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THE POPULATION DYNAMICS AND GROWTH OF THE FRESHWATER CRAYFISH *Austropotamobius pallipes* IN AN AQUEDUCT IN NORTHUMBRIA

by

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ABSTRACT

Despite the wide distribution and abundance of the freshwater crayfish *Austropotamobius pallipes* in Britain, little is known of its population biology. The dynamics and growth of a Northumbrian population of *A. pallipes* were studied using an intensive-mark-recapture programme.

The seasonal timing of moulting and reproduction was found to be predictable and probably related to water temperature. Stomach contents showed crayfish to be omnivorous, with plant material forming the bulk of the diet.

Population size, survival and recruitment were estimated from mark-recapture data at frequent intervals. Two principal types of mortality were identified: moult-associated mortality, which was relatively intense and of short (2-3 weeks) duration, and overwinter mortality, which operated at a much lower estimated weekly rate over a period of some 30 weeks. Mortality was shown to be highly variable throughout the year. Population size generally showed a midsummer peak as recruitment into the catchable size classes occurred. Thereafter numbers declined slightly towards the end of the growth season, followed by an overwinter decline of some 50% of total numbers. Longevity was estimated to be at least eleven years.

The relationship between size, age and weight was established and males shown to have faster growth rates than females after the size of sexual maturity. Growth increments and moult frequency were shown to differ between the sexes and according to body size. Reproductive females omitted one moult while carrying eggs. Growth rates were depressed by the parasite *Thelohania contejeani* and by the regeneration of a major chela. The fecundity of females and the probability of being reproductive increased with body size.

The annual production of the study population was estimated at 196.49 kg ha^{-1} in 1977, 116.80 kg ha^{-1} in 1978 and 87.79 kg ha^{-1} in 1979.

Detailed life histories of many marked individuals were collected which support the conclusions drawn at the population level.

Chapter One

GENERAL INTRODUCTION

Crayfish are widely distributed throughout temperate fresh waters, where they are usually the largest invertebrate present. They are, however, absent from equatorial regions. Huxley (1878,1880) suggested that their disjunct occurrence is attributable to their evolution from a widely distributed marine ancestor which subsequently disappeared. Of the present day species, some 250 are found in North America (Avault 1973), approximately 100 in Australasia (Huxley 1880; Frost 1975) and only four are native to Europe. A few species are known from South America and the Far East. It is probable that the large number of North American crayfish is related to the great diversity of habitats: many species have adapted to unpredictable or adverse environments by developing a plastic life history (Bovbjerg 1952; Caldwell & Bovbjerg 1969) or by burrowing when the habitat dries out, e.g. *Procambarus clarkii* and *Orconectes immunis* (Fielder 1972; Avault 1973). Hobbs (1975) has described several species adapted to cave dwelling. A feature of the subfamily Cambarinae, which comprises the majority of the North American species, is their relatively short lifespan, e.g. 2½ years in *Orconectes neglectus chaenodactylus* (Price & Payne 1979) and 3 years in *O. palmeri palmeri* (Price & Payne 1977), while *Procambarus pictus* is believed to be an annual species (Franz 1977).

The native European species have certain features distinguishing them from the North American Cambarinae. They are relatively long-lived, e.g. at least 11 years in *Austropotamobius pallipes*, up to 13 years in *Astacus leptodactylus eichwaldi* (Cherkashina 1975) and 8 years in *Astacus astacus* (Cukerzis 1975), and have similar life histories, which, together with the consistent timing of the growth season and reproductive cycle (Abrahamsson 1971; Kossakowski 1971) are features which are typical of members of the subfamily Astacinae (as defined by Hobbs 1974).

There are relatively few published reports of studies of the population biology of freshwater crayfish. This is somewhat surprising, for in several countries they are economically important and natural populations are cropped as a food source. In addition, crayfish are generally prominent members of their habitats by virtue of their relatively large size and their occurrence in high densities. The existing literature is confined largely to descriptions of their life histories and distribution, e.g. Rhoades (1962); Smart (1962); Aiken (1965); Fielder (1972); Payne (1972); Weagle & Ozburn (1972); Lake & Newcombe (1975); Berrill (1978); Boyd & Page (1978); Caine (1978). Of the studies reporting on the population dynamics of crayfish, those of Abrahamsson (1966); Momot (1967a, 1967b, 1978); Cukerzis (1975); Mason (1975) and Momot & Gowing (1977a, 1977b, 1977c) are notable.

Literature concerning the only freshwater crayfish native to the British Isles, *Austropotamobius pallipes* (Lereboullet 1858) is particularly sparse. It is clear from early references to crayfish as a food item that it was widespread and well known in Britain at least from medieval times. In an edition of a work dating from 1577, Harrison (1878) referred to 'the little crafishes taken plentifullie in our fresh rivers', while Fuller (1702) recorded the stocking of the River Yower with 'crevishes'. The species was reported to be found 'in most chalk streams ... and in many ponds and other rivers' by Cameron (1917).

The first scientific work on the biology of the species was the classic work of Huxley (1880), which relied heavily on published continental sources supplemented by detailed information of distribution and life history of the native species obtained from local sources. Duffield (1933, 1936) presented details of reports of local fluctuations in crayfish numbers in southern England, but the general lack of interest in crayfish biology is apparent from the dearth of published work on the subject until the last decade. Davies (1964) reported a density of four adults per square yard in the River Stour and mistakenly stated that crayfish are found only in rivers. Thomas & Ingle (1971) gave a short account of the general biology and bionomics of the species in Britain, while Moriarty (1973) reported on the timing of events in the life history of an Irish population of *A. pallipes*. More recently, Holdich, Jay & Goddard (1978) have provided a synopsis of the status of *A. pallipes* in the British Isles, while the work of Brown (1979) is the first to include any details of the dynamics of a natural population of the species. Growth in a population of *A. pallipes* in southern England has been studied by Pratten (1980), who found evidence of different growth patterns to those discussed in Chapter 4, almost certainly a corollary of the warmer temperature regime of this more southerly population.

In contrast to the position in many European countries, particularly Scandinavia, and in North America, where crayfish have long been of commercial importance, there has been little interest until recently in the commercial exploitation of crayfish in Britain. Consumption of *A. pallipes* is common only locally (Holdich, Jay & Goddard 1978), catering outlets relying almost exclusively on imported crayfish. The reasons for this are not clear. While *A. pallipes* is, in general, slightly smaller than *Astacus astacus*, the most common European species, it is comparable in every respect in its acceptability for the table. A lack of knowledge of the species may well be an important reason for the low level of its consumption in Britain. This lack of knowledge is reflected in the scarcity of scientific studies of *Austropotamobius pallipes*. Indeed, the species is often ignored in freshwater biology texts, e.g. Macan (1973); Moss (1980).

It is commonly held that crayfish in Britain are inhabitants only of swift-flowing chalk streams. Davies (1964) erroneously stated that they inhabit only rivers. They are, however, much more widely distributed than is generally believed, being found in canals, gravel pits and reservoirs as well as rivers and streams (personal observations; Holdich, Jay & Goddard 1978; Bowler 1979). Dense populations exist in Kent and the Home Counties, the West Country and south Wales, the Midlands, the Lake District, Yorkshire, Northumbria and Ireland. The absence of *A. pallipes* from Scotland (except where introduced) is believed to be attributable to the greater acidity of the waters of the Central Lowland, which may act as a barrier to more northerly distribution (Jay & Holdich 1977).

A. pallipes is widespread in western Europe, notably in France, Spain, West Germany and Switzerland (Thomas & Ingle 1971; Laurent 1973). The most common species native to Europe, however, is *Astacus astacus* L., which ranges from Italy to Scandinavia and from France to Poland. Two further species, *Astacus leptodactylus* Eschscholtz and *Austropotamobius torrentium* (Schrank) occur in eastern Europe and upland areas of central Europe respectively. The range of each of the native European species has been reduced by the crayfish plague, an infection by the fungus *Aphanomyces astaci* Schikora which is fatal to European crayfish.

The plague was probably first introduced to Europe in 1860 with 100 specimens of a resistant North American crayfish, *Orconectes limosus* Rafinesque (Svardson 1965; Unestam 1972) and has since spread rapidly, devastating stocks of the highly susceptible native crayfish. The loss of economically important stocks of *Astacus astacus* has led to their attempted replacement by the introduction of the plague-resistant *Orconectes limosus* and (more importantly) *Pacifastacus leniusculus* Dana, which has been widely transplanted. The rapid spread of crayfish plague throughout mainland Europe and the introduction of *P. leniusculus* to many countries to replace native stocks has been well documented (Abrahamsson 1973 ; Hastein & Gladhaug 1973, 1975; Herfort-Michieli 1973; Kossakowski 1973; Schweng 1973; Spitzy 1973; Westman 1973; Brinck 1975).

The resistance of *P. leniusculus* to the plague fungus has been established by Unestam (1969, 1973). However, although resistant this species acts as a reservoir of infection for the highly susceptible *Astacus astacus*, continually allowing fresh outbreaks of the plague. Contrary to some reports (Anon. 1976; Richards & Fuke 1977; Karlsson 1977, 1978), there is no evidence that crayfish plague has reached Britain (Behrendt 1979; Bowler 1979; Goddard & Holdich 1979). While there is no doubt that local extinctions of *Austropotamobius pallipes* have occurred (Duffield 1933, 1936; Ingle & Thomas 1978) and that the species is less widespread than a century ago, as for many other species it is probable that this has been caused by human modification or pollution of habitats.

P. leniusculus has now been introduced to Britain (Richards & Fuke 1977). The absence of any legislation restricting the import of wild-caught crayfish leaves the native population of *Austropotamobius pallipes* vulnerable. Even in the absence of crayfish plague the indiscriminate introduction of *P. leniusculus* may have indirect effects on stocks of *A. pallipes* by competition and by the production of sterile hybrids (Richards & Fuke 1977). The introduction of exotic crayfish species to new areas has already had highly undesirable effects in some cases, e.g. the introduced *Procambarus clarkii* is a serious pest of the rice crop in Japan (Unestam 1975). Similarly, *P. clarkii* introduced to Lake Naivasha, Kenya, has affected the local fishery by damaging net-caught fish and the nets themselves (Lowery & Mendes 1977). In order that the status of *A. pallipes* be understood and that the possible effects of the introduction of exotic crayfish may be assessed, it is necessary to obtain detailed information on the biology of the species. The question is not a trivial one: while *A. pallipes* in Britain lacks the economic importance of *Astacus astacus* in mainland Europe, there is a growing awareness of the important rôle of crayfish in freshwater ecosystems. Abrahamsson (1966) reported the reduction of macrophytes in a Swedish pond by a population of *Astacus astacus*, the removal of crayfish by the plague and the subsequent resurgence of the vegetation. Further examples of the importance of crayfish in keeping waterways open are given by Dean (1969); Taub (1972); Rickett (1974); Magnuson *et al.* (1975) and Lorman & Magnuson (1978). Moreover, it is now apparent that in many ecosystems crayfish make a significant contribution to the recycling of nutrients from detritus and macrophytes and their conversion to animal protein (Rundquist, Gall & Goldman 1977; Lorman & Magnuson 1978; Momot, Gowing & Jones 1978).

There are therefore three important reasons why there is a need for a comprehensive statement of the biology of *Austropotamobius pallipes*. The species is Britain's only native crayfish and is poorly understood, indeed, often ignored by freshwater biologists and laymen alike. Despite this, it is probable that crayfish are important components in terms of their biomass and of their function in large water bodies over a wide area. Finally, the possible introduction of crayfish plague and exotic crayfish species to Britain poses a threat to the balance of some freshwater ecosystems which cannot be assessed until the status of *A. pallipes* has been determined.

Chapter Two

THE STUDY AREA AND THE BIOLOGY OF THE SPECIES

2.1 INTRODUCTION

In any study of population biology an adequate description of the physical and biological features of the field site is essential in that it allows work to be placed in the context of similar studies on other populations and on other species. Such comparisons are valuable in that they allow a distinction to be made between general principles applying to all populations of a species and those which are peculiar to a field site, type of environment or species. It will become clear that the timing of the principal events of the life cycle of *Austropotamobius pallipes* is very dependent on water temperature. However, this conclusion was reached only after a comparison of data with those of workers on populations in different temperature regimes.

There are certain features peculiar to the study area. The aqueduct is man-made, being lined with sandstone blocks, and the water level and flow rate are relatively constant. However, as populations of *A. pallipes* exist naturally in a variety of habitats, including swift-flowing streams, canals, large reservoirs and lakes, it is unlikely that these features have an 'unnatural' effect on the dynamics of the population. One particularly important feature is the facility for draining the aqueduct, thereby enabling intensive sampling of the population.

2.2 THE STUDY AREA

The population of this study inhabits a stretch of aqueduct feeding Hallington Reservoir East in Northumbria, part of the North Tyne catchment area under the control of the Newcastle and Gateshead Water Company. The water flowing through the aqueduct originates from the Catcleugh and Colt Crag reservoirs, from where it flows through pipes and open aqueduct to Little Swinburn Reservoir. From there the water flows by tunnel and open aqueduct to Hallington, where there are two small reservoirs. The aqueduct is used principally to feed Hallington Reservoir East, which was constructed in 1871 and has a capacity of 2.593 x 10^9 litres (Newcastle & Gateshead Water Company 1969). The west reservoir (capacity 2.813 x 10^9 litres), having no outlet of its own, is used for storage and to replenish the east reservoir, from which the water flows to the Whittle Dene reservoir complex and ultimately supplies the Tyneside area.

Fig. 2.1 shows the relationship of the aqueduct to the two reservoirs and the position of the sluice gates controlling water levels in the aqueduct. Since the west reservoir has no outlet of its own, the sluice gates are normally positioned to ensure the maximum flow through the aqueduct into the east reservoir.

2.3 THE AQUEDUCT

The stretch of aqueduct inhabited by the population of this study is 746 m long, 2 m wide at water level, which is usually at least 1 m, and 1 m wide at the floor. Upstream of the sluice gates the aqueduct is lined with concrete, while below the sluice gates it is brick lined for 153 m. The remaining 593 m are lined with large sandstone blocks (Fig. 2.1). The outflow to the east reservoir is torrential and the water in the aqueduct accelerates rapidly towards the outflow. While the brick and sandstone sections contain an abundance of cracks and crevices suitable for crayfish hides, the concrete-lined stretch contains none. Repeated trapping in this area has shown immigration of crayfish from upstream to be negligible. Since immigration from downstream against the torrential outflow is extremely improbable, the study population is believed to be almost completely reproductively isolated.

During sampling of the population (3.2.3) the water level in the aqueduct was lowered to less than 10 cm by closing the sluice gate at the top of the aqueduct, thereby diverting water into the west reservoir. The lowering of the water level causes large numbers of crayfish to leave their hides in the aqueduct walls and descend to the floor, where they are readily collected by hand.

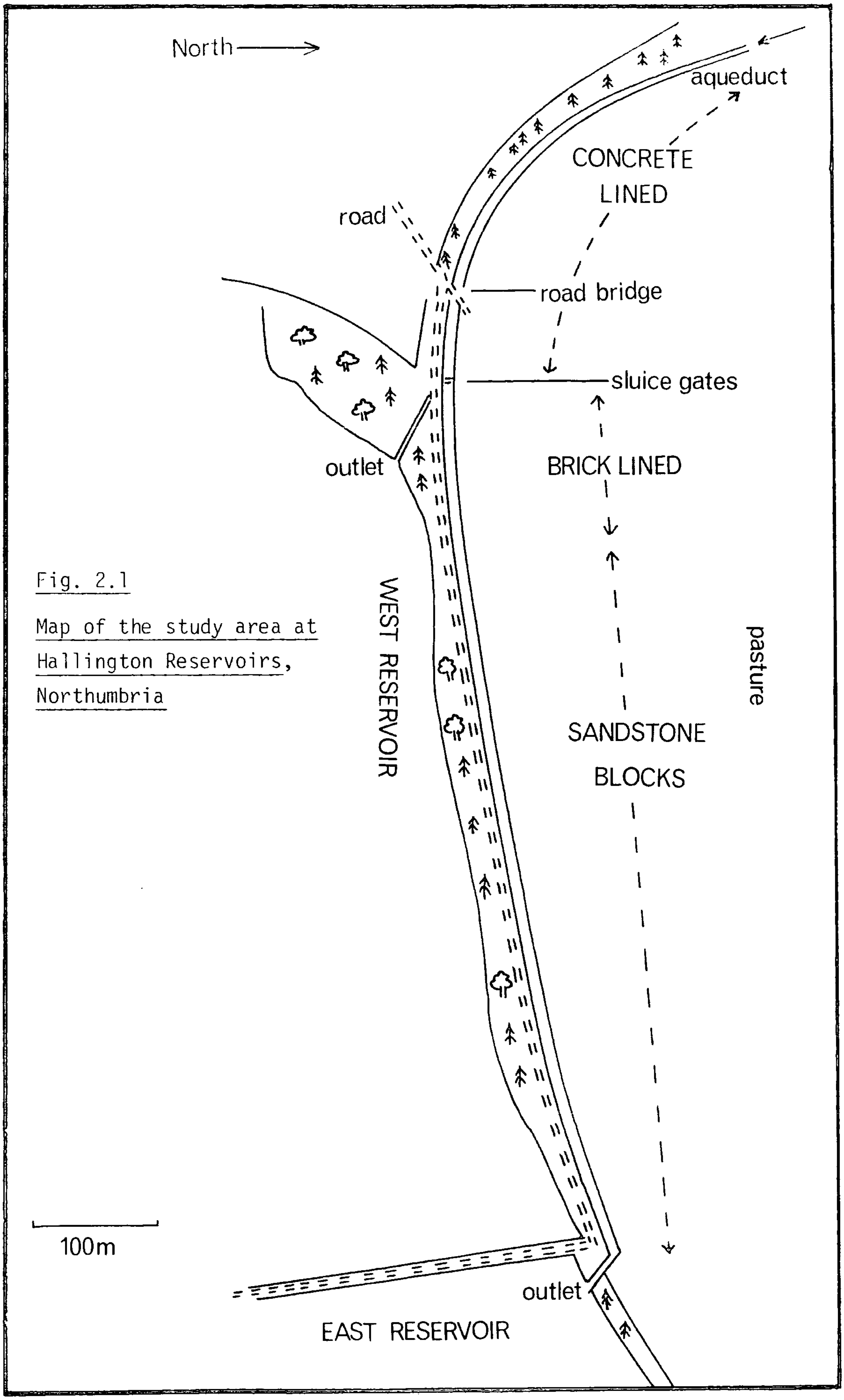


Fig. 2.1

Map of the study area at Hallington Reservoirs, Northumbria

2.3.1 Physical features of the aqueduct

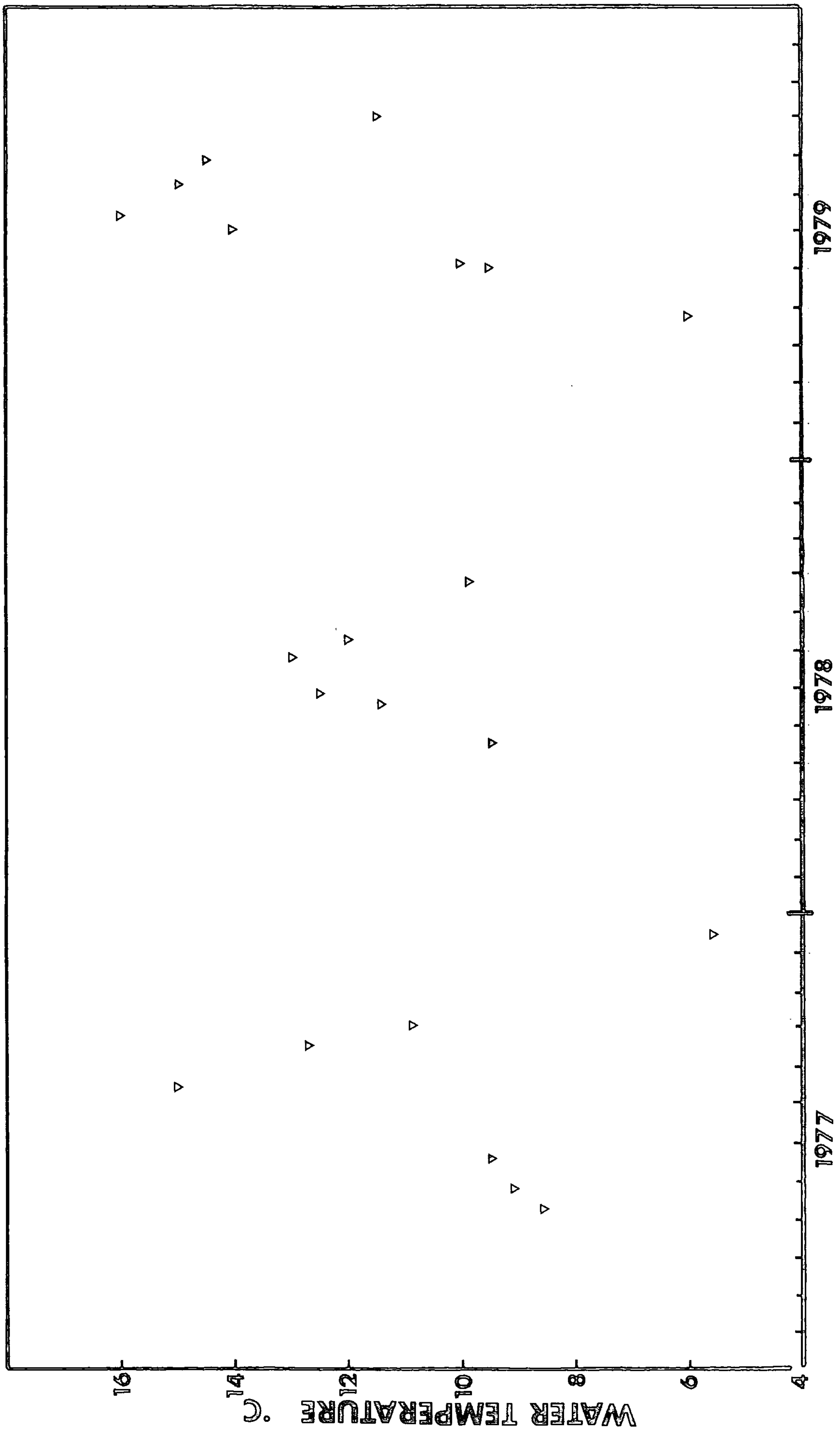
The calcium concentration in water from the aqueduct was determined by Brown (1979) as 18.61 ± 1.01 ppm, while the pH of the water was 7.84 ± 0.21. Nygaard (1955) found that *'Astacus fluviatilis'* (presumably *Austropotamobius pallipes*) was reproducing successfully in a calcium concentration of 1.8 mg L^{-1}.

Water temperature in the aqueduct was measured on each of the sample dates throughout the three years of the study. Fig. 2.2 shows that the seasonal changes in water temperature were similar in each of the three years. The regularity of the water temperature regime at this site was also reported by Brown (1979), who found cycles very similar to those of Fig. 2.2 for the years 1974-76. Temperatures during the most active period in the crayfish life cycle (from the end of May until October at this latitude) did not fall below 8^{o}C. The importance of the water temperature regime in determining the timing of the main events of the crayfish year, a recurring theme of this study, is discussed in 2.6.

At Hallington moulting has stopped almost completely by mid-October, by which time water temperature has fallen to 9-10^{o}C (Fig. 2.2). There then follows the long overwinter period (some 30 weeks in Northumbria) during which time crayfish activity is greatly reduced. Movement becomes very limited: hand fishing the full length of the aqueduct during the winter generally yielded 100-200 crayfish compared to the 1000-2000 collected from approximately one third of the aqueduct's length during the summer months (Table A1). As will be seen (3.5, 3.6), a significant amount of mortality occurs overwinter which may be attributable to a combination of low temperature and nutritional stress. Stomach contents collected from the aqueduct during the winter months generally revealed little evidence of feeding.

The torpid crayfish become more active as water temperatures approach 8^{o}C in late April and May and moulting reaches the first peak of the year during late June and July, when water temperatures are 10-13^{o}C. A second moulting peak occurs in September when temperatures are still relatively high. Copulation and egglaying occur in late October and November at temperatures of 9-10^{o}C.

Fig. 2.2 Water temperature in the aqueduct on each sampling date 1977-79



2.3.2 Biological features of the aqueduct

Whilst it was not the purpose of this study to investigate the trophic relationships of the crayfish population, many qualitative observations were made during the course of field work which will indicate more clearly the type of environment inhabited by the study population.

The dominant plant in the aqueduct was the moss *Fontinalis antipyretica* Hedw., which grew in clumps on the walls and accumulated around any stones on the floor of the aqueduct, considerable quantities being washed downstream. The generally smooth character of the floor and the speed of the current in the aqueduct prevented the accumulation of detritus except where stones were to be found. During the autumn months considerable quantities of fallen tree leaves were to be found on the aqueduct floor. These included leaves of the oak (*Quercus robur* L.) and elm (*Ulmus campestris* L.) as well as those of conifers lining the side of the aqueduct (Fig. 2.1). This seasonal input of fallen leaves from upstream (oak and elm are not found near the aqueduct) and the year-round input of *Fontinalis* formed the major part of the allochthonous material entering the aqueduct. Apart from *Fontinalis*, the only macrophyte found in the aqueduct was the goose pondweed *Potamogeton obtusifolius*, which formed a few isolated clumps.

Vertebrate fauna of the aqueduct included the perch (*Perca fluviatilis*), the stone loach (*Nemacheilus barbatulus*), the rainbow trout (*Salvelinus* sp.), the frog (*Rana temporaria*) and the water vole (*Arvicola amphibius*). In addition, a single specimen of the eel (*Anguilla anguilla*) was seen and mink (*Mustela vison*) and otter (*Lutra lutra*) were known to be present in the area. Grey heron (*Ardea cinerea*) were also seen occasionally. Of these species, however, only the water vole and the stone loach were seen on each visit to the aqueduct, the remainder being present in relatively small numbers. The principal invertebrates were *Gammarus* sp. and larvae of Ephemeroptera and Chironomidae among the detritus and *Austropotamobius pallipes* inhabiting crevices in the walls of the aqueduct and beneath stones on the floor. Also present were the freshwater sponge (*Ephydatia*) and the gastropod mollusc *Potamopyrgus jenkinsi*.

2.3.3 Possible predators of crayfish

Whilst no detailed study of predation on crayfish was carried out, it is considered that the following general statement can be made. Of the fauna of the aqueduct and the surrounding area, the mink, otter, eel, perch and trout have been reported as important predators of crayfish (Gerell 1967, 1968; Day & Linn 1972; Erlinge 1972; Svardson 1972). Mink and otter were believed not to be sufficiently numerous locally to be important regulators of crayfish population size. The only direct evidence of predation on the study population, pieces of carapace scattered infrequently along the banks of the aqueduct, was almost certainly the result of predation by one of these species. Svardson (1972) has reported on the great importance of the eel as a crayfish predator, but only a single specimen was seen during the three years of the study. Watson (unpubl.) reported the occurrence of crayfish in perch stomachs at 38% and in rainbow trout stomachs at 20%. Despite their abundance in nearby waters, however, these two species occurred only sporadically in the aqueduct. Predation was therefore believed to be unimportant as a regulator of the size of the crayfish population.

2.3.4 The diet of *Austropotamobius pallipes*

A. pallipes is commonly referred to simply as a scavenger, e.g. Huxley (1880); Howes (1962); Karlsson (1977); Richards & Fuke (1977); Fuke (1978). No detailed study of the diet in the field exists, however. Whilst it was not a primary aim of this study to investigate the diet of *A. pallipes*, many observations were made which it is felt are of value in view of the lack of objective work on the subject.

(A) Evidence from stomach contents in the field

Stomach contents were obtained from crayfish in the field by the withdrawal of fluid using disposable plastic pipettes. Samples were taken throughout the year from adult crayfish at several sites in Northumbria. Stomach contents were examined under a binocular microscope. The fragmentation of material by the gastric mill made identification of contents very difficult and no attempt was made to identify them to species or to quantify the various constituents.

The overwhelming bulk of the stomach contents at all times of year was found to consist of plant material. *Fontinalis antipyretica* occurred frequently, together with colonial algae, diatoms and many higher plant fragments, principally allochthonous leaf material. Arthropod setae, probably indicating consumption of *Gammarus*, also occurred occasionally.

(B) Laboratory experiments

Six macrophytes common in the fresh waters of northern England were presented singly to adult *A. pallipes* in 13-litre aquaria. After two days the mechanical damage and consumption of the plants were assessed. *Nitella sp.* was attacked most avidly, consumption ending only when the plant had been fragmented to such an extent that it was very difficult for the crayfish to manipulate. *Potamogeton sp.*, which occurs in isolated clumps at the field site, and *Rorippa nasturtium-aquaticum* were consumed less readily but mechanical damage was marked. Consumption of *Myriophyllum spicatum* and *Fontinalis antipyretica* was low but mechanical damage was still appreciable. *Elodea canadensis* was consumed least readily of any of the six species used and mechanical damage was slight.

Gammarus sp. and *Potamopyrgus jenkinsi*, two of the most abundant benthic invertebrates of the field site, were readily accepted by laboratory-maintained crayfish, as was raw ox liver, which was used as bait in crayfish traps. Decaying leaves of oak (*Quercus*), elm (*Ulmus*) and sycamore (*Acer*) were also accepted in the laboratory.

2.4 CRAYFISH STUDIES IN BRITAIN

Despite the wide distribution of *A. pallipes* (Chapter 1; Bowler 1979) and its position as Britain's only native crayfish species, scientific studies of the population biology of the species are remarkably rare. There is no doubt that this is attributable at least in part to the secretive and largely nocturnal habit of the animal and to the difficulties involved in quantifying parameters of dense populations of large mobile organisms inhabiting large bodies of water. One effect of this has been that popular knowledge of the species, where it exists, is often anecdotal, verging on folklore. Davies (1964) mistakenly stated that crayfish are found only in rivers, while many reports, e.g. Grove & Newell (1958) suggest that they are common only in waters of high calcium content. Some freshwater biology texts omit any mention of crayfish, e.g. Macan (1973); Willoughby (1976); Moss (1980), while others contain only cursory notes, e.g. Maitland (1978). A further complication is that many early scientific reports, principally on the behaviour and distribution of crayfish, do not specify to which species the work refers, e.g. Lereboullet (1850, 1951); Coste (1858); Soubeiran (1865); Chantran (1870, 1871, 1872a, 1872b, 1873); Parker (1876); Drouin de Bouville (1905), although it is probable that most refer to *Astacus astacus*. More recently, there have been attempts to resolve the confusion as to the nomenclature of the native British crayfish (Stiles & Baker 1926; Curra 1967; Thomas & Ingle 1971) and the species is now properly designated *Austropotamobius pallipes* (Lereboullet 1858).

Reports on the biology of *A. pallipes* have been very limited in number. One early exception is that of Couch (1837), who compared the process of moulting in *A. pallipes* with that in prawns and lobsters. Huxley (1880) produced a classic text on the biology of the species (*Astacus fluviatilis* Milne-Edwards, as it was then designated) which is still of value today. Since that time, however, there have been only a few reports on some aspects of the lifestyle of *Austropotamobius pallipes*, e.g. Moriarty (1973); Bowler & Brown (1977); Brown & Bowler (1977); Pratten (1980). Thomas & Ingle (1971) and Holdich, Jay & Goddard (1978) summarised the life cycle of *A. pallipes* in southern England and in the Midlands respectively, while the work of Brown (1979) at the site of the present study is the first to attempt to study the dynamics of a natural population of *A. pallipes*. The growth season was reported to extend over thirteen weeks in Northumbria and population size was estimated (Brown 1979). No comprehensive statement of the dynamics of *A. pallipes* exists, however.

2.5 CRAYFISH BIOLOGY IN NORTHUMBRIA

The life history of *A. pallipes* is dominated by the events of reproduction and moulting, the timing of which is discussed below. It should be emphasised, however, that these timings apply only to *A. pallipes* in Northumbria and differ for other populations according to the temperature regime of the environment. For example, Pratten (1980) reported that growth rates and the timing of the events of the life history in a population in southern England differ considerably from those in Northumbria. Further examples of different timings in more southerly populations are given by Thomas & Ingle (1971) and Holdich, Jay & Goddard (1978).

The reproductive cycle of *A. pallipes* begins with mating, which in Northumbria occurs in late October. Fertilised females were readily identified in the field by the presence of white spermatophores on the sternum. Such females were seen in the aqueduct on the following dates: 22 October and 29 October 1978 and 18 October and 25 October 1979. Egg laying occurs within two weeks of fertilisation, the female extruding the eggs ventrally into glair. The eggs become firmly attached to modified pleopod setae (Ingle & Thomas 1974) in which position the female, now said to be 'in berry', carries them for some nine months. The fecundity of females in the study population is discussed in detail in 5.3. Egg hatching occurs in late July and early August in Northumbria, the hatchlings remaining attached to the modified pleopod setae of the mother by means of their modified chelae. These possess sharp tips and are used to cling to the old egg membranes, which are not shed from the body of the mother until her first moult (Thomas 1973). Females carrying hatched young were seen on 12 August 1977, 10 August 1978 and 9 August 1979. Hatchlings remain attached to or near their mother for 2-3 weeks after emerging from the egg, during which time they undergo two moults (Thomas 1973). Hatchlings from the aqueduct had a carapace length of 5.42 ± 0.35 mm. By the end of the growth season in October they had reached a mean carapace length of

8.49 mm (4.3.1). The number of moults required to reach this size is not known with certainty, but is estimated to be five. (Moult frequency is examined in detail in 4.3.5).

Brown (1979) reported that the growth season in Northumbria extended from late June to mid-September. However, field observations during the present study showed that the growth season is longer than this. In 1978 the first moults of the year were recorded on 14 June, while twenty-seven marked individuals were recaptured during the course of the study which were known to have moulted after 16 September. Indeed, in 1978 three crayfish are known to have moulted after 22 October. While these numbers appear to be low, it should be borne in mind that the probability of recapturing any one individual both before and after a particular moult late in the growth season is very low: these crayfish may therefore represent an appreciable proportion of late-moulting crayfish. Throughout the three years of the study no crayfish was found to have moulted while water temperature was below $9^{o}C$ (Fig. 2.2).

The minimum size for sexual maturity in this population was 22 mm carapace length (CL) (Brown 1979), while all crayfish were believed to be adult at 27 mm CL. In general, adults moulted twice each year, once in late June-July and once in September. Moult frequency was higher in juveniles (4.3.5) and its timing was less strictly confined to these two major moult periods. Variations in moult frequency and in size of moult increments are discussed in Chapter 4.

Females carrying eggs necessarily show large modifications in their behaviour and in their moulting patterns. Since eggs are laid in early November and do not hatch until late July or early August, reproductive females omit to moult during the first major moult period, i.e. late June-July. Only after the eggs have hatched and the young have been released can a reproductive female moult (during the second major moult period of the year, i.e. September). The omission of a moult and the characteristically small post-reproductive moult increment inevitably leads to breeding females falling behind the growth rates of nonreproductive females of similar size (4.3.2). The behavior of egg-bearing females is modified in that they become much more secretive than usual. In order to avoid any biasing of results because of their changed behaviour, berried females were treated as a separate subpopulation in the estimation of population parameters (3.4, 3.5).

A feature of this crayfish population is the presence of the microsporidian endoparasite *Thelohania contejeani* Henneguy. Some 3% of the total population was found to be infected by *Thelohania*, which progressively invades the muscular tissue of the host crayfish, filling it with spores. The effect is to render the host increasingly sluggish and to decrease growth rate (6.3.2). The disease, which is eventually fatal (Kudo 1924) is readily identifiable in the field by the characteristic opaque white colour of the abdominal musculature. *Thelohania* is known to have been present in this population for at least twelve years (Cossins & Bowler 1974) and, while the mode of transmission is not certain, it is believed to be by cannibalism of infected crayfish. The occurrence of *Thelohania* in the study population is discussed in detail in Chapter 6.

The habit of omnivory among crayfish extends to cannibalism, a factor which is of particular concern to crayfish culturists (Richards & Fuke 1977; Behrendt 1979). Following a moult the new carapace requires some 3-4 days to acquire a rigidity approaching that of the old (Stevenson 1975). During this time a newly-moulted crayfish is vulnerable to cannibalism even by individuals smaller than itself. Behaviour during this vulnerable period is greatly changed, being much more secretive than is usual. Many moulting crayfish are believed to retire to hides for several days until the new carapace is sufficiently rigid for them to emerge safely. The general concentration of moulting in adult crayfish into two major moult periods each year is undoubtedly adaptive in that it reduces the risk of cannibalism. This synchronisation of moulting in juveniles is not possible, however, as moulting occurs more than twice each year (4.3.5). Laboratory and field observations indicate that few crayfish fail to complete a moult successfuly. The strong association of the major moult periods with heavy mortality in all subpopulations is therefore believed to be attributable to cannibalism of soft-shelled crayfish.

2.6 DISCUSSION

The regularity of the water temperature regime at the field site (Fig. 2.2; Brown 1979) accords well with the very limited amount of variation between the timing of the major features of the life cycle from year to year. Comparative data are invariably from more southerly populations, since Northumbria is at the northern limit of the species range in Britain. Thus Thomas & Ingle (1971) found that mating of *Austropotamobius pallipes* in Kent occurred in the last week of September and that in 1963 egg laying occurred between 30 October and 6 November. Mating was not recorded before late October in Northumbria, with egg laying following during the next two weeks. Brown (1979) recorded egg hatching at the site of the present study as early as 24 July in 1974. It is interesting to note that on 24 July 1978 all reproductive females at this site were still carrying unhatched eggs. In more southerly English populations, however, egg hatching is much earlier: Thomas & Ingle (1971) record hatching on 10-17 June 1964 in Kent, Holdich, Jay & Goddard (1978) give May-June as the hatching time in the Midlands and Pratten (1980) found hatching occurred in June in Buckinghamshire.

The warmer temperature regimes of these populations have more profound effects than simply to bring forward the dates of egg hatching and moulting, however. Pratten (1980) stated that male crayfish in the River Ouse show three periods of moulting activity - in early June, in late July and in September. Only two major moult periods were recorded in Northumbria (2.5). Furthermore, the earlier hatching date of the Ouse population means that newly hatched crayfish have a longer growth season before facing their first winter. They are therefore able to undergo seven or eight moults compared to the five estimated for hatchlings in Northumbria: overwintering hatchlings in the River Ouse have a modal size of 12.7 mm CL compared to the 8.49 mm CL of Northumbrian hatchlings. Holdich, Jay & Goddard (1978) reported that *A. pallipes* in the Midlands moulted six or seven times in their first year and may reach sexual maturity in their third or fourth year. This is not reached until the fourth or fifth year at Hallington (4.3.8). The failure of *A. pallipes* in Northumbria to moult at water temperatures of less than 9°C is also reported by Pratten (1980) for laboratory-maintained crayfish at 10°C, while Momot & Gowing (1977b) noted that the American crayfish

Orconectes virilis did not moult below this temperature. Passano (1960a, 1960b) has described the endocrinological basis of the low temperature blockage of moulting in the crab *Uca pugnax* and other crustaceans: a similar mechanism presumably applies in *A. pallipes*.

Several workers have suggested that other factors, particularly photoperiod, also play a part in regulating the reproductive cycles of crayfish. Stephens (1952, 1955) demonstrated the effect of photoperiod on the regulation of the reproductive and moulting cycles of *Cambarus*. Goldman (1973) considered photoperiod to be important in establishing the breeding regime of *Pacifastacus leniusculus*, a North American species with a similar life history to that of *Austropotamobius pallipes*, while Aiken (1969), although accepting the influence of photoperiod, considered water temperature to be a more important factor. (Female *Orconectes virilis* subjected to a normal winter temperature and light regime followed by exposure to long daylengths but cold water temperatures failed to produce eggs). Armitage, Birkema & Willems (1973) also considered water temperature to be the more important factor, while Momot & Gowing (1977a, 1977b, 1977c) have produced some evidence to show a density-dependent effect on reproductive success. The strong regulatory effect of water temperature on many crayfish populations seems clear, however. Lowery & Mendes (1977) found that *Procambarus clarkii* removed from its normal seasonally fluctuating temperature regime by introduction to the warm waters of Lake Naivasha, Kenya, lost its regular reproductive cycle and bred all year round.

The clear limiting effect of water temperature on the distribution of *Astacus astacus* in Sweden has been reported by Abrahamsson (1973), who found that introduced populations of the species could survive and grow at latitudes up to 68^{0}N, but that reproduction was limited to those areas where water temperatures averaged 15^{0}C for three months or more. It may well be, however, that water temperature is not the sole limiting factor on the northern distribution of *Austropotamobius pallipes* in Britain. Jay & Holdich (1977) have attributed the absence of the species from Scotland to the barrier formed by the acidic waters of the Central Lowland: conditions further north may be suitable for crayfish, but they are unable to colonise the area. Nevertheless, it is clear that water temperature is a highly important factor, as the occurrence of the life history events of *A. pallipes* in Northumbria is invariably later than in more southerly populations (Thomas & Ingle 1971; Holdich, Jay & Goddard 1978; Pratten 1980).

There was a marked correlation of the activity levels of *A. pallipes* with water temperature (2.3.1), a relationship mirrored almost exactly in a study by Flint (1977) on an American species, *Pacifastacus leniusculus*. *P. leniusculus* was found still to be sluggish in its movements at temperatures of 8-10^{o}C in late May, while increasing water temperatures in June and July stimulated greater activity in a manner very similar to that of *A. pallipes* (2.3.1).

The wide range of items in the diet of *A. pallipes* has led to reports that it is a scavenger, e.g. Huxley (1880); Howes (1962); Karlsson (1977); Richards & Fuke (1977); Fuke (1978). The experiments described in 2.3.4, however, indicate that it is, whenever possible, a selective feeder. Feeding is essentially opportunistic: although plant material probably forms the bulk of the diet in most cases, there is a marked preference for animal material whenever it is available. This is supported by the high catch rate of traps baited with raw liver (personal observations). Moriarty (1973) concluded that *A. pallipes* was selective even for certain types of animal material, as certain baits actually repelled crayfish. Cannibalism may be regarded as an example of opportunistic feeding. Fox (1975) considered that where it is not ascribable to any obvious factor, cannibalism may be a response primarily to the presence of vulnerable individuals, while Brown (1967), commenting on cannibalism in gull populations, considered it to be an extension of normal hunting behaviour. This may well be true of *A. pallipes* also.

Despite the demonstrable preference of *A. pallipes* for animal material, it is generally incapable of catching any but the most sluggish of benthic invertebrates. Laboratory and field observations show that the major chelae of crayfish are too cumbersome to be useful in catching prey, a fact recognised by Chidester as long ago as 1908. The capture and manipulation of food is carried out by the minor chelae on the first two pairs of ambulatory limbs. This general inability to catch active prey is undoubtedly an important reason for the preponderance of plant material in crayfish stomachs (Chidester 1908; van Deventer 1937; Tack 1941; Dean 1969; Caine 1975;

Momot 1978). The presence of a cellulase in the digestive systems of crayfish enabling them to utilise plant material has been reported by Yokoe (1960) and Kooiman (1964), who suggested that the wide range of carbohydrases present in *A. pallipes* was related to the importance of detritus in the diet.

Evidence of selective feeding in crayfish was found by Chidester (1908) and Seroll & Coler (1975) and it is apparent from the feeding experiments described in 2.3.4 that *A. pallipes* prefers certain macrophytes to others, showing the strongest affinity for *Nitella* and the lowest for *Elodea canadensis*. Although the moss *Fontinalis antipyretica* is virtually the only macrophyte present at the principal field site (2.3.2), it is not one of the species most preferred by *A. pallipes*. It may be that this plant is of low food value (Pratten 1980). An important feature of these experiments was the destructive nature of the feeding of *A. pallipes*. Besides consumption of parts of plants, stems and leaves were frequently severed and plants damaged mechanically. The effect of a natural population of crayfish is therefore likely to extend far beyond its powers to consume macrophytes. Thus Abrahamsson (1966) reported the control of macrophytes in several lakes by populations of the crayfish *Orconectes causeyi*. Among the controlled species was *Elodea canadensis*, the species which proved least attractive to *Austropotamobius pallipes* (2.3.4).

Whilst activity levels in the study population were strongly correlated with water temperature (2.3.1), there was no evidence that feeding habits changed during the year, although the frequency of feeding was apparently much reduced during the winter months. These findings are similar to those of Flint (1977), who reported that feeding in a population of *Pacifastacus leniusculus* was occasional during the winter and that general activity was much reduced. The lower feeding activity in *A. pallipes* is probably related to low water temperatures, as at several sites near the study area the larger aquatic macrophytes remained in good condition into January and February.

It has been suggested that filter feeding is the method used by juvenile crayfish to obtain a large proportion of their nutrition (Budd, Lewis & Tracey 1978), while adults retain the ability to filter feed (a method which may be particularly valuable while the carapace hardens during the immediate postmoult condition). It is apparent that crayfish feature in at least three trophic levels in most freshwater systems, being active consumers of detritus, macrophytes and animal material. Their importance as recyclers of nutrients has been suggested by Taub (1972); Lorman & Magnuson (1978) and Rundquist, Gall & Goldman (1977). Penn (1950); Franz & Cordone (1970); Jacobsen (1977) and Gowing & Momot (1979) recognised the value of crayfish as food for various species of fish. However, it is believed that predation of *A. pallipes* was not important in the regulation of population size during this study.

Chapter Three

POPULATION DYNAMICS

3.1 INTRODUCTION

There have been very few reports of the biology of *Austropotamobius pallipes* and even fewer have made any attempt to quantify population parameters. Duffield (1933, 1936) presented a series of local reports suggesting a 13-14-year cycle of abundance and decline in crayfish populations in southern England and speculated that the cause 'may turn out to be *Thelohania contejeani* or *Bacillus pestis astaci*' (now designated *Aphanomyces astaci*, the crayfish plague fungus). There is no evidence that crayfish plague, which is characterised by the rapid and almost total elimination of crayfish populations, has reached Britain (Behrendt 1979; Bowler 1979), and in the population of this study *Thelohania* is not believed to be important in the regulation of population size (6.4).

Thomas & Ingle (1971), while providing a valuable account of the general biology of the species, gave only brief details of the size of hatchlings and reproductive females. The work of Holdich, Jay & Goddard (1978) includes similar details for crayfish in the Midlands, while that of Pratten (1980) reported in detail on growth rates in a population of *A. pallipes*, without reference to dynamics. Whilst Brown (1979) has produced the first attempt to quantify some of the parameters of the dynamics of a population of *A. pallipes*, there remains a large body of questions about the biology of the species at the population level. Many of these questions can be answered only by a detailed long term study of population dynamics. The only previous attempt at such a long term study is the work of Momot (1967a, 1967b, 1978) and Momot & Gowing (1977a, 1977b, 1977c) on populations of the American crayfish *Orconectes virilis*, in which year class fluctuation in the age structure was identified (the species is comparatively short-lived, with a maximum lifespan of three years). Population size was found to be relatively stable with most of the year-to-year differences in biomass being produced by changes in mortality rather than growth rates. In the absence of a comparable study on *Austropotamobius pallipes* it has not been possible to assess how far these conclusions are applicable to this species.

3.2 METHODS

3.2.1 Marking Techniques

The marking of crayfish poses special problems in that a method must be found which ensures that a mark is not lost when the exoskeleton is shed during a moult. This precludes the use of many types of colour marking used principally on insects (see, for example, Manly & Parr 1968). In addition to the usual requirements for a marking system, i.e. that the marks must not affect the growth, survival and behaviour of individuals, there were certain extra constraints upon the technique to be used for this study, since one of the principal objectives was to follow growth in the field as well as to study population dynamics. It was essential that the chosen technique be readily applicable under field conditions and capable of dealing with large numbers of individuals. Most of the established marking methods fail to fulfil at least one of these criteria.

As Southwood (1978) noted, most invertebrate marking methods have been developed for insects and are intended to give date-specific as opposed to individual-specific marks. Simple surface labelling of the crayfish exoskeleton would be inadequate as marks would be lost at the first moult of the individual: in adult *A. pallipes* moulting generally occurs twice each year and juveniles moult more frequently (4.3.5). Various types of mutilation have been used to mark crustaceans, e.g. by Thomas (1958); Momot (1966); Hopkins (1967a); Hepper (1972), and while these punches or clippings may persist for several moults (Simpson 1963) they are eventually lost by regeneration of the deformed appendage. In addition, it is difficult to adapt such a system to mark many animals with individual marks. Goellner (1943); Slack (1955) and Penn (1975) attempted the use of injected dyes for marking with limited success. Penn (1976) and Pollock & Roscoe (1977) used tags inserted in the carapace of *Penaeus latisulcatus* and *Jasus tristani* respectively, but Davis (1978), in a field evaluation of a tag for juvenile spiny lobsters (*Panulirus argus*), found a mean monthly tag loss of 3.8% or approximately 10% per moult for the first three moults after tagging.

Bearing in mind the requirements of this study and the above observations on alternative marking techniques, it was decided to use the method of branding spots on the dorsal carapace. The original description of this method of marking crayfish was given by Abrahamsson (1965), although the number coding system (Fig. 3.2) was used in a slightly different form by Richards & Waloff (1954) for marking grasshoppers. Moriarty (1973) used branding on an Irish population of *A. pallipes* and Brown (1979) found that this method satisfied the requirements in the field for his study of the species.

The marking instrument which was used was a nichrome filament heated to red heat by a heavy duty battery. Application of the filament to the dorsal carapace produced a small but easily visible mark which experience showed persisted through at least two moults as the initial branding affects the integumentary layers below the external carapace. All marks became less distinct with each moult but could be reinforced as necessary upon subsequent recapture. This had the great advantage of extending considerably the period over which individual histories of growth and reproduction could be followed.

The first mark given to a captured crayfish was a date-specific mark on the uropods (Fig. 3.1). Upon recapture a crayfish carrying a date-specific mark was given an individual 'number' after the method of Abrahamsson (1965) modified by the addition of marks on the abdominal segments in order to permit the numbering of animals up to 25 599 (Fig. 3.2). The use of this combination of date-specific uropod marks and individual-specific numbers meant that many individuals carried both types of mark. When the number of a crayfish was in doubt it was often possible to identify it by reference to the uropod mark, size or sex, thereby eliminating other possibilities. Throughout the study there was no evidence to suggest that the use of this marking system interfered with moulting or affected crayfish survival in any other way.

3.2.2 Recording of field data

The confinement of the crayfish population in a narrow aqueduct and the ease with which it could be sampled when the water had been drained after closure of the sluice gate (2.3) meant that it was the number of animals which could be 'processed' in the field rather than the number which could be caught which was the limiting factor, at least in midsummer, when water temperatures were at their highest.

Fig. 3.1 The coding system of the fifteen date-specific uropod marks

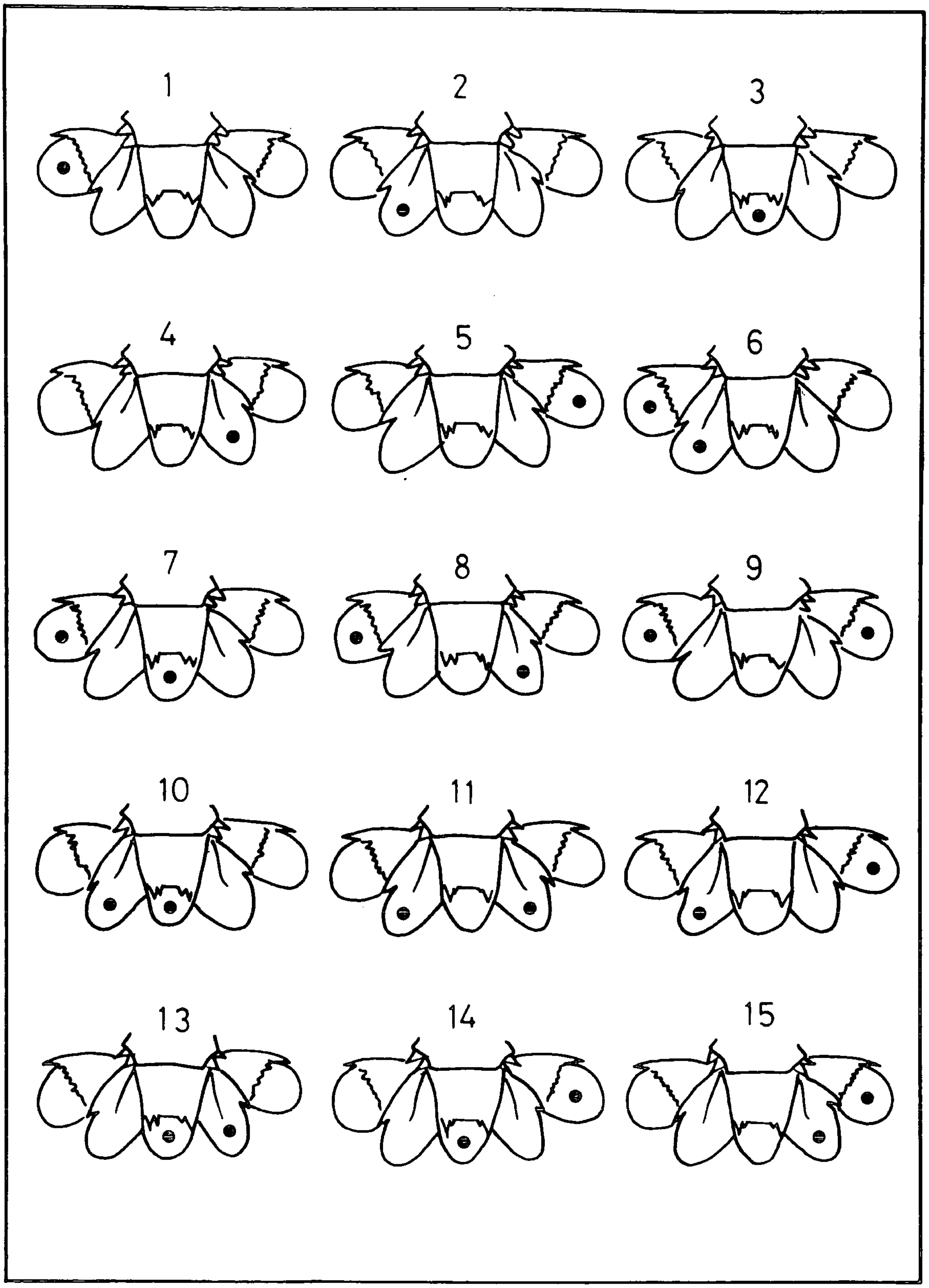
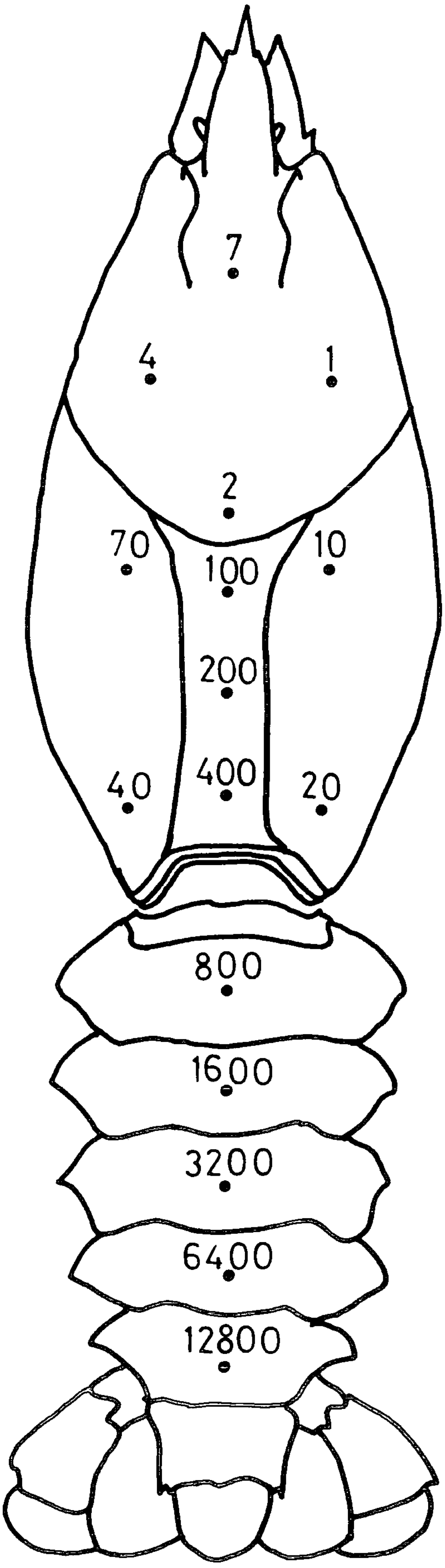


Fig. 3.2 The system used to number individual crayfish (after Abrahamsson 1965)



Accordingly, the details listed below were recorded only for individually numbered crayfish. Previously unmarked animals were given a date-specific uropod mark, sexed and classified as adult or juvenile. For crayfish bearing a number or a uropod mark, the following details were recorded:

i) The number and uropod mark or 'daymark' (where present).

ii) Carapace length, defined as the distance from the rostral apex to the posterior median edge of the cephalothorax. This distance is almost exactly half of the total body length and was preferred as the index of size because of the flexibility of the abdomen. During the first part of the study the width of the carapace was also recorded, but this was later dispensed with as the measurement of carapace length proved to be sufficiently accurate.

iii) The sex of small juveniles can, with practice, be determined readily in the field because of the presence of two pairs of modified pleopods in the male. Thomas (1977) reported that juvenile *A. pallipes* can be sexed at a carapace length of 8 mm. Since the smallest animals caught in this study had carapace lengths of some 13 mm, sexing was readily done in the field.

iv) Reproductive females were easily identified by the presence of a large 'berry' of eggs attached to the pleopods. For a period of some two weeks after hatching the young remain clinging to these pleopods before becoming free living. In addition, for a short period following mating in late October and early November fertilised females can be recognised by the presence of white spermatophores on the ventral surface.

v) The loss or damage of the major chelae is a common feature in crayfish. Records were made of individuals with lost, damaged or regenerating chelae and of the size of regenerating chelae (measured from the tip of the propodus to the carpal joint).

vi) The projecting nature of the rostrum of *A. pallipes* renders it vulnerable to damage. However, its characteristic shape

vi) (Gordon 1963; Thomas 1974; Gledhill, Sutcliffe & Williams 1976) makes damage readily identifiable.

vii) A feature of this population is the presence of the microsporidian endoparasite *Thelohania contejeani* Henneguy (Microsporidia: Nosematidae). During the period of the study some 3% of the population was found to be infected by the parasite, these crayfish being identified by the opaque white colour of the abdominal musculature (6.1).

The above details of numbered crayfish were recorded in field notebooks. Because of the large numbers which were sampled a coding system was developed to enable this information to be stored in a file on an IBM 370 computer. This file was enlarged and updated at each successive sample and proved to be very efficient and flexible in the statistical manipulations which were required. The principal programmes used to analyse the data were the SPSS package of Nie *et al.* (1975) and a purpose-written FORTRAN programme by Davies (1971) to produce estimates of population size, survival and recruitment.

3.2.3 Sampling methods

For the purposes of sampling, the aqueduct was divided into 120 6-metre sections after the method of Brown (1979), the area of rapid flow adjacent to the outlet being excluded from sampling. On each sampling occasion thirty to forty sections chosen at random were fished by hand after the sluice gates had been positioned to drain water from the aqueduct (2.3). The catch from each section was held separately during the recording of data and returned to a section which was chosen randomly from those which had been fished that day. This procedure was adopted to ensure the thorough random mixing of marked crayfish with the rest of the population as required by the population model of Jolly (1965), which was the principal method used to produce estimates of population parameters. Such a stratified random method of sampling the population is considered by Southwood (1966) to be preferable for most ecological work.

The importance of a knowledge of the life history of the subject species of a population study has been stressed by Malley & Reynolds

(1979). Throughout this study the timing of sampling was adjusted so as to span the periods of moulting and reproductive activities.

Of the 27 569 crayfish which were given a date-specific mark during the three years of the study, 4332 were recaptured once (NB: crayfish were given an individual number at first recapture). A further 1256 were recaptured twice, 456 three times, 172 four times, 63 five times, 27 six times, 8 seven times, 4 eight times and 1 nine times.

3.3 REQUIREMENTS OF THE MARK-RECAPTURE STUDY

The practical difficulties facing workers on growth in crustaceans are discussed in detail in 4.1. The principal difficulties apply also to studies of population dynamics. In particular, the problems of obtaining sufficiently large representative samples from large populations have hindered workers on this group as on many others. Indeed, Rose & Armentrout (1974) concluded that the estimation of population size of urodeles is often 'a difficult and meaningless task'. Roff (1973b) lists some reasons for the appearance of bias in some mark-recapture studies, among which are differential behaviour, temporary emigration, differential survival of age groups, insufficient mixing of marked animals, homing, a population composed of mobile and static components and tagging mortality.

As discussed earlier (2.3), the aqueduct inhabited by the crayfish population of this study has certain features which allowed the catching of large samples. In addition, the method of hand fishing which was used ensured that the entire population of a size larger than 13 mm carapace length was almost completely fished out of a representative sample of the aqueduct (3.2.3), thereby ensuring that an unbiased sample was obtained.

Any effect of the differential behaviour of reproductive females (2.5) was dealt with by treating this subpopulation separately in the estimation of population parameters (3.4, 3.5). Similarly, adult males, adult nonreproductive females and juveniles were treated separately. The importance of the use of biological insight to produce homogeneous groups for the estimation of population parameters is stressed by Bishop & Sheppard (1973).

The thorough mixing of marked animals with the rest of the population was assisted by the method of returning the catch from a fished section of the aqueduct to a section chosen randomly from those which had been fished that day (3.2.3). Studies by Camougis & Hichar (1959); Black (1963); Mobberly & Pfrimmer (1967) and Merkle (1969) indicate that there are no territorial tendencies in crayfish, although individuals may occupy one particular hide for several days at a time. The generally random nature of movements and hide selection further assist the mixing of marked crayfish. Furthermore, Brown (1979) found that the movements of adult crayfish in this aqueduct in summer were extensive, frequently exceeding 100 m between trapping dates. While the lowering of the water level during hand fishing (2.3) undoubtedly disturbed the population, it is believed that this served to aid further the random mixing of marked animals. The system of marking which was used (3.2.1) satisfied the requirements common to the most widely used mark-recapture methods (Southwood 1966; Seber 1973). In particular, the date of last capture of marked individuals was known from records of the uropod marks or the individual numbers. There was no evidence to suggest that marking modified behaviour or affected the chances of survival. Samples could also be regarded as 'instantaneous', i.e. sampling time was negligible with respect to the length of the study.

The most widely used mark-recapture models are all derivatives of the Lincoln Index (Lincoln 1930). The relative merits and disadvantages of these have been reported by many workers, e.g. Southwood (1966); Manly (1970); Bishop & Sheppard (1973); Roff (1973a); Rose & Armentrout (1974), and it is not proposed to discuss these in detail. Manly (1970), in a simulation study of several models, concluded that the method of Fisher and Ford (1947) is as accurate as that of Jolly (1965) when its assumptions are valid, but that it can produce strongly biased estimates if mortality rates are age-dependent. (An important limitation of the Fisher-Ford model is its assumption of a single constant survival rate). The method of Bailey (1951, 1952) is considered by Southwood (1966) to utilise an inefficient grouping of data. Jolly's method was recommended for use by Manly (1970) where samples are moderately large and where mortality rates are not strongly affected by age. The method of Manly & Parr (1968), like that of Jolly, calculates a separate survival rate for each intersample period, but (unlike Jolly's method) does not assume that mortality is independent of age. In this study, however, intersample periods were relatively short and because of the separate treatment of several subpopulations it could be assumed that mortality was independent of age during these short periods. In such a case the method of Jolly is superior (Manly & Parr 1968).

Southwood (1966) stated that 'Jolly's method would appear to be the most appropriate method for use in studies including three or more successive samples where both dilution and loss is occurring, that is in most studies of invertebrate populations'. It was decided that the method of Jolly (1965) is the most appropriate model for this study and that the assumptions implicit in its use (see above) are satisfied for this population. This method was used earlier by Brown (1979), who sampled almost exclusively adult crayfish in a study at this field site.

3.4 THE CALCULATION OF POPULATION ESTIMATES

Estimates of population parameters were made after the method of Jolly (1965). Davies (1971) produced a FORTRAN programme which calculates estimates according to Jolly's equations when data are entered as a trellis of last recapture date frequencies together with sample sizes. This programme was compiled and run on an IBM 370 computer to produce estimates for each subpopulation studied. Estimates of survival and recruitment were produced for each intersample period. Since the periods between samples varied, these estimates were converted to weekly rates in order that direct comparisons could be made. For the estimates of recruitment, this conversion was achieved by a simple ratio method varying according to the length of the intersample period. Estimates of survival (S) were converted to weekly mortality rates (M) by the equation

$$M = (1 - e^{\frac{\ln(S)}{\text{time}}}) \times 100$$

The general utility of Jolly's model for use in studies involving long series of mark-recapture samples is widely recognised (Southwood 1966; Manly & Parr 1968). There was, however, a limiting factor on the length of the recapture series used to produce population estimates in this study. This was the progressive loss of marks with each successive moult. Experience showed that the marks persisted through at least two moults (3.2.1). The computation of estimates of population parameters was therefore limited to recapture series extending over no more than two major moult periods. Since any one sample could be included in two or more such series, it was often possible to produce two or more partially independent estimates of each parameter for any one sample date. In such cases each estimate is given in Appendix Tables A1-A8. On no occasion do any two such estimates differ significantly: indeed, a feature of the data is the very close agreement between them. Sections 3.5-3.6 discuss in detail the seasonal changes in the estimated parameters of the subpopulations which are presented in Figs 3.3-3.6. Population size (N) is represented as $\log_{10}$ in these figures as this transformation is more descriptive of relative changes in numbers (Williamson 1972).

The large numbers of marked crayfish in the population and the increased sampling intensity, particularly of juvenile crayfish, after May 1978 allowed the subdivision of the juvenile subpopulation into the year classes 2+ and 3+ on the basis of carapace length. Section 4.3.8 describes the detailed analysis of the relationship between carapace length (CL) and age and places the sizes of these two year classes at 13.00-18.25 mm CL and 18.25-24.74 mm CL (males) and 18.25-26.32 mm CL (females) respectively. In the absence of this data at the beginning of the study a somewhat subjective estimate of these sizes was made and crayfish in the range 13-18 mm CL were classified as year 2+ while crayfish of 18-25 mm CL were classified as year 3+. The method of hand fishing which was used to sample the population excluded almost entirely animals of year 1+ (8.49-13.00 mm CL).

The subdivision of the juvenile subpopulation in this way reduced the numbers of recaptures in the cells of the trellis required by the model of Jolly (1965) as the basis for estimating population parameters. Thus the standard errors of the estimates for the juvenile year classes are generally proportionately larger than those of the three principal subpopulations studied (Tables A1-A8), and although less reliability may be placed on their accuracy it is nevertheless possible to distinguish certain similarities to the estimates for other subpopulations.

3.5 RESULTS

The detailed estimates of population size, mortality and recruitment are given in Tables A1-A8 and are summarised in Figs 3.3-3.6. Only the salient points will be treated here.

Estimates of total population size were generally stable during the first half of 1977 (Table A1). There followed a large midsummer peak in numbers which is attributable to the increase in size of the juvenile subpopulation. Thus the largest estimate of total population size in 1977 was 21 821 (95% confidence limits = 16 066 - 27 576) on 12 August. Thereafter the estimates indicate a slight fall in numbers towards the end of the year. The apparent large increase in numbers during the winter of 1977-78 (when no moulting and therefore no recruitment occurred) is believed to be an artefact caused by the increased intensity with which the population was sampled from 1978 onwards. Similar 'increases' are to be seen in the adult male and adult female subpopulations.

While total population size remained relatively stable during the first half of 1978 (Fig. 3.3), there was no midsummer peak in numbers comparable to that of 1977. Indeed, there is clear evidence of a substantial fall in numbers during August and September and a further fall overwinter: both estimates of 29 October 1978 are significantly greater ($P<0.05$) than the estimate of 4128 (95% CL = 3336-4920) on 24 April 1979. Similar large overwinter declines of up to 50% of original numbers occurred in the adult male and juvenile subpopulations, although the trend is less clear in the adult female subpopulation (Figs 3.4-3.6). The largest estimate of total population size in 1979 is 14 612 (95% CL = 11 882-17 342) on 18 July. This was followed by a decline: estimated numbers on 2 October were significantly lower ($P<0.05$) than numbers on 18 July and on 9 August (Table A1). The final estimate of 4871 (95% CL = 3366-6376) indicates that the population had failed to recover to the level prior to the decline of late 1978.

The available estimates of survival rates in the total population (Table A1, Fig. 3.3) show that mortality was generally highest during the major moult periods (2.5) and during May and early June.

Fig. 3.3 Population estimates for the total population. Error bars are 95% confidence limits. OW = Overwinter.

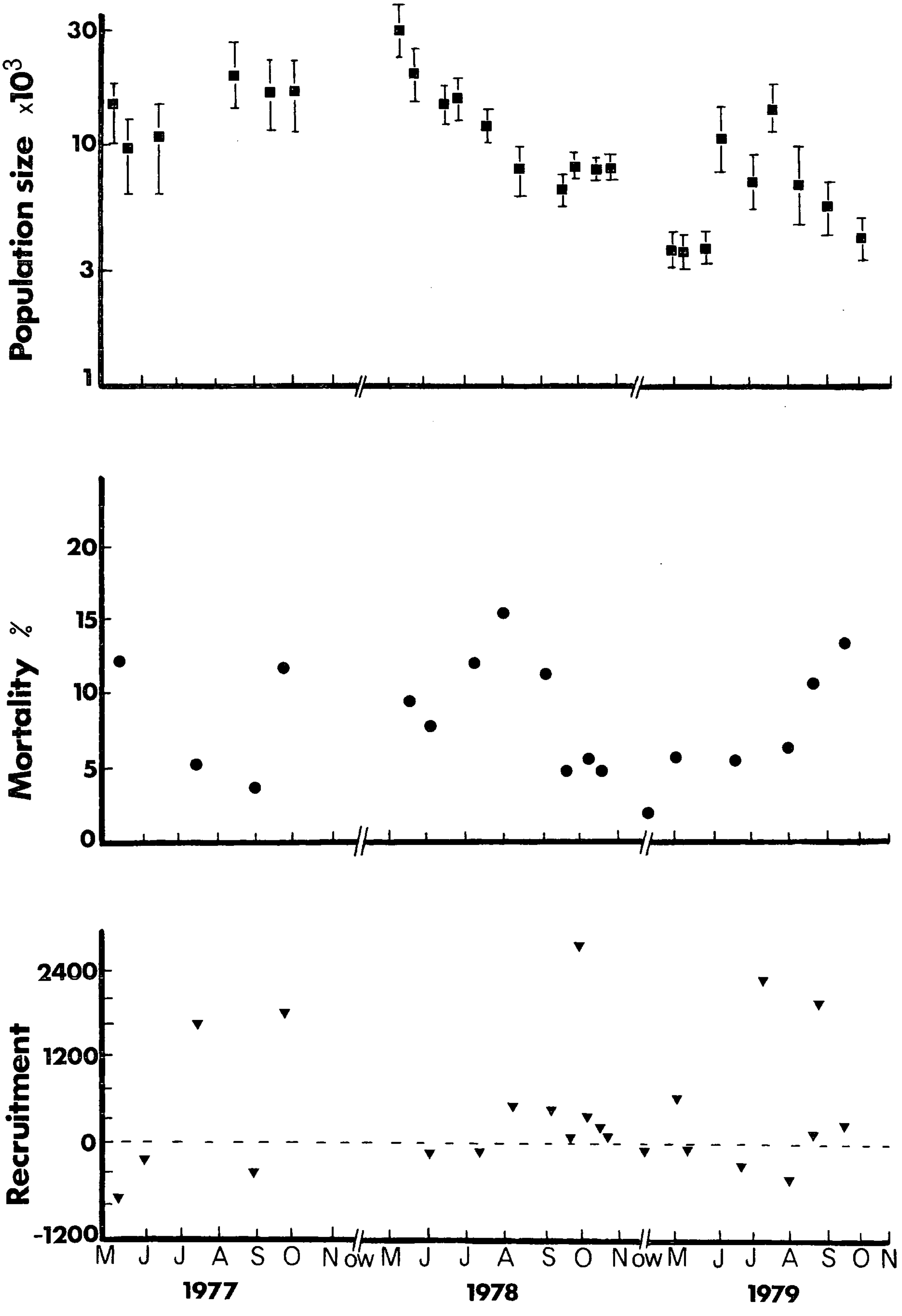


Fig. 3.4 Population estimates for the adult male subpopulation. Error bars are 95% confidence limits. OW = Overwinter.

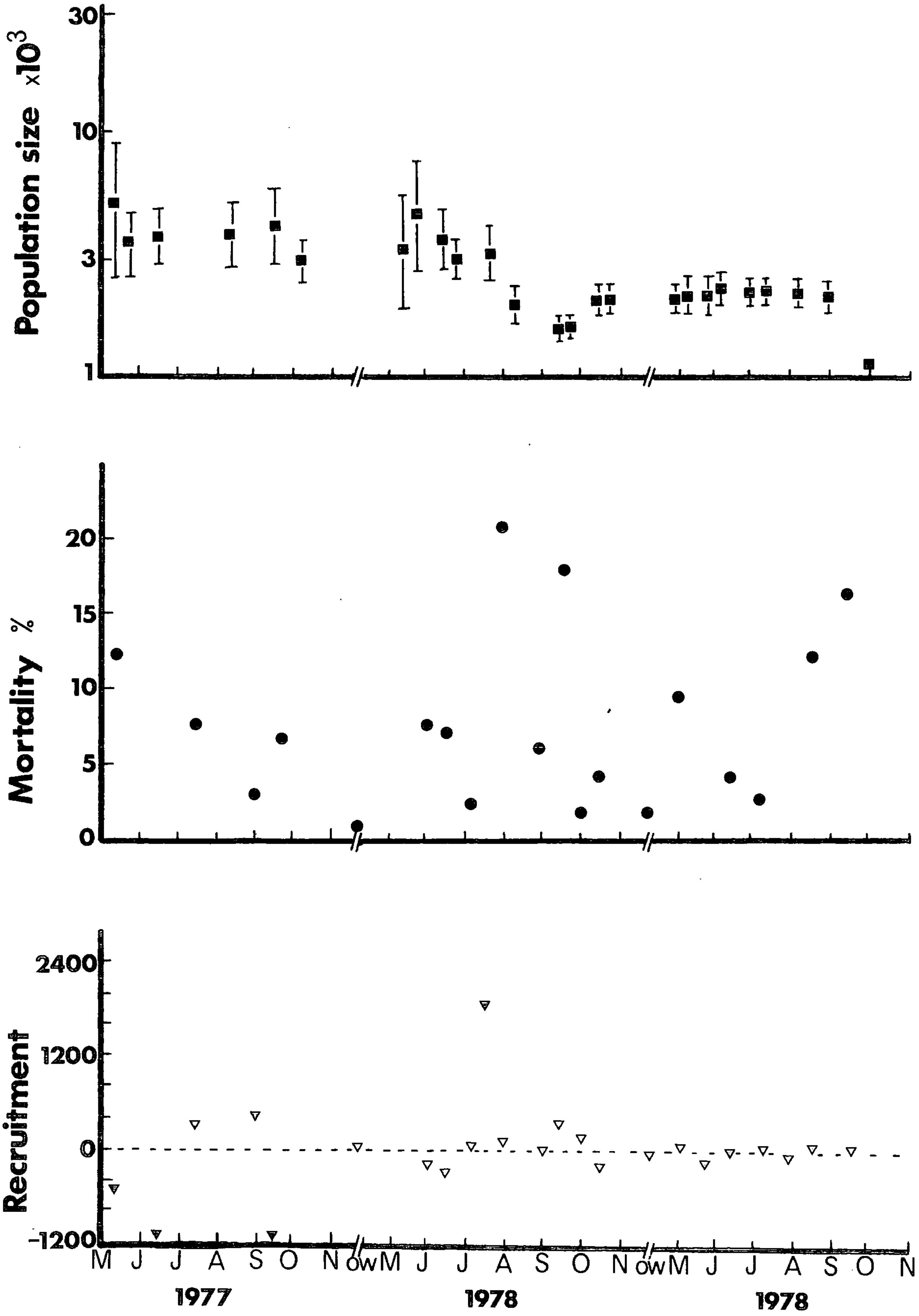


Fig. 3.5 Population estimates for the adult female sub-population. Error bars are 95% confidence limits. OW = Overwinter.

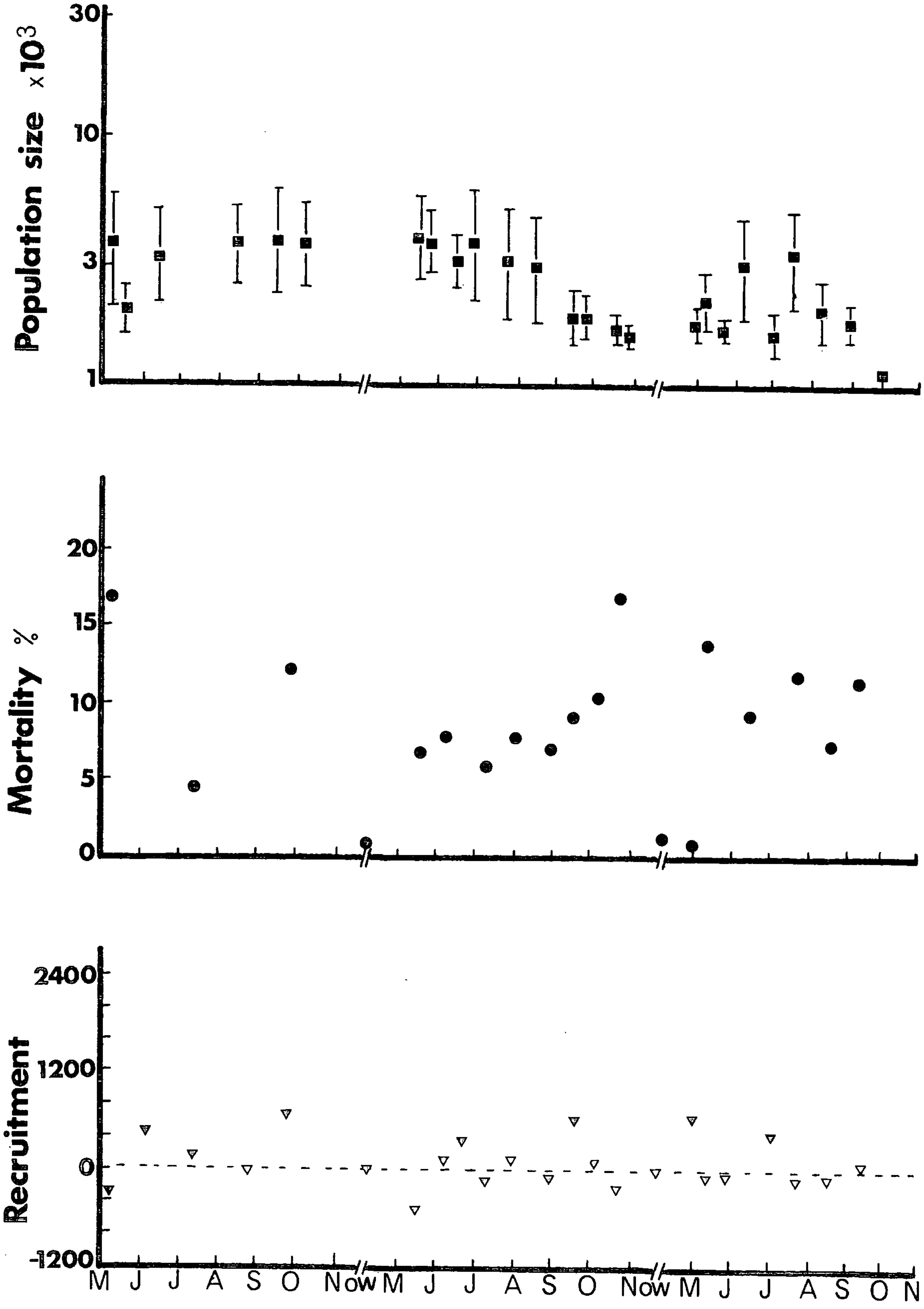
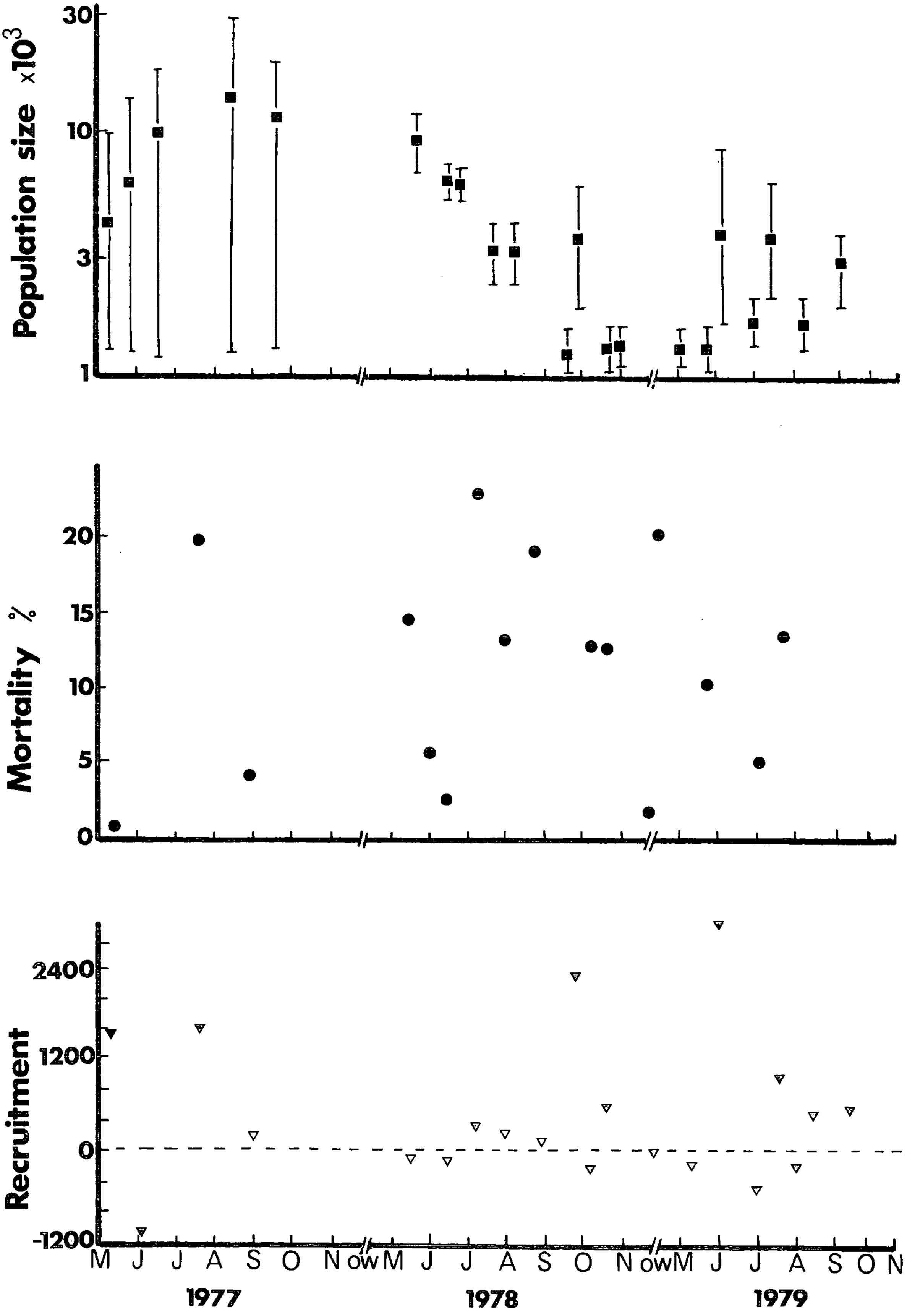


Fig. 3.6 Population estimates for the juvenile subpopulation. Error bars are 95% confidence limits. OW = Overwinter.



The apparent mortality during the latter period is believed to be spurious and to be attributable to biased sampling of the population while water temperatures were too low to allow full activity of crayfish (2.5, 3.6). Trends are clearer in the mortality rates estimated for the separate subpopulations. There is a tendency in the adult subpopulations for the periods of highest mortality to coincide with the major moult periods (Tables A2-A3, Figs 3.4-3.5). Rates at these times are commonly 8-12% week^{-1}, while in the mid-summer period between the major moult periods there is generally an appreciable fall in the mortality rate. This trend is not apparent in estimates for the juvenile subpopulation, however, in which mortality tended to be high throughout the summer period, in several cases approaching 15% week^{-1} (Table A4, Fig. 3.6). Over-winter mortality rates (calculated on the basis of a constant weekly rate) were very similar (1-2% week^{-1}) in each subpopulation.

Estimates of weekly recruitment to the total population in 1977 show two large peaks covering the periods June to August and the second half of September when recruitment was estimated to exceed 1500 crayfish week^{-1} (Table A1, Fig. 3.3). Between these two periods, i.e. in August and early September, a low negative estimate was obtained. Positive estimates of recruitment for the winter of 1977-78 and contradictory estimates of recruitment in the subpopulations during May-June in each year are believed to be effects of the increased sampling effort from 1978 onwards and of the low water temperatures at this time of year (2.5, 3.6). Relatively high recruitment to the total population, as in 1977, occurred during the period June-August in 1978, followed by a second peak in September. A similar trend is evident in the estimates for 1979.

The intensity of sampling of the juvenile subpopulation was relatively low because of its comparatively large size. Consequently the standard errors attached to the estimates for this subpopulation are generally larger than those for other subpopulations. It was nevertheless possible to recognise certain features of the juvenile subpopulation. Chief among these is the appearance of positive recruitment rates during June, August and September (Table A4, Fig. 3.6). As in other subpopulations, mortality rates were particularly high in midsummer, although high rates were also recorded in May 1978 and May 1979. The sole estimate of mortality available for the winter of 1978-79 is a rate of 1.92% week^{-1} for year 3+ females (Table A6), a rate strikingly similar to those of the two adult subpopulations.

3.6 DISCUSSION

In view of the need for a rigorous interpretation of the dynamics of the population, it is necessary to place in a statistical context the accuracy of the estimates of the population parameters. Roff (1973a) used the ratio $SE/\hat{N}$ as a measure of the accuracy of estimates of population size and proposed that such estimates be considered acceptable only if this ratio is below 0.05. However, he also noted that it is questionable whether the sampling intensities required to achieve this can be achieved in practice. As Table 3.1 shows, this ratio declined throughout the period of the study to levels approaching Roff's stringent limit, something rarely achieved in studies of open populations. It was possible in this study because the sampling intensity (estimated as m_i/M_i : Roff 1973b) was 30-50% for each subpopulation.

Some estimates of survival rate (Tables A1-A8) are greater than one, although not significantly so. Such figures occur occasionally in series of Jolly estimates: Parr (1965) includes several examples. Bishop & Sheppard (1973) noted the tendency for Jolly's model to overestimate survival rates. Such values were assumed to be equal to one. Of the estimates of survival rate which were less than one, most are not significantly different from this figure (significance levels are indicated in Tables A1-A8). It was nevertheless possible to calculate weekly mortality rates from such estimates. In view of the absence of any significant deviation from one of the original survival estimates, no great degree of reliance can be placed on such mortality rates. Similarly, the standard errors attached to the estimates of recruitment rates are generally rather large: few estimates differ significantly from zero (significance levels are given in Tables A1-A8). If, then, these estimates are regarded as indicators of general trends rather than accurate estimates a definite seasonal pattern can be distinguished.

There is evidence that mortality occurs in the population throughout

Table 3.1

The ratio SE/$\hat{N}$ for the total population on some sample dates during the study

Date		SE/$\hat{N}$ (%)
May	1977	20.4
June		15.8
August		13.5
October		12.5
May	1978	8.3
June		6.6
July		10.3
August		8.5
September		7.3
April	1979	9.8
June		10.3
July		8.8
August		9.3

the year, but that the nature and intensity of this mortality varies in different subpopulations and according to the time of year. One important period of mortality is the long overwinter period of some 30 weeks during which crayfish become torpid. Estimates for each subpopulation and for the population as a whole consistently place the overwinter mortality rate at 1-2% week^{-1}. This low weekly rate has the effect of reducing population size by some 40-60% because of the long period over which it is effective (Tables A1-A8, Figs. 3.3-3.6). The proportion of this reduction which is attributable to emigration or cannibalism is believed to be very low because of the greatly reduced activity levels of crayfish at winter temperatures (2.5). In the absence of any direct evidence as to the nature of overwinter mortality the most likely cause appears to be low temperature and/or nutritional stress. Some circumstantial evidence to support such a density-independent source of mortality is the consistency of the overwinter mortality rate in adult and juvenile subpopulations.

Two further important periods of mortality exist, coinciding with the two major moult periods which have been identified (2.5). Unlike overwinter mortality, rates during these periods are typically 8-12% week^{-1} in the adult subpopulations and are effective for periods of 2-3 weeks. In the juvenile subpopulation the rates are generally higher at 15% week^{-1} or more and tend to remain in effect for longer periods. There is good reason to believe that this type of mortality, operating at appreciably higher rates and over well defined shorter periods than overwinter mortality, is attributable to cannibalism of recently moulted crayfish. Cannibalistic tendencies in crayfish are well documented (Huxley 1880; Cossins & Bowler 1974; Behrendt 1979; Cuellar & Coll 1979) and field observations indicate that they are marked in *Austropotamobius pallipes* (2.5). The confinement of these high mortality rates to the major moulting periods is strong circumstantial evidence of cannibalism. (Laboratory and field observations indicate that few individuals fail to complete a moult successfully). The more frequent moulting of juveniles (4.3.5) and the consequent lack of synchrony with the major moult periods of adults accounts for the higher mortality rates operating over longer periods in this subpopulation. The presence of a strong tendency for moulting in adults to be synchronous (2.5) can therefore be regarded as an adaptation to reduce the risk of cannibalism. Mortality rates between major moult periods fell markedly to levels approaching the overwinter rate, which may thus be regarded as being a 'background' mortality rate.

Also strongly related to the moult periods is the level of recruitment. Clearly, crayfish may enter the catchable size range (>13 mm CL) only by moulting. Thus the marked overwinter decline in numbers is followed by an increase during the growth season and results in a midsummer peak in population size. Thereafter numbers remain relatively stable, with recruitment apparently being balanced by mortality, until the overwinter decline begins once more.

There is one point upon which the estimates of the population parameters consistently contradict this pattern. This is the apparent presence of very high mortality rates, causing a marked decline in population size, during the month of May (before any moulting was recorded in any year). Whilst some mortality would be expected at this time as part of the overwinter losses (water temperature is typically 8-9^{0}C in May, too low for full activity of crayfish - 2.5), the losses estimated far exceeded this level for three of the four subpopulations in 1977 and 1978. The exceptions are the juvenile subpopulation, for which a large recruitment was estimated in May 1977 (Table A4), and the adult male subpopulation, for which a similar large increase was estimated in May 1978 (Table A2). Samples taken later in these years produced estimates conforming to the pattern expected from a knowledge of the biology of the species. In an attempt to elucidate the reasons for these unexpected results a sample was taken earlier in 1979 (on 24 April). Estimates for the period between this date and 3 May 1979 indicate that recruitment occurred in each subpopulation, although only the estimate for the total population is significant. While the reasons for these inconsistent results, which appeared during the same period in each year of the study, are unknown, they may reasonably be considered to be related to the low water temperatures (e.g. 6^{0}C on 24 April 1979). Crayfish activity does not reach its 'normal' summer level until water temperatures reach approximately 10^{0}C, and hand fishing at lower temperatures invariably yields smaller samples. Thus the samples taken during April and May were consistently the smallest samples of the entire three-year period (Table A1). Furthermore, there is the possibility that because of the reduced activity of crayfish at lower temperatures, marked crayfish returned to the aqueduct in April and May did not mix randomly with the rest of the population, thereby violating an important assumption of the capture-recapture model. In this respect it is important to note that the inter-sample periods did not exceed fifteen days in April and May in any year of the study: at the reduced activity levels then prevailing this may have been insufficient time to allow thorough mixing of the marked animals with the rest of the population.

There remains one further possible reason for these anomalies. The method of sampling used depends on the disturbance of crayfish from their hides in the walls of the aqueduct and their consequent availability to capture on the floor of the aqueduct. Many of these hides extend to a considerable distance into the aqueduct walls, however, and it may be that sampling at the low water temperatures of April and May failed to flush out semi-torpid crayfish in such deep hides. Only the more accessible crayfish would then have been available to capture. The same conditions may well have prevailed at the next sample some fifteen days later, when once more the same subset of the population would have been available to capture, so producing highly biased estimates of population parameters.

In an earlier study at this site, Brown & Brewis (1979) compared trapping and hand fishing as sampling methods. They concluded that trap-caught samples were strongly biased towards large males, many of which became 'trap-happy' on repeated sampling. This bias resulted in an approximate three-fold underestimation of population size, while estimates derived from the recapture of hand fished samples in traps did not differ significantly from those derived from samples which were hand fished at both mark and recapture (Brown & Brewis 1979). In consequence, trapping was not used as a method of estimating population size in the present study, the 'passive' method of hand fishing being strongly preferred in view of its more representative sampling of the entire population.

The cause of the marked decline in numbers (from some 15 000 to 6-8000) which occurred in late 1978 is unknown. While the winter of 1978-79 was particularly severe, the decline occurred well before water temperatures approached the typical winter temperatures of 2-4^{0}C (2.5^{0}C on 8 March 1979). Furthermore, the overwinter mortality rates were estimated to be at normal levels for each subpopulation (Figs. 3.3-3.6). Duffield (1933, 1936) collated a series of local reports suggesting that crayfish populations in southern England undergo approximately thirteen-year cycles of abundance and decline. There was no apparent change in the environmental parameters of the aqueduct which may have caused such a decline, and there was little evidence of a resurgence in numbers in 1979 (Fig. 3.3, Table A1). All other fluctuations in total population size are consistent with the seasonal pattern described above.

Reproductive females in Northumbria carry eggs between November and early August (2.5). Estimates of their numbers are therefore available from samples taken during this period. These are presented in Table 3.2. It can be seen that the estimates of numbers in 1979 are generally smaller than those in either of the two preceding years. The estimate of 600 (95% CL = 304-896) on 31 May 1979 is significantly less ($P<0.05$) than that on 23 May 1978: 1889 (95% CL = 1042-2736). The lower numbers in 1979 reflect the smaller total population size in that year. Estimates of the numbers of reproductive females remained fairly constant within each year, as would be expected in a subpopulation to which no recruitment was possible. None of the estimated survival rates are significantly different from one and the weekly mortality rates derived from these are generally below 10% week^{-1}, showing none of the periodic peaks and declines of the other subpopulations (Table 3.2, Figs. 3.3-3.6). Some 45% of all adult females were reproductive in any one year (5.2). The relationship between size, fecundity and frequency of reproduction is discussed in Chapter 5.

Brown (1979), in a previous study of this population, was able to identify certain of the features of the annual population cycle described above, but did not achieve sufficiently high sampling intensities to demonstrate year-round mortality. He estimated population size to have been in the region of 20 000 individuals during the summer of 1974, 1975 and 1976. The decline of late 1978 therefore occurred after a relatively stable period of at least four years.

The consistent timing of the moulting and reproductive cycles from year to year observed in this population of *A. pallipes* is typical of members of the subfamily Astacinae (as defined by Hobbs 1974). Similar life histories have been described for *Astacus astacus*

Table 3.2

Population estimates for the reproductive female subpopulation

Date	N	Population size ± S.E.	Survival rate ± S.E.	Recruitment ± S.E.	Mortality (% week^{-1})	Weekly Recruitment
12 May 1977	155		0.673 ± 0.195		16.86	
27 May 1977	124	996 ± 374	2.452 ± 1.349	1549 ± 1379		516
17 June 1977	136	3989 ± 2304				
17 May 1978	205		0.959 ± 0.127		4.74	
23 May 1978	221	1889 ± 432	0.886 ± 0.126	173 ± 392	3.63	53
15 June 1978	280	1846 ± 315	0.978 ± 0.196	-316 ± 268	1.27	-184
27 June 1978	177	1490 ± 310	0.681 ± 0.215	-53 ± 129	9.48	-14
24 July 1978	132	962 ± 278				
24 April 1979	94		0.977 ± 0.191		1.82	
3 May 1979	69	704 ± 250	0.930 ± 0.207	-55 ± 223	1.81	-14
31 May 1979	102	600 ± 151	0.955 ± 0.262	330 ± 230	4.52	330
7 June 1979	89	902 ± 293	1.440 ± 0.602	-119 ± 341		-32
3 July 1979	75	1180 ± 479	0.576 ± 0.315	46 ± 182	22.68	21
18 July 1979	50	726 ± 347				

(Abrahamsson 1971; Kossakowski 1971), *Astacus leptodactylus* (Kossakowski 1971) and *Pacifastacus leniusculus* (Abrahamsson 1971; Mason 1975). These consistent patterns are probably related to the more predictable variations in water level and temperature compared to the more plastic life histories of some members of the Cambarinae, which generally inhabit less predictable environments (Bovbjerg 1952; Caldwell & Bovbjerg 1969). In the terms of Pianka (1978) *Austropotamobius pallipes* appears to be a K-strategist in this population in that population size is relatively constant over a long period, that mortality is strongly 'directed' rather than 'catastrophic' and that no recolonisation is necessary. Of the factors limiting the size of this population, cannibalism (which is probably density-dependent) and the availability of suitable hides would appear to be the most important, although the availability of food must also be considered. Within the aqueduct the moss *Fontinalis antipyretica* is virtually the only macrophyte present and it has been found in the stomachs of all crayfish which have been examined (2.3.4). Other material present included arthropod fragments (probably Gammarus sp.), colonial algae, diatoms and higher plant fragments from leaves washed into the aqueduct. While there is no evidence that the population is food-limited, this may be an important factor in overwinter mortality as the *Fontinalis* dies back and little allochthonous material enters the aqueduct. In general, however, workers have concentrated on estimating the size and production of crayfish populations and understanding of the mechanisms regulating these factors is very limited.

The estimates of annual production of the population (Table 4.14) correspond to 196.49 kg ha^{-1} in 1977, 116.80 kg ha^{-1} in 1978 and 87.79 kg ha^{-1} in 1979. Brown (1979) estimated annual production at this site to be 170.5 kg ha^{-1}. The annual production of a natural Russian population of Europe's most heavily commercially exploited crayfish, *Astacus astacus*, was estimated by Cukerzis (1975) to be 42 kg ha^{-1}. Mason (1975) estimated 133 kg ha^{-1} for a stream population of *Pacifastacus leniusculus trowbridgii*, while Momot & Gowing (1977b) give values of 60.2-133.4 kg ha^{-1} for natural populations of *Orconectes virilis* from biomasses smaller than those of *Austropotamobius pallipes* in the present study. Morrissy (1980) estimated the annual production of marron (*Cherax tenuimanus*), a large Australian crayfish, at 384-1033 kg ha^{-1} in farm dams, where the biomass often far exceeded the levels found in the study population of *A. pallipes*. The same author gives five examples of cultured marron populations exceeding 2000 kg ha^{-1} annual production, while Avault (1973) gives the annual production of pond-farmed *Procambarus clarkii* in Louisiana as 224-898 kg ha^{-1}.

In a comparison of the production/biomass (P/B) ratios of several crayfish populations, Momot (1978) found that values ranged from 0.5 to 2.0 and were typically 0.7-1.5. A value of 0.7 was obtained by Cukerzis (1975) for a population of *Astacus astacus*, the species most similar to *Austropotamobius pallipes* in its life history and longevity. The P/B ratios calculated for *A. pallipes* during the three years of the present study (0.40, 0.27, and 0.27) are considerably lower. An important factor in this is undoubtedly the short growing season in Northumbria (2.5). Momot, Gowing & Jones (1978), in a review of the rôle of crayfish in freshwater ecosystems, found that P/B ratios in four species of crayfish were similar and speculated that the production of crayfish populations can be approximated from a knowledge of their standing crops. While this may, in general, be true, it appears that for the population of this study, on which the limiting effect of the environment is pronounced, the relationship does not hold. The effect of temperature on P/B ratios was stressed by Waters (1977), who noted that the ratio is lower for zooplankton in cold habitats than for the same species elsewhere. It is probable that the comparatively low values obtained for the P/B ratio in the present study are at least partially attributable to the cold water temperature regime at the northern limit of the range of *A. pallipes*.

The work of Momot (1967a, 1967b, 1978) and Momot & Gowing (1977a, 1977b, 1977c) on *Orconectes virilis* comprises the most closely comparable study of crayfish population biology, although this work concentrates primarily on changes from year to year rather than seasonal changes. The lifespan of *O. virilis* is typically 3-4 years compared to eleven or more in *A. pallipes* (4.3.8). In common with *A. pallipes*, however, the growth rates of males are faster than those of females (4.3.7) and predation was not considered to be important as a population control mechanism (2.5, Momot 1967b). Whilst direct evidence of the rôle of cannibalism is difficult to obtain, the conclusions of Momot (1967b) agree with those of the present study, i.e. that population size is probably regulated principally by cannibalism at moulting. Fluctuations in mortality were reported to be the most important factor producing year-to-year differences in populations of *O. virilis* (Momot & Gowing 1977b), and mortality has been shown to have considerable seasonal variation in the study population of *A. pallipes* (Figs. 3.3-3.6).

The importance of the rôle in freshwater ecosystems of crayfish has been suggested by Momot, Gowing & Jones (1978). The precise function of crayfish is difficult to define since they operate at three trophic levels - those of detritivore, primary consumer and secondary consumer. It has been suggested (Momot, Gowing & Jones 1978) that crayfish may be most important in waters of low phytoplankton production, where they are important agents of energy flow. It is clear, however, that crayfish are significant at the ecosystem level both in terms of their biomass and of their function.

Chapter Four

GROWTH

4.1 INTRODUCTION

The nature of the incremental growth characteristic of the Crustacea presents problems to workers on growth studies. The two factors of paramount importance are moult frequency and the size of the moult increment. The study of growth in decapod crustaceans is complicated by the variability of both. These two factors may vary both between individuals and within the same individual from time to time. Many workers have used indirect methods to estimate moult frequencies and the size of moult increments. This has been necessary because the problems associated with the study of a large population of mobile animals make the recapture rates necessary to use direct methods difficult to attain. In addition, it is often necessary to treat certain parts of the population separately because of fundamental differences in their growth patterns. Differential growth rates between the sexes have been reported in the shrimp *Caridina nilotica* (Hart 1980), in the lobster *Homarus vulgaris* (Thomas 1958; Hepper 1972) and in the crawfish *Jasus tristani* (Pollock & Roscoe 1977) as well as the crab *Pachygrapsus crassipes* (Hiatt 1948). Furthermore, definite species differences exist in the relationship between size (age) and growth. This has two facets. First, the size of the increment at successive moults may fall, as has been reported for the crayfish *Paranephrops planifrons* larger than 20 mm carapace length (Hopkins 1967b) and for *Jasus tristani* (Pollock & Roscoe 1977), whereas in *Homarus vulgaris* Hewett (1974) reported that the growth increment increased with age. In general, however, when decapod growth is expressed relative to body size the growth increment falls with age. Second, moult frequency may decline with age (Hopkins 1967b; Farmer 1973; Hewett 1974).

The determination of age is in itself a major problem, as the moulting of the complete carapace prevents the use of techniques such as the aging of fish by the number of rings in the otolith. Farmer (1973) attempted a method of instar determination in *Nephrops norvegicus* using the numbers of aesthatasc-bearing segments of the antennule and the numbers of lamellae in the endocuticle but found these to be unreliable indicators of age. Consequently, many studies of decapod growth use size-frequency plots to estimate modal sizes of year classes and from these to estimate the size of the moult increment, e.g. Hopkins (1966, 1967b); Pratten (1980). It is often possible to distinguish only the first two or three year classes using this method, however, as variations in moult frequency and moult increment obscure the modal progression of year classes.

The regeneration of damaged or lost limbs may also obscure underlying growth patterns, e.g. it has been shown that limb regeneration in *Austropotamobius pallipes* is linked to a smaller moult increment (Bowler & Brown 1977). Bennett (1973) demonstrated that the marginal reduction of body growth by less severe limb loss in the crab Cancer pagurus is accentuated in the case of severe limb loss to a reduction of up to 25%, although this is counteracted to some extent by more frequent moulting. A further complicating factor may be the debilitating effect of parasites on some members of the population, e.g. Bowler & Brown (1977) reported that individuals of *A. pallipes* infected by the parasite *Thelohania contejeani* had smaller moult increments than normal animals. Finally, the omission of one or more moults by reproductive females and their small post-reproductive moult increments as in *Paranephrops planifrons* (Hopkins 1967a) and in *A. pallipes* (4.3.2) inevitably leads to their falling behind the growth rates of nonreproductive females of similar size. There is, then, no reliable method of determining whether animals of the same size are the same age, for they may have experienced a different number of moults of different moult increments.

The problems posed by many of these factors are often insuperable for particular populations and field sites and it is common for reports to present growth statistics as a mean value for the entire population or for males and females separately. As will be shown, this practice may be a gross oversimplification and it has the further disadvantage of submerging individual variations, preventing the identification of characteristically fast- or slow-growing individuals where they exist. One method commonly used to overcome these problems is to study the growth of captive animals in order to estimate moult increments. This practice, however, has been shown to be unreliable as several authors have reported that growth in the laboratory is less than that in the field (Hiatt 1948; Brown 1979; Bowler pers. comm.).

4.2 METHODS

The system of marking used in this study (3.2.1) enabled the consistent identification of individual crayfish. Since all numbered crayfish were measured on each occasion of capture, increments of growth were frequently recorded in those individuals which were recaptured on more than one occasion. These increments of growth were measured as increases in carapace length (3.2.2) and will be referred to as moult increments (MIs). Since carapace length was measured from the tip of the rostrum all crayfish with damaged rostra were omitted from the analysis of growth statistics. From a knowledge of the size of the typical moult increment it was possible to determine with a high degree of certainty which crayfish had moulted more than once since the date of last capture and to exclude multiple moult increments from the analysis.

Multiple recaptures of individuals in a single intermoult period provided a check on the accuracy of the measurement of carapace length, which was taken with Vernier calipers to the nearest 0.1 mm. While a measuring error of 0.1-0.2 mm was common, an error as large as 0.5 mm was very rare and was in any case insignificant in assessing moult frequency as moult increments almost invariably exceeded 2 mm. Many crayfish were recaptured sufficiently often to ascertain the number of moults undergone during a complete year. From these individuals a detailed analysis of moult frequency was derived (4.3.5).

The instantaneous growth rates (g) of size classes of crayfish are presented in 4.3.7. These rates were calculated as follows:

$$g = \log_e (W_t/W_o),$$

where W_t = weight after one year

W_o = weight at beginning of year

The modal sizes of the overwintering year classes 1+ and 2+ were estimated from a size-frequency diagram after the method of Cassie (1954).

From the regressions calculated for the relationship between postmoult carapace length and premoult carapace length for the size classes of Figs. 4.4-4.11, the mean moult increment for a crayfish of any given size and sex could be predicted. With the addition of the known modal sizes for the overwintering year classes 0+ and 1+ and a knowledge of moult frequency thereafter (Table 4.5) the relationship between size and age for each sex throughout the life cycle was estimated (Fig. 4.22).

4.3 RESULTS

4.3.1 Year classes

The year class 0+ was not sampled at the Hallington aqueduct, but data from other sites in Northumbria indicate that the mean overwintering size of this year class was 8.49 ± 0.09 mm CL (n = 181). This compares with a size of 5.42 ± 0.08 mm CL (n = 20) in newly hatched crayfish (hatching occurs in early August in Northumbria).

Presentation of data as a size-frequency plot revealed two inflexion points marking the presence of year classes (Cassie 1954). For males these inflexion points occurred at 13.00 ± 0.34 mm CL and 18.25 ± 1.35 mm CL (mean ± SE), and represent the year classes 1+ and 2+. For females these two year classes occurred at 11.1 ± 1.70 mm CL and 18.75 ± 0.08 mm CL. It was not possible to identify year classes beyond 2+ for either sex using this method. From a knowledge of the size of moult increments (4.3.2), the number of moults completed in the first growth season was estimated at five, in the second growth season at four and in the third and fourth at three (Fig. 4.22).

4.3.2 Moult increments

Bearing in mind the marked differences between the sexes and the decline in the size of the moult increment with age which have been reported in other Crustacea (4.1), it was considered advisable to begin the analysis of growth in *A. pallipes* with a plot of the moult increment as a function of the carapace length prior to the moult for each sex. The principal feature of this plot (Fig. 4.1) is the larger moult increment of male crayfish, the mean of

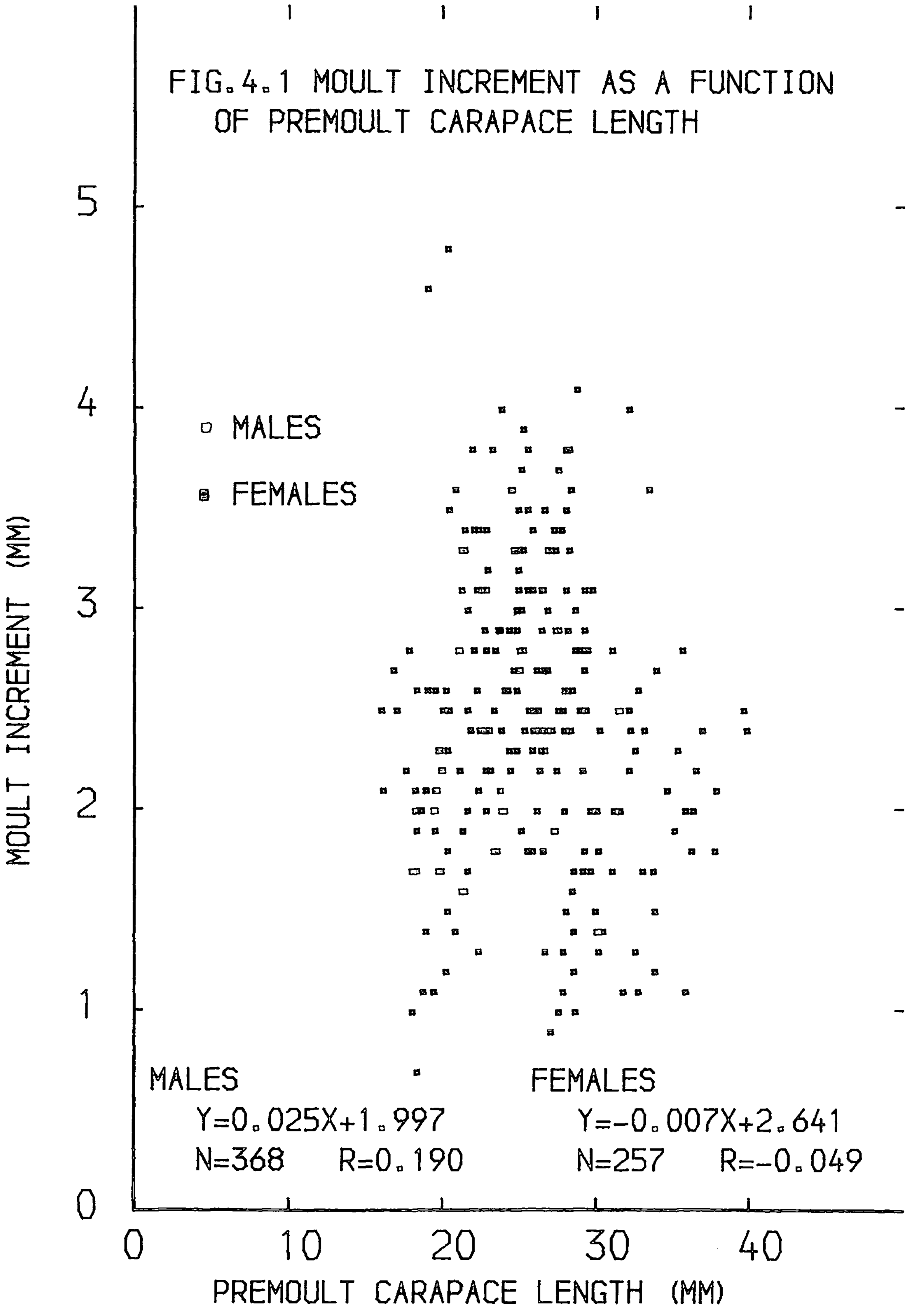


FIG. 4.1 MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH

2.69 ± 0.04 mm (n = 368) being significantly larger ($P<0.01$) than the mean nonreproductive female increment of 2.45 ± 0.05 mm (n = 257). Both of these figures are significantly larger ($P<0.001$) than the mean increment of reproductive females (1.90 ± 0.04 mm, n = 171).

A second method of expressing increments of growth is to present the moult increment as a percentage of premoult carapace length (the percentage moult increment, PCMI). Fig. 4.2 indicates that there is no significant difference between the PCMIs of males (mean = 9.9 ± 0.17, n = 368) and nonreproductive females (9.8 ± 0.22, n = 257). Both of these figures, however, are significantly larger ($P<0.001$) than the mean PCMI of 5.7 ± 0.14 (n = 171) of reproductive females.

Hiatt (1948) introduced the use of postmoult carapace length as a function of premoult carapace length and the method has since become widely adopted in studies of the growth of crustaceans. Fig. 4.3 presents such a Hiatt plot for the full size range of males and nonreproductive females known to have moulted once only since the date of last capture. It can be seen that the slope of the male regression is greater than that of the females.

Appendix Figs. A1 and A2 present the frequency histograms of the 368 male and 257 nonreproductive female single moult increments which were used for the detailed analysis of growth expressed as the absolute moult increment (Fig. A1) and as the percentage moult increment (Fig. A2). The distributions of both figures are clearly normal (Gaussian) distributions and the use of the t-test to differentiate between the means of subpopulations and size classes is justified.

4.3.3 Variation in growth within and between subpopulations

As noted earlier (4.1), the practice of presenting growth statistics as mean values for entire populations obscures the possibility that differences in growth may occur between different size classes and between the sexes. There is the further possibility that growth may vary from year to year. The intensity of the mark-recapture programme of this study meant that it was often possible to identify the growth increment of an individual as having occurred during a particular major moult period (2.5). Table 4.1 presents the moult

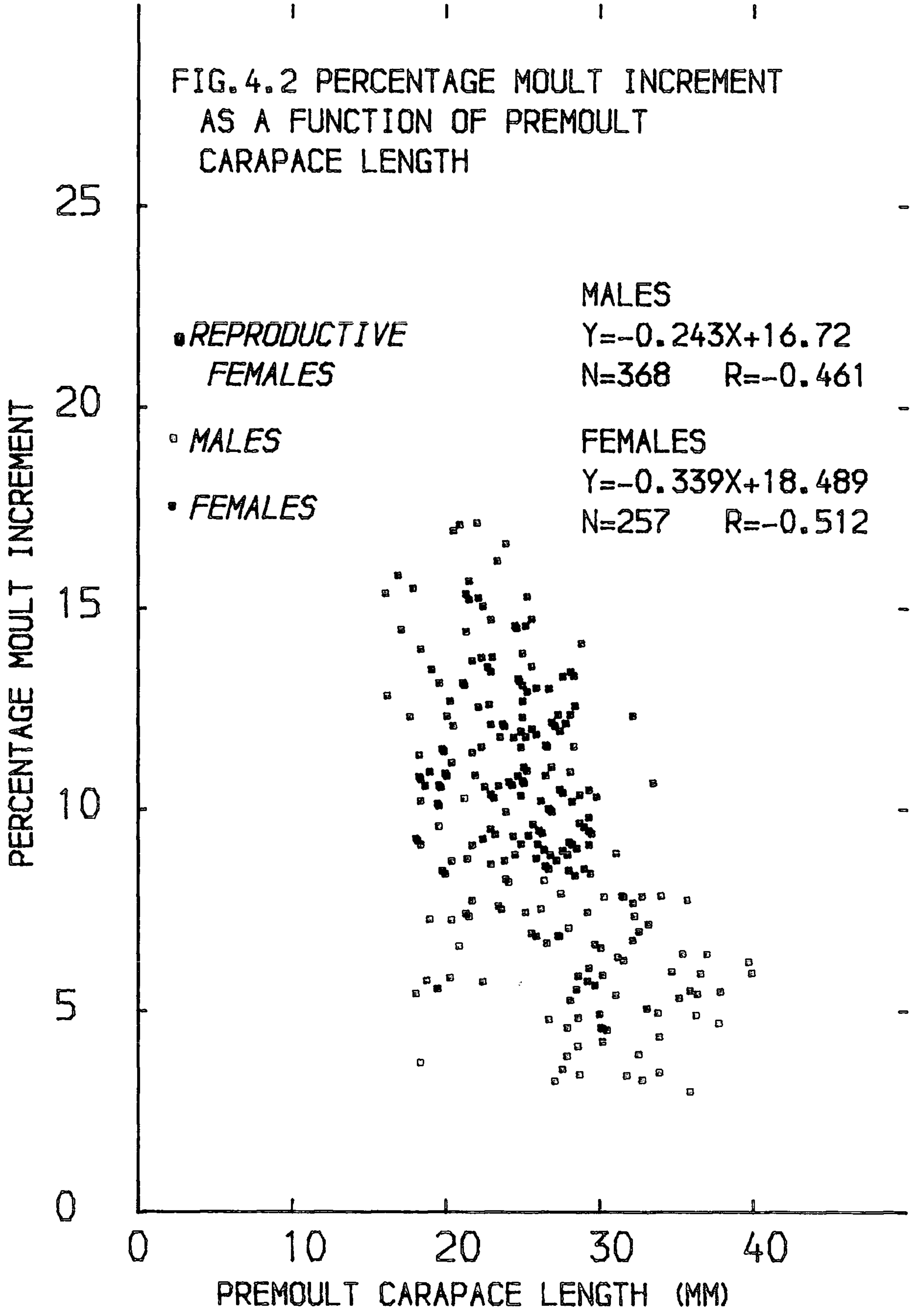


FIG. 4.2 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH

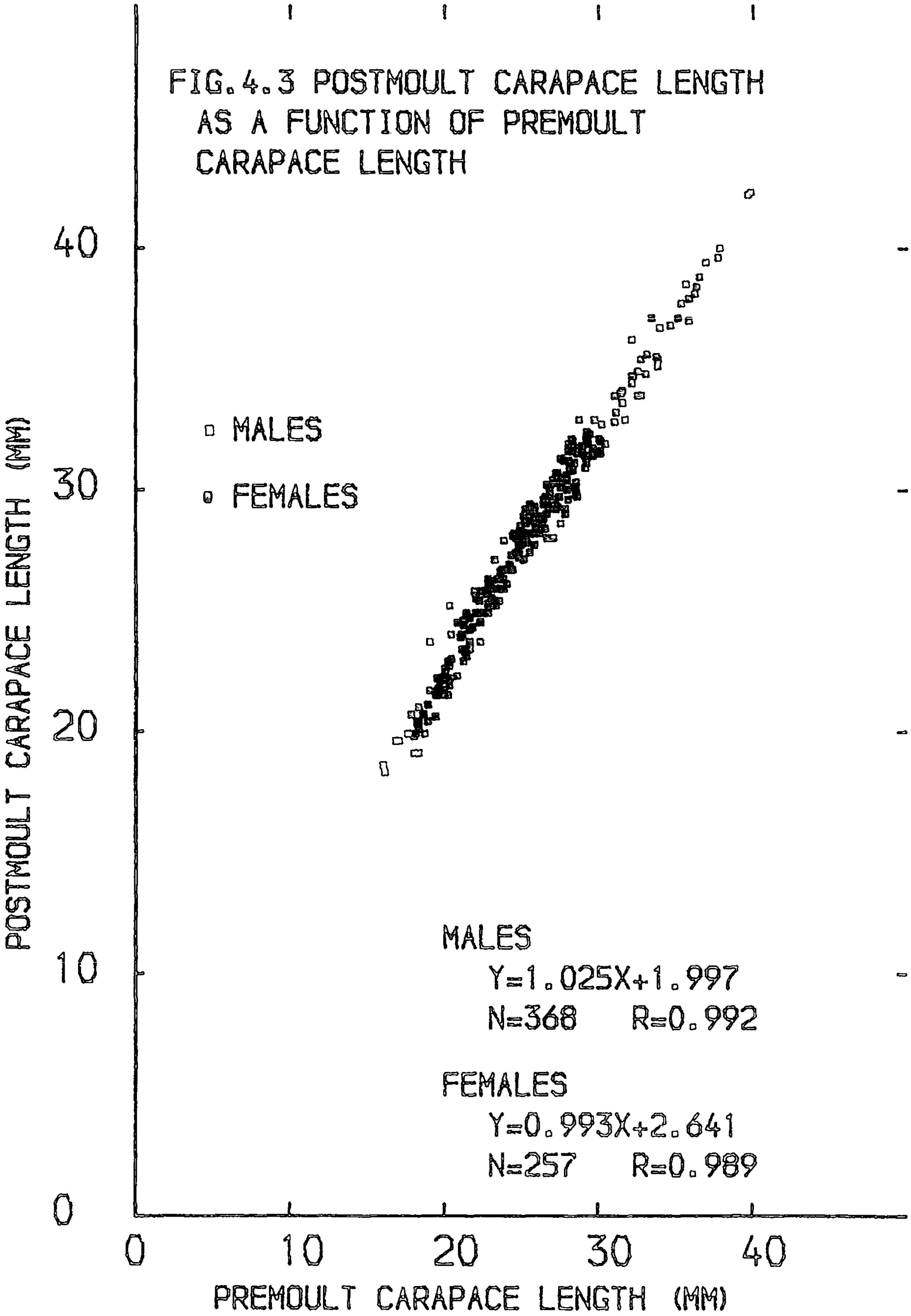


FIG. 4.3 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH

MALES
Y=1.025X+1.997
N=368 R=0.992

FEMALES
Y=0.993X+2.641
N=257 R=0.989

increments in absolute terms (MIs) and as percentage moult increments (PCMIs) for the adult male, adult nonreproductive female, reproductive female and juvenile subpopulations in each major moult period during the three years of the study. The subpopulation of reproductive females comprised those females known to have been berried during the first moult period of a particular year and which were recaptured after their first postreproductive moult (which occurred during the second major moult period of the same year). Table 4.1 indicates that there is a tendency for the MIs of adult males to be larger than the corresponding values for nonreproductive females. The MIs of juveniles tend to be smaller than those of the adult male and nonreproductive female subpopulations.

The overall trend in the size of moult increments is adult males > non-reproductive females > juveniles > reproductive females (Table 4.1). When increments in growth are expressed as a percentage of premoult carapace length (i.e. as percentage moult increment, PCMI) - a more rigorous treatment of the data - a different pattern emerges. The trend then becomes juveniles > adult males > nonreproductive females > reproductive females. Thus the PCMIs of juveniles during the second major moult period of 1978 and the first moult period of 1979 were significantly larger ($P<0.05$, $P<0.01$) than those of adult males and those of nonreproductive females ($P<0.002$, $P<0.002$). Reproductive females had significantly smaller PCMIs than nonreproductive females during the second moult periods of 1977 and 1978 ($P<0.002$, $P<0.001$).

A further point to arise from Table 4.1 is the tendency for the growth increment (expressed as both MI and as PCMI) during the first moult period of a year to be larger than that during the second. Significant differences between increments in different years are also in evidence, e.g. the adult male MI and PCMI during the second moult period of 1978 were larger ($P<0.02$ in both cases) than those during the corresponding period of 1977. The MI and PCMI of adult males in the first moult period of 1978 were also significantly larger than those in the first moult period of 1979 ($P<0.05$ in both cases). Examples of this type are also to be seen in the reproductive female subpopulation, in which the MI and PCMI in 1979 were significantly larger than those in 1977 and 1978 ($P<0.05$ in all cases).

Whether or not these differences in growth increments within and

Table 4.1

Absolute (MI) and percentage (PCMI) moult increments of crayfish during specific moult periods 1977-79

	1977						1978						1979					
	1st Moult Period			2nd Moult Period			1st Moult Period			2nd Moult Period			1st Moult Period			2nd Moult Period		
	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N
Adult Males (>22 mm CL)	2.9 ± 0.13	9.4 ± 0.55	29	2.4 ± 0.12	8.5 ± 0.42	32	3.1 ± 0.11	11.1 ± 0.40	44	2.8 ± 0.09	9.8 ± 0.30	71	2.8 ± 0.09	9.8 ± 0.40	79	2.6 ± 0.11	8.6 ± 0.35	53
Nonreproductive Adult Females (>22 mm CL)	2.5 ± 0.14	8.9 ± 0.44	15	2.4 ± 0.19	8.4 ± 0.79	19	2.7 ± 0.26	9.9 ± 1.02	12	2.6 ± 0.11	9.0 ± 0.44	46	2.5 ± 0.11	8.9 ± 0.49	24	2.3 ± 0.14	7.6 ± 0.57	34
Reproductive Females				1.8 ± 0.11	5.4 ± 0.31	24				1.9 ± 0.06	5.6 ± 0.18	109				2.1 ± 0.09	6.4 ± 0.28	34
Juveniles (>22 mm CL)	2.7 ± 0.67	13.3 ± 3.4	3	2.1 ± 0.20	11.4 ± 2.04	3	2.1 ± 0.10	11.1 ± 0.53	57	2.2 ± 0.10	11.2 ± 0.46	40	2.6 ± 0.23	13.4 ± 1.06	16	1.8 ± 0.30	8.8 ± 1.33	5

between subpopulations have a biological significance is not clear as these data were collected from a wide size range within each subpopulation. It is possible, therefore, that the differences were produced by size composition effects within and between the subpopulations. In order to examine this possibility Table 4.2 presents data which have been derived from those of Table 4.1 by matching to within ± 0.5 mm carapace length as many individuals as possible from each moult period with crayfish from every other moult period within a particular subpopulation. Although the tendency for the increment during the first moult period of a year to be larger than that during the second is still evident in the adult male subpopulation, none of the differences are significant and this tendency is in fact reversed in the nonreproductive female subpopulation. There are no significant differences between increments during corresponding moult periods of different years in any subpopulation (Table 4.2). From the limited data available on the juvenile subpopulation, there are no significant differences in increments either within or between years.

Accepting the evidence of this analysis, i.e. that there are no significant differences between increments in corresponding moult periods of different years, then it is permissible to pool these data. Table 4.3 presents these pooled data and again reveals the tendency in the adult male subpopulation for the increment during the first moult period of a year to be larger than that during the second. No such tendency is present in any other subpopulation. The differences between growth increments of the subpopulations are in agreement with those previously described. Thus the MI and PCMI of reproductive females are significantly smaller than those of every other subpopulation during the pooled second moult periods. In order to remove completely the possibility that the differences between the growth of reproductive and nonreproductive females are due to size composition effects, the two subpopulations were matched for carapace length. From Table 4.3, the increments of nonreproductive females are significantly larger ($P<0.02$ for MI, $P<0.05$ for PCMI). The largest PCMIs are once more to be seen in the juvenile subpopulation, these being significantly larger ($P<0.05$) than those of nonreproductive females during the first moult periods. The largest MIs occur in the adult male subpopulation, these being significantly larger than those of juveniles in both moult periods ($P<0.01$, $P<0.02$ respectively).

Table 4.2

Absolute (MI) and percentage (PCMI) moult increments of crayfish matched to within ± 0.5 mm CL in each subpopulation

	1977						1978						1979					
	1st Moult Period			2nd Moult Period			1st Moult Period			2nd Moult Period			1st Moult Period			2nd Moult Period		
	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N	MI ± SE	PCMI ± SE	N
Adult Males (>22 mm CL)	3.0 ± 0.19	10.2 ± 0.73	16	2.4 ± 0.15	8.1 ± 0.42	15	2.9 ± 0.18	10.0 ± 0.55	15	2.6 ± 0.12	9.1 ± 0.80	14	2.7 ± 0.24	9.3 ± 0.82	14	2.6 ± 0.20	8.6 ± 0.57	16
Nonreproductive Adult Females (>22 mm CL)	2.6 ± 0.12	9.4 ± 0.37	7	2.8 ± 0.20	9.9 ± 0.74	8	2.7 ± 0.25	9.5 ± 0.89	12	2.73 ± 0.19	10.0 ± 0.88	10	2.8 ± 0.15	10.2 ± 0.72	10	2.9 ± 0.26	10.6 ± 1.12	8
Reproductive Females				1.8 ± 0.11	5.4 ± 0.31	24				1.8 ± 0.13	5.2 ± 0.38	24				2.2 ± 0.11	6.5 ± 0.36	21
Juveniles (>22 mm CL)							2.1 ± 0.25	10.9 ± 0.88	14	2.2 ± 0.22	9.5 ± 1.01	12	2.6 ± 0.24	13.3 ± 1.13	15	1.8 ± 0.30	8.8 ± 1.33	5

Table 4.3

Absolute (MI) and percentage (PCMI) moult increments of crayfish matched to within ± 0.5 mm CL in each subpopulation

	FIRST MOULT PERIODS				SECOND MOULT PERIODS			
	MI (mm)	PCMI	Mean Carapace Length (mm)	N	MI (mm)	PCMI	Mean Carapace Length (mm)	N
ADULT MALES (>22 mm CL)	2.8 ± 0.12	9.8 ± 0.42	29.5 ± 0.56	45	2.6 ± 0.11	8.6 ± 0.36	29.8 ± 0.57	45
NONREPRODUCTIVE FEMALES	2.6 ± 0.07	9.9 ± 0.31	26.8 ± 0.41	65	2.6 ± 0.09	9.8 ± 0.39	27.25 ± 0.48	65
Matched to reproductive females (below)					2.2 ± 0.10	6.9 ± 0.40		45
REPRODUCTIVE FEMALES Matched to nonreproductive females (above)					1.8 ± 0.07	5.8 ± 0.27		45
JUVENILES (<22 mm CL)	2.3 ± 0.14	11.5 ± 0.72	20.0 ± 0.72	41	2.2 ± 0.10	11.01 ± 0.49	20.1 ± 0.20	41

4.3.4 The relationship between size and growth increments

The preceding analyses have examined variation in growth increments within and between years and subpopulations. However, in order to study the relationship between body size and growth increment it is necessary to define size classes much more closely. Table 4.4 presents the data from Fig. 4.3 for 5 mm CL size classes of each subpopulation during the years 1977-79. In the male subpopulation the 27-32 mm CL size class had the largest mean MI during the first moult periods, it being significantly larger than those of the male size classes of <22 mm CL and 37-42 mm CL ($P<0.001$, $P<0.02$ respectively). The class of juvenile males (<22 mm CL) had, in fact, a significantly smaller MI than that of any other male size class during the first moult periods. During the second moult periods the male size class of 32-37 mm CL had the largest mean MI, it being significantly larger than those of the male size classes of<22 mm CL and 22-27 mm CL ($P<0.01$, $P<0.05$ respectively).

In the nonreproductive female subpopulation the smallest size class (<22 mm CL) had the smallest MI during the first moult periods. The 32-37 mm CL class had the largest MI, although the differences are not significant. During the second moult periods the 22-27 mm CL size class had the largest MI (Table 4.4), it being significantly larger than those of the <22 mm CL size class ($P<0.001$), the 27-32 mm CL size class ($P<0.02$) and the 32-37 mm CL size class ($P<0.001$).

There is a clear inverse correlation between PCMI and carapace length in both sexes. From Table 4.4, the PCMIs of the male size classes of <22 mm CL, 22-27 mm CL and 27-32 mm CL are significantly larger than those of the 32-37 mm CL and 37-42 mm CL size classes during the first moult periods ($P<0.01$ in each case). Similarly, the nonreproductive female size class of <22 mm CL had a mean PCMI during the first moult periods which is significantly larger than those of the 27-32 mm CL and 32-37 mm CL size classes ($P<0.001$, $P<0.02$ respectively). The PCMI of the female 22-27 mm CL size class is also significantly larger ($P<0.001$) than that of the 27-32 mm CL class. Similar trends are present in the PCMIs of both sexes during the second moult periods.

Table 4.4

Absolute (MI) and percentage (PCMI) moult increments of size classes of crayfish

	First Moult Periods			Second Moult Periods		
	MI (mm) ± SE	PCMI ± SE	N	MI (mm) ± SE	PCMI ± SE	N
Males CL < 22 mm	2.2 ± 0.11	11.4 ± 0.61	41	2.4 ± 0.15	11.7 ± 0.83	19
Males CL = 22-27 mm	2.9 ± 0.09	11.9 ± 0.39	57	2.5 ± 0.11	10.0 ± 0.42	51
Males CL = 27-32 mm	3.1 ± 0.10	10.7 ± 0.37	43	2.7 ± 0.09	8.9 ± 0.31	54
Males CL = 32-37 mm	2.8 ± 0.16	8.2 ± 0.48	33	2.9 ± 0.11	8.7 ± 0.31	43
Males CL = 37-42 mm	2.6 ± 0.19	6.8 ± 0.51	17	2.8 ± 0.37	7.2 ± 1.00	7
Nonreproductive Females CL < 22 mm	2.4 ± 0.16	12.0 ± 0.79	34	2.1 ± 0.09	10.4 ± 0.46	29
Nonreproductive Females CL = 22-27 mm	2.7 ± 0.08	11.0 ± 0.34	47	2.8 ± 0.09	11.3 ± 0.39	46
Nonreproductive Females CL = 27-32 mm	2.4 ± 0.13	8.2 ± 0.49	23	2.4 ± 0.13	8.4 ± 0.46	49
Nonreproductive Females CL = 32-37 mm	2.8 ± 0.33	8.4 ± 1.06	6	1.9 ± 0.13	5.6 ± 0.37	18
Nonreproductive Females CL = 37-42 mm				2.2 ± 0.13	5.8 ± 0.31	5
Reproductive Females CL = 27-32 mm				1.9 ± 0.07	6.4 ± 0.24	53
Reproductive Females CL = 32-37 mm				1.9 ± 0.06	5.5 ± 0.18	95
Reproductive Females CL > 37 mm				2.0 ± 0.15	5.1 ± 0.40	18

There are no significant differences between the increments of juvenile males and juvenile females, i.e. those crayfish of <22mm CL. Some differences between the sexes are apparent, however. Both the MI and PCMI of the male 27-32 mm CL size class are significantly larger than those of the corresponding non-reproductive females size class in the first moult periods ($P<0.001$ in both cases), while the same is true of the male size class of 32-37 mm CL during the second moult periods ($P<0.001$ in both cases).

The characteristic small increments of females at the first post-reproductive moult have been noted earlier. From Table 4.4, the increments of the size classes of reproductive females are smaller in every instance than those of the corresponding nonreproductive female size class. Thus the MI and PCMI of the 27-32 mm CL size class of nonreproductive females are significantly larger than those of reproductive females of the same size range ($P<0.001$ in both cases). Also, the MIs and PCMIs of nonreproductive females in the 22-27 mm CL and 27-32 mm CL classes during the second moult periods are significantly larger than those of reproductive females in the >37 mm CL size class.

Evidence of a larger increment during the first moult periods compared to the second comes from the male size classes of 22-27 mm CL and 27-32 mm CL (Table 4.4), within which the differences are significant ($P<0.01$ for MIs and PCMIs). A significant difference of this type is also present in the nonreproductive female size class of 32-37 mm CL. It appears that this, however, may be caused by the large mean MI obtained for the first moult periods from a sample of only six.

Figs. 4.4-4.11 present the regressions of postmoult carapace length on premoult carapace length for the 5 mm CL size classes of each subpopulation. There is a tendency for the slope of the male regression to be greater than that of the corresponding female regression. The exceptions are the juvenile size class of <22 mm CL, in which the greater female slope is not significantly different from that of the males, and the size class of >37 mm CL, in which the female sample of five is inadequate for reliable statistical testing. In the size class of 32-37 mm CL the male slope is significantly greater ($P<0.02$). In the reproductive female

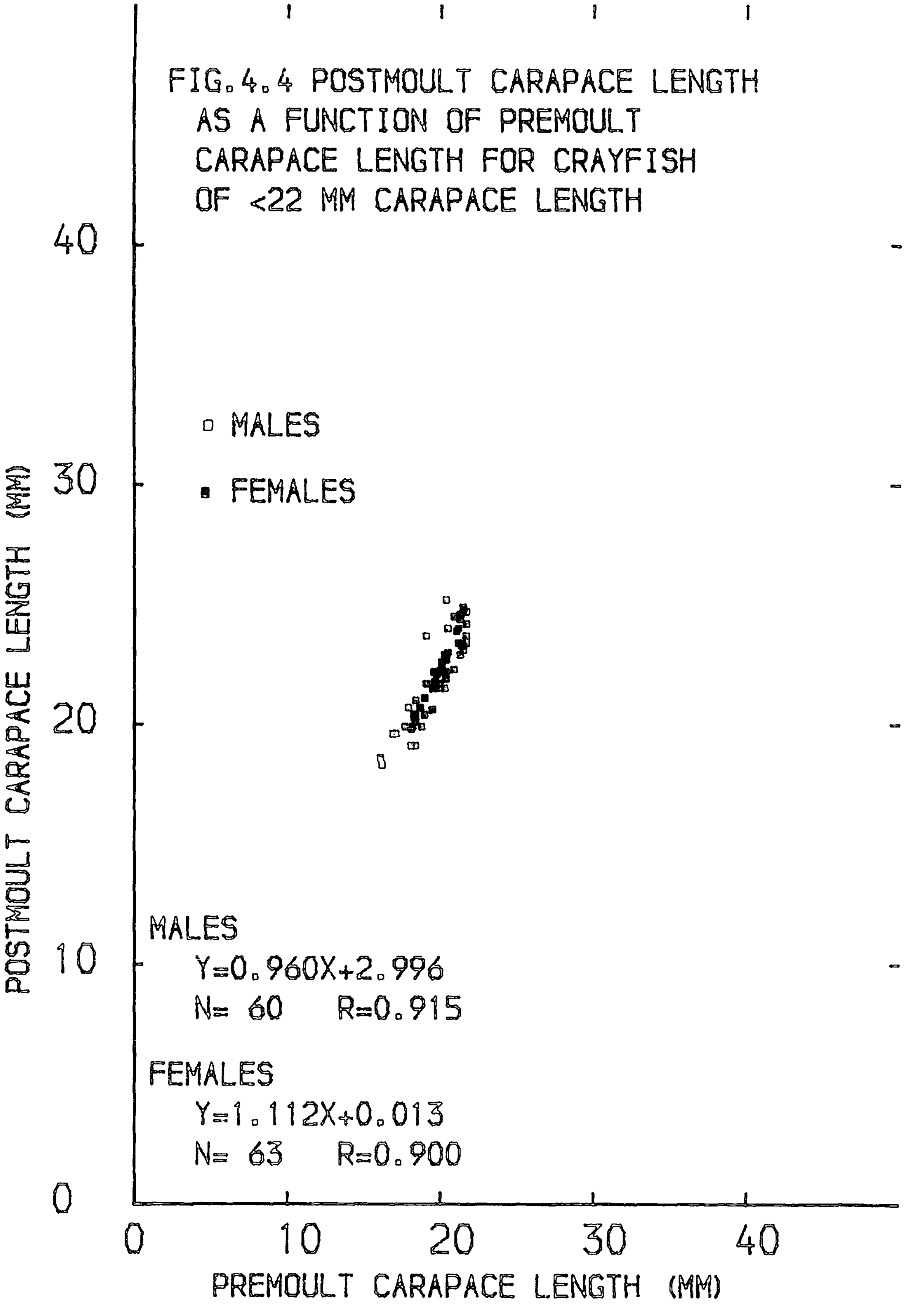


FIG. 4.4 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF <22 MM CARAPACE LENGTH

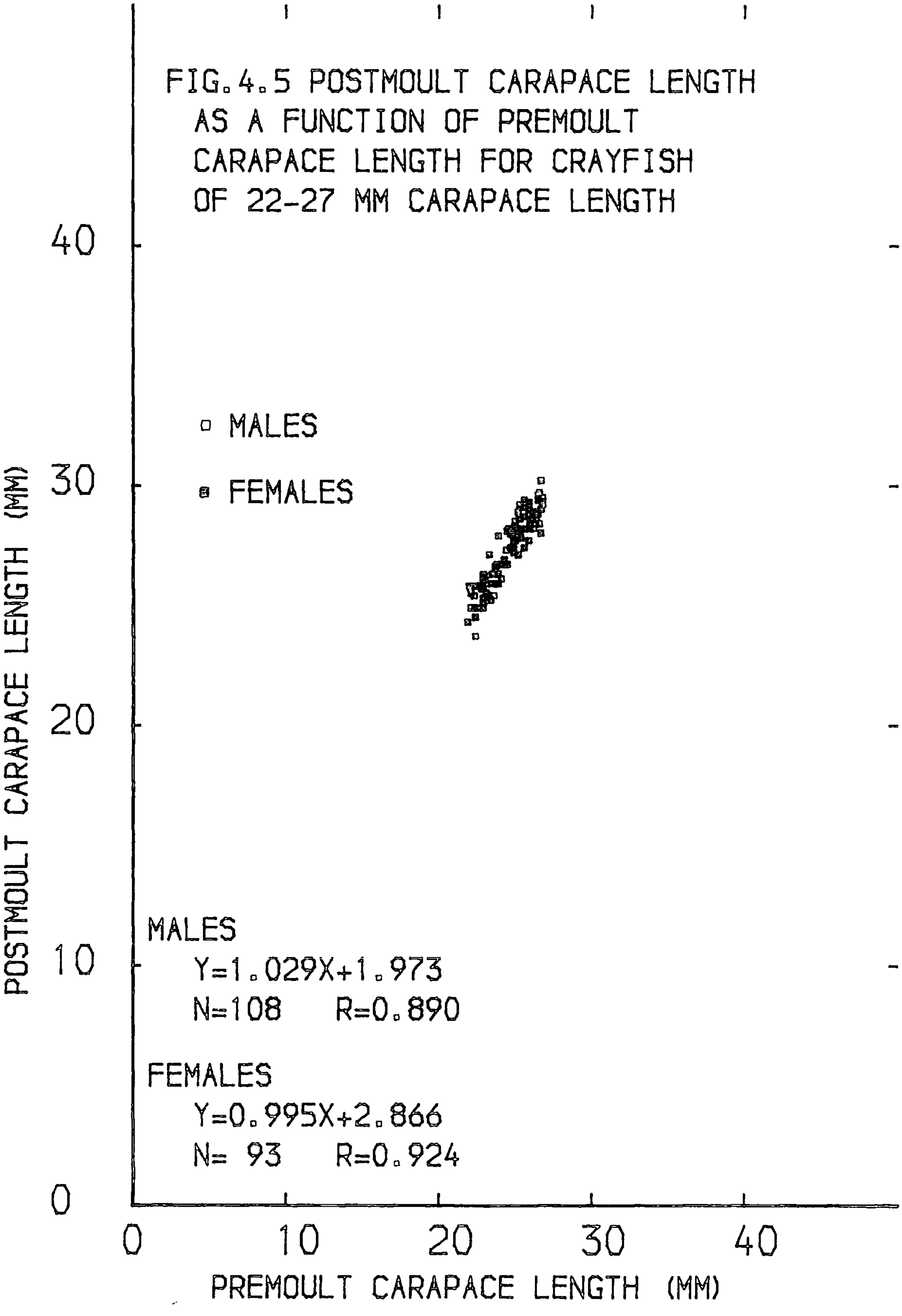


FIG. 4.5 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF 22-27 MM CARAPACE LENGTH

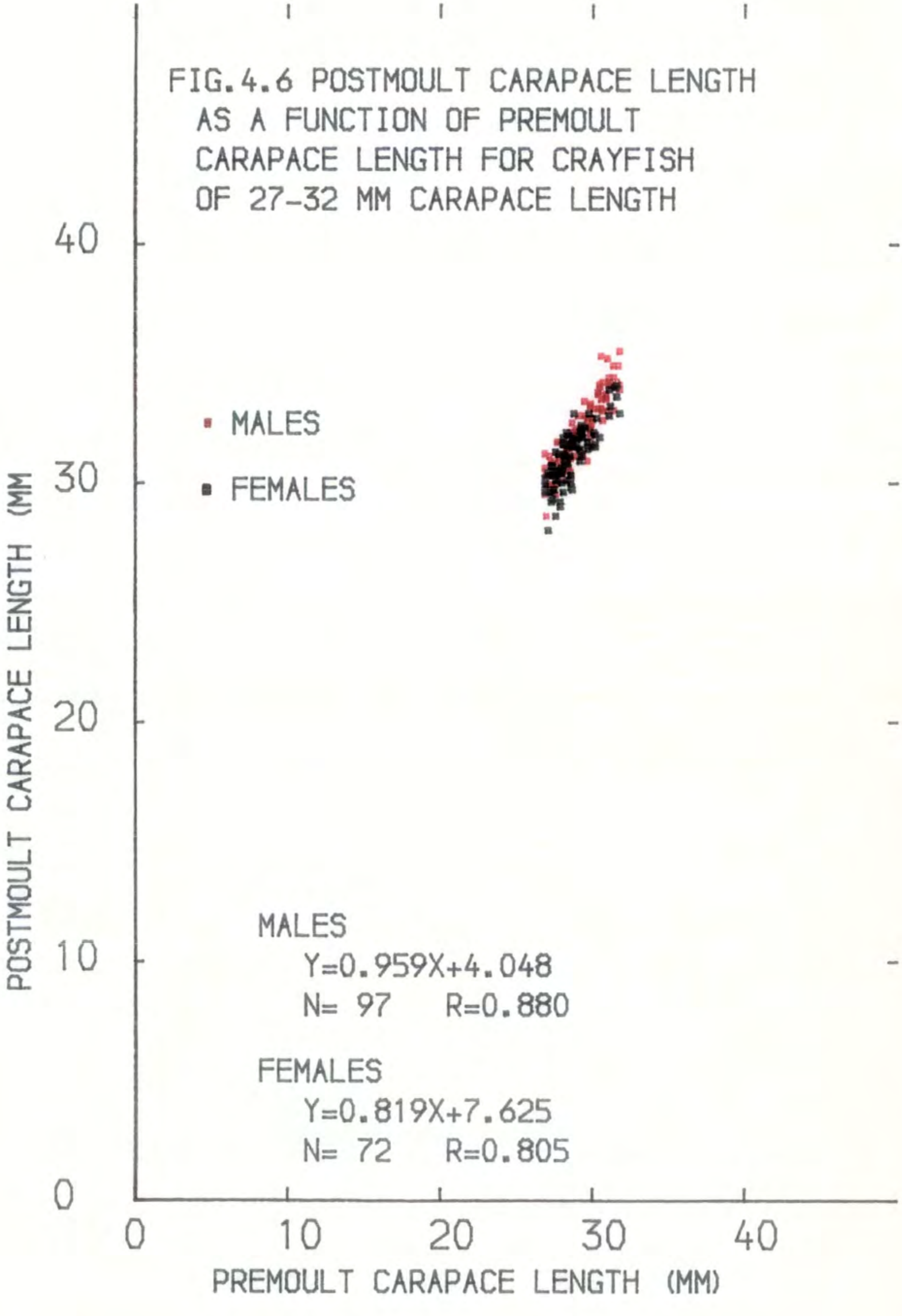


FIG. 4.6 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF 27-32 MM CARAPACE LENGTH

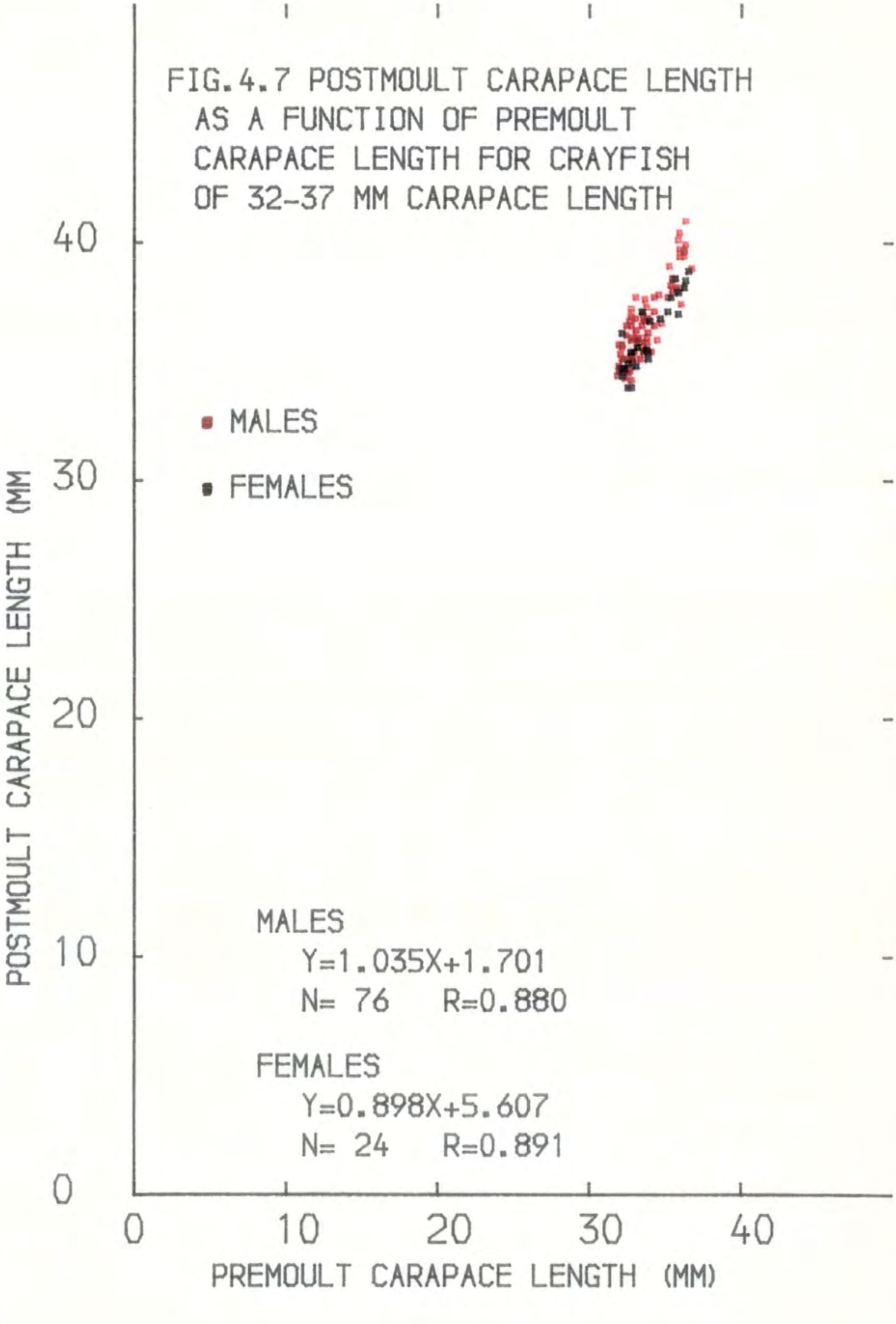


FIG.4.7 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF 32-37 MM CARAPACE LENGTH

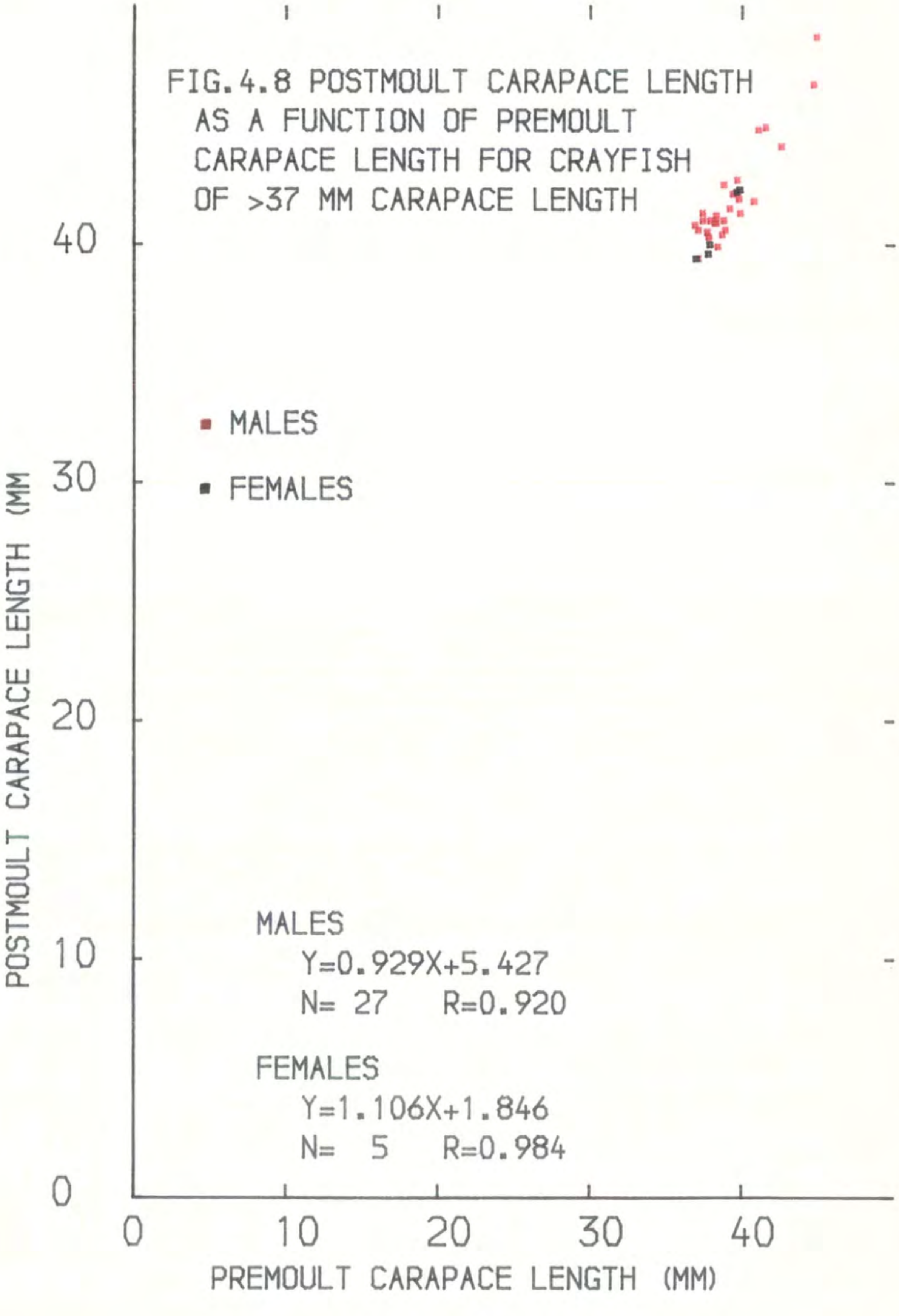


FIG.4.8 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF >37 MM CARAPACE LENGTH

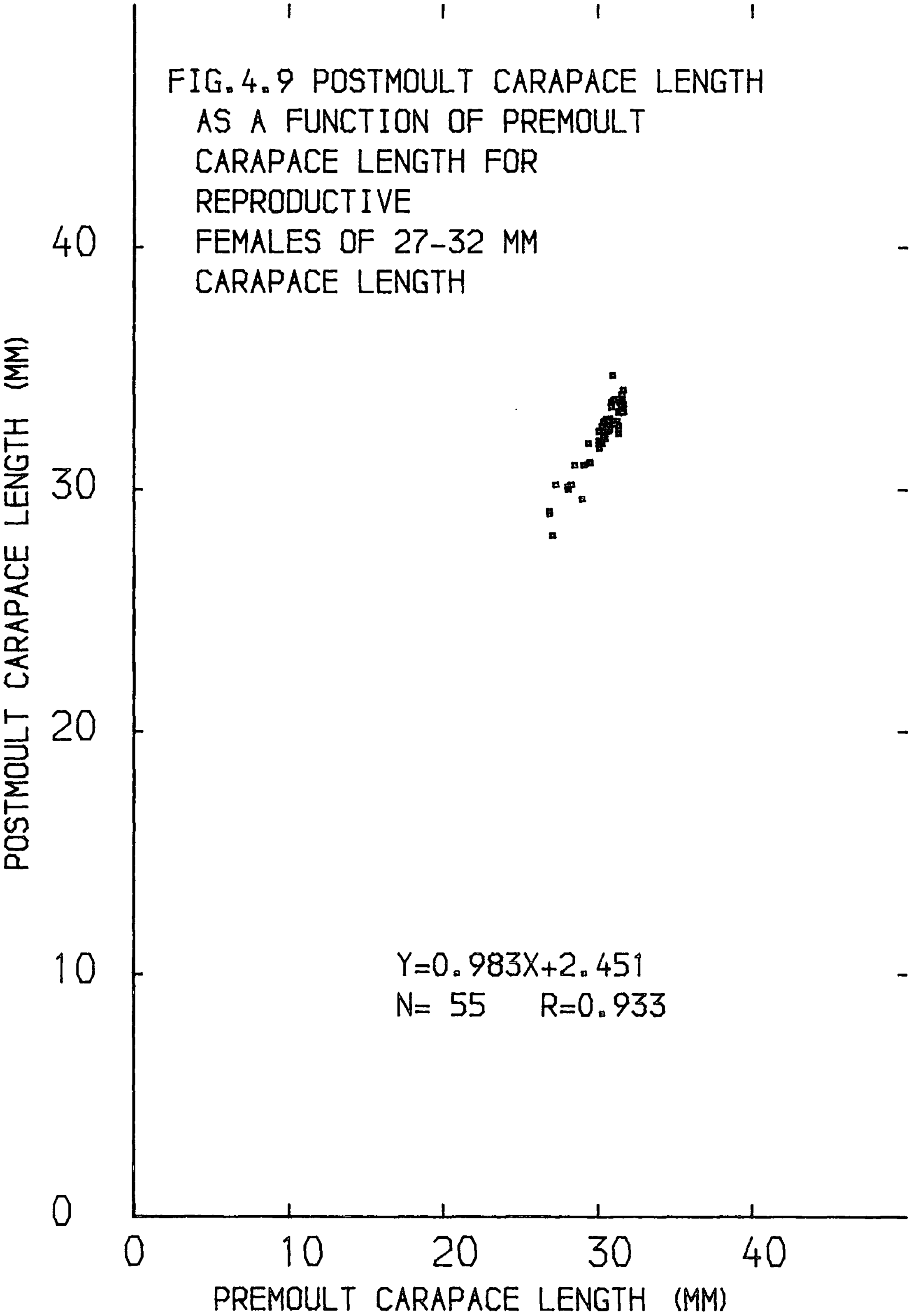


FIG.4.9 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR REPRODUCTIVE FEMALES OF 27-32 MM CARAPACE LENGTH

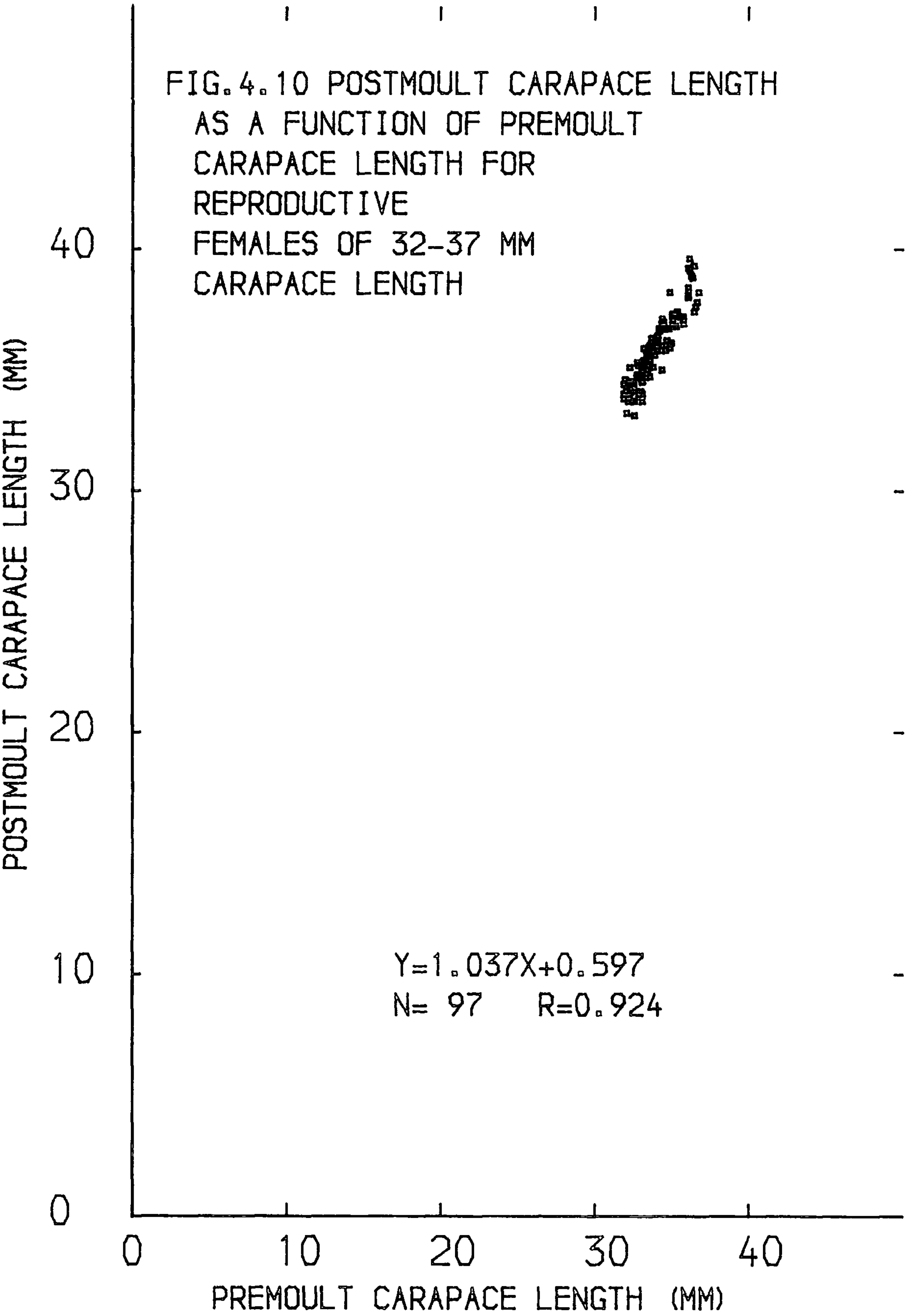


FIG. 4.10 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR REPRODUCTIVE FEMALES OF 32-37 MM CARAPACE LENGTH

Y=1.037X+0.597
N= 97 R=0.924

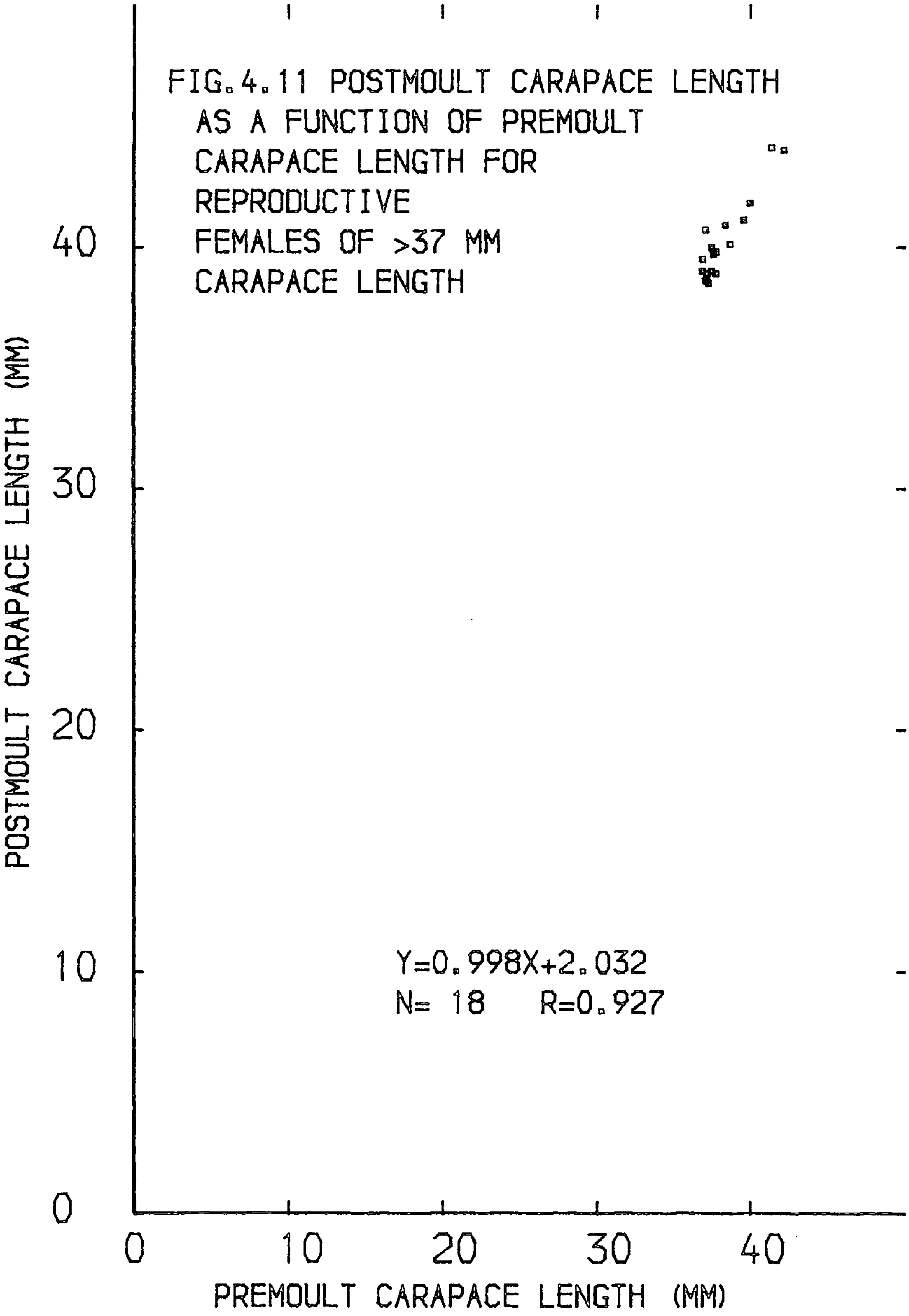


FIG. 4.11 POSTMOULT CARAPACE LENGTH AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR REPRODUCTIVE FEMALES OF >37 MM CARAPACE LENGTH

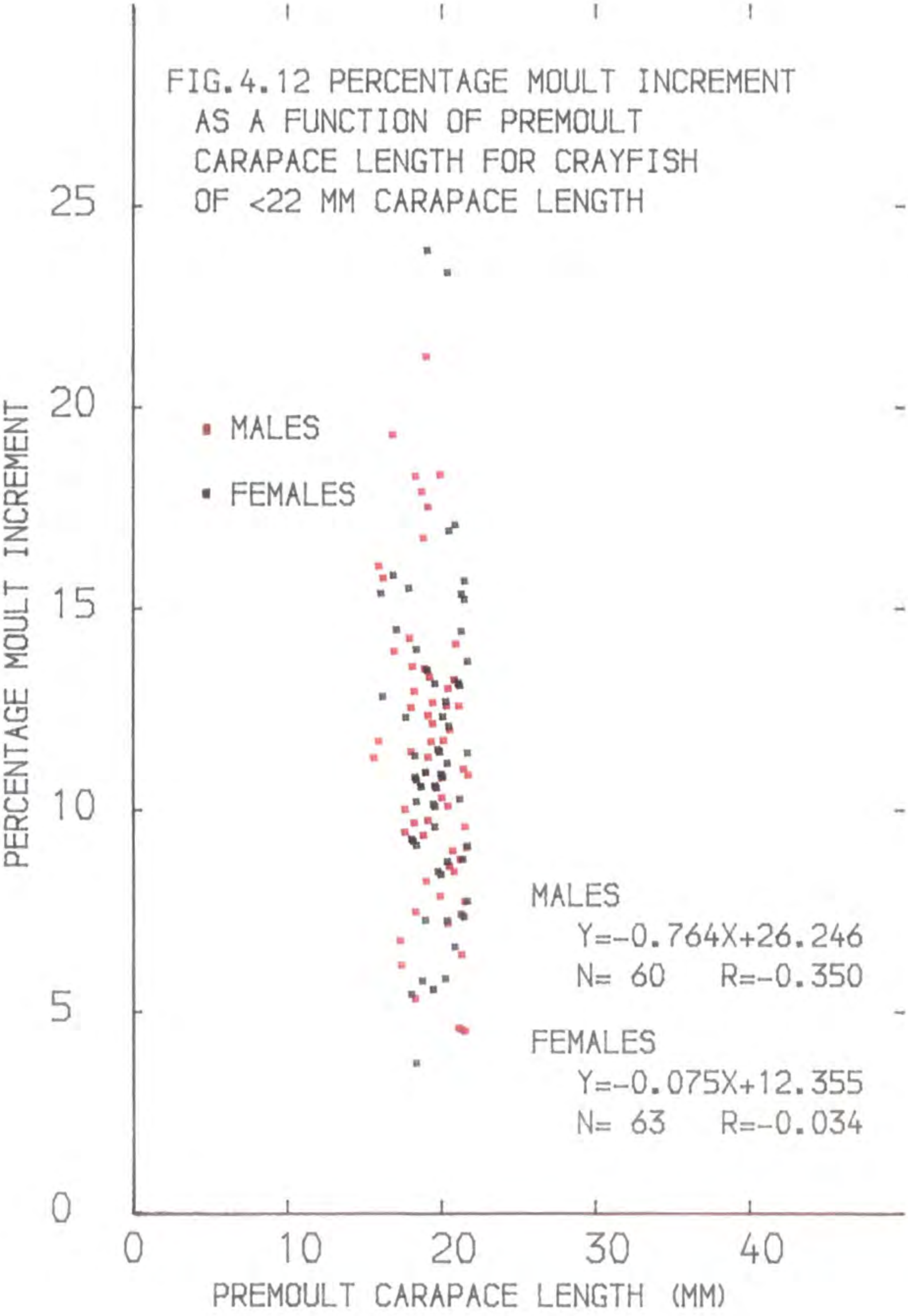


FIG.4.12 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF <22 MM CARAPACE LENGTH

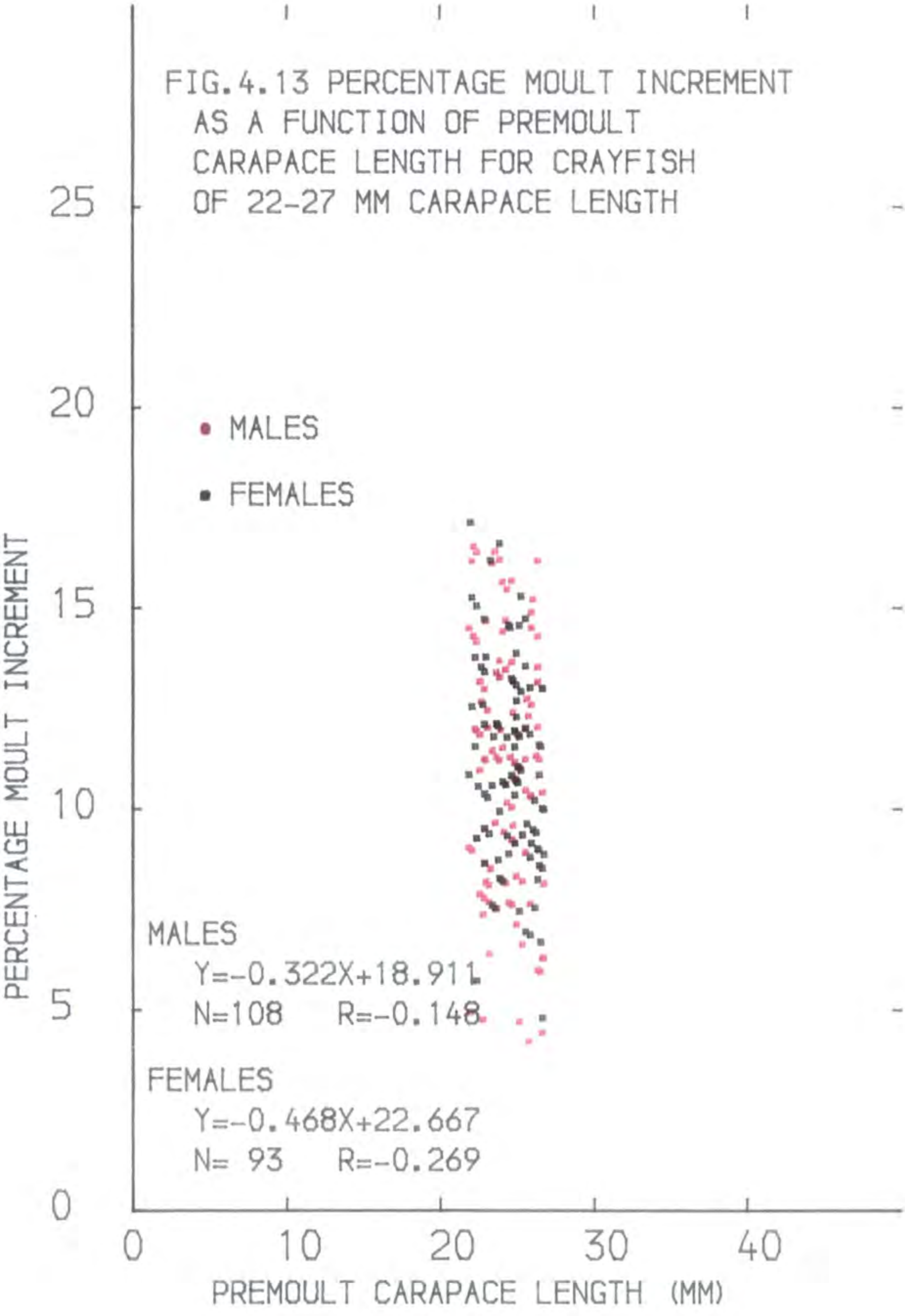


FIG.4.13 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF 22-27 MM CARAPACE LENGTH

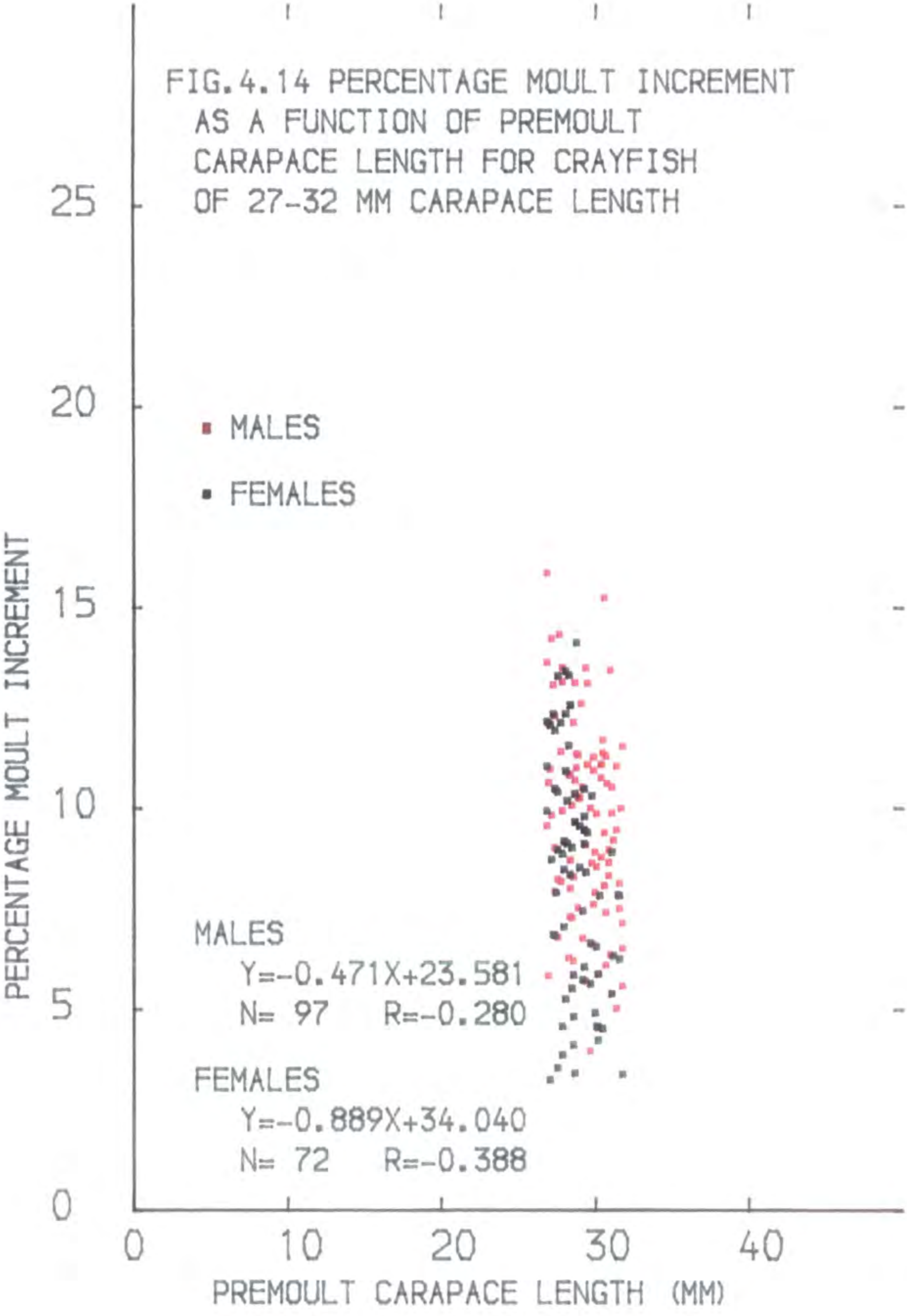


FIG.4.14 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF 27-32 MM CARAPACE LENGTH

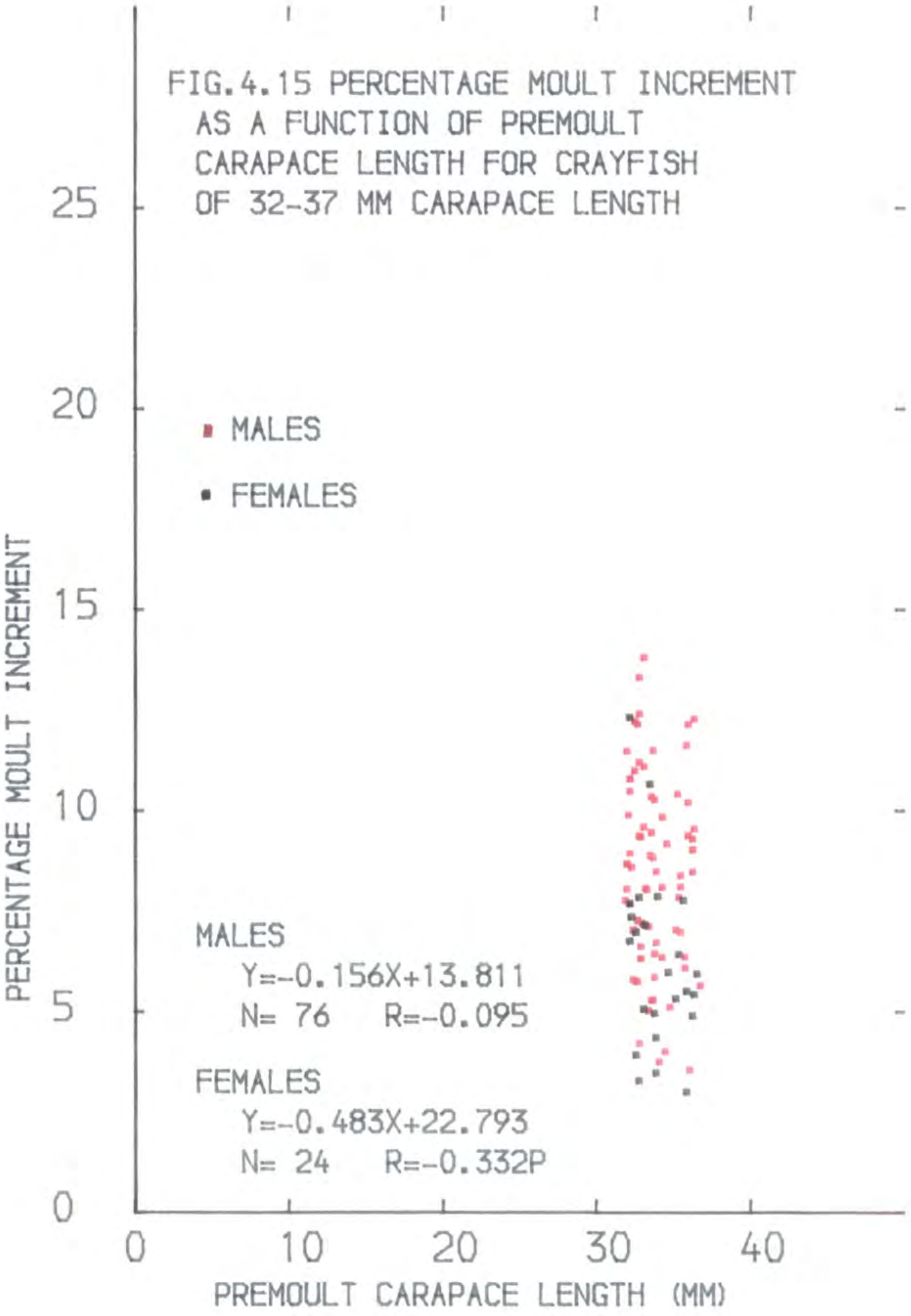


FIG.4.15 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF 32-37 MM CARAPACE LENGTH

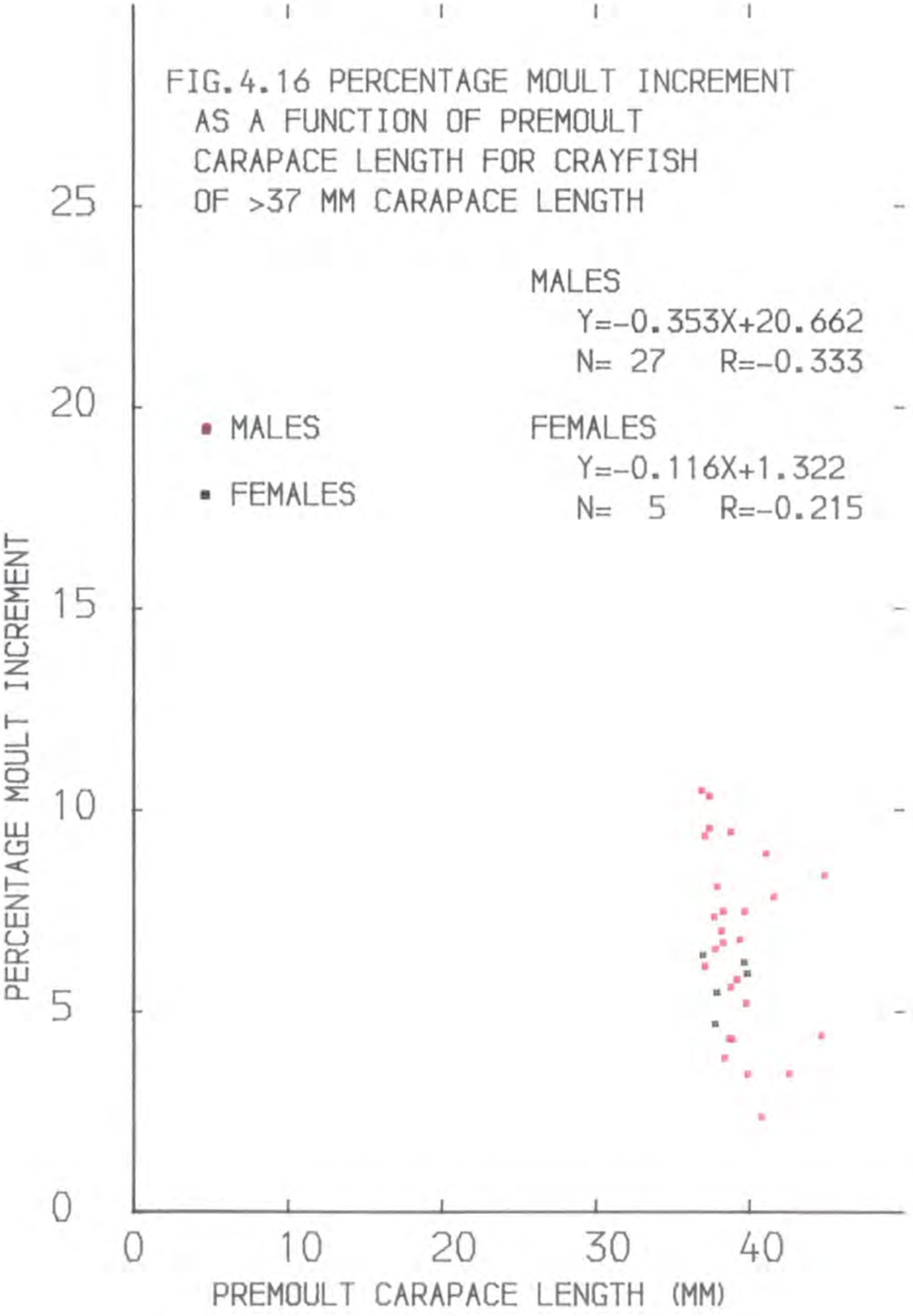


FIG.4.16 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR CRAYFISH OF >37 MM CARAPACE LENGTH

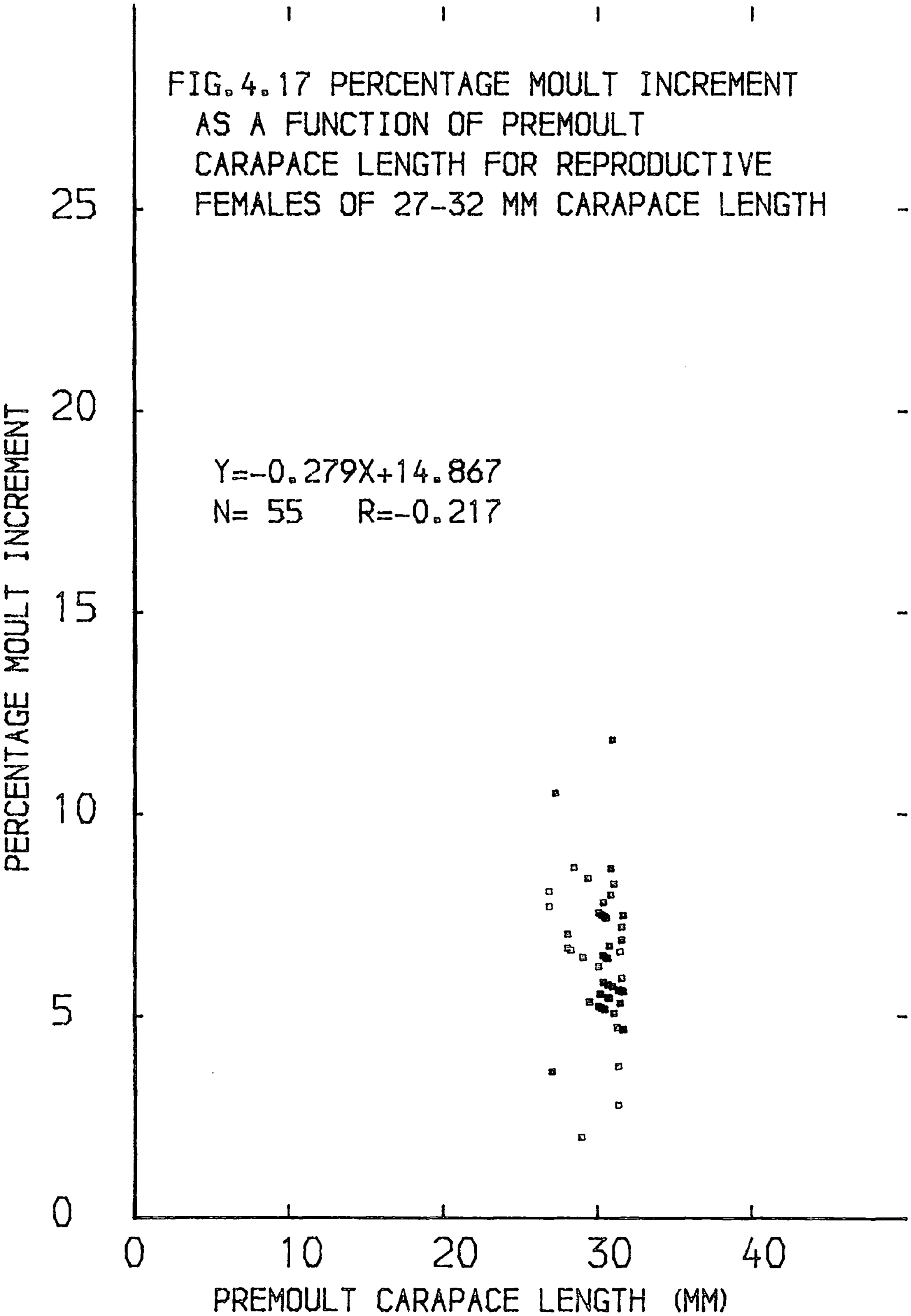


FIG. 4.17 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR REPRODUCTIVE FEMALES OF 27-32 MM CARAPACE LENGTH

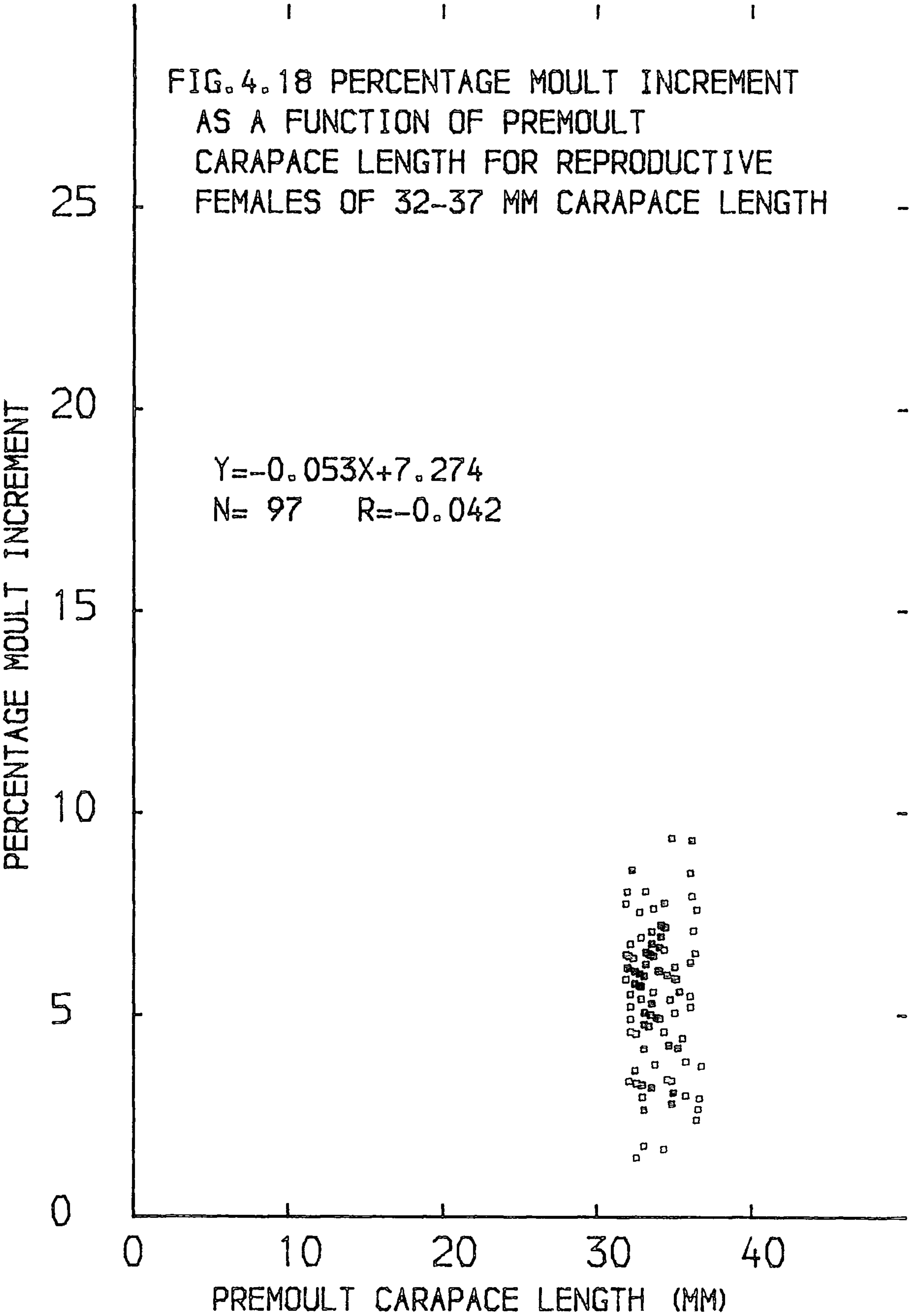


FIG. 4.18 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR REPRODUCTIVE FEMALES OF 32-37 MM CARAPACE LENGTH

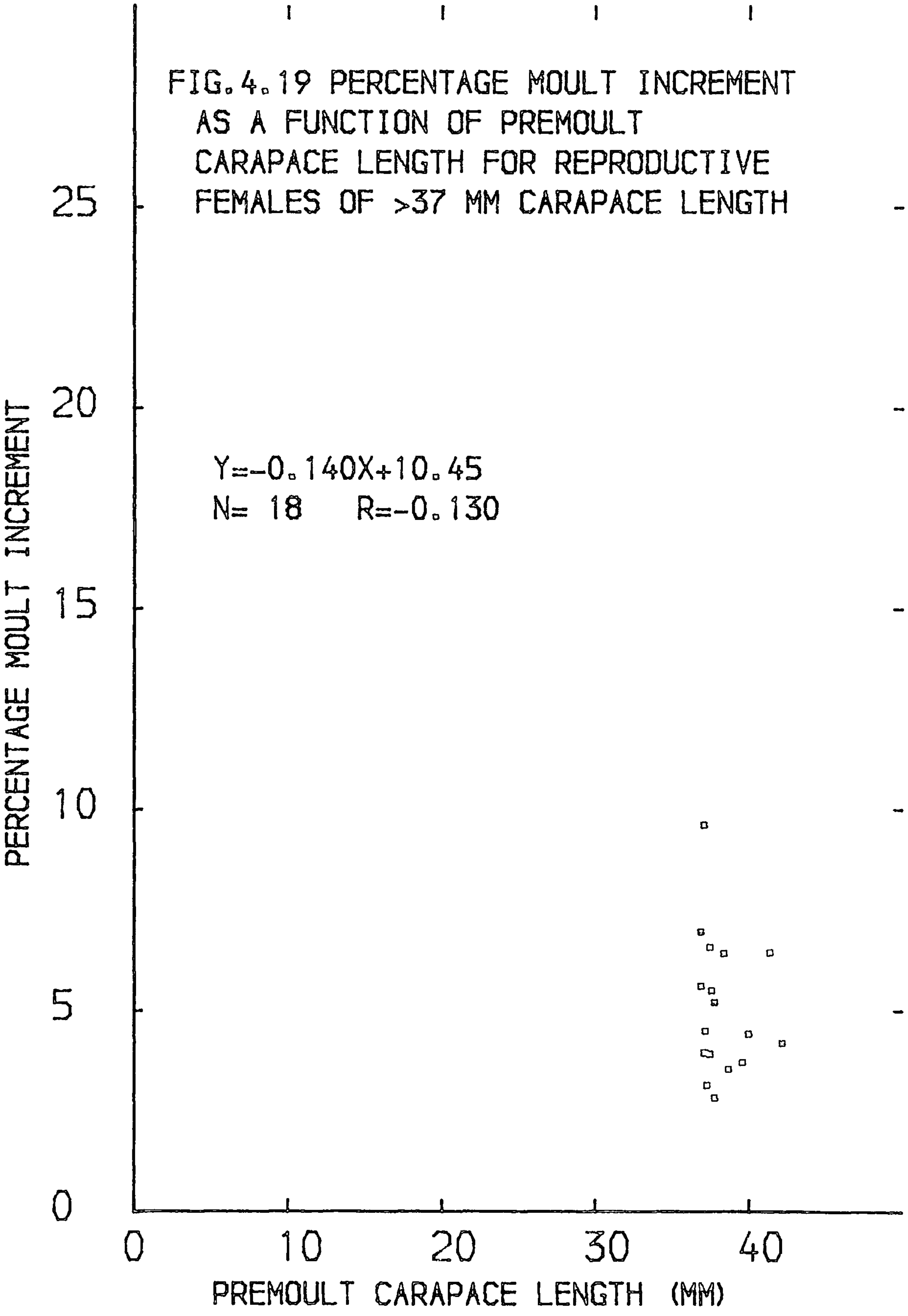


FIG.4.19 PERCENTAGE MOULT INCREMENT AS A FUNCTION OF PREMOULT CARAPACE LENGTH FOR REPRODUCTIVE FEMALES OF >37 MM CARAPACE LENGTH

subpopulation there are no significant differences between the slopes of the three size classes studied (Figs. 4.9-4.11), but the trend is for the slope to increase to the 32-37 mm CL size class and to fall thereafter.

The plots of percentage moult increment against premoult carapace length (Figs. 4.12-4.19) indicate that the correlation of the two within any one size class is low, generally of the order 0.2-0.3. While the slopes of the male regressions are generally greater than those of the female regressions, this is compensated for by the larger intercepts of the female plots. A comparison of Figs. 4.17-4.19 with Figs. 4.14-4.16 indicates that the rate of decline of percentage moult increment with increasing size is more rapid in nonreproductive females than in reproductive females, except for the largest size class (>37 mm CL), in which the rates are very similar. As has already been seen, however, the percentage moult increments of reproductive females are significantly smaller than those of comparable nonreproductive females.

4.3.5 Moult frequency and timing of moulting

Table 4.5 comprises data from crayfish which were individually marked and recaptured sufficiently often to allow unequivocal determination of moult frequency during one complete growth season. The data include two examples of juveniles which moulted three times in one year. Most adults moulted twice annually up to the 26-28 mm CL size class. In this population the minimum size at sexual maturity is 22 mm CL (Brown 1979), whilst all crayfish are believed to be mature at 27 mm CL. From this size onwards there was an increasing tendency among females to moult once only in each growth season, whilst this tendency was not apparent in males until 32 mm CL (Table 4.5). Beyond this size some individuals of both sexes did not moult at all during some years.

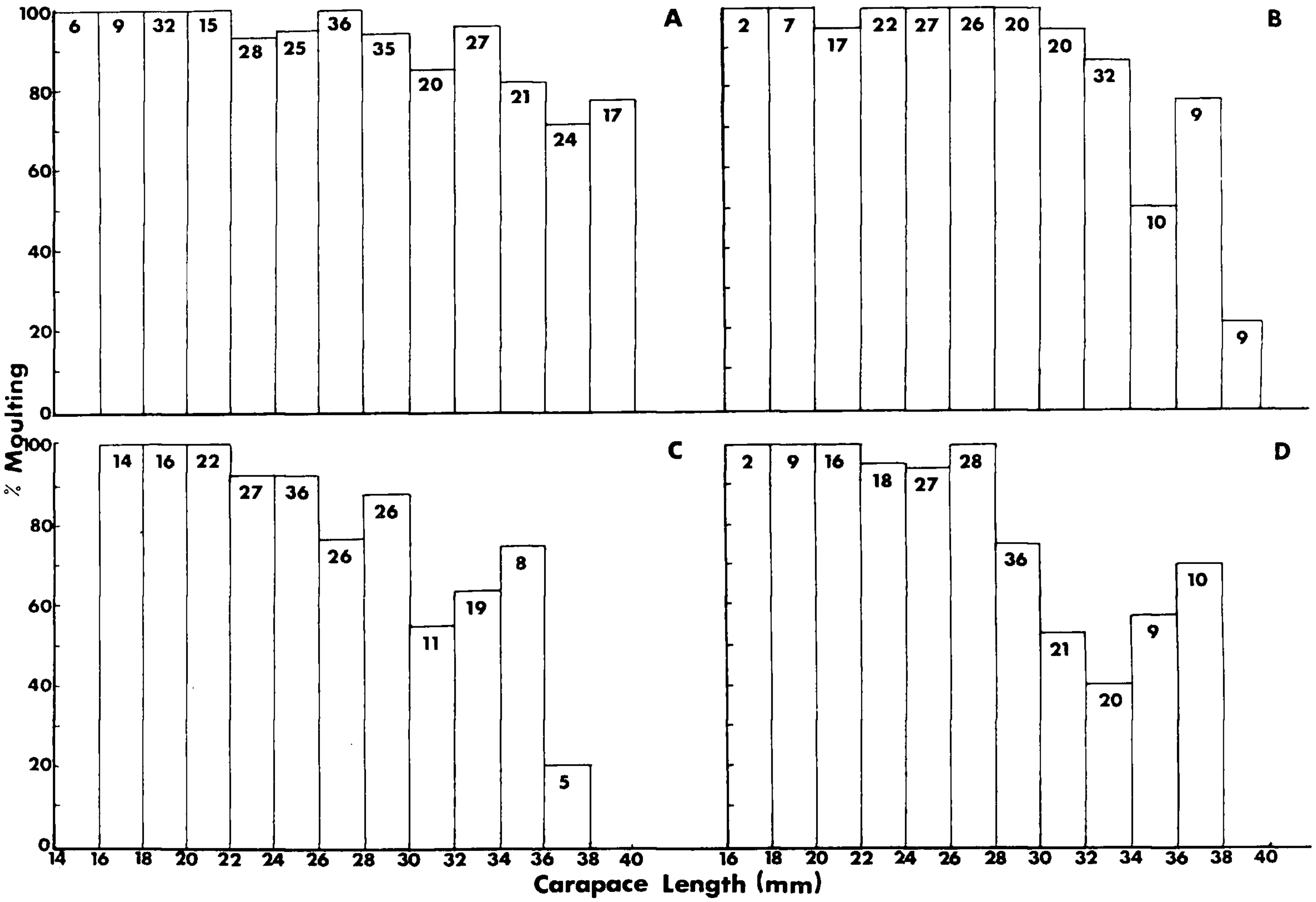
This decline of moult frequency with increasing size is also seen in Fig. 4.20, which shows the percentage of crayfish in each 2-mm CL size class which moulted during the first and second major moult periods during the study. (The two major moult periods of the year, during which moulting is most concentrated, fall in late June-July and in September in Northumbria). The high proportions of the size

Table 4.5

Annual moult frequencies of individually marked crayfish

Carapace length (mm)	MALES				FEMALES			
	Number of moults per year				Number of moults per year			
	0	1	2	3	0	1	2	3
14-16							1	
16-18							1	
18-20			4	1			4	1
20-22			3				5	
22-24		1	4				4	
24-26			6			1	5	
26-28	1	2	6			8	1	
28-30		2	5			12		
30-32		5	2			1		
32-34	1	24	1		1	4		
34-36	1	9				2		
36-38	1	16				1		
38-40	2	4						
40-42	1	6				2		
42-44		1				1		
44-46		2						

Fig. 4.20 The percentages of crayfish in 2-mm carapace length size classes moulting in the first and second major moult periods. (A) Males, first moult periods (B) Males, second moult periods (C) Females, first moult periods (D) Females, second moult periods



classes of both sexes of less than 28 mm CL which moulted in both moult periods is further evidence of the strong tendency for these individuals to moult at least twice each year (Table 4.5). There is no apparent significant difference between the proportions of crayfish of the two sexes which moulted during the two major moult periods.

Tables 4.6 and 4.7 present summaries of the growth of individually numbered male and female crayfish respectively over periods of some eighteen months or more. As in all decapods, growth in *Austropotamobius pallipes* is a function of moult increment and moult frequency. The tables include the number of moults completed by each crayfish together with the maximum number of moults which it was possible to have completed during the period for which growth was followed. The latter figure was calculated by assuming that each crayfish completed two moults in each growth season except for reproductive females, which omitted the first moult of the year, animals of a carapace length less than 25 mm, for which it was estimated that three moults were possible, and animals larger than 35 mm CL, for which it was estimated that one moult only was completed in each growth season. Evidence to support the choice of these moult frequencies is provided by the data given in Table 4.5. In many cases the growth of an individual was followed over one complete growth season and part of the preceding or following season. Since Fig. 4.20 indicates no differential moulting by either sex in favour of one or the other of the major moult periods, in the calculation of the maximum possible number of moults it was assumed that one moult was possible in such a period regardless of whether it was the beginning or end of the growth season.

The growth increment of each individual as measured in the field and the predicted increment calculated from the regression of postmoult carapace length on premoult carapace length for the 5-mm CL size class appropriate to each individual's particular size, sex, reproductive condition and number of moults are also included in Tables 4.6 and 4.7. The ratio of the actual increment to the calculated increment is then a measure of the size of the individual's growth increment in relation to the average predicted increment for an animal of that particular size and sex. It can be seen that twenty-two of the forty-four males in Table 4.6 and

Table 4.6 Growth of individual male crayfish 1977 - 1979

NUMBER	CARAPACE LENGTH (mm)	NUMBER OF MOULTS	NUMBER OF MOULTS POSSIBLE	ACTUAL GROWTH INCREMENT (mm)	CALCULATED GROWTH INCREMENT (mm)	ESTIMATED MAXIMUM INCREMENT (mm)	ACTUAL/ CALCULATED INCREMENT (%)	ACTUAL/ ESTIMATED MAXIMUM INCREMENT (%)
775	23.0	5	6	13.1	13.91	16.90	94.18	77.51
1342	25.5	4	5	11.5	11.26	14.25	102.13	80.70
2059	26.7	2	5	5.3	5.59	14.18	94.81	37.38
272	27.0	3	6	10.0	8.61	16.52	116.14	60.53
182	28.0	3	6	7.5	8.56	16.16	87.62	46.41
2631	28.3	3	3	8.9	8.55	8.55	104.09	104.09
4293	28.6	2	5	5.8	5.64	13.98	102.84	41.49
2824	28.9	3	5	7.1	8.52	13.87	83.33	51.19
621	29.0	3	6	8.4	8.51	15.76	98.71	53.30
4332	29.6	3	5	10.1	8.61	13.69	117.31	73.78
2821	29.9	3	4	8.1	8.62	11.37	93.97	71.24
2906	30.7	2	3	6.5	5.66	8.63	114.84	75.32
4643	31.2	2	4	7.2	5.66	11.15	127.21	64.57
2420	32.3	3	4	9.2	8.59	10.89	107.10	84.48
2476	32.8	3	5	8.5	8.53	12.55	99.65	67.73
3352	33.0	2	4	5.5	5.82	10.69	94.50	51.45
2657	33.1	3	4	8.5	8.49	10.66	100.12	79.74
4120	33.1	1	4	3.4	2.86	10.66	118.88	31.89
2934	33.1	2	3	5.6	5.82	8.49	99.12	65.96
3095	33.7	2	3	6.3	5.86	8.41	107.51	74.91
4126	33.9	1	3	2.2	2.89	8.39	76.12	26.22
10	34.0	3	7	8.5	8.37	14.44	101.55	59.00
454	34.0	2	4	5.5	5.88	10.39	93.54	52.94
3763	34.4	2	4	4.2	5.88	10.25	71.42	40.98
138	35.0	2	2	4.7	5.79	5.79	81.17	81.17
381	35.0	2	2	5.3	5.79	5.79	91.54	91.54
3335	35.1	2	2	5.4	5.77	5.77	93.59	93.59
1746	35.8	2	2	4.8	5.65	5.65	84.96	84.96
1474	35.9	2	2	7.3	5.64	5.64	129.43	129.43
2453	36.0	3	4	10.5	7.78	9.54	134.96	110.06
3368	36.0	3	3	9.6	7.78	7.78	123.39	123.39
2373	36.2	2	2	6.1	5.59	5.59	109.12	109.12
1374	36.4	2	2	5.3	5.56	5.56	95.32	95.32
3623	36.8	1	3	3.0	2.99	7.53	100.33	39.84
3410	36.9	2	3	5.1	5.48	7.50	93.07	68.00
36	37.0	2	2	5.8	5.49	5.49	105.65	105.65
985	37.0	1	2	3.2	2.89	5.49	110.73	58.29
1052	37.0	2	3	4.9	5.49	7.49	89.25	65.42
4852	37.9	1	3	4.1	2.86	7.07	143.36	57.99
2902	38.2	3	3	10.6	6.94	6.94	152.74	152.74
3503	38.6	2	3	3.8	4.95	6.75	76.77	56.30
3945	38.8	2	2	4.2	4.88	6.66	86.07	73.27
2896	39.9	2	3	5.1	4.51	6.15	113.08	82.93
3510	40.7	2	2	6.7	4.24	4.24	158.02	158.02

Table 4.7 Growth of individual female crayfish 1977 - 1979

N - normal moult increment B - postreproductive moult increment

NUMBER	CARAPACE LENGTH (mm)	NUMBER AND TYPE OF MOULTS	NUMBER OF MOULTS POSSIBLE	ACTUAL GROWTH INCREMENT (mm)	CALCULATED GROWTH INCREMENT (mm)	ESTIMATED MAXIMUM INCREMENT (mm)	ACTUAL/ CALCULATED INCREMENT (%)	ACTUAL/ ESTIMATED MAXIMUM INCREMENT (%)
3438	23.5	N-N-N	5	7.3	7.86	12.05	92.88	60.58
4872	24.8	N-N-B	4	7.8	7.33	8.89	106.41	87.74
1332	25.5	N-N-N-N	5	9.8	9.60	11.47	102.08	85.44
4837	27.5	N-N	5	3.6	4.82	9.67	74.69	37.23
4563	27.8	B-N-N	5	5.8	6.60	10.39	87.88	55.82
2343	28.3	N-N	3	6.4	4.55	6.84	140.66	93.57
616	29.0	B-N	3	3.6	4.00	5.65	90.00	63.72
1637	29.1	N-N-N-B	7	9.0	8.44	15.54	106.64	57.92
2026	29.3	N-B	3	4.3	4.23	5.94	101.65	72.39
4447	29.4	N-B	3	4.7	4.21	5.93	111.64	79.26
3085	29.8	N-B	3	4.3	4.02	5.76	106.97	74.65
3792	29.8	N-N	3	4.1	4.60	6.73	89.13	60.92
197	30.0	N-N	4	4.2	4.55	8.57	92.31	49.01
3588	30.0	B-B	2	3.4	3.86	3.86	88.08	88.08
4710	31.0	B-B	3	3.7	3.76	5.60	98.40	66.07
4323	31.2	B-N-N	5	6.9	6.21	10.67	111.11	64.67
1945	32.0	B-B	2	5.0	3.65	3.65	136.99	136.99
4366	32.0	B-B-B	3	10.3	5.57	5.57	184.92	184.92
3392	32.1	N-B-N	5	5.8	6.18	10.84	93.85	53.51
4269	32.9	B-B	2	3.8	3.71	3.71	102.43	102.43
4415	32.9	B-N	3	3.1	3.92	5.98	79.08	51.84
4363	34.1	B-N-N	5	8.7	6.02	11.09	144.52	78.45
4066	34.4	N-B-B	5	5.4	6.05	10.39	89.26	51.97
65	35.0	N	2	3.2	2.07	4.15	154.59	77.11
3582	35.7	B-N	2	3.9	4.07	4.07	95.82	95.82
4355	35.7	B-B	2	2.1	3.89	3.89	53.98	53.98
5021	38.2	B-N	2	4.3	4.37	4.37	98.40	98.40

thirteen of the twenty-seven females in Table 4.7 fall within ± 10% of the 100% level for this ratio. The estimated maximum growth increment of an individual (see Tables 4.6 and 4.7) was calculated in a manner similar to that for the average predicted increment (see above) and by assuming that it moulted on every occasion possible, i.e. by an extrapolation from the field data. The ratio of the actual growth increment to the estimated maximum growth increment is then a measure of the individual's growth performance relative to its potential growth. By presenting the data in this manner it is possible to identify crayfish with higher or lower growth rates than the average for the population. From Table 4.6, number 272, a male of 27.0 mm CL, had moult increments larger than predicted (actual/calculated increment ratio = 116%) but moulted on only three occasions out of a possible six and therefore had a poor overall growth performance (actual/estimated maximum increment ratio = 60%). Similarly, number 4643 (31.2 mm CL) had a much larger increment than predicted for the two moults which it completed and failed to fulfil more than 65% of its potential growth because of the omission of two further possible moults. Number 4852 (37.9 mm CL), despite having a very large increment at a single moult, had an actual/estimated maximum increment ratio of less than 60% since it did not moult on two further occasions. Numbers 1474 (35.9 mm CL), 3368 (36.0 mm CL) and 2902 (38.2 mm CL) produced much better growth performances than expected because of their large growth increments and because each moulted on every occasion possible. In the cases of numbers 2824 (28.9 mm CL) and 4126 (33.9 mm CL), a smaller growth increment than predicted combined with a relatively low moult frequency produced very low actual/estimated maximum increment ratios. A further type of growth pattern is displayed by numbers 3335 (35.1 mm CL) and 1746 (35.8 mm CL), which moulted on every occasion possible but because of their small moult increments fell somewhat below their maximum potential growth (Table 4.6).

Examples of some of these types of growth patterns are also to be seen among the females presented in Table 4.7. Thus numbers 4837 (27.5 mm CL) and 197 (30.0 mm CL) each fulfilled less than half of their potential growth over the period for which they were studied because of a combination of low moult increments and a low moult frequency. Number 1332 (25.5 mm CL) had moult increments slightly larger than the norm but fell well below its potential growth increment because of the omission of a moult, while number 2343 (28.3 mm CL) came close to its estimated maximum increment despite the omission of a moult because of its very large increment over the two moults which it did compete. Most other cases in this table involve at least one post-reproductive moult. In such cases the calculation of the estimated maximum growth increment takes into account the fact that reproductive females moult once only each year and that at the first post-reproductive moult (B) the increment tends to be smaller than that at a normal moult (N), particularly in the smaller reproductive females. There is some evidence to suggest that the effect of reproduction on the growth of individuals may vary greatly, e.g. numbers 1945 and 4366, both females of 32.0 mm CL, were able to exceed considerably their estimated maximum growth increment despite having produced eggs in successive years, while numbers 4710 (31.0 mm CL) and 4355 (35.7 mm CL), which also reproduced in successive years, fell well below this figure.

4.3.6 The effect of chela regeneration on growth

The growth of crayfish regenerating a major chela is much reduced (Table 4.8). Moult increments are generally smaller than predicted for such individuals, whilst moult frequency is apparently not affected to the same extent. In common with crayfish infected by *Thelohania* (6.3.2), there is much variation between individuals regenerating a major chela in the degree to which growth is affected. The two individuals suffering from additional disabilities (number 4471, a male of 22.6 mm CL regenerating both major chelae, and number 5789, a female of 29.2 mm CL regenerating both major chelae and infected by *Thelohania*) both showed very low growth rates (Table 4.8).

4.3.7 Instantaneous growth rates

The decline in instantaneous growth rate throughout the life of each subpopulation is shown in Table 4.9. The decline is particularly rapid in the largest (oldest) size classes of nonreproductive females. The growth rates of males and females can be seen to be very similar until the size of 27 mm CL is reached. At this size it is estimated that all crayfish in this population are sexually

Table 4.8

Growth of individual crayfish regenerating chelae

* regenerating both chelae   † regenerating both chelae, thelohaniasis

Number	Carapace Length (mm)	Number of Moults	Number of Moults possible	Actual Growth Increment (mm)	Calculated Growth Increment (mm)	Estimated Max. Growth Increment (mm)	Actual/ Calculated Increment (%)	Actual/ Estimated Maximum Increment (%)
(A) MALES 6414	18.0	3	3	6.0	7.08	7.08	84.8	84.8
8296	19.4	3	3	4.9	7.01	7.01	69.9	69.9
5660	19.6	2	3	5.0	4.33	7.00	115.5	71.4
4591	21.5	2	3	2.6	4.80	7.54	54.2	34.5
* 4471	22.6	1	3	0.6	2.63	8.23	22.8	7.3
4993	26.0	2	2	4.8	5.60	5.60	85.7	85.7
6692	33.2	1	2	2.7	2.86	5.82	94.4	46.4
5995	37.3	1	1	1.7	2.97	2.97	57.2	57.2
6361	38.6	1	1	2.8	2.73	2.73	102.6	102.6
6298	44.1	1	1	0.8	1.70	1.70	47.1	47.1
(B)FEMALES 5697	18.2	2	3	3.2	4.33	7.08	73.9	45.2
6745	26.5	1	2	1.4	2.73	5.06	51.3	27.7
5768	26.8	1	2	2.7	2.74	5.14	98.5	52.5
6205	27.2	2	2	4.2	4.91	4.91	85.5	85.5
† 5789	29.2	1	2	1.8	2.34	4.26	76.9	42.3
4555	29.6	1	2	2.5	2.27	4.12	110.1	60.7
6297	30.2	2	2	4.3	4.50	4.50	95.6	95.6

Table 4.9

Instantaneous growth rates over a one-year period of size classes of *A.pallipes* in Northumbria

Carapace Length	Males	N	Nonreproductive Females	N	Reproductive Females	N
17-22 mm	0.832 ± 0.039	7	0.878 ± 0.095	12	-	-
22-27 mm	0.639 ± 0.043	18	0.612 ± 0.040	20	-	-
27-32 mm	0.415 ± 0.032	35	0.283 ± 0.024	22	0.176 ± 0.007	53
32-37 mm	0.277 ± 0.007	127	0.225 ± 0.024	12	0.178 ± 0.006	95
37-45 mm	0.231 ± 0.006	90	0.053 ± 0.010	6	0.060 ± 0.005	18

mature, and it is notable that after this size has been attained males maintain consistently higher growth rates than females, the rates of males being significantly faster in the 27-32 mm CL size class ($P<0.01$), the 32-37 mm CL size class ($P<0.05$) and the 37-45 mm CL class ($P<0.001$).

The instantaneous growth rate of the smallest reproductive females in this population, i.e. the 27-32 mm CL size class, is significantly slower than that of nonreproductive females of the same size range. In the next size class, however, the difference is less marked and is not statistically significant, while in the largest size class of all the growth rates of reproductive and nonreproductive females are very similar (Table 4.9).

Fig. 4.21 presents the relationship between instantaneous growth rate and carapce length for individually marked male and female crayfish during one complete year. The marked inverse correlation between carapace length and instantaneous growth rate is clearly shown in this figure and in Table 4.9. The rate of decline of instantaneous growth rate is more rapid in females than in males.

Also indicated on Fig. 4.21 are the instantaneous growth rates of individuals infected by *Thelohania contejeani* or regenerating a major chela. The general reduction in growth rate caused by these conditions can be clearly seen, the majority of such crayfish having growth rates below the mean for the population as a whole.

4.3.8 The relationship between size and age

Data on the modal sizes of overwintering year classes (4.3.1), on moult frequency (4.3.5) and on the size of moult increments (4.3.2-4.3.4) were utilised in the construction of Fig. 4.22, which presents the estimated relationship between size and age for the crayfish of the study population. The figure indicates that males first become larger than females of the same age at approximately 32 mm CL, a fact which is supported by the tendency for males to maintain higher moult frequencies than females above sizes of 26-28 mm CL (Table 4.5). The figure represents the most likely of the many different possible patterns of growth which an individual may follow because of the variations in moult frequency indicated in

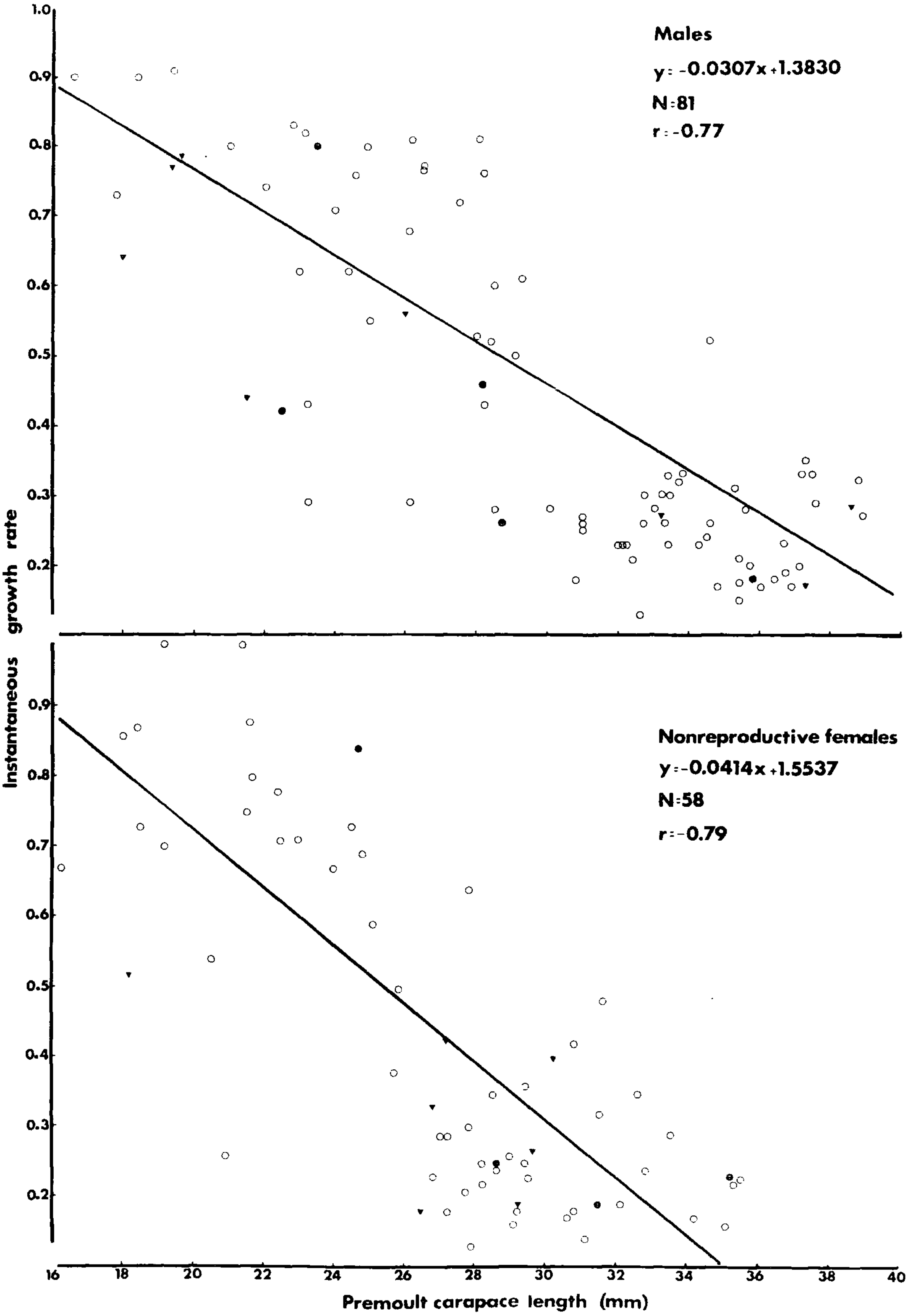


Fig. 4.21 The relationship between instantaneous growth rate and carapace length in *A. pallipes* from Northumbria

●Infected by *Thelohania* ▼Regenerating a major chela

Fig. 4.22 The relationship between size and age throughout the lifespan of *A. pallipes* in Northumbria

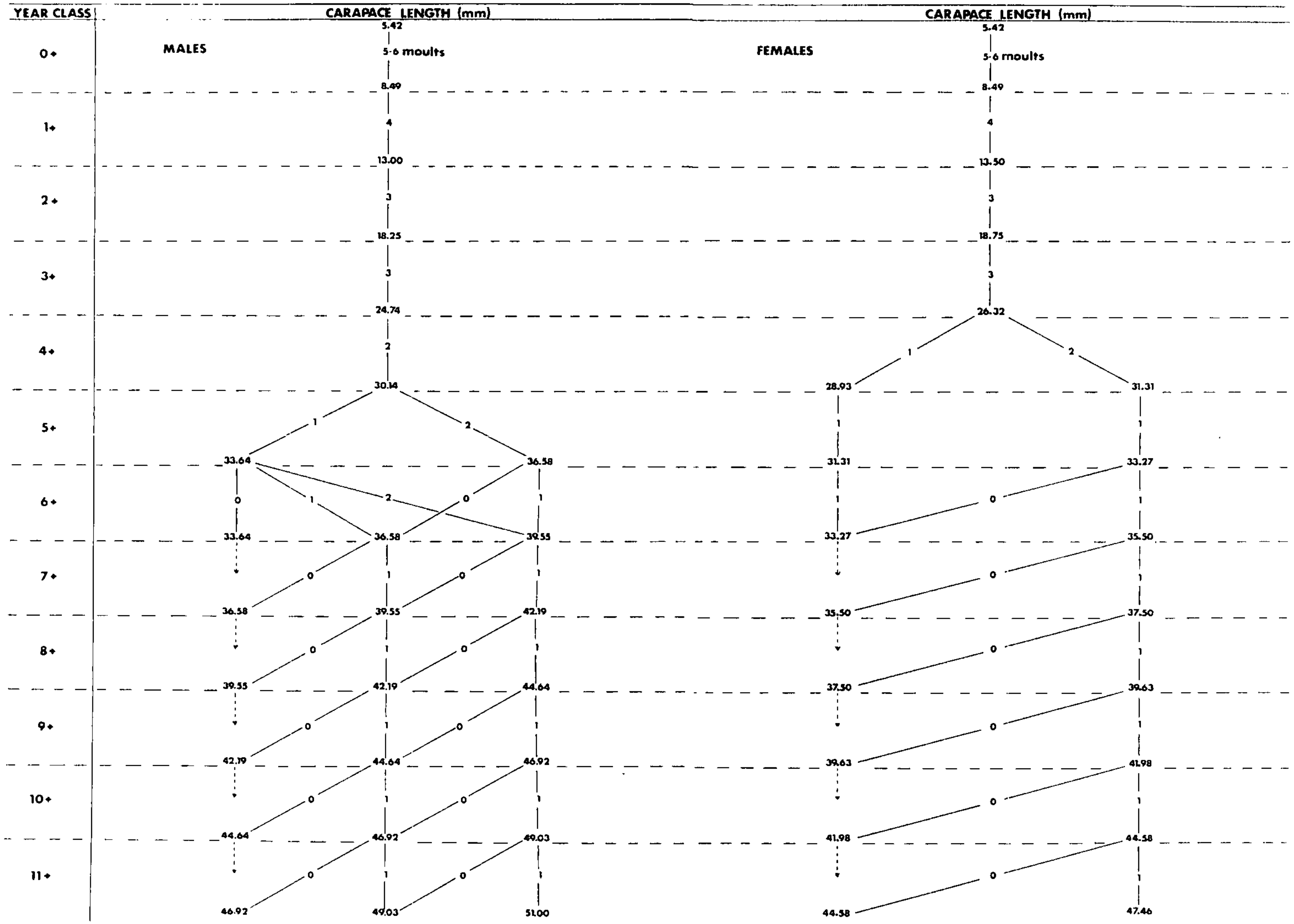


Table 4.5. Since the largest crayfish which were caught during the study had carapace lengths of 49.6 mm (male) and 46.1 mm (female), it was estimated that the oldest animals in the population were at least eleven years old (*cf*. Brown & Bowler 1979).

4.3.9 The relationship between size and weight

Live wet weights of crayfish collected throughout the year from several sites in Northumbria were used to establish the relationship between size (measured as carapace length) and weight. From samples of 200 of each sex the following relationships between weight (y) and carapace length (x) were derived:

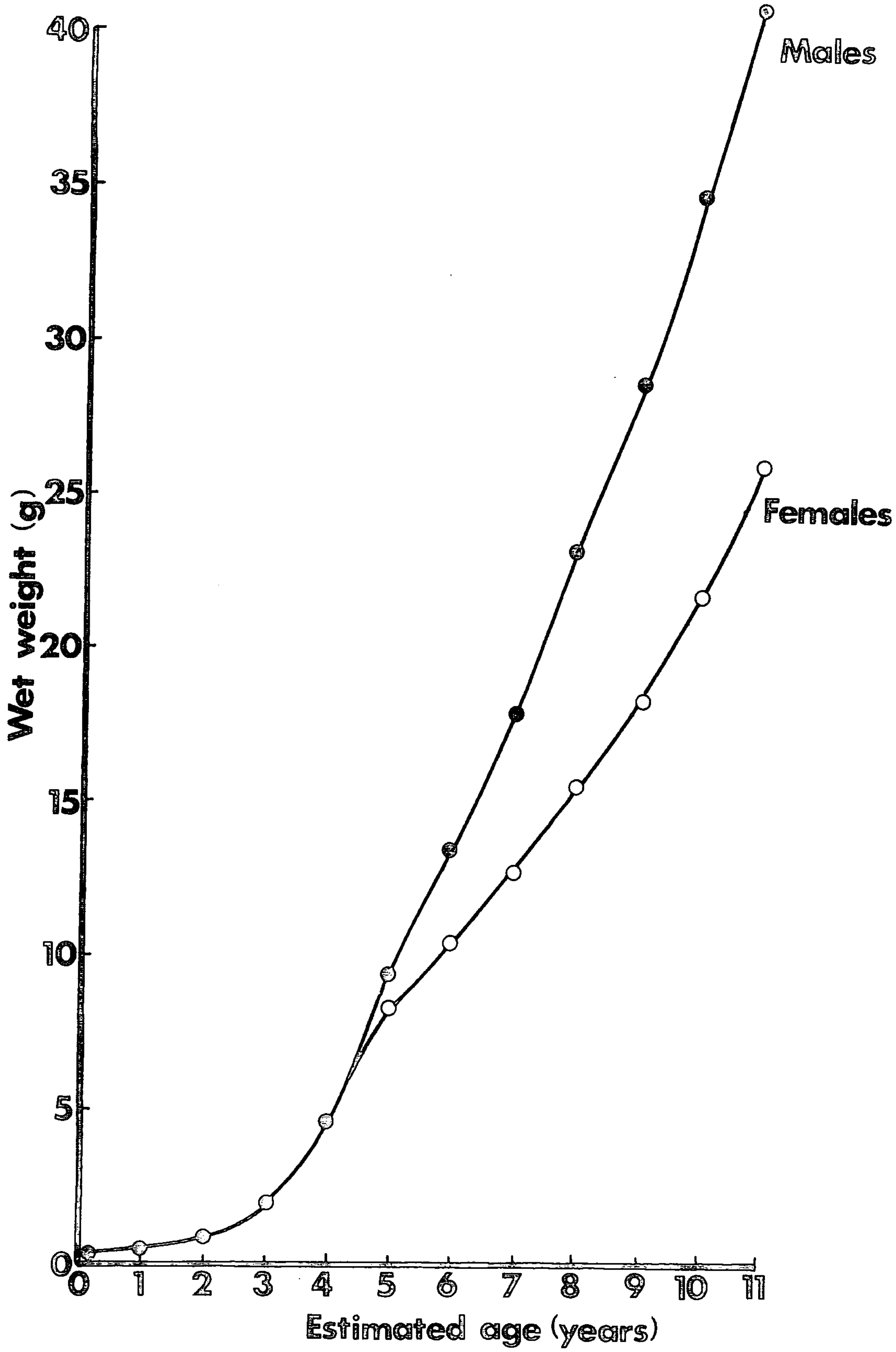
juveniles $\log_e y = 2.791 \log_e x - 7.444$
males (>25 mm CL) $\log_e y = 3.330 \log_e x - 9.110$
females (>25 mm CL) $\log_e y = 3.078 \log_e x - 8.249$

These relationships were used to estimate the wet weights of crayfish at sizes corresponding to a particular year class (from Fig. 4.22). These weights are shown in relation to estimated age in Fig. 4.23. In the construction of this figure it was assumed that for males one moult took place in year 5+ and one per year thereafter. For females, one moult was assumed in year 4+ and one per year thereafter (see Table 4.5). It can be seen that the oldest individuals in the population had weights of some 40g (males, at a carapace length of some 47 mm) and 26g (females, at a carapace length of some 42 mm). There was a clear fall in growth rate in both sexes during the fourth and fifth years of life (Fig. 4.23).

4.3.10 The estimation of annual production

From the detailed estimates of population size (3.5) and a knowledge of the relationship between size and weight (4.3.9) estimates of the annual production of the study population were made. The mean carapace length of crayfish in each of the three subpopulations (adult male, adult female and juvenile) at the start of each growth season was known and the length at the end of the growth season was estimated from the relationships between postmoult carapace length and premoult carapace length given in Figs. 4.4-4.8. It was assumed that adults completed one moult and juveniles three during the full

Fig. 4.23 The relationship between age and wet weight throughout the lifespan of *A.pallipes* in Northumbria



growth season (see Table 4.5 for the relationship between size and moult frequency). The carapace lengths were converted to wet weights using the equations given in 4.3.9. The estimated numbers in each subpopulation at the beginning (N_1) and end (N_2) of each growth season were known (Tables A1-A4), together with their survival rates during the growth season. The mean subpopulation size (excluding recruits) during the growth season was estimated as $(N_1+N_2)/2$. The biomass at the beginning of the growth season and production by the survivors of the initial population was then calculated (Table 4.10).

The contribution to production by recruits to each subpopulation during the growth season is estimated in Table 4.11. Calculations are as for the estimation of production in Table 4.10 with the additional assumption that all recruitment occurred midway through the growth season and therefore one moult was completed by the adult subpopulations and two by juveniles.

The estimates of total production are presented in Table 4.12, which sums the contributions made by growth (Table 4.10), recruitment (Table 4.11) and egg production, the latter being calculated from the number of eggs produced in each year (5.4) and the weight of each egg (13.11 mg).

Estimates of biomass at the beginning of the growth season for the study population of crayfish range from 122.93 kg (495.29 kg ha^{-1}) in 1977 to 79.26 kg (319.34 kg ha^{-1}) in 1979 (Table 4.12). The much lower value for 1979 is a reflection of the smaller population during that year (3.5). The proportion of total production attributable to recruitment was much smaller in 1978 and 1979 than in 1977. This is an index of the general failure of recruitment in 1978, the consequent fall in population size and the failure to regain former numbers in 1979 (3.5). Annual production was estimated at 48.77 kg (196.49 kg ha^{-1}) in 1977, 28.99 kg (116.80 kg ha^{-1}) in 1978 and 21.79 kg (87.79 kg ha^{-1}) in 1979. The ratio of annual production to the initial biomass (P/B ratio) was 0.40 in 1977, 0.27 in 1978 and 0.27 in 1979.

Table 4.10

The estimation of annual production from growth of the standing crop at the beginning of the growth season

	ADULT MALES	ADULT FEMALES	JUVENILES	TOTALS
1977				
Mean individual weight (g)	14.19	10.80	3.02	
N_1 (at beginning of year)	4178	3600	8200	
Initial biomass (kg)	59.29	38.88	24.76	122.93
Survival to end of year	0.379	0.486	0.134	
N_2 (at end of year)	1583	1750	1099	
$(N_1 + N_2)/2$	2881	2675	4650	
Mean individual weight (g)	18.60	13.97	4.52	
Production (kg)	12.71	8.48	6.98	28.17
1978				
Mean individual weight (g)	12.85	10.91	2.57	
N_1 (at beginning of year)	3906	3379	7401	
Initial biomass (kg)	50.19	36.86	19.02	106.07
Survival to end of year	0.237	0.254	0.036	
N_2 (at end of year)	926	858	266	
$(N_1 + N_2)/2$	2416	2119	3834	
Mean individual weight (g)	16.92	14.09	3.78	
Production (kg)	9.83	6.74	4.64	21.21
1979				
Mean individual weight (g)	12.22	10.91	3.14	
N_1 (at beginning of year)	2687	2928	4610	
Initial biomass (kg)	32.84	31.94	14.48	79.26
Survival to end of year	0.233	0.214	0.450	
N_2 (at end of year)	626	627	2075	
$(N_1 + N_2)/2$	1657	1778	3343	
Mean individual weight (g)	16.12	14.09	4.72	
Production (kg)	6.46	5.65	5.28	17.39

Table 4.11

The estimation of production from recruitment to the population

	ADULT MALES	ADULT FEMALES	JUVENILES	TOTALS
1977				
Recruitment (N_1)	2772	3333	13 705	
Mean individual weight (g)	5.00	5.25	0.75	
Survival to end of year	0.721	0.709	0.455	
N_2 (at end of year)	1999	2363	11 046	
$(N_1 + N_2)/2$	2386	2848	12 378	
Mean individual weight (g)	7.03	7.23	1.46	
Production (kg)	4.84	5.64	8.79	19.27
1978				
Recruitment (N_1)	2108	1920	4625	
Mean indivudual weight (g)	5.00	5.25	0.75	
Survival to end of year	0.520	0.394	0.146	
N_2 (at end of year)	1096	756	675	
$(N_1 + N_2)/2$	1602	1338	2650	
Mean indivudual weight (g)	7.03	7.23	1.46	
Production (kg)	3.25	2.65	1.88	7.78
1979				
Recruitment (N_1)	581	1082	3038	
Mean individual weight (g)	5.00	5.25	0.75	
Survival to end of year	0.289	0.455	0.146	
N_2 (at end of year)	168	492	444	
$(N_1 + N_2)/2$	375	787	1741	
Mean individual weight (g)	7.03	7.23	1.46	
Production (kg)	0.76	1.56	1.24	3.56

Table 4.12

Annual production of *Austropotamobius pallipes* in Northumbria

		ADULT MALES	ADULT FEMALES	JUVENILES	TOTALS
1977	Production from:				
	growth	12.71	8.48	6.98	28.17
	recruitment	4.84	5.64	8.79	19.27
	egg production	-	1.33	-	1.33
	TOTAL PRODUCTION (kg)	17.55	15.45	15.77	48.77
	INITIAL BIOMASS (kg)	59.29	38.88	24.76	122.93
1978	Production from:				
	growth	9.83	6.74	4.64	21.21
	recruitment	3.25	2.65	1.88	7.78
	egg production	-	1.59	-	1.59
	TOTAL PRODUCTION (kg)	13.08	9.39	6.52	28.99
	INITIAL BIOMASS (kg)	50.19	36.86	19.02	106.07
1979	Production from:				
	growth	6.46	5.65	5.28	17.39
	recruitment	0.76	1.56	1.24	3.56
	egg production	-	0.84	-	0.84
	TOTAL PRODUCTION (kg)	7.22	8.05	6.52	21.79
	INITIAL BIOMASS (kg)	32.84	31.94	14.48	79.26

4.4 DISCUSSION

The problem of identifying year classes in populations of decapod Crustacea is widely reported. The most usual method of attempting to determine modal sizes of year classes is the size-frequency plot. Several workers on species of freshwater crayfish have found that whilst it is easy to pick out the first two or three year modes with this method, subsequent modes are obscured by the overlapping in size between year classes (Hopkins 1966; Momot 1967b; Mason 1975; Brown & Bowler 1977). This is a serious limitation in a study of growth in a long-lived species such as *Austropotamobius pallipes*. The treatment of size-frequency data after the method of Cassie (1954) provides a less subjective method of estimating modal sizes. Brown (1979), using this method on data for *A. pallipes*, identified for each sex three clear modes and three further tentative ones representing year classes from the same field site as used in the present study. The modal sizes of the first two of these year classes correspond closely with those derived from a size-frequency plot of overwintering crayfish in the present study (4.3.1), with the exception of that of the female year class 1+. Brown (1979) found this to be 12.6 mm CL, whereas in the present study it was determined at 11.1 ± 1.7 mm CL. There is reason to believe that the latter mean is too low, for data obtained from juvenile females from nearby sites suggest a mode of 13.0 mm CL. An interesting geographical comparison is afforded by the work of Pratten (1980), who reported that *A. pallipes* in the River Ouse reaches 12.7 mm CL at the end of the first year of life (*cf.* 8.49 mm CL in Northumbria) and 20.0 mm CL at the end of the second. The difference between this population and that in Northumbria is attributable to the higher temperatures and the earlier hatching date in the more southerly population. Reservations must be made on the accuracy of some published data as it is not made clear that the measurements used to establish size-frequency relationships were collected when the crayfish were in the overwinter condition and therefore all in the same intermoult phase.

The decline of percentage moult increment (y) with carapace length (x) in *A. pallipes* was reported by Bowler & Brown (1977), who fitted the equations $y = -0.316x + 17.89$ ($n = 61$) for females and $y = -0.296x + 19.08$ ($n = 207$) for males. These equations agree well with those obtained in the present study for larger samples, i.e. $y = -0.505x + 23.376$ (n = 194) for adult females and $y = -0.284x + 18.041$ (n = 308) for adult males. Mason (1975) tabulates values for *Pacifastacus leniusculus trowbridgii* from which the similar relationship $y = -0.431x + 26.28$ can be derived.

Such treatment of growth data assumes that the incremental growth in crayfish of a specific size and sex is independent of the time of moulting within the growth season or of the growth season itself. This study indicates that, at least for some male size classes of *A. pallipes*, this may not be true, while Momot & Gowing (1977b) have shown that considerable annual variations in the production of populations of the crayfish *Orconectes virilis* may occur.

In view of the inverse relationship between percentage moult increment and body size revealed in this study and the variation of the absolute moult increment with size, it is important to explore the possibility that a different size composition of the same subpopulation at different sampling times may either obscure or produce differences. In this respect the matching of individuals for size is of particular importance and is a technique which has been little used by other workers. The tendency apparent from the unmatched data of Table 4.1 for increments to be larger during the first moult period than during the second is revealed by further analysis of individuals matched for carapace length to be spurious, with the possible exception of the adult male subpopulation. The smaller increments of females at the first post-reproductive moult compared to those of nonreproductive females are also revealed in subpopulations matched for carapace length (see Table 4.3). Hopkins (1967a) reported a similar phenomenon in a population of the New Zealand crayfish *Paranephrops planifrons*. The analysis of growth in juveniles is more complex than in adult populations since, as stressed earlier (2.5, Table 4.5) juveniles undergo more than two moults in a year.

The division of the subpopulations of *A. pallipes* into 5-mm CL size classes (Table 4.4) shows that the relationship between growth increment and body size is more complex than is evident from the preceding tables. Whilst the decline of percentage moult increment with size is well marked in both sexes, including reproductive females, the absolute moult increment at first increases with size before declining in the larger size classes (Table 4.4). Mason (1975) reported the same trend in *Pacifastacus leniusculus trowbridgii*. In males it can be seen that only in the 22-32 mm CL size range is there a significant difference between the size of the increments in the first and second moult periods (Table 4.4). It may be pertinent that in this population it is only this size range of males which regularly moult twice each year, moult frequency tending to decline thereafter (Table 4.5). This may also explain why the pooled data of Table 4.3, which are derived principally from animals of this size range, displays this difference between the first and second moult periods only in the adult male subpopulation.

An important point to emerge from a comparison of growth increments in reproductive and nonreproductive females is that only in the smallest size class (27-32 mm CL) is the size of the increment in the former subpopulation significantly smaller. This is also true of the instantaneous growth rates presented in Table 4.9. In the largest size class the instantaneous growth rates of reproductive and nonreproductive females are very similar. The inference is that reproduction has a severe effect on growth only in the youngest breeding females. Whilst Table 4.9 reveals a marked decline in growth rates throughout the lifespan for both sexes, it also reveals important differences between the two. Growth rates are very similar until the 27 mm CL size is reached. At this point it is believed that all crayfish in this population are sexually mature. At all sizes larger than this the growth rates of males are significantly faster than those of females, the difference being particularly marked in the largest size class. The fall from the rapid growth rates of juvenile life occurs during the fourth and fifth years of life, i.e. at about the time of sexual maturity. Thereafter males maintain consistently faster growth rates than females. This observation is compatible with those of Table 4.5 and Fig. 4.23. Since there are many possible variations in moult frequency, however (Table 4.5), there will be many gradations between the curves given in Fig. 4.23 as being typical of each sex. In addition, variations caused by differences in moult increments, parasitism by *Thelohania*, regeneration of chelae and small post-reproductive moults exist, so that the true picture is undoubtedly better represented as a band of growth curves about the two lines of Fig. 4.23.

The ability to determine annual moult frequencies of individuals (Table 4.5) is invaluable in that it enables conclusions to be drawn about moult frequencies in a population where the modal progression of a size-frequency plot has disappeared. Hopkins (1967a) used this technique in a study of *Paranephrops planifrons*. Most workers, however, are unable to attain the necessary recapture rate in order to be able to determine individual moult frequencies directly in the field. Fig. 4.22, constructed with regard to the moult frequencies given in Table 4.5, illustrates the manner in which individuals of the same age may come to differ widely in size because of their different moult frequencies. Conversely, a given size class of individuals may differ widely in their ages, particularly at the larger end of the size range. Even the variation depicted in this figure must be regarded as being simplified, as the effects of *Thelohania*, the regeneration of limbs, characteristically large or small moult increments in individuals and (in females) reproduction on growth rates have not been allowed for. Similarly, the size-age relationships given by Mason (1975) for *Pacifastacus leniusculus trowbridgii* and Price & Payne (1979) for *Orconectes neglectus chaenodactylus* assume a rigid moult frequency and uniform moult increments, a fact recognised by Mason (1975), who speculated that his postulated year classes VI-VIII may be spillovers from preceding age classes which maintained high individual growth rates. The close agreement between the data in Fig. 4.22 and those given independently by Brown & Bowler (1979) for the minimum life span of *A. pallipes* suggests that this is an accurate representation of the size-age relationship in this population.

A striking feature of the data presented in Tables 4.6 and 4.7 and Fig. 4.22 is the large variation in growth between individuals of comparable size and sex. The two statistics which account for this variation are moult frequency and the actual/calculated increment ratio. Where this ratio is low it identifies an individual of characteristically small moult increments and where it is high it identifies an individual of characteristically large moult increments. Both of these characteristics may be combined with either a high or a low moult frequency to produce the variations in growth pattern which have been examined earlier. As can be seen from Tables 4.6 and 4.7, many gradations between these extremes exist, with the majority of the individuals studied tending to cluster around the mean. However, few crayfish of either sex approached fulfilment of their estimated maximum growth. Of the very few which exceeded this figure, most were large individuals.

In the calculation of the estimated maximum increment for female crayfish, allowance was made for the smaller moult increment and lower moult frequency associated with reproduction (4.3.2). It could be argued, however, that no such allowance should be made and that the estimated maximum increments of reproductive females are larger than the figures given in Table 4.7. This would have the effect of reducing the ratio of the actual increment to the estimated maximum increment. Clearly, there is a complex collection of selective pressures bearing on such females. Reproduction is effected at the expense of a lower growth rate and, because of the strong correlation between body size and number of eggs produced (5.3; Brown & Bowler 1977), results in a lower potential production of eggs in future years. However, Table 4.9 indicates that in large females there is no difference between the growth rates of reproductive and nonreproductive individuals. Reproduction may also confer an advantage on the smaller females in that it reduces the risk of moult-associated mortality (chiefly cannibalism) by reducing moult frequency. In larger females moult frequency is unaffected by reproduction (Table 4.5).

The selective pressures upon males are no less complex. In order to be able to copulate with a female a male must be able to overturn her with his chelae interlocked in hers (Ingle & Thomas 1974). Furthermore, large body size probably enables a male to copulate with larger females, thereby taking advantage of the positive correlation which exists between female body size and number of eggs produced (5.3: Brown & Bowler 1977). Greenspan (1980) has described such a relationship in the fiddler crab *Uca rapax*. It appears, therefore, that large body size is an advantage to a male and that selection has been directed towards its attainment by the maintenance of a faster growth rate than found in females in adult life

(Table 4.5, Figs. 4.22-4.23). The important function of the major chelae of both sexes during copulation (Ingle & Thomas 1974; Stein 1976) may also account for the regeneration of lost or damaged chelae at the expense of body growth in general (Table 4.8, Fig. 4.21). The variation in the effect of regenerating a major chela upon the growth of individuals can be explained by taking into account the degree to which regeneration was completed during the study. Examination of individual cases showed that in general those individuals showing little fall in growth rate were those in which regeneration was almost complete.

The reasons for the variation in the effect of the parasite *Thelohania contejeani* upon individual growth rates are less obvious. However, from the time when infection can first be identified in the field to the death of the host crayfish is between one and two years (6.4) and the variation in the effect of the parasite on growth rates can be attributed to differences in the extent to which the infection had developed.

The size classes for which instantaneous growth rates are presented in Table 4.9 correspond to the year classes 2+ and above (4.3.1, Fig. 4.22). The instantaneous growth rates for the year classes 0+ and 1+ were estimated to be 0.62 and 1.30 respectively for males and 0.71 and 1.44 respectively for females. These compare with rates of 3.03 (0+) and 1.71 (1+) for both sexes recalculated from Pratten (1980), the higher rates of the latter reflecting the longer growth season afforded by the generally higher water temperatures of this population. The disparity between the growth rates of these two English populations of *Austropotamobius pallipes* indicates the importance of water temperature: it is pertinent that the Northumbrian population is at the northern limit of the species range.

The estimated P/B ratios (0.40, 0.27, 0.27) of the study population of *A. pallipes* (4.3.10) are considerably lower than those estimated for other crayfish species, which vary from 0.5 to 2.0 but are typically 0.7-1.5 (Cukerzis 1975; Momot 1978). Waters (1977) has stressed the effects of voltinism and water temperature (among other factors) on aquatic secondary production and gave examples of the variation with environment of P/B ratios of species of fish.

Heal & MacLean (1975) also emphasised the effect of temperature on the P/B ratio and noted that this figure tends to decline as longevity increases: *A. pallipes* is much longer-lived than the North American crayfish. Voltinism in the crayfish species for which P/B ratios have been estimated is one: it is probable that the longevity of *A. pallipes* and the cold water temperature regime in Northumbria are the principal reasons for the comparatively low P/B ratio of the study population.

Direct comparison of many of the data which have been presented here is not possible as few similar data on the growth of other crustaceans, particularly freshwater crayfish, have been published. It is apparent that few individuals in this population of *A. pallipes* fulfil their potential growth over any appreciable period. As discussed earlier, the reasons for this may include disease, a small post-reproductive moult increment in the case of females and the regeneration of missing limbs. Other individuals characteristically show high or low moult frequencies and large or small moult increments. Whether the failure to fulfil growth potential is genetically, environmentally or socially determined, it is apparent that further detailed studies on the growth of marked individuals can help reveal more of the principles governing growth in crustaceans.

Chapter five

REPRODUCTIVE FEMALES

5.1 INTRODUCTION

An assessment of the number of breeding females is clearly a very important factor in any population study. However, the difficulties of adequately sampling crayfish populations have prevented workers from reporting any but the most brief details.

It has been a feature of several reports that adult female crayfish do not always carry eggs each year. Steffenberg (1872), as quoted by Thomas & Ingle (1971), reported that females of *Astacus fluviatilis* did not breed each year. Thomas & Ingle (1971) themselves found that 96% of females exceeding 27 mm carapace length bore eggs in a population of *Austropotamobius pallipes* in Kent. The size composition of this sample is not given, however. Brown (1979) estimated the proportion of adult females (i.e. those larger than 25 mm carapace length) which was berried at 31.57% in 1974-75, 47.21% in 1975-76 and 48.35% in 1976-77 at the Hallington site in Northumbria and also reported that a greater proportion of the larger size classes bore eggs. The purpose of this study was to estimate numbers of breeding females, their fecundity and the potential recruitment into the study population each year.

5.2 NUMBERS OF REPRODUCTIVE FEMALES

Table 5.1 presents the numbers of reproductive females which were collected in the hand fished samples taken during the periods when eggs were being carried from 1977-79. The mean proportion of berried females for the three-year period was 40.65%. However, in each year a sudden fall in the proportion of reproductive females occurred in samples taken during early August (Table 5.1). This is the time of egg hatching and release of young (2.5) and it is probable that this fall is attributable to the earlier hatching and release of some broods. If these samples are omitted from the analysis the mean proportions of reproductive females are 47.21% in 1977, 44.73% in 1978 and 42.45% in 1979, with an overall mean of 44.80%.

TABLE 5.1

Numbers of reproductive females in hand fished samples 1977-79

DATE	REPRODUCTIVE	NONREPRODUCTIVE	% REPRODUCTIVE
12 May 1977	154	162	48.73
27 May 1977	124	135	47.88
17 June 1977	137	167	45.07
9 August 1977	51	219	18.89
12 August 1977	130	372	25.90
17 May 1978	205	213	49.04
23 May 1978	221	275	44.56
15 June 1978	280	219	56.11
27 June 1978	177	264	40.14
24 July 1978	132	283	31.81
10 August 1978	107	162	39.78
24 April 1979	94	93	50.27
3 May 1979	69	43	61.61
31 May 1979	102	114	47.22
7 June 1979	88	106	45.36
3 July 1979	75	96	43.86
18 July 1979	50	196	20.33
9 August 1979	72	192	27.27

Estimates of the size of the adult female subpopulation during the period when eggs were being carried, i.e. November - August, are available from Table A3. The mean of all the available estimates was taken as being the most accurate estimate of subpopulation size. This figure was chosen in preference to the Jolly estimates of numbers of reproductive females (Table 3.2) because of the suspected bias in these estimates resulting from the modification of behaviour of berried females (2.5) and because of the accuracy with which the proportion of reproductive females was determined from large samples (Table 5.1). Estimates of the numbers of reproductive females in each year of the study are then given by:

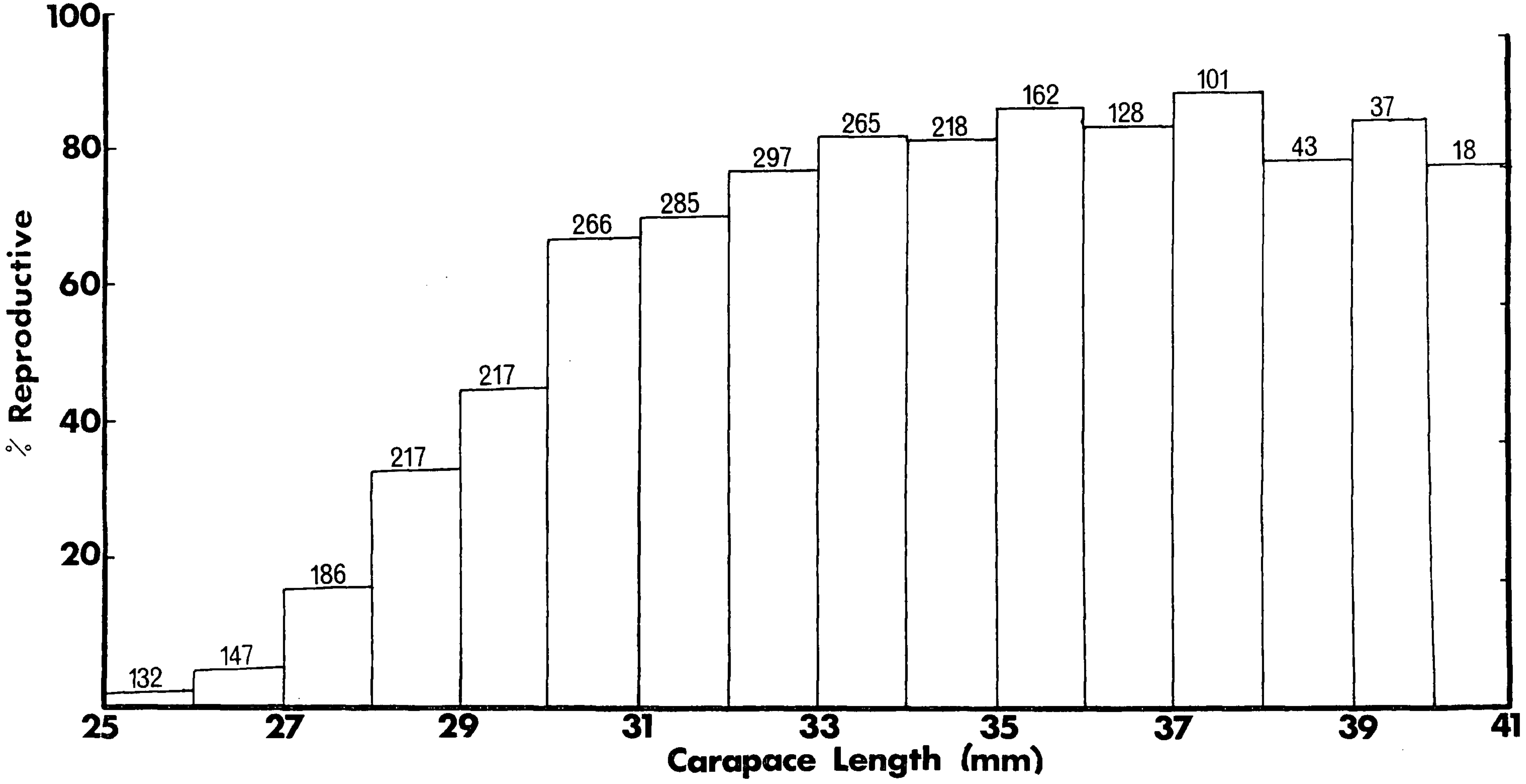
1976-77 47.21% x 3276 = 1547 reproductive females
1977-78 44.73% x 4265 = 1908 reproductive females
1978-79 42.45% x 2329 = 989 reproductive females

The proportion of reproductive females in each 1-mm carapace length size class during the three years of the study is given in Fig. 5.1. These data indicate that the proportion of reproductive females reaches a plateau at approximately 33 mm carapace length and thereafter remains at 80-90%. The smallest breeding female had a carapace length of 25 mm.

5.3 FECUNDITY

No berried females were taken from the field site in order not to disturb the dynamics of the study population. Consequently, few such females were available to determine the relationship between body size and number of pleopod eggs (few berried females were caught by trapping at other sites because of their trap-shyness). However, the equation $y = 4.235x - 75.125$ ($n=21$) was obtained, where y = number of eggs and x = carapace length. The largest number of eggs counted was 113 on a female of 37.0 mm carapace length, and larger individuals in the study population almost certainly bore more: Thomas & Ingle (1971) recorded 130 eggs on a female of 42 mm carapace length. The number of eggs typically varied from 40-80 in Northumbria. Throughout the study females were occasionally found with far fewer eggs than would be expected for their size (e.g. 7.2.9). In some cases individual eggs were

Fig. 5.1 The proportions of reproductive females in 1-mm carapace length size classes 1977-79. (Numbers are sample sizes)



seen to be lighter in colour than normal, probably because of fungal infection or sterility, and it is believed that such eggs are eventually lost. Other females were found carrying a small number of apparently healthy eggs. One such individual recaptured on 24 April 1979 was carrying ten eggs, while the number had fallen to six on 3 May 1979. The reason for the loss of such apparently healthy eggs is uncertain, long experience in the field having shown that losses because of handling are negligible.

5.4 POTENTIAL RECRUITMENT

The mean carapace length of reproductive females collected in the sampling programme was 33.4 ± 0.19 mm in 1977 (n=205), 32.9 ± 0.12 mm in 1978 (n=605) and 33.0 ± 0.14 mm in 1979 (n=457). From the equation given in 5.3 and the estimated numbers of reproductive females in each year (5.2) the potential recruitment to the population was estimated as follows:

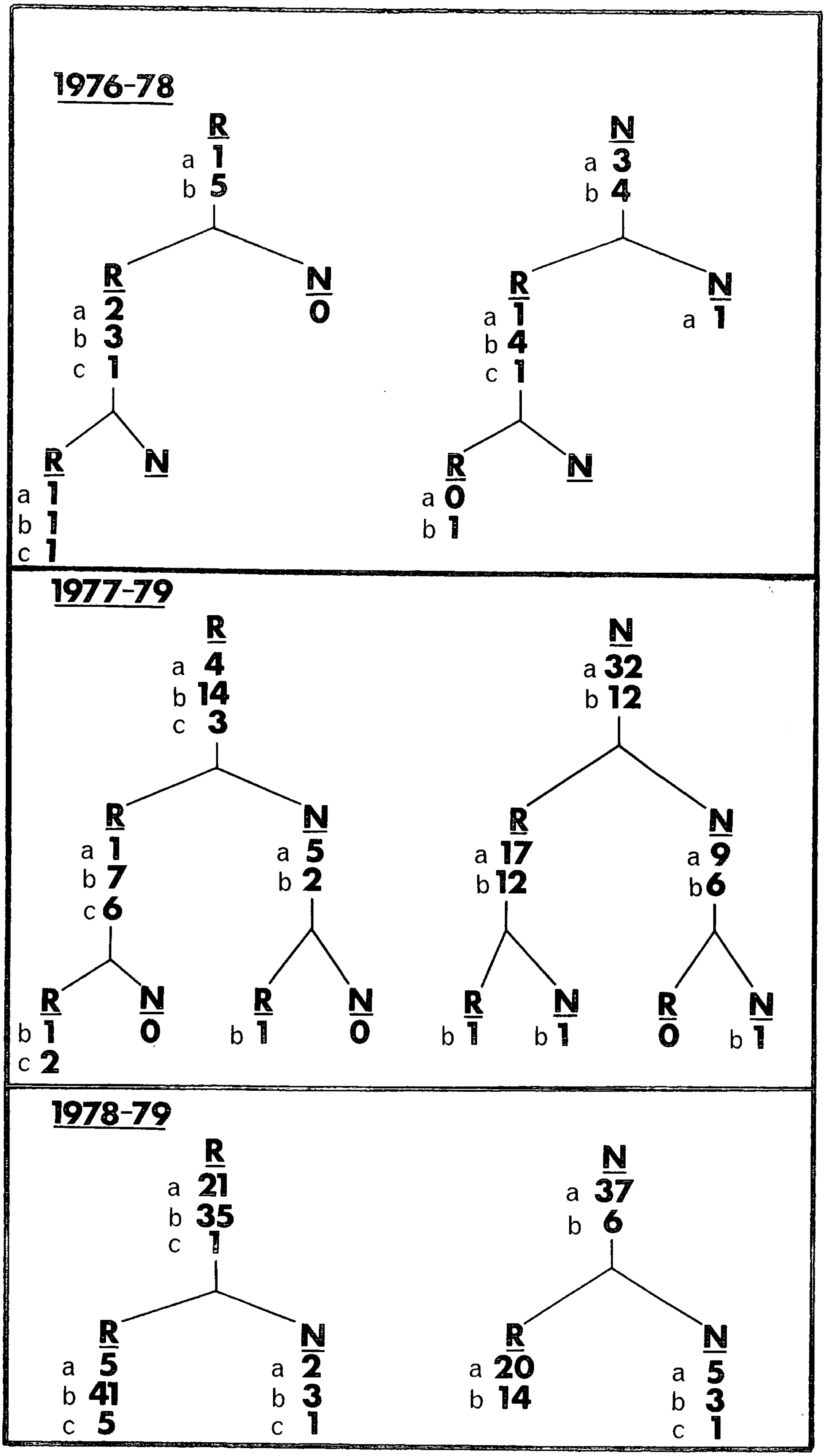
Number of eggs produced in 1976-77 1547 x 66 = 102 102
" " " " " 1977-78 1908 x 64 = 122 112
" " " " " 1978-79 989 x 65 = 64 285

The much lower figure for 1978-79 is a reflection of the smaller estimated population size in 1978 (3.5).

5.5 REPRODUCTIVE HISTORIES

The strong relationship between body size and the probability of being reproductive is described in 5.2 and Fig. 5.1. However, it is possible that other factors, such as previous reproductive history, are also important in determining reproductive status. The validity of this view can be tested only by following the reproductive histories of individually marked females over periods of at least two years. The high recapture rates achieved during this study made it possible to ascertain the reproductive status of 178 females in two or three successive years. These data are presented in Fig. 5.2. It can be seen that in each case a very high proportion of reproductive females was reproductive again the following year (e.g. 51 out of 57 in 1979). A somewhat smaller proportion of those females which did not breed in any one year did so in the next

Fig. 5.2 Reproductive histories of individual female crayfish.
R - reproductive. N - nonreproductive.
a - <32mm CL b - 32-37mm CL c - >37mm CL



(e.g. 29 out of 44 in 1977-78 and 34 out of 43 in 1978-79). The data indicate that it is rare for a female of reproductive size to go through more than two years without breeding: of the eleven females recaptured in three successive years, only one did not breed at all during that time. The relationship between size and propensity to breed indicated in Fig. 5.1 is supported by the data of Fig. 5.2, in which there is a tendency for the smallest size class to have a lower proportion of reproductive females in any given year.

5.6 DISCUSSION

An increase in the proportion of reproductive females with size similar to that reported here has been described for *Pacifastacus leniusculus* (Abrahamsson & Goldman 1970), for *Astacus astacus* (Abrahamsson 1972) and for *Austropotamobius pallipes* (Brown 1979). It therefore appears to be a feature common to crayfish with life histories similar to that of *A. pallipes*.

The size of the smallest reproductive female of this study population (25 mm carapace length) compares with a figure of 27 mm for *A. pallipes* in a Kent population (Thomas & Ingle 1971) and 28.3 mm in Ireland (Moriarty 1973), although both of these populations were sampled much less intensively and the latter by trapping only. The much higher proportion (96%) of females larger than 27 mm carapace length which was reproductive in the population studied by Thomas & Ingle (1971) contrasts markedly with the present study in which 44.80% of females larger than 25.0 mm carapace length were reproductive (5.2) and with the figure of 38.61% given by Brown (1979). While the causes of these differences are unknown they may reflect differential sampling of the population as well as a temperature effect (see below).

Clearly, it is important to have precise information not only on the relationship between size and reproductive frequency but also on that between size and number of eggs produced if accurate estimations of potential recruitment are to be made. Brown (1979) gave the relationship between number of eggs produced (y) and carapace length (x) as $y = 7.87x - 207.17$ for *A. pallipes* in Northumbria in 1974-76. This contrasts with the relationship presented earlier (5.3). In particular, it underestimates the contribution to potential recruitment made by the smaller reproductive females. For a female of 33.0 mm carapace length (the mean size of all reproductive females recaptured during the present study) the relationship given in 5.3 estimates that 65 eggs are produced. The equation given by Brown (1979) estimates only 53 eggs. This may partially explain why his maximum estimate of potential recruitment was some 47 000, less than half of that estimated in this study for the years 1977 and 1978 (5.4).

The loss of eggs after the initial attachment to the abdomen has been reported by Brown (1979) for *A. pallipes* in Northumbria: 4% of females known to have been berried were recaptured before the time of egg hatching having lost all their eggs. Partial or total loss of the egg complement was known or suspected to have happened in certain marked females during the present study (e.g. 5.3, 6.2.8).

Kossakowski (1975) found that some 33% of female *Orconectes limosus* in Poland did not reproduce in a given year and earlier (1971) suggested that females may reproduce only in alternate years. Similarly, Abrahamsson (1973) reported that *Astacus astacus* females breed each year in certain waters of northern Germany but only every second year in waters with lower food availability. The data of Figs. 5.1-5.2 do not exclude the possibility that breeding in alternate years may be a characteristic of a small proportion of mature females in the study population of *Austropotamobius pallipes*. Others, however, display a distinct tendency to reproduce in each year, while comparatively few fail to breed in successive years.

The factors controlling the frequency of reproduction by females have not been positively identified, but may be surmised. If, as seems probable, water temperatures are important (albeit indirectly), then the general tendency for a greater proportion of larger females to be reproductively active (Figs. 5.1-5.2) may be explained by their relatively higher ability to withstand lower temperatures and the associated stresses, which may be nutritional and physiological. Abrahamsson (1972) recognised the importance of water temperatures in Swedish populations of *Astacus astacus*: reproduction was found to be confined to those waters where temperatures averaged 15^{0}C or more for at least three months, although survival and growth were possible in colder waters. The same worker also found that the proportions of reproductive females of *Astacus astacus* were greater in populations inhabiting warmer waters. Furthermore, the frequency of reproduction of females of more than 100 mm in length (i.e. about 50 mm carapace length) was little influenced by water temperatures. It would appear, therefore, that the limiting effect of water temperature is exerted on the smaller females: from Fig. 5.2, the nonreproductive females tend to be of the smaller size classes. Where this limiting effect is removed the reproductive cycle may lose its regularity, e.g. Lowery & Mendes (1977) found that the normally seasonally breeding *Procambarus clarkii* reproduced all year round when introduced to the warm waters of Lake Naivasha, Kenya.

Another reason for the larger proportion of reproductively active females in the larger size classes is the progressively diminishing cost to the individual of reproduction with age: Table 4.9 indicates that the growth rates of large reproductive and nonreproductive females are very similar, whereas in smaller size classes reproductive individuals have significantly slower growth rates. Thus, in the terms of Gadgil & Bossert (1970), it becomes more advantageous (or less disadvantageous) to breed with increasing age.

As a consequence of the complexity of the relationships between female size, fecundity and probability of reproduction, it is essential to have a detailed knowledge of each in order to make an accurate assessment of potential recruitment. As can be seen from the above discussion, however, the practical difficulties of obtaining adequate data on each have limited most workers to a treatment of separate aspects of the problem.

Chapter Six

THE INCIDENCE OF *THELOHANIA CONTEJEANI* AND ITS EFFECT ON THE GROWTH OF *AUSTROPOTAMOBIUS PALLIPES*

6.1 INTRODUCTION

The microsporidian endoparasite *Thelohania contejeani* Henneguy (Microsporidia: Nosematidae) has been present in the study population of *A. pallipes* for at least twelve years (Cossins & Bowler 1974). The full time course of the infection is unknown as identification of *Thelohania* in the field is not possible until infection is at an advanced stage, when the spores of the parasite cause the entire abdominal musculature of the host to become an opaque white. Infected crayfish are commonly more sluggish than normal because of the progressive invasion of muscle fibres by the parasite. The full life cycle of *Thelohania* is also unknown, but is generally summarised in the manner of Johnson (1977), i.e. schizogony and sporulation in the host followed by the release of spores and infection of other individuals by an unknown route. This route is widely believed to be that of cannibalism (Cossins & Bowler 1974; Quilter 1976; Mazylis 1979).

6.2 METHODS

The low incidence of the parasite (see below) prevented the accurate estimation of the size of the infected subpopulation of crayfish by Jolly's method as recapture rates were too low. The incidence of the parasite was therefore estimated from sample compositions.

The recording of growth data in the field and the calculation of growth rates of crayfish infected by *Thelohania* were carried out according to the methods given in 3.2 and 4.2.

6.3 RESULTS

6.3.1 Incidence of *Thelohania contejeani*

Table 6.1 presents the incidence of crayfish with visible infections

Table 6.1

The incidence of the parasite *Thelohania contejeani* 1977-79

	ADULT MALES			ADULT FEMALES			ALL ADULTS		
	Diseased	Normal	% Diseased	Diseased	Normal	% Diseased	Diseased	Normal	% Diseased
Before 17 June	100	2642	3.79	152	2948	5.16	252	5590	4.51
18 June-30 Sept	154	4067	3.79	193	3954	4.88	347	8021	4.33
1 Oct-30 Dec	54	1002	5.39	55	1203	4.57	109	2205	4.94
TOTALS	308	7711	3.99	400	8105	4.94	708	15816	4.48

of the parasite at three times of year: prior to the growth season (before 17 June), during the growth season (18 June - 30 September) and after the growth season (after 30 September). The overall incidence in the adult subpopulation was 4.48% (n=15 816) and 1.31% (n=12 797) in the juvenile subpopulation, giving a figure for the entire population of 3.21%. The incidence of *Thelohania* among adult females (some 5%) was slightly greater than among adult males (4%). There is no clear trend in the incidence of infection of either sex throughout the year (Table 6.1).

6.3.2 The effect of *Thelohania* on the growth of *A. pallipes*

The effect of infection by *Thelohania* on the growth of *A. pallipes* is presented in Table 6.2, which compares the growth of the adult male, nonreproductive female and reproductive female subpopulations affected by *Thelohania* with those of healthy crayfish matched to within ± 0.5 mm carapace length. As the number of infected crayfish for which growth data were obtained was relatively small and as the effect of pairing infected crayfish with healthy crayfish for carapace length was to exclude some data, no distinction is made between moult periods in Table 6.2 in order to produce reasonably large subgroups for statistical testing. The sole significant difference to emerge from this analysis is between the moult increments of diseased and healthy nonreproductive females, the latter being significantly larger ($P<0.05$). Although no other significant differences are in evidence there is a clear tendency among nonreproductive females and adult males for both the absolute moult increment and the percentage moult increment to be larger in healthy crayfish. In the case of reproductive females the growth statistics of healthy and infected crayfish are very similar. The depression of crayfish growth rates by *Thelohania* can also be seen in Fig. 4.21, in which the instantaneous growth rates of infected individuals are generally below the mean for the population as a whole.

Table 6.3 contains details of the growth of individually marked crayfish infected by *Thelohania contejeani*. From the ratios of the actual / estimated maximum increments (4.3.5) it can be seen that the effect of the parasite on crayfish may vary greatly. In general, however, *Thelohania* causes a marked depression of growth similar to that of crayfish regenerating a major chela (Table 4.8, Fig. 4.21).

Table 6.2

The effect of infection by *Thelohania contejeani* upon the absolute (MI) and percentage (PCMI) moult increments of crayfish matched to within ± 0.5 mm CL in each subpopulation

	Infected by *Thelohania*			Disease-Free		
	MI (mm) ± SE	PCMI ± SE	N	MI (mm) ± SE	PCMI ± SE	N
Adult Males (>22 mm CL)	2.3 ± 0.12	7.8 ± 0.55	26	2.6 ± 0.15	9.0 ± 0.63	26
Nonreproductive Females (>22 mm CL)	2.1 ± 0.17	7.3 ± 0.72	18	2.5 ± 0.13	8.7 ± 0.61	18
Reproductive Females	1.9 ± 0.19	5.7 ± 0.61	14	1.8 ± 0.18	5.5 ± 0.51	14

Table 6.3

Growth of individual crayfish infected by *Thelohania contejeani*

Number	Carapace Length (mm)	Number of Moults	Number of Moults possible	Actual Growth Increment (mm)	Calculated Growth Increment (mm)	Estimated Max. Growth Increment (mm)	Actual/ Calculated Increment (%)	Actual/ Estimated Maximum Increment (%)
(A) MALES								
4222	22.5	2	3	3.5	5.33	8.24	65.7	42.5
4210	23.5	2	3	6.7	5.38	8.24	124.5	81.3
4542	28.2	2	2	4.2	5.66	5.66	74.2	74.2
6335	28.7	1	2	2.2	2.87	5.62	76.7	39.2
5195	35.8	1	1	2.2	2.95	2.95	74.6	74.6
4997	41.5	1	1	2.3	2.19	2.19	105.0	105.0
(B) FEMALES								
6460	24.7	3	3	7.4	7.58	7.58	97.6	97.6
5225	28.6	1	2	2.4	2.45	4.45	98.0	53.9
4352	31.6	1	2	2.2	1.91	4.13	115.2	53.3
5454	35.2	1	1	1.8	2.05	2.05	87.8	87.8
4888	38.6	1	1	2.6	2.25	2.25	115.6	115.6

6.4 DISCUSSION

The presence of *Thelohania contejeani* in crayfish populations has been reported by several workers. Kudo (1924) and Schaperclaus (1954) referred to economically important outbreaks of the infection in Europe. Vey & Vago (1973) and Cossins (1974) reported incidences of some 10% in populations of *Austropotamobius pallipes* in France and England respectively, while Quilter (1976) reported similar levels in a New Zealand population of *Paranephrops zealandicus*. Mazylis (1979) recorded levels of 0.7-3.7% in Lithuanian populations of *Astacus astacus*, levels very similar to those of the present study (6.3.2). Brown (1979) consistently estimated the incidence of *Thelohania* at the site of this study during 1974-76 at 6-8%. This higher figure is probably the result of samples consisting almost entirely of adult crayfish and may also have been caused by a lower sampling intensity, at which slow-moving parasitised crayfish were over-represented in samples. The thorough sampling of all sub-populations during the present study ensured that this did not occur.

Fluctuations in the incidence of *Thelohania* throughout the year (Table 6.1) were not sufficiently large to suggest that there was any significant change. However, on the basis of data obtained from numerous recaptures of diseased crayfish the following series of events may be proposed as being typical of the time course of the infection. It is known that the disease can not be identified in the field until it is at an advanced stage (6.1). It therefore seems reasonable to assume that the parasite requires one full growth season to reach that stage, sporulation occurring rapidly in the warm summer water temperatures. Many marked individuals are known to have survived for more than a year after the identification of the disease in the field. It therefore seems probable that the time course of the infection is at least two years and it may be that most crayfish mortality caused by *Thelohania* occurs in the winter following the second full growth season of the parasite in the host.

Bowler & Brown (1977) described the reduction of growth increments in adult male *A. pallipes* infected by *Thelohania*. Table 6.2 clearly displays the same trend, although only in the case of nonreproductive females is the difference between healthy and infected crayfish significant. It is of interest that the small increment at the first post-reproductive moult of females is not further reduced by the effects of *Thelohania*. This fact suggests that the cost of reproduction alone to the individual female is so high as to depress growth to such a level that it can be little affected further by the effects of the parasite. Mazylis (1979) reported that female *Astacus astacus* infected by *Thelohania* did not lay eggs when fertilised by healthy males, whereas fifteen *Austropotamobius pallipes* females infected by *Thelohania* and carrying eggs were captured during the course of this study.

Although eventually fatal (Kudo 1924), the disease is not considered to be a major cause of mortality in the study population of *A. pallipes* because of its low incidence and the fact that marked infected individuals are known to have survived for more than a year. If, as is widely believed, cannibalism is the main pathway of infection, then the greater proportion of infected adults compared to juveniles (6.3.1) may simply reflect the larger number of cannibalistic opportunities experienced by older animals. The presence of the parasite at comparable levels for at least twelve years (Cossins & Bowler 1974) suggests that *Thelohania* is a parasite well adapted to its crayfish host and that an equilibrium exists between the two. It appears unlikely that *Thelohania* is responsible for large fluctuations in the size of populations of *Austropotamobius pallipes* as suggested by Duffield (1933) and Pixell-Goodrich (1956).

Chapter Seven

INDIVIDUAL HISTORIES

7.1 INTRODUCTION

The biology of *Austropotamobius pallipes* has been discussed in detail in Chapter 2, followed by the results of an investigation of the dynamics, growth and reproduction of the study population (Chapters 3,4,5). Many of the data presented on each aspect of the population biology are mean values for particular subpopulations or size classes. In particular, the detailed analysis of growth data was done in this way. It is clear from these analyses that there are marked differences in the regularity and frequency of moulting and reproduction and in the size of the growth increment between different subpopulations. Such analyses provide invaluable information on life history patterns and the extent of the variation in each factor in the population of this study, as well as permitting comparisons with data from other populations. The data which were collected, however, were a series of observations and measurements on individual crayfish. Much variation in the factors mentioned above was, by definition, detectable only over a long period. The marking system used (3.2.1) enabled the identification of individuals through at least two moults. Many crayfish which were recaptured before the original mark had been lost were remarked, thereby extending greatly the period over which they could be identified. Multiple recaptures of such individuals enabled their life histories to be followed in detail. The ten histories set out below were obtained from such multiple recaptures and give a valuable insight into the variety of patterns displayed by individuals in the study population.

7.2 INDIVIDUAL HISTORIES

7.2.1 Number 10

This male crayfish was one of the first marked by Brown (1979) in a previous population study at this site. On 8 October 1973 it had a carapace length (CL) of 34.0 mm. It was not recaptured until 28 June 1975, having moulted once in 1974 and attained a CL of 36.9 mm, a percentage moult increment (PCMI) of 8.53%. It was caught again on 15 August 1975, having moulted once to a size of 39.8 mm CL (PCMI = 7.86%). Further recaptures on 18 August and 28 October 1975 and on 27 June 1976 showed that no further moulting had occurred in 1975. By 15 October 1976 one more moult had taken place. At the final recapture date (27 May 1977) this male measured 42.5 mm CL, a PCMI of 6.78%. It had therefore moulted once in each of three growth seasons in accordance with the low moult frequency of large individuals indicated in Table 4.5.

7.2.2 Number 3622

Number 3622, a female, was first captured on 30 May 1976 when it was carrying eggs at a carapace length of 35.2 mm. On 12 August 1977 it was carrying hatched young, having attained a size of 36.6 mm CL. This increment, a PCMI of only 3.98%, was therefore the result of a single post-reproductive moult after the hatching of eggs in 1976. The increment at the first post-reproductive moult is characteristically small (4.3.2, 4.3.3). This female was last recaptured on 23 May 1978 at a size of 38.8 mm CL. This increment was again the result of a single post-reproductive moult after the release of hatchlings in 1977. The PCMI was again low (6.01%). The white colour of the abdominal musculature at this last recapture revealed the presence of the parasite *Thelohania contejeani* (Chapter 6) and is a good example of the progressive nature of the infection as it had not been visible on previous recapture dates.

7.2.3 Number 3623

This male was first recorded at a size of 36.8 mm CL on 30 May 1976. The same measurement was recorded at recapture on 13 June 1976. By 17 June 1977 its size had increased to 39.7 mm CL (PCMI = 7.88%). Since no moulting was known to occur before 14 June in any year (2.5), this increment was certainly the result of a single moult in 1976. Further recaptures were made on 3 July and 18 July 1979, when no further growth had occurred. This large male had therefore moulted only once in three complete growth seasons.

7.2.4 Number 3692

This individual, a male of 38.9 mm CL, was first captured on 11 June 1976. More than three years later, on 9 August 1979, positive identification was still possible as only one moult had occurred during the intervening period, increasing the size to 41.1 mm CL (PCMI = 5.66%). Table 4.5 includes details of other large crayfish which were known not to have moulted in a particular year.

7.2.5 Number 3837

At first capture on 13 June 1976 this female was berried and had a carapace length of 35.6 mm. The next recapture occurred on 12 August 1977, when it was carrying hatched young and measured 37.4 mm CL. This increment, a PCMI of only 5.06%, was the result of a small post-reproductive moult in 1976. The last recapture of this female occurred on 15 June 1978, when it was recorded as carrying eggs for the third year in succession (see 5.5 and Fig. 5.2 for typical reproductive histories of females). Its carapace length on this occasion had increased to 39.4 mm (PCMI = 5.35%), the result of a post-reproductive moult in 1977.

7.2.6 Number 4066

Number 4066, a female, was first recorded at 34.4 mm CL on 31 August 1976. Since its size was unchanged on 26 October 1976, this crayfish had omitted to moult during the second major moult period of that year. On 17 May 1978 it was berried and its size had increased to 36.0 mm CL. The small size of this increment (PCMI = 4.35%) is characteristic of a post-reproductive moult and suggests that this female was berried in 1976-77. Its size had increased to 37.7 mm CL on 20 September 1978, the result of a single post-reproductive moult (PCMI = 2.72%). At subsequent recaptures on 24 April and 18 July 1979 the size was unchanged, but this female was carrying eggs on these occasions. If, as seems probable, this female was berried in 1976-77, then this individual too reproduced in three successive years.

7.2.7 Number 5447

This male increased in size from 32.7 mm CL on 17 May 1978 to 35.3 mm CL on 3 July 1979, a PCMI of 7.95%. Since there is little chance that this male had moulted before 3 July in 1979 (see 2.5 for a discussion of moult periods), the increase was almost certainly the result of a single moult in 1978. On 30 August 1979 its size had grown to 38.2 mm CL, one more moult having occurred in the first major moult period of the year. From a knowledge of the moult frequencies of males in this size class it could be predicted that no further moult would occur in 1979 (4.3.5). Furthermore, this male was then at a size where it would become increasingly likely that no moult would occur in some complete growth seasons.

7.2.8 Number 5502

On 23 May 1978 this male crayfish had a carapace length of 23.0 mm. This increased to 26.0 mm by 24 July 1978 and to 28.7 mm by 20 September 1978. No further moult had occurred by the date of its last recapture, 17 April 1979. This male therefore completed two moults in 1978, one in each of the two major moult periods (2.5). The PCMIs of 13.04% and 10.38% are larger than those of the males discussed above, all of which were larger in size (see 4.3.4 and Fig. 4.2 for the inverse correlation between body size and PCMI).

7.2.9 Number 6170

This female (36.3 mm CL) was recorded as bearing eggs on 15 June 1978. Upon recapture on 3 July 1979 it was again found to be carrying eggs and its size had increased to 37.2 mm CL. In addition, infection by *Thelohania* was then visible in the abdominal musculature and this may have played a part in reducing the PCMI of this single post-reproductive moult to 2.48% (6.3.2). The number of eggs carried on this last occasion was only five. Since the expected number of eggs for a female of this size is 82 (see 5.3 for the relationship between body size and fecundity) it is clear that most had been lost overwinter. Whether the infection by *Thelohania* played any part in this it is not possible to determine. This female was one of fifteen individuals which were known to have been berried while being infected by *Thelohania*, a condition which Mazylis (1979) states does not occur in *Astacus astacus*.

7.2.10 Number 6642

This male crayfish was first marked as a juvenile of 18.4 mm CL on 27 June 1978. By 24 July 1978 a single moult had increased this to 20.2 mm CL (PCMI = 9.78%). A further moult occurred between this date and 20 September 1978, when the size was recorded as 22.4 mm CL (PCMI = 10.89%). The next recapture occurred on 22 October 1978, by which time the size had reached 24.5 mm CL (PCMI = 9.38%). This increase was therefore the result of a moult which occurred after 20 September, which is beyond the end of the growth season as determined by Brown (1979). In fact, twenty-seven individuals are known to have moulted after 16 September during the three-year study and it is therefore clear that crayfish may moult at this latitude much later than previously believed (2.5). No change in the size of this male had occurred on its seventh capture on 7 June 1979, but a single moult increased its size to 27.7 mm CL (PCMI = 13.06%) by 18 July 1979. A further moult, taking the size to 30.0 mm CL (PCMI = 8.30%) had occurred by 2 October 1979. This very fast-growing individual had therefore moulted three times in 1978 and twice in 1979 (once in each major moult period) and had increased in size from 18.4 mm CL to 30.0 mm CL in two growth seasons.

7.3 DISCUSSION

The individuals of which details are presented above were selected as examples of the various types of life histories which have been identified in previous chapters. Since the probability of recapturing any one crayfish was low, few individuals were caught as often as those listed above. Many more, however, were caught on two or three occasions (3.2.3), sufficiently often to enable records of moult increments and timings, reproduction and parasitism to be made. Few workers have been able to achieve a sufficiently high recapture rate to follow the histories of particular individuals in this manner. Hopkins (1967b) was able to determine moult timing and frequency of thirty-seven *Paranephrops planifrons* only by removing selected marked individuals to a small side stream. Other workers, e.g. Hopkins (1966); Momot (1967b), Mason (1975); Pratten (1980), have relied on size-frequency plots or the growth of captive animals. Both methods have their limitations (4.1). Mean values for moult increments and moult frequencies as well as the timing of life history events may readily be derived from data from populations containing individuals widely disparate in these factors. The value of detailed histories of individuals lies in the evidence which they provide that the values derived from such data are representative of most members of the population.

Chapter Eight

GENERAL DISCUSSION

Austropotamobius pallipes has a special status as Britain's only native freshwater crayfish. It is widespread and locally common throughout England, Wales and Ireland but is reported to be absent from Scotland (Jay & Holdich 1977). Although *A. pallipes* is also found in western Europe, the most important and widespread continental crayfish is *Astacus astacus*. While *A. astacus* has long been in great demand as a food item, *Austropotamobius pallipes* has not received the same attention in Britain. However, there is evidence to show that the species has been well known as a food item in Britain at least for several centuries (Fuller 1702; Harrison 1878; Cameron 1917; Thomas & Ingle 1971) and it is still consumed in some areas (Holdich, Jay & Goddard 1978). The species has never had the economic importance which *Astacus astacus* has in mainland Europe, however, and scientific reports of its biology have been few until recent interest in the commercial exploitation of crayfish in Britain (Richards & Fuke 1977; Fuke 1978).

Knowledge of the biology of *Austropotamobius pallipes* has, despite the early contribution of Huxley (1880), remained largely anecdotal, so much so that unsubstantiated and incorrect statements about life style and distribution are a feature of the current state of understanding. The works of Thomas & Ingle (1971) and Brown (1979) have been the most important reports on the subject to date, the latter including some details of population dynamics. Holdich, Jay & Goddard (1978) have summarised the status of the species in the British Isles, while Pratten (1980) studied growth in a population of *A. pallipes* in southern England. There remained a need, however, for a comprehensive study of the biology of a natural population of the species which it is hoped will be satisfied by this work.

The problems of studying the biology of a natural population of decapod Crustacea are discussed in detail in 4.1 with particular reference to the study of growth. The intensity of sampling, the density of the study population and the ability to drain the aqueduct during sampling were important advantages in overcoming these difficulties and in ensuring a high recapture rate.

A detailed account of the timing of the events in the life cycle of the Northumbrian crayfish population which was studied is given in 2.5. The principal events are mating and egg laying, which occur in late October and November. Eggs are carried by reproductive females overwinter, during which period the entire population becomes generally inactive. Egg hatching occurs in late July and early August, followed by the release of the hatchlings from the parent some two weeks later. Moulting in adult crayfish is generally fairly regular: most adults moult twice annually, once in late June-July and once in September. Juveniles, however, moult more frequently and reproductive females omit the first moult of the year while carrying eggs. The timing of these events was found to be very predictable from year to year during the course of this study and the previous work of Brown (1979) at this site and is probably regulated by water temperature. Crayfish activity was strongly related to temperature, being greatest during the summer months and much reduced in winter. No moulting took place when water temperature was below 9°C.

One aspect of the biology of *A. pallipes* which has been particularly neglected is that of its diet. References to the species simply as a scavenger, e.g. Huxley (1880); Howes (1962), Maitland (1978), are probably oversimplified. Whilst laboratory feeding experiments show a clear preference for animal material (2.3.4), examination of stomach contents from the field reveals that the bulk of the diet is plant material, almost certainly because of the general inability of *A. pallipes* to catch any but the most sluggish of benthic invertebrates. Evidence of selectivity of feeding on certain aquatic macrophytes was also found. In addition, *A. pallipes* is highly cannibalistic and it is clear that much work remains to be done to establish the trophic status of the species (Reynolds 1979).

The practical problems associated with a study of the dynamics of a large dense population of mobile animals (3.1, 3.2, 3.3, 4.1) are great, and no comprehensive study of the dynamics of a natural population of *A. pallipes* exists. The size of the population of the present study was estimated to be some 15 000 (3.5) during 1977 and most of 1978, a size comparable to that estimated by Brown (1979) during earlier work at the same site. There was a marked fall in numbers in late 1978 which was caused by a partial failure of recruitment (5.4). There was little evidence of recovery of former numbers in 1979.

This study is the first to show the regular occurrence of moult-associated mortality in *A. pallipes* (3.5). It is probable that this phenomenon is common in many crayfish species but has been little reported as most population studies have concentrated on year-to-year rather than seasonal changes in dynamics. In this respect the present study is particularly important, as the three principal periods of mortality in each year have been clearly identified (see below). The more frequent moulting of juveniles (4.3.5) results in mortality in this subpopulation being less concentrated in the two major moult periods of adults and extending over a greater part of the growth season. This lack of synchrony between the moulting cycles of adults and juveniles causes differences in the patterns of recruitment to the two subpopulations. Recruitment to the adult subpopulation is limited to the two major moult periods, whereas recruitment into the catchable size classes of juveniles (i.e. >13 mm CL) occurred throughout the growth season (3.5).

The principal mechanisms regulating population size appear to be moult-associated mortality, most probably acting through cannibalism, and overwinter mortality, most probably caused by low temperature and/or nutritional stress. The former is intense, of relatively short duration and is detectable during the major moult periods, while the latter presumably operates at a much lower weekly rate over a much longer period (some thirty weeks in Northumbria). Juvenile mortality during the growth season, i.e. moult-associated mortality, is generally much greater than that of adults. It may well be that the lack of synchrony of juvenile moulting with the adult cycle is an important reason for this, as recently moulted juveniles will more often be exposed to cannibalistic adults. In this respect the synchrony of moulting in mature crayfish may be regarded as an adaptation to reduce the risk of being cannibalised.

The problems of studying growth in a large natural population are similar to those of studying dynamics (3.1-3.3). Differences in moult frequency and size of moult increments between and within the sexes compounded by the effects of regenerating limbs, parasites and the omission of moults by reproductive females cause the modes of size-frequency plots (each mode representing a year class) to become obscured rapidly. This is a serious limitation in the study of growth in a long-lived species such as *A. pallipes*. The system of individual marking (3.2.1) and the intensive mark-recapture programme used to overcome the problems of studying dynamics also satisfied the requirements of a study of growth, and a large number of data on growth were collected as a result of the multiple recapture of marked individuals over long periods.

Males were shown to have faster growth rates than females after the size of sexual maturity (4.3.7). The more frequent moulting of juveniles is reflected in their higher instantaneous growth rates. Instantaneous growth rates decline markedly with increasing body size in both sexes (4.3.7). A detailed analysis of the variations in the size of growth increments is presented in 4.3.2-4.3.4. A notable feature is the significantly smaller increment of females at the first post-reproductive moult (4.3.2, Fig. 4.2), which may be interpreted as the energetic cost of reproduction. A similar reduction in growth increment is caused by the parasite *Thelohania contejeani* (6.3.2) and by the regeneration of a major chela (4.3.6). From a detailed knowledge of moult frequencies and the size of moult increments throughout the lifespan the relationship between size and age was calculated (Fig. 4.22) and the longevity of *A. pallipes* estimated to be at least eleven years (4.3.8).

From the growth data which were collected during the course of this study (Chapter 4), it is evident that a large number of different patterns of growth occur in the field, e.g. Fig. 4.22. However, few crayfish approached fulfilment of their potential growth (4.3.5) and there is evidence to show that the population contains 'fast' and 'slow' growers.

Of particular importance to any population study is an estimate of the number of breeding females. The system of individually marking crayfish (3.2.1) was invaluable in this respect in that it allowed an assessment of reproductive frequency in marked females to be made (Fig. 5.2). The factors affecting the frequency of reproduction are not clearly understood, but it is evident that it is related to size, albeit probably indirectly (5.2, 5.6). Greater proportions of large females were reproductive in any one year and large females also showed a distinctly stronger tendency to reproduce in successive years (5.2, 5.5, Figs. 5.1-5.2), and there was a positive correlation between body size and number of eggs produced (5.3).

An interesting feature of the study population is the presence of the microsporidian endoparasite *Thelohania contejeani*, which is known to have been present for at least twelve years (Cossins & Bowler 1974). The overall incidence of *Thelohania* was 3.21%. Whilst the full life cycle and mode of transmission of the parasite remain unknown, the higher incidence among adults (6.3.1) supports the view that transmission is by cannibalism of infected crayfish (adults will have experienced a larger number of cannibalistic encounters than juveniles). *Thelohania* was also shown to cause a decline in growth rates of infected crayfish by reducing the size of the moult increment (6.3.2). Despite the reports of Kudo (1924) and Schaperclaus (1954) of economically important outbreaks of the parasite in crayfish populations, there is no evidence that *Thelohania* in England is anything other than a parasite well adapted to its host existing at a low and stable level. The earlier higher estimates of the incidence of *Thelohania* by Brown (1979) at the site of this study may be explained by a less thorough sampling technique. There is no evidence to support the suggestion of Duffield (1933) and Pixell-Goodrich (1956) that *Thelohania* is responsible for large fluctuations in numbers of *A. pallipes*.

The basis of this study was the multiple recapture of marked individuals. While Chapters 2 and 4 note the variations in the timing of events of the life history and in individual growth patterns, it is evident from the collected data that most individuals display a strong tendency to conform to the population mean in both respects (7.2.1-7.2.10): there was no evidence of differential timing of events or of polymodality in the size of growth increments within subpopulations.

The termination of this study at the end of the 1979 growth season is particularly regrettable in that further work offered the opportunity to study several interesting aspects of the dynamics of the population in the light of the fall in numbers in late 1978. Several qualitative predictions could have been tested by investigation in the field. Among these were that reproductive success, growth rates and juvenile survival would increase in a density-dependent manner. Momot & Gowing (1977b) reported larger numbers of attached eggs per breeding female in populations of the North American crayfish *Orconectes virilis* when density was low and also (1977a) identified increased survival and egg production as the major response of a population of *O. virilis* to exploitation. If, as seems probable, the transmission of the parasite *Thelohania contejeani* in the study population is by cannibalism, then the incidence of infection might be expected to decline in the smaller crayfish population as the number of potentially cannibalistic encounters would fall. These factors are almost certainly density-dependent. Overwinter mortality, however, is likely to be density-independent because of the probable nature of its action (3.6) and as such would be expected to be unaffected in its magnitude by a smaller population size. The lower numbers in the population would have presented a particularly valuable opportunity to resolve these questions as a much greater sampling intensity would have been possible in a continuation of the study.

It is clear that water temperature is a very important factor affecting the timing of the major events in the life cycle of *A. pallipes*, i.e. the stages of moulting and reproduction (2.5, 2.6), and plays a large part in determining growth rates (4.4). In every case where comparative data are available the timing of events in the life cycle is later and growth rates are slower in the Northumbrian population of this study than those of populations of *A. pallipes* inhabiting warmer waters. Thus the population in southern England studied by Pratten (1980) had generally faster growth rates than the population of the present study, which is close to the northern limit of the species range in Britain. It appears that this difference is attributable to a shortening of the intermoult period to as little as fifty days, compared to some ninety days in Northumbria (2.5, 4.3.5). The dates given by Thomas & Ingle (1971) and Holdich, Jay & Goddard (1978) for reproduction and moulting in more southerly populations of *A. pallipes* are also earlier than those in Northumbria.

It is known from the present study (2.2.1) and from earlier work at the same site (Brown 1979) that the water temperature regime is very predictable from year to year, and this is probably the principal reason for the consistent timing of the reproductive and moulting cycles of this population of *A. pallipes*. Although there is some evidence that photoperiod can influence the moulting and reproductive cycles of crayfish (Stephens 1952, 1955; Aiken 1969), it is not believed to be important in this respect in the population of this study, upon which the limiting effect of the temperature regime is so pronounced. Furthermore, laboratory-maintained *A. pallipes* at 15°C moult regularly approximately every ninety days in a variety of light : dark regimes (Bowler, pers. comm.). Ninety days is also the approximate intermoult period in the field (2.5), where summer water temperatures are near 15°C for some weeks.

As well as the cycles of moulting and reproduction, an annual cycle of population size can be discerned. There is a midsummer peak in numbers (3.5) as recruitment occurs during the growth season. Thereafter numbers remain relatively stable until the end of the growth season, probably because recruitment is effectively balanced by moult-associated mortality. Up to 50% of the population is lost overwinter (3.5), possibly because of the stresses associated with low temperatures. The population becomes more active as water temperatures rise in April and May and numbers remain relatively constant until the beginning of the growth season in June, followed once more by the characteristic midsummer peak in numbers. Cooper (1965), describing the annual population cycle of the freshwater amphipod *Hyalella azteca*, the details of which are in many respects analogous to that of *A. pallipes*, stated 'the numerical maxima in the summer .... and the numerical minima in the winter is felt to be the most characteristic pattern for natural invertebrate populations'.

In populations of the crayfish *Orconectes virilis* Momot & Gowing (1977b) considered that most of the year-to-year differences in biomass were produced by changes in mortality rather than in growth rates. Figs. 3.3-3.6 indicate the highly variable nature of mortality rates throughout the year in the study population of *A. pallipes* and it has been shown (3.5, 3.6) that these seasonal changes are reflected in changes of the total population size. The fall in numbers in late 1978 was caused by a general failure of recruitment: the reason for this is unknown. In common with the present study, Momot & Gowing (1977a, 1977b, 1977c) considered predation to be unimportant as a population control mechanism in populations of *Orconectes virilis*. Although several potential predators of *A. pallipes* were present in the study area (2.3.3), there was no evidence of any significant predation on crayfish in the aqueduct.

In a species such as *A. pallipes*, where most mortality falls on juveniles (3.5, Table A4), selection would be expected to favour rapid growth through this stage at the expense of early maturity (Wilbur, Tinkle & Collins 1974). Such rapid growth among juveniles relative to adults has been demonstrated (4.3.7) and maturity is delayed until the fourth or fifth year of life.

In common with many other decapods, crayfish show a marked decline of moult frequency with age (4.3.5, Fig. 4.22). Juveniles have at least three moults annually, while larger adults commonly moult once each year and some large individuals do not moult at all in some growth seasons (4.3.5, 7.2.3). It is likely that this progressive decline in moult frequency is adaptive in that it balances the advantages of attaining the adult size as quickly as possible against the risks of moult-associated mortality. Since chela size is strongly related to body size (Bowler & Brown 1977) and the chelae play an important rôle in mating (Ingle & Thomas 1974), it may well be that the reason for the continuing decline of moult frequency among the larger size classes of *A. pallipes* is the progressively diminishing return, in terms of increased reproductive success, which accrues for further increases in body size. The greater proportions of reproductive females in the larger size classes of the population (5.2) and also reported by Abrahamsson (1972), Abrahamsson & Goldman (1970) and Brown (1979) are predicted from the theory of Gadgil & Bossert (1970), which states that reproductive effort should increase with age in an iteroparous species since the cost is a continuously decreasing function of age.

The sexual dimorphism which is a feature of many different crayfish species does not become apparent in *A. pallipes* until after the time of sexual maturity, i.e. the fourth or fifth year of life. Apart from the primary sexual differences (Thomas 1977) there is conspicuous dimorphism in secondary sexual characters, principally in the larger major chelae of the male and the broader abdomen of the female. The latter may be presumed to be related to the shelter of eggs and young (Stein, Murphy & Magnuson 1977), but the function of large chelae in the male is not clearly understood. Ingle & Thomas (1974) have described the rôle of the male's chelae in copulation. The male overturns the female and holds her in position by interlocking the chelae in order to achieve insemination. The importance of the chelae is emphasised by the fact that chela regeneration is rapid and is made at the expense of body growth in general (4.3.6, Fig. 4.21). Further to this, Stein (1976) has shown in the American species *Orconectes propinquus* that between males of comparable size a male with large chelae is more likely to mate with a female than a male with small chelae. In consequence, a large body size (and therefore large chela size) is probably an advantage to males in that they are more likely to mate successfully. It may also confer the advantage of being able to mate with larger females, thereby benefiting from the positive correlation between female body size and fecundity (5.3).

From the growth data which were collected in this study it is clear that a wide range of patterns of growth (i.e. variations in moult frequency and size of moult increment) exist in the population, e.g. Fig. 4.22. It would seem a rewarding line of research to attempt to evaluate these growth strategies for each sex in terms of egg potential. This could be done by a laboratory investigation into the effect of body size on the selection of mating partners (see above) and by a detailed field study of the risks of moult-associated mortality. From a knowledge of moult frequency and the size of moult increments (Chapter 4) an assessment could be made of the probability of survival of an individual following a particular growth pattern and an estimate of its reproductive success could be obtained from the laboratory experiments. Such an approach has been discussed by Calow (1978), who emphasised the complexity of the relationship between current reproductive effort and residual reproductive value of the individual. Where residual reproductive value is relatively insensitive to current reproductive effort, iteroparity becomes more feasible as a life history strategy. Although *A. pallipes* is iteroparous it is clear that the effect of current reproductive effort on residual reproductive value is appreciable: the small size of the post-reproductive moult increment of females and the omission of a moult while carrying eggs has a direct effect on future fecundity because of the relationship between body size and egg production (5.3). Furthermore, few small crayfish tend to be berried in successive years (5.5, Fig. 5.2).

Comparable literature on crayfish life styles is devoted largely to North American cambarinid species, which differ from *A. pallipes* in several important respects. Most significantly, their longevity is much less (often only 2-3 years) and because they tend to inhabit less predictable environments they generally exhibit greater plasticity in their responses to environmental changes, e.g. *Orconectes immunis* and *Procambarus clarkii* burrow in response to drying of their habitat (Fielder 1972; Avault 1973), while Lowery & Mendes (1977) found that *P. clarkii* bred throughout the year when introduced to the constantly warm waters of Lake Naivasha, Kenya. A characteristic of the cambarinids is the summer moulting of males to a breeding form (the 'first form') and their return at the next moult to the 'second form'. No such specialised moult occurs in the native European crayfish. In addition, the greater longevity of the European species means that they have much more complex population structures, e.g. Cukerzis (1975) recognised eight year classes in a population of *Astacus astacus*. In the population of this study the estimated lifespan of *Austropotamobius pallipes* was at least eleven years (4.3.8). In this population at least, *A. pallipes* can be said to exhibit many of the characteristics of a so-called K-selected species in that it has a long generation time, a large size, a low level of dispersal, iteroparity, (presumably) a high level of intraspecific competition and a relatively constant population size (Southwood 1977; Stearns 1977). Murphy (1968) has stated that 'evolutionary pressure for long life, later maturity and many reproductions may be generated either by an environment in which density-independent factors cause wide variation in the survival of pre-reproductives or by an environment that is biologically inhospitable to pre-reproductives because of intense competition with the reproductives'. The environment of *A. pallipes* in Northumbria may be deemed as being of the second type: heavy mortality of juveniles during the growth season has been demonstrated (3.5, 3.6). Their greater moult frequency and lack of synchronisation of moulting with adults is probably an important factor in this.

The estimates of annual production obtained in this study may have important implications for prospective crayfish culturists, of whom there is an increasing number in Britain. While the faster growth rate and greater reproductive potential of *Pacifastacus leniusculus*, the species most widely favoured for introduction and culture, is well documented, e.g. Abrahamsson & Goldman (1970), this may not be so important in natural or semi-natural stocks consisting of fully structured populations which are cropped annually and allowed to replace the shortfall by natural recruitment or in populations cultured at high densities, continually cropped and artificially stocked with juveniles. It is significant that the economically important crayfisheries of Europe have long been based on the controlled exploitation of natural stocks rather than cultured populations. Although there has as yet been little interest in exploiting *A. pallipes* in Britain, natural stocks may well be capable of satisfying much of the demand for crayfish (Goddard & Holdich 1979).

The need for a comprehensive study of the biology of a natural population of *A. pallipes* has become more pressing in view of the increasing awareness of the important rôle of crayfish in freshwater systems. Their very large biomass and the complexity of their trophic relationships, particularly as feeders on detritus and macrophytes, enables them to make significant contributions to keeping waterways open (Abrahamsson 1966; Dean 1969; Taub 1972; Rickett 1974; Magnuson *et al.* 1975) and in recycling nutrients from detritus (Lorman & Magnuson 1978; Momot, Gowing & Jones 1978). The importance of detritivores in aquatic production is now recognised, e.g. Minshall (1967); Kaushik & Hynes (1971); Jonasson (1975); Cummins & Klug (1979). Indeed, Rundquist, Gall & Goldman (1977) have described an experimental system using crayfish as efficient converters of nutrients from enriched waters to animal protein. The continuing spread of the crayfish plague, a fungal disease fatal to crayfish, in mainland Europe and the increasing interest in importing exotic crayfish into Britain for commercial purposes makes a study of the native species even more pertinent. There is no evidence that the plague fungus has reached Britain (Behrendt 1979; Bowler 1979), but the unrestricted importing of plague-resistant but potentially plague-carrying species leaves the highly susceptible native species vulnerable. The catastrophic effects of the plague fungus on economically important stocks of *Astacus astacus* in Europe and the attempts to replace them by introducing the plague-resistant American species *Pacifastacus leniusculus* have been well documented (Abrahamsson 1973; Hastein & Gladhaug 1973, 1975; Herfort-Michieli 1973; Kossakowski 1973; Schweng 1973; Spitzy 1973; Westman 1973; Brinck 1975; Geelen 1975). Some examples of the harmful effects of ill-considered introductions of animals to new environments are given by Paine & Zaret (1975). More particularly, Dean (1969); Abrahamsson & Goldman (1970); Abrahamsson (1973); Magnuson *et al.* (1975); Unestam (1975); Lowery & Mendes (1977) and Unestam *et al.*(1977) have warned of the dangers of the indiscriminate introduction of new crayfish species.

This study provides the most detailed account available of the population biology of Britain's only native freshwater crayfish. It is evident that some of the features described, particularly the timing and frequency of moulting and reproduction, may be uniquely related to the field site. However, these features provide a basis for comparison with other populations of *Austropotamobius pallipes* and with other crayfish species. It is therefore desirable that similar studies on other populations be carried out, for only in this way can the factors regulating crayfish population biology be established with certainty. How far the principles underlying the patterns of growth and population dynamics of *A. pallipes* can be extended to other populations and species of crayfish is not known. However, it is likely that these patterns will prove to be generally applicable to the univoltine astacine crayfish. Many of the available comparative data, however, are based on studies of the Cambarinae, which differ in some important respects (see above). The increasingly apparent functional importance of crayfish in aquatic systems makes such studies even more appropriate.

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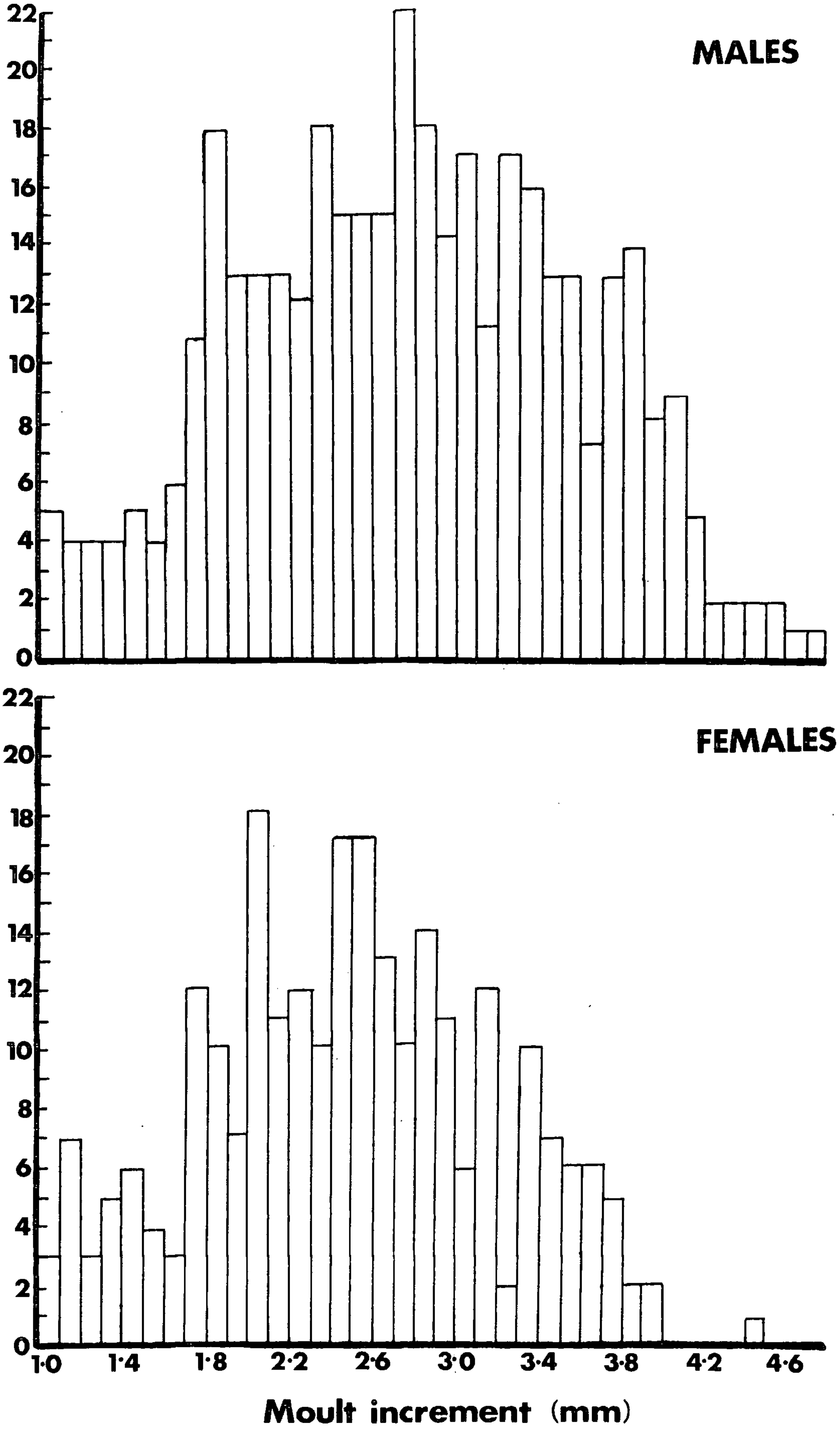
APPENDIX

Fig. A1 The distributions of the moult increments used in the analysis of growth.



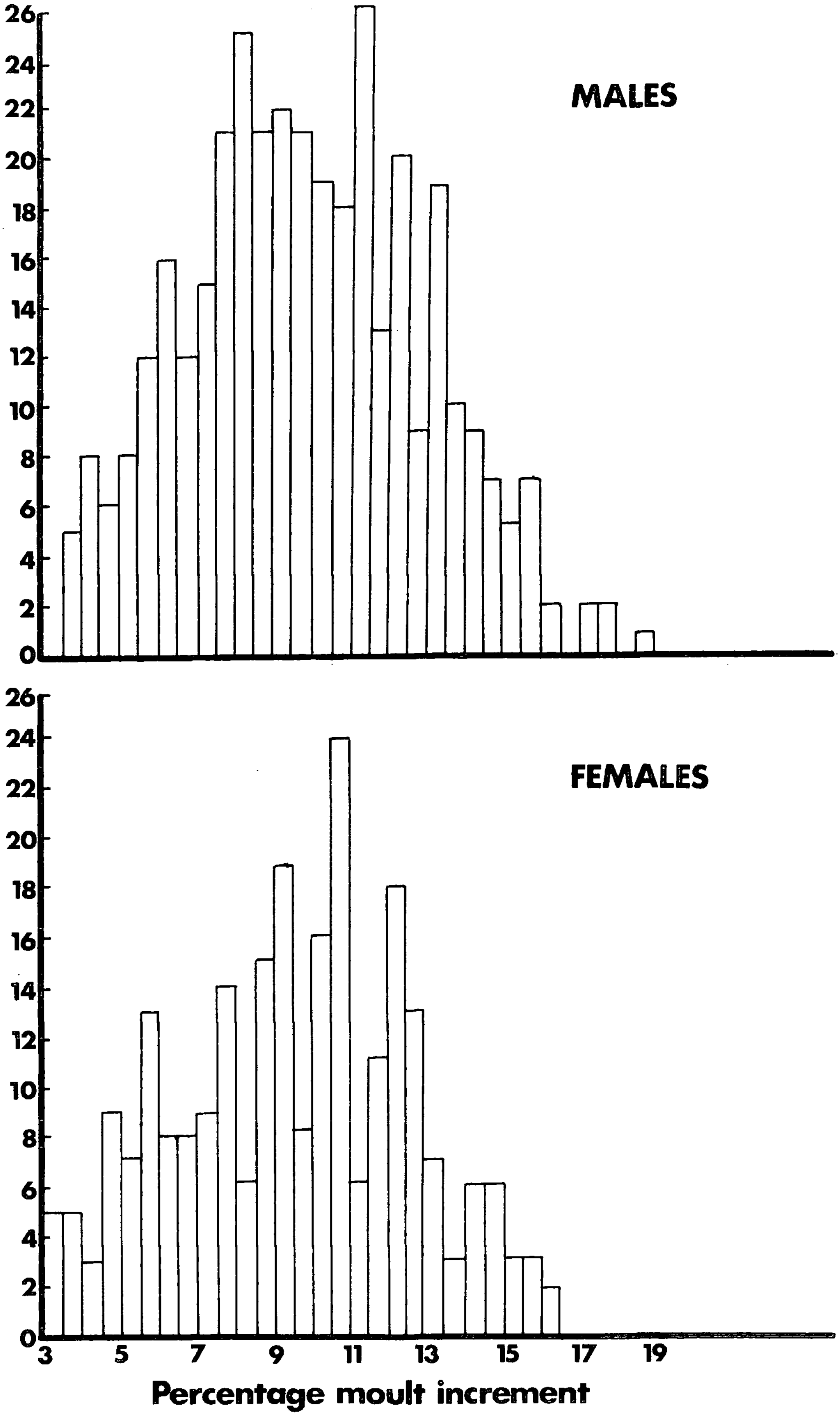


Fig. A2 The distributions of the percentage moult increments used in the analysis of growth.

Table A1

Population estimates for the total population

Significantly less than 1 : * $P<0.05$ ** $P<0.01$ *** $P<0.001$ † Significantly greater than 0

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
12 May 1977	778	14079 ± 2874	0.735 ± 0.126*	-1493 ± 1691	13.40	-697
		15430 ± 2675	0.782 ± 0.098	-1338 ± 2226	10.87	-624
		Mean = 14755	Mean = 0.759	Mean = -1416	Mean = 12.14	Mean = -661
27 May 1977	674	9663 ± 1499	1.273 ± 0.234	-1215 ± 1644		-405
		9845 ± 1721	1.354 ± 0.182	491 ± 2350		164
		9745 ± 1686				
		Mean = 9751	Mean = 1.314	Mean = -362		Mean = -121
17 Jun 1977	703	11088 ± 2063				
		13685 ± 2160	0.652 ± 0.093***	12904 ± 2427†	5.12	1585
12 Aug 1977	1841	21821 ± 2936	0.799 ± 0.144	-1683 ± 2029	4.39	-337
			0.847 ± 0.064*		3.28	
			Mean = 0.823		Mean = 3.84	
16 Sep 1977	1132	15751 ± 2905				
		15877 ± 1826	0.720 ± 0.064***	4551 ± 1941†	11.41	1677
		Mean = 15814				
5 Oct 1977	732	15978 ± 2002	1.067 ± 0.091	11974 ± 2807†		374
			1.086 ± 0.067			
			Mean = 1.077			

continued ...

Table A1 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
17 May 1978	1815	29028 ± 2794	1.006 ± 0.092	-6018 ± 2460†		-7021
		27733 ± 4063	0.914 ± 0.048	-4156 ± 3734	9.95	-4849
			0.919 ± 0.045		9.37	
		Mean = 28381	Mean = 0.946	Mean = -5087	Mean = 9.66	Mean =-5935
23 May 1978	2231	23188 ± 2143				
		21194 ± 1586	0.773 ± 0.044***	-556 ± 1230	7.55	-169
		20666 ± 1720	0.747 ± 0.037***	90 ± 1364	8.49	27
		Mean = 21683	Mean = 0.760	Mean = -233	Mean = 8.02	Mean = -71
15 Jun 1978	1677	15819 ± 1062	1.054 ± 0.079	-143 ± 951		-83
		15530 ± 1031	1.081 ± 0.065	-159 ± 1044		-93
		Mean = 15675	Mean = 1.068	Mean = -151		Mean = -88
27 Jun 1978	1914	16526 ± 1226	0.603 ± 0.067***	2019 ± 575†	12.30	523
		16633 ± 1066	0.612 ± 0.043***	2116 ± 593†	11.95	549
		Mean = 16580	Mean = 0.608	Mean = 2068	Mean = 12.13	Mean = 536
24 Jul 1978	1706	11979 ± 1241	0.639 ± 0.047***		16.82	
		12295 ± 1267	0.675 ± 0.057***	1267 ± 536†	14.94	522
		Mean = 12137	Mean = 0.657		Mean = 15.88	
10 Aug 1978	911	9564 ± 816	0.458 ± 0.040***	34 ± 271	12.47	6
		9013 ± 1001	0.540 ± 0.038***	516 ± 577	9.98	88
		Mean = 9289	Mean = 0.499	Mean = 275	Mean = 11.23	Mean = 47

continued ...

<u>Table A1</u> (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
20 Sep 1978	802	4418 ± 323	0.940 ± 0.085	2779 ± 434†	6.03	2779
		5386 ± 469	0.965 ± 0.064	2554 ± 629†	3.50	2554
		Mean = 4902	Mean = 0.953	Mean = 2667	Mean = 4.77	Mean = 2667
27 Sep 1978	851	6931 ± 634	0.753 ± 0.086**	1448 ± 422†	7.64	405
		7752 ± 666	0.879 ± 0.062*	1398 ± 622†	3.54	391
		Mean = 7342	Mean = 0.816	Mean = 1423	Mean = 5.59	Mean = 398
22 Oct 1978	1010	6665 ± 709	0.975 ± 0.059		2.47	
		8211 ± 643	0.947 ± 0.080	286 ± 575	5.27	286
		Mean = 7438	Mean = 0.961		Mean = 3.87	
29 Oct 1978	802	8063 ± 715	0.612 ± 0.064***	-805 ± 328†	1.92	-32
		7175 ± 743	0.653 ± 0.044***	74 ± 575	1.67	3
		Mean = 7619	Mean = 0.633	Mean = -366	Mean = 1.80	Mean = -15
24 Apr 1979	435	4128 ± 404	0.979 ± 0.135	934 ± 395†	1.61	727
		4760 ± 481	0.911 ± 0.068	831 ± 623	7.03	646
			0.880 ± 0.061*		9.44	
		Mean = 4445	Mean = 0.923	Mean = 883	Mean = 6.03	Mean = 687
3 May 1979	298	4975 ± 662	1.064 ± 0.183	6 ± 405		2
		4057 ± 755	1.147 ± 0.080	-25 ± 898		-6
		5163 ± 598	1.151 ± 0.088	-564 ± 642		-141
		Mean = 4732	Mean = 1.121	Mean = -194		Mean = -48

continued ...

Table A1 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
31 May 1979	663	5297 ± 747				
		4627 ± 474	1.212 ± 0.097	5895 ± 1304†		5895
		5376 ± 417	1.207 ± 0.104	4711 ± 930†		4711
		Mean = 5100	Mean = 1.210	Mean = 5303		Mean = 5303
7 Jun 1979	612	11200 ± 1153	0.789 ± 0.074**	-1094 ± 761	6.18	-295
		11502 ± 1414	0.795 ± 0.068**	-1136 ± 1084	6.00	-306
		Mean = 11351	Mean = 0.792	Mean = -1115	Mean = 6.09	Mean = -301
3 Jul 1979	689	7740 ± 682	1.205 ± 0.119	5287 ± 998†		2467
		8004 ± 776	1.167 ± 0.100	4038 ± 1077†		1884
		Mean = 7872	Mean = 1.186	Mean = 4663		Mean = 2176
18 Jul 1979	1101	14612 ± 1393	0.755 ± 0.099*	-2358 ± 727†	8.54	-750
		13378 ± 1237	0.764 ± 0.075**	-1243 ± 755	8.22	-396
		Mean = 13995	Mean = 0.760	Mean = -1801	Mean = 8.33	Mean = -573
9 Aug 1979	1082	8678 ± 1045				
		8975 ± 839	0.707 ± 0.095**	505 ± 462	10.90	168
		Mean = 8827				
30 Aug 1979	675	6853 ± 879	0.508 ± 0.091***	1390 ± 386†	13.38	295
2 Oct 1979	679	4871 ± 768				

Table A2

Population estimates for the adult male subpopulation

Significantly less than 1 : * P<0.05 ** P<0.01 *** P<0.001 † Significantly greater than 0

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
12 May 1977	235	6653 ± 2159	0.691 ± 0.198	-804 ± 1302	15.83	-375
		5961 ± 2330	0.801 ± 0.15	-783 ± 1905	9.86	-365
		Mean = 6307	Mean = 0.746	Mean = -794	Mean =	Mean = -370
					12.85	
27 May 1977	231	3793 ± 1115				
		3987 ± 1083	1.778 ± 0.554	-3301 ± 1889		-1100
		4756 ± 1623	1.713 ± 0.390	-3579 ± 2732		-1193
		Mean = 4179	Mean = 1.746	Mean = -3440		Mean = -1147
17 Jun 1977	232	3788 ± 1194				
		4568 ± 1203	0.525 ± 0.130***	2323 ± 797†	7.61	285
		Mean = 4178				
12 Aug 1977	539	4721 ± 1008	0.802 ± 0.237	449 ± 748	4.31	90
			0.941 ± 0.118		1.22	
			Mean = 0.872		Mean =	
					2.77	
16 Sep 1977	334	4235 ± 1284				
		5131 ± 1044	0.827 ± 0.146	-1236 ± 858	6.76	-455
		Mean = 4683				
5 Oct 1977	158	3005 ± 649	0.905 ± 0.167	1754 ± 713†	0.31	55
			0.792 ± 0.101*		0.73	
			Mean = 0.849		Mean =	
					0.52	

continued ...

Table A2 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
17 May 1978	333	4472 ± 789	1.095 ± 0.203	187 ± 743		218
		3474 ± 1028	1.148 ± 0.113	1400 ± 1336		1633
			1.171 ± 0.103			
		Mean = 3973	Mean = 1.143	Mean = 794		Mean = 926
23 May 1978	506	5082 ± 922				
		5386 ± 869	0.738 ± 0.074***	-277 ± 652	8.85	-84
		5618 ± 1014	0.813 ± 0.074*	-452 ± 859	6.10	-138
		Mean = 5362	Mean = 0.776	Mean = -365	Mean = 7.48	Mean = -111
15 Jun 1978	424	3695 ± 471	0.929 ± 0.108	-407 ± 393	4.19	-237
		4117 ± 536	0.839 ± 0.082*	-584 ± 418	9.73	-341
		Mean = 3906	Mean = 0.884	Mean = -496	Mean = 6.96	Mean = -289
27 Jun 1978	410	3027 ± 367	0.949 ± 0.171	369 ± 268	1.35	96
		2869 ± 309	0.870 ± 0.096	433 ± 242	3.55	112
		Mean = 2948	Mean = 0.910	Mean = 401	Mean = 2.45	Mean = 104
24 Jul 1978	535	3240 ± 553	0.560 ± 0.062***		21.22	
		2928 ± 316	0.572 ± 0.075***	367 ± 182†	20.55	151
		Mean = 3084	Mean = 0.566		Mean = 20.89	
10 Aug 1978	278	2041 ± 270	0.642 ± 0.092***	321 ± 159†	7.28	55
		2185 ± 384	0.721 ± 0.079***	149 ± 299	5.43	25
		Mean = 2113	Mean = 0.682	Mean = 235	Mean = 6.36	Mean = 40

continued ...

Table A2 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
20 Sep 1978	262	1632 ± 218	0.793 ± 0.124	374 ± 172†	20.73	374
		1725 ± 240	0.847 ± 0.092	440 ± 254	15.26	440
		Mean = 1679	Mean = 0.820	Mean = 407	Mean = 18.00	Mean = 407
27 Sep 1978	239	1667 ± 256	0.915 ± 0.190	624 ± 236†	2.45	175
		1901 ± 261	0.944 ± 0.108	771 ± 313†	1.59	216
		Mean = 1784	Mean = 0.930	Mean = 698	Mean = 2.02	Mean = 196
22 Oct 1978	301	2150 ± 422	1.090 ± 0.096	-175 ± 303	4.47	-175
		2566 ± 341	0.955 ± 0.127			
		Mean = 2358	Mean = 1.023			
29 Oct 1978	234	2276 ± 323	0.660 ± 0.104**	-272 ± 160	1.63	-11
		2476 ± 455	0.626 ± 0.057***	-281 ± 305	1.84	-11
		Mean = 2376	Mean = 0.643	Mean = -277	Mean = 1.74	Mean = -11
24 Apr 1979	149	1229 ± 178	0.890 ± 0.166	69 ± 123	8.65	54
		1266 ± 186	1.051 ± 0.096	198 ± 268		154
			1.033 ± 0.091			
		Mean = 1248	Mean = 0.991	Mean = 134		Mean = 104
3 May 1979	119	1161 ± 199	1.079 ± 0.249	207 ± 138		52
		1526 ± 240	1.086 ± 0.106	-129 ± 251		-38
		2007 ± 651	0.999 ± 0.088	-891 ± 642	0.02	-223
		Mean = 1565	Mean = 1.055	Mean = -271		Mean = -70

continued ...

Table A2 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
31 May 1979	230	1460 ± 287				
		1529 ± 166	1.276 ± 0.158	735 ± 314†		735
		1114 ± 146	1.323 ± 0.149	1213 ± 422†		1213
		Mean = 1368	Mean = 1.300	Mean = 974		Mean = 974
7 Jun 1979	181	2686 ± 401	0.837 ± 0.118	66 ± 291	4.69	18
		2687 ± 470	0.866 ± 0.112	146 ± 422	3.81	39
		Mean = 2687	Mean = 0.852	Mean = 106	Mean = 4.25	Mean = 29
3 Jul 1979	226	2312 ± 300	0.963 ± 0.130	240 ± 241	1.76	112
		2472 ± 362	0.926 ± 0.111	32 ± 309	3.51	15
		Mean = 2392	Mean = 0.945	Mean = 136	Mean = 2.64	Mean = 64
18 Jul 1979	329	2466 ± 303	1.015 ± 0.197	-251 ± 199		-80
		2322 ± 281	1.019 ± 0.148	-18 ± 231		-6
		Mean = 2394	Mean = 1.017	Mean = -135		Mean = -43
9 Aug 1979	346	2253 ± 409				
		2347 ± 332	0.674 ± 0.144*	131 ± 156	12.32	44
		Mean = 2300				
30 Aug 1979	222	1713 ± 339	0.429 ± 0.123***	208 ± 104†	16.43	44
2 Oct 1979	190	943 ± 234				

Table A3

Population estimates for the adult female subpopulation

Significantly less than 1 = * $P<0.05$ ** $P<0.01$ *** $P<0.001$ † Significantly greater than 0

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% $WEEK^{-1}$)	WEEKLY RECRUITMENT
12 May 1977	318	4347 ± 983	0.647 ± 0.150*	-715 ± 529	18.41	-334
		4118 ± 1099	0.695 ± 0.119*	-895 ± 721	15.63	-418
		Mean = 4233	Mean = 0.671	Mean = -805	Mean = 17.02	Mean = -376
27 May 1977	259	2095 ± 483				
		1927 ± 403	1.142 ± 0.267	972 ± 515		324
		1967 ± 389	1.277 ± 0.210	1521 ± 742†		507
		Mean = 1996	Mean = 1.210	Mean = 1247		Mean = 416
17 Jun 1977	304	3218 ± 773				
		3982 ± 826	0.686 ± 0.119**	1484 ± 643†	4.52	182
		Mean = 3600				
12 Aug 1977	502	4217 ± 730	1.042 ± 0.260	-66 ± 645		-13
			1.076 ± 0.111			
			Mean = 1.059			
16 Sep 1977	432	4328 ± 1090				
		3957 ± 615	0.709 ± 0.090**	1562 ± 767†	11.88	575
		Mean = 4143				
5 Oct 1977	236	4369 ± 820	1.197 ± 0.165	287 ± 971		9
			0.991 ± 0.101		0.03	
			Mean = 1.094			

continued ...

Table A3 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
17 May 1978	418	5517 ± 823	0.932 ± 0.149	-595 ± 619	7.85	-694
		4442 ± 990	0.957 ± 0.076	-153 ± 960	5.01	-177
			0.941 ± 0.088		6.83	
		Mean = 4980	Mean = 0.943	Mean = -374	Mean = 6.56	Mean = -436
23 May 1978	496	4548 ± 695				
		4028 ± 537	0.795 ± 0.079**	213 ± 430	6.75	65
		4133 ± 628	0.734 ± 0.055***	306 ± 505	8.97	93
		Mean = 4236	Mean = 0.765	Mean = 260	Mean = 7.86	Mean = 79
15 Jun 1978	499	3416 ± 388	1.103 ± 0.144	680 ± 437		397
		3341 ± 359	1.167 ± 0.101	588 ± 485		343
		Mean = 3379	Mean = 1.135	Mean = 634		Mean = 370
27 Jun 1978	441	4445 ± 612	0.795 ± 0.162	-354 ± 322	5.77	-92
		4485 ± 492	0.766 ± 0.078**	-337 ± 324	6.67	-87
		Mean = 4465	Mean = 0.781	Mean = -346	Mean = 6.22	Mean = -90
24 Jul 1978	415	3182 ± 598	0.802 ± 0.079*		8.71	
		3099 ± 310	0.850 ± 0.102	356 ± 267	6.50	147
		Mean = 3141	Mean = 0.826		Mean = 7.61	
10 Aug 1978	269	2987 ± 371	0.590 ± 0.070***	-104 ± 152	8.62	-18
		2983 ± 569	0.724 ± 0.068***	-129 ± 415	5.36	-22
		Mean = 2985	Mean = 0.657	Mean = -117	Mean = 6.99	Mean = -20

continued ...

Table A3 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
20 Sep 1978	363	1658 ± 153	0.877 ± 0.102	668 ± 153†	12.34	668
		2030 ± 243	0.942 ± 0.081	605 ± 282†	5.77	605
		Mean = 1844	Mean = 0.910	Mean = 637	Mean = 9.06	Mean = 637
27 Sep 1978	365	2121 ± 245	0.730 ± 0.109*	376 ± 151†	8.45	105
		2518 ± 282	0.635 ± 0.056***	209 ± 183	11.96	59
		Mean = 2320	Mean = 0.683	Mean = 293	Mean = 10.21	Mean = 82
22 Oct 1978	374	1922 ± 269	0.831 ± 0.078*		16.86	
		1812 ± 174	1.097 ± 0.126	-290 ± 164		-290
		Mean = 1867	Mean = 0.964			
29 Oct 1978	245	1557 ± 186	0.642 ± 0.094***	102 ± 93	1.73	4
		1381 ± 198	0.768 ± 0.083**	609 ± 249†	1.04	24
		Mean = 1469	Mean = 0.705	Mean = 356	Mean = 1.39	Mean = 14
24 Apr 1979	187	1065 ± 138	3.424 ± 0.824	1202 ± 612†		935
		1670 ± 260	0.991 ± 0.119		0.72	
			1.058 ± 0.145	640 ± 469		498
		Mean = 1368	Mean = 1.824	Mean = 921		Mean = 717
3 May 1979	112	4590 ± 1128	0.391 ± 0.116***	-475 ± 236†	20.91	-118
		1729 ± 503	0.441 ± 0.116***	-17 ± 491	18.51	-4
		2406 ± 500	0.863 ± 0.120	-516 ± 378	3.61	-129
		Mean = 2908	Mean = 0.565	Mean = -336	Mean = 14.34	Mean = -84

continued ...

Table A3 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
31 May 1979	216	1362 ± 301				
		1611 ± 278	1.189 ± 0.153	1143 ± 555†		1143
		1561 ± 197	1.155 ± 0.162	994 ± 362†		994
		Mean = 1511	Mean = 1.172	Mean = 1069		Mean = 1069
7 Jun 1979	194	2797 ± 457	0.737 ± 0.115*	-316 ± 280	7.88	-85
		3059 ± 586	0.648 ± 0.087***	-311 ± 367	11.04	-84
		Mean = 2928	Mean = 0.693	Mean = -314	Mean = 9.46	Mean = -85
3 Jul 1979	171	1745 ± 259	1.540 ± 0.288	1134 ± 455†		529
		1669 ± 258	1.556 ± 0.227	682 ± 460		318
		Mean = 1707	Mean = 1.548	Mean = 908		Mean = 424
18 Jul 1979	246	3821 ± 699	0.642 ± 0.146*	-516 ± 274	13.15	-164
		3279 ± 537	0.716 ± 0.119*	-169 ± 298	10.08	-54
		Mean = 3550	Mean = 0.679	Mean = -343	Mean = 11.62	Mean = -109
9 Aug 1979	264	1937 ± 369				
		2179 ± 326	0.799 ± 0.155	-36 ± 189	7.22	-12
		Mean = 2058				
30 Aug 1979	216	1705 ± 308	0.569 ± 0.153**	174 ± 116	11.28	37
2 Oct 1979	224	1144 ± 273				

Table A4

Population estimates for the juvenile subpopulation

Significantly less than 1 = * P<0.05 ** P<0.01 *** P<0.001 † Significantly greater than 0

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
12 May 1977	224	5600 ± 2574	1.183 ± 0.591	1766 ± 3222		824
		4405 ± 2456	0.982 ± 0.379	4779 ± 4284	0.84	2230
			1.043 ± 0.426			
		Mean = 5003	Mean = 1.069	Mean = 3273		Mean = 1527
27 May 1977	214	8392 ± 4495	1.131 ± 0.930			
		9373 ± 4830	1.614 ± 1.080	-4212 ± 5312		-1404
		7847 ± 4345		-2648 ± 6338		-882
		Mean = 8537	Mean = 1.373	Mean = -3430		Mean = -1143
17 Jun 1977	203	6384 ± 5197				
		10015 ± 6902	0.166 ± 0.112***	12865 ± 7636	19.82	1580
		Mean = 8200				
12 Aug 1977	798	14522 ± 8200	0.806 ± 0.392	840 ± 6515	4.22	168
16 Sep 1977	366	12544 ± 6558				
17 May 1978	940		0.869 ± 0.068		15.06	
23 May 1978	1133	9545 ± 1145	0.821 ± 0.075*	-436 ± 956	5.82	-133
15 Jun 1978	681	7401 ± 822	0.951 ± 0.120	-55 ± 632	2.87	-32
27 Jun 1978	915	6986 ± 841	0.358 ± 0.053***	1199 ± 312†	23.36	311

continued ...

Table A4 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
24 Jul 1978	623	3702 ± 507	0.700 ± 0.150* 0.749 ± 0.159 Mean = 0.725	628 ± 351	13.67 11.21 Mean = 12.44	259
10 Aug 1978	308	3219 ± 689 3423 ± 863 Mean = 3321	0.272 ± 0.065*** 0.280 ± 0.061*** Mean = 0.276	281 ± 167 769 ± 407 Mean = 525	19.95 19.54 Mean = 19.75	48 131 Mean = 90
20 Sep 1978	160	1156 ± 242 1727 ± 453 Mean = 1442	1.196 ± 0.299 1.095 ± 0.213 Mean = 1.146	2690 ± 984† 1856 ± 966 Mean = 2273		2690 1856 Mean = 2273
27 Sep 1978	178	4071 ± 1175 3746 ± 1038 Mean = 3909	0.587 ± 0.164* 0.630 ± 0.117** Mean = 0.609	-548 ± 530 -572 ± 579 Mean = -560	13.84 12.15 Mean = 13.00	-153 -160 Mean = -157
22 Oct 1978	258	1843 ± 457 1786 ± 3291 Mean = 1815	0.913 ± 0.112 0.828 ± 0.153 Mean = 0.871	564 ± 318	8.70 17.19 Mean = 12.95	564
29 Oct 1978	234	2043 ± 410 2252 ± 496 Mean = 2148	0.611 ± 0.150** 1.070 ± 0.205 Mean = 0.841	-123 ± 228 -78 ± 678 Mean = -101	1.93	-5 -3 Mean = -4

continued ...

Table A4 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
24 Apr 1979	84	1125 ± 293	1.255 ± 0.480	856 ± 645		666
		2332 ± 653	0.521 ± 0.111***	25 ± 405	39.79	19
			0.490 ± 0.093***		42.55	
		Mean = 1729	Mean = 0.755	Mean = 441	Mean = 41.17	Mean = 343
3 May 1979	53	2268 ± 930	1.265 ± 0.598	-606 ± 754		-152
		1240 ± 353	1.777 ± 0.328	-214 ± 591		-54
		312 ± 116	1.930 ± 0.353	1228 ± 511†		31
		Mean = 1273	Mean = 1.657	Mean = 136		Mean = -58
31 May 1979	174	2262 ± 840	0.836 ± 0.158	3032 ± 1445†	16.42	3032
		1991 ± 372	0.946 ± 0.186	2776 ± 960†	5.43	2776
		1830 ± 535				
		Mean = 2028	Mean = 0.891	Mean = 2904	Mean = 10.93	Mean = 2904
7 Jun 1979	184	4658 ± 1102	0.771 ± 0.148	-1430 ± 714†	6.77	-385
		4561 ± 1503	0.878 ± 0.161	-1743 ± 1244	3.44	-469
		Mean = 4610	Mean = 0.825	Mean =-1587	Mean = 5.11	Mean = -427
3 Jul 1979	237	2161 ± 377	0.921 ± 0.180	2179 ± 629†	3.77	1017
		2262 ± 463	0.793 ± 0.145	1733 ± 607†	10.24	809
		Mean = 2212	Mean = 0.857	Mean = 1956	Mean = 7.01	Mean = 913

continued ...

Table A4 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
18 Jul 1979	318	4169 ± 823	0.657 ± 0.177	-771 ± 417	12.50	-245
		3528 ± 717	0.614 ± 0.120***	-401 ± 366	14.39	-128
		Mean = 3849	Mean = 0.636	Mean = -586	Mean = 13.45	Mean = -187
9 Aug 1979	310	1969 ± 498				
		1764 ± 339	1.088 ± 0.369	1082 ± 570		361
30 Aug 1979	157	3001 ± 1046	6.915 ± 7.240	26327 ± 28103		559
2 Oct 1979	205	47079 ± 48332				

Table A5

Population estimates for year 3+ males

*** Significantly less than 1 (P 0.001)   Significantly greater than 0

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
17 May 1978	37		0.441 ± 0.077***			
23 May 1978	301	1984 ± 448	0.771 ± 0.162	246 ± 374	7.62	75
15 Jun 1978	179	1776 ± 429	0.921 ± 0.377	182 ± 309	4.71	106
27 Jun 1978	236	1817 ± 719	0.183 ± 0.085***	1453 ± 750	35.60	377
24 Jul 1978	110	1786 ± 841	2.942 ± 3.042	-947 ± 2351		-390
10 Aug 1978	55	4307 ± 4535	0.044 ± 0.046***	46 ± 95	41.38	8
20 Sep 1978	29	235 ± 123	6.916 ± 7.195	20606 ± 30491		20 606
27 Sep 1978	24	22231 ± 31666	0.064 ± 0.066***	-1199 ± 1495	53.72	-336
22 Oct 1978	78	219 ± 108				

Table A6

Population estimates for year 3+ females

Significantly less than 1 = * P 0.05 *** P 0.001

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
17 May 1978	44		4.7151 ± 0.1789			
23 May 1978	351	2626 ± 674	1.195 ± 0.232	-93 ± 845		-28
15 Jun 1978	213	3045 ± 749	1.164 ± 0.351	-622 ± 660		-363
27 Jun 1978	224	2921 ± 838	0.197 ± 0.067***	-84 ± 90	34.36	-22
24 Jul 1978	232	492 ± 140	0.316 ± 0.133***	11 ± 29	37.75	5
10 Aug 1978	113	167 ± 66 1205 ± 402 Mean = 686	0.492 ± 0.261* 0.369 ± 0.099*** Mean = 0.431	1489 ± 1666 -33 ± 147 Mean = 728	11.39 15.64 Mean = 13.52	254 14 Mean = 134
20 Sep 1978	50	1571 ± 1681 412 ± 129 Mean = 992	2.215 ± 1.697 0.876 ± 0.202 Mean = 1.546	-1295 ± 3832 322 ± 193 Mean = -487	12.39	-1295 322 Mean = -487
27 Sep 1978	74	2184 ± 2142 682 ± 204 Mean = 1433	1.574 ± 1.556 0.915 ± 0.194 Mean = 1.245	-655 ± 2528 -14 ± 177 Mean = -335	2.46	-183 -392 Mean = -288
22 Oct 1978	107	2782 ± 2279 611 ± 140 Mean = 1697	0.872 ± 0.126 0.803 ± 0.202 Mean = 0.838	105 ± 126	12.83 19.75 Mean = 16.29	105

continued ...

Table A6 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
29 Oct 1978	67	595 ± 165	0.612 ± 0.179*	-77 ± 77	1.92	-3
		781 ± 276	1.119 ± 0.246	-375 ± 309		-15
		Mean = 688	Mean = 0.866	Mean = -226		Mean = -9
24 Apr 1979	41	287 ± 78	1.539 ± 0.763	150 ± 166		117
		499 ± 146	0.926 ± 0.293	5 ± 153	5.78	4
		Mean = 393	Mean = 1.233	Mean = 78		Mean = 61
3 May 1979	23	592 ± 304	1.106 ± 0.681	93 ± 192		23
		467 ± 172	1.020 ± 0.318	117 ± 157		29
		Mean = 530	Mean = 1.113	Mean = 155		Mean = 26
31 May 1979	65	748 ± 345	0.741 ± 0.184	398 ± 256	25.92	398
		593 ± 152	0.909 ± 0.241	377 ± 233	9.06	377
		Mean = 671	Mean = 0.825	Mean = 388	Mean = 17.49	Mean = 388
7 Jun 1979	62	916 ± 279	0.717 ± 0.183	-202 ± 160	8.58	-54
		1061 ± 266	0.853 ± 0.201	-110 ± 216	4.19	-30
		Mean = 989	Mean = 0.785	Mean = -156	Mean = 6.39	Mean = -42
3 Jul 1979	78	455 ± 102	1.384 ± 0.451	346 ± 186		161
		454 ± 124	0.965 ± 0.258	246 ± 157	1.67	115
		Mean = 455	Mean = 1.175	Mean = 296		Mean = 138

continued ...

Table A6 (continued)

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% WEEK^{-1})	WEEKLY RECRUITMENT
18 Jul 1979	92	976 ± 318	0.622 ± 0.278	63 ± 137	14.00	20
		684 ± 201	0.587 ± 0.171*	145 ± 134	15.58	46
		Mean = 830	Mean = 0.605	Mean = 104	Mean = 14.79	Mean = 33
9 Aug 1979	72	670 ± 268				
		546 ± 166	2.107 ± 1.098	72 ± 309		24
		Mean = 608				
30 Aug 1979	67	1223 ± 642	0.414 ± 0.280*	201 ± 218	17.06	43
2 Oct 1979	46	707 ± 395				

Table A7

Population estimates for year 2+ males

Significantly less than 1: * $P<0.05$ *** $P<0.001$ † significantly greater than 0

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% $WEEK^{-1}$)	WEEKLY RECRUITMENT
17 May 1978	378		0.869 ± 0.068		15.06	
23 May 1978	172	9545 ± 1145	0.821 ± 0.075*	-436 ± 956	5.82	-133
15 Jun 1978	119	7401 ± 822	0.951 ± 0.120	-55 ± 632	2.87	-32
27 Jun 1978	188	6986 ± 841	0.358 ± 0.053***	1199 ± 312†	23.36	311
24 Jul 1978	135	3702 ± 507	0.700 ± 0.150*	628 ± 351	13.67	259
10 Aug 1978	72	3219 ± 689	0.272 ± 0.065***	281 ± 167	19.95	48
20 Sep 1978	35	1156 ± 242	1.196 ± 0.299	2690 ± 984†		2690
27 Sep 1978	37	4071 ± 1175	0.587 ± 0.164*	-548 ± 530	13.84	153
22 Oct 1978	30	1843 ± 457				

Table A8

Population estimates for year 2+ females

Significantly less than 1: * $P<0.05$ ** $P<0.01$ *** $P<0.001$

DATE	N	POPULATION SIZE ± S.E.	SURVIVAL RATE ± S.E.	RECRUITMENT ± S.E.	MORTALITY (% $WEEK^{-1}$)	WEEKLY RECRUITMENT
17 May 1978	481		0.503 ± 0.112***		55.18	
23 May 1978	309	1816 ± 552	0.701 ± 0.184	94 ± 396	10.25	29
15 Jun 1978	170	1367 ± 409	0.690 ± 0.257	14 ± 221	19.46	8
27 Jun 1978	267	956 ± 337	0.413 ± 0.173***	1934 ± 1010	20.49	501
24 Jul 1978	146	2329 ± 1111	1.707 ± 1.290	-1094 ± 1770		-450
10 Aug 1978	68	2880 ± 2233	0.073 ± 0.057***	-72 ± 77	36.11	-12
20 Sep 1978	46	137 ± 66	4.660 ± 4.939	3049 ± 3758		3049
27 Sep 1978	43	3688 ± 4326	0.057 ± 0.061***	-129 ± 142	55.14	-36
22 Oct 1978	43	81 ± 46				