 408). Tucker (1958) studied the physical characteristics of 16 ponds, 6 of which contained *A. meridianus*, 2 *A. aquaticus*, and 8 no *Asellus*. There is no correlation between any of the physical characteristics noted by Tucker and his recorded distribution of *Asellus*.

2. Associated flora and fauna.

Differences in the associated flora and fauna were investigated by a study of 20 localities on Merseyside. The position of and the species of *Asellus* at each of these localities are indicated below:

Localities containing only *A. aquaticus*.

109/279650 (Buckley Lake)
109/455859
109/325814
109/233890
109/330810

Localities containing only A. meridianus.

109/278620 (Padeswood Lake)
109/322814
109/258860
109/260861
109/320830
109/325804
109/460843
109/321804

Localities containing both A. aquaticus and A. meridianus.

109/553722 (Hatchmere)
109/418889
109/462853
109/320793

Localities containing neither species of Asellus.

109/1575675 (Oakmere)
109/322814
109/250877

All of these localities are lentic and most of those without names are small eutrophic ponds. At each locality the absence or presence of Asellus, and the species of Asellus were determined from numerous samples collected at various points on the periphery. In most cases these samples were collected on more than one occas--sion.

Only brief notes of the associated flora were made, and these referred to only the more common macrophytic species. The following species were noted in some localities containing both species of _Asellus_, in some localities containing only _A. aquaticus_, and in some localities containing only _A. meridianus_.

Lemna minor
L. trisulca
Carex sp.
Juncus spp.
Sparganium sp.
Glyceria sp.
Iris sp.
Typha latifolia
Phragmites communis
Callitriche spp.
Potamogeton spp.
Elodea canadensis
Equisetum sp.
Nymphaea sp.

The following species were recorded from localities containing no _Asellus_:

Lemnor minor
L. trisulca
Carex sp.
Juncus sp.
Littorella uniflora

Only one species, _Myriophyllum_ sp., was found restricted to localities containing only _A. aquaticus_; and only one species, _Phalaris arundinacea_, was found restricted to localities containing only _A. meridianus_. _Littorella uniflora_ was recorded from two localities, one of which contained both species of _Asellus_, and the other no _Asellus_. No species were found restricted to localities containing both species of _Asellus_, or to localities containing no *Asellus*.

Both *Myriophyllum* sp. and *Phalaris arundinacea* are present at Llyn Llywenan, and it is thus evident that these species cannot be considered as differentiating localities, containing, respectively, only *A. aquaticus*, and only *A. meridianus*. Similarly, *Littorella uniflora* is present elsewhere in Britain in localities containing only *A. aquaticus* or only *A. meridianus* (e.g. in Bassenthwaite which contains only *A. meridianus* and in Loch Lomond which contains only *A. aquaticus*). It would appear, therefore, that as far as the more common macrophytes are concerned there are no constant specific differences between localities containing both species of *Asellus*, or only one or other of the species. It would appear, however, that fewer species of macrophytes are present in localities which contain no *Asellus*.

On pages 6.41 , 6.42 and 6.43 are presented lists of the associated macroscopic fauna recorded from the 20 localities investigated. The species have been grouped into four lists, each list showing the species recorded from some of the localities containing, respectively, only *A. aquaticus*, only *A. meridianus*, both species of *Asellus*, and no *Asellus*. The lists were compiled from a single series of samples collected on the 27th July, 1960.

By extrapolation from these lists it can be seen that, although no species were restricted to localities in which *Asellus* was absent, a number of species were found restricted to localities containing only *A. aquaticus*, to localities containing only *A. meridianus*, or to localities containing both species of *Asellus*. For convenience, these species are indicated in the table below:

Species restricted to localities containing:

only *A. aquaticus*	only *A. meridianus*	both *A. aquaticus* and *A. meridianus*
Dendrocoelum lacteum	*Physa fontinalis*	*Planorbis carinatus*
Haemopis sanguisuga	*Planorbis laevis*	*Corixa moesta*
* *Anodonta cygnaea*	*Eurycercus lamellatus*	Tanypodinae
Theromyzon tessulatum	*Nemurella picteti*	*Noterus* sp.
Planorbis complanatus	*Corixa praeusta*	*Gyrinus* sp.
Corixa fossarum	*C. sahlbergi*	*Dytiscus* sp.
* *Ilyocoris cimicoides*	Sericostomatidae	*Cyprinus* sp.
Leptoceridae	Orthocladiinae	
* Tabanidae	* Helodidae	
Hydroporus sp.	* *Hygrobia hermanni*	
Hyphydrus ovatus		

Most of the above species, however, cannot be regarded as peculiar to only those localities containing the species of

Asellus indicated, for an examination of the literature and other records reveals that most can occur with both species of Asellus. The papers of Humphries (1936), Pyefinch (1937), Macan (1949), Dunn (1952), Macan & Lund (1954), Weerekoon (1956), Hynes (1957) and Tucker (1958) have been most useful in this connection. The exceptions are marked in the table by an asterisk; for these species I have been unable to obtain from the literature or other sources any records of an association with Asellus. It can be seen that the exceptions comprize five species, three peculiar to localities containing only A. aquaticus and two peculiar to localities containing only A. meridianus. But, it is difficult to see how these species are correlated with the absence or presence of the relevant species of Asellus, for all were scarce and each occurred in only one pond. It seems probable, in fact, that there is no correlation, the association being merely the result of chance. The conclusion follows, therefore, that as far as the macroscopic species of associated fauna are concerned there would appear to be no consistent differences between localities containing both species of Asellus, or only one or other of the species. Some correlation, nevertheless, would seem to exist between the number of associated species and the absence or presence of Asellus; it appears that localities containing Asellus differ from those in which it is absent in that they contain a wider variety of associated animals.

Using the papers indicated in the preceding paragraph, and a few others, it is possible to prepare extremely long lists of the associated fauna and flora recorded from localities containing both species of Asellus, only one or other of the species, or no Asellus. Most of the associated species are common to all of the four sorts of locality, although a few are apparently more restricted. However, as before, it is difficult to see how the restrictions are correlated with the absence or presence of Asellus, and it seems probable, in fact, that there is no causal correlation. The study of the literature indicates also that the number of associated species of animals and plants in localities containing no Asellus (and which would appear suitable) is only slightly less than in the localities containing Asellus; in Malham tarn, for example, which contains no Asellus, there is an extremely rich and abundant flora and fauna (see Holmes, 1956).

Thus, from a consideration of both the investigation of the 20 Merseyside localities and the literature, it seems not unreasonable to conclude that there are no marked differences in the associated flora and fauna between localities containing both species of Asellus or only one or other of the species, and that localities containing no Asellus are perhaps distinguished by the smaller numbers of associated species present.

3. Concentrations of certain solutes.

During the investigations of the chemical differences between various localities, water samples were subjected to analysis for eight major solutes. Seven of these were inorganic, and comprized bicarbonate, sulphate, chloride, magnesium, calcium, sodium and potassium ions; the eighth was dissolved organic matter. All water samples were collected in 1500 ml. polythene bottles, and were obtained by wading out as far as possible and drawing water into the bottle from about one foot beneath the surface. Each sample was analysed as soon as possible after collection; in most cases the analyses were made the day after collection. Before analysis all samples were filtered. The concentrations of the solutes were obtained as follows:

Bicarbonate ; by titration against a standard solution of Hydrochloric acid (Mackereth, 1957); and also by subtraction of the sum of the ionic concentrations of sulphate and chloride from the total ionic concentration.

Sulphate & Chloride ; by ion-exchange prodcedures as described by Mackereth (1955, 1955a), but employing a somewhat modified apparatus and technique. The ionic concentrations in the final effluents from the resin columns were estimated using a conductivity meter and a prepared calibration chart. No corrections were made for the variations in the temperature.

Magnesium & Calcium ; by titration with standard sodium versenate solution (Heron & Mackereth, 1955).

Sodium & Potassium ; by flame photometer (Mackereth, 1957).

Dissolved organic matter ; by reduction using potassium permanganate. The results are expressed as the amount of oxygen obsorbed in mg/L. under the experimental conditions described by Mackereth (1957,p.28).

Using the analytical methods indicated above, the chemical composition of water samples from 19 localities on Merseyside was determined. Six of these localities contained only A. aquaticus, 8 only A. meridianus, 1 both species, and 4 no Asellus. The water samples were collected during March 1959. The results of the analyses, and the position of each locality and the species of Asellus contained (if any) are shown in the table on p.6.44.

Further information concerning the chemical differences between localities containing both, only one, or no species of Asellus, and involving all seven of the principal inorganic ions, has been obtained from two major sources; information has been obtained by determining the species of, or the absence of Asellus, in a number of Shropshire and Cheshire meres for which full chemical analyses were already available (Gorham 1957, 1957a); and information has been obtained by combining the results of

Moon's investigations of the distribution of *Asellus* in the Lake District with the results of full chemical analyses of the localities visited by him. These analyses were provided by the Mr. J.F.H. Mackereth (pers. comm.). Minor sources of information include the analyses of water samples from Bala Lake (Ball 1957), Llyn Idwal and Llywenan, and Buckley and Padeswood Lakes. All the further infromation is collected together and shown in the table on pages 6.45, 6.46. The species of *Asellus* or their absence at each locality is also shown in the tables.

It is apparent from an examination of these tables that there are no consistent differences between localities which contain both species of *Asellus*, or only one or other of the species. Thus, neither the range of concentration of any one solute, nor the ratios of the concentrations of various ions to each other, serve to distinguish localities containing only *A. aquaticus*, only *A. meridienns*, or both species. But, there would appear to be some distinction in ionic composition between localities containing *Asellus* and those in which it is absent. This distinction is most obvious when the concentrations of calcium and total ions are considered. Thus, referring to the scatter diagrams (pages 6.49 and 6.50), which show for two separate areas the relationship between the occurrence of *Asellus* and the concentrations of calcium and total ions, it can be seen that all localities containing no *Asellus* are characterized by their restriction to those parts of the scatter diagrams indicating low concentations of calcium and total ions.

This phenomenon is plainly in support of the hypothesis recently advanced by Reynoldson (pers. comm.; in press) that the occurrence of <u>Asellus</u> is correlated with the concentrations of calcium and total dissolved matter (hereafter T.D.M.).

Reynoldson based his hypothesis upon an investigation of 65 localities located in areas in mid-Scotland, the Lake District, Northern Ireland, Anglesey and North Wales. Briefly, he suggested that in localities containing more than 0.625 meq./L. of calcium and 110 mg/L. of T.D.M. <u>Asellus</u> was usually present; that in localities containing 0.35 - 0.65 meq./L. of calcium and 70 - 110 mg/L. of T.D.M. <u>Asellus</u> was either present or absent; and that in localities containing less than 0.25 meq./L. of calcium and 70 mg/L. of T.D.M. <u>Asellus</u> was usually absent. A summary of his data is produced below:

Concentration of calcium:

No. of localities <u>Asellus</u> present	 <u>Asellus</u> absent	Concentration of calcium
26	4	>0.625 meq./L.
5	6	0.35-0.625 meq./L.
2	22	<0. 25 meq./L.

Concentration of T.D.M.

No. of localities		
Asellus present	*Asellus* absent	Concentration of T.D.M.
26	4	>110 mg/L.
5	6	70-110 mg/L.
0	20	<70 mg/L.

Reynoldson subjected his data to statistical tests of significance; he found that both sets of data were highly significant, i.e. there was a distinct correlation between the concentrations of both calcium and T.D.M. and the absence or presence of *Asellus*. In addition, he noted that his hypothesis was also supported by a statistical analysis of the data of Moon (1957b) referring to the Lake district, the data of Macan and Lund (1954) referring to a number of Irish Lakes, and the data of Tucker (1958) referring to a number of ponds in southern England.

No support for Reynoldson's hypothesis, however, is given by the results of an investigation of the concentration of calcium in 67 localities in areas of Scotland outside that previously considered by Reynoldson. But these results are not regarded as invalidating Reynoldson's conclusions; it is suggested that the incomplete dispersal of *Asellus* in Scotland (see p.3.32) coupled with the remote position of many of the localities investigated is responsible for the fact that Asellus is absent from many localities containing more than 0.625 meq./L. of calcium[1], whilst, on the other hand, special circumstances explain the presence of Asellus in localities containing less than 0.25 meq./L. of calcium.

The information concerning the calcium concentration and the occurrence of Asellus in 37 of the localities was obtained during May, 1959, and is shown in tabular form on p.6.47,48; the similar information for the remaining 30 localities has been provided by Reynoldson (pers. comm.), and is summarized below:

No. of localities		
Asellus present	Asellus absent	Concentration of calcium
5	14	< 0.25 meq./L.
1	10	> 0.25 meq./L.

It can be seen from the above table and the table on p.6.48 that Asellus was found in 5 localities containing less than 0.25 meq./L. of calcium. It is suggested, however, that these occurrences do not provide valid exceptions to Reynoldson's hypothesis, for four of the localities were large, a characteristic which is generally regarded (see, for example, Macan, 1950) as compensating for low calcium concentrations, whilst the remaining

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Footnote 1. Reynoldson himself invoked this explanation to explain the absence of Asellus from 11 localities on Islay containing more than 0.626 meq./L. of calcium (chemical data in Reynoldson, 1958).

one was unusual in that it contained a high concentration of magnesium (0.51 meq./L.).

If the suggested explanations concerning the occurrences of *Asellus* are accepted, it seems not unreasonable to conclude that for areas which have been subject to colonization by *Asellus* for some time there is, in fact, a correlation between the occurrence of *Asellus* and the concentration of calcium. But even in these areas there would seem to be a number of factors which have a modifying affect upon the correlation. Such factors probably include altitude, the size of the locality, the amount of vegetable debris present, etc. Thus, Jarhnfelt (Reynoldson, in press, in discuss.), for example, noted that in Finland *A. aquaticus* is abundant, and yet the concentration of calcium in Finnish localities seldom reaches 0.25 meq./L. Similarly, Tucker noted that the thresh-hold for calcium was higher for *Asellus* when decomposing vegetable matter was abundant.

It is perhaps of interest at this point to note that Borutskii (1929: quoted by Birstein, 1951) published a quantitative class--ification of habitats which related the abundace of *A. aquaticus* to the productivity of the locality. He stated that *A. aquaticus* was most abundant in habitats which were "oligotrophic with features of eutrophy", and least abundant in habitats which were dystrophic. However, as Birstein (1951) pointed out, the applicability of the classification is limited; in Karelia, for instance, *A. aqaticus* is most abundant in dystrophic lakes.

Associated fauna

From localities containing only *A. aquaticus* :

Dendrocoelum lacteum (Müll.)
Polycelis sp.
Stylaria lacustris
Tubificidae
other oligochaetes
Haemopis sanguisuga
Glossosiphonia complanata
Helobdella stagnalis (L.)
Erpobdella sp.
Theromyzon tessulatum
Limnaea pereger
L. stagnalis L.
Planorbis vortex L.
P. albus
P. complanatus
Hydrobia jenkinsi
Bithynia tentaculata
Pisidium sp.
Sphaerium sp.
Anodonta cygnaea L.
Simocephalus vetulus (Müll.)
Copepoda
Ostracoda
Gammarus pulex
G. lacustris
Hydracarina
Caenis sp.
Chloeon sp.
Ischnura elegans
Corixa dorsalis
C. falleni
C. fossarum
C. punctata
C. linnei (Fieb.)
Notonecta glauca
Nepa cinerea
Ilyocoris cimicoides (L.)
Gerris spp.
Limnophilidae
Polycentropidae
Phryganeidae
Leptoceridae
Sialis lutaria
Eristalis sp.
Chironominae
Anopheles sp.
Tabanidae
Tipulidae
Ptychoptera sp.
Haliplus sp.
Hydroporus sp.
Ilybius sp.
Hyphydrus ovatus L.
Gasterosteus sp.

Associated fauna :

From localities containing only *A. meridianus* :

Polycelis sp.
Stylaria lacustris
Tubificidae
other oligochaetes
Glossosiphonia complanata
Helobdella stagnalis
Erpobdella sp.
Planorbis albus
P. laevis Alder
Limnaea pereger
Physa fontinalis
Hydrobia jenkinsi
Pisidium sp.
Sphaerium sp.
Eurycercus lamellatus (Müll.)
Copepoda
Ostracoda
Gammarus pulex
Hydracarina
Argyroneta aquatica
Caenis sp.
Chloeon sp.
Nemurella picteti
Ischnura elegans
Nepa cinerea
Corixa praeusta
C. falleni
C. sahlbergi (Fieb.)
Notonecta glauca
Gerris spp.
Limnophilidae
Polycentropidae
Sericostomatidae
Phryganeidae
Sialis lutaria
Orthocladiinae
Chironominae
Anopheles sp.
Corethra sp.
Ptychoptera sp.
Haliplus sp.
Helodidae
Laccophilus sp.
Hygrobia hermanni F.
Ilybius sp.
Nymphula sp.
Gasterosteus aculeatus

Associated fauna

From localities containing both *A. aquaticus* and *A. meridianus* :

Polycelis sp.
oligochaetes
Erpobdella sp.
Glossosiphonia complanata
Helobdella stagnalis
Limnaea pereger
L. stagnalis
Planorbis vortex
P. carinatus
Bithynia tentaculata
Pisidium sp.
Sphaerium sp.
Simocephalus vetulus
Copepoda
Ostracoda
Gammarus pulex
G. lacustris
Hydracarina
Argyroneta aquatica
Chloeon sp.
Leptophlebia sp.
Nepa cinerea
Notonecta glauca
Corixa linnei
C. dorsalis
C. falleni
C. punctata
C. moesta
Gerris sp.
Limnophilidae
Phryganeidae
Polycentropidae
Molanna sp.
Sialis lutaria
Chironominae
Tanypodinae
Anopheles sp.
Eristalis sp.
Tipulidae
Laccophilus sp.
Gyrinus sp.
Noterus sp.
Nymphula sp.
Cyprinus sp.
Gasterosteus aculeatus

From localities with no *Asellus* :

oligochaetes
Theromyzon tessulatum
Erpobdella sp.
Limnaea pereger
Sphaerium sp.
Copepoda
Hydracarina
Argyroneta aquatica
Leptophlebia sp.
Nemurella picteti
Corixa praeusta
Molanna sp.
Sialis lutaria
Chironominae
Eristalis sp.

A = <u>A. aquaticus</u>
M = <u>A. meridianus</u>

Posn. of locality	Sp. of Asellus	Total salts	HCO_3	SO_4	Cl	Mg	Ca	Na	K	Dissolved org. matter
273993	A	5.97	3.72	0.48	1.77	0.12	3.86	2.00	0.16	17.0
233890	A	4.55	2.70	0.35	1.50	0.99	1.98	1.36	0.12	13.3
242885	A	2.76	1.93	0.22	0.61	0.44	1.48	0.51	0.30	9.0
313853	A	6.70	3.00	2.90	0.80	0.90	5.15	0.60	0.06	16.7
325814	A	1.76	0.74	0.65	0.37	0.16	1.14	0.24	0.10	18.7
330810	A	5.45	3.00	1.62	0.83	0.80	4.20	0.10	0.27	14.0
260861	M	6.84	3.59	1.16	2.09	1.50	3.33	1.92	1.16	18.4
276854	M	2.88	0.64	1.02	1.22	0.73	0.85	1.24	0.09	21.7
302843	M	2.32	1.64	0.35	0.33	0.36	1.59	0.50	0.10	16.3
320830	M	3.68	2.38	0.80	0.50	0.80	3.35	0.18	0.11	8.8
325804	M	2.27	0.77	0.62	0.88	0.84	1.20	0.17	0.08	15.2
321804	M	1.91	0.51	0.49	0.91	0.17	1.07	0.14	0.13	18.0
396873	M	3.43	1.53	0.77	1.13	0.33	2.64	0.41	0.09	16.8
322814^{1}	M	2.75	0.50	0.95	1.30	0.22	2.35	0.15	0.05	26.4
307850	A & M	5.46	2.06	1.25	2.15	1.32	2.52	1.80	0.28	26.0
250877	0	1.88	0.98	0.60	0.30	0.39	1.25	0.18	0.01	11.8
242859	0	1.85	0.00	0.88	0.97	0.50	0.66	0.78	0.06	0.0
248858	0	1.54	0.34	0.70	0.50	0.43	0.57	0.50	0.04	11.4
322814^{2}	0	1.44	0.44	0.60	0.40	0.24	0.48	0.39	0.20	14.0

<u>Table showing the species of Asellus in and the ionic composition of 19 localities on Merseyside</u>.

<u>Note</u>: All concentrations are in milliequivalents/litre except for those of the dissolved organic matter.

A = <u>A. aquaticus</u>
M = <u>A. meridianus</u>

Name of locality	Sp. of Asellus	Total salts	HCO_3	SO_4	Cl	Mg	Ca	Na	K	Dissolved org. matter
Budworth pool	A	3.61	1.59	1.20	0.68	1.04	1.94	0.53	0.10	-
Budworth mere	A	6.99	3.10	2.51	1.30	1.88	3.65	1.30	0.16	-
Pickmere	A	6.01	2.93	2.09	0.96	1.66	3.35	0.89	0.12	-
Newton mere	A	1.06	0.30	0.30	0.42	0.11	0.37	0.37	0.20	-
Whitemere	A	2.13	1.12	0.59	0.44	0.12	1.50	0.36	0.13	-
Rostherne mere	A	4.28	2.00	1.50	0.68	0.98	2.60	0.62	0.11	-
Hatchmere	A & M	3.22	1.65	0.94	0.62	0.97	1.67	0.48	0.10	-
Oakmere	0	1.05	0.00	0.54	0.50	0.21	0.38	0.39	0.06	-
Buckley Lake	A	10.60	5.88	2.54	2.16	5.43	2.11	2.17	0.74	-
Padeswood Lake	M	8.54	5.22	2.23	0.98	1.20	5.75	1.22	0.24	-
Llyn Idwal	0	0.30	0.07	0.07	0.16	0.05	0.10	0.10	0.01	0.0
Bala Lake	M	0.35	0.08	0.10	0.18	0.04	0.13	0.16	0.02	-
Llyn Llywenan	A & M	1.55	-	-	-	0.28	0.60	0.61	0.06	-

<u>Table showing the species of Asellus in and the ionic composition of various localities in Cheshire and North Wales.</u>

<u>Note</u>: All concentrations are in milliequivalents/litre.

A = <u>A. aquaticus</u>
M = <u>A. meridianus</u>

Name of locality	Sp. of Asellus	Total salts	HCO_3	SO_4	Cl	Mg	Ca	Na	K
Crook Resv.	M	0.98	0.62	0.19	0.17	0.18	0.61	0.17	0.01
Green Haws	A	0.73	0.13	0.29	0.31	0.10	0.33	0.26	0.02
Lilymere	A	0.55	0.14	0.19	0.21	0.09	0.26	0.18	0.01
Middlerigg	A	0.92	0.39	0.26	0.26	0.16	0.53	0.19	0.01
Rose Castle	A & M	0.85	0.32	0.21	0.32	0.17	0.49	0.19	0.01
Scale	A	0.50	0.13	0.19	0.18	0.07	0.25	0.19	0.01
Tarn Hows	A & M	0.57	0.21	0.11	0.25	0.10	0.27	0.17	0.01
Whimfell	A	3.08	2.68	0.18	0.22	0.91	1.90	0.22	0.05
Wynandermere	A	1.03	0.51	0.25	0.27	0.14	0.63	0.20	0.03
Bassenthwaite	M	0.56	0.16	0.15	0.25	0.10	0.25	0.21	0.01
Bros. water	O	0.47	0.16	0.16	0.15	0.07	0.27	0.14	0.01
Buttermere	O	0.32	0.05	0.08	0.19	0.06	0.10	0.14	0.01
Conistan	O	0.56	0.16	0.19	0.21	0.08	0.30	0.19	0.01
Crummock	O	0.34	0.04	0.10	0.20	0.06	0.10	0.16	0.01
Derwentwater	O	0.50	0.10	0.10	0.30	0.05	0.23	0.21	0.01
Ennerdale	O	0.35	0.06	0.09	0.20	0.07	0.12	0.16	0.01
Esthwaite	A	0.73	0.31	0.21	0.21	0.12	0.41	0.20	0.02
Grasmere	A	0.45	0.12	0.15	0.18	0.05	0.25	0.15	0.01
Haweswater	O	0.43	0.16	0.12	0.15	0.06	0.24	0.13	0.01
Loweswater	O	0.55	0.15	0.16	0.24	0.10	0.23	0.22	0.01
Rydal	A	0.50	0.16	0.15	0.19	0.06	0.27	0.16	0.01
Ullswater	O	0.52	0.21	0.14	0.17	0.08	0.29	0.14	0.01
Wastwater	O	0.32	0.05	0.10	0.17	0.06	0.10	0.15	0.01
Windermere	A & M	0.53	0.18	0.17	0.18	0.06	0.30	0.16	0.01
Brathay	M	2.40	1.27	0.95	0.18	0.51	1.83	0.17	0.02
Cleabarrow	A	1.25	0.60	0.37	0.28	0.20	0.70	0.27	0.04

<u>Table showing the species of Asellus in and the ionic composition of various localities in the Lake District.</u>

<u>Note:</u> All concentrations are in milliequivalents/litre.

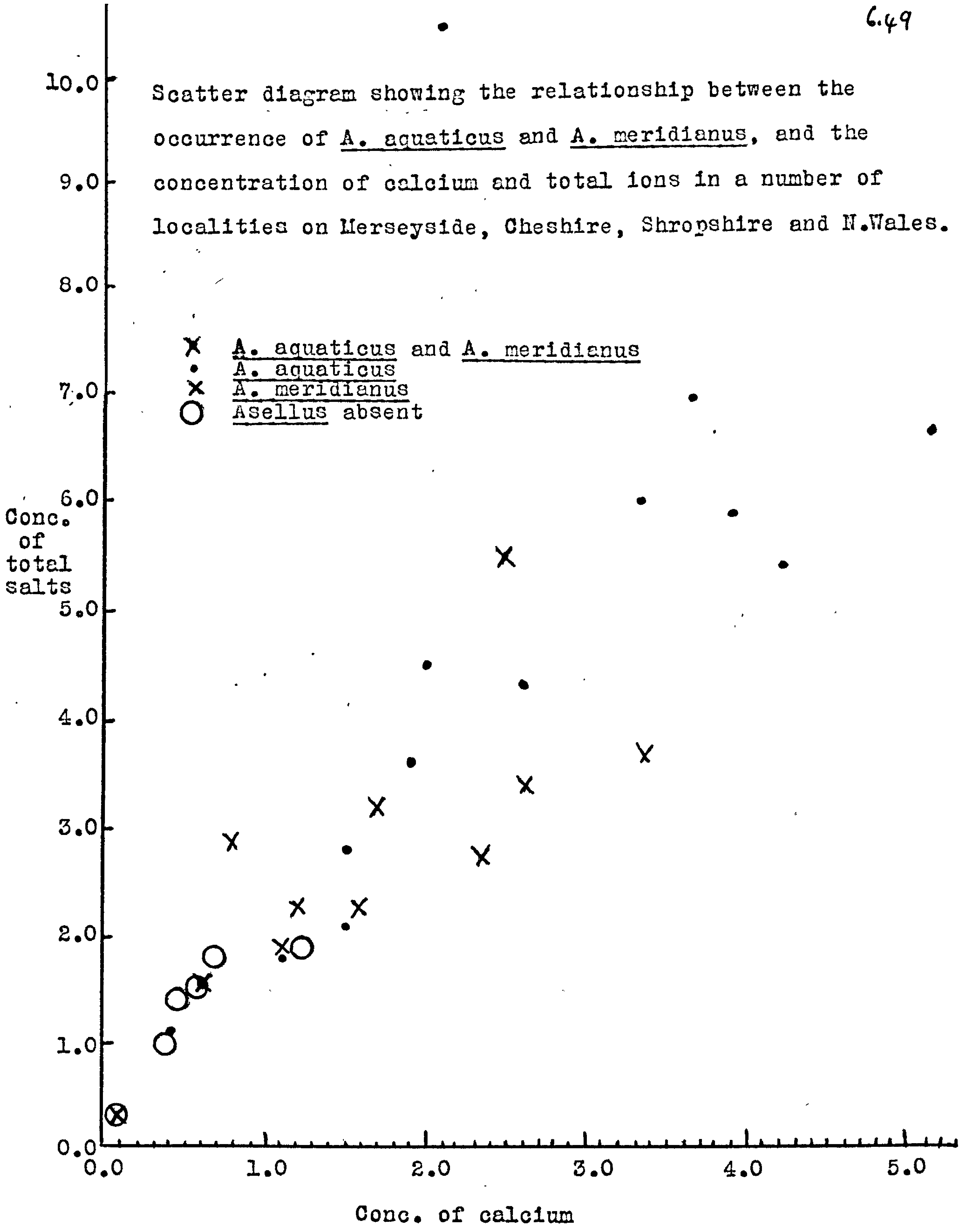
Table showing the relationship between the occurrence of Asellus and the concentration of calcium for a number of Scottish localities. (Data collected during May, 1959).

A = A. aquaticus
M = A. meridianus

Locality	sp. of Asellus	Conc. of Ca (meq./L.)
Garnkirk Sta.	A	6.24
Gartman Dam	0	3.31
Gordonstoun pond	M	3.13
Hirsel Loch	M	2.85
Carlingswark Loch	M	2.34
Yetholm Loch	0	2.26
Williestruther Loch	0	2.25
Woodend Loch	A	2.10
Sheriffside Loch	0	2.06
Pond nr. Witton L.	0	2.05
Cuilc Brae	A	2.00
Auchenreoch Loch	0	1.90
Black Loch	0	1.70
Loch Lindores	0	1.42
Loch Na Bo	0	1.35
Witton Loch	0	1.20
Horslaw Loch	0	1.17
Loriston Loch	M	1.10

Table continued......

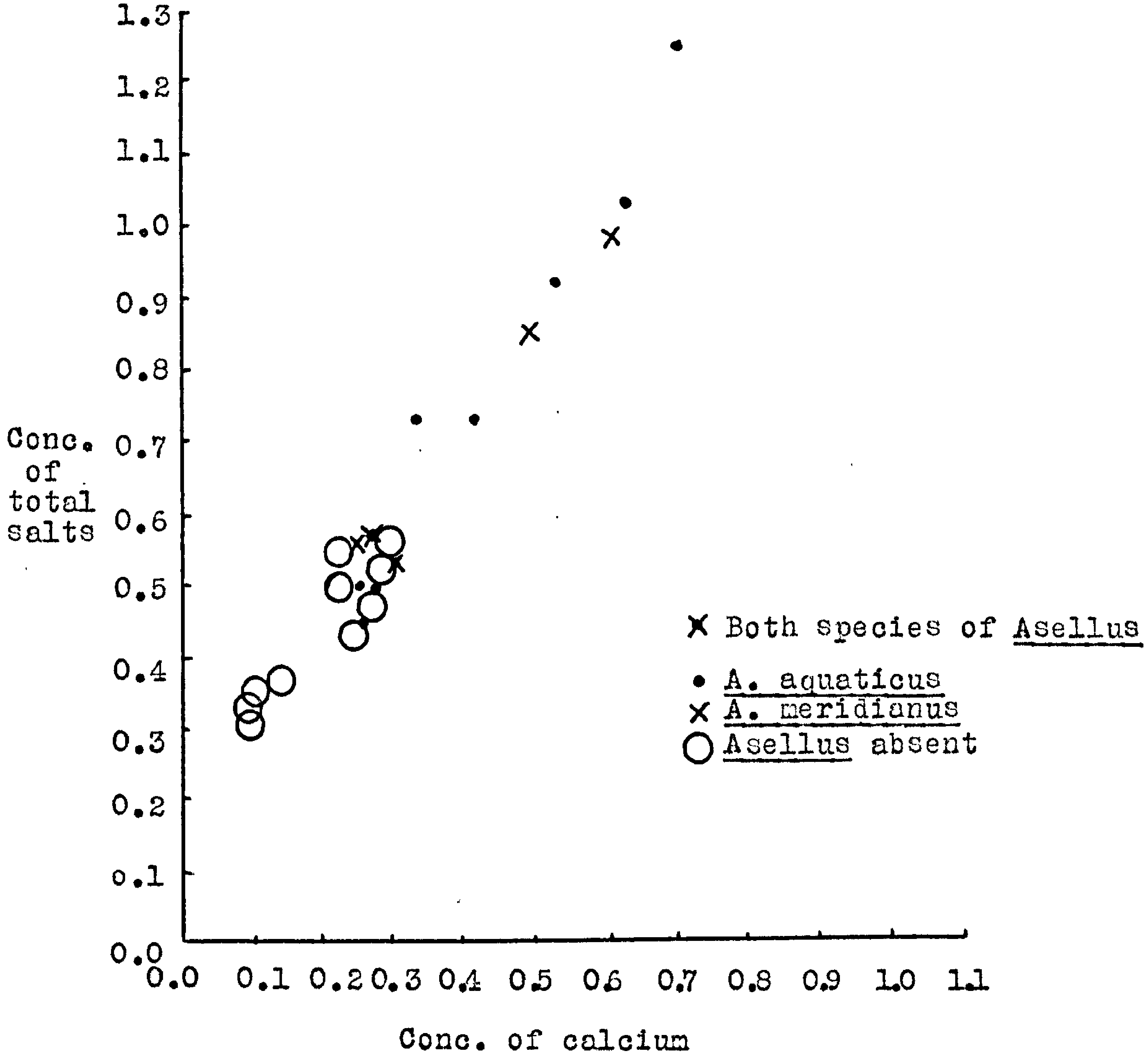
Locality	sp. of *Asellus*	Conc. of Ca (meq./L.)
Pond nr. Douglas	O	1.05
River Tweed nr. Peebles	A	1.01
Kirk Loch	O	0.99
Castle Loch	O	0.95
Pond nr. Dalry	M	0.63
Pond nr. Innerleithen	A	0.59
Pond nr. Peebles	M	0.52
Stare Dam	A	0.50
St. Mary's Loch	M	0.49
Loch na Ba Ruidhe	O	0.46
Loch of Lowes	O	0.43
Loch Bog	O	0.43
River Falloch	A	0.27
Loch Ness	A	0.18
Loch Ken	M	0.15
Loch Lomond	A	0.14
Loch Oich	A	0.12
Loch Achtriochatan	O	0.10
L'Na Achlaise	O	0.08
Loch Muck	O	0.07



Scatter diagram showing the relationship between the occurrence of *A. aquaticus* and *A. meridianus*, and the concentration of calcium and total ions in a number of localities on Merseyside, Cheshire, Shropshire and N.Wales.

(all concs. in meq/L.)

Scatter diagram showing the relationship between the Occurrence of A. aquaticus and A. meridianus, and the concentration of calcium and total ions in a number of localities in the Lake District.



(all conc. in meq/L.)

INTERSPECIFIC COMPETITION

It has already been seen that a study of the geographical distribution of A. aquaticus and A. meridianus suggests that these species are in competition (chapter III). However, as previously noted (p.3.36), such geographical evidence is only indirect, and further evidence is necessary before interspecific competition can be regarded with certainty as an actual and extant process. A number of investigations, therefore, were undertaken in an attempt to provide this further information, and these comprized both field and laboratory investigations.

1. Field investigations.

(a). The distribution of Asellus on Merseyside.

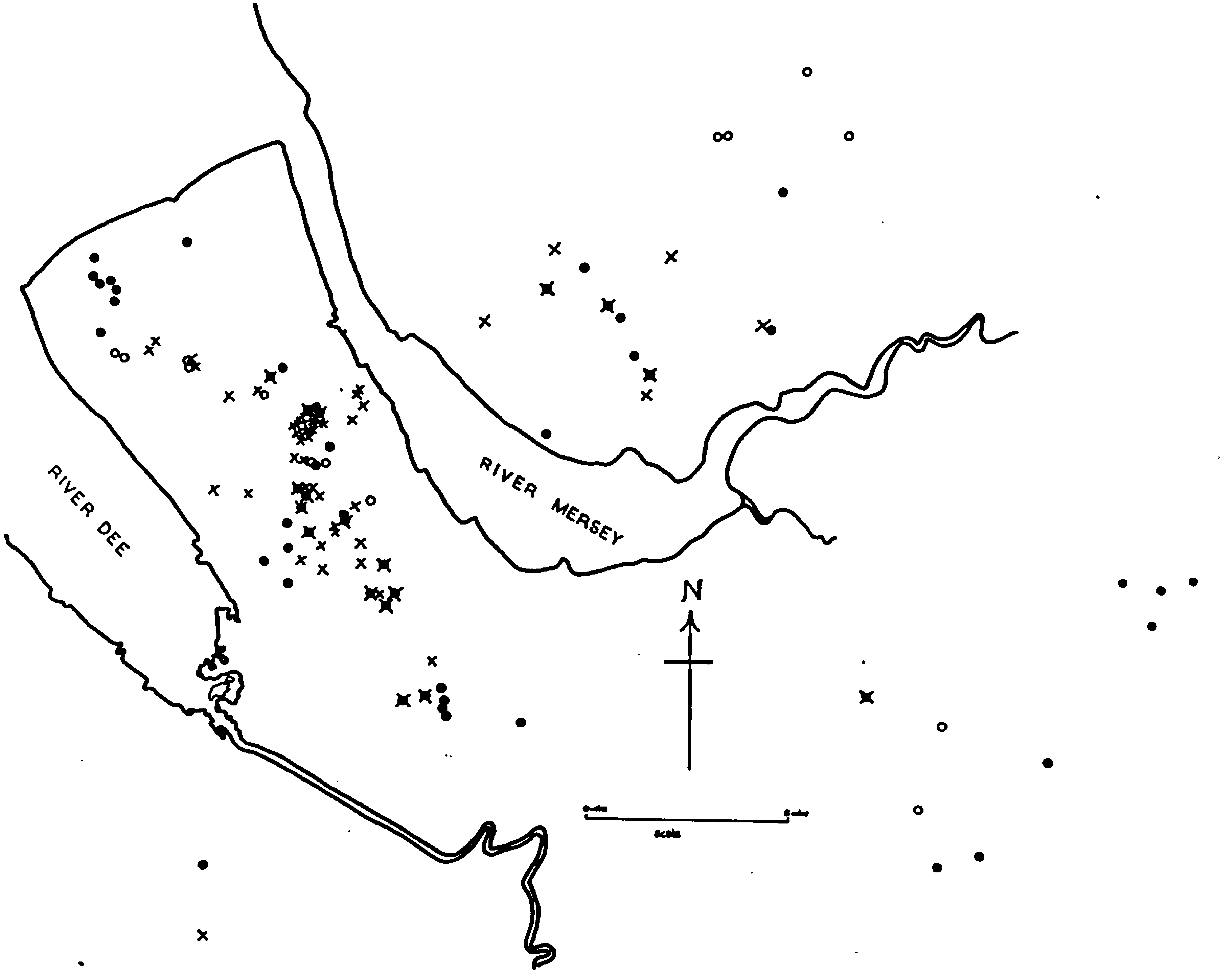
Several authors (e.g. Gurney, 1904; Elton, 1927,1929; Carl, 1940; Thienemann, 1950) have postulated competitive relationships amongst various groups of species on the basis of specific differences in local distribution. The most detailed work is perhaps that of Carl (1940), who studied the distribution in British Columbia of a number of species of various genera of Cladocera and free-living Copepoda. He found that in most cases the percentage of localities containing more than one species of a genus was extremely low, and concluded that this phenomenon resulted from interspecific competition; "it appears that the

7.2

Fig. 27 The distribution of *Asellus* on Merseyside and in adjoining areas

Key:

- ● localities containing only *A. aquaticus*
- × localities containing only *A. meridianus*
- ✗ localities containing both species of *Asellus*
- ○ localities containing no *Asellus*


RIVER MERSEY
RIVER DEE
N
scale

different genera occupy different "niches" within the association and when these "niches" are occupied by one species others are prevented from becoming established" (p. 97-98).

Fig. 27 , p.7.2 shows the details of the distribution of <u>A. aquaticus</u> and <u>A. meridianus</u> on Merseyside, and is based upon collections from 115 localities. At each locality collections were made from at least three points on the periphery, on one occasion, but many of the localities were visited on a number of occasions and numerous collections were taken.

It can be seen from the map that 36 of the localities contain only <u>A. aquaticus</u>, 45 only <u>A. meridianus</u>, 18 both species, and 16 no <u>Asellus</u>. In order to determine whether such a pattern of distribution could have arisen by chance (i.e. if the distrib--utions of the species were random with respect to each other), these figures were analysed statistically. The statistical analysis revealed that it is extremely unlikely that the observed pattern of distribution has arisen by chance, and it must be concluded, therefore, that in some manner populations of the two species interact. The analysis cannot of course supply any information concerning the nature of this interaction; it indicates merely that the percentage of uni-specific localities is higher than expected if it is assumed that the presence of one species has no affect upon the presence of the other.

The statistical analysis involved the use of a 2 X 2 contingency table and a chi-squared test:

		A. aquaticus		
		present	absent	total
	present	18	45	63
A. meridianus	absent	36	16	52
	total	54	61	115

$\chi^2 = 18.9$

with 1 d.f. $P = <0.001$.

(b). The distribution of Asellus in Lake Windermere

Moon (1934) in 1932 and Humpries (1936) in 1934 found only A. meridianus in Lake Windermere. Moon (1957), however, during the nine years prior to 1957, found that both species were present, and, on the basis of a detailed survey of their relative distributions in the lake, suggested that A. meridianus was the older inhabitant of the two, and was in competition with and being replaced by A. aquaticus.

In order to examine Moon's suggestion and to determine whether there had been any change in the relative distribution of the two species since his survey, a partial resurvey was underaken during April 1960, when the distribution of the two species on the central islands and on the western shore of the northern end of the lake was investigated. During this resurvey a total of 62 shore collections and 30 collections from deeper water were made, all of which corresponded exactly in position with stations previously investigated by Moon; the loan of the original data and 6" maps, and the communication of much unpublished information by Professor Moon proved especially useful in this connection. The shore collections were made using a stramin hand-net in a similar manner to that described on p.33 and also employed by Moon (1957a, p.113); the collections from deeper water were made using an Ekman grab of 0.23 sq.ft. 'grab-area'.

Except for two collections, the results of the collections using the Ekman grab have already been presented (p.6.15); the results of the shore collections are summarized in the table below:

		The no. of stations at which both, only one, or no species of <u>Asellus</u> were recorded in 1960.				
		A & M	A	M	0	totals
The no. of stations at which both, only one, or no species of <u>Asellus</u> were re--corded during the period 1947-1956.	A & M	0	10	0	6	16
	A	0	6	0	8	14
	M	0	20	0	4	24
	0	0	1	0	7	8
	totals	0	37	0	25	62

A = Stations at which only <u>A. aquaticus</u> was collected.
M = Stations at which only <u>A. meridianus</u> was collected.
A & M = Stations at which both species were collected.
0 = Stations at which no <u>Asellus</u> was collected.

The first of the two extra collections using the Ekman grab was made just south of Rough Holme at a depth of two metres, when 32 specimens of A. aquaticus and one of A. meridianus were taken; the second was made west of Thompson's Holme at a depth of 3 metres, when 5 specimens of A. aquaticus were taken.

The results of both the shore collections and the collections from deeper water are shown also in map form in **fig. 28, p.7.7**, which compares the distribution of the two species as recorded by Moon (map (a)), and as recorded in 1960 (map (b)).

It is clear from an examination of the results that, at least in the area resurveyed, A. meridianus would seem to have almost completely disappeared, its place having been taken by A. aquaticus. Thus, considering only the shore collections, it can be seen from the table (p. 7.5) that in April 1960 A. meridianus was never collected at any of the 30 stations where Moon had previously collected either both species or only A. meridianus. Similarly, considering the results of the collections from deeper water, it can be seen that, although A. meridianus is still present, A. aquaticus is now the dominant species at all levels.

It must be concluded, therefore, that, since there is no reason to suspect that the disappearance of A. meridianus is not causally related to the presence of A. aquaticus or restricted

Fig. 28 The distribution of *Asellus* in Lake Windermere.

(a) as recorded by Moon (1957a) for the period 1947-56,

(b) as recorded in April 1960.

Note:

The positions at which collections are indicated are identical in both maps.

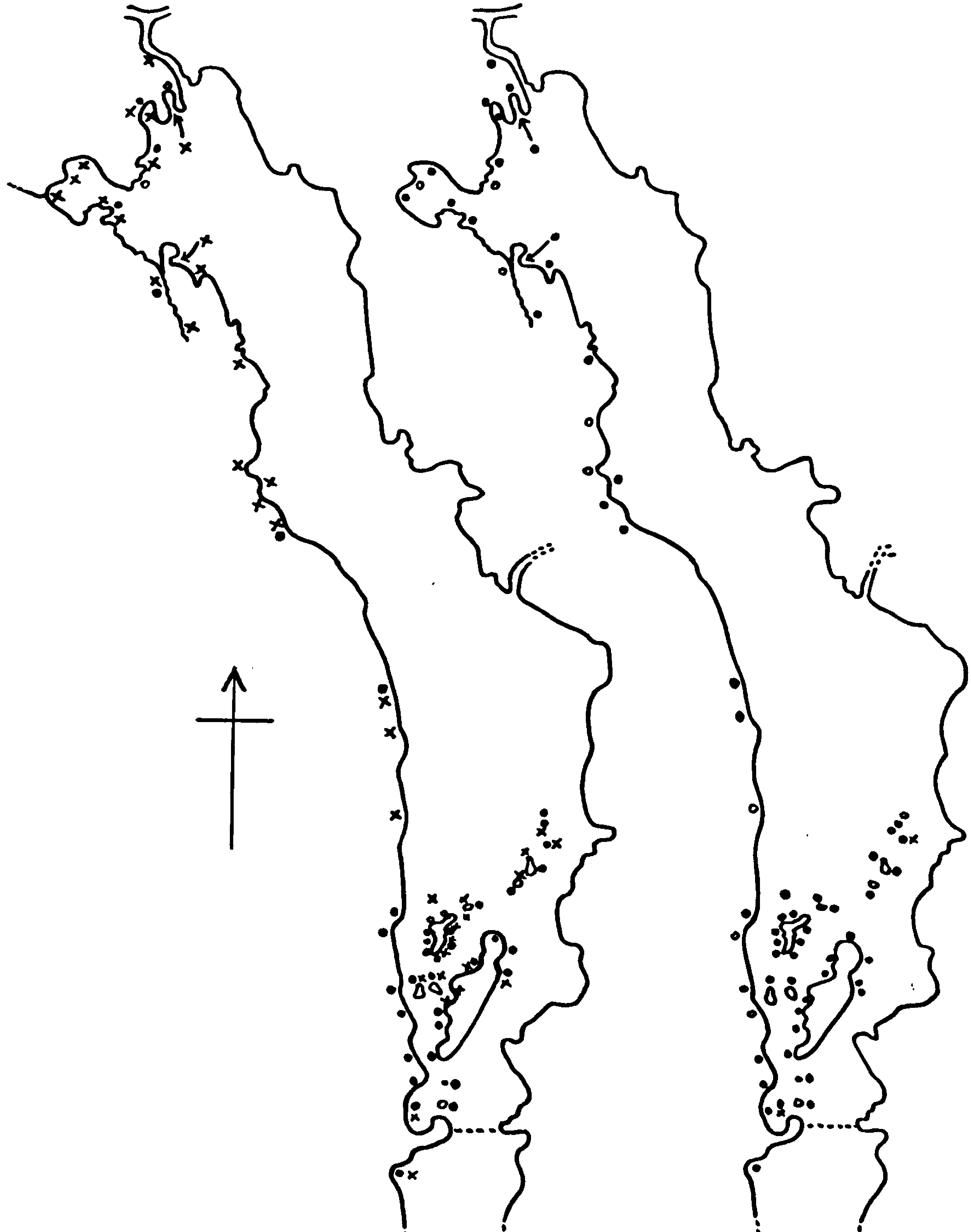
Key:

• Positions at which only *A. aquaticus* was collected

× Positions at which only *A. meridianus* was collected

✖ Positions at which both species were collected

○ Positions at which no *Asellus* was collected.



(a) (b)

to only that part of the lake surveyed, the investigation completely supports Moon's suggestion, and the tentative conclusions advanced from the study of the geographical distribution of the two species.

(c). The temporal change in the specific ratio in localities containing both species of Asellus.

Fig.29 , p.7.9 shows the change in the numerical ratio of A. aquaticus and A. meridianus at Llyn Llywenan, Anglesey, over a 10 year interval of time. This figure is based upon information which has been obtained from a number of sources: the information for 1950 and 1953 has been obtained from samples collected by Dr. H.B.N. Hynes and now in the possession of Prof. H.P. Moon (information communicated privately by Prof. Moon); the information for 1957 and 1958 has been obtained from samples[1] collected by Dr. Hynes and analysed during the present research; and the information for 1959 and 1960 has been obtained from samples collected personally. All the samples were obtained from the northern end of the lake where the road is immediately adjacent to the shore-line. In all samples, the specimens of Asellus were separated from the vegetable and other debris by hand sorting.

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[1] Footnote 1. These samples were used also to provide information concerning the life-history of the two species (see p.4.35).

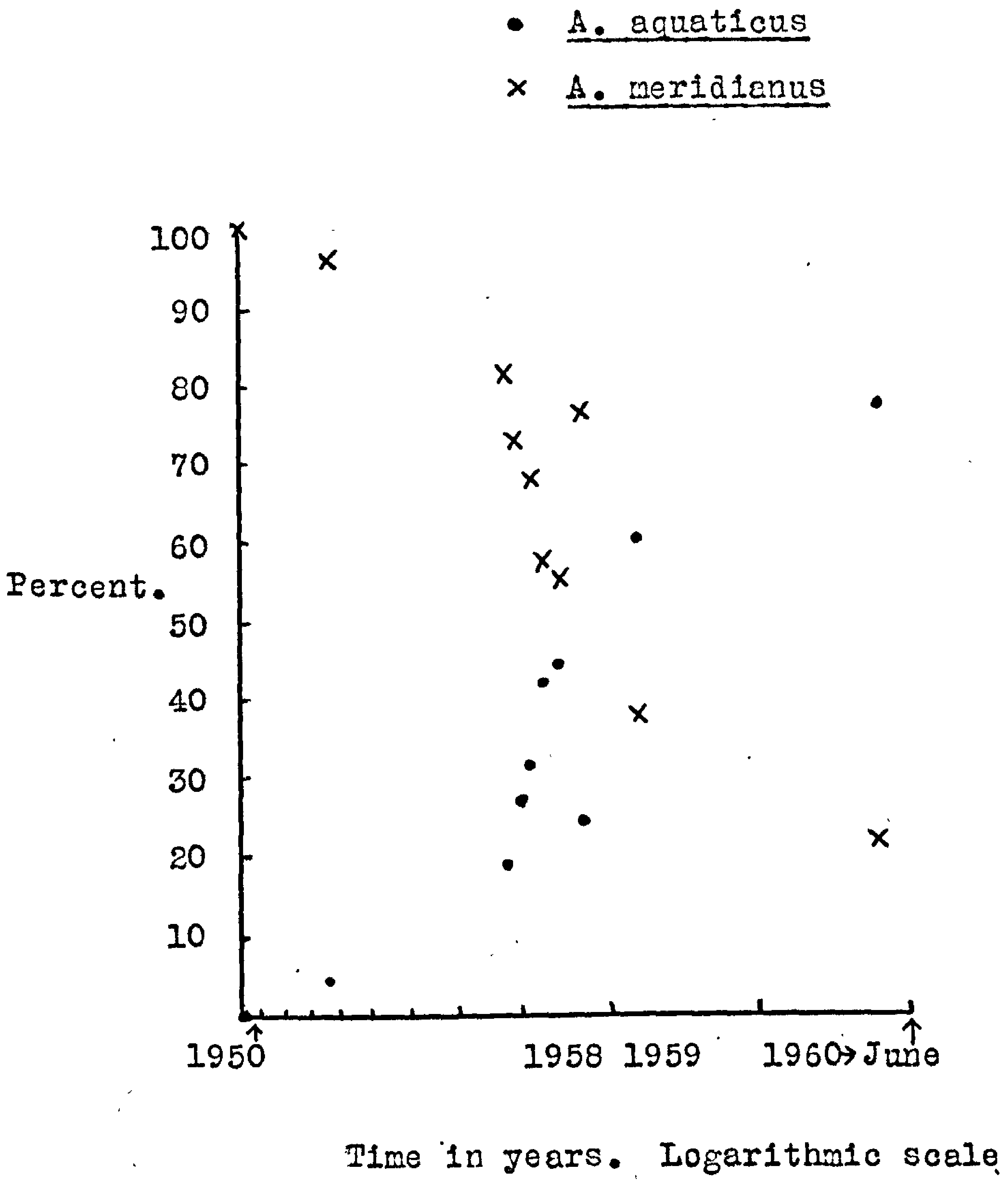


Fig. 29 Diagram showing the change in the ratio of A. aquaticus and A. meridianus at Llyn Llywenan over a ten year interval (1950 - 1960); the ratios are expressed as specific percentages of the total population of Asellus.

The details of the data upon which the figure is based are shown in the table below:

Date of sampling		A. meridianus		A. aquaticus		Total no. in sample
		No.	%	No.	%	
6th Jan.	1950	7	100	0	0	7
10th Oct.	1953	50	96	2	4	52
10th Oct.	1957	297	82	65	18	362
12th Dec.	1957	234	73	85	27	319
21st.Feb.	1958	212	68	100	32	312
17th April.	1958	174	58	129	42	303
30th June.	1958	263	55	212	45	475
21st Sept.	1958	115	76	37	24	154
31st Mar.	1959	56	38	90	62	146
7th May.	1960	63	22	230	78	293

It can be seen from the above table that, as only 7 specimens of *Asellus* were present in the 1950 sample, it is not certain that *A. meridianus* was the only species occurring at Llyn Llywenan at that time. Nevertheless, the table and the figure clearly indicate that there has been an obvious change in the specific ratio over the past 10 years such that *A. aquaticus* is now the predominant species whereas formerly *A. meridianus* predominated. Since there has been no marked apparent change in either the total abundance of *Asellus* from at least 1957, or the condition of the lake during the periods 1950-1957 (Hynes; pers. comm.) and 1958-1960, it seems reasonable to conclude that the most likely explanation for this decline in the proportion of *A. meridianus* involves the relationship between this species and A. aquaticus. It seems, in fact, that the situation parallels that suggested for Lake Windermere; A. meridianus is the older inhabitant of Llyn Llywenan, and is now in competition with and being replaced by A. aquaticus.

Apart from indicating an overall decline in the proportion of A. meridianus at Llyn Llywenan, fig. 29 indicates also that over short periods of time it would seem that reversals occur in the general direction of the change in the specific ratios. Thus, it can be seen that in the latter half of 1958 there was a marked apparent increase in the proportion of A. meridianus, and, correspondingly, a marked decline in the proportion of A. aquaticus. This suggested at first that there might be a seasonal rhythm of change in the specific ratios such that during the earlier part of the year A. aquaticus was favoured whilst during the later part of the year A. meridianus was favoured. To investigate this suggestion, the specific ratios were determined in a number of regular samples from (a) a different part of Llyn Llywenan, viz., about mid-way along the western shore, and (b) Hatchmere, Cheshire. The additional samples from Llyn Llywenan were collected between Oct. 1957 and Sept. 1958, and, as before, were obtained by Dr. H.B.N. Hynes; the samples from Hatchmere were collected from the northern end of the lake at irregualr intervals between June 1959 and July

1960, and were partly obtained during the study of the life-cycle of <u>Asellus</u> (see p.4.35). The detailed results of the determinations are presented in the tables below and in fig. 30 p.7.13.

Date of sampling	A. meridianus No.	A. meridianus %	A. aquaticus No.	A. aquaticus %	Total No. in sample
		<u>Llyn Llywenan</u> (western shore)			
10th Oct. 1957	64	38	106	62	170
12th Dec. 1957	16	11	127	89	143
21st Feb. 1958	31	12	237	88	268
17th April. 1958	162	34	309	66	471
30th June. 1958	104	35	196	65	300
21st Sept. 1958	26	9.5	246	90.5	272
	<u>Hatchmere</u>				
10th June. 1959	191	53.5	185	46.5	346
30th June. 1959	310	48	332	52	642
14th July. 1959	286	56	228	44	514
31st July. 1959	197	55	160	45	357
13th Aug. 1959	160	41	233	59	393
7th Sept. 1959	197	32	414	68	611
10th Sept. 1959	148	37	247	63	395
7th Oct. 1959	82	29	204	71	286
19th Oct. 1959	111	40	166	60	277
2nd Nov. 1959	17	22	62	78	79
16th Nov. 1959	53	14	336	86	389
30th Nov. 1959	49	25	149	75	198
11th April. 1960	56	24	173	76	229
16th May. 1960	17	6	297	94	314
30th June. 1960	93	28	241	72	334
26th July. 1960	87	28	225	72	312

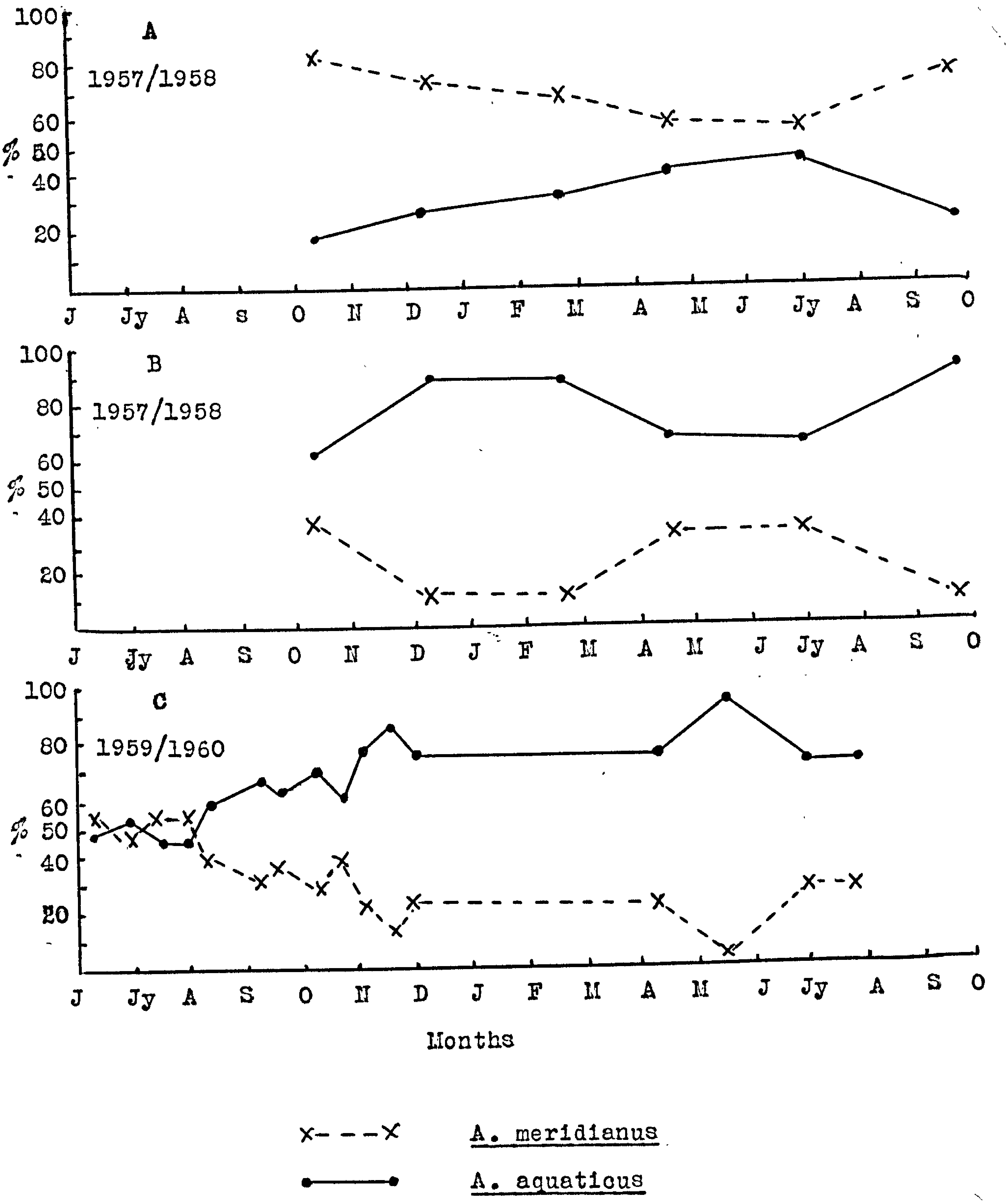
Fig. 30 Graphs showing the change in the ratio of *A. aquaticus* and *A. meridianus* at three stations over a period of one year.

The ratios are expressed as specific percentages of the total population of *Asellus*.

Graph A:
The change in the specific ratio at Llyn Llywenan (northern end) over the period Oct. 1957-Oct. 1958.

Graph B:
The change in the specific ratio at Llyn Llywenan (western Shore) over the period Oct. 1957-Oct. 1958.

Graph C:
The change in the specific ratio at Hatchmere over the period June 1959-July 1960.


A
1957/1958
B
1957/1958
C
1959/1960
%
100
80
60
50
40
20
J
Jy
A
S
O
N
D
J
F
M
A
M
J
Jy
A
S
O
Months
A. meridianus
A. aquaticus

For comparative purposes, fig.30 shows also the change in the specific ratio at the northern end of Llyn Llywenan between Oct. 1957 and Sept. 1958. The figure is so arranged that, by reading vertically, the direction of change in the specific ratios at all three stations can be immediately compared for any period of the year. Comparing the stations in this manner, it is evident that there were no consistent seasonal changes, and it must be concluded, therefore, that there is little evidence supporting the suggestion that there is a defined seasonal rhythm of change in the specific ratios.

(d). Transference experiments.

Ideally, it would seem that field transference experiments provide the most satisfactory method of testing conclusions concerning the ecological relationships of Asellus. Two simple transference experiments were therefore carried out in 1959, the first involving the transference of A. aquaticus to a locality containing only A. meridianus, and the second involving the transference of A. meridianus to a locality containing only A. aquaticus. Since it was felt that these experiments would produce meaningful results only after a relatively long period, they were primarily undertaken in order to provide a basis for a future long-term investigation. After only one year, however, certain conclusions can be derived from the experiments, and for this reason they are discussed fully below;

On the 14th Aug. 1959 a random sample of A. aquaticus was transferred to a small pond, M.R. 109/330775, near Willaston, Cheshire, and a random sample of A. meridianus was transferred to a small pond, M.R. 100/273903, near Bidston, Cheshire. It was known that before the transferences the former pond contained only A. meridianus and the latter only A. aquaticus. Each random sample contained an estimated 2,000 specimens. A careful note was made of the exact position at which each sample was added. After approximately one year had elapsed since the transferences, a small sample was collected from each of the positions noted and the specific ratio within this sample determined. The results of the determinations are shown below:

Date of sampling	A. meridianus		A. aquaticus		Total No. in sample
	No.	%	No.	%	
Sample from pond initially containing only A. meridianus:					
15th Sept. 1960.	22	47	25	53	47
Sample from pond initially containing only A. aquaticus:					
15th Sept. 1960.	0	0	133	100	133

The above figures clearly indicate that the transferred population of A. aquaticus successfully managed to establish itself, whereas, in contrast, the transferred population of

A. meridianus completely failed to do so. It is evident, therefore, that the results so far gained from the transference experiments provide prima facie evidence of the competitive superiority of A. aquaticus, and as such support the tentative conclusions already advanced concerning the inter-specific relationships of the two species.

There is, however, one important methodological point of criticism which must be noted, and which prevents the unreserved acceptance of the results. This is that the initial abundance of Asellus in the two ponds was rather different, the abundance in the pond initially containing A. meridianus being far less than in the other pond. It is possible, therefore, that the severity of competition differed in the two ponds, and this may have accounted for the results independently of any difference in specific competitive ability. On the other hand, it is necessary to note that the severity of competition may be of only secondary importance, for even in the absence of competition transferences are not always successful. Thus, in 1957 Prof. H.P. Moon (pers. comm.) transferred 200 specimens of Asellus (sic) to each of two Lake District tarns which contained no Asellus but which appeared subjectively suitable. It would appear that these specimens failed to establish themselves, for even after two years he was unable to find any Asellus in either tarn.

2. Laboratory investigations.

The laboratory investigations were designed on the same lines as the experimental investigations of Gause's hypothesis (see p.1.6). Thus, fundamentally they were designed to compare the ability of the two species to survive when reared together, and when reared in isolation.

(a). Investigation 1.

At various times in June, July and August 1959, twenty-one large jars were set aside, and into each was put either a number of soaked elm leaves or a small sample of the substratum from Buckley Lake, Padeswood Lake, Hatchmere or "Jackson's pond" (M.R. 109/418889). It is to be noted that the first two of these localities contain, respectively, only *A. aquaticus*, and only *A. meridianus*, whilst the last two contain both species. Each jar was then almost filled with tap-water, and to each was added a certain number of variously sized ovigerous females of only one or both species of *Asellus*. These had been recently collected from the field. The preparation of a variety of experimental conditions within the jars was undertaken since the original aim of the investigation was to determine not only whether one species would be replaced by the other in the jars initially containing both species, but also whether, assuming there was such a replacement, its direction was always constant. The details of the preparations are shown in the table on p. 7.19. Referring to this table, it can be seen that those jars containing elm leaves possessed either 20 specimens of A. aquaticus, 20 specimens of A. meridianus, or specimens of both species in the proportions 10:10 or 5:15 (and vice versa); and those jars containing small samples of natural substratum possessed either 20 specimens of A. aquaticus, 20 specimens of A. meridianus, or 10 specimens of each species. All the jars were maintained at room temperatures (18-21°C).

In October 1959, i.e. after an interval of a few months, a count was made of the number of individuals of each species in each jar. Specific identification of the individuals in the jars containing both species was based upon the pattern of pigmentation on the dorsal surface of the head. The results of the count are shown in the table on p. 7.19.

Three principal points arize from the examination of the results. Firstly, it is clear that they exhibit a wide range of variation, and not all of this can be attributed solely to the differing experimental conditions. Secondly, in six of the nine jars which initially contained both species, A. aquaticus greatly outnumbered A. meridianus, whilst in the remaining three A. meridianus was totally absent. And thirdly, the two species persisted in all of the jars in which, initially, only one of them was

Key: A = *A. aquaticus*
M = *A. meridianus*
s.s. = sample of substratum

Experimental conditions of each jar.	initial specific ratio (ovig.♀♀) A	: M	Date of commencement (1959)	Date of count (1959)	Results of counts A	: M
Elm leaves	20	0	20.June	9.Oct.	376	0
Elm leaves	20	0	20.June	10.Oct.	201	0
s.s. from Buckley Lake	20	0	31.July	10.Oct.	139	0
s.s.from Padeswood "	20	0	24.July	12.Oct.	143	0
s.s.from Hatchmere	20	0	25.June	12.Oct.	38	0
s.s.from"Jackson's pond"	20	0	14.July	13.Oct.	53	0
Elm leaves	0	20	22.June	7.Oct.	0	130
Elm leaves	0	20	23.June	9.Oct.	0	83
s.s. from Buckley Lake	0	20	31.July	10.Oct.	0	85
s.s.from Padeswood "	0	20	24.July	12.Oct.	0	15
s.s.from Hatchmere	0	20	15.July	12.Oct.	0	7
s.s.from"Jackson's pond"	0	20	14.July	13.Oct.	0	14
Elm leaves	10	10	22.June	7.Oct.	250	1
Elm leaves	10	10	13.Aug.	9.Oct.	95	18
s.s. from Buckley Lake	10	10	31.July	12.Oct.	112	16
s.s.from Padeswood "	10	10	24.July	12.Oct.	181	17
s.s.from Hatchmere	10	10	16.July	12.Oct.	15	0
s.s.from"Jackson's pond"	10	10	11.July	13.Oct.	190	0
Elm leaves	5	15	22.June	9.Oct.	170	0
Elm leaves	5	15	23.June	9.Oct.	134	11
Elm leaves	15	5	25.June	9.Oct.	293	1

present. At face value, the results appear to indicate, there-fore, that A. meridianus was unable to compete with A. aquaticus in any of the jars, and, considering the short time for which the investigation was allowed to run, that A. aquaticus directly prevented the survival of A. meridianus. However, it is necessary to study the abundance of A. meridianus in those jars in which it was the only species present. It can be seen that in half of these the abundance of the species was of the same order of abundance as in those jars containing both species. It seems possible, therefore, that the small number of individuals of A. meridianus in the jars containing both species had no causal relation to the presence of A. aquaticus; the low numbers of A. meridianus in these jars had perhaps resulted from the same factors causing the low numbers in some of the jars initially containing only this species. Subjection of the data to statistical analysis provided no clarification; using a t-test, Dr. P.M. Sheppard found that it was just concievably possible that there was no causal relation between the abundances of the two species in the mixed species jars. The only conclusion it is, therefore, safe to make from the investigation is that A. aquaticus survived better under the experimental conditions than did A. meridianus.

(b). Investigation 2.

This investigation was primarily designed to clarify the results of investigation 1.

In March 1960, fifteen large jars were set aside, and into each was put an amount of washed sand sufficient to cover the bottom, some Elodea and Callitriche, and a number of soaked elm leaves. Each jar was then almost filled with tap-water, and to each was added a certain number of variously sized ovigerous females of only one or both species of Asellus. These had been recently collected from the field. The details of the preparations are shown in the table on p.7.22. Referring to this table, it can be seen that five of the jars contained 10 specimens of A. aquaticus per jar, five 10 specimens of A. meridianus per jar, and five 5 specimens of both species per jar. All the jars were maintained at room temperatures (18-21°C), and were constantly aerated.

After an interval of approximately three months a count was made of the number of individuals of each species in each jar. Specific identifications were made using the same method as was used in investigation 1. The results of the count are shown in the table on p.7.22.

An examination of these results shows that, broadly, they exhibit a similar pattern to those of investigation 1. Thus, the largest populations of both species occurred in those jars

A. = <u>A. aquaticus</u>
M. = <u>A. meridianus</u>

Initial specific ratio (ovig.♀♀)		Date of commencement (1959)	Date of count (1959)	Results of count	
A :	M			A :	M
10	0	15th March	5th June	411	0
10	0	15th March	20th June	204	0
10	0	15th March	21st June	427	0
10	0	14th March	20th June	535	0
10	0	11th March	21st June	456	0
0	10	11th March	5th June	0	247
0	10	11th March	20th June	0	0
0	10	11th March	20th June	0	171
0	10	11th March	18th June	0	385
0	10	11th March	20th June	0	57
5	5	11th March	20th June	270	28
5	5	11th March	21st June	321	15
5	5	11th March	5th June	131	34
5	5	11th March	18th June	184	10
5	5	11th March	20th June	370	41

containing only one of them, and in all the jars containing both species, *A. aquaticus* greatly outnumbered *A. meridianus*, again indicating a *direct* interference of *A. aquaticus* with *A. meridianus*. In contrast to the previous investigation, it can be seen that in one of the jars initially containing only *A. meridianus*, this species became extinct. This result, therefore, as before, precludes the drawing of a definitive conclusion concerning a causal relationship between the abundance of *A. meridianus* and the presence of *A. aquaticus* in the mixed species jars. As in the previous investigation, subjection of the results to statistical analysis provided no clarification; Dr. P.M. Sheppard, using a t-test, found that it was just possible that the small numbers of *A. meridianus* in the mixed species jars had not been caused by the presence of *A. aquaticus*. It is evident, therefore, that this second investigation failed to clarify the results of the first. Once more, the only safe conclusion that can be drawn is that *A. aquaticus* survived better under the experimental conditions than did *A. meridianus*.

(c). *Investigation 3*.

This investigation likewise was primarily designed to clarify the results of investigation 1. In this case, however, the investigation was designed to determine whether the suggested *direct* influence of *A. aquaticus* upon *A. meridianus* took place between the adults of the species.

In December 1959, into each of 90 petri-dishes of 3" diameter were put a single soaked elm leaf and sufficient tap-water almost to fill the dish. The dishes were arranged in three series, 30 in each. Into each dish of the first series were then put 2 specimens of *A. aquaticus*, into each dish of the second series 2 specimens of *A. meridianus*, and into each dish of the third series 1 specimen of each species. Only adult specimens which had been acclimatized to room temperatures were used, and no attention was paid to their sex. In those dishes in which the specimens were of the same species there was a large specimen and a smaller specimen; in those dishes in which the specimens were of differing species, the specimen of *A. aquaticus* was always slightly larger than that of *A. meridianus*. The dishes were left at room temperatures for approximately three months, during which time they were observed at irregular intervals. At each observation, the number of dead specimens of each species was noted, and fresh elm leaves or water were added where necessary, Dishes containing only one live specimen were discarded.

The results of the observations are presented in the following table, in which they are shown as the number of specimens surviving as a percentage of the initial number present. In the compilation of these percentages, those single live specimens that were discarded have been regarded as having survived until the end of the investigation, and thus the percentage survival is not the actual one, but merely the complement of the *observed* mortality.

Date of observations (1959/60)	Dishes containing two specimens of *A. aquaticus* % survival	Dishes containing one specimen of each species of *Asellus* % survival		Dishes containing two specimens of *A. meridianus* % survival
		A :	M	
17th Dec.	100	100	100	100
29th Dec.	100	90	100	100
12th Jan.	100	90	100	100
30th Jan.	95	83.3	93	96.7
29th Feb.	78.3	70	76.7	83.3
25th Mar.	60	66.7	63.3	63.3

As the above table clearly shows, there was very little difference between the final percentage survival in all four columns, and none between the third and fourth. The investigation indicates, therefore, that the presence of adults of *A. aquaticus* does not appear to have influenced the survival of adults of *A. meridianus*; it is evident that if there was any direct interspecific interference in investigations 1. and 2., then this must have involved juvenile individuals.

(d). Investigation 4.

This last investigation was essentially a continuation of an investigation initiated by Dr. H.B.N. Hynes. As in investigations 1. and 2., it involved the maintenace of single and mixed species populations of Asellus, but, in contrast to these investigations, the populations were kept out-of-doors and thus experienced an approximately similar temperature regime as occurred in the field.

Only four populations at a time were maintained, and these were kept in four large tanks, each being about 6' long, 1.5' wide and 3' deep, and formed by partitioning with wood two larger tanks. The investigation was begun in April 1958 by Dr. Hynes, who, after filling the tanks with sufficient water, placed in the first 240 specimens of A. aquaticus, in the second 240 specimens of A. meridianus, and in the third and fourth 120 specimens of each species. These specimens were random with respect to size and sex. To each tank were also added a number of pond snails, some Elodea and a fairly large quantity of dried elm leaves to serve as food.

The populations were left in situ for a period of 8 months, at the end of which the number of individuals of each species in each of the tanks was counted. Specific identifications were made using the same method as was used in investigation 1. The results of the count are shown in the table on p.7.27 in which the tanks are referred to as tanks 1-4.

A = *A. aquaticus*
M = *A. meridianus*
* = ovigerous females

Tank No.	Initial specific ratio A	: M	Date of commencement	Date of count	Specific ratio at count A	: M
1	240	0	April 1958	1st Dec.58.	800	681
2	0	240	April 1958	1st Dec.58.	1002	989
3	120	120	April 1958	1st Dec.58.	4096	788
4	120	120	April 1958	1st Dec.58.	568	199
1_1	200	0	12.Dec.1958	14th Dec.59.	800	0
2_1	0	200	12.Dec.1958	14th Dec.59.	0	360
3_1	4096	788	12.Dec.1958	14th Dec.59.	0	0
4_1	568	199	12.Dec.1958	14th Dec.59.	0	0
1_2	50*	50*	5.April 1959	15th Sept.60.	724	512
2_2	50*	50*	5.April 1959	15th Sept.60.	548	222
3_2	100*	0	5.April 1959	15th Sept.60.	2735	0
4_2	0	100*	5.April 1959	15th Sept.60	(41)	262

Two main points emerge from the examination of the results. Firstly, it is clear that the partition between tanks 1 and 2 had been ineffective so that all tanks contained mixed species populations. And secondly, despite the great variability of the results, *A. aquaticus* was numerically superior in all the tanks, although only just so in tank 2. The results indicate, therefore, that under the given experimental conditions *A. aquaticus* survived better than did *A. meridianus*; but, in the absence of comparative data from single species populations, they do not indicate whether the numerical inferiority of *A. meridianus* was due to competition. At all events, the results from tanks 1 and 2 suggest that under certain circumstances populations of the two species may co-exist over long periods of time with perhaps only slight changes in the specific ratio favouring *A. aquaticus*.

After the count, the populations from tanks 1 and 2 were discarded. The populations from tanks 3 and 4, however, were replaced, and, in addition, the two empty tanks were restocked with respectively, 200 specimens of *A. aquaticus*, and 200 specimens of *A. meridianus*. These specimens were random with respect to size and sex. As before, each tank was also stocked with a number of pond snails, some *Elodea* and a fairly large quantity of elm leaves to serve as food. Before the restocking of the tanks, in an attempt to isolate them effectively, the floor of all four was covered with a thick layer of washed sand: it was known that the largest gaps in the partitions occurred where they met the floors of the tanks.

The tanks were left for a period of 12 months, and then, once more, the number of individuals of each species in each tank was counted. The results of this count also are shown in the table on p. 7.27, and here the tanks are referred to as tanks $1_1 - 4_1$.

Referring to the table, it can be seen that, whilst in tanks 1_1 and 2_1 the populations of <u>Asellus</u> had persisted, in tanks 31 and 4_1 the populations had become extinct. No further information, unfortunately, was therefore given concerning the specific ratios of the mixed species populations which had been prepared in April 1958. The extinction of these populations would seem to have been caused by the large number of beetle larvae (<u>Agabus</u> sp., and Hydroporini) which had entered the tanks at some time during the preceding 12 months. Moreover, since these larvae had also entered tanks 1_1 and 2_1 but in differing proportions (tank 2_1 contained many more than did tank 1_1)., it is doubtful if any importance can be attached to the difference in the abundance of the populations in these two tanks. It is evident that this part of investigation 4. provided no information.

One further attempt was made to obtain information using the tanks. This time, however, to ensure that no beetle larvae interfered with the investigation, the tanks were entirely covered with a fine plastic mesh, and, to ensure that there were no gaps in the wooden partitions, these were cemented over.

After filling with sufficient water, the tanks were restocked with ovigerous females, the first and second each containing 50 specimens of both species, and the third and fourth 100 specimens of, respectively, A. aquaticus, and A. meridianus. As before, pond snails, some Elodea and a fairly large quantity of elm leaves were also added to each tank.

The number of individuals of each species in each tank was counted after an interval of about six months. These numbers are indicated in the table on p. 7.27, and here the tanks are referred to as tanks 1_2 - 4_2.

The table shows that in the two tanks initially containing both species A. aquaticus was numerically superior to A. meridianus, and that in the two tanks initially containing only one species both species persisted, although A. aquaticus was vastly more abundant than was A. meridianus. (The presence of a small number of specimens of A. aquaticus in tank 4_2 is difficult to explain, for it seems unlikely that they entered through gaps in the partition). The results indicate, therefore, that under the experimental conditions A. aquaticus survived better than did A. meridianus. However, the results do not indicate that it is possible to attribute the discrepancy between the numbers of the two species in the mixed species populations to interspecific competition, for, assuming that the small numbers of *A. aquaticus* in tank 4_2 had had no affect, the number of *A. meridianus* in tank 4_2 falls within the range of the numbers in tanks 1_2 and 2_2.

Discussion.

From a consideration of the data presented in the preceding chapters, it is not possible to arrive at any firm conclusions concerning the factors which govern the distribution of A. aquaticus and A. meridianus in Britain. It is possible, nevertheless, to indicate some preliminary ideas, which, it is suggested, provide a reasonable explanation of the distribution, and which would seem to be the most reasonable ones that can be drawn from the data.

Apart from the gross specific differences, the investigation of the geographical distribution of the two species (see chapter III) reveals two particularly salient differences: it is only in Britain that A. meridianus is widely distributed north of the southernmost limit reached by the ice-sheet during the Ice-age; and in all of the most isolated parts of Britain (and in parts of France also) A. meridianus is the predominant if not the only species of Asellus present. It is suggested (chapter III) that these differences can be explained by considering the post-glacial history of the two species, and by assuming that they compete. Thus, to reiterate briefly, it is thought that both species originated before or during the Ice-age, A. aquaticus in central Asia, and A. meridianus in the Mediterrenean region. After the retreat of the ice, A. meridianus spread northwards, whilst, contemporaneously, A. aquaticus spread westwards along the margin of the ice-sheet. A. meridianus may have either survived the Ice-age in refuges in Britain, or arrived subsequently via the early post-glacial land-bridge across the English Channel; but, at all events, this species was present in Britain before A. aquaticus, and became widely distributed throughout the British Isles during the early post-glacial period. On the continent, the westwardly immigrating A. aquaticus either replaced A. meridianus in most of the post-glacially colonized regions north of the southernmost limit of the Glacial ice-sheet, or, as is considered more likely, it prevented the colonization of such areas by A. meridianus. By the time A. aquaticus had spread as far as northwestern France, however, the land-bridge across the English Channel had disappeared and this hindered the further spread of the species in this region, and allowed A. meridianus to survive in Britain. During compararatively recent historical time A. aquaticus has been able to overcome the barrier of the English Channel, and, probably aided by Man in a number of diverse ways, has spread and is spreading throughout Britain, where it is gradually replacing A. meridianus.

The above suggested scheme of events would certainly seem to be supported by three, or perhaps four, further investigations of the present research. Firstly, the resurvey of the distribution of Asellus in Windermere (p. 7.4) indicates that whereas A. meridianus was formerly the most common species in that lake, *A. aquaticus* is now the most common; and, in fact, *A. meridianus* seems to have almost completely disappeared. Secondly, the investigation of the change in the specific ratio at Llyn Llywenan (pp.7.7) shows that between 1950 and 1960 there was a complete reversal in the ratio, *A. meridianus* predominating during the early and middle part of the decade, and *A. aquaticus* during the final part. It is to be emphasized at this point that, since there do not appear to have been any marked changes in the condition of Windermere and Llyn Llywenan over the period of these changes, it can only be concluded that the decreases in the abundance of *A. meridianus* resulted from competition with *A. aquaticus*. Thirdly, the investigation of the detailed local specific distribution on Merseyside (pp.7.1) provides statistical evidence for competitive exclusion. And fourthly, the transference experiments (p. 7.14) indicate perhaps the competitive superiority of *A. aquaticus*.

Thus, to summarise, it is suggested that both the regional and local distribution of *A. aquaticus* and *A. meridianus* in Britain can be explained in the following terms:

A. meridianus was the first species to arrive in Britain, where it became widespread. A. aquaticus arrived much later, and is now spreading throughout the British Isles and replacing A. meridianus, with which, therefore, it is in competition.

But, whether this explanation is accepted or not, it is clear that previous ones cannot. Thus, the investigations of localities containing both, only one, or no species of <u>Asellus</u> (p. 6.26), and of the specific microhabitats (p. 6.9) provide no support for Needham's (1942) suggestion (see p. 1.13), and Maury's (1927) hypothesis (see p. 1.13) that there is a specific differentiation in habitat. Similarly, the investigation of the distribution of the two species on Merseyside (p. 7.1) provides no support for the alternative suggestion of Needham (1942) (see p.1.13) that the distribution of both species is entirely fortuitous. The suggestion (anon., 1944)(see p.1.13) that the two species can co-exist (in the sense that they constitute an exception to Gause's hypothesis), also, cannot be accepted, when the results of the investigations on Lake Windermere (p. 7.4) and on Llyn Llywenan (p. 7.7) are considered.

<u>Unfortunately, however, the present research provides no DIRECT evidence of inter-specific competition</u>, and it is not possible, therefore, to put forward any reliable suggestions as to how the phenomenon operates. It is possible, nevertheless, to indicate a number of bases upon which it presumably does <u>not</u> operate. Thus, it is clear that the interspecific competition cannot be explained in terms of a difference in the life-cycle (chapter IV) or biotic potential (chapter V) of the two species. Moreover, considering the type of food of <u>Asellus</u> (p. 6.1), it is

difficult to see how this could provide a basis for competition. And, as indicated by investigation 3 (p. 7.23), direct inter-specific interference between the adults of the species would seem to be ruled out.

The present research likewise provides no information concerning those factors responsible for the control of the population size of the two species; and on this account, also, it is not pssible to put forward any reliable suggestions as to how the two species actually compete. However, it is perhaps relevant to note here that predation would seem to be one of the most important of these controlling factors, for a brief survey of the literature on the food of fresh-water fish[1] revealed that both species of Asellus are a major item in the diet of many fish species; and, as shown by the second part of investigation 4 (p. 7.28), Asellus is probably eaten by numerous inverterates also.

It would seem that previous research on the ecology of closely related and sympatric species falls into two principal categoreis: firstly, research which shows that there are specific differences in food, microhabitat, etc. (i.e. "niche"), and which then infers that these differences have resulted or result

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[1] Footnote 1. In this connection, the works of the following authors have been most useful; Slack (1964), Radforth(1940), Hartley (1947,1948), Hynes (1950), Dunn (1954), Graham (1960), Ball (in m.s.), Chubb (pers. comm.).

from interspecific competition (see pages 1.7 and 1.8 for examples); and secondly, research which shows that there are apparently no specific differences in "niche", but which provides no evidence of any interspecific competition (see p. 1.8 for examples). Insofar as the tentative conclusions of the present work are accepted, it can be seen that the present research fits into neither of these categories: the two species of *Asellus*do not appear to exhibit any differences in "niche", but, at the same time, there *is* evidence for interspecific competition. Morevoer, it would appear that this evidence is somewhat more satisfactory than that of previous researches, for, as Andrewartha & Birch (1954) and other authors have pointed out, the exhibition of specific differences in "niche" in no way proves the presence of interspecific competition.

It would seem, therefore, that the present research provides a natural example of two closely related species which possess no differences in "niche", and between which competition is a significant and extant process.

And as such, it is evident that the present research is in accordance with Gause's hypothesis, since it is to be expected that the present geographical co-existence of the two species is only a temporary transitory stage.

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Appendix A.

Table 1.

Details of the distributional records of Asellus in Britain.

ENGLAND AND WALES.

Vice - county No.	 Name	Number of records of : A. aquaticus	 A. meridianus
0	Channel Isles	0	2
1	Cornwall, W.	0	2
2	Cornwall, E.	0	1
3	Devon, S.	1	2
4	Devon, N.	1	0
5	Somerset, S.	1	0
6	Somerset, N.	0	1
7	Wiltshire, N.	2	4
8	Wiltshire, S.	1	0
9	Dorset	2	2
10	Isle of Wight	0	2
11	Hants, S.	3	3
12	Hants, N.	0	1
13	Sussex, S.	3	4
14	Sussex, E.	2	4
15	Kent, E.	0	0
16	Kent, W.	1	2
17	Surrey	2	2
18	Essex, S.	6	3
19	Essex, N.	1	0
20	Herts.	5	2
21	Middlesex	3	1
22	Berks.	2	2
23	Oxford	1	1
24	Bucks.	8	0
25	Suffolk, E.	1	1
26	Suffolk, W.	2	0
27	Norfolk, E.	3	1
28	Norfolk, W.	1	0
29	Cambridge	2	1
30	Bedford.	4	1
31	Hunts.	1	1
32	Northants.	1	3
33	Glos., E.	1	1
34	Glos., W.	0	0
35	Monmouth	0	0

Vice - County No.	Name	Number of records of : *A. aquaticus*	 *A. meridianus*
36	Hereford	2	0
37	Worcs.	3	3
38	Warwick	4	2
39	Stafford	4	0
40	Salop	6	1
41	Glamorgan	1	4
42	Brecon	0	0
43	Radnor	0	0
44	Carmarthen	0	0
45	Pembroke	0	1
46	Cardigan	1	0
47	Mont.	6	0
48	Merioneth	0	2
49	Caerns.	0	4
50	Denbigh	1	0
51	Flint	1	1
52	Anglesey	5	39
53	Lincs., S.	0	0
54	Lincs., N.	0	1
55	Leics. & Rutland	1	1
56	Notts.	3	0
57	Derby	2	1
58	Cheshire	∞	∞
59	Lancs., S.	∞	∞
60	Lancs., Mid	3	0
61	Yorks., S.E.	3	1
62	Yorks., N.E.	1	0
63	Yorks., S.W.	2	2
64	Yorks., Mid. W.	3	0
65	Yorks., N.W.	0	0
66	Durham	0	2
67	Northum., S.	1	0
68	Cheviot land	1	0
69	Westmor.& N.Lancs.	∞	∞
70	Cumberland	∞	∞
71	Isle of Man	0	4

SCOTLAND.

Vice - county No.	 Name	Number of records of : A. aquaticus	 A. meridianus
72	Dumfries	0	0
73	Kirkcudbright	0	3
74	Wigtown	0	1
75	Ayr	1	1
76	Renfrew	1	0
77	Lanark	3	0
78	Peebles	2	1
79	Selkirk	1	2
80	Roxburgh	1	0
81	Berwick	1	1
82	Haddington	5	1
83	Edinburgh	12	7
84	Linlithgow	7	3
85	Fife & Kinross	2	1
86	Stirling	4	2
87	Pth., S. & Clkn.	2	0
88	Perth, Mid.	6	0
89	Perth, N.(or E.)	0	0
90	Porfar	0	0
91	Kincardine	0	1
92	Aberdeen, S.	1	2
93	Aberdeen, N.	0	0
94	Banff	0	0
95	Elgin	0	3
96	Easterness	1	0
97	Westerness	1	0
98	Main Argyll	0	0
99	Dumbarton	1	0
100	Clyde Isles	0	0
101	Cantire	0	0
102	Ebudes, S.	0	0
103	Ebudes, Mid.	0	0
104	Ebudes, N.	0	0
105	Ross, W.	0	0
106	Ross, E.	0	0
107	Sutherland, E.	0	0
108	Sutherland, W.	0	0
109	Caithness	2	0
110	Hebrides	0	0
111	Orkneys	0	0
112	Shetlands	0	0

IRELAND.

Vice - county		Number of records of :	
No.	Name	A. aquaticus	A. meridianus
1	Kerry, S.	0	0
2	Kerry, N.	0	0
3	Cork, W.	0	0
4	Cork, Mid.	0	0
5	Cork, E.	0	0
6	Waterford	0	0
7	Tipperary, S.	0	0
8	Limerick	0	0
9	Clare	1	1
10	Tipperary, N.	1	0
11	Kilkenny	0	0
12	Wexford	0	0
13	Carlow	0	0
14	Queen's Co.	0	0
15	Galway, S.E.	1	0
16	Galway, W.	0	1
17	Galway, N.E.	1	0
18	Kings's Co.	0	0
19	Kildare	1	0
20	Wicklow	0	0
21	Dublin	2	1
22	Meath	1	0
23	Westmeath	1	0
24	Longford	0	2
25	Roscommon	0	0
26	Mayo, E.	0	0
27	Mayo, W.	0	2
28	Sligo	2	1
29	Leitrim	2	0
30	Cavan	2	2
31	Louth	0	0
32	Monaghan	0	0
33	Fermanagh	1	0
34	Donegal, E.(or S.)	0	0
35	Donegal, W.(or N.)	0	0
36	Tyrone	2	0
37	Armagh	6	0
38	Down	3	0
39	Antrim	5	0
40	Derry	1	0 .

OFFSHORE ISLANDS (other than those mentioned above)

Name of island	Number of records of :	
	A. aquaticus	*A. meridianus*
Lundy Isle	0	2
Scilly Isles	0	1
Bardsey Isle	0	7
Skokholm	0	1

Appendix B.

Table 1.

Details of the two samples of A. meridianus collected from Padeswood Lake, Flintshire, on the 27th October 1958.

Sample I. Total number in sample, 263.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
7.5	3	3	1.1	-	-	-	-	-	-
6.5	14	6	2.3	7	2.7	-	-	-	-
5.5	56	25	9.5	23	8.7	4	1.5	4	1.5
4.5	78	33	12.5	43	16.3	2	0.8	-	-
3.5	68	25.8%)							
2.5	33	12.5%)	unsexable						
1.5	11	4.2%)							
		Sample II.			Total number in sample, 255.				
7.5	4	2	0.8	2	0.8	-	-	-	-
6.5	6	3	1.1	3	1.1	-	-	-	-
5.5	38	16	6.3	20	7.8	1	0.4	1	0.4
4.5	72	30	11.4	38	14.9	3	1.1	1	0.4
3.5	62	24.3%)							
2.5	48	18.4%)	unsexable						
1.5	25	9.8%)							

Appendix B.

Table 2.

Details of a sample of *A. aquaticus* from Buckley Lake, Flintshire.

A. Based on specimens obtained by the sieve-method only.

Total number in sample, 207.

Size of in group m.m.	Total in group	Males No.	%	Females with small lamellae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
13.5	2	2	1.0	-	-	-	-	-	-
12.5	14	14	6.8	-	-	-	-	-	-
11.5	16	16	7.7	-	-	-	-	-	-
10.5	23	16	7.7	-	-	7	3.4	-	-
9.5	22	16	7.7	-	-	5	2.4	1	0.5
8.5	32	13	6.3	-	-	17	8.2	2	1.0
7.5	35	10	4.8	1	0.5	22	10.6	2	1.0
6.5	28	6	2.9	9	4.3	10	4.8	3	1.4
5.5	19	4	1.9	11	5.3	3	1.4	1	0.5
4.5	7	2	1.0	5	2.4	-	-	-	-
3.5	2	1.0%)	unsexable.						
2.5	5	2.4%)							
1.5	2	1.0%)							

B. Based on the 'total' number of specimens present in the sample (i.e. specimens obtained by the sieve-method and Hand-sorting.)

Total number in sample, 218.

13.5	2	2	0.9	-	-	-	-	-	-
12.5	15	15	6.9	-	-	-	-	-	-
11.5	16	16	7.3	-	-	-	-	-	-
10.5	23	16	7.3	-	-	7	3.2	-	-
9.5	23	17	7.8	-	-	5	2.3	1	0.4
8.5	36	15	6.9	-	-	17	7.8	4	1.8
7.5	38	11	5.0	1	0.4	23	10.1	4	1.8
6.5	29	6	2.7	9	4.1	11	5.0	3	1.4
5.5	20	5	2.3	11	5.0	3	1.4	1	0.4
4.5	7	2	0.9	5	2.3	-	-	-	-
3.5	2	0.9%)							
2.5	5	2.3%)	unsexable.						
1.5	2	0.9%)							

Appendix B.

Table 3.

Details of a sample of *A. aquaticus* from Hatchmere, Cheshire.

A. Based on specimens obtained by the sieve-method only.

Total number in sample, 173.

Size of in group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
13.5	1	1	0.6	-	-	-	-	-	-
12.5	1	1	0.6	-	-	-	-	-	-
11.5	5	4	2.3	-	-	1	0.6	-	-
10.5	7	5	2.9	-	-	2	1.2	-	-
9.5	7	6	3.5	-	-	1	0.6	-	-
8.5	19	8	4.6	2	1.2	9	5.2	-	-
7.5	25	11	6.4	7	4.0	7	4.0	-	-
6.5	36	17	9.8	19	11.0	-	-	-	-
5.5	29	12	6.9	17	9.8	-	-	-	-
4.5	22	13	7.5	9	5.2	-	-	-	-
3.5	17	9.8%	) unsexable.						
2.5	4	2.3%	)						

B. Based on the 'total' number of specimens present in the sample (i.e. specimens obtained by the sieve-method and hand-sorting.)

Total number in sample, 183.

13.5	1	1	0.5	-	-	-	-	-	-
12.5	1	1	0.5	-	-	-	-	-	-
11.5	6	5	2.7	-	-	1	0.5	-	-
10.5	7	5	2.7	-	-	2	1.1	-	-
9.5	8	6	3.3	-	-	2	1.1	-	-
8.5	20	9	4.9	2	1.1	9	4.9	-	-
7.5	25	11	6.0	7	3.8	7	3.8	-	-
6.5	38	17	9.3	20	10.9	1	0.5	-	-
5.5	30	13	7.1	17	9.3	-	-	-	-
4.5	26	16	8.7	10	5.5	-	-	-	-
3.5	17	9.3%	} unsexable.						
2.5	4	2.2%	}						

Appendix B.

Table 4.

Details of a sample of *A. meridianus* from Padeswood Lake, Flintsh.

A. Based on specimens obtained by the sieve-method only.

Total number in sample, 374.

Size of group in m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
8.5	4	4	1.1	-	-	-	-	-	-
7.5	19	15	4.0	-	-	3	0.8	1	0.3
6.5	58	39	10.4	-	-	17	4.5	2	0.5
5.5	76	39	10.4	2	0.5	33	8.8	2	0.5
4.5	91	43	11.5	25	6.7	23	6.1	-	-
3.5	90	34	9.1	50	13.4	6	1.6	-	-
2.5	31	8.3%)	unsexable.						
1.5	5	1.3%)							

B. Based on the 'total' number of specimens present in the sample (i.e. specimens obtained by the sieve-method and hand-sorting.)

Total number in sample, 494.

Size of group in m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
8.5	5	5	1.0	-	-	-	-	-	-
7.5	27	21	4.2	1	0.2	3	0.6	2	0.4
6.5	81	56	11.3	-	-	23	4.7	2	0.4
5.5	108	47	9.5	3	0.6	55	11.1	3	0.6
4.5	114	53	10.7	37	7.5	24	4.9	-	-
3.5	112	44	8.9	62	12.6	6	1.2	-	-
2.5	42	8.5%)	unsexable.						
1.5	5	1.0%)							

Appendix B.

Table 5.

Details of a sample of *A. meridianus* from Hatchmere, Cheshire.

A. Based on specimens obtained by the sieve-method only.

Total number in sample, 56.

Size of in group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
8.5	1	1	1.8	-	-	-	-	-	-
7.5	3	3	5.4	-	-	-	-	-	-
6.5	7	7	12.5	-	--	-	-	-	-
5.5	17	13	23.2	-	-	4	7.1	-	-
4.5	13	3	5.4	7	12.5	3	5.4	-	-
3.5	15	3	5.4	12	21.4	-	-	-	-

B. Based on the 'total' number of specimens present in the sample (i.e. specimens obtained by the sieve-method and hand-sorting.)

Total number in sample, 69.

Size of in group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
8.5	1	1	1.4	-	-	-	-	-	-
7.5	3	3	4.3	-	-	-	-	-	-
6.5	9	9	13.0	-	-	-	-	-	-
5.5	21	14	20.3	-	-	7	10.1	-	-
4.5	17	4	5.8	8	11.6	5	7.2	-	-
3.5	18	4	5.8	14	20.3				

Appendix C

Table 1. Details of the monthly samples of *A. aquaticus* from Buckley Lake, Flintshire, collected from the 24th October 1957 until the 2nd November 1959.

Details of the monthly samples.

<u>A. aquaticus L.</u>, Buckley Lake, Flintshire.

Date of sampling: 24.X.57. Total number in sample, 264.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
11.5	2	2	0.8	-	-	-	-	-	-
10.5	3	3	1.1	-	-	-	-	-	-
9.5	11	9	3.4	2	0.8	-	-	-	-
8.5	26	23	8.6	3	1.1	-	-	-	-
7.5	24	16	6.0	8	3.0	-	-	-	-
6.5	29	16	6.0	13	4.9	-	-	-	-
5.5	33	20	7.5	13	4.9	-	-	2	0.8
4.5	53	27	10.2	26	9.7	-	-	-	-
3.5	43	16.2%)							
2.5	31	11.7%)		unsexable.					
1.5	9	3.4%)							

Date of sampling: 28.XI.57. Total number in sample, 221.

12.5	1	1	0.5	-	-	-	-	-	-
11.5	4	4	1.8	-	-	-	-	-	-
10.5	18	17	7.7	1	0.5	-	-	-	-
9.5	21	17	7.7	4	1.8	-	-	-	-
8.5	48	23	10.4	25	11.3	-	-	-	-
7.5	40	13	5.9	27	12.2	-	-	-	-
6.5	12	3	1.4	9	4.1	-	-	-	-
5.5	16	7	3.2	9	4.1	-	-	-	-
4.5	16	5	2.3	11	5.0	-	-	-	-
3.5	18	8.1%)							
2.5	20	9.1%)		unsexable.					
1.5	7	3.2%)							

Details of the monthly samples.

A. aquaticus L., Buckley Lake, Flintshire.

Date of sampling: 23.X11.57. Total number in sample, 301.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
12.5	5	5	1.7	-	-	-	-	-	-
11.5	11	11	3.7	-	-	-	-	-	-
10.5	23	21	7.0	2	0.7	-	-	-	-
9.5	44	34	11.3	10	3.3	-	-	-	-
8.5	76	40	13.3	35	11.7	1	0.3	-	-
7.5	47	12	4.0	35	11.7	-	-	-	-
6.5	17	7	2.3	10	3.3	-	-	-	-
5.5	31	9	3.0	22	7.3	-	-	-	-
4.5	27	15	5.0	12	4.0	-	-	-	-
3.5	16	5.3%)							
2.5	3	1.0%)		unsexable.					
1.5	1	0.3%)							

Date of sampling: 29.I.58. Total number in sample, 383.

12.5	3	3	0.8	-	-	-	-	-	-
11.5	3	3	0.8	-	-	-	-	-	-
10.5	20	17	4.4	3	0.8	-	-	-	-
9.5	25	15	3.9	10	2.6	-	-	-	-
8.5	52	21	5.5	31	8.1	-	-	-	-
7.5	42	11	2.9	31	8.1	-	-	-	-
6.5	39	9	2.3	30	7.8	-	-	-	-
5.5	51	22	5.8	29	7.5	-	-	-	-
4.5	44	17	4.4	27	7.0	-	-	-	-
3.5	49	12.8%)							
2.5	45	11.8%)		unsexable.					
1.5	10	2.6%)							

Details of the monthly samples.

<u>A. aquaticus L.</u>, Buckley Lake, Flintshire.

Date of sampling: 27.II.58. Total number in sample, 346.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
12.5	1	1	0.3	-	-	-	-	-	-
11.5	11	11	3.2	-	-	-	-	-	-
10.5	13	13	3.8	-	-	-	-	-	-
9.5	23	14	4.1	5	1.4	4	1.2	-	-
8.5	42	16	4.6	23	6.7	2	0.6	1	0.3
7.5	36	10	2.9	23	6.7	1	0.3	2	0.6
6.5	28	5	1.4	23	6.7	-	-	-	-
5.5	44	23	6.7	21	6.1	-	-	-	-
4.5	52	31	9.0	21	6.1	-	-	-	-
3.5	56	16.2%)							
2.5	30	8.7%)		unsexable.					
1.5	10	2.9%)							

Date of sampling: 27.III.58. Total number in sample, 330.

12.5	1	1	0.3	-	-	-	-	-	-
11.5	3	3	0.9	-	-	-	-	-	-
10.5	14	12	3.6	-	-	2	0.6	-	-
9.5	27	22	6.7	1	0.3	4	1.2	-	-
8.5	37	23	7.0	2	0.6	11	3.3	1	0.3
7.5	42	9	2.7	16	4.8	16	4.8	1	0.3
6.5	43	13	3.9	26	7.9	4	1.2	-	-
5.5	52	20	6.1	32	9.7	-	-	-	-
4.5	48	25	7.6	23	7.0	-	-	-	-
3.5	37	11.2%)							
2.5	22	7.3%)		unsexable.					
1.5	4	1.2%)							

Details of the monthly samples.

<u>A. aquaticus L.</u>, Buckley Lake, Flintshire.

Date of sampling: 25.1V.58. Total number in sample. 157.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
9.5	6	5	3.2	-	-	1	0.6	-	-
8.5	14	8	5.1	-	-	6	3.8	-	-
7.5	23	6	3.8	1	0.6	14	8.9	2	1.3
6.5	22	5	3.2	6	3.8	8	5.1	3	1.9
5.5	43	19	12.1	20	12.7	3	1.9	1	0.6
4.5	20	8	5.1	12	7.6	-	-	-	-
3.5	19	12.1%)							
2.5	7	4.5%)	unsexable,						
1.5	3	1.9%)							

Date of sampling : 27.V.58. Total number in sample. 240.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
11.5	2	2	0.8	-	-	-	-	-	-
10.5	2	1	0.4	-	-	1	0.4	-	-
9.5	9	6	2.5	-	-	2	0.8	1	0.4
8.5	26	16	6.7	9	3.9	1	0.4	-	-
7.5	47	32	13.3	5	2.1	5	2.1	5	2.1
6.5	55	23	9.6	18	7.5	8	3.3	6	2.5
5.5	51	16	6.7	24	10.0	8	3.3	3	1.2
4.5	34	11	4.6	22	9.2	-	-	1	0.4
3.5	6	2.5%)							
2.5	1	0.4%)	unsexable.						
1.5	7	2.9%)							

Details of the monthly samples.

A. aquaticus L., Buckley Lake, Flintshire.

Date of sampling: 25.VI.58. Total number in sample. 355.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches	
		No.	%.	No.	%.	No.	%.	No.	%.
10.5	2	2	0.6	-	-	-	-	-	-
9.5	5	4	1.1	-	-	-	-	1	0.3
8.5	25	18	5.1	5	1.4	-	-	2	0.6
7.5	18	3	0.8	5	1.4	7	2.0	3	0.8
6.5	38	10	2.8	13	3.6	12	3.4	3	0.8
5.5	55	27	7.6	23	6.5	3	0.8	2	0.6
4.5	70	32	9.0	38	10.7	-	-	-	-
3.5	79	22.3%)							
2.5	36	10.2%)		unsexable.					
1.5	27	7.6%)							

Date of sampling: 25.VII.58 Total number in sample. 524.

9.5	2	2	0.4	-	-	-	-	-	-
8.5	15	14	2.9	1	0.2	-	-	-	-
7.5	25	22	4.2	3	0.6	-	-	-	-
6.5	41	29	5.5	5	1.0	4	0.8	3	0.6
5.5	73	31	5.9	19	3.6	14	2.9	9	1.7
4.5	70	24	4.6	37	7.1	5	1.0	4	0.8
3.5	74	14.1%)							
2.5	144	27.5%)		unsexable.					
1.5	80	15.3%)							

Details of the monthly samples.

A. aquaticus L., Buckley Lake, Flintshire.

Date of sampling: 24.V111.58. Total number in sample, 157.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
10.5	1	1	0.6	-	-	-	-	-	-
9.5	0	-	-	-	-	-	-	-	-
8.5	4	4	2.5	-	-	-	-	-	-
7.5	10	10	6.4	-	-	-	-	-	-
6.5	13	7	4.5	2	1.3	4	2.5	-	-
5.5	25	13	8.3	6	3.8	5	3.2	1	0.6
4.5	31	13	8.3	16	10.2	2	1.3	-	-
3.5	27	17.2%)							
2.5	20	12.7%)	unsexable.						
1.5	26	16.6%)							

Date of sampling: 8.1X.58. Total number in sample, 165.

8.5	2	2	1.2	-	-	-	-	-	-
7.5	8	8	5.5	-	-	-	-	-	-
6.5	15	12	7.3	3	1.8	-	-	-	-
5.5	24	17	10.3	7	4.2	-	-	-	-
4.5	29	12	7.3	17	10.4	-	-	-	-
3.5	30	18.2%)							
2.5	27	16.4%)	unsexable.						
1.5	30	18.2%)							

Date of sampling: 27.1X.58. Total number in sample, 142.

8.5	1	1	0.7	-	-	-	-	-	-
7.5	3	3	2.1	-	-	-	-	-	-
6.5	15	15	10.6	-	-	-	-	-	-
5.5	15	7	4.9	7	4.9	1	0.7	-	-
4.5	24	11	7.7	13	9.1	-	-	-	-
3.5	22	15.5%)							
2.5	41	28.9%)	unsexable.						
1.5	21	14.8%)							

Details of the monthly samples.

A. aquaticus L., Buckley Lake, Flintshire.

Date of sampling: 24.X.58. Total number in sample, 169.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
10.5	2	2	1.2	-	-	-	-	-	-
9.5	10	10	5.9	-	-	-	-	-	-
8.5	10	6	3.6	4	2.4	-	-	-	-
7.5	23	13	7.7	10	5.9	-	-	-	-
6.5	31	16	9.5	15	8.9	-	-	-	-
5.5	33	21	12.5	12	7.1	-	-	-	-
4.5	29	14	8.3	15	8.9	-	-	-	-
3.5	21	12.5%)							
2.5	9	5.3%)		unsexable.					
1.5	1	0.6%)							

Date of sampling: 29.XI.58. Total number in sample, 282.

12.5	3	3	1.1	-	-	-	-	-	-
11.5	19	19	6.7	-	-	-	-	-	-
10.5	29	28	9.9	1	0.3	-	-	-	-
9.5	28	22	7.8	6	2.1	-	-	-	-
8.5	53	30	10.6	23	8.2	-	-	-	-
7.5	36	16	5.7	20	7.1	-	-	-	-
6.5	24	12	4.3	12	4.3	-	-	-	-
5.5	42	17	6.0	25	8.8	-	-	-	-
4.5	28	9	3.2	19	6.7	-	-	-	-
3.5	17	6.0%)							
2.5	3	1.1%)		unsexable.					

Details of the monthly samples.

A. aquaticus L., Buckley Lake, Flintshire.

Date of sampling: 22.XII.58. Total number in sample, 122.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
12.5	1	1	0.8	-	-	-	-	-	-
11.5	11	11	9.0	-	-	-	-	-	-
10.5	11	10	8.2	1	0.8	-	-	-	-
9.5	21	15	12.3	6	4.9	-	-	-	-
8.5	20	15	12.3	5	4.1	-	-	-	-
7.5	12	8	6.6	4	3.3	-	-	-	-
6.5	11	5	4.1	6	4.9	-	-	-	-
5.5	11	5	4.1	6	4.9	-	-	-	-
4.5	16	8	6.6	8	6.6	-	-	-	-
3.5	8		6.6%)	Unsexable.					

Date of sampling: 24.I.59. Total number in sample, 99.

12.5	5	5	5.0	-	-	-	-	-	-
11.5	8	7	7.1	1	1.0	-	-	-	-
10.5	15	12	12.1	3	3.0	-	-	-	-
9.5	9	6	6.1	3	3.0	-	-	-	-
8.5	18	9	9.1	9	9.1	-	-	-	-
7.5	18	8	8.1	10	10.1	-	-	-	-
6.5	6	3	3.0	3	3.0	-	-	-	-
5.5	13	7	7.1	6	6.1	-	-	-	-
4.5	5	3	3.0	2	2.0	-	-	-	-
3.5	2		2.0%)	unsexable.					

10.19

Details of the monthly samples.

<u>A. aquaticus L.</u>, Buckley Lake, Flintshire.

Date of sampling: 3.111.59. Total number in sample, 358.

Size of group m.m.	Total in group	Males No.	%	Females with small lamellae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
12.5	1	1	0.3	-	-	-	-	-	-
11.5	3	3	0.8	-	-	-	-	-	-
10.5	17	17	4.7	-	-	-	-	-	-
9.5	22	22	6.1	-	-	-	-	-	-
8.5	44	26	7.3	17	4.7	1	0.3	-	-
7.5	44	21	5.9	21	5.9	2	0.6	-	-
6.5	32	13	3.6	17	4.7	2	0.6	-	-
5.5	37	18	5.0	19	5.3	-	-	-	-
4.5	43	17	4.7	26	7.3	-	-	-	-
3.5	51	14.2%)							
2.5	50	14.0%) unsexable.							
1.5	14	3.9%)							

Date of sampling: 30.111.59. Total number in sample, 173.

12.5	3	3	1.7	-	-	-	-	-	-
11.5	3	3	1.7	-	-	-	-	-	-
10.5	9	9	5.2	-	-	-	-	-	-
9.5	7	4	2.3	-	-	3	1.7	-	-
8.5	15	12	7.0	-	-	3	1.7	-	-
7.5	14	4	2.3	1	0.6	7	4.0	2	1.2
6.5	17	7	4.0	6	3.4	4	2.3	-	-
5.5	19	7	4.0	11	6.4	1	0.6	-	-
4.5	29	14	8.1	15	8.7	-	-	-	-
3.5	36	21.0%)							
2.5	20	11.6%) unsexable.							
1.5	1	0.6%)							

Details of the monthly samples.

<u>A. aquaticus L.</u>, Buckley Lake, Flintshire.

Date of sampling: 27.lV.59. Total number in sample, 178.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
12.5	1	1	0.6	-	-	-	-	-	-
11.5	2	2	1.2	-	-	-	-	-	-
10.5	3	3	1.7	-	-	-	-	-	-
9.5	3	2	1.2	-	-	1	0.6	-	-
8.5	18	10	5.6	-	-	6	3.4	2	1.2
7.5	19	8	4.5	-	-	9	5.0	2	1.2
6.5	22	11	6.2	3	1.7	8	4.5	-	-
5.5	47	16	9.0	21	11.8	10	5.6	1	0.6
4.5	30	13	7.3	16	9.0	-	-	-	-
3.5	27	15.2%)							
2.5	5	2.8%) unsexable.							
1.5	1	0.6%)							

Date of sampling: 27.V.59. Total number in sample, 168.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
10.5	1	1	0.6	-	-	-	-	-	-
9.5	0	-	-	-	-	-	-	-	-
8.5	1	1	0.6	-	-	-	-	-	-
7.5	3	3	1.8	-	-	-	-	-	-
6.5	7	1	0.6	-	-	6	3.6	-	-
5.5	13	6	3.6	2	1.2	4	2.4	1	0.6
4.5	9	2	1.2	6	3.6	1	0.6	-	-
3.5	13	7.7%)							
2.5	57	33.9%) unsexable.							
1.5	64	38.1%)							

Details of the monthly samples.

A. aquaticus L., Buckley Lake, Flintshire.

Date of sampling: 30.VI.59. Total number in sample, 188.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
7.5	1	1	0.5	-	-	-	-	-	-
6.5	16	15	8.0	1	0.5	-	-	-	-
5.5	42	17	9.0	14	7.4	10	5.3	1	0.5
4.5	54	20	10.6	28	14.9	4	2.1	2	1.1
3.5	36	19.2%)							
2.5	20	10.6%)	unsexable.						
1.5	19	10.1%)							

Date of sampling: 30.VII.59. Total number in sample, 155.

7.5	6	6	3.9	-	-	-	-	-	-
6.5	19	18	11.6	1	0.6	-	-	-	-
5.5	36	24	15.5	5	3.2	7	4.5	-	-
4.5	39	11	7.1	20	12.9	7	4.5	1	0.6
3.5	27	17.4%)							
2.5	19	12.3%)	unsexable.						
1.5	9	5.8%)							

Date of sampling: 7.IX.59. Total number in sample, 236.

8.5	1	1	0.4	-	-	-	-	-	-
7.5	8	8	3.4	-	-	-	-	-	-
6.5	39	38	16.1	1	0.4	-	-	-	-
5.5	56	42	17.8	10	4.2	4	1.7	-	-
4.5	58	30	12.7	17	7.2	10	4.2	1	0.4
3.5	35	14.8%)							
2.5	25	10.6%)	unsexable.						
1.5	14	5.9%)							

Details of the monthly samples.

<u>A. aquaticus L.</u>, Buckley Lake, Flintshire.

Date of sampling: 6.X.59. Total number in sample, 279.

Size of in group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
8.5	7	7	2.5	-	-	-	-	-	-
7.5	46	44	15.8	2	0.7	-	-	-	-
6.5	58	41	14.7	17	6.1	-	-	-	-
5.5	73	40	14.3	31	11.1	2	0.7	-	-
4.5	41	16	5.7	25	9.0	-	-	-	-
3.5	25	9.0%)							
2.5	22	7.9%)	unsexable.						
1.5	7	2.5%)							

Date of sampling: 2.XI.59. Total number in sample, 202.

Size of in group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
9.5	3	3	1.5	-	-	-	-	-	-
8.5	10	9	4.4	1	0.5	-	-	-	-
7.5	33	22	10.9	11	5.5	-	-	-	-
6.5	52	25	12.4	27	13.4	-	-	-	-
5.5	45	16	7.9	29	14.3	-	-	-	-
4.5	24	12	5.9	12	5.9	-	-	-	-
3.5	19	9.4%o)							
2.5	13	6.4%)	unsexable.						
1.5	3	1.5%)							

Appendix C

Table 2. Details of the monthly samples of *A. meridianus* from Padeswood Lake, Flintshire, collected from the 24th October 1957 until the 2nd November 1959.

Details of the monthly samples.

A. meridianus Rac., Padeswood Lake, Flintshire.

Date of sampling: 24.X.57. Total number in sample, 261.

Size of group in m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
8.5	1	1	0.5	-	-	-	-	-	-
7.5	9	6	2.4	2	0.8	1	0.4	-	-
6.5	14	7	2.7	4	1.6	2	0.8	1	0.4
5.5	53	37	14.2	8	3.1	7	2.7	1	0.4
4.5	75	27	10.3	47	18.0	1	0.4	-	-
3.5	53	10	3.4	43	16.9	-	-	-	-
2.5	41	15.7%)	unsexable						
1.5	15	5.7%)							

Date of sampling: 28.XI.57. Total number in sample, 262.

Size of group in m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
8.5	2	2	0.8	-	-	-	-	-	-
7.5	2	2	0.8	-	-	-	-	-	-
6.5	12	9	3.4	3	1.2	-	-	-	-
5.5	62	38	14.5	23	8.8	1	0.4	-	-
4.5	72	31	11.8	41	15.6	-	-	-	-
3.5	57	29	11.1	28	10.7	-	-	-	-
2.5	36	13.6%)	unsexable.						
1.5	19	7.3%)							

Details of the monthly samples.

<u>A. meridianus</u> Rac., Padeswood Lake, Flintshire.

Date of sampling: 23.XII.57. Total number in sample, 899.
(only ¼ of sample actually analysed)

Size of in group m.m.	Total in group	Males		Females with small lamallae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
9.5	0.5	0.5	0.2	-	-	-	-	-	-
8.5	3.2	2.2	1.0	1	0.4	-	-	-	-
7.5	13.5	8.5	3.8	5	2.2	-	-	-	-
6.5	35	17	7.6	18	8.0	-	-	-	-
5.5	53	22	9.8	31	13.8	-	-	-	-
4.5	60	23	10.2	37	16.5	-	-	-	-
3.5	37	11	4.9	26	11.6	-	-	-	-
2.5	17.5	7.8%)	unsexable.						
1.5	5	2.2%)							

Date of sampling: 29.1.58. Total number in sample, 375.

Size of in group m.m.	Total in group	Males		Females with small lamallae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
9.5	2	2	0.5	-	-	-	-	-	-
8.5	6	5	1.3	1	0.3	-	-	-	-
7.5	8	3	0.8	5	1.3	-	-	-	-
6.5	43	14	3.7	28	7.5	1	0.3	-	-
5.5	105	30	8.0	74	19.8	1	0.3	-	-
4.5	120	27	7.2	93	24.9	-	-	-	-
3.5	51	16	4.2	35	9.5	-	-	-	-
2.5	27	7.2%)	unsexable.						
1.5	13	3.4%)							

Details of the monthly samples.

A. meridianus Rac., Padeswood Lake, Flintshire.

Date of sampling: 27.11.58. Total number in sample, 209.

Size of in group m.m.	Total in group	Males No.	%	Females with small lamallae No.	%	Ovigerous females No.	%	Females with empty pouches No.	%
10.5	1	1	0.5	-	-	-	-	-	-
9.5	3	3	1.5	-	-	-	-	-	-
8.5	9	5	2.5	1	0.5	3	1.5	-	-
7.5	36	7	3.3	16	7.7	12	5.7	1	0.5
6.5	59	3	1.5	45	21.5	10	4.8	1	0.5
5.5	56	14	6.7	40	19.1	2	1.0	-	-
4.5	32	7	3.3	25	12.0	-	-	-	-
3.5	11	3	1.5	8	3.8	-	-	-	-
2.5	2	1.0%) unsexable.							

Date of sampling: 27.111.58. Total number in sample, 328.

9.5	8	3	0.9	-	-	3	0.9	2	0.6
8.5	19	10	3.0	1	0.3	5	1.5	3	0.9
7.5	40	12	3.7	1	0.3	26	7.9	1	0.3
6.5	104	17	5.2	9	2.7	75	22.9	3	0.9
5.5	85	5	1.5	29	8.8	49	14.9	2	0.6
4.5	49	14	4.3	33	10.1	2	0.6	-	-
3.5	19	11	3.3	8	2.5	-	-	-	-
2.5	4	1.2%) unsexable.							

Date of sampling: 25.1V.58. Total number in sample, 530.
(only ½ of sample analysed).

9.5	3.5	2	0.8	0.5	0.2	0.5	0.2	0.5	0.2
8.5	13	3	1.1	2	0.8	6	2.3	2	0.8
7.5	77	9	3.4	2	0.8	52	19.6	14	5.3
6.5	88	10	3.8	-	-	73	27.5	5	1.9
5.5	62	5	1.9	20	7.5	34	12.8	3	1.1
4.5	16	3.5	1.3	12.5	4.7	-	-	-	-
3.5	4	3	1.1	1	0.4	-	-	-	-
2.5	0.5	0.2%)							
1.5	1	0.4%) unsexable.							

Details of the monthly samples.

<u>A. meridianus</u> Rac., Padeswood Lake, Flintshire.

Date of sampling: 27.V.58. Total number in sample, 632.

Size of in group m.m.	Total in group	Males No.	%	Females with small lamallae No.	%	Ovigerous females No.	%	Females with empty pouches No.	%
9.5	6	2	0.3	-	-	4	0.6	-	-
8.5	17	1	0.2	3	0.5	12	1.9	1	0.2
7.5	44	10	1.6	13	2.1	15	2.3	6	0.9
6.5	51	17	2.7	7	1.1	17	2.7	10	1.6
5.5	41	11	1.7	6	0.9	20	3.2	4	0.6
4.5	20	8	1.3	9	1.5	2	0.3	1	0.2
3.5	34	11	1.7	23	3.7	-	-	-	-
2.5	175	27.7%	)	unsexable.					
1.5	244	38.6%	)						

Date of sampling: 25.Vl.58. Total number in sample 870.

8.5	7	1	0.1	2	0.2	-	-	4	0.4
7.5	7	1	0.1	-	-	2	0.2	4	0.4
6.5	14	6	0.7	2	0.2	3	0.3	3	0.3
5.5	17	7	0.8	7	0.8	1	0.1	2	0.2
4.5	85	59	6.8	25	2.9	1	0.1	-	-
3.5	193	77	8.9	116	13.3	-	-	-	-
2.5	274	31.5%	)	unsexable.					
1.5	273	31.4%	)						

Date of sampling: 25.Vll.58. Total number in sample, 882.

8.5	1	-	-	1	0.1	-	-	-	-
7.5	2	-	-	1	0.1	1	0.1	-	-
6.5	8	5	0.6	2	0.2	1	0.1	-	-
5.5	35	24	2.7	5	0.6	5	0.6	1	0.1
4.5	94	58	6.6	19	2.2	17	2.0	-	-
3.5	191	111	12.6	80	9.0	-	-	-	-
2.5	270	30.6%	)	unsexable.					
1.5	281	31.8%	)						

Details of the monthly samples.

A. meridianus Rac., Padeswood Lake, Flintshire.

Date of sampling: 24.VII.58. Total number in sample, 487.

Size of in group m.m.	Total in group	Males No.	%	Females with small lamallae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
6.5	6	3	0.6	2	0.4	1	0.2	-	-
5.5	57	36	7.4	6	1.2	13	2.7	2	0.4
4.5	106	29	5.9	41	8.4	33	6.7	3	0.6
3.5	127	46	9.5	81	16.6	-	-	-	-
2.5	149	30.6%	)	unsexable.					
1.5	42	8.6%	)						

Date of sampling: 27.IX.58. Total number in sample, 342.

6.5	10	9	2.6	-	-	1	0.3	-	-
5.5	38	16	4.7	6	1.8	16	4.7	-	-
4.5	89	27	7.9	30	8.8	31	9.1	1	0.3
3.5	67	29	8.5	38	11.1	-	-	-	-
2.5	98	28.8%	)	unsexable.					
1.5	40	11.7%	)						

Date of sampling 24.X.58. Total number in sample, 255.

7.5	4	2	0.8	2	0.8	-	-	-	-
6.5	6	3	1.1	3	1.1	-	-	-	-
5.5	38	16	6.3	20	7.8	1	0.4	1	0.4
4.5	72	30	11.4	38	14.9	3	1.1	1	0.4
3.5	62	28	10.6	34	13.4	-	-	-	-
2.5	48	18.4%	)	unsexable.					
1.5	25	9.8%	)						

Details of the monthly samples.

A. meridianus Rac., Padeswood Lake, Flintshire.

Date of sampling 29.Xl.58. Total number in sample, 272.

Size of in group m.m.	Total in group	Males No.	Males %.	Females with small lamallea No.	Females with small lamallea %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
8.5	6	6	2.2	-	-	-	-	-	-
7.5	11	8	2.9	3	1.1	-	-	-	-
6.5	28	13	4.8	15	5.5	-	-	-	-
5.5	57	26	9.6	30	11.0	-	-	1	0.4
4.5	80	28	10.3	52	19.1	-	-	-	-
3.5	55	14	5.1	41	15.1	-	-	-	-
2.5	27	9.9%)		unsexable.					
1.5	8	2.9%)							

Date of sampling 22.X11.58. Total number in sample, 189.

9.5	2	2	1.0	-	-	-	-	-	-
8.5	3	3	1.6	-	-	-	-	-	-
7.5	4	3	1.6	1	0.5	-	-	-	-
6.5	22	10	5.3	12	6.3	-	-	-	-
5.5	44	20	10.6	24	12.7	-	-	-	-
4.5	62	17	9.0	44	23.3	-	-	1	0.5
3.5	33	6	3.2	27	14.3	-	-	-	-
2.5	16	8.6%)		unsexable.					
1.5	3	1.6%)							

Date of sampling 24.1.59. Total number in sample, 255.

9.5	3	2	0.8	1	0.4	-	-	-	-
8.5	7	7	2.8	-	-	-	-	-	-
7.5	22	15	5.9	7	2.8	-	-	-	-
6.5	47	17	6.7	30	11.8	-	-	-	-
5.5	63	14	5.5	49	19.2	-	-	-	-
4.5	67	13	5.1	54	21.2	-	-	-	-
3.5	34	5	1.9	29	11.4	-	-	-	-
2.5	10	3.9%)		unsexable.					
1.5	2	0.8%)							

Details of the monthly samples.

<u>A. meridianus</u> Rac., Padeswood Lake, Flintshire.

Date of sampling: 3.111.59. Total number in sample, 315.

Size of in f group m.m.	Total in group	Males No.	%	Females with small lamallae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
9.5	3	3	1.0	-	-	-	-	-	-
8.5	14	14	4.4	-	-	-	-	-	-
7.5	15	10	3.2	-	-	5	1.6	-	-
6.5	36	17	5.4	10	3.2	9	2.9	-	-
5.5	86	25	7.9	57	18.1	4	1.2	-	-
4.5	85	20	6.3	65	20.6	-	-	-	-
3.5	43	14	4.4	29	9.2	-	-	-	-
2.5	26	8.2%)	unsexable.						
1.5	7	2.2%)							

Date of sampling: 30.111.59. Total number in sample, 177.

Size of in f group m.m.	Total in group	Males No.	%	Females with small lamallae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
8.5	2	2	1.1	-	-	-	-	-	-
7.5	15	8	4.5	1	0.5	5	2.8	1	0.5
6.5	24	9	5.0	1	0.5	13	7.3	1	0.5
5.5	35	5	2.8	23	13.0	7	4.0	-	-
4.5	40	11	6.2	28	16.0	1	0.5	-	-
3.5	36	12	6.7	24	13.5	-	-	-	-
2.5	19	10.7%)	unsexable.						
1.5	6	3.4%)							

Date of sampling: 27.1V.59. Total number in sample, 133.

Size of in f group m.m.	Total in group	Males No.	%	Females with small lamallae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
8.5	1	1	0.7	-	-	-	-	-	-
7.5	2	-	-	1	0.7	-	-	1	0.7
6.5	20	5	3.7	3	2.2	10	7.5	2	1.5
5.5	24	5	3.7	6	4.5	12	9.0	1	0.7
4.5	30	13	10.0	17	13.0	-	-	-	-
3.5	25	14	11.5	11	8.3	-	-	-	-
2.5	29	21.8%)	unsexable.						
1.5	2	1.5%)							

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Details of the monthly samples.

A. meridianus Rac., Padeswood Lake, Flintshire.

Date of sampling 27.V.59. Total number in sample, 153.

Size of in group m.m.	Total in group	Males No.	Males %.	Females with small lamallae No.	Females with small lamallae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
7.5	3	-	-	1	0.7	2	1.3	-	-
6.5	9	6	4.0	1	0.7	2	1.3	-	-
5.5	27	6	4.0	4	2.6	12	8.0	5	3.3
4.5	23	11	7.0	10	6.5	2	1.3	-	-
3.5	27	15	9.9	12	7.8	-	-	-	-
2.5	32	20.8%)		unsexable.					
1.5	32	20.8%)							

Date of sampling 30.vl.59. Total number in sample, 112.

7.5	3	-	-	-	-	-	-	3	2.7
6.5	1	1	0.9	-	-	-	-	-	-
5.5	3	1	0.9	-	-	2	1.8	-	-
4.5	12	6	5.4	1	0.9	5	4.5	-	-
3.5	20	11	9.9	9	8.0	-	-	-	-
2.5	27	24.1%)		unsexable.					
1.5	46	41.1%)							

Date of sampling 30.Vll.59. Total number in sample, 192.

6.5	7	7	3.6	-	-	-	-	-	-
5.5	38	33	17.2	1	0.5	2	1.0	2	1.0
4.5	69	13	6.7	24	12.5	32	16.7	-	-
3.5	49	16	8.3	32	16.7	1	0.5	-	-
2.5	27	14.1%)		unsexable.					
1.5	2	1.0%)							

Details of the monthly samples.

A. meridianus Rac., Padeswood Lake, Flintshire.

Date of sampling 7.1X.59. Total number in sample, 104.

Size of in group m.m.	Total in group	Males		Females with small lamallae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
7.5	3	2.9	-	-	-	-	-	-	-
6.5	10	7	6.7	1	1.0	1	1.0	1	1.0
5.5	20	7	6.7	6	5.7	6	5.7	1	1.0
4.5	28	6	5.7	12	11.4	10	9.5	-	-
3.5	19	8	7.7	11	10.5	-	--	-	-
2.5	20	19.0%)	unsexable.						
1.5	4	3.8-%)							

Date of sampling 6.X.59. Total number in sample, 122.

7.5	1	1	0.9	-	-	-	-	--	-
6.5	3	3	2.4	-	-	-	-	-	-
5.5	14	7	5.7	3	2.4	2	1.6	2	1.6
4.5	14	3	2.4	6	4.9	3	2.4	2	1.6
3.5	35	18	14.6	17	13.8	-	-	-	-
2.5	37	30.1%)	unsexable						
1.5	18	14.6%)							

Date of sampling 2.X1.59. Total number in sample, 134.

8.5	1	1	0.7	-	-	-	-	-	-
7.5	2	2	1.5	-	-	-	-	-	-
6.5	15	10	7.5	5	3.7	-	-	-	-
5.5	33	15	11.1	18	13.4	-	-	-	-
4.5	37	12	9.0	25	18.6	-	-	-	-
3.5	33	13	9.7	20	15.0	-	-	-	-
2.5	10	7.5%)	unsexable.						
1.5	3	2.2%)							

Details of the regular samples from Llyn Llywenan, Anglesey.

<u>A. aquaticus</u> (L.)

Date of sampling 10.X.57. Total number in sample, 69.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
9.5	1	-	-	1	1.5	-	-	-	-
8.5	4	4	5.8	-	-	-	-	-	-
7.5	14	7	10.1	7	10.1	-	-	-	-
6.5	15	9	13.0	6	8.7	-	-	-	-
5.5	12	8	11.6	4	5.8	-	-	-	-
4.5	16	7	10.1	9	13.0	-	-	-	-
3.5	7	10.1%)	unsexable.						

Date of sampling 12.X11.57. Total number in sample, 85.

11.5	1	1	1.2	-	-	-	-	-	-
10.5	4	4	4.7	-	-	-	-	-	-
9.5	2	1	1.2	1	1.2	-	-	-	-
8.5	7	5	5.9	2	2.4	-	-	-	-
7.5	19	12	14.1	7	8.2	-	-	-	-
6.5	9	4	4.7	5	5.9	-	-	-	-
5.5	12	3	3.5	9	10.6	-	-	-	-
4.5	5	2	2.4	3	3.5	-	-	-	-
3.5	15	17.7%)							
2.5	7	8.2%)	unsexable.						
1.5	4	4.7%)							

Details of the regular samples from Llyn Llywenan, Anglesey.

A. aquaticus (L.)

Date of sampling 21.11.58. Total number in sample, 100.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches	
		No.	%.	No.	%.	No.	%.	No.	%.
11.5	3	3	3	-	-	-	-	-	-
10.5	3	3	3	-	-	-	-	-	-
9.5	12	12	12	-	-	-	-	-	-
8.5	22	16	16	2	2	4	4	-	-
7.5	26	9	9	13	13	4	4	-	-
6.5	19	2	2	14	14	3	3	-	-
5.5	6	3	3	3	3	-	-	-	-
4.5	6	1	1	5	5	-	-	-	-
3.5	2	2%)	Unsexable.						
2.5	1	1%)							

Date of sampling 17.1V.58. Total number in sample, 129.

9.5	4	-	-	-	-	4	3.1	-	-
8.5	25	2	1.6	-	-	22	16.5	1	0.8
7.5	41	5	3.9	-	-	33	25.6	3	2.3
6.5	18	3	2.3	3	2.3	12	9.3	-	-
5.5	16	10	7.8	6	4.6	-	-	-	-
4.5	9	4	3.1	5	3.9	-	-	-	-
3.5	12	9.3%)							
2.5	4	3.1%) unsexable.							

Details of the regualr samples from Llyn Llywenan, Anglesey.

A. aquaticus (L.)

Date of sampling 30.Vl.58. Total number in sample, 212.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
8.5	1	1	0.5	-	-	-	-	-	-
7.5	5	4	1.9	1	1.5	-	-	-	-
6.5	4	3	1.4	1	1.5	-	-	-	-
5.5	28	21	9.9	3	1.4	3	1.4	1	0.5
4.5	56	29	13.7	24	11.3	2	1.0	1	0.5
3.5	61	28.8%)							
2.5	47	22.2%)	unsexable.						
1.5	10	4.7%)							

Date of sampling 21.1X.58. Total number in sample, 284.

8.5	1	-	-	1	0.4	-	-	-	-
7.5	1	1	0.4	-	-	-	-	-	-
6.5	7	6	2.1	-	-	1	0.4	-	-
5.5	32	18	6.3	12	4.2	2	0.7	-	-
4.5	66	21	7.4	43	15.2	-	-	2	0.7
3.5	65	22.9%)							
2.5	71	25.0%)	unsexable).						
1.5	42	14.8%)							

Details of the regular samples from Llyn Llywenan, Anglesey.

A. meridianus Rac.

Date of sampling 10.X.57. Total number in sample, 293.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches	
		No.	%.	No.	%.	No.	%.	No.	%.
7.5	1	1	0.3	-	-	-	-	-	-
6.5	20	20	6.8	-	-	-	-	-	-
5.5	79	73	24.9	5	1.7	1	0.3	-	-
4.5	77	41	14.0	25	8.5	10	3.4	1	0.3
3.5	58	24	8.2	23	7.8	8	2.7	3	1.0
2.5	39	13.3%)	unsexable.						
1.5	19	6.5%)							

Date of sampling 12.X11.57. Total number in sample, 234.

9.5	2	2	0.9	-	-	-	-	-	-
8.5	1	1	0.4	-	-	-	-	-	-
7.5	8	8	3.4	-	-	-	-	-	-
6.5	18	16	6.8	2	0.9	-	-	-	-
5.5	36	23	9.8	13	5.5	-	-	-	-
4.5	57	33	14.1	24	10.3	-	-	-	-
3.5	59	30	12.8	29	12.4	-	-	-	-
2.5	36	15.4%)	unsexable.						
1.5	17	7.3%)							

Date of sampling 21.11.58. Total number in sample, 212.

9.5	1	1	0.5	-	-	-	-	-	-
8.5	3	3	1.4	-	-	-	-	-	-
7.5	32	30	14.1	1	0.5	1	0.5	-	-
6.5	43	32	15.1	6	2.8	5	2.4	-	-
5.5	64	23	10.8	31	14.6	10	4.7	-	-
4.5	34	15	7.1	18	8.5	1	0.5	-	-
3.5	19	7	8	12	5.7	-	-	-	-
2.5	16	7.5 %)	unsexable.						

Details of the regular samples from Llyn Llywenan, Anglesey.

A. meridianus Rac.

Date of sampling 17.1V.58. Total number in sample, 173

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
7.5	1	1	0.6	-	-	-	-	-	-
6.5	11	9	5.2	-	-	1	0.6	1	0.6
5.5	38	20	11.5	2	1.2	12	6.9	4	2.3
4.5	58	26	14.9	20	11.5	12	6.9	0	-
3.5	45	25	14.4	20	11.5	2	-	-	-
2.5	20	11.5%) unsexable.							

6

Date of sampling 30.Vl.58. Total number in sample, 261.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
6.5	3	3	1.1	-	-	-	-	-	-
5.5	11	8	3.1	-	-	-	-	3	1.1
4.5	25	17	6.5	4	1.5	3	1.1	1	0.4
3.5	88	53	20.3	25	9.6	10	3.8	-	-
2.5	105	39.9%) unsexable.							
1.5	29	11.0%)							

2

Date of sampling 21.1X.58. Total number in sample,140.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
5.5	3	2	1.4	1	0.7	-	-	-	-
4.5	49	40	28.5	4	2.8	5	3.6	-	-
3.5	33	18	12.8	10	7.1	5	3.6	-	-
2.5	42	30.0%) unsexable.							
1.5	13	9.3%)							

[illegible]

Appendix C

Table 4. Details of the regular samples of *A. aquaticus* and *A. meridianus* from Hatchmere, Cheshire, collected from the 10th June 1959 until the 30th November 1959.

Details of the regular samples from Hatchmere, Cheshire.

A. aquaticus L.

Date of sampling 10.VI.59. Total number in sample, 185.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty puches. No.	Females with empty puches. %.
8.5	2	2	1.1	-	-	-	-	-	-
7.5	3	1	0.5	1	0.5	1	0.5	-	-
6.5	7	2	1.1	4	2.2	1	0.5	-	-
5.5	14	7	3.8	5	2.7	2	1.1	-	-
4.5	33	20	10.8	13	7.0	-	-	-	-
3.5	46	24.9%)							
2.5	60	32.4%)	unsexable.						
1.5	20	10.8%)							

Date of sampling 30.VI.59. Total number in sample, 332.

8.5	6	5	1.5	-	-	1	0.3	-	-
7.5	8	7	2.1	1	0.3	-	-	-	-
6.5	19	14	4.2	-	-	4	1.2	1	0.3
5.5	40	14	4.2	20	6.0	5	1.5	1	0.3
4.5	62	25	7.5	34	10.2	3	0.9	-	-
3.5	49	14.8%)							
2.5	56	16.9%)	unsexable.						
1.5	92	27.7%)							

Date of sampling 14.VII.59. Total number in sample, 228.

8.5	1	-	-	1	0.4	-	-	-	-
7.5	5	5	2.2	-	-	-	-	-	-
6.5	5	4	1.8	-	-	1	0.4	-	-
5.5	20	3	1.3	10	4.4	7	3.1	-	--
4.5	29	17	7.4	11	4.8	1	0.4	-	-
3.5	34	14.9%)							
2.5	56	24.6%)	unsexable.						
1.5	78	34.2%)							

Details of the regular samples from Hatchmere, Cheshire.

A. aquaticus L.

Date of sampling 31.V11.59 Total number in sample, 160.

Size of group m.m.	Total in group	Males No.	%	Females with small lamellae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
7.5	3	2	1.3	1	0.6	-	-	-	-
6.5	7	5	3.1	-	-	-	-	2	1.2
5.5	16	9	5.6	3	1.9	3	1.9	1	0.6
4.5	23	12	7.5	9	5.6	1	0.6	1	0.6
3.5	27	16.9%)							
2.5	54	33.7%)	unsexable.						
1.5	30	18.7%)							

Date of sampling 13.V111.59 Total number in sample, 233.

Size of group m.m.	Total in group	Males No.	%	Females with small lamellae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
8.5	1	1	0.4	-	-	-	-	-	-
7.5	5	5	2.1	-	-	-	-	-	-
6.5	6	6	2.6	-	-	-	-	-	-
5.5	20	8	3.4	2	0.8	9	3.9	1	0.4
4.5	25	14	6.0	9	3.9	2	0.8	-	-
3.5	52	22.3%)							
2.5	66	28.3%)	unsexable.						
1.5	58	24.9%)							

Date of sampling 7.1X.59. Total number in sample, 418.

Size of group m.m.	Total in group	Males No.	%	Females with small lamellae No.	%	Ovigerous females No.	%	Females with empty pouches. No.	%
7.5	4	4	1.0	-	-	-	-	-	-
6.5	17	17	4.1	-	-	-	-	-	-
5.5	47	32	7.7	8	1.9	4	1.0	3	0.7
4.5	70	46	11.0	22	5.3	2	0.5	-	-
3.5	88	21.0%)							
2.5	110	26.3%)	unsexable.						
1.5	82	19.6%)							

Details of the regular samples from Hatchmere, Cheshire.

A. aquaticus L.

Date of sampling 16.1X.59. Total number in sample, 247.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
8.5	1	1	0.4	-	-	-	-	-	-
7.5	3	3	1.2	-	-	-	-	-	-
6.5	14	12	4.9	1	0.4	1	0.4	-	-
5.5	34	23	9.3	9	3.6	-	-	2	0.8
4.5	44	29	11.7	15	6.1	-	-	-	-
3.5	55	22.3%	)						
2.5	36	14.6%	)	unsexable.					
1.5	60	24.3%	)						

Date of sampling 7.X.59. Total number in sample, 204.

8.5	4	4	2.0	-	-	-	-	-	-
7.5	3	3	1.5	-	-	-	-	-	-
6.5	22	17	8.3	5	2.5	-	-	-	-
5.5	44	23	11.3	21	10.3	-	-	-	-
4.5	34	17	8.3	17	8.3	-	-	-	-
3.5	35	17.2%	)						
2.5	24	10.8%	)	unsexable.					
1.5	38	18.6%	)						

Date of sampling 19.X.59. Total number in sample, 166.

9.5	1	1	0.6	-	-	-	-	-	-
8.5	13	12	7.3	1	0.6	-	-	-	-
7.5	21	10	6.0	11	6.6	-	-	-	-
6.5	20	13	7.9	7	4.2	-	-	-	-
5.5	14	10	6.0	4	2.4	-	-	-	-
4.5	17	10	6.0	7	4.2	-	-	-	-
3.5	19	11.4%	)						
2.5	36	21.7%	)	unsexable.					
1.5	25	15.1%	)						

Details of the regular samples from Hatchmere, Cheshire.

A. aquaticus L.

Date of sampling 2.XI.59. Total number in sample, 62.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
9.5	2	1	1.6	1	1.6	-	-	-	-
8.5	2	2	3.2	-	-	-	-	-	-
7.5	8	4	6.4	4	6.4	-	-	-	-
6.5	7	3	4.8	4	6.4	-	-	-	-
5.5	6	5	8.1	1	1.6	-	-	-	-
4.5	6	5	8.1	1	1.6	-	-	-	-
3.5	7	11.3%)							
2.5	13	21.0%) unsexable.							
1.5	11	17.7%)							

Date of sampling 16.XI.59. Total number in sample, 336.

11.5	2	2	0.6	-	-	-	-	-	-
10.5	15	14	4.2	1	0.3	-	-	-	-
9.5	29	20	5.9	9	2.7	-	-	-	-
8.5	47	33	9.8	14	4.2	-	-	-	-
7.5	54	27	8.0	27	8.0	-	-	-	-
6.5	34	17	5.1	17	5.1	-	-	-	-
5.5	35	18	5.4	17	5.1	-	-	-	-
4.5	36	16	4.8	20	5.9	-	-	-	-
3.5	27	8.0%)							
2.5	40	11.9%) unsexable.							
1.5	17	5.1%)							

Details of the regular samples from Hatchmere, Cheshire.

<u>A. aquaticus L.</u>

Date of sampling 30.X1.59. Total number in sample, 149.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches.	
		No.	%.	No.	%.	No.	%.	No.	%.
12.5	2	2	1.3	-	-	-	-	-	-
11.5	6	5	3.4	1	0.7	-	-	-	-
10.5	11	9	6.0	2	1.3	-	-	-	-
9.5	12	6	4.0	6	4.0	-	-	-	-
8.5	13	5	3.4	8	5.4	-	-	-	-
7.5	21	11	7.4	10	6.7	-	-	-	-
6.5	16	5	3.4	11	7.4	-	-	-	-
5.5	13	2	1.3	11	7.4	-	-	-	-
4.5	18	7	4.7	11	7.4	-	-	-	-
3.5	23	15.4%)							
2.5	13	8.7%)	unsexable.						
1.5	1	0.7%)							

Details of the regular samples from Hatchmere, Cheshire.

A. meridianus Rac.

Date of sampling 10.V1.59. Total number in sample, 191.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
5.5	13	5	2.6	1	0.5	4	2.1	3	1.6
4.5	10	4	2.1	5	2.6	1	0.5	-	-
3.5	24	12	6.2	10	5.2	1	0.5	1	0.5
2.5	96	50.3%)							
1.5	48	25.1%)	unsexable.						

Date of sampling 30.V1.59. Total number in sample, 310.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
5.5	3	3	1.0	-	-	-	-	-	-
4.5	11	8	2.6	1	0.3	2	0.6	-	-
3.5	76	46	15.0	28	8.7	2	0.6	-	-
2.5	122	39.4%)							
1.5	98	31.6%)	unsexable.						

Date of sampling 14.V11.59. Total number in sample, 287.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
5.5	1	1	0.3	-	-	-	-	-	-
4.5	3	3	1.0	-	-	-	-	-	-
3.5	41	21	7.3	9	3.2	10	3.5	1	0.3
2.5	106	37.1%)							
1.5	136	47.5%)	unsexable.						

Date of sampling 31.V11.59. Total number in sample, 197.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches. No.	Females with empty pouches. %.
5.5	2	2	1.0	-	-	-	-	-	-
4.5	4	3	1.5	-	-	1	0.5	-	-
3.5	39	18	9.1	7	3.5	14	7.1	-	-
2.5	78	39.6%)							
1.5	74	37.6%)	unsexable.						

Details of the regular samples from Hatchmere, Cheshire.

A. meridianus Rac.

Date of sampling 13.V111.59. Total number in sample, 160.

Size of group m.m.	Total in group	Males No.	Males %.	Females with small lamellae No.	Females with small lamellae %.	Ovigerous females No.	Ovigerous females %.	Females with empty pouches No.	Females with empty pouches %.
5.5	1	1	0.6	-	-	-	-	-	-
4.5	15	14	8.7	-	-	1	0.6	-	-
3.5	44	18	11.3	13	8.1	11	6.9	2	1.2
2.5	70	43.7%)							
1.5	30	18.7%)	unsexable.						

Date of sampling 7.1X.59. Total number in sample, 192.

4.5	17	15	7.8	1	0.5	1	0.5	-	-
3.5	59	40	20.8	14	7.3	2	1.0	3	1.6
2.5	80	41.7%)							
1.5	36	18.7%)	unsexable.						

606

Date of sampling 16.1X.59. Total number in sample, 148.

4.5	6	5	3.4	-	-	1	0.7	-	-
3.5	43	30	20.2	8	5.4	5	3.4	-	-
2.5	60	40.5%)							
1.5	39	26.4%)	unsexable.						

Date of sampling 7.X.59. Total number in sample, 82.

4.5	2	2	2.4	-	-	-	-	-	-
3.5	19	8	9.9	9	10.9	1	1.2	1	1.2
2.5	28	34.1%)							
1.5	33	40.2%)	unsexable.						

Details of the regular samples from Hatchmere, Cheshire.

<u>A. meridianus Rac.</u>

Date of sampling 19.X.59. Total number in sample, 111.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches	
		No.	%.	No.	%.	No.	%.	No.	%.
5.5	2	1	0.9	1	0.9	-	-	-	-
4.5	16	10	9.1	5	4.5	-	-	1	0.9
3.5	32	21	18.8	11	10.0	-	-	-	-
2.5	45	40.5%)							
1.5	16	14.4%)	unsexable.						

Date of sampling 2.X1.59. Total number in sample, 17.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches	
		No.	%.	No.	%.	No.	%.	No.	%.
5.5	1	1	5.9	-	-	-	-	-	-
4.5	3	3	17.6	-	-	-	-	-	-
3.5	9	7	41.2	2	11.8	-	-	-	-
2.5	4	25.5%)	unsexable.						

Date of sampling 16.X1.59. Total number in sample, 53.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches	
		No.	%.	No.	%.	No.	%.	No.	%.
5.5	1	-	-	1	1.9	-	-	-	-
4.5	10	6	11.3	4	7.5	-	-	-	-
3.5	20	9	16.9	11	20.8	-	-	-	-
2.5	18	33.9%)							
1.5	4	7.5%)	unsexable.						

Date of sampling 30.X1.59. Total number in sample, 49.

Size of group m.m.	Total in group	Males		Females with small lamellae		Ovigerous females		Females with empty pouches	
		No.	%.	No.	%.	No.	%.	No.	%.
6.5	3	3	6.1	-	-	-	-	-	-
5.5	10	5	10.2	5	10.2	-	-	-	-
4.5	14	7	14.3	7	14.3	-	-	-	-
3.5	11	3	6.1	8	16.5	-	-	-	-
2.5	7	14.3%)							
1.5	4	8.2%)	unsexable.						

Appendix C.

Table 5.

Details of the sample of *A. aquaticus* from a pond near Bidston, Cheshire.

Date of Sampling, 30.VI.59. Total number in sample, 148.

Size of group m.m.	Total in group	Males No.	Males %	Females with small lamellae No.	Females with small lamellae %	Ovigerous females No.	Ovigerous females %	Females with empty pouches No.	Females with empty pouches %
9.5	1	1	0.7	-	-	-	-	-	-
8.5	1	1	0.7	-	-	-	-	-	-
7.5	3	2	1.4	1	0.7	-	-	-	-
6.5	11	8	5.4	1	0.7	2	1.4	-	-
5.5	32	5	3.4	9	6.1	18	12.2	-	-
4.5	24	11	7.5	10	6.8	3	2.0	-	-
3.5	21	14.2%)							
2.5	27	18.2%)	unsexable						
1.5	28	19.0%)							

Details of the sample of *A. meridianus* from a pond near Storeton, Cheshire.

Date of sampling, 30.VI.59. Total number in sample, 211.

Size of group m.m.	Total in group	Males No.	Males %	Females with small lamellae No.	Females with small lamellae %	Ovigerous females No.	Ovigerous females %	Females with empty pouches No.	Females with empty pouches %
7.5	1	-	-	-	-	1	0.5	-	-
6.5	4	3	1.4	-	-	1	0.5	-	-
5.5	28	23	10.9	4	1.9	1	0.5	-	-
4.5	43	23	10.9	2	1.0	18	8.5	-	-
3.5	60	20	9.5	29	13.6	9	4.3	2	1.0
2.5	41	19.4%)	unsexable						
1.5	34	16.1%)							

Appendix D.

Details of the investigation of the length of time of incubation at various temperatures. *A. aquaticus*

Date on which ♀ first became ovigerous	Date on which ♀ began to release juveniles	Length of incubation in days	Mean temp. °C
1st July 1959	13th July 1959	13	23.5
4th July 1959	14th July 1959	11	23.5
6th July 1959	18th July 1959	12	23.5
10th July 1959	22nd July 1959	13	23.5
16th July 1959	28th July 1959	13	23.5
16th July 1959	28th July 1959	13	23.5
15th June 1959	29th June 1959	15	21
13th June 1959	29th June 1959	17	21
15th July 1959	29th July 1959	15	21
15th July 1959	29th July 1959	15	21
15th July 1959	29th July 1959	15	21
15th July 1959	30th July 1959	16	21
16th July 1959	30th July 1959	15	21
16th July 1959	30th July 1959	15	21
23rd Feb. 1960	9th Mar. 1960	15	21
18th July 1959	1st Aug. 1959	15	21
18th July 1959	31st July 1959	14	21
19th June 1959	6th July 1959	18	20
20th June 1959	9th July 1959	20	20
20th June 1959	8th July 1959	19	20
20th June 1959	9th July 1959	20	20
20th June 1959	6th July 1959	17	20
22nd June 1959	8th July 1959	17	20
22nd June 1959	7th July 1959	16	20
22nd June 1959	9th July 1959	18	20
26th Feb. 1960	16th Mar. 1960	19	19
23rd Feb. 1960	13th Mar. 1960	19	19
6th July 1959	23rd July 1959	18	18
9th July 1959	29th July 1959	21	18
10th July 1959	29th July 1959	20	18
10th July 1959	29th July 1959	20	18
14th July 1959	31st July 1959	18	18
23rd Mar. 1959	7th May 1959	46	10
25th Mar. 1959	8th May 1959	45	10
31st Mar. 1959	14th May 1959	45	10
23rd June 1959	Some date later than 11th Aug. 1959	50+	8.5
24th June 1959		49+	8.5
24th June 1959		49+	8.5
24th June 1959		49+	8.5
24th June 1959		49+	8.5

Table continued...... <u>A. meridianus</u>

Date on which ♀ first became ovigerous	Date on which ♀ began to release juveniles	Length of incubation in days	Mean temp. °C
4th July 1959	15th July 1959	12	23.5
16th July 1959	29th July 1959	14	23.5
26th Feb. 1960	11th March 1960	15	21
13th June 1959	27th June 1959	15	21
13th June 1959	27th June 1959	15	21
8th July 1959	21st July 1959	14	21
23rd June 1959	11th July 1959	19	20
23rd June 1959	11th July 1959	19	20
23rd June 1959	10th July 1959	18	20
24th June 1959	11th July 1959	18	20
26th Feb. 1960	14th Mar. 1960	18	19
26th Feb. 1960	14th Mar. 1960	18	19
26th Feb. 1960	15th Mar. 1960	19	19
26th Feb. 1960	16th Mar. 1960	20	19
6th July 1959	25th July 1959	20	18
11th June 1959	3rd July 1959	23	18
6th July 1959	24th July 1959	19	18
6th July 1959	26th July 1959	21	18
11th June 1959	3rd July 1959	23	18
11th July 1959	31st July 1959	21	18
4th July 1959	20th July 1959	17	18
10th July 1959	31st July 1959	22	18
2nd April 1959	14th May 1959	43	10
20th Mar. 1959	30th April 1959	42	10
25th June 1959)	Some date later than 11th Aug. 1959	48+	8.5
25th June 1959)		48+	8.5
26th June 1959)		47+	8.5
27th June 1959)		46+	8.5

Appendix E.

Details of the numbers of eggs or embryos within the brood puches of ovigerous females of *A. aquaticus* and *A. meridianus*.

A. aquaticus

Size of female (mm.)	Month	Average no. of eggs or embryos ((a)-(c) only)	No. of females upon which average is based
10.5	May	161.0	1
9.5	February	114.5	4
9.5	March	144.0	5
9.5	April	142.7	3
9.5	May	106.5	2
8.5	February	101.5	2
8.5	March	106.5	14
8.5	April	95.8	18
8.5	May	108.0	1
7.5	February	62.7	3
7.5	March	82.2	19
7.5	April	92.0	31
7.5	May	63.5	4
7.5	June	41.7	3
6.5	March	62.7	6
6.5	April	60.0	24
6.5	May	52.9	11
6.5	June	32.4	8
6.5	July	42.7	3
6.5	September	44.5	2
5.5	April	36.3	10
5.5	May	35.1	9
5.5	June	26.0	15
5.5	July	24.8	23
5.5	August	30.1	15
5.5	September	24.5	2
4.5	May	24.0	1
4.5	June	10.7	6
4.5	July	18.3	11
4.5	August	18.3	10

A. meridianus

Size of female (mm.)	Month	Average no. of eggs or embryos ((a)-(c) only)	No. of females upon which average is based
9.5	March	99.0	1
9.5	May	116.5	2
8.5	February	72.0	3
8.5	March	80.0	1
8.5	May	67.0	8
7.5	February	59.7	16
7.5	March	60.0	26
7.5	April	59.7	20
7.5	May	58.5	11
7.5	July	41.0	1
6.5	February	49.0	15
6.5	March	53.8	75
6.5	April	44.0	52
6.5	May	39.9	13
6.5	June	26.0	1
6.5	September	40.0	1
5.5	February	37.6	5
5.5	March	45.0	50
5.5	April	35.1	37
5.5	May	26.7	23
5.5	June	29.5	2
5.5	July	18.8	5
5.5	August	25.2	15
5.5	September	30.9	12
4.5	March	38.0	3
4.5	May	19.0	4
4.5	June	18.5	4
4.5	July	17.9	45
4.5	August	17.7	33
4.5	September	18.9	27
3.5	June	9.3	11
3.5	July	10.8	21
3.5	August	10.4	9
3.5	September	10.1	10
3.5	October	13.7	6