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A STUDY OF THE POPULATION BIOLOGY OF THE BRITISH FRESHWATER CRAYFISH *Austropotamobius pallipes* (Lereboullet)

by

Duncan J. Brown, B.Sc. (Dunelm)

Being a thesis submitted for the degree of
Doctor of Philosophy
of the University of Durham,
March 1979

Grey College,
University of Durham

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GLOSSARY

1. General abbreviations

C.L.	carapace length in mm. (see section 2.1)
Pre M.C.L.	premoult carapace length in mm.
Post M.C.L.	postmoult carapace length in mm.
M.I.	moult increment in mm. (Post M.C.L. - Pre M.C.L.)
% M.I.	percentage moult increment (M.I./ Pre M.C.L. x 100)
PCF	percentage cumulative frequency (Cassie 1954)
0+	age during the first year of life; thus 1+ and 2+ are the ages during the second and third years of life, and so on.
CV	calorific value of whole crayfish
$\hat{P}a$	estimated annual production for the whole population of A. pallipes in the aqueduct (Winberg 1971)
$\bar{B}$	estimated mean annual biomass (Winberg 1971)

2. General statistical notation (see section 2.4)

c.t.	contingency table
d.f.	degrees of freedom
Y.C.	Yates correction
χ^2	chi squared
t	Students t
SE	standard error
SD	standard deviation
p	probability
m,c	slope (m) and intercept (c) in a regression equation of the form; $y = mx + c$
r	Bravais-Pearson correlation coefficient

3. Categories of trapped samples (see section 6.2.4)

b. ↓ '75	Samples obtained by baited traps
b. ↓ '76	when the water level was not lowered between setting and emptying in 1975 and 1976.
n.b. ↓ '75	Samples obtained by non-baited
n.b. ↓ '76	traps when the water level was lowered between setting and emptying in 1975 and 1976.
n.b. ↓ '75	Samples obtained by non-baited traps when the water level was not lowered between setting and emptying in 1975.

4. Statistical notation for the estimation of population parameters (see Chapters 5, 6 & 7

Lincoln index notation:-

n_1	number of crayfish in the first sample
n_2	number of crayfish in the second sample
m_2	number of crayfish from the first sample recaptured in the second sample
$\hat{N}$	estimate of the number of crayfish of carapace length $\geqslant$ 13 mm. in the aqueduct; usually applying to the time when the first sample was collected (see text).

The notation of Jolly's stochastic model (1965):-

n_i	number captured in the i'th sample
m_i	number of marked crayfish in the i'th sample
s_i	number released from the i'th sample after marking
$\hat{M}_i$	estimated total number of marked crayfish in the population at time i
n_{ij}	number in i'th sample last captured in the j'th sample ($1 \leqslant j \leqslant i - 1$)
$\hat{a}_i$	alpha; the estimated proportion of the population marked at time i
$\hat{\phi}_i$	phi; the estimated probability that an animal alive at the moment

	of release of the i'th sample will survive till the time of capture of the i + 1'th sample (emigration and death being synonymous for this purpose)
$\hat{B}_i$	estimated number of new animals joining the population in the interval between the i and i + 1'th samples and alive at time i + 1
$\hat{N}_i$	estimated number in the population when the i'th sample is captured

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ABSTRACT

The general biology and population dynamics of the freshwater crayfish, Austropotamobius pallipes, were studied in a man-made aqueduct in Northumbria. The paucity of ecological knowledge of this species; the threat of the pathogenic crayfish 'plague' fungus, which has destroyed many European crayfish stocks; and several features of this aqueduct which made it particularly suitable for a population study inspired this investigation. The latter features were: the population was delimited to a known area (ca. 0.25 ha.); immigration was unlikely and the water level could be artificially manipulated allowing the collection of many crayfish by hand. Two sampling methods, hand-collection and funnel traps, and two marking schemes, one date-specific and one individual-specific were used to monitor the population. Over 4,500 crayfish were numbered and over 6,000 given a date-specific mark between March 1974 and June 1977. Moulting and growth were followed and found to occur only between late June and mid-September; this was limited by higher summer water temperatures. A potential life span of 10-13 years was projected. Fecundity was estimated for individuals and the whole population. No recognizable 'home range' was observed. An attempt was made to describe crayfish diel activity patterns and trophic inter-relationships. The effects of a protozoan parasite were observed under natural conditions. It was demonstrated that hand-collection provided relatively unbiased mark-recapture estimates of population size; trap samples seriously underestimated this parameter. The density of crayfish of body length $\geqslant$ 26 mm. was estimated as 8+/m^2 in the summers of 1974 and 1975 and to have varied between 10.4/m^2 and 3.8/m^2 from June 1976 to May 1977. Annual production (ca. 170.5 Kg./ha.) and mean annual biomass (ca. 409.7 Kg./ha.) were estimated in 1976.

GENERAL INTRODUCTION

The only species of freshwater crayfish native to the British Isles is Austropotamobius pallipes (Lereboullet) (Gledhill et al. 1976, Huxley 1896, Thomas & Ingle 1971). This is very much in contrast to the many different crayfish species described from the North American continent (Hobbs 1972, 1974b), Australia and New Zealand (Chapman & Lewis 1976, Riek 1969). On the European continent there are four native species of freshwater crayfish (A. pallipes, Austropotamobius torrentium, Astacus astacus, Astacus leptodactylus: Gledhill et al. 1976, Huxley 1896, Kossakowski 1971). That A. pallipes is the only member of the family Astacidae indigenous to the U.K. is generally attributed to the effects of the Pleistocene ice ages. This has resulted in A. pallipes having a wider ecological range here than on the continent of Europe where it is confined to small streams (as is A. torrentium), with the other two species occupying the larger streams and rivers (Huxley 1896, Hynes 1972).

There is a considerable amount of evidence that A. pallipes is widely distributed, and abundant in many places where it does occur, in England, Ireland and

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Wales (see Chapter 5; Davies 1964, Holdich et al. 1978, Howes 1962, Huxley 1896, Moriarty 1972, Thomas & Ingle 1971; pers. communications, Aston, Bowler, Langford, Pratten & Thomas); although some anecdotal reports give the impression that the opposite is the case (Anonymous 1976 as quoted by Holdich et al. 1978, Carpenter 1928, Conran 1978, Jackman 1977, Stellan Karlsson 1978).

Despite the fact that there is only one native species represented by so many individuals relatively little is known of the ecology (e.g. Moriarty 1972, Thomas & Ingle 1971, Watson unpubl.), or even the natural history, of this species (Howe 1962). This is rather different to the extent of knowledge of the genus Astacus (e.g. Abrahamsson 1966, 1971a, 1971b, 1972a; Cukerzis 1968, 1974; Kossakowski 1965, 1967, 1971) and that of many North American species (e.g. Abrahamsson & Goldman 1970; Avault 1974; Capelli 1975; Flint 1975a, 1975b; Mason 1974; Momot 1964, 1966, 1967a; Penn 1943; Tack 1941). However, there exists no comprehensive body of ecological knowledge for any species of freshwater crayfish. This deficiency is mainly due to the inaccessibility to direct sampling of these benthic, largely nocturnal and in many cases burrowing freshwater invertebrates (see also section 5.1). Indirect sampling methods such as baited traps and drop nets are usually effective but do not provide representative samples of the whole population (traps usually catch few adult females and very few juveniles,

see also Chapter 6). Sutcliffe (1978), when reviewing a book on the freshwater Crustacea of New Zealand, has said that "more is known about the life cycle of one of the two species of crayfish (Koura) in New Zealand than is known about the only native species in Britain!" despite "the limited data for the New Zealand fauna". Indeed, the latest comprehensive work on the field biology of this species is by T. H. Huxley (1896) and, since this was written as a general "Introduction to Zoology" as a subject, it often relies on "the authority of M. Carbonnier (L'Écrevisse. Paris, 1869); but this obviously applies only to the large 'Écrevisse à pieds rouges' of France" (A. astacus) "and not to the English crayfish, which appears to be identical with the 'Écrevisse à pieds blancs" (A. pallipes).

There are several good reasons, apart from any esoteric considerations, why a much greater knowledge of the ecology of A. pallipes is necessary. All of these reasons (which concern the ultimate fate of our native stocks with possible far reaching effects on the trophic ecology of our waterways) are associated with the appearance of an epidemic crayfish disease on the continent of Europe in the late nineteenth century (Kossakowski 1971, Schweng 1972, Spitzy 1972). This disease (the 'crayfish plague') was, apparently, introduced into Italy in association with the North American crayfish species, Orconectes limosus; this species is 'tolerant' of the plague, as are all North American species (Unestam 1969, 1972a, 1972b; Unestam

& Weiss 1970). The plague was identified as the parasitic fungus Aphanomyces astaci in the mid-nineteen thirties (Schäperclaus 1954); this fungus is endemic among North American crayfish species which all show high but not complete resistance (Unestam 1969, 1972a; Fürst & Boström 1978). A. astaci has spread through Europe and into Scandinavia and destroyed many populations of crayfish, particularly of A. astacus and A. leptodactylus, which were much appreciated gastronomically in many areas and important economically as an export (e.g. Abrahamsson 1972a, Brinck 1974, Fürst 1977, Hynes 1972, Laurent 1972, Spitzy 1972, Westman 1972, 1974).

O. limosus has become quite widely distributed in France, Germany and Poland and is abundant in some areas (Grünwald 1975; Jungbluth 1975; Kossakowski 1971, 1974; Schweng 1972). It is, however, less esteemed gastronomically than Astacus sp. (Lindqvist pers. comm., Kossakowski 1971). The major efforts to restore European crayfish waters affected by the plague have been concentrated on the introduction of the tolerant North American species Pacifastacus leniusculus; first with live adults from the U.S.A. and now with hatchlings produced from infection-free stock animals in Sweden, to avoid the re-introduction of plague spores (Abrahamsson 1972c; Brinck 1974, 1976; Fürst 1977; Goldman 1972; Spitzy 1972). There is now some evidence to suggest that this can be successful and some waters may be restored to their former productivities (Brinck

1976, Fürst 1977). However, some P. leniusculus (which is the 'normal' host of the plague fungus in the U.S.A.) have been found to be infected in most Swedish waters to which they have been introduced (Fürst 1977, Fürst & Boström 1978, Unestam et al. 1976). As many European countries are also striving to preserve their surviving stocks of A. astacus the establishment of populations of a 'tolerant' foreign species, which may act as a reservoir for fungal spores, must be carefully considered and if carried out must be done in a planned and controlled way if native stocks are not to be endangered.

There is no evidence that crayfish plague has had any effect on crayfish abundance or, indeed, has even gained a foothold in the U.K. (see Holdich et al. 1978 and the Introduction to Chapter 5 for a detailed examination of this point). That this may occur in the future is, however, a possibility which deserves serious consideration. The decline of crayfish stocks on the European continent has resulted in considerable importation of frozen crayfish to meet the home demand, mainly from the U.S.A. and Turkey; and consequent high market prices for this luxury food item (e.g. £8 - £12/Kg., ca. 50p. - 70p./crayfish, Fuke 1978; Fürst 1977; Westman 1972, 1974). The upsurge of interest in freshwater crayfish in Europe over the past decade, together with these high prices, has resulted in commercial aquaculturists in the U.K. becoming interested in rearing these animals for sale. The large maximum size and relatively rapid growth rates that have been reported for some introduced populations of P. leniusculus

(Abrahamsson 1971b, Fuke 1978, Richards & Fuke 1977), and possibly also the lack of knowledge of the native species, has resulted in many of these persons interested in culture importing P. leniusculus into the U.K. (Bowler, Pratten pers. communications; Fuke 1978, Richards & Fuke 1977). Despite the fact that these P. leniusculus have, as far as is known, come from plague-free stocks in Sweden the threat to our native species is obvious; once established these foreign crayfish are a potential reservoir of fungal spores from which the plague could proliferate into our native stocks of A. pallipes. As there is, at present, no legislation concerning the introduction of foreign crayfish species into England, Ireland and Wales (although recent legislation may cover this with respect to Scotland, Stott pers. comm.), and since small numbers of adult Procambarus sp. are known to have been brought in (Bowler pers. comm.), it would seem to be only a matter of time before A. astaci is also introduced.

Although A. pallipes is a small species (maximum wet weight of males $\simeq$ 60 gms.) the larger specimens (> ca. 30 gms. wet weight) compare favourably to A. astacus in a gastronomic sense (Lindqvist, Tirri, pers. communications). They are not widely consumed in the U.K. (Holdich et al. 1978) but in view of their abundance could prove a valuable export. One consequence of the lack of interest in eating A. pallipes in the U.K. would be that if our stocks were seriously affected by A. astaci

there would be no incentive to restock as is being attempted in Europe. The loss of crayfish from many areas could have serious consequences as there is a growing body of evidence that they can have a considerable effect on the abundance of some aquatic macrophytes (see section 3.5). Abrahamsson (1966) has reported ponds in Sweden becoming 'choked' with macrophytes and algae following the extermination of the population of A. astacus by the plague. Because these ponds were used as water reservoirs weed-cutting had to be considered; it is possible, therefore, that the prolonged absence of crayfish from some water bodies may create serious problems in terms of keeping the watercourse free-flowing and, perhaps, accessible to anglers and/or boat traffic.

It is clear, therefore, that a study of the general biology, growth, abundance and population dynamics of A. pallipes is of considerable importance so that the possible effects of the introduction of A. astaci, along with foreign crayfish species, may be foreseen and that these may be averted by an objective assessment of the potential of our existing native stocks for exploitation and their subsequent protection.

The study area chosen for the investigation of the population biology of A. pallipes had several unique advantages which made it particularly suitable for this purpose; these features are described in detail in Chapter 1. Briefly, these features were that the population was delimited to a known area (a stretch of

man-made aqueduct), immigration into this stretch of aqueduct was unlikely and the population could be sampled by direct hand-collection when the water was drained away by closing a sluice gate. The opportunities presented by these advantages, particularly the ability to collect large numbers of crayfish of both sexes and all sizes, may provide information of general value in the study of crayfish populations. Indeed, there is a general lack of information concerning the population biology of long-lived freshwater invertebrates (maximum life span of A. pallipes in the study area was 10-13 years, see Chapter 4; also Hynes 1972, Chapter 5). This deficiency may be limiting our understanding of the functioning of freshwater ecosystems.

The frequency of the hand-collections and the time for which the sluice gate could be closed were determined by the owners of the aqueduct; hand-sampling was, therefore, not possible over certain periods owing to the high demand for water (Chapter 5). The variations in the density of crayfish over the consistently catchable size (i.e. attempted capture was almost always successful; 13 mm. carapace length) were, however, determined with reasonable accuracy, by mark and recapture methods, over a period of one year (3.8-10.4 crayfish/m^2 between May 1976 and June 1977, see section 5.4.5). Several other, more approximate, estimates indicated that the density was ca. 8+ crayfish/m^2 in the summer months of 1974 and 1975.

CHAPTER 1

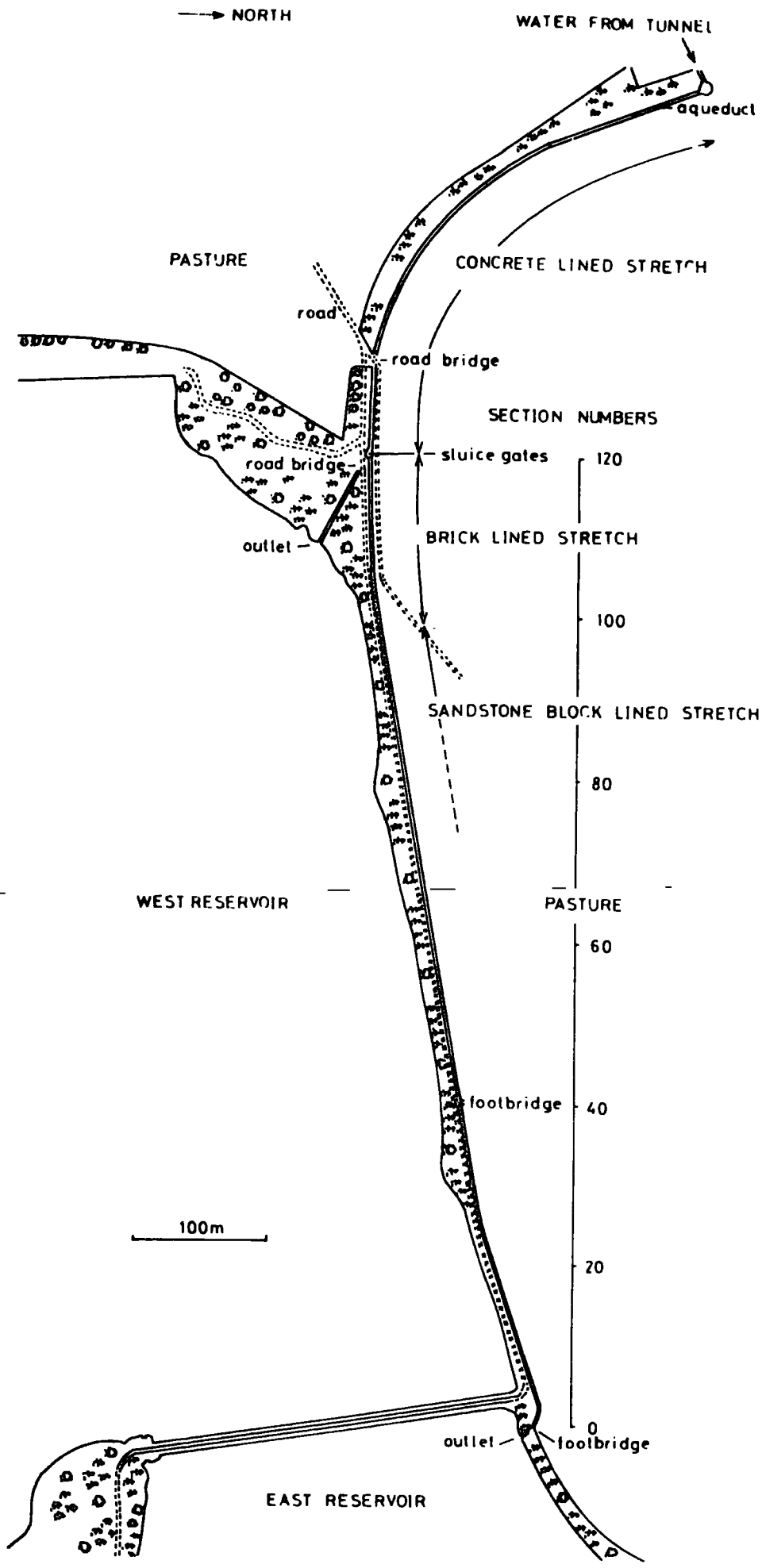
Description of the study area

1.1 Topography

The study area is a stretch of man-made aqueduct that is the main inflow to Hallington Reservoirs, Northumbria. The part of the aqueduct containing the study population (subsequently referred to as the aqueduct) flows from map reference NY 96127626 to NY 96847638 and lies approximately 2 km. to the west of Hallington village.

A map of the whole aqueduct is shown on Fig. 1.1. The original source of the water is Catcleugh and Colt Crag reservoirs, the water flows via tunnel, open aqueduct and cast iron pipes into Little Swinburn reservoir and then goes underground to emerge from a tunnel into the concrete lined stretch above the aqueduct at Hallington (Newcastle and Gateshead Water Company 1969). The two sluice gates which control the flow of water into the East and West reservoirs (Fig. 1.1; Plate 1.1a) are usually arranged so that the maximum flow runs through the aqueduct into the East reservoir, this is because the outflow to Whittle Dene reservoirs is drawn entirely from the East reservoir, the West reservoir

Fig. 1.1: Map showing the pertinent features of the whole aqueduct system which is the main inflow to Hallington reservoirs. The brick and sandstone lined stretches contained most of the study population and are subsequently referred to as the aqueduct


NORTH
WATER FROM TUNNEL
aqueduct
PASTURE
CONCRETE LINED STRETCH
road
road bridge
SECTION NUMBERS
sluice gates
120
road bridge
BRICK LINED STRETCH
outlet
100
SANDSTONE BLOCK LINED STRETCH
80
WEST RESERVOIR
PASTURE
60
footbridge
40
100m
20
0
outlet
footbridge
EAST RESERVOIR

being purely storage (Newcastle and Gateshead Water Company 1969). At least half the water from Little Swinburn is always allowed to flow through the aqueduct so the minimum depth is approximately two thirds the maximum depth (ca. 1.2 m) due to the aqueduct being narrower than the outflow into the West reservoir. The usual flow rate through the aqueduct is ca. 54×10^6 L. day^{-1} or 24.5 $m.min^{-1}$.

The first 390 meters of aqueduct is concrete lined as is the outflow into the West reservoir. Below the sluice gates the aqueduct lining is brick for 153 meters and sandstone blocks for the remaining 593 meters (Fig. 1.1).

The rapid nature of the run off from the aqueduct into the East reservoir (Plate 1.2b) and the unsuitability of the concrete substrate for crayfish at the inflow suggested that the crayfish population was reproductively isolated and largely limited to between the sluice gates and the outflow, this was later shown to be the case (section 3.6.1). This stretch of aqueduct was therefore divided into 122 equal sections, measured as 6.096 m. (20 feet) each (Fig. 1.1). The length of this stretch as calculated from Ordnance Survey Plan NY 9676 (scale 2,500:1) was 746 m., the actual length of a section was therefore 6.115 m. and a measurement error of ca. 0.31% existed.

Plates 1.1 and 1.2 show the nature of the inflow to and outflow from the aqueduct, the normal water level and the wall structure in the sandstone block lined stretch when the water level had been lowered to < 10 cm. by

Plate 1.1a: The two sluice gates with the concrete lined stretch in the foreground

Plate 1.1b: The aqueduct at normal water level near the middle of the sandstone block lined stretch

Plate 1.2a: The aqueduct with the water level at its lowest in the sandstone block lined stretch. Scale ca. 8 : 1 in foreground

Plate 1.2b: The outlet of the aqueduct into the East reservoir; the far side of the stone bridge was the beginning of the first six meter section (Fig. 1.1)

closing the sluice gate at the top of the aqueduct. A diagrammatic representation of the walls and substratum of the aqueduct in the sandstone block lined stretch is shown on Fig. 1.2. When the water level was lowered (Plate 1.2a) crayfish left their hides in the walls of the aqueduct in large numbers to seek alternative hides on the aqueduct floor. Normal water level was 1.05 m. (Plate 1.1b) and the brick lined and sandstone block lined stretches were 1.98 m. and 1.90 m. wide at the top and 1.18 m. and 1.02 m. wide at the bottom respectively. The total wall and floor area of the aqueduct can therefore be estimated as approximately 2,482 m^2.

1.2 Physical parameters of the study area

1.2.1 Turbidity

The water flowing through the aqueduct was usually very clear except during occasional spates and when the pipes and tunnels were cleaned out by the water company, a practice carried out less than once each year.

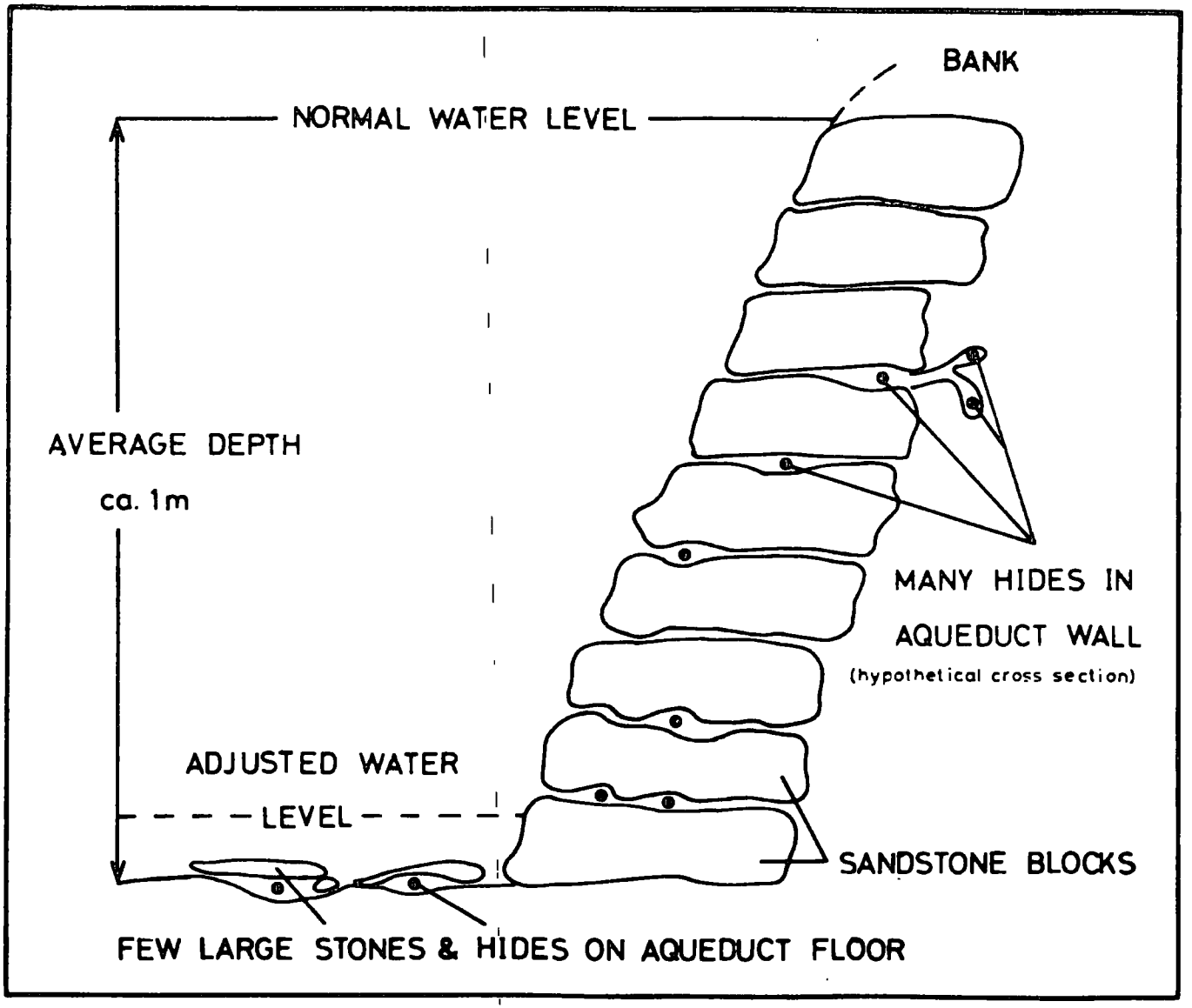
1.2.2 Calcium concentration

The calcium concentration in water from the aqueduct was determined by the method of Willis (1961) using a Pye Unicam SP 90 atomic absorbtion spectrophotometer. The mean calcium concentration on nine occasions in 1974-75 was 18.61 $\pm$ 1.01 ppm Ca (range 16.0-25.5 ppm).

1.2.3 pH

The pH of the water flowing through the aqueduct was 7.84 $\pm$ 0.21 (n=5).

Fig. 1.2: A generalized cross section of the aqueduct in the sandstone block lined stretch showing the type of hides occupied by crayfish ⩾ 13 mm. carapace length


BANK
NORMAL WATER LEVEL
AVERAGE DEPTH
ca. 1m
MANY HIDES IN
AQUEDUCT WALL
(hypothetical cross section)
ADJUSTED WATER
LEVEL
SANDSTONE BLOCKS
FEW LARGE STONES & HIDES ON AQUEDUCT FLOOR

1.2.4 Oxygen concentration

The percentage oxygen saturation varied from 69% at 3.8°C to 98% at 13.3°C. The mean percentage saturation of oxygen in water taken from the aqueduct around mid-morning was 85.61 ± 2.01% (n=15).

1.2.5 Temperature

The temperature of the water in the aqueduct was measured in three ways:-

i) on most visits throughout the study a thermometer reading was taken around mid-morning

ii) the mean water temperature between nine visits in 1974 was estimated using a sucrose inversion technique as described by Lawton (1969)

iii) thermometer readings were taken at three hourly intervals for twenty-four hours on two occasions in August 1975.

The means of the thermometer readings on the days on which the sucrose tubes were set and removed were in all cases similar to the mean water temperatures as estimated by the inversion of the acid sucrose solution in the tubes (Table 1.1). This suggested that the water temperature in the aqueduct did not vary irregularly and there was probably a progressive seasonal trend of water temperature in the aqueduct. Five of the eight sucrose inversion estimates during the warmest part of the year were higher than the mean thermometer readings. This may have been because the effect of temperature on the inversion of sucrose is not linear but exponential,

Table 1.1

Estimates of mean water temperature in the aqueduct between dates by thermometer readings and sucrose inversion

Date	Thermometer reading °C	Mean thermometer reading °C	Sucrose inversion estimate °C
29. 5.74	10.7		
		11.15	12.5
12. 6.	11.6		
		12.45	13.9
18. 7.	13.3		
		13.00	13.4
24. 7.	12.7		
		13.25	13.8
31. 7.	13.8		
		13.80	14.3
7. 8.	13.8		
		12.70	12.7
11. 9.	11.6		
		9.10	8.2
28.10.	6.6		
		6.40	5.6
7.11.	6.2		
	mean	11.48 ± 0.89	11.80 ± 1.12

higher temperatures therefore had a disproportionate weight in the mean (Edington 1964).

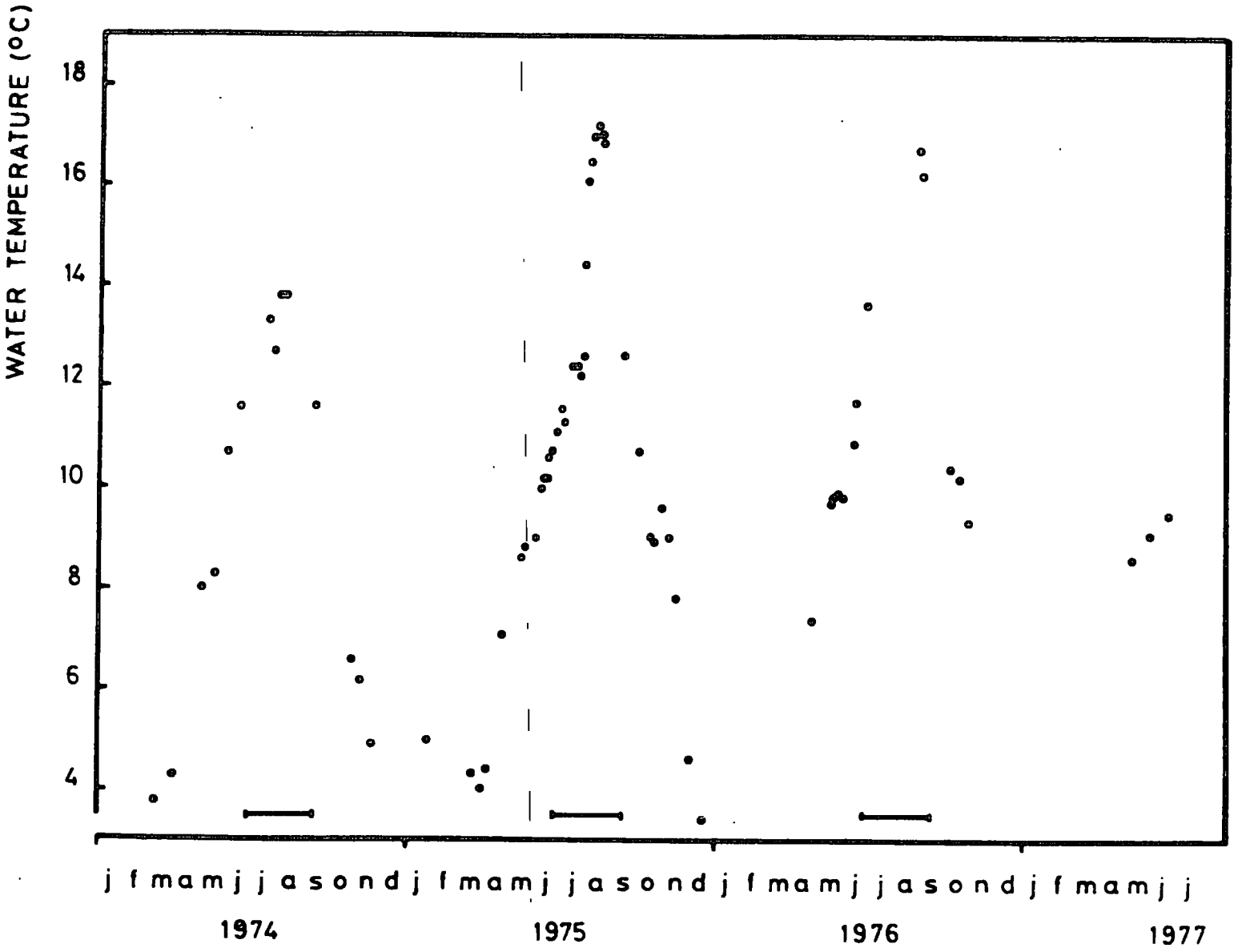
The diel temperature range on two occasions in August 1975 (when the diel range would be expected to be among the largest throughout the year, Crisp and Le Cren 1970) was 0.4 and 0.6°C. This may have been due to the many underground sections before this watercourse came to the surface and the many trees screening the southern bank (Fig. 1.1). The small diel range and the similarity between mean thermometer readings and sucrose inversion estimates indicated that the thermometer readings were an adequate measure of seasonal trends of water temperature in the aqueduct with respect to the various stages of the life history of the animal (Fig. 1.3, Fig. 3.1). The temperature cycle was very similar from year to year (1974-77) except for the lower summer temperatures in 1974.

1.3 Biological parameters of the study area

1.3.1 Detritus

The floor of the aqueduct was constructed in the same manner as the sides and there was only a small amount of loose substrate on account of the current. What little there was gathered around the bases of small boulders (> 10 cm. mean diameter) and branches. The detritus food chain would therefore appear to be a relatively minor component in the energy flow of the aqueduct community.

Fig. 1.3: Mid-morning thermometer readings from water in the aqueduct as a function of date. The solid horizontal bars represent the period over which moulting occurred


WATER TEMPERATURE (°C)
18
16
14
12
10
8
6
4
j f m a m j j a s o n d j f m a m j j a s o n d j f m a m j j a s o n d j f m a m j j
1974
1975
1976
1977

1.3.2 Flora

By far the most abundant aquatic plant, and indeed organic material of any sort, in the aqueduct was the moss Fontinalis antipyretica. Not only were there large growths of this moss in situ but considerable quantities were washed downstream from the source (1.1) and became entangled around any projection. There were also a very few growths of Potamogeton obtusifolius. Despite the considerable area of mixed woodland along the banks of the aqueduct (Fig. 1.1) very little allochthonous organic matter was found in the aqueduct. Such material did not collect on projections as did the long strands of F. antipyretica and would be carried straight through.

1.3.3 Fauna

The fauna of the aqueduct was quite rich in species but none (with the exception of A. pallipes) were particularly abundant (personal observations) when considered in terms of numbers per m^2 averaged out over the whole of the floor and wall area of the aqueduct (2482 m^2, 1.1). For the Gammarus sp and insect larvae present this was due to the relatively small amount of detritus and its localized distribution (1.3.1) and the fact that although present in considerable quantity the growths of F. antipyretica and the loose strands which collected around projections were mainly clumped in distribution (1.3.2). Also present were the freshwater sponge, Ephydatia sp., the gastropod, Potamopyrgus jenkinsi, the stone loach, Nemacheilus barbatulus, the rainbow trout, Salvelinus sp., and the water vole, Arvicola amphibius.

Crayfish collected from many areas in Northumberland have been identified as the subspecies Austropotamobius pallipes pallipes (Lereboullet) according to the key of Gledhill, Sutcliffe and Williams (1976).

Some years prior to the present study several hundred large crayfish (> 40 mm. carapace length) were removed from the aqueduct for physiological studies at Durham. This was a considerable proportion of the largest crayfish which were the least numerous in the aqueduct. (< 1% of the total population, 5.4.5, Figs. 4.7 & 4.8). Growth during the period 1973-77 has resulted in crayfish > 40 mm. carapace length being caught much more frequently as indicated by the increase in mean carapace length of the samples collected by hand in successive years (Table 1.2).

Table 1.2

Mean size of hand collected samples

Year	Mean carapace length ± SE	
1974	24.32 ± 0.19	
		$p < 0.001$
1975	28.96 ± 0.56	
		$p < 0.001$
1976	32.27 ± 0.27	
		$p < 0.01$
1977	31.10 ± 0.30	

These large animals were such a small proportion of the total population that the removal of several hundred had no noticeable effect on the population dynamics of A. pallipes in the aqueduct. (5.4.5)

A. pallipes of ≥ 13 mm. carapace length were present at densities ranging from 3.8 to 10.4/m^2 between June 1975

and June 1977 (5.4.5). Smaller crayfish were very abundant but were clumped in distribution owing to their tendency to hide in the clumps of F. antipyretica. Mean potential recruitment (i.e. estimated total number of eggs carried prior to hatching) was 18 individuals/m^2 in 1975, 76 and 77 (3.4).

CHAPTER 2

Methods

The two ways by which samples were collected from the aqueduct population (trapping and hand collecting) and how these samples were returned to the aqueduct are considered in detail in Chapters 5 & 6. The means by which all the crayfish in each sample were processed before returning them to the aqueduct was pertinent to all aspects of the field data and is the subject of this chapter.

2.1 Measurements

Measurements were taken with vernier calipers to the nearest 0.1 mm. Only individually numbered crayfish were measured. Date-specific marked animals were sexed and size classed as either adult or juvenile (see section 2.3).

For reasons developed below all measured crayfish had the carapace length (minimum distance from tip of rostral spine to posterior carapace rim) taken, in addition the large majority had their carapace width (maximum width of carapace) taken and during the initial part of the study the total body length (minimum distance

from tip of rostral spine to posterior rim of telson, excluding setae, with tail in horizontal position and unstretched) was measured. In some cases chela lengths (maximum distance from propodus tip to hardened exoskeletal rim of chela nearest to hinge with carpus) were also taken.

The measuring errors associated with these sets of observations can be determined. These errors in measurement were analysed as the differences in any of the above measurements between consecutive recaptures in any one intermoult period (see sections 2.2 & 2.3). All animals with damaged rostra were excluded (Fig. 2.1).

Carapace length was the most accurate measurement with 99% confidence limits about the mean ($2\frac{1}{2}$ SD) of $\pm$ 0.53 mm; errors greater than this were thus encountered very rarely, indeed most measurements were a good deal more accurate than this with only 30% of the recorded errors $> \pm$ 0.1 mm. This measurement was therefore selected as an index of growth.

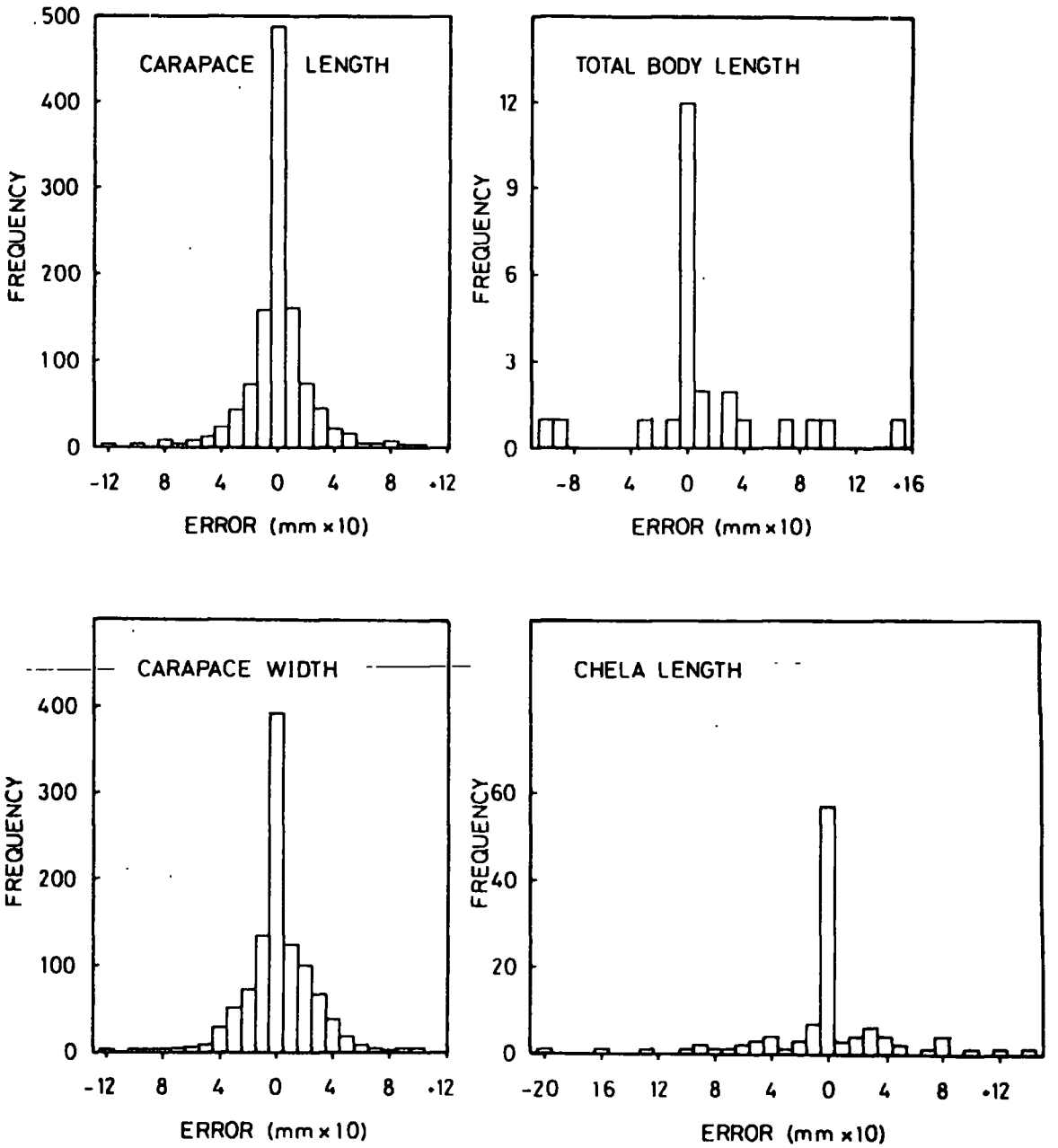
Carapace width was slightly less accurate ($2\frac{1}{2}$ SD = 0.58 mm.) probably because the carapace could be laterally compressed, particularly in early postmoult.

Chela lengths showed considerably more variation ($2\frac{1}{2}$ SD = 1.20 mm.) as a result of the problems in manipulation of a live crayfish in obtaining this measurement.

Total body length was the least accurate ($2\frac{1}{2}$ SD = 1.27 mm.) as expected due to the flexibility of the abdomen.

Fig. 2.1: Frequency histograms of the errors in measurement of crayfish that were recaptured and measured several times in the same inter-moult period; see text

	Mean error (mm.)	$2\frac{1}{2}$ SD
Carapace length	-3.50×10^{-4}	0.53
Carapace width	1.66×10^{-2}	0.58
Total length	1.20×10^{-1}	1.27
Chela length	1.86×10^{-2}	1.20


CARAPACE LENGTH
FREQUENCY
500
400
300
200
100
0
-12 8 4 0 4 8 +12
ERROR (mm x 10)
TOTAL BODY LENGTH
FREQUENCY
12
9
6
3
0
-8 4 0 4 8 12 +16
ERROR (mm x 10)
CARAPACE WIDTH
FREQUENCY
400
300
200
100
0
-12 8 4 0 4 8 +12
ERROR (mm x 10)
CHELA LENGTH
FREQUENCY
60
40
20
0
-20 16 12 8 4 0 4 8 +12
ERROR (mm x 10)

The symmetry of the histograms on Fig. 2.1 suggested that most errors were observational and supported the view that the rostral spine was of a characteristic shape such that any damage was usually obvious (see sections 2.2.2 & 4.2.1).

Wet weights of crayfish in the size range 8-55 mm. carapace length were determined in the laboratory and in the field. Each crayfish was dried with filter paper to remove as much external water as possible and weighed to the nearest 0.01 gm. This drying was carried out either until no more wet areas appeared on the filter paper or for a maximum of thirty seconds in an attempt to compromise between removing all external water and evaporation loss of internal water. A constant error was water in the branchial chambers; these weights were therefore always slightly too high by a constant proportion.

2.2 Observations on the 'condition' of each animal

Several observations were made in accordance to predetermined criteria and the results recorded in coded form as part of the processing routine for each crayfish that was individually numbered.

2.2.1 Life-history

(i) All individuals of carapace length > 11 mm. were easily sexed by eye due to the presence of the fully developed first two pairs of modified pleopods of the males (Huxley 1896, Thomas 1976).

(ii) When a white spermatophore deposit was present in the region of the openings of the female oviducts this was recorded as fertilization having occurred (Ingle & Thomas 1974). Those females bearing eggs attached to the pleopods or 'in berry' were also recorded, as were hatched young clinging to the pleopods.

(iii) Those crayfish which could be recognised as infested by the microsporidian parasite Thelohania contejeani were also recorded (see Chapter 3).

(iv) Moulted (M) was used to describe a crayfish that was free of the dark epizootic growths which occurred on the integument overwinter, this showed that it had moulted at least once that year.

(v) Moult imminent (MI) was recorded when the old exoskeleton had become separated from the new that was being formed underneath (Stage D_3, lasts about 3 days, Ross Stevenson 1974).

(vi) Moult very imminent (MVI) described the condition of an animal within hours of moulting (Stage D_4, Ross Stevenson 1974).

(vii) Recently moulted (RM) referred to animals which had not fully hardened their new shells after shedding the old (up to about 100 hours postmoult; stages A_1, A_2 & B, Ross Stevenson 1974).

2.2.2 Injuries

(i) Chela loss and regeneration is a fairly common feature in crayfish (see Chapter 4) and in order to study this in field conditions chela lengths were measured when

either one of both chelipeds had been missing or were regenerating (size difference ⩾ 1 mm. between normal and regenerating chela).

(ii) The loss and/or regeneration of, or damage to, walking legs and pleopods was noted.

(iii) Any damage to the rostrum was readily apparent as this has a characteristic shape when intact (Gledhill et al 1976, Gordon 1963, Thomas 1974).

The records of size, sex, moult stage, reproductive status and abnormalities provided a very useful check on field identification by the numbering system (section 2.3).

2.3 Marking techniques

Arthropods are notoriously difficult to mark with any degree of permanence because any mark applied only to the outer exoskeleton is lost when the animal moults and induced, codified mutilations are frequently regenerated. Before looking to the literature to see what techniques had been developed for decapods the requirements of any marking technique to be employed in the intended study were formulated:-

(i) The marks must not be lost at the moult due to the old exoskeleton having been shed or regeneration.

(ii) Marking must not directly or indirectly affect survival.

(iii) There should be very little chance of confusing marks with natural mutilations and abnormalities.

(iv) Ecdysis should not be hindered in any way or the animal more than normally weakened upon its completion.

(v) Marking should not produce any abnormal behaviour patterns e.g. limb tags may hinder locomotion, defence or offence or the animal may attempt to remove them (Goellner 1943, Slack 1955).

(vi) Growth and mating must be unaffected.

(vii) As the population was to be sampled continuously any marking technique had to be equally applicable and harmless at all stages of the moult cycle.

(viii) The technique must be simple, quick and effective under field conditions.

(ix) Any system for individual recognition must be able to cope with large numbers of animals.

The majority of the methods already developed have some shortcomings compared to the above requirements. Limb removal is obviously limited in scope, prone to confusion with natural mutilation and liable to disappear on regeneration apart from possible behavioural abnormalities (Goellner 1943, Slack 1955, Svärdson 1949, Tack 1941, Van Deventer 1937). Some of the other mutilation techniques have similar disadvantages but pleural clipping and cutting or punching holes in the telson, and uropods may last several moults (Bumpus 1901, George 1957, Goellner 1943, Simpson 1961, Templeman 1940, Thomas 1958, Wilder 1953, Woodland 1967). Injection and staining methods are awkward to apply and do not allow individual recognition (Costello & Allen 1961, Goellner 1943, Loosanoff 1953, Lucas et al. 1972, Penn 1975, Slack 1955, Woodland 1967). Some tags have been developed that are effective through the moult and

are relatively easy to apply but growth has often been shown to be affected and some post-marking mortalities usually occurred, particularly when tags were attached to animals in early post-moult (Butler 1957, Cooper 1970, Gunderson 1967, Lindner 1939, Penn 1975, Rounsefell & Eberhardt 1953, Scarrat & Elson 1965, Simpson 1963, Smith 1940, Von Bonde 1928).

The only method that seemed likely to approach the requirements of this study was the cauterisation of small areas of integument (Abrahamsson 1965, Cooper 1970, Dybern 1965, Flint 1975, Moriarty 1972, Watson unpubl.). Cooper (1970) compared this method to two tagging techniques and was critical of the durability of the cauterised marks. The marks of Cooper (1970) were, however, applied to a relatively large area (a cross on the carapace) with a relatively cool heat source (a soldering iron). All the other applications of this method have employed red-hot heat sources to discrete areas for short time periods and have proved successful (Abrahamsson 1965, Dybern 1965, Flint 1975, Moriarty 1972, Watson unpubl.). The use of relatively high temperatures to discrete areas not only ensures that the hypodermal cells beneath the integument are cauterised but also that marking is completed before any significant amount of heat is conducted to the surrounding tissues.

Crayfish of both sexes of 13-55 mm. carapace length were marked with this technique and held in the laboratory. No marking mortalities were observed over a period of eighteen months. The marks persisted and were easily

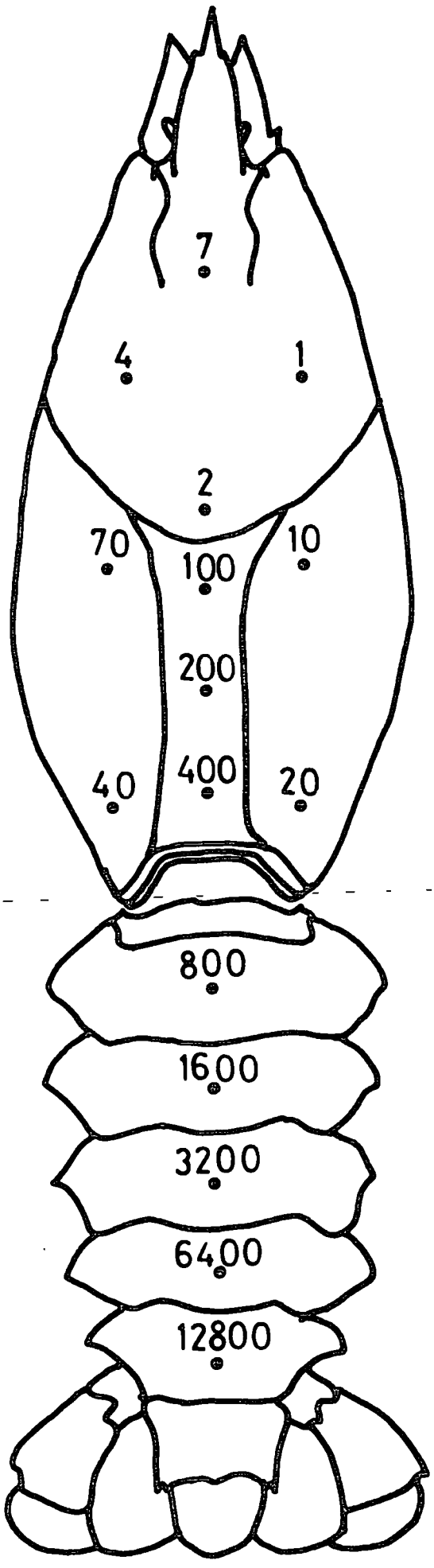
recognizable after at least two moults, some crayfish moulted four times in captivity and could still be recognized. These moults appeared to occur normally and moult increments were comparable to laboratory held controls. Behaviour of marked crayfish showed no noticeable abnormalities and with practice the technique could be applied to all sizes at all moult stages with equally effective results.

An electrically heated needle which glowed red almost immediately a switch connecting it with a 12 volt car battery was closed was used for speed and convenience in the field. This produced black marks with red edges 1-1½ mm. in diameter which were easily visible as paler areas 2-3 mm. in diameter after one or two moults.

The marking scheme used to apply individual numbers was a modification of that of Abrahamsson (1965) and is shown on Fig. 2.2. This provided ample scope as the maximum number of individuals that could be marked was 25,599.

Crayfish which bore a clear number on recapture but did not correspond to any of the parameters previously recorded for that number (sections 2.2 & 2.3) were few. Of the 4,595 crayfish individually numbered, 889 were recaptured once, 282 twice, 109 three times, 43 four times, 32 five times, 3 six times, 5 seven times, 2 eight times and one ten times. Only twenty-five marked animals were recaptured and could not be placed. Many animals had moulted twice (36) and some three times (11) between marking and recapture and still bore recognizable

Fig. 2.2: System used for numerical marking of crayfish by cauterisation; on the head the units, on the sides of the carapace the position of the tens, and between the branchiocardial lines, the hundreds (after Abrahamsson 1965). This system was extended onto abdominal somites 16 to 20 as shown; 25,599 individual marks were then possible


7
4
1
2
70
100
10
200
40
400
20
800
1600
3200
6400
12800

numbers; all numbers were reinforced before release if the animal had moulted since the initial marking, this allowed long term recognition of a few individuals.

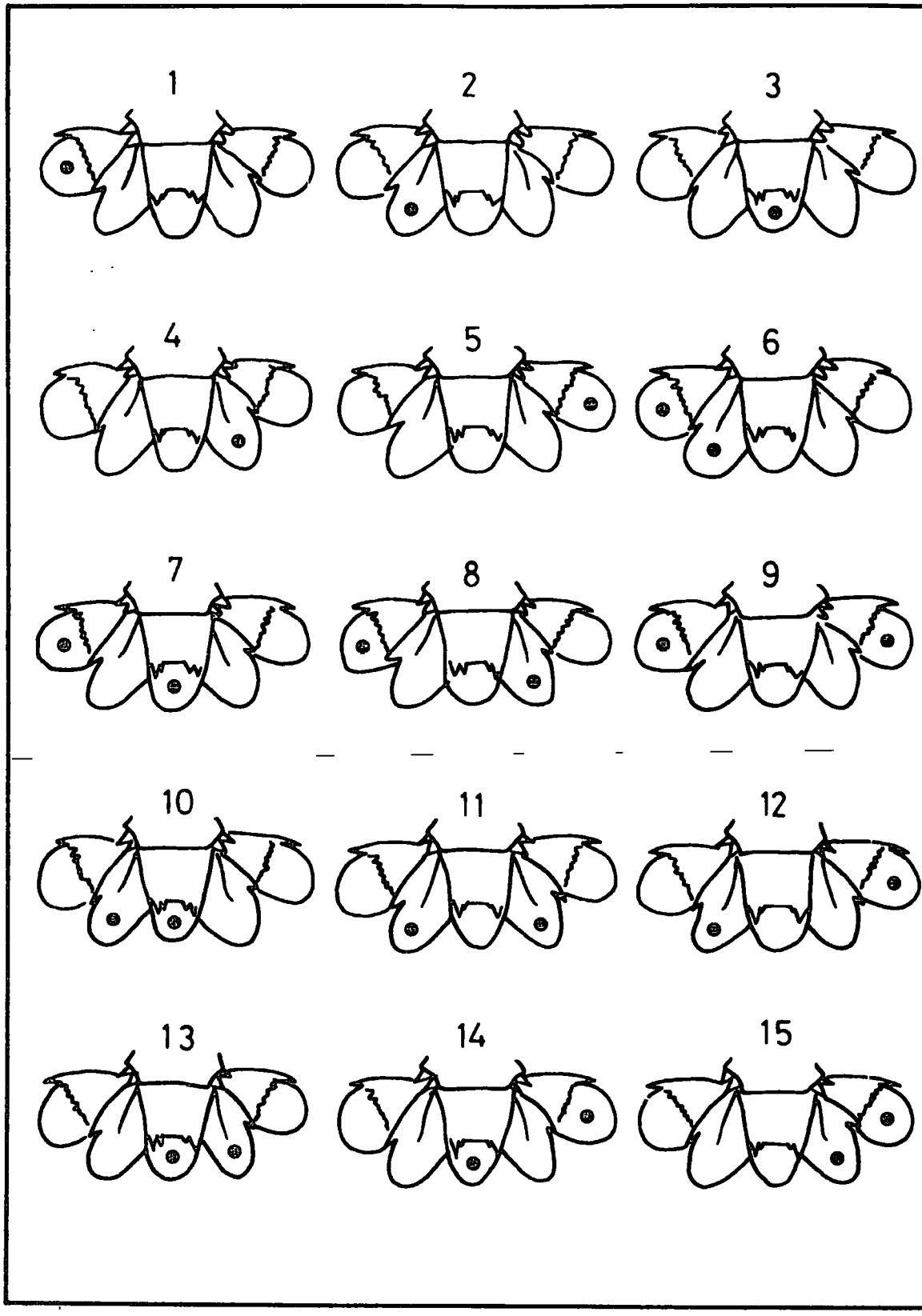
The above observations indicated that mistakes due to human error were few and that the marking technique was very reliable under field conditions. If this had not been the case many errors in identification would have been expected to occur as some marks persisted and others disappeared from the same animal.

Date-specific or 'Day' marks were applied to the uropods and telson in the same manner as individual numbers were to the carapace (Fig. 2.3). These were superceded by an individual mark on first recapture in order that the complete recapture history of all individuals marked was known. This also meant that some animals bore both marks and since the numbering system was known to have been effective in the laboratory and the field for at least two moults these animals were used to follow the fate of the 'Day' marks (5.4.4). These marks were shown to be reliable for at least a whole growth season or overwinter from the end of one growth season to the beginning of another but not for the whole of both these periods, in all animals re-captured.

2.4 Statistical methods

The methods of data analysis and the statistical tests of significance used in this study were either derived from first principles or taken from the texts of

Fig. 2.3: System used for date specific marking of crayfish by cauterisation of discrete areas on the telson and uropods; only fifteen different 'Day' marks were possible by marking one or two of the uropods and/or telson


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Bailey (1959), Davies (1971), Elliot (1971), Ricker (1971), Seber (1973) and Winberg(1971).

CHAPTER 3

The general biology of A. pallipes

3.1 Introduction

The only British species of freshwater crayfish, Austropotamobius pallipes, has been little studied either by freshwater biologists or students of natural history (Huxley 1896, Moriarty 1972, Sutcliffe 1978, Thomas & Ingle 1971, Watson unpubl.).

The recent upsurge of European interest in freshwater crayfish has been caused by the dramatic effects the crayfish plague fungus, Aphanomyces astaci, has had on European stocks (Kossakowski 1971, Unestam 1969, Unestam & Weiss 1970). The disappearance of crayfish from many continental waters, particularly since the last war, has meant not only a decrease in revenue for local fishermen and the loss of a sport fishery but has also resulted in some waters becoming weed choked (Abrahamsson 1966). Whether or not the crayfish plague has crossed the Channel and infected British crayfish stocks is in contention (see section 5.1). What is clear, however, is that the greatly increased European demand for crayfish and consequent high prices

(£8-12/Kg., Fuke 1978; Fürst 1977) have resulted in several people in the U.K. becoming interested in the farming of crayfish, particularly Pacifastacus leniusculus and other fast growing, large species (Bowler pers. communications, Fuke 1978, Jackman 1977, Pratten pers. comm., Richards & Fuke 1977). The risks inherent in introducing non-indigenous crayfish species which can in many cases tolerate and therefore may carry fungal spores (Fürst & Boström1978) have often been stressed (Unestam 1972, 1974, Unestam & Weiss 1970) but there is, as yet, no legislation to prevent the importation of such crayfish into England (Stott pers. comm.).

There is therefore a good case for encouraging interest in the exploitation of our native species rather than importing exotic ones. Otherwise in the future, we may find that this potentially valuable natural resource is disappearing from our waters due to the plague while our knowledge of the biology of the native species is still meagre, as has already been seen to occur with continental species.

The results obtained concerning various aspects of the general biology of A. pallipes in this study were mainly a spin-off from the programme of sampling, marking and returning crayfish to the aqueduct as part of the study of the population dynamics of this species (Chapters 5 and 7) and so have not been systematically followed up in some cases. Nevertheless, in the light of our limited knowledge of this species, these results

provided several useful pointers to some aspects of the general biology of A. pallipes.

3.2 Geographical distribution

A. pallipes is the only species of freshwater crayfish native to the British Isles and is widely distributed and often abundant in waters in England, Ireland and Wales but is apparently absent from most of Scotland (Carpenter 1928, Huxley 1896, Jay pers. comm., Moriarty 1972, Thomas & Ingle 1971). It is also present in several European countries including France, Germany, Italy, Spain and Switzerland (Huxley 1896, Thomas & Ingle 1971). This was very much in contrast with the popular misconception that British freshwater crayfish were typical inhabitants of clear chalk streams (e.g. Conran 1978). Indeed, A. pallipes appeared to be relatively eurytopic with respect to calcium as it thrived in the fairly soft waters of the aqueduct (16-25.5., mean 18.61 ppm. Ca., 1.2.2, Macan & Worthington 1951) and was abundant in Lough Lea, Northern Ireland (11.5 ppm. Ca., Watson unpubl.) but could not moult successfully in water from Lake Windermere (ca. 5 ppm. Ca., Sutcliffe pers. comm.). The lower limit of water hardness which must limit the distribution of this species was not known but was clearly well to the 'soft' end of the scale. Also A. pallipes was no more susceptible to heavy metal pollutants than many other aquatic invertebrates (Chaisemartin 1972) and was not, as was generally assumed to be the case, restricted to totally

unpolluted waters (Aston, Langford pers. comm.). Other factors which limit the distribution of A. pallipes are pH (Jay & Holdich 1976) and water temperatures.

During this study, a short collaboration with CERL biologists at Ratcliffe-on-Soar Power Station, near Nottingham, established that A. pallipes could survive and moult successfully in the ponds beneath the cooling towers. This water contained much of the waste heat discharged from the generators (annual range 10-25°C) and was well aerated. It did, however, also contain free chlorine and chloramine (mean total chlorine ca. 0.15 ppm., but surges much higher than this at chlorination, Aston & Brown 1974) as a result of the sterilization of the cooling system and these were fatal to many fish including trout. As a consequence, crayfish culture in these ponds was a possible way in which this waste energy could be utilized without the capital outlay for heat exchangers that would be necessary with salmoniids.

It would appear that A. pallipes is eurytopic with respect to several aspects of water quality as demonstrated by direct observations and indirectly from its wide distribution.

Discussion

The fact that A. pallipes is the only species of freshwater crayfish native to the U.K. has been attributed to the effects of the Pleistocene ice ages by Hynes (1972) and also by Huxley (1896) to A. pallipes having been the only crayfish species in much of

Western Europe when the British Isles and Europe were separated by the Channel. According to Huxley (1896), Astacus astacus later spread into Western Europe from the East as Astacus leptodactylus has spread into Russia (Huxley 1896) and Western Europe (Cukerzis 1968) in contemporary times. A. pallipes is still the most abundant crayfish species in France however (Laurent & Suscillon 1962).

Several species of freshwater crayfish have been introduced to the British Isles. Gledhill, Sutcliffe & Williams (1976) consider it probable that A. astacus has been introduced and Davies (1964) reports that it has colonized some southern rivers. Pacifastacus leniusculus juveniles have recently been extensively introduced from Sweden (Fuke 1978, Pratten pers. comm.). Procambarus clarkii and A. leptodactylus are also believed to have been imported on a small scale (Bowler pers. comm.).

A. pallipes is considerably more eurytopic than its widely upheld image as a typical chalk stream inhabitant would suggest. Most other crayfish species are similarly tolerant, to varying degrees, of a wide spectrum of different aspects of water quality (e.g. Albaugh 1973, Avault 1974, Hobbs & Hall 1974, Momot 1978, Schweng 1972, Spohrer et al. 1974, Tack 1941).

3.3 The life cycle in the aqueduct

The timing of several of the stages in the life cycle of A. pallipes that were observed on any of the

sampling occasions during 1974-76 were summarized on Table 3.1 and Fig. 3.1. Moulting was restricted to a short growth season from late June to mid-September in the three years 1974-76. The recorded water temperatures were highest at this time of year ranging from 10.2 to 11.6°C in late June and from 11.3 to 12.6°C in mid-September (Fig. 3.1). Even during this time of year, the water temperature readings only exceeded 14°C in 1975 (maximum recorded water temperature 17.2°C) and 1976 (maximum recorded water temperature 16.7°C) in the month of August; the exception was in 1974 when the maximum recorded water temperature was 13.8°C (Fig. 3.1). The crayfish population bred successfully in the aqueduct every year from 1974-77 (section 3.4); A. pallipes is therefore clearly a cold water species and if the literature was accurate the study population must be near to its northern limit of distribution.

Upper and lower confidence limits for the length of the growth season in 1974 and 75 were obtained from the length of time between those visits when moulting was first and last observed and the time between the visits closest to these when no moulting was observed i.e. moulting may have begun or ended at any time between these adjacent visits. The moulting season was 83-96 days in 1974 and 80-90 days in 1975 (Table 3.1).

Fertilization took place during about three weeks in late October - early November and egg laying was completed in all individuals between one and two weeks

Table 3.1: Details of the life history of A. pallipes from the aqueduct: the River Ouse, Bucks. (Pratten pers. comm.): the River Darent, Kent (Thomas and Ingle 1971): Lough Lea, County Fermanagh, Northern Ireland (Watson unpubl.) and White Lake, Eire (Moriarty 1972)

		Aqueduct			R. Ouse		R. Darent		L. Lea	White Lake
Moulting season	Previous visit:	12. 6.74	19. 6.75	12. 6.76				10. 5.64		
	Moulting first observed:	20. 6.74	25. 6.75	27. 6.76	26. 5.76	2. 6.77	16. 5.63	16. 5.64	June 70	July 69
	Moulting last observed:	11. 9.74	13. 9.75		late 9.76		- .10.63	-.10.64	Oct. 70	Sept.69
	Next visit:	16. 9.74	17. 9.75							
Reproductive cycle	Hatching first observed:	24. 7.74	2. 8.75		9. 6.76	20. 6.77		10. 6.64	June 70	June 69
	Hatching last observed:	7. 8.74	12. 8.75		14. 6.76	26. 6.77		17. 6.64	July 70	
	Fertilization first observed:	16.10.74	12.10.75	15.10.76	10.10.76	14.10.77	23. 9.63	25. 9.64	Oct. 70	18. 9.69
	Fertilization last observed:	7.11.74	4.11.75					30.10.64		
	All reproductive females have attached eggs:	20.11.74	12.11.75				6.11.63		Nov. 70	Nov. 69

Fig. 3.1: Seasonal variations in mid-morning thermometer readings taken from water in the aqueduct in comparison to the timing of several aspects of the life history of A. pallipes in 1974, 75, 76 and 77

o - 1974 ▵ - 1976
● - 1975 ▫ - 1977

Trend lines fitted by eye:-

– – – – – – 1974 ———— 1975

–·–·–·– 1976

Life history:-

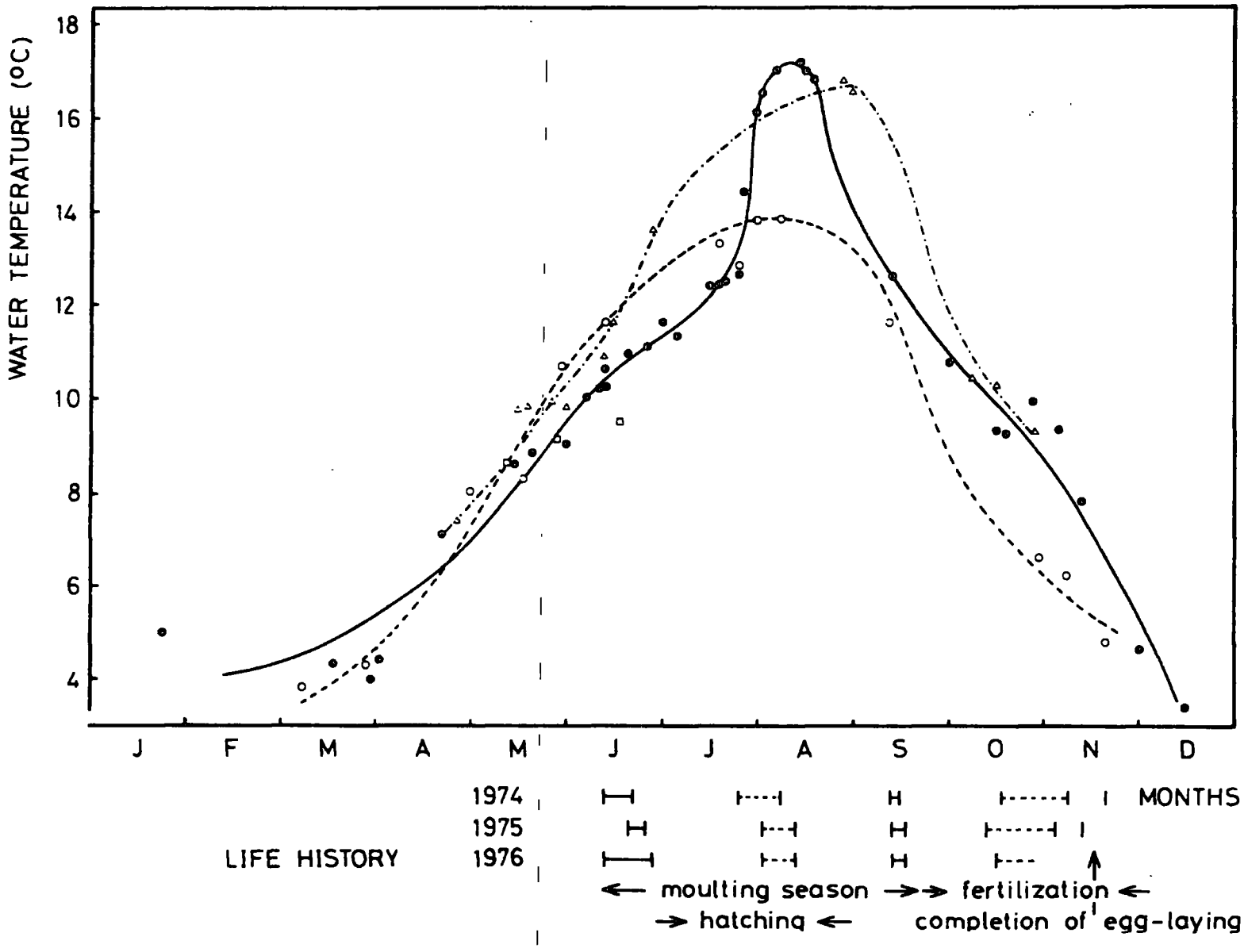
├ – – – – –┤- period over which a particular stage in the life cycle was observed to occur

├————————┤- period between last visit on which evidence of moulting was or was not present and the next visit on which this condition was reversed (i.e. upper and lower confidence limits on the length of the moulting season, see also Table 3.1)

Hatching - that period between hatching of the eggs attached to the pleopods and release of the young.

Fertilization - that period for which females were observed with a white spermatophore deposit (Ingle & Thomas 1974)

Completion of egg-laying - that date on which all females that had been fertilized bore eggs on the pleopods


WATER TEMPERATURE (°C)
18
16
14
12
10
8
6
4
J
F
M
A
M
J
J
A
S
O
N
D
1974
1975
1976
MONTHS
LIFE HISTORY
moulting season
fertilization
hatching
completion of egg-laying

later (Fig. 3.1). These eggs hatched the following year in the first half of August; the young were designated as year class 0+ in the first year after hatching, as 1+ in the second year etc.

Annual trends in water temperature and the timing of the life cycle were very similar from year to year (Fig. 3.1). It was possible to account for some of the small variations in the timing of the stages of the life cycle in 1975 by the initially cooler (mid-May to mid-July) and later warmer water temperatures (late July-August) in comparison to 1974 and 76. Thus moulting and hatching began later after the initial cooler than usual period and fertilization began earlier and egg-laying was completed sooner than usual after the later warmer period. This suggested that water temperature was a major factor influencing the timing of the life cycle.

Further evidence for this conclusion was obtained by comparison with other populations of A. pallipes from the River Ouse, Bucks; River Darent, Kent; Lough Lea, County Fermanagh, Northern Ireland; and White Lake, Eire (Table 3.1). All these populations were far to the south of the aqueduct and in all cases except White Lake, where the annual temperature range was similar to that in the aqueduct (3-21°C), the moulting season was longer, hatching occurred earlier and (with the exceptions of Lough Lea and White Lake) fertilization and the completion of egg-laying were also earlier. Similar trends in the timing of the life cycle of A. astacus have been observed by Abrahamsson (1972a) in Sweden.

Moulting occurred throughout the growth season but was more frequent in the first half of this period particularly for the juveniles (Fig. 3.2). All juveniles for which data were collected ($\geq$ 17 mm. CL) moulted at least twice each year, some adults also moulted twice with an increasing tendency to moult only once with age (4.3.2). Although many crayfish moulted almost simultaneously at the start of the growth season, there was no evidence that the second moult of the year for animals $\geq$ 17 mm. CL occurred during any particular period.

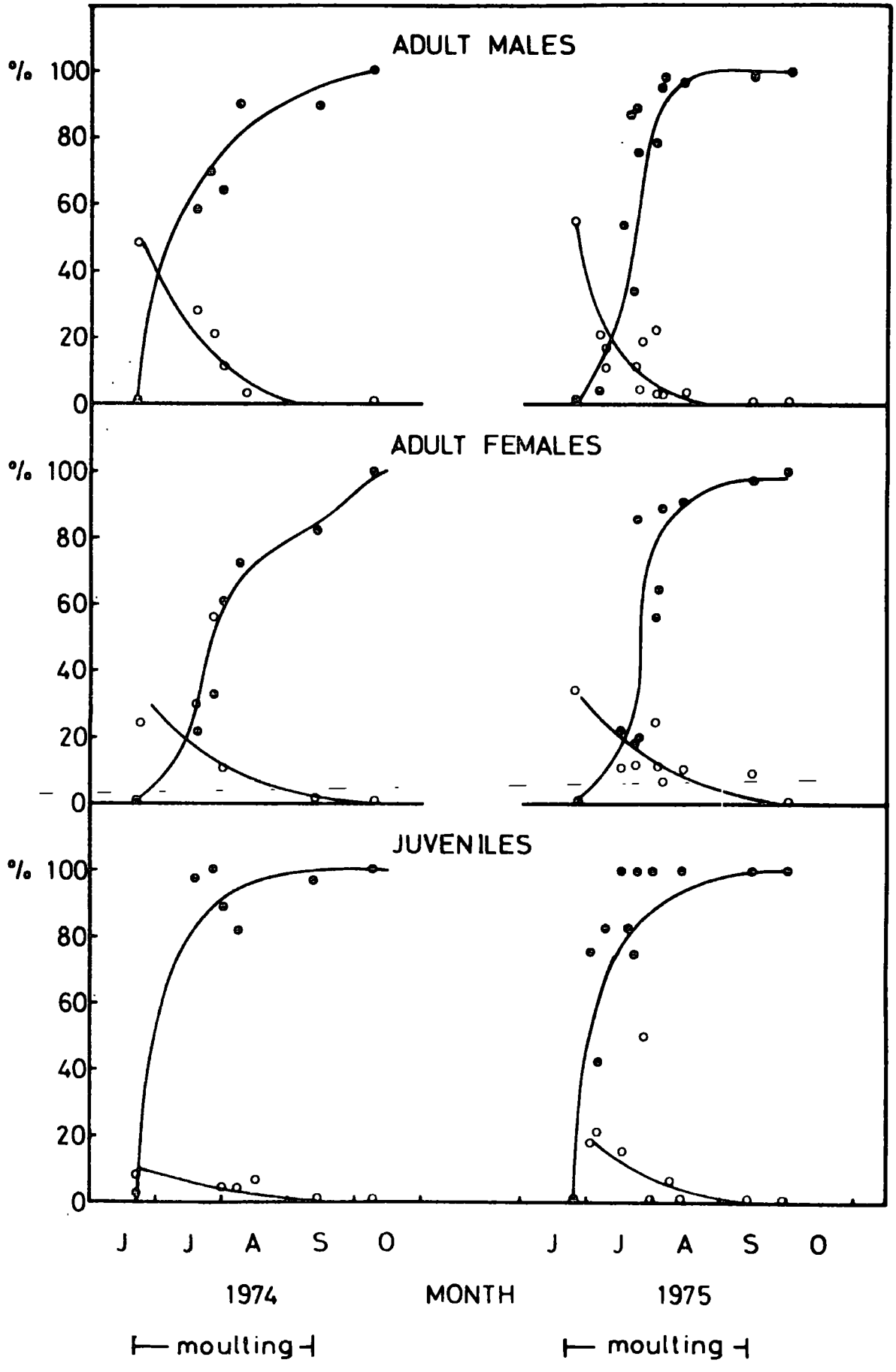
A mean growth pattern throughout the life cycle for A. pallipes in the aqueduct was postulated on the basis of the analysis of size frequency distributions and the percentage moult increment in mms. carapace length (4.3.3). This pattern suggested much higher moult frequencies in smaller juvenile A. pallipes with up to six moults occurring in the first growth season.

Females that were berried moulted only once in the following moulting season between mid-August and mid-September, after the hatching of the eggs. All animals moulted at least once each year.

Discussion

All species of freshwater crayfish belong to two families, the Astacidae and the Parastacidae, which are indigenous to the northern and southern hemispheres respectively (Hobbs 1974b, Huxley 1896, Kaestner 1970). The Astacidae are divided into two major subfamilies;

Fig. 3.2: Percentage of crayfish in hand and trap samples that had moulted that growth season (●) and the percentage for which a moult was imminent (o) as a function of date in 1974 and 1975. For criteria used in moult staging see Chapter 2. Trend lines fitted by eye


ADULT MALES
% 100
80
60
40
20
0
ADULT FEMALES
% 100
80
60
40
20
0
JUVENILES
% 100
80
60
40
20
0
J J A S O
1974
MONTH
J J A S O
1975
moulting
moulting

the Astacinae, which includes all native European species and the frequently introduced P. leniusculus (Bowler pers. comm., Fuke 1978, Pratten pers. comm.) and the Cambarinae which includes all the North American genera, except Pacifastacus and the minor subfamilies Cambaroidinae and Cambarellinae (Hobbs 1972, 1974b, Kaestner 1970).

The life history of A. pallipes is typical of the Astacinae; moulting is restricted to the summer months, fertilization and egg-laying occur in late autumn and the eggs are carried on the mother's pleopods over-winter to hatch in early summer (Table 3.1; Astacus astacus, P. leniusculus, Abrahamsson 1971b; A. astacus, A. leptodactylus, Kossakowski 1971; Pacifastacus leniusculus trowbridgii, Mason 1974).

The reproductive cycle of the Cambarinae differs in several respects, some of the most obvious of which are summarized here. Only members of the subfamily Cambarinae show a change of form of the adult male, Form I (sexually competent) to Form II (not sexually competent), which occurs at the post-reproductive moult (Creaser 1933, Momot 1964). The cycle is less synchronous in most populations than that observed in the Astacinae. However, the peak of mating activity is still the autumn but the eggs are not usually laid until the following spring to early summer, the sperm having been stored in the annulus ventralis of the female; hatching generally occurs one or two months later

(Orconectes immunis, Orconectes virilis, Caldwell & Bovbjerg 1969; Orconectes propinquus, Capelli 1975; Procambarus pictus, Franz 1977; Cambarus (Orconectes) immunis, Goellner 1943; Kaestner 1970; O. virilis, Momot 1964; Procambarus clarkii, Penn 1943; O. virilis, Weagle & Ozburn 1972).

Life cycles of crayfish species of the subfamily Cambarinae show much more variability than Astacine types both between and within species. For example, some populations of the genus Procambarus had year round recruitment (P. acutus & P. hinei, Albaugh 1973; P. clarkii, de la Brettone & Avault 1976), and in O. immunis some females may carry eggs overwinter (Goellner 1943, Tack 1941).

There appeared to be no common overall pattern in the reproductive cycles of species belonging to the family Parastacidae with some species spawning and hatching out eggs in the summer (Cherax tenuimanus, Morrisy 1970; Engaeus cisternarius, Engaeus fossor, Suter 1977; Cherax albidus, Woodland 1967).and others bearing eggs overwinter (Paranephrops planifrons, Hopkins 1967; Parastacoides tasmanicus, Lake & Newcombe 1975).

The life histories of the two closely related species, O. virilis and O. immunis, were investigated by Caldwell & Bovbjerg (1969) in a region where they are sympatric and have a similar range. They found that the life cycle of O. virilis was relatively 'fixed' and

that of O. immunis more 'flexible' from year to year, this difference was interpreted as having survival value for the latter species as O. virilis typically occurs in running water whereas O. immunis is a pond species where variations in the water level would be more likely to be sufficient to interfere with reproduction. A similar relationship has been described for O. propinquus and C. fodiens by Bovbjerg (1952). The variability in the pattern of life history among the Cambarinae as compared to the Astacinae may, therefore reflect the wider variety of habitat types inhabited by members of the former subfamily by virtue of the highly developed burrowing habits of some species (e.g. Albaugh 1973, Bardach et al. 1972, Momot 1964, Payne 1972, Tack 1941, Williams et al. 1974).

The variations in the timing of the stages of the reproductive cycle of A. pallipes in the aqueduct have been small over the three years 1974-76 (Table 3.1). Although some of the variations may have been due to small differences in water temperature (Fig. 3.1), this did not rule out the possibility of an endogenous circannual rhythm. Such a rhythm has been demonstrated in the cave dwelling crayfish Orconectes pellucidus inermis and the advantages of "(1) anticipating future environmental situations and (2) temporally programming conflicting or competing physiological processes" have been discussed (Jegla & Poulson 1970).

3.4 Individual and population fecundity

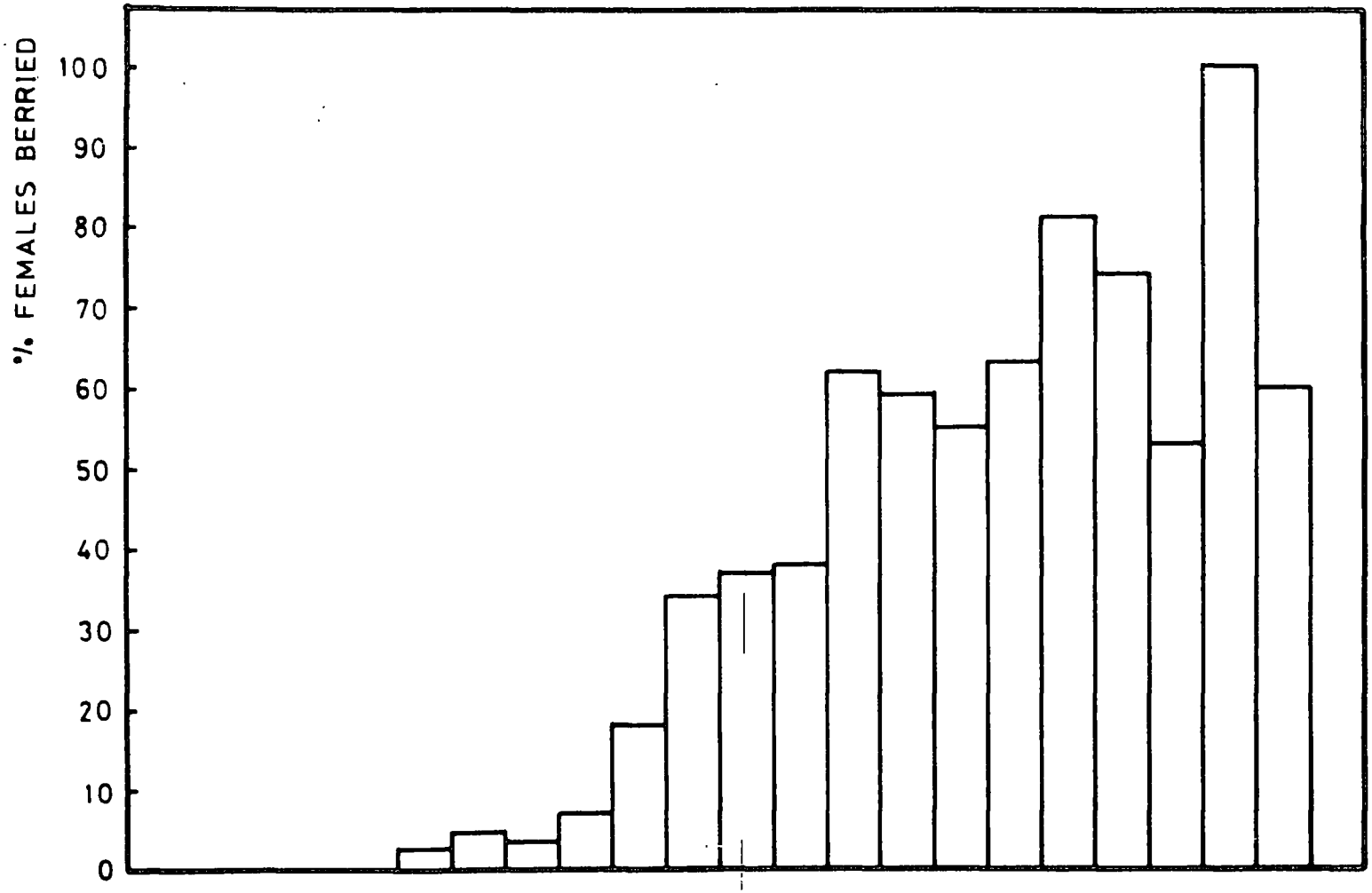
The smallest female crayfish seen to be carrying eggs were 25 mm. carapace length (Fig. 3.3). During the period of fertilization several males (n = 16) were observed whilst copulating in the laboratory and a small number (n = 26) from the aqueduct had some of the white spermatophore deposit (Ingle & Thomas 1974) adhering to the first two pairs of pleopods at this time; the smallest of these males was 22 mm. carapace length.

These minimum carapace lengths at sexual maturity were similar to those observed in other studies of A. pallipes; females - 28 mm., Moriarty(1972); females and males - 26 mm., Pratten (pers. comm.); females - 27 mm., males - 23 mm., Thomas & Ingle (1971); females - 20 mm., Watson (unpubl.).

Although the minimum size at which sexual maturity was apparent in females was 25 mm. carapace length, many females larger than this did not bear eggs (Table 3.2). The estimates of the percentage of 'adult' females (i.e. above the minimum size at which sexual maturity was attained) that bore eggs as calculated from the proportions in hand and trap collections were of a similar magnitude in all three years (32 - 49%).

Trapping had a strong bias towards the capture of adult males throughout the period of ca. 8½ months when the reproductive females bore eggs (Table 3.1, Fig. 3.1, 6.3.1, 6.3.4). However, the proportion of adult females that were berried in the trapped samples (32% in 1974-75

Fig. 3.3: The percentage of females berried from each 1 mm. size class 20 mm. carapace length (e.g. 20 mm. size class = 20.0 - 20.9 mm. carapace length) in the four reproductive cycles from 1973-77. The absolute numbers of berried females and total females in each size class are also shown



	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	
No BERRIED FEMALES						2	3	3	6	18	33	50	53	74	67	53	33	35	24	10	6	3	CARAPACE LENGTH (mms)
TOTAL No FEMALES	44	42	37	53	62	71	73	87	87	98	98	134	138	120	114	96	52	43	32	19	6	5	TOTAL No FEMALES

Table 3.2: Estimates of the proportion of adult females that were berried in the aqueduct in the four reproductive cycles during this study

Reproductive cycle	Number of samples	Total number adult females observed	Estimated mean percentage of adult females berried	Method of estimation and capture
1973-74	6	143	33.22 ± 5.35	Proportion in hand collections
1974-75	13	262	31.57 ± 3.60	Proportion in trapped samples
1975-76	2	492	38.99 ± 6.94	Proportion in hand collections
"	9	276	49.04 ± 8.16	Proportion in trapped samples
"	11	768	47.21 ± 6.78	Proportion in all samples
"	2	492	24.53 ± 14.16	Mark-recapture on hand collections
1976-77	3	841	48.35 ± 1.26	Proportion in hand collections
"	2	561	35.08 ± 18.03	Mark-recapture on hand collections
"	2	524	66.22 ± 32.88	Mark-recapture on hand collections

& 49% in 1975-76) was comparable to that in the hand collections (39% in 1975-76). This indicated that adult females responded to traps in a similar way irrespective of reproductive status.

The mark-recapture estimates of the percentage of adult females berried showed much more sample variation and ranged from 24 to 66%. However, the fact that the mark-recapture estimates encompassed those from sample composition indicated that there was no major bias in the proportion of reproductive females from the hand collections.

The percentage of berried females in 1976-77, as estimated from sample composition (48%), was significantly higher than that in 1973-74 and 1974-75 (33 and 32%, $p < 0.05$ and $p < 0.01$ respectively). The proportion of adult females berried in all samples in 1975-76 was also relatively high (49%). That more females were estimated to have produced eggs in the aqueduct population in 1975-76 and 1976-77 may have been due to an increased nutritional status of the females following the relatively warm summer water temperatures in 1975 and 1976 (Figs. 1.3 and 3.1).

The overall mean percentage of adult females berried in all four reproductive cycles as estimated by sample composition was $38.61 \pm 3.16\%$.

There were two possible interpretations either or both of which could account for less than half of the adult females bearing eggs:-

(i) Only a proportion were fertilized or capable of producing viable ova.

(ii) All females produced viable ova, were fertilized and attached the eggs to the pleopods but many lost their eggs overwinter.

If the second situation were a major factor contributing to this lowered fecundity, a close negative correlation between time since egg attachment and the percentage of females berried would have been expected; there was no suggestion of such a correlation in samples taken from the aqueduct. Some numbered females known to have been berried were recaptured without eggs before hatching had begun in that cycle but these were few in number (n = 21, 4% of the total). The first set of circumstances was therefore believed to have been by far the most important factor contributing to the lowered potential fecundity in the aqueduct.

The A. pallipes population in White Lake, Eire (Moriarty 1972), which had an annual temperature range only slightly broader than that in the aqueduct (3-21°C), had a mean proportion of 41.6 ± 4.2% adult females berried. In this case, there was some evidence that the second explanation was also important as there was a progressive decrease in the proportion of adult females berried from November 1967 (71%) to June 1968 (22%). Low overwinter temperatures could have produced such an effect in White Lake just as the short growth season may have accounted for the low initial breeding success

in the aqueduct. The facts that the proportion of adult females berried was 96% in the River Darent, Kent in November 1963 (Thomas & Ingle 1971) and 55% in the River Ouse, Bucks. in March 1977 (Pratten pers. comm.), both of which were well to the south of the aqueduct and White Lake supported this.

The percentage of females that bore eggs increased with carapace length (Fig. 3.3) as expected, if water temperature and the length of the growth season were limiting factors to reproductive success. Only 3% of the females in the 25.0-25.9 mm. carapace length size class were berried in the breeding cycle from 1973-77, this increased to between 50 and 100% in the size classes above 33mm. carapace length.

It has been suggested that in crayfish populations where all females do not reproduce each year, that those females that are not carrying eggs are 'resting' and bear eggs in alternate years (Kossakowski 1971). In order to account for any other proportion than 50% of the adult females being berried, this effect would have to be superimposed on an increasing probability of bearing eggs for the first time with increasing size. Indeed, there may be two conflicting processes:-

(i) The larger the female the more likely that it will produce eggs (this was clearly important in the aqueduct, Fig. 3.3).

(ii) Bearing eggs in one year reduces the likelihood that a female will bear eggs the following year.

That both these processes were important in the aqueduct was clear from a consideration of numbered adult females, the reproductive status of which was known in consecutive years (Table 3.3). Despite the fact that the majority of females that bore eggs in the first year and were numbered (32) also bore eggs in the second year (23), 28% (9) reverted to a non-reproductive or 'resting' condition. The females which did not bear eggs in the first year (39) were approximately equally divided between staying non-berried (19) and bearing eggs (20) in the second year.

There was a significant positive correlation between the number of pleopod eggs (y) and carapace length (x) in a sample of females (n = 59) taken from the aqueduct within two months of the completion of egg laying (Fig. 3.4). The equation for the regression line was:-

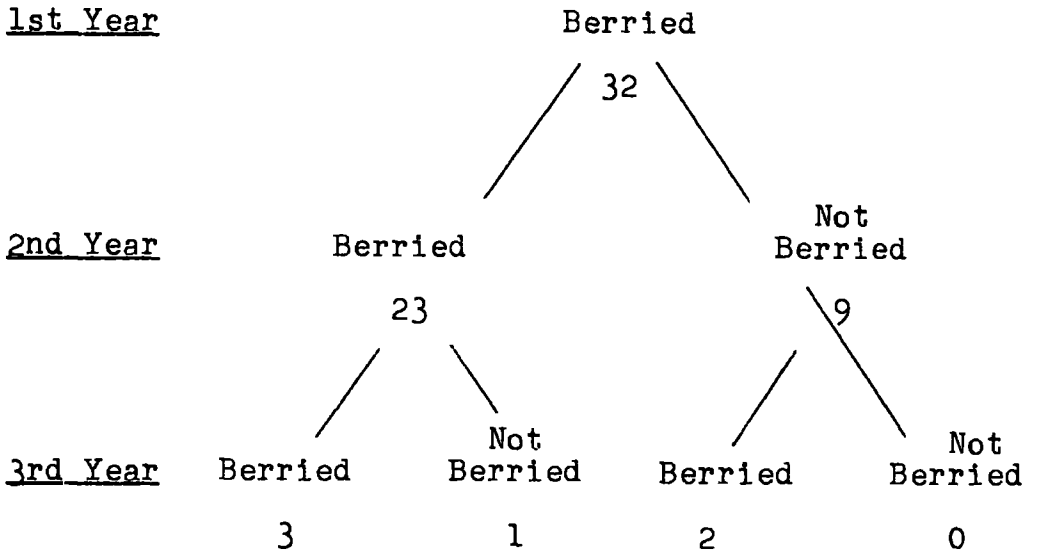
$$y = 7.87x - 207.17 \quad (r = 0.93,\ p < 0.001)$$

The correlation between these two parameters was also calculated for A. pallipes from Lough Lea by Watson (unpubl.):-

$$y = 3.64x - 44.77 \quad (n = 33,\ p < 0.01)$$

This indicated that although the larger females (> 37 mm. carapace length) from both locations bore similar numbers of eggs (> 84), the smaller ones bore far fewer in the aqueduct (e.g. at 32 mm. carapace length mean number eggs per female in the aqueduct was 45 and in Lough Lea was 72). Thomas and Ingle (1971) reported the largest egg bearing female (42 mm.

Table 3.3: Reproductive history of adult female crayfish from the aqueduct in the years 1973-77. Only females whose reproductive status was known for consecutive years were included, thus all of those caught in the first year were caught in the second and only some for a third time



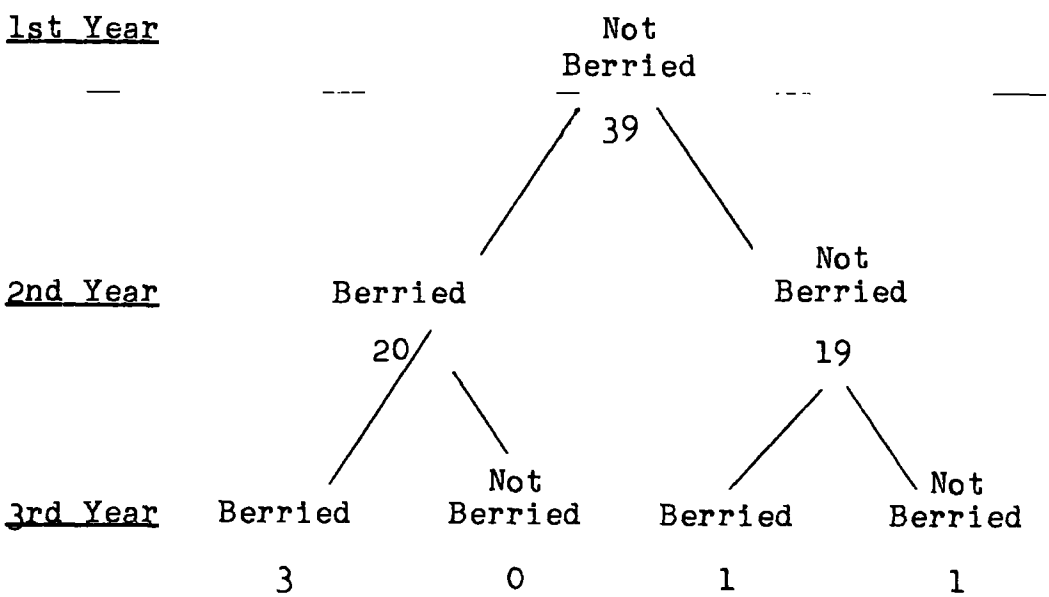
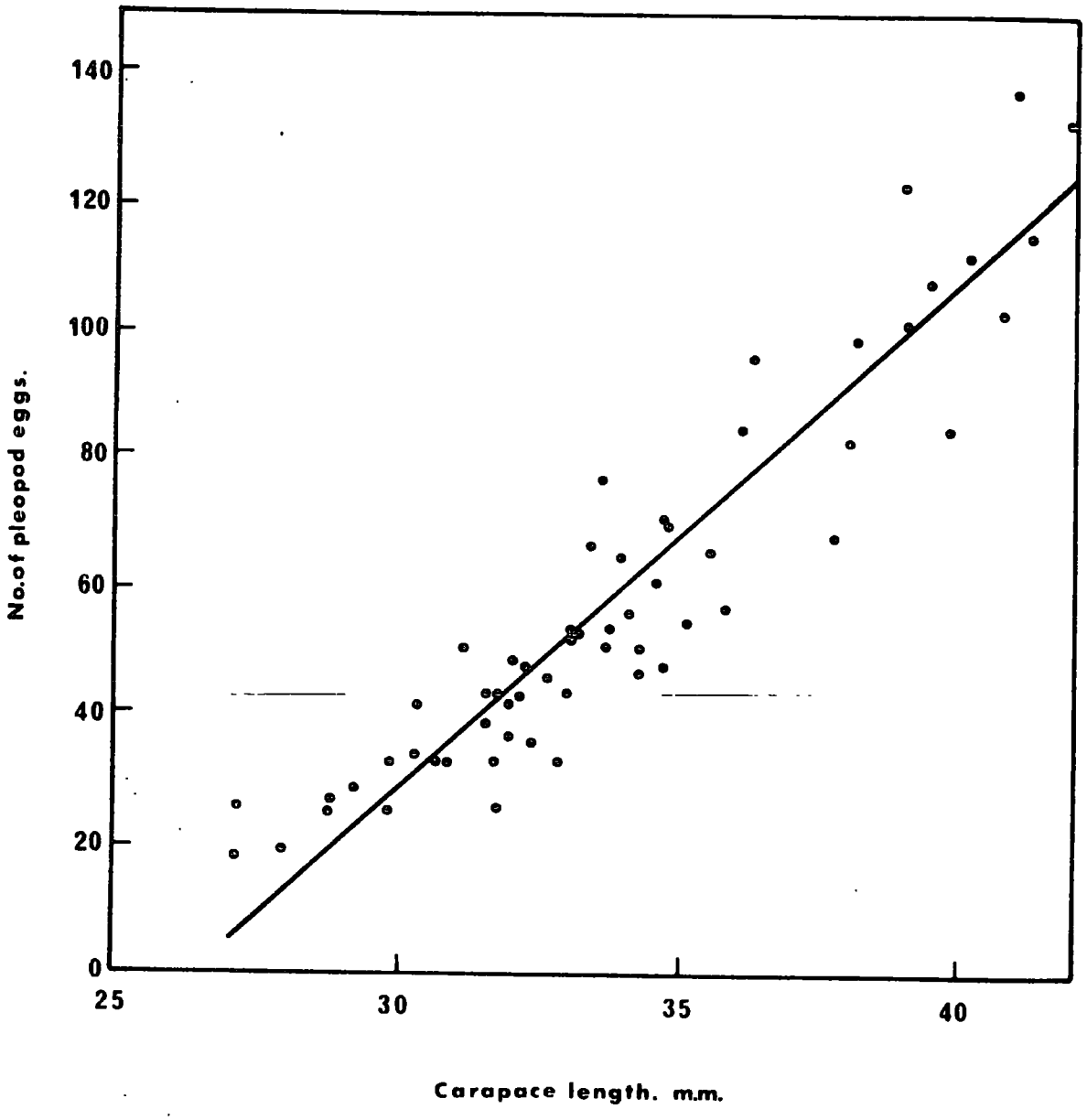


Fig. 3.4: The number of eggs attached to the pleopods as a function of carapace length for A. pallipes from the aqueduct. This sample was taken in November and December as some females lost some, and occasionally all, of their eggs overwinter

$y = 7.87x - 207.17$ ($n = 59$)

SE slope = 0.41

$r = 0.93$, $t = 19.07$, $p < 0.001$


140
120
100
80
60
40
20
0
25
30
35
40
No.of pleopod eggs.
Carapace length. m.m.

carapace length) from the River Darent to have borne 130 eggs (cf. 123 eggs predicted at this size in the aqueduct, Fig. 3.4); whereas smaller females (27 mm. carapace length) bore as many as 70 eggs. These differences amongst the smaller females may have been another consequence of the relatively low water temperatures and/or poor nutritional state of these females in the aqueduct.

An estimate of the potential fecundity each breeding season in any crayfish population is possible if three pieces of information are known, the number of adult females that bear eggs in the period prior to hatching, the size frequency distribution of the adult female sub-population and the relationship between the mean number of eggs per female and size (Fig. 3.4). The number of eggs borne by each size class of females could then be estimated and the total calculated. An alternative method would be to treat the adult female sub-population as a whole and estimate the proportion berried in each size class from the relationship shown on Fig. 3.3; this method could not be employed to give independent estimates for different years in this study, as only numbered individuals were measured (2.1, 5.2), and the relationship between the percentage of females in each size class that bore eggs and carapace length was, therefore, only apparent by pooling all the data. The overall mean percentage of adult females that bore eggs was, however, known in each year. These two

methods gave very similar results when applied to these data (all differences less than two thousand eggs).

These estimates were all slightly too high due to the correlation between number of eggs per female and carapace length having been established soon after egg attachment and the fact that low numbers of females (< 4%) were observed to lose some eggs overwinter.

The potential recruitment in the 1974-75 breeding season (Table 3.4) was calculated from the mean of three mark-recapture estimates of the size of the adult sub-population in the two months prior to hatching (5.4.5), an assumed one to one sex ratio (5.4.5), and the overwinter size frequency distribution shown on Fig. 4.8. Estimates of potential recruitment in the 1975-76 and 1976-77 reproductive seasons (Table 3.4) both relied on a mean of two mark-recapture estimates of the adult female sub-population (5.4.5) and as no size frequency distribution was available in these years the mean of the 1973-74 and 1974-75 distributions (Figs. 4.7 and 4.8) was taken as an approximation. This was unlikely to bias these estimates seriously as it has already been shown that the overall mean percentage of adult females that were berried was an adequate description of fecundity throughout the population; this proportion was in all cases estimated as the proportion of adult females that were berried in trapped and hand collected samples (Table 3.2).

There were no significant differences between years for any of the estimated parameters listed on Table 3.4,

Table 3.4: Estimated potential recruitment ± SE in the years 1974-77

Season	Percentage of adult females berried	Number of adult females	Number of adult females berried	Potential recruitment
1974-75	31.57	5,013 ± 1,652	1,583 ± 522	43,191 ± 14,244
1975-76	47.21	3,444 ± 928	1,626 ± 438	47,142 ± 12,700
1976-77	48.35	3,108 ± 696	1,503 ± 337	43,500 ± 9,753

including the estimated number of potential recruits to the aqueduct population. This was because, although the estimated number of adult females present prior to the hatching of the eggs fell from 1974-77, the percentage of them bearing eggs increased and this resulted in the estimated number of berried females and potential recruitment remaining fairly constant. Momot and Gowing (1977) have suggested that fecundity is density dependent in O. virilis.

General discussion

There was a significant positive correlation between the maximum number of eggs borne on the pleopods and the size of the largest female for twenty-two species of freshwater crayfish ($r = 0.73$, $p < 0.001$; Fig. 3.5). This was also often the case for individuals of the same species of varying sizes (e.g. Fig. 3.4; P. acutus, P. hinei, Albaugh 1973; P. leniusculus, Flint 1975; C. (O.) immunis, Goellner 1943; P. planifrons, Hopkins 1967; O. virilis, Weagle & Ozburn 1972). This suggests that there is a minimum size below which no crayfish egg would be viable.

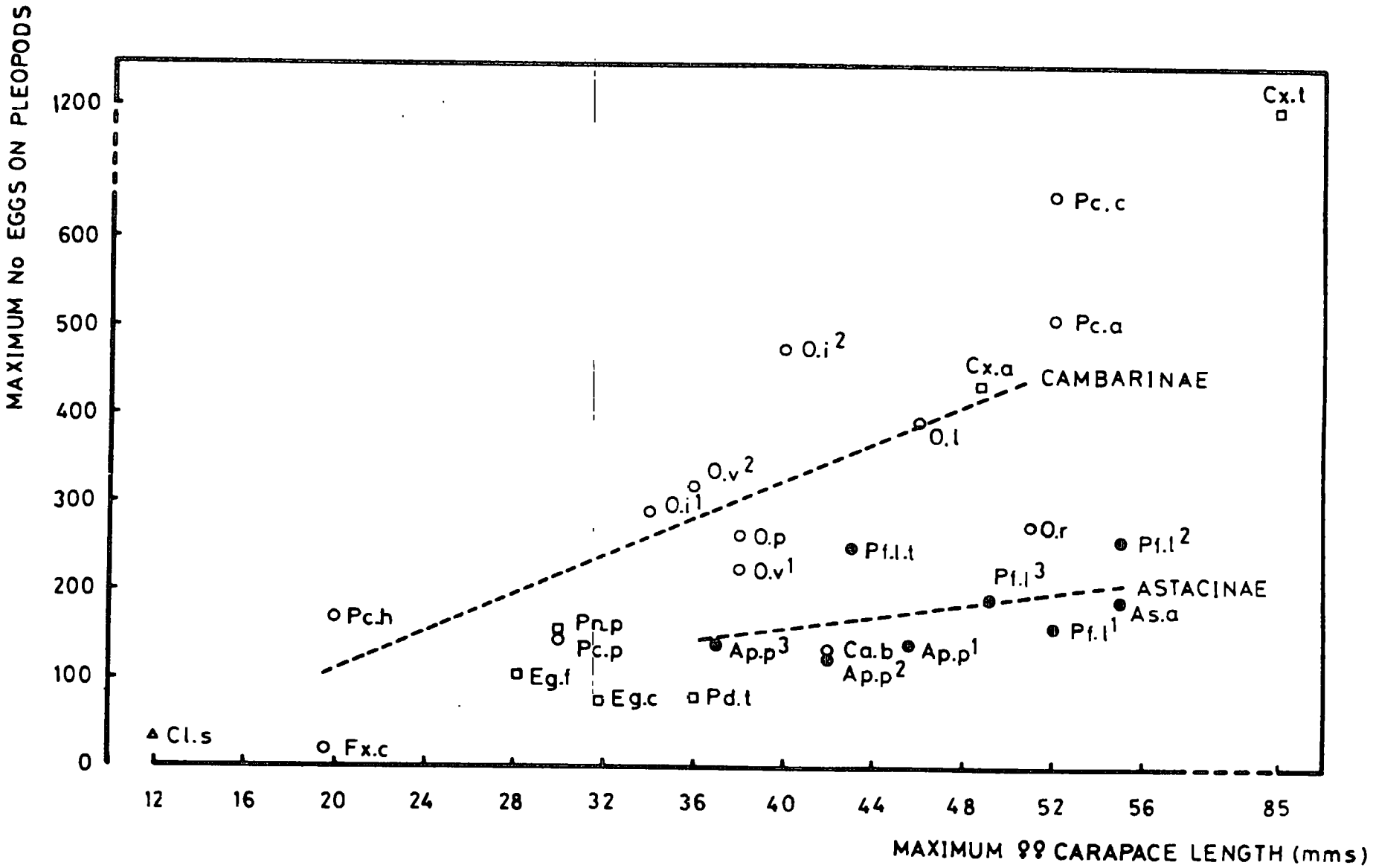
As shown in the broken regression lines on Fig. 3.5, members of the subfamily Astacinae have a lower reproductive potential than the subfamily Cambarinae (mean maximum number of eggs 182.50 ± 17.77, 297.85 ± 48.16 respectively, $t = 2.25$, $p < 0.05$). The reproductive potential of all the parastacid species except C. albidus and C. tenuimanus were similar to those of the astacin types.

Fig. 3.5: The maximum number of eggs borne on the pleopods as a function of the size of the largest female in mm. carapace length (when only total length was stated carapace length was assumed to have been half this value, Fig. 3.9) for twenty-two species of crayfish

Family Astacidae:- Astacinae - ●
Cambarinae - o
Cambarellinae - △

Family Parastacidae:- □

	Species	Source of Reference
As.a	Astacus astacus	Abrahamsson 1971a
Ap.p[1]	Austropotamobius pallipes	Author
Ap.p[2]	"	Thomas and Ingle 1971
Ap.p[3]	"	Watson unpubl.
Ca.b	Cambarus bartoni	Penn 1950
Cl.s	Cambarellus shufeldtii	" "
Cx.a	Cherax albidus	Woodland 1967
Cx.t	Cherax tenuimanus	Morrissy 1970
Eg.c	Engaeus cisternarius	Suter 1977
Eg.f	Engaeus fossor	" "
Fx.c	Orconectes (Faxonella) clypeatus	Smith 1953
O.i[1]	Cambarus (Orconectes) immunis	Goellner 1943
O.i[2]	Orconectes immunis	Penn 1950
O.l	Orconectes limosus	Kossakowski 1971
O.p	Orconectes propinquus	Capelli 1975
O.r	Orconectes rusticus	Penn 1950
O.v[1]	Orconectes virilis	Momot 1964
O.v[2]	"	Weagle and Ozburn 1972
Pf.l[1]	Pacifastacus leniusculus	Abrahamsson and Goldman 1970
Pf.l[2]	"	Abrahamsson 1971a
Pf.l[3]	"	Flint 1975
Pf.l.t	P. l. trowbridgii	Mason 1974
Pn.p	Paranephrops planifrons	Hopkins 1967
Pd.t	Parastacoides tasmanicus	Lake and Newcombe 1975
Pc.a	Procambarus acutus	Albaugh 1973
Pc.c	Procambarus clarkii	Penn 1950
Pc.h	Procambarus hinei	Albaugh 1973
Pc.p	Procambarus pictus	Franz 1977


MAXIMUM No EGGS ON PLEOPODS
1200
600
500
400
300
200
100
0
12
16
20
24
28
32
36
40
44
48
52
56
85
MAXIMUM ♀♀ CARAPACE LENGTH (mms)
Cx.t
Pc.c
Pc.a
O.i 2
Cx.a
CAMBARINAE
O.l
O.v 2
O.i 1
O.p
O.v 1
Pf.l.t
O.r
Pf.l 2
Pf.l 3
ASTACINAE
As.a
Pf.l 1
Pc.h
Pn.p
Pc.p
Ap.p 3
Ca.b
Ap.p 2
Ap.p 1
Eg.f
Eg.c
Pd.t
Cl.s
Fx.c

The proportion of adult females that bore eggs in any one year varied from the vast majority (A. astacus, P. leniusculus, Abrahamsson, 1971b; P. leniusculus, Abrahamsson & Goldman 1970; O. propinquus, Capelli 1975; O. (F.) clypeatus, Smith 1953; C. albidus, Woodland 1967) to less than half (C.(O.) immunis, Goellner 1943; P. tasmanicus, Lake & Newcombe 1975; C. tenuimanus, Morrissy 1970). The frequency of spawners in a year class usually does not approach 100% in the first one or two years after some individuals first become sexually mature (Fig. 3.3; Morrissy 1970). The fact that all animals did not become sexually mature at the same size (although all animals above the minimum size for sexual maturity are often classed as adult) did not altogether account for the low frequency of spawners in the aqueduct (ca. 42%) or the variation from 39-63% observed for C. tenuimanus by Morrissy (1970). These instances of lowered breeding success may have been due to some environmental factor, such as water temperature or food availability.

Abrahamsson (1972a) has shown that in populations of A. astacus near to its northern limit of distribution in Sweden the frequency of spawning females is low, particularly for the smaller females. The spawning frequency of the larger females was little affected by latitude. He concluded that water temperature was the most important factor but that food supply also influenced reproductive success in lakes at similar

latitudes. This was consistent with the marked increase in the percentage of females bearing eggs with carapace length in the aqueduct (Fig. 3.3) and the conclusion that this population was near to the northern limit of distribution for A. pallipes.

The loss of some eggs from the pleopods before hatching due to physical damage and disease also occurred particularly in the subfamily Astacinae which carry the eggs overwinter (3.3; Kossakowski 1971).

There is very little data on the actual reproductive rates of freshwater crayfish due to the difficulty in sampling hatchlings once they become independent of the mother. Kaestner (1970) reports about 20 hatchling A. astacus survive to a postlarval stage from each brood, Kossakowski (1971) assumed a mean of 16 A. astacus survived to the first autumn and Lake & Newcombe (1975) observed up to 10 independent hatchlings per brood in P. tasmanicus.

Recruitment to natural populations of freshwater crayfish is, therefore, clearly well below the theoretical maximum for a number of reasons.

3.5 Trophic relationships

The body of knowledge regarding the position or positions of A. pallipes in the food web is meagre but it is clearly a complex one. It is preyed upon by a wide variety of animals ranging from its own kind to fish, mammals and birds (Table 3.5) and it is an omnivore in the broadest sense of the term taking plant

Table 3.5: A summary of the known and suspected predators on A. pallipes

Common name	Latin name	Source of reference (percentage occurrence)
Crow	Corvus sp.	Pratten pers. comm.
Eel	Anguilla anguilla	Watson unpubl. (11%)
Heron *	Ardea cinerea	Author (possible) Pratten pers. comm. Macan & Worthington 1951
Otter	Lutra lutra	Pratten pers. comm. Macan & Worthington 1951
Perch	Perca fluviatilis	Mann 1978 Watson unpubl. (38%)
Brown trout	Salmo trutta	Frost & Brown 1967 Pratten pers. comm.
Rainbow trout	Salmo gairdneri	Watson unpubl. (20%)
Canadian brook trout*	Salvelinus sp.	Author (possible)
Water voles *	Arvicola amphibius	Lawrence & Brown 1967 Southern 1964 Author (possible)
Cannibalism*	A. pallipes	Author (frequent) Pratten pers. comm. Watson unpubl.

* predators present in the study area

and animal material both living and dead (personal observations, Pratten pers. comm., Watson unpubl.).

The trophic ecology of A. pallipes was not systematically studied during the course of this project. However, so much of the recorded 'information' concerning this aspect of the biology of A. pallipes is anecdotal and/or simply inaccurate that the small amount of information collected in this study and that from several others, either unpublished or still in progress, is summarized below.

Twenty-two gut contents of A. pallipes were fixed in Bouins solution, stained with Safranin O and Light Green and mounted in DPX. These gut contents were taken from animals that had been hand collected by inserting a plastic Pasteur pipette between the mandibles and into the oesophagus within half an hour of capture. The most abundant species of macrophyte and some types of terrestrial leaf litter found at the collection site were fed to A. pallipes held in the laboratory (these crayfish were starved for 48 hours, prior to feeding, to clear the gut). The gut contents from these animals were treated as above and 'type' slides of these plants prepared.

All the samples analysed as above contained large amounts of finely divided material of vegetable origin that could not be further identified but which appeared, in comparison to the 'type' slides, to have been decomposing before ingestion and was thus designated as

detritus. Also some inorganics were always present in the form of sand or silt, as would have been expected if the animals had been feeding on detritus. The results of the examination of twelve gut contents of A. pallipes from the aqueduct, five females and seven males, are listed below:-

All 12 contained fragments of the aquatic moss Fontinalis antipyretica.

3 contained various diatoms of species that were typically associated with plants and substratum species.

1 contained fragments of terrestrial leaf litter of unknown species.

1 contained a fragment (< 1 mm.) of arthropod limb that bore many fine setae and was therefore probably not of A. pallipes but of Gammarus sp. or an insect larva.

Gut contents of crayfish collected from other areas within the Whittle Dene/Hallington reservoir complex were similar, with the exception that often none of the plant material was identified. Potamogeton crispus was identified in several crayfish guts from a feeder stream where it was abundant.

Laboratory-held crayfish readily ate all forms of aquatic vegetation collected from areas where they themselves occurred including Elodea canadensis, F. antipyretica, Myriophyllum spicatum, Nitella sp., P. crispus and Rorippa sp. Plant material was usually bound at the base of the stem with lead wire to ensure it held bottom. The overall effect of these crayfish

when grazing over four days was observed to be that not only were significant amounts of all the plants tried ingested but that in all plants some stems, and with M. spicatum and Nitella sp. all stems, were eaten through. It would, therefore, be predicted that the impact of the grazing of A. pallipes on aquatic macrophytes would be far in excess of the amount of plant material actually ingested. In flowing waters, much of the severed plant material would be washed away, whereas in still waters, it would enter the detritus food web of which A. pallipes is also a part.

A. pallipes in tanks showed a very marked preference for meat, particularly highlyvascular offal, such as liver and spleen, and fish over vegetable matter. That this preference also existed in the wild was confirmed by the much larger catches when traps were baited with ox-liver (6.3.1, Moriarty 1972).

The characteristics of animals which had been cannibalised in the laboratory were unmistakable, the ventral integument at the carapace/abdominal junction was eaten through and the contents of the thorax and less often the tail ingested. Animals in a very early postmoult condition were often completely devoured. There was much evidence of cannibalism in the laboratory, usually of crayfish in the first few days following a moult; such animals were also occasionally found in the aqueduct.

That crayfish were omnivorous, taking macrophytes

and detritus, and had a preference for animal material when available has also been found by Pratten (pers. comm.) and Watson (unpubl.).

The known and suspected predators on A. pallipes are listed on Table 3.5. Specimens of all species listed as possible predators on the aqueduct population (with the exception of the heron) were examined but no evidence of predation was found. The nature of the bank and sides of the aqueduct (Plates 1.1 & 1.2) would make the heron seem an unlikely predator on this population. Several water voles were caught and drowned in traps, the reason for these trap entries was not known; however some sources claim this species is not wholly herbivorous (Lawrence & Brown 1967, Southern 1964).

General Discussion

There is a commonly held opinion that astacuran decapods are primarily carnivorous (e.g. Davies 1964, Emadi 1974) or are scavengers (e.g. Albaugh 1973, Crocker & Barr 1968, Kossakowski 1971). There is no direct evidence to support this opinion which has been perpetuated anecdotally and probably originated from the strong preference for animal matter shown by captive animals (e.g. Emadi 1974, Kossakowski 1971) and the fact that members of the closely related and better known family Homaridae are largely carnivores or scavengers (e.g. Heydorn 1969, Kaestner 1970). However, it is now well established that many species of freshwater

crayfish are omnivorous in the broadest sense; feeding on aquatic and terrestrial plants, living and dead animal matter and detritus; in varying proportions depending on species, age and availability (e.g. Abrahamsson 1966, Albaugh 1973, Caldwell & Bovbjerg 1969, Capelli 1975, Chapman & Lewis 1976, Creaser 1934, Crocker & Barr 1968, Flint 1975, Koslucher & Minshall 1973, Kossakowski 1971, Lake & Newcombe 1975, Suter & Richardson 1977, Tack 1941, Thomas 1978, Woodland 1967). The broad spectrum of material taken as food suggests an element of opportunism; there is, however, a growing body of evidence to support the view that feeding is not random on what is available but that preferences do exist which vary with age and also possibly with sex (e.g. Albaugh 1973, Capelli 1975, Flint 1975 & Mason 1963). It has also been suggested that very small individuals may be filter feeders (Thomas 1978).

All species of freshwater crayfish show a marked preference for animal material in the wild as carrion or trap bait and in captivity (e.g. Albaugh 1973, Bardach et al. 1972, Capelli 1975, Chapman & Lewis 1976, Moriarty 1972, Norton 1942, Suter & Richardson 1977, Woodland 1967) but their clumsy movements render them inept as predators on small active prey (Abrahamsson 1966, Albaugh 1973, Woodland 1967). In some species, the juveniles have been shown to prey extensively upon invertebrates but this is probably explained by their common preferred habitat amongst aquatic macrophytes (Capelli 1975, Creaser 1934, Flint 1975). Cannibalism, particularly at the moult, is also

universal, to varying degrees, among freshwater crayfish (e.g. Abrahamsson 1966, Bardach et al. 1972, Capelli 1975, Chapman & Lewis 1976, Flint 1975, Kossakowski 1971, Momot 1967, Woodland 1967).

A wide variety of animals have been reported to prey on freshwater crayfish at varying intensities; from invertebrates (e.g. Dye & Jones 1974) to fish, amphibians, reptiles, birds and mammals (e.g. Caldwell & Bovbjerg 1969, Capelli 1975, Chapman & Lewis 1976, Crocker & Barr 1968, Lagler & Lagler 1943, Lagler & Ostenson 1942, Lowe 1921, Momot 1967b, Penn 1950, Tack 1941, Woodland 1967). Crayfish as a food source were, however, generally underutilized by predators (Momot 1964, 1967a, 1967b and Momot & Gowing 1977) including man (Bardach et al. 1972).

3.6 Displacements of crayfish in the aqueduct

3.6.1 Migration into and out of the study area

The population being studied at any one time was defined as all crayfish between a point eighteen meters above the outlet from the aqueduct and the sluice gates at the upper end (i.e. between sections 6 and 122 was the study area, one section = 6 meters, 1.1). There were believed to be few crayfish in the aqueduct outside this stretch for the following reasons:-

(a) The lowest eighteen meters of aqueduct leading into the East Pond is at an increasing slope and the run off is very rapid (Plate 1.2b). Hand-collecting in this stretch when the water level was lowered produced few

crayfish (< 10). Traps set in the East Pond near the outlet produced a total of fifteen crayfish, on the four occasions when they were not damaged or washed away by the current, none of these was marked. Despite this fact, emigration must have occurred from this part of the aqueduct but it was unlikely that immigration would have been significant due to the strength of the current at this end of the aqueduct.

(b) Up to the sluice gates (section 122), the walls of the aqueduct are made of sandstone blocks or brick; above this point the floor and sides are concrete for the 390 meters before the watercourse emerges from below ground (Fig. 1.1). Hand collecting, on three occasions along the alternative route for the water flow (into the West Pond) when the total flow was diverted into the stretch containing the study population, produced no crayfish. Four traps were baited and set on twelve occasions in the 24 meters of concrete lined stretch above the sluice gates. The mean catches in these traps were inversely proportional to the distance above the sluice gates:-

Section number	Mean trap catch
122	3.41 ± 0.24
126	0.92 ± 0.06
130	0.84 ± 0.06
134	0.67 ± 0.05

The overall mean catch in these traps (1.46 ± 0.39) was significantly less than that in the traps from lower

down the aqueduct (4.29 ± 0.28; $t = 5.89$, $p < 0.001$). The lower numbers of crayfish in the concrete lined stretch were believed to be mainly foragers from the study population (possibly as a result of putting baited traps in). This was because of the relatively high proportions of those crayfish trapped in, and returned to, the concrete lined stretch that were initially caught (46%), or subsequently recaptured (57%), below the sluice gates compared to the overall trap recapture rate within the study population (9%).

All gains to the study population were, therefore, believed to be internal; losses could occur due to both death and emigration.

3.6.2 Displacements within the study area

Successive captures of individually numbered crayfish provided data on how far these animals had been displaced between captures. If movements were not always progressive, these displacements were the minimum or net distance moved between captures (upstream distances were defined as positive and downstream distances as negative). As lowering the water level to hand collect must have caused considerable disturbance to the population (5.2), only the distances 'moved' between trapped samples during periods when the water level was not adjusted were considered as being representative of movements under natural conditions.

Numbers of individuals that moved up and downstream

	Trapped			Hand collected		
	Males	Females		Males	Females	
Upstream	202	17	219	29	23	52
Downstream	181	16	197	26	26	52
No displacement	33	5	38	3	4	7

The numbers of individuals that moved upstream and downstream were similar for both trapped ($\chi^2 = 0.02$, $p < 0.80$) and hand collected samples ($\chi^2 = 0.35$, $p < 0.50$). In both cases few animals were recaptured in the same section to which they were returned (hand 6.31%, trap 8.37%). That movements were not usually progressive in either direction was clearly shown by considering the displacements of twenty-one randomly selected animals that were trapped at least four times (Fig. 3.6). If crayfish had recognizable home ranges in the aqueduct, displacements, such as that of individual number XVIII, would have been expected to be much more frequent. Instead, the vast majority of displacements between captures were greater than 5 sections (30 meters) e.g. individual numbers II, IV, V, VIII, IX, X etc.

These displacements and the mean net distance 'moved' of 19.56 $\pm$ 154.26 (SD) meters (Table 3.6) suggests that A. pallipes did not have a recognisable home range in the aqueduct.

The mean and range of the net distances moved between samples of different types are listed in

Fig. 3.6: The displacements of twenty-one (I -XXI) randomly selected individuals between trapped samples during periods when the water level was left unadjusted. Capture positions in terms of section number (1 section = 6 meters) read from left to right or are indicated where necessary (↑)

● - Position of capture

o - Capture and recapture in same section

– – – - Randomized from one section to another between capture and return to the aqueduct

The mean net distance moved ± 2 SD (upstream = positive, downstream = negative) is also shown on a separate scale marked off in sections

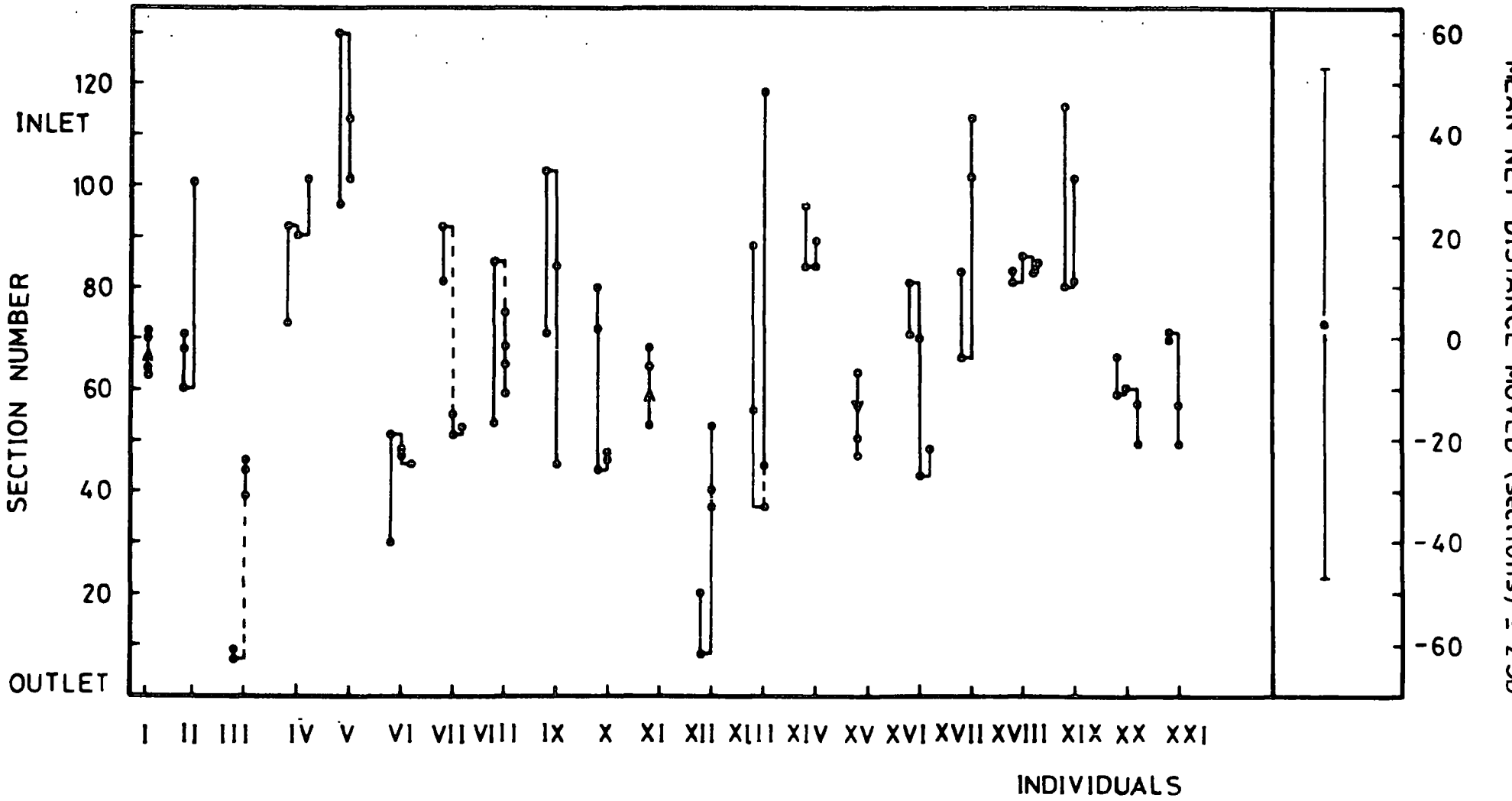

INLET
OUTLET
SECTION NUMBER
120
100
80
60
40
20
I II III IV V VI VII VIII IX X XI XII XIII XIV XV XVI XVII XVIII XIX XX XXI
INDIVIDUALS
60
40
20
0
-20
-40
-60
MEAN NET DISTANCE MOVED (sections) ± 2SD

Table 3.6: Mean net distances moved between successive captures by the different sampling methods

Sampling method	Mean net distance moved (m.) ± SE	Range net distance moved (m.) ± SE	Number of observations
Trapping			
1. Normal	14.75 ± 9.61	-354, + 582	236
2. Randomized	64.78 ± 19.75	-558, + 660	103
3. Consecutive	-13.72 ± 9.11	-312, + 360	108
4. Randomized and Consecutive	30.00 ± 79.58	-174, + 486	7
Total trapped	19.56 ± 7.24	-558, + 660	454
Hand collection	32.70 ± 14.71	-324, + 480	111

Categories of trapped samples:-

	Crayfish returned to section caught from	Crayfish captured on consecutive occasions
1. Normal	Yes	No
2. Randomized	No	No
3. Consecutive	Yes	Yes
4. Randomized and Consecutive	No	Yes

Table 3.6. The only net downstream movement was observed between the trapped samples that were taken on consecutive trapping visits, although this was not significantly less than zero (-13 meters, $t = 1.51$, $p > 0.10$). This was also the smallest mean net movement calculated and this was probably associated with the practice of releasing the catch and resetting baited traps on the same day (6.2.3, 6.3.5). Those crayfish that were not returned to the same section as they were caught from were said to have been randomized and showed the largest mean net movement which was significant in an upstream direction (65 meters, $t = 3.28$, $p < 0.01$). This overall positive rheotactic response may have been due to more intense hide seeking behaviour in the new surroundings. Mean net movement between normal trapped samples (15 meters, $t = 1.53$, $p > 0.10$) and between samples that were randomized and consecutive (30 meters, $t = 0.38$, $p > 0.70$) were not significant. However, the means of the net movements between all trapped samples and between all the hand samples were both significant in an upstream direction (20 & 33 meters, $t = 2.70$, $p < 0.01$ & $t = 2.22$, $p < 0.05$, respectively).

All hand collected samples were randomized in an attempt to increase movements and facilitate thorough mixing of marked and unmarked crayfish; an essential assumption inherent in the mark-recapture estimation of population parameters. This was successful as the mean total distance moved (i.e. irrespective of direction)

between hand samples was also calculated as 110.00 ± 10.77 meters; this was significantly greater than the calculated mean total distance of 16.76 ± 0.92 meters between the trapped samples ($t = 8.63$, $p \ll 0.001$). It was calculated that these displacements between trapped and hand samples represented a mean total 'movement' of 5.25 meters/day with a maximum of 104 meters/day! A. pallipes is therefore a vagrant animal.

3.6.3 Diel activity patterns in the aqueduct

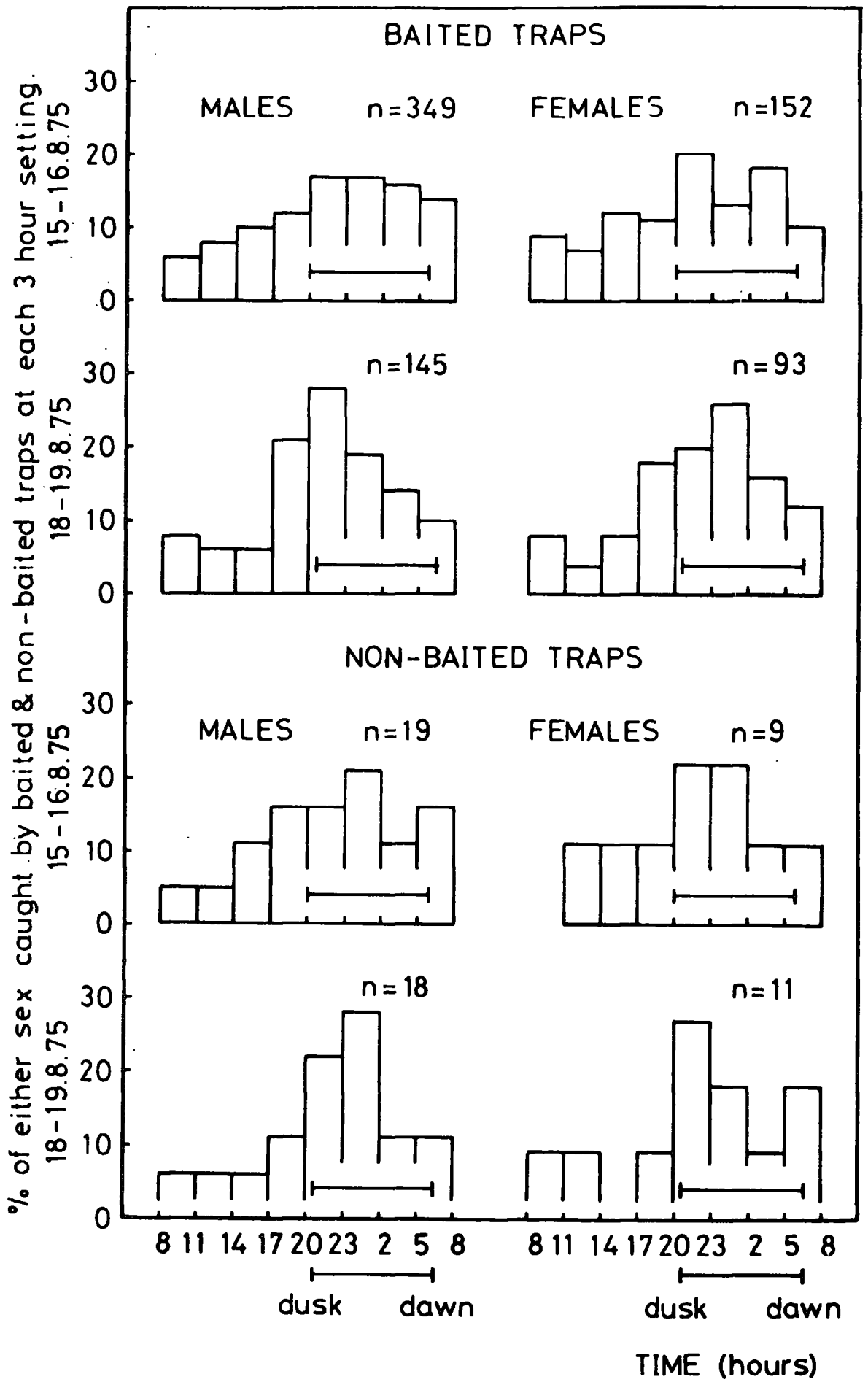
The activity pattern was studied over two twenty four hour periods by continually setting and emptying fourteen baited and fourteen non-baited traps arranged alternately at six meter intervals along the aqueduct. These traps were emptied and reset every three hours and all catches were retained and returned at the end of the study period. Catch/trap can only be an indirect index of activity and baited and non-baited traps were employed in an attempt to differentiate between feeding and hide seeking activity.

The percentages of males and females caught in each three hour period in baited and unbaited traps on both of the days 16. 8 and 19. 8.75, are shown on Fig. 3.7. All crayfish species are generally assumed to be principally nocturnal feeders and to be much less active at other times (with the possible exception of cave-dwelling species such as Orconectes inermis inermis, Hobbs 1974a). As can be seen from Fig. 3.7, the highest catches always occurred at night (up to a mean value of 6.35 crayfish/

Fig. 3.7: The percentage of crayfish of either sex caught in each 3 hour trapping period on 16. 8.75 and 19. 8.75 for the 14 baited and 14 non-baited traps.

n = total sample size

⊢—⊣ = dusk to dawn from personal observation


BAITED TRAPS
MALES
n=349
FEMALES
n=152
15-16.8.75
n=145
n=93
18-19.8.75
NON-BAITED TRAPS
MALES
n=19
FEMALES
n=9
15-16.8.75
n=18
n=11
18-19.8.75
% of either sex caught by baited & non-baited traps at each 3 hour setting.
0
10
20
30
8 11 14 17 20 23 2 5 8
dusk
dawn
TIME (hours)

trap/3 hours in the baited traps and 0.43 crayfish/trap/3 hours in the non-baited traps). Daytime catches were, however, not as low as would have been expected for a principally nocturnal animal; if catch/trap was a reasonably good index of activity (up to a mean of 4.21 crayfish/trap/3 hours and 0.29 crayfish/trap/3 hours respectively). There was no obvious difference in the pattern of diel activity as shown by baited and non-baited traps.

General Discussion

Individually marked A. pallipes were frequently displaced considerable distances apparently at random between successive trap captures in the aqueduct. As only sequences of trapped samples taken when the water level was not lowered were considered, these movements must represent the minimum distance moved under as near natural conditions as was possible; assuming that any effects due to the lowering of the water level lasted no longer than about one month. There was no evidence to suggest that A. pallipes had a recognisable home range in the aqueduct. However, some individuals, particularly large adult males, may behave territorially in that they defend whichever hide they occupy (personal observations in laboratory and field conditions).

Reports of extensive movements of marked freshwater crayfish are numerous (e.g. Abrahamsson 1971a, Camougis & Hichar 1959, Capelli 1975, Flint 1975, 1977, Kossakowski 1965, Mobberley & Pfrimmer 1967, Momot &

Gowing 1972). Some authors have observed migrations that have been associated with breeding (e.g. Henry 1951) and compensation for the effects of floods (e.g. Momot 1966). The greater net distances moved in an upstream direction by A. pallipes in the aqueduct may have been a result of a response to maintain position in the aqueduct, or to spread upstream and colonize new areas as observed in the mitten crab, Eriocheir sinensis (Hynes 1972). Only in two studies of freshwater crayfish has a measurable home range been reported. Black (1963) estimated the home range of two species of the genus Procambarus as less than thirty meters and Merkle (1969) stated that the "home areas" of Orconectes juvenalis varied in length from 9.4 to 47 meters. Whether freshwater crayfish are territorial and/or have a measurable home range or not, they are highly mobile benthic invertebrates.

The mobility of the reptant decapods is exemplified by the spiny lobster Panulirus argus which undergoes mass migrations in long queues with one animal touching its anterior pereiopods to the abdomen of the one in front; such queues are sometimes more than 1,000 individuals in length. Experimentally displaced lobsters have a remarkable homing instinct and groups of lobsters taken from queues and put into aquaria have remained linked up and continued marching for an estimated 500 miles! (Herrnkind 1969).

It is widely accepted that most decapods of the superfamily Nephropsidea feed nocturnally and remain in

hides by day (Kaestner 1970). Assuming that trap returns were a reliable index of activity, A. pallipes in the aqueduct was approximately twice as active by night as by day (Fig. 3.7):-

	Mean % of total catch/3 hours	
	Day	Night
Baited traps	10.47	17.57
Non-baited traps	9.00	16.57

These trap returns may have over-represented daytime activity, as even the possibly small number of animals that were active by day could have been exposed to a saturation of traps, and trap returns at night may have been limited by the number of traps set. There are, however, several other reports based on direct observations using SCUBA of considerable daytime activity (> 25% of nocturnal activity) which has in some cases been attributed to crayfish leaving their hides to feed even when they might be exposed to predators in "overcrowded" populations (Abrahamsson 1971a, Capelli 1975, Flint 1975, 1977).

3.7 Infestation of A. pallipes in the aqueduct by the microsporidian parasite Thelohania contejeani Henneguy

T. contejeani is a pathogenic endoparasite of both A. pallipes (Cossins & Bowler 1974, Vey & Vago 1972) and Astacus astacus (Kossakowski 1971, Voronin 1971). It has been prevalent in the aqueduct and other areas of Northumberland for at least 11 years, is widespread in

England (Cossins 1974) and has also been reported in Russia (Voronin 1971), Poland (Kossakowski 1971), Finland (Sumari & Westman 1969), Germany (Schäperclaus 1954) and France (Vey & Vago 1972). This chronic condition is also known as porcelain disease as it can only be easily recognized by eye in the later stages when all striated muscle blocks in the body are infested and appear white, as compared to the normal translucent muscle (Cossins 1972). The spread of the parasite through the hosts muscle fibres results in a progressive deterioration in muscle function and ultimately death (Kudo 1924).

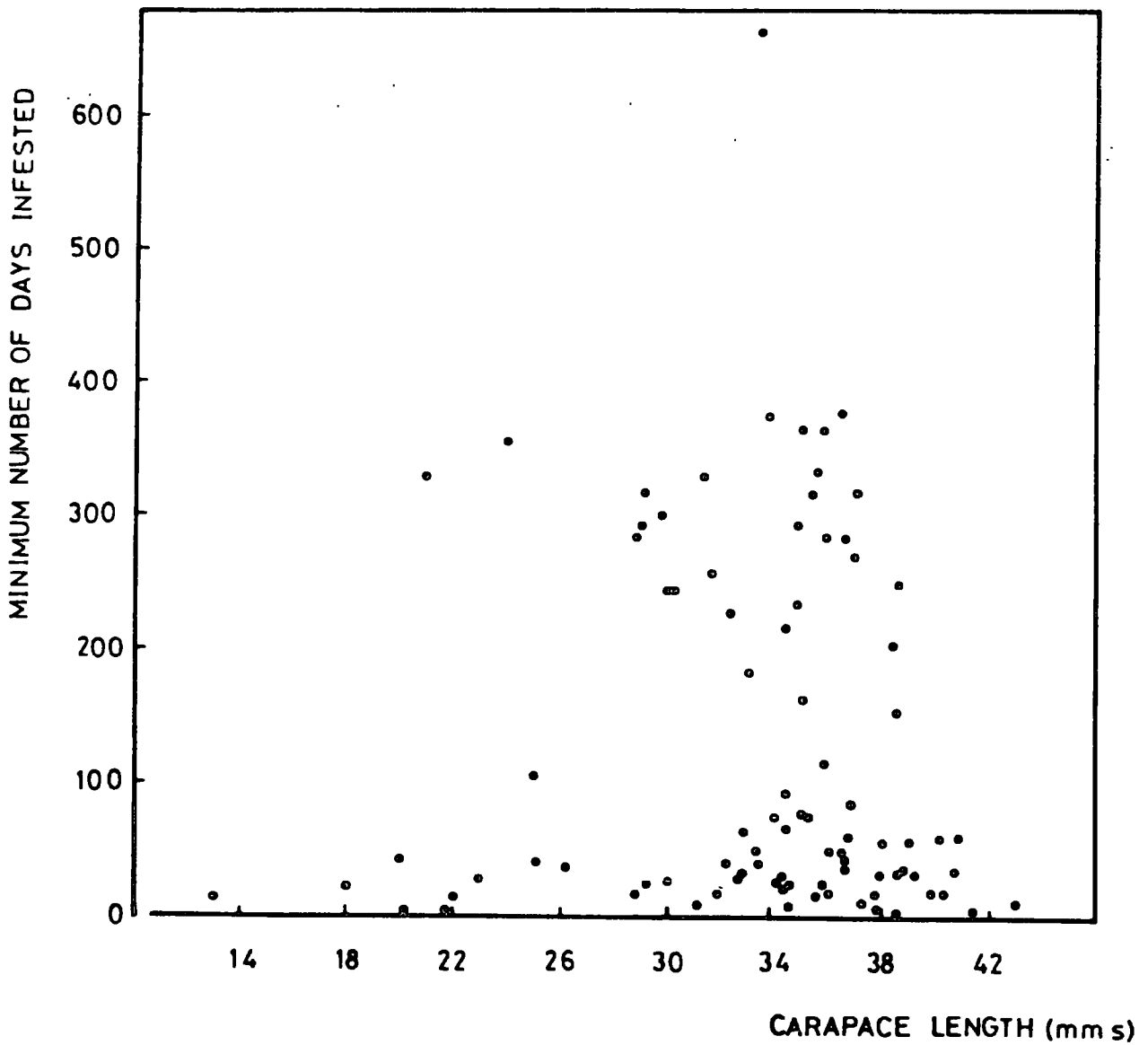
It was probable that all stages of the life cycle of A. pallipes were affected by this parasite as the smallest individual which was recognized as parasitized was 13 mm. carapace length (Fig. 3.8). There was no information available concerning the time course of this disease before it becomes apparent on external examination. As a crayfish of the 13 mm. carapace length was in the 1+ year class (4.3.3), this stage must have been a year or less in this size of animal. Once a spore which has transmitted this infection to a crayfish has undergone any intermediate stages, a progressive invasion of the host's muscle blocks will begin. Therefore, the disease might be expected to take longer to become apparent in larger individuals.

The percentage incidence of crayfish at a recognizable stage of infestation in five size classes is

Fig. 3.8: The total number of days that individual crayfish (which were caught several times) were recognised as infested by Thelohania contejeani as a function of carapace length

● - alive at last capture

o - dead at last capture


MINIMUM NUMBER OF DAYS INFESTED
600
500
400
300
200
100
0
14
18
22
26
30
34
38
42
CARAPACE LENGTH (mm s)

shown in Table 3.7. The level of infestation showed a clear trend to increase with size from 1.43 and 0.91% in the males and females < 20 mm. carapace length to 8.41 and 12.90% in the males and females ⩾ 35 mm. carapace length. This trend may have been entirely due to the progressive nature of the disease but smaller crayfish being less cannibalistic may also contribute, if this is how the disease is transmitted (Cossins 1972). In addition, older crayfish had been exposed to infection for a longer period.

The overall incidence of the parasite as shown in Table 3.7 was very similar in males (6.54%) and females (6.59%).

It was possible to estimate the size of the sub-population parasitized by mark and recapture on three occasions in 1976 (5.4.5 and Table 3.8). This varied from 936 (12.0% of total estimate) individuals in June to 193 (1.8% of total estimate) in October. The percentage parasitized, as estimated from sample composition, varied from 8.0-6.4% over the same period indicating that there was no major bias in the catchability of parasitized animals by hand.

Parasitized crayfish were observed to moult and reproduce successfully although moult increments were smaller than in normal crayfish (4.3.1). The lowest survival rate for any sub-population as estimated by the Jolly model (1965) was for the crayfish recognized as parasitized; survival rate (Phi) = 0.2860 $\pm$ 0.1358 over 41 days in September to October 1976, mean weekly

Table 3.7: The percentage of crayfish parasitized by Thelohania contejeani in five size classes as estimated by the proportional composition of all trapped and hand collected samples 1975-77

Carapace length in mm.	Males			Females		
	Number parasitized*	Total number	Percentage parasitized*	Number parasitized*	Total number	Percentage parasitized*
< 20	5	350	1.43	3	329	0.91
20.0 - 24.9	11	308	3.57	17	326	5.21
25.0 - 29.9	26	648	4.01	20	542	3.69
30.0 - 34.9	86	1,159	7.42	72	895	8.05
⩾ 35	149	1,771	8.41	53	411	12.90
Total	277	4,236	6.54	165	2,503	6.59

parasitized* - refers to crayfish that were infested by T. contejeani to an extent where this was apparent on external examination

mortality = 19.24% (5.4.5). This corresponded to the fall in the percentage parasitized, as estimated by mark and recapture, from 5.5% to 1.8% over the same period (Table 3.8).

Repeated recaptures of individually marked crayfish which either developed the disease in a recognizable form during capture and survived until last capture or were diagnosed at first capture irrespective of their ultimate fate provided an estimate of the minimum time course for the recognizable stages of the disease (Fig. 3.8). This appeared to be around one year, with the exception of one male which survived for 663 days following first capture when the disease was noted. Only one animal fell into the category where infestation was not noted at first capture but was observed later and the animal subsequently died; the actual time course of the recognizable stages of the disease in this one male was 284 days.

General Discussion

Reports of the infestation of crayfish populations by the microsporidian endoparasite Thelohania contejeani indicate that usually only a relatively low proportion of individuals are past that stage of infestation which can be diagnosed by eye (8.2%, Cossins & Bowler 1974; 7.7% and 17.9%, Pixell Goodrich 1956; 0.7-3.7%, Mazylis 1978 and mean 6.57% in the aqueduct, Table 3.7). It is clear that these low proportions can exist for long periods as the disease has been present below the 10%

Table 3.8: The size of the sub-population recognized as parasitized by T. contejeani 1976-77

Date	Day	Total population size	SE	Parasitized population size*	SE	%*	Sample size	Parasitized sample size*	%*
26. 5.76	8						972	75	7.7
11. 6.76	9	11,625	2,044	1,393	936	12.0	1,017	81	8.0
27. 8.76	11	25,917	4,776	1,427	914	5.5	951	82	8.6
8.10.76	12	20.776	3,861	382	193	1.8	885	57	6.4
26.10.76	14						1,018	80	7.9
12. 5.77	1A	15,310	2,646				778	31	4.0
27. 5.77	2A	9,329	1,613				677	32	4.7
17. 6.77	3A						703	35	5.0

Parasitized population size* and parasitized sample size* refer only to those animals that were recognized as parasitized by T. contejeani.

%* - parasitized* as a percentage of population size or sample size.

level in several populations of A. pallipes in Northumberland over at least the past 11 years (Cossins 1972). There are, however, reports that the disease has assumed plague proportions in some continental populations (Kossakowski 1971, Kudo 1924, Schäperclaus 1954) and it has been suggested that it may be one of the factors responsible for fluctuations in numbers of A. pallipes in the British Isles (Duffield 1933, Pixell Goodrich 1956).

Repeated recaptures of marked individuals that were infested has shown the usual time course of the recognizable stages of the disease to be approximately one year (Fig. 3.8). At the time of death all skeletal muscle blocks are infested with huge numbers of spores (Cossins 1972) and these presumably propagate the disease to the next host. The way in which this occurs has not been elucidated for T. contejeani but it seems likely from data on related species that the disease is transmitted when the new host cannibalizes infested muscle tissue from a dead animal (Cossins 1972, Johnson 1977, Sumari & Westman 1969). Pixell Goodrich (1956) has suggested that spores may enter directly into the haemolymph via injuries sustained during moulting. Whatever the actual mode of transmission, it must, in common with the above two hypotheses, expose only a small proportion of the crayfish population to infection. If this were not the case, the many spores from a dead animal would have catastrophic results in a dense population, such as those in Northumberland, but this has not happened over the past decade.

The evidence from the U.K. therefore suggests that European crayfish and T. contejeani have existed sympatrically over a long period. This parasite has adapted to its host so that the two may coexist in the same water body for long periods, as the ability to wipe out populations of its host has no survival value for a parasite. Such an interrelationship is very much in contrast to the fungal plague, Aphanomyces astaci, which is native to North America and can co-exist with American species of crayfish. However, after its accidental introduction to Europe, it was found to be fatal to all the European crayfish in every water body it infected (Unestam 1972b, 1974).

3.8 The analysis of the body form of A. pallipes

The measurements of carapace length, carapace width, total length, chela length and total wet weight (as defined in section 2.1) that were taken in laboratory and field were analysed so that the body form of A. pallipes could be biometrically defined. Carapace length was used as an index of overall body size as it was the measurement subject to the least variation (2.1) and has been widely used for this purpose in studies of crayfish and other macruran species.

The relationship between total length (y) and carapace length (x) is shown on Fig. 3.9:-

males $y = 1.9537x + 2.1309$ ($p \ll 0.001$)

females $y = 2.0461x + 0.9621$ ($p \ll 0.001$)

Fig. 3.9: Total length as a function of carapace length for males (solid line) and females (broken line) with undamaged rostra

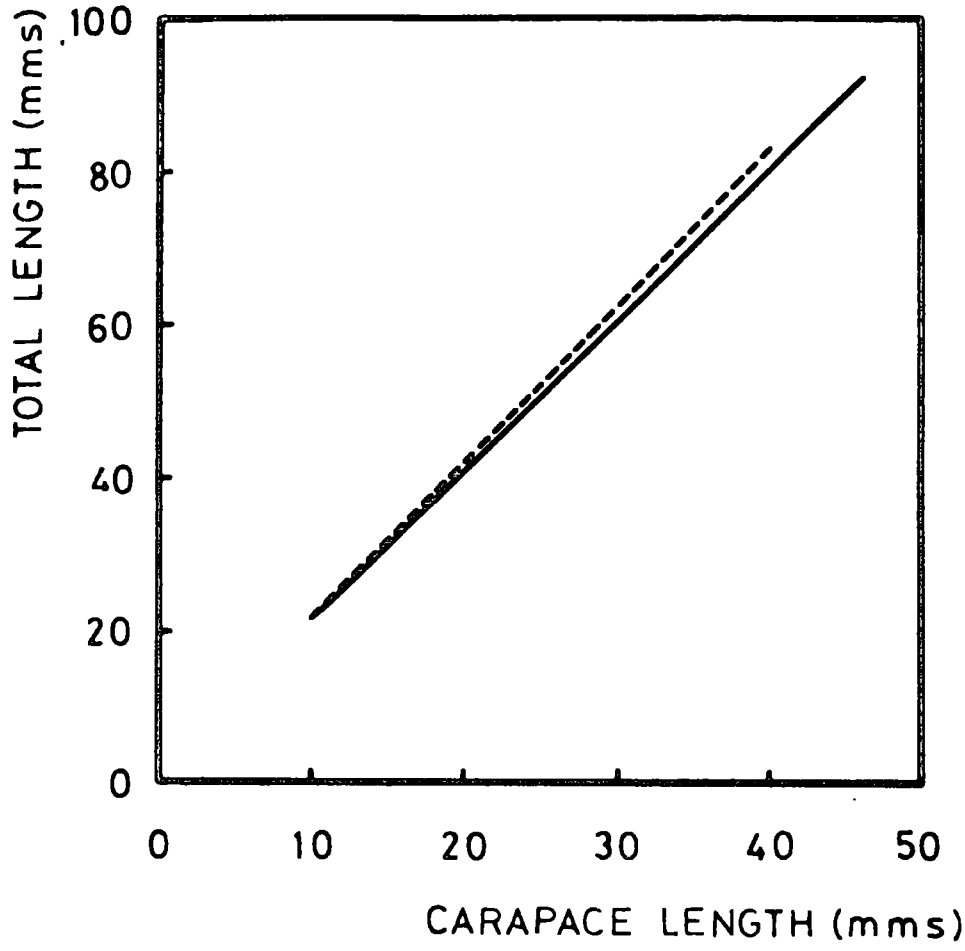
males:- $y = 1.9537x + 2.1309$ $(n = 273)$
$r = 0.9974$, $t = 226.17$,
$p \ll 0.001$
SE slope $= 8.64 \times 10^{-3}$

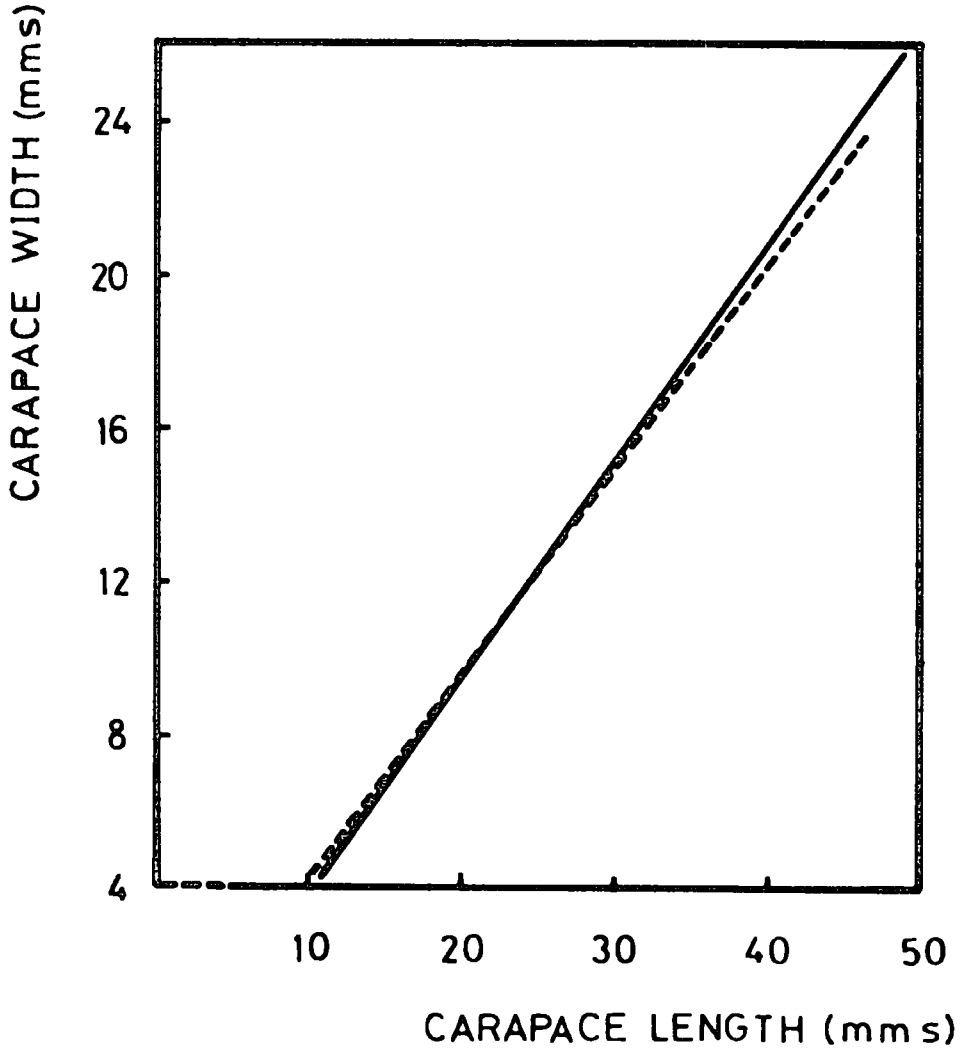
females:- $y = 2.0461x + 0.9621$ $(n = 271)$
$r = 0.9954$, $t = 170.02$,
$p \ll 0.001$
SE slope $= 1.20 \times 10^{-2}$

Carapace width as a function of carapace length for males (solid line) and females (broken line) without damage to the carapace

males:- $y = 0.5544x - 1.7157$ $(n = 4243)$
$r = 0.9893$, $t = 441.86$,
$p \ll 0.001$
SE slope $= 1.25 \times 10^{-3}$

females:- $y = 0.5389x - 1.1673$ $(n = 2731)$
$r = 0.9907$, $t = 379.88$,
$p \ll 0.001$
SE slope $= 1.42 \times 10^{-3}$


TOTAL LENGTH (mms)
100
80
60
40
20
0
0
10
20
30
40
50
CARAPACE LENGTH (mms)


CARAPACE WIDTH (mms)
24
20
16
12
8
4
10
20
30
40
50
CARAPACE LENGTH (mms)

There was a significant difference between the slopes of these two regression lines ($t = 6.25$, $p < 0.001$).

The relationship between carapace width (y) and carapace length (x) is also shown on Fig. 3.9:-

males $y = 0.5544x - 1.7157$ ($p \ll 0.001$)

females $y = 0.5389x - 1.1673$ ($p \ll 0.001$)

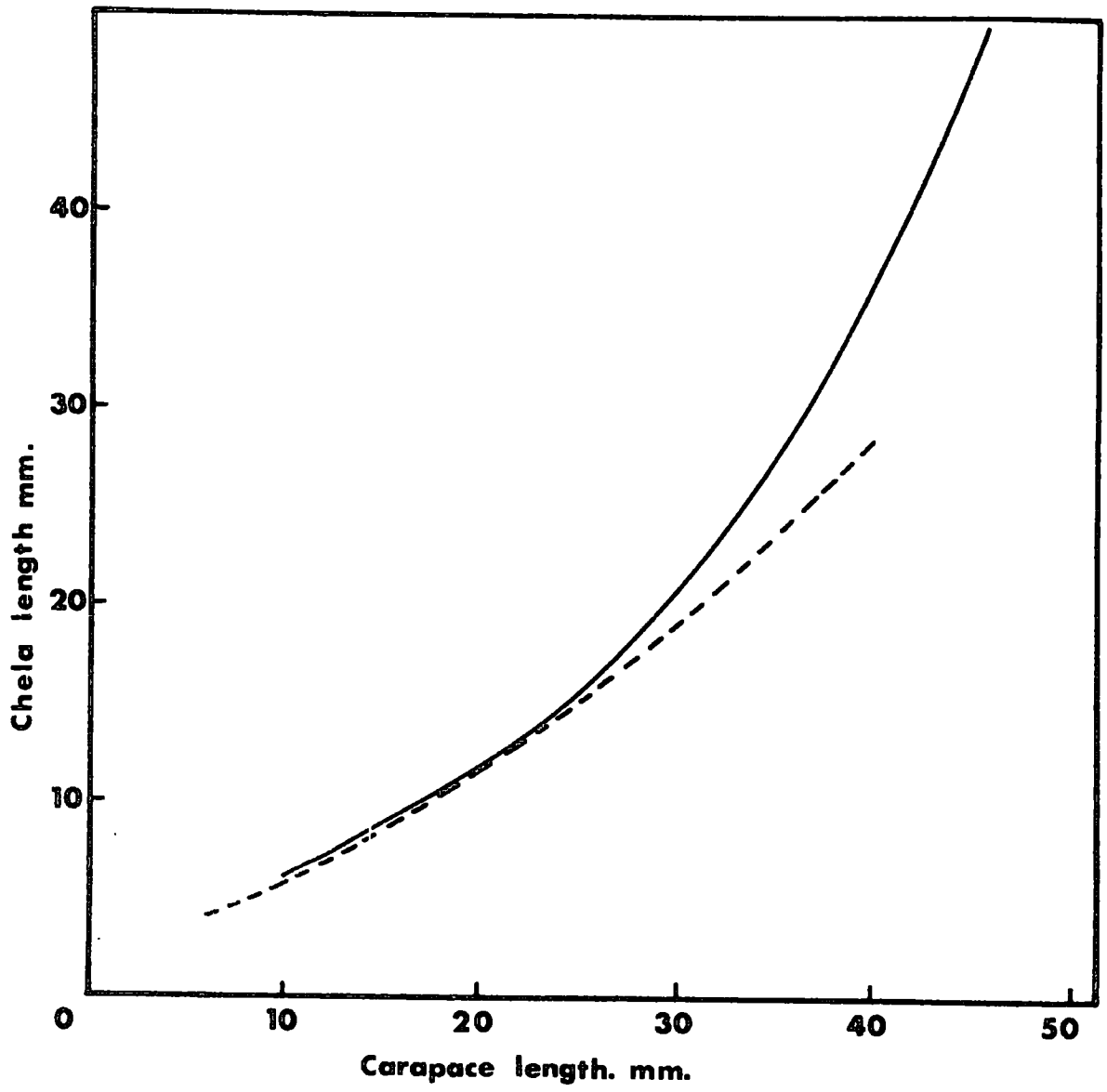
There was a significant difference between the slopes of these two regression lines ($t = 8.19$, $p < 0.001$).

Therefore, as body size increased, females became relatively longer in terms of total body length and narrower in the carapace with respect to males. The abdomen of mature female crayfish is much broader than that of males of similar carapace length (Huxley 1896) and this together with it also being longer facilitates the attachment of large numbers of eggs to the pleopods. There was no obvious reason for the relatively wider carapace of the males.

The relative proportions of the three measurements total length : carapace length : carapace width for any one individual of either sex is therefore approximately 4 : 2 : 1.

A detailed statistical analysis of the correlation between chela length and carapace length in normal animals has been included in 4.2.1. The mean chela length of mm. size classes was estimated from the regression lines fitted to Fig. 4.1 and shown as a function of carapace length on Fig. 3.10. For both

Fig. 3.10: Mean chela length of one mm. size classes as a function of carapace length for males (solid line) and females (broken line) which showed a length difference of less than 1 mm. between both the chelae. The mean values were calculated from the regression lines fitted to Fig. 4.1


40
30
20
10
0
10
20
30
40
50
Chela length mm.
Carapace length. mm.

males and females the relationship is approximately linear from 10-20 mm. carapace length, above this size the chelae grow allometrically in both sexes but to a much greater extent in the males. This sexual dimorphism in adults is associated with the important role the chelae play in offence, defence and mating behaviour (e.g. Bovbjerg 1956, Ingle & Thomas 1974, Stein 1976, Stein & Magnuson 1976).

The relationship between length and weight can be expressed in the general form:-

$$w = ql^b$$

where q and b are constants, w = weight and l = length (Winberg 1971). When this equation was expressed in its logarithmic form log w = log q + b log l, there was a highly significant positive linear correlation between $\log_{10}$ wet weight and $\log_{10}$ carapace length in both sexes ($p \ll 0.001$, Fig. 3.11):-

males $w = 1.1803 \times 10^{-4} l^{3.2768}$

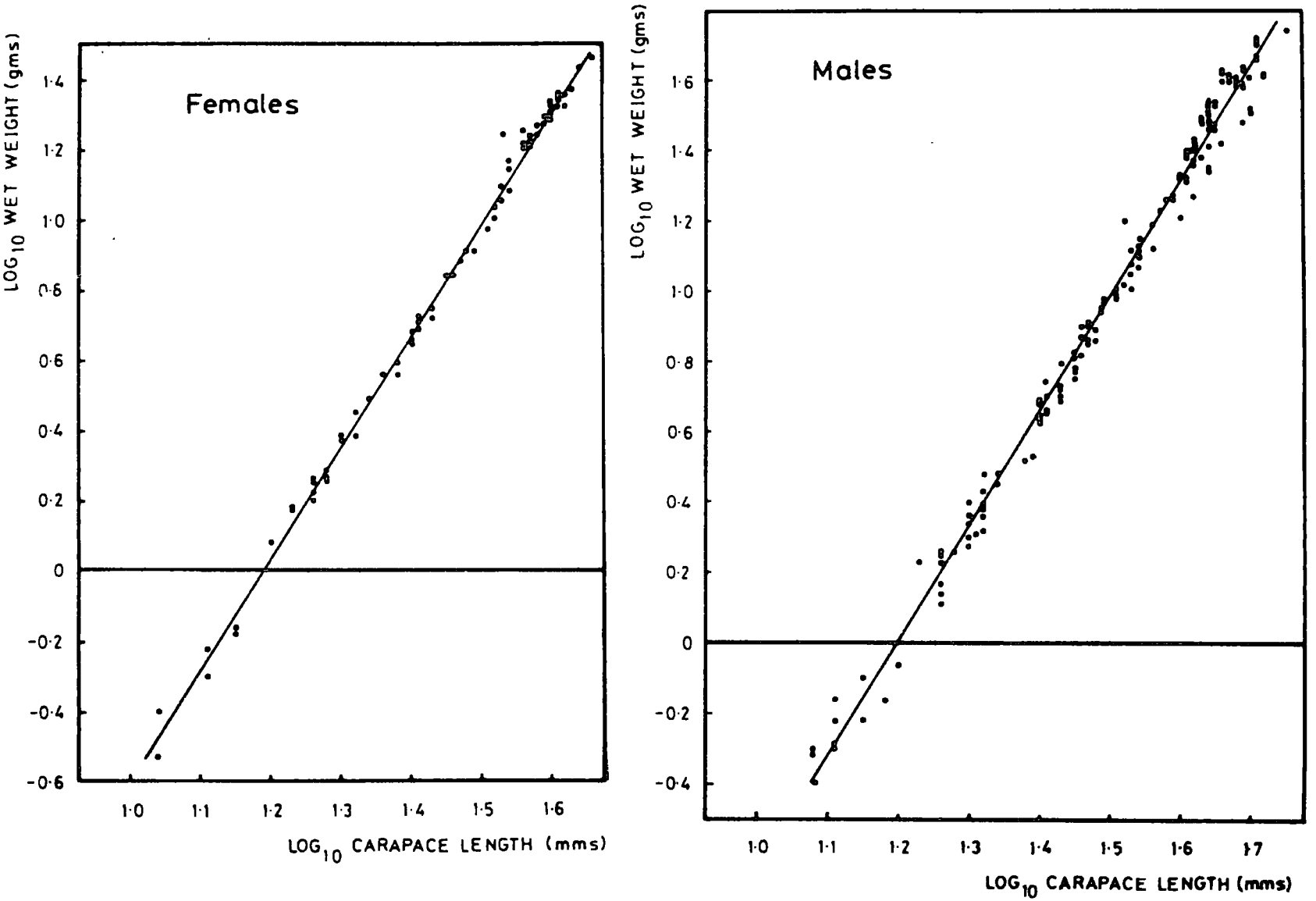
females $w = 1.7480 \times 10^{-4} l^{3.1548}$

"When the geometric proportions of the body are not changed, that is, there is no alteration in the body form, b = 3" (Winberg 1971). Both values of b for male (3.2768 ± 0.0223) and female crayfish (3.1548 ± 0.0280) were significantly greater than 3 ($t = 12.41$, $p < 0.001$; $t = 5.52$, $p < 0.001$ respectively) and the overall body form therefore changes during growth so that the ratio of carapace length to weight decreases. The facts that the relationships of total length and carapace width

Fig. 3.11: Log_{10} wet weight (gms.) as a function of log_{10} carapace length (mms.) for males and females respectively

males:- $y = 3.2768x - 3.9280$ ($n = 173$)
$r = 0.9961$, $t = 147.63$,
$p \ll 0.001$
SE slope $= 2.2308 \times 10^{-2}$

females:- $y = 3.1548x - 3.7486$ ($n = 77$)
$r = 0.9971$, $t = 113.47$,
$p \ll 0.001$
SE slope $= 2.8025 \times 10^{-2}$


Females
Males
LOG10 WET WEIGHT (gms)
LOG10 CARAPACE LENGTH (mms)
1·4
1·2
1·0
0·6
0·4
0·2
0
-0·2
-0·4
-0·6
1·6
0·8
1·0
1·1
1·2
1·3
1·4
1·5
1·6
1·7

with carapace length were linear (Figs. 3.9 and 3.10) suggests that this was due entirely to the profound positive allometric growth of the chelae in the males and the same trend in the females, although less pronounced, together with the broadening of the abdomen. All these changes occur around the time at which sexual maturity is attained.

Similar trends in the magnitude of the parameters considered above, as carapace length increased, have been observed for other species of freshwater crayfish (total length, Flint 1975; female abdominal width, Stein 1977; chela size, Abrahamsson 1966, Kossakowski 1967, 1971, Stein 1977; wet weight, Miller & Hyning 1970, Momot 1967, Nefedov & Mazanov 1973 and Romaire et al. 1977).

CHAPTER 4

Growth of A. pallipes in the aqueduct and in the laboratory

4.1 Introduction

The stepwise increases in size, which occur as arthropods shed their hardened, outer cuticular layer at ecdysis, have been extensively studied, particularly within the decapod crustacea (e.g. Allen 1966, Kurata 1962, Passano 1960). Many of these studies have described growth in normal animals both in the laboratory (e.g. Adelung 1971, Edwards 1965, Emadi 1974, Hughes & Sullivan 1972) and in the field (e.g. Abrahamsson 1972a, Farmer 1973, Flint 1975b, Hepper 1972, Hewett 1974, Hiatt 1948, Hopkins 1967, Kossakowski 1971, Lindberg 1955, Rumyantsev 1973). Others have reported the effects of limb-regeneration and reproduction on growth in the laboratory (e.g. Adelung 1971, Bennett 1973, Bittner & Kopanda 1973, Durand 1960, Emmel 1907) but less often has such comparative data been available from field studies (e.g. Kossakowski 1971, Sheard 1949, Woodland 1967).

As a consequence of the stepwise nature of arthropod growth all of these studies have described linear and/or gravimetric growth and not growth in terms of cell

division or energetics which is, as in all other phyla, a continuous process with growth of the soft tissues occurring throughout the intermoult period to replace the water with which the soft shell was expanded during early postmoult (Emadi 1974, Carlisle 1960, Needham 1965, Sather 1966).

There are three general methods by which moult increment data has been analysed in previous studies of decapod growth. These were the relationships between premoult carapace length and postmoult carapace length (e.g. Hiatt 1948, Mason 1974), absolute moult increment and premoult carapace length (length increments, e.g. Abrahamsson 1971b; weight increments, e.g. Hewett 1974) and relative moult increment expressed as the increment as a percentage of premoult size (length increments, e.g. Hopkins 1967; weight increments, e.g. Bennett 1973).

Kurata (1962) has characterised growth patterns in the Crustacea into three types according to the slope (m) of the regression line, $y = mx + c$, of postmoult carapace length as a function of premoult carapace length:-

(i) progressive geometric growth $m \geqslant 1.05$

(ii) arithmetic growth $1.05 > m \geqslant 0.95$

(iii) retrogressive geometric growth $m < 0.95$

The limits chosen to distinguish these three growth patterns were apparently completely arbitrary as they did not take sample variation into account. It was not possible, therefore, to test the statistical significance

of any observed growth pattern. The author considered that the only rigorous interpretation of these growth patterns was whether m was significantly different from unity or not; as only in the latter case can true arithmetic growth be said to have been observed.

The periodic shedding of all hardened exoskeletal body parts that occurs in the decapoda at ecdysis rules out the possibility of any of these parts showing annual growth rings such as those of the scales and otoliths of fish (Tesch 1971). A method of instar determination that has been used successfully with several of the Isopoda, which was based on the number and arrangement of the aesthetascs on the antennules and antennae (Holdich 1968), has also proved unadaptable to the decapoda (Farmer 1973, Holdich pers. comm.). As far as was known there exist no structures by which the age of any decapod species can be directly determined.

This situation has resulted in extensive use having been made of the interrelationship between size and age (e.g. Abrahamsson 1971b, Hopkins 1967, Kurata 1962, Woodland 1967). These methods involve either extensive knowledge of the variations in moult increment and frequency throughout the life cycle or the analysis of the polymodal size frequency distribution of the population, which is found in many of the longer lived crustacean species, by means of cumulative probability curves (e.g. Cassie 1954, Harding 1949). Once the distribution was separated and the mean of each modal

group determined each was usually considered to constitute a year class, normally with some moult increment and frequency data to substantiate the inherent assumptions.

There is very little information in the literature concerning moulting and growth in A. pallipes (Moriarty 1972, Thomas & Ingle 1971, Watson unpubl.). The fact that many crayfish caught during the population studies were given an individual mark (2.3) allowed the growth increments and moult frequencies for many individual animals to be followed in the aqueduct. An estimation of the interrelationship between size and age throughout the life cycle of A. pallipes in the aqueduct was also calculated using a combination of the above two methods for ageing decapods (4.3.3). Growth was also studied under controlled laboratory conditions (4.4).

Population growth and mortality were the two major factors which determined annual production (Chapter 7) and this latter parameter was of particular interest for the aqueduct population, not only because it had not been previously estimated for this species, but also as it seemed likely that this population was near to the northern limit of distribution for this species (3.2).

4.2 Methods

4.2.1 Moult increments

(i) All length measurements were made with vernier calipers to the nearest 0.1 mm. as described in Chapter 2. The rostral spine has a characteristic shape when intact (Gledhill et al. 1976, Gordon 1963) and all

carapace length data from animals showing evidence of damage in this area were rejected.

(ii) Transformations of the allometric relationships between chela length and carapace length (Fig. 3.10) for normal males and females (< 1 mm. difference in lengths of chelae, Chapter 2) were shown on Fig. 4.1. Any crayfish which had one or both chelae of a size which fell below the 99% confidence limits of these relationships was classified as limb-regenerating. The sexual dimorphism of chela growth has already been discussed (3.8).

4.2.2 Moult frequency

The interrelationships between premoult carapace length (Pre M.C.L.) and postmoult carapace length (Post M.C.L.) for males and females are shown on Fig. 4.2. These data were derived from measurements made on marked individuals (Chapter 2) which had undergone a single moult between successive recaptures. There were obviously a number of instances in which the recapture interval was sufficiently long for two or more moults to have occurred. These individuals were easy to identify as if their growth increment was treated as a single moult increment then it fell well outside the 99% confidence limits of Fig. 4.2. Indeed, the close correlation of Pre M.C.L. and Post M.C.L. ($r > 0.94$, $p \ll 0.001$ in all cases) allowed the number of moults to be estimated in these animals. For any crayfish showing a Post M.C.L. above the upper confidence limit for its Pre M.C.L. on the

Fig. 4.1A: Chela length$^{\frac{1}{2}}$ (measured as the longest distance from propodus tip to hardened exoskeletal rim of propodus nearest to hinge with carpus) for normal females (showing less than 1 mm. difference in length of either chela) as a function of carapace length

$y^{\frac{1}{2}} = 0.0975x + 1.4454$ (n = 187)

SE slope = 9.54×10^{-4}

$r = 0.9912$, $p < 0.001$

B: Log_{10} chela length for normal males as a function of carapace length

$\text{Log}_{10}y = 0.0248x + 0.5721$ (n = 186)

SE slope = 3.13×10^{-4}

$r = 0.9856$, $p < 0.001$

These criteria were used to determine whether an animal was regenerating one or both chelae; i.e. if chela length fell below the lower 99% confidence limit (broken line)

The above transformations were used as they provided the highest correlation coefficients over the size range under consideration

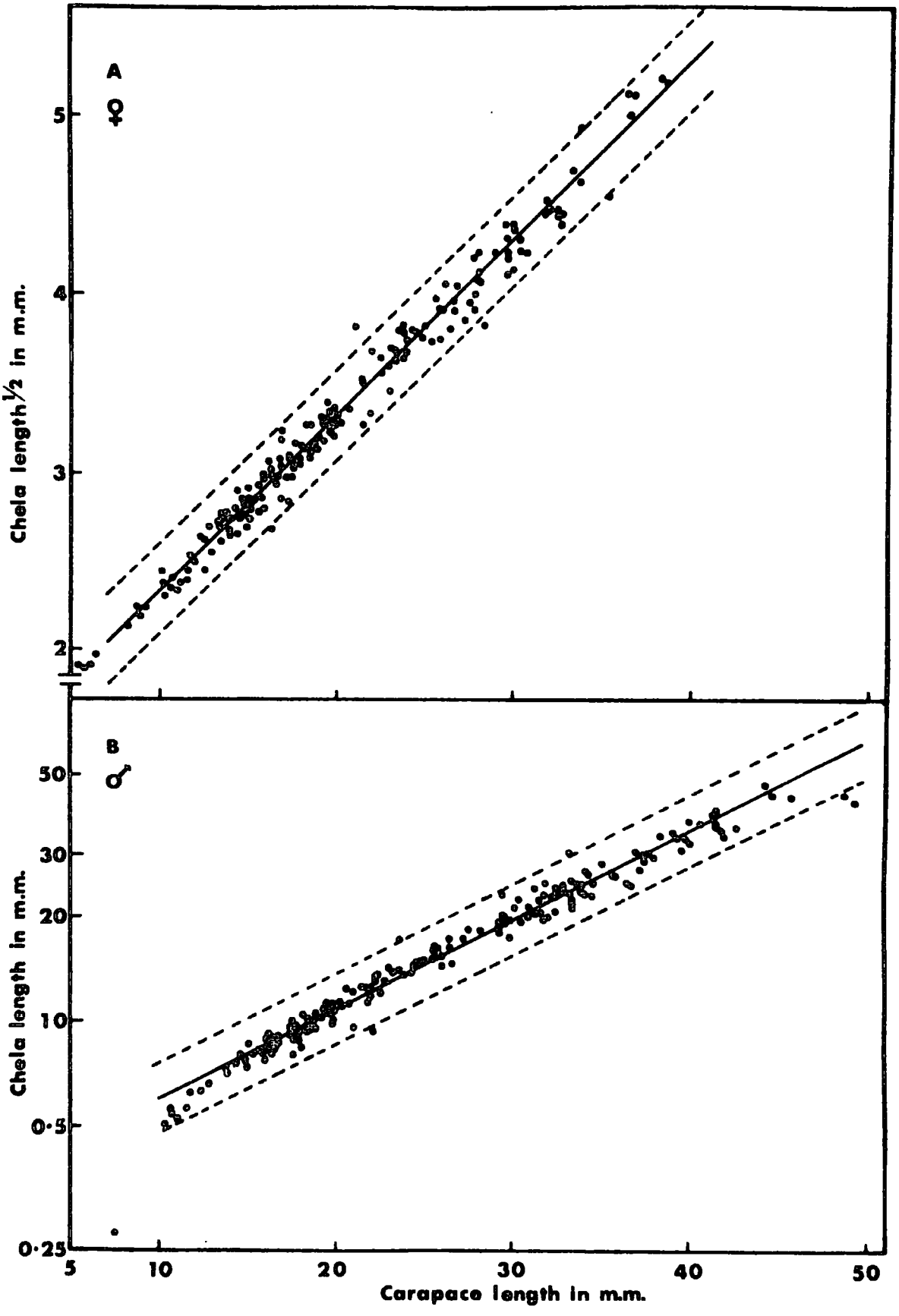

A
♀
B
♂
Chela length½ in m.m.
Chela length in m.m.
Carapace length in m.m.
5
4
3
2
50
30
20
10
0·5
0·25
5
10
20
30
40
50

Fig. 4.2: Postmoult carapace length (Post M.C.L.) as a function of premoult carapace length (Pre M.C.L.) for normal crayfish that were recaptured at two points sufficiently close in time that only one moult could have occurred in the intervening period (M = minimum size at sexual maturity)

males (i) $CL \leq 28$ mm.

$y = 1.0847x + 0.6084$
$(n = 43)$

SE slope = 0.0351

$r = 0.9828$, $t = 34.08$,
$p \ll 0.001$

(ii) $CL > 28$ mm.

$y = 0.9736x + 3.8502$
$(n = 374)$

SE slope = 0.0095

$r = 0.9792$, $t = 93.08$
$p \ll 0.001$

females (i) $CL \leq 28$ mm.

$y = 1.0517x + 0.9451$
$(n = 27)$

SE slope = 0.0645

$r = 0.9560$, $t = 16.29$
$p \ll 0.001$

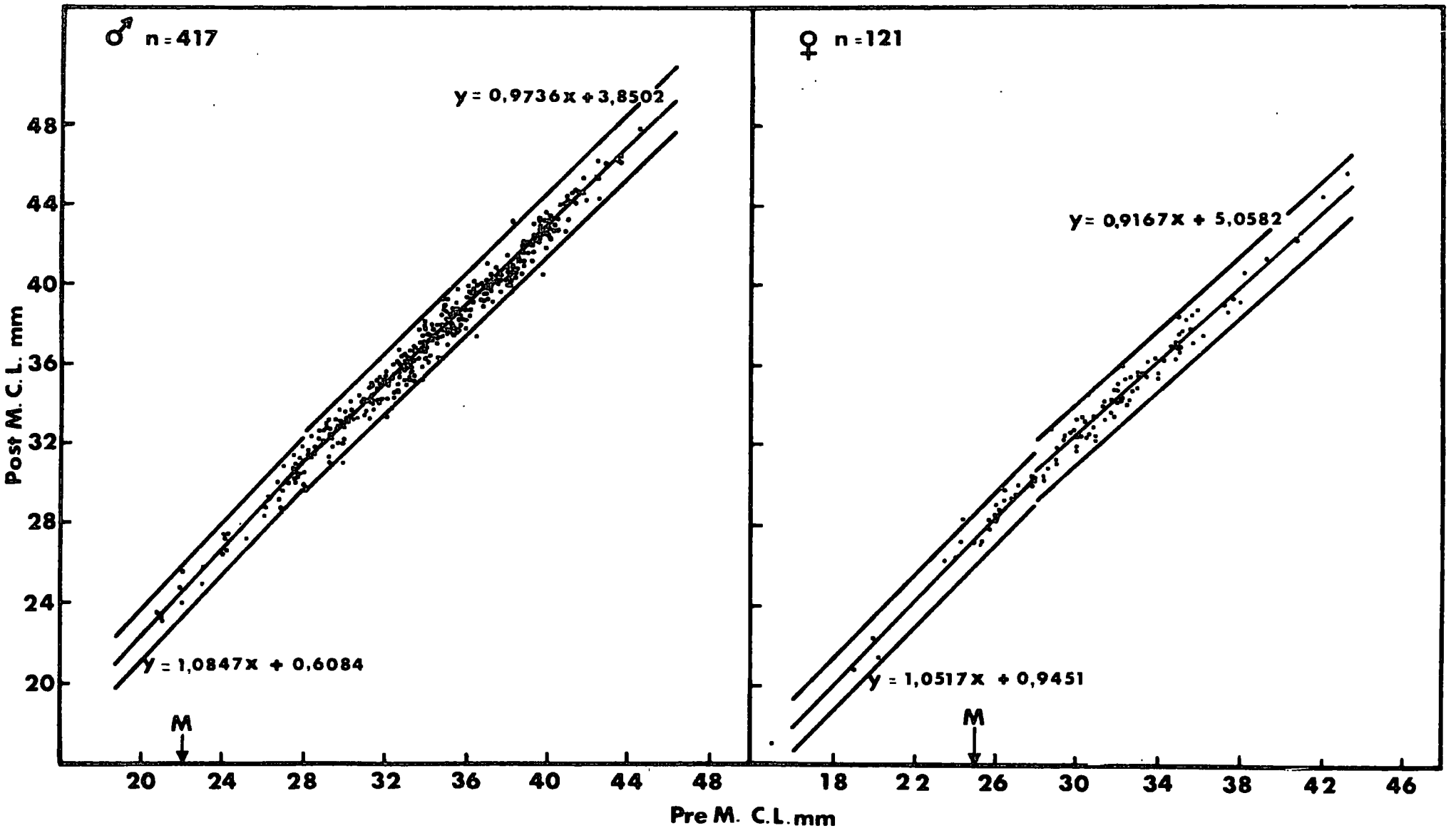
(ii) $CL > 28$ mm.

$y = 0.9167x + 5.0582$
$(n = 94)$

SE slope = 0.0328

$r = 0.9482$, $t = 28.63$,
$p \ll 0.001$

The 99% confidence limits fitted to all four regression lines were used to estimate moult frequency in animals which had moulted more than once between captures (4.2.2)


♂ n = 417
y = 0,9736x + 3,8502
y = 1,0847x + 0,6084
M
♀ n = 121
y = 0,9167x + 5,0582
y = 1,0517x + 0,9451
M
Post M. C. L. mm
Pre M. C. L. mm
20
24
28
32
36
40
44
48
18
22
26
30
34
38
42
46

previous recapture occasion, the growth increment was divided by 2 or 3 or 4 until the Pre M.C.L. and calculated values of Post M.C.L. fell within the 99% confidence limits of Fig. 4.2. In all cases only one integer value resulted, this gave the estimated number of moults occurring between the two recapture occasions. As this technique only 'averaged' the moult increments at successive moults it was used only to establish moult frequency in animals of different size classes.

Details of the marking technique, moult staging and all other relevant methods are given in Chapter 2.

4.3 Linear growth of A. pallipes in the aqueduct

4.3.1 Moult increments

The correlation between Pre M.C.L. (x) and Post M.C.L. (y), one aspect of which has already been described in section 4.2.2, is shown on Fig. 4.2. This correlation was highly significant for both sexes when the regression parameters were calculated over the whole size range (males $r = 0.96$, $p < 0.001$; females $r = 0.94$, $p < 0.001$). However, the regression lines which best 'fitted' these data had a decrease in slope in the region of 28 mm. Pre M.C.L.; two sets of regression parameters were therefore calculated for each sex, one for crayfish of $\leqslant$ 28 mm. Pre M.C.L. and another for larger individuals. This interpretation suggests that a change in growth pattern occurs just after sexual maturity (minimum carapace length at sexual maturity was 25 mm. for females and 22 mm. for males, 3.4).

The regression parameters were as follows:-

Males Pre M.C.L. $\leq$ 28 mm.

$y = 1.0847x + 0.6084$ ($n = 43$, $r = 0.98$)

Females Pre M.C.L. $\leq$ 28 mm.

$y = 1.0517x + 0.9451$ ($n = 27$, $r = 0.96$)

Males Pre M.C.L. $>$ 28 mm.

$y = 0.9736x + 3.8502$ ($n = 374$, $r = 0.98$)

Females Pre M.C.L. $>$ 28 mm.

$y = 0.9167x + 5.0582$ ($n = 94$, $r = 0.95$)

The only interpretation of these growth patterns that was considered was whether or not the slope of the lines fitted to Fig. 4.2 differed significantly from unity (arithmetic growth, 4.1, Kurata 1962).

Sex	Pre M.C.L.	n	slope ± SE	p (difference from 1)
Males	$\leq$ 28 mm.	43	1.0847 ± 0.0531	< 0.02
	$>$ 28 mm.	374	0.9736 ± 0.0095	< 0.01
Females	$\leq$ 28 mm.	27	1.0517 ± 0.0645	> 0.40
	$>$ 28 mm.	94	0.9167 ± 0.0328	< 0.02

In the males the slope was significantly different from one for both juveniles and adults. For juveniles, this value is greater than unity and consequently suggests that progressive geometric growth occurs. In adults of both sexes, this value is significantly less than one implying retrogressive geometric growth. Only in juvenile females is a value for the slope obtained which

did not differ significantly from unity. This implies that juvenile female growth is an arithmetical progression, however the large sample variation and small sample size precludes a definite statement. According to the criteria of Kurata (1962), this would have been interpreted as progressive geometric growth ($m \geqslant 1.05$).

That the slope of the regression line decreased at about 28 mm. Pre M.C.L. in the males ($t = 3.06$, $p < 0.01$) and appeared to do so in the females ($t = 1.87$, $p < 0.10$) suggested that absolute moult increments increased with increasing size, at least in the males, until sexual maturity and decreased thereafter.

The relationships between the absolute moult increment in mm. carapace length (MI., y) and Pre M.C.L. (x) for normal males and females are shown on Figs. 4.3a and b respectively. There was considerable variability between individual moult increments, however the equations for the regression lines were as follows:-

Males Pre M.C.L. $\leqslant$ 28 mm.

$y = 0.0848x + 0.6081$ ($n = 43$, $r = 0.35$)

Females Pre M.C.L. $\leqslant$ 28 mm.

$y = 0.0839x + 0.3272$ ($n = 27$, $r = 0.47$)

Males Pre M.C.L. $>$ 28 mm.

$y = -0.0232x + 3.7534$ ($n = 374$, $r = -0.14$)

Females Pre M.C.L. $>$ 28 mm.

$y = -0.0571x + 4.2575$ ($n = 94$, $r = -0.22$)

Fig. 4.3a: Individual moult increments in mm. carapace length (M.I.) as a function of premoult carapace length (Pre M.C.L.) for male crayfish parasitized by Thelohania contejeani, those regenerating chelipeds (and/or pereiopods in a few cases) and normal animals

The regression parameters for normal males were calculated for crayfish of Pre M.C.L. $\leq$ 28 mm. and $>$ 28 mm. because of the change in growth patters at this size (Fig. 4.2). The regression lines fitted to the data for normal crayfish are also shown on the plots of parasitized and limb-regenerating M.I.'s for comparison

normal males $\leq$ 28 mm. Pre M.C.L.:-

$y = 0.0848x + 0.6081$ ($n = 43$)

SE slope = 0.0351

$r = 0.3531$, $t = 2.42$, $p < 0.05$

normal males $>$ 28 mm. Pre M.C.L.:-

$y = -0.0232x + 3.7534$ ($n = 374$)

SE slope = 0.0083

$r = -0.1446$, $t = 2.79$, $p < 0.01$

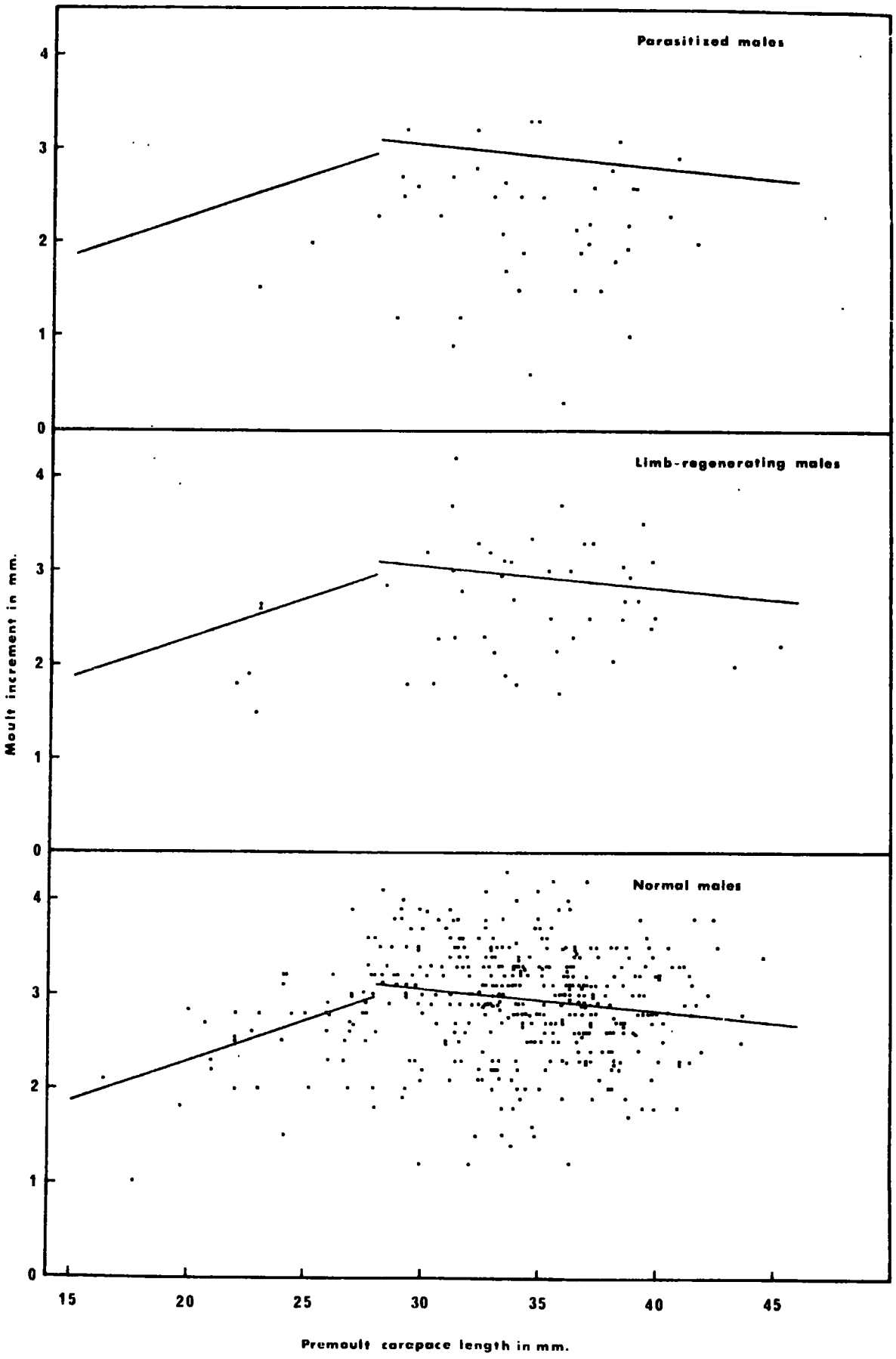

Parasitized males
Limb-regenerating males
Normal males
Moult increment in mm.
Premoult carapace length in mm.
0
1
2
3
4
15
20
25
30
35
40
45

Fig. 4.3b: Individual moult increments in mm. carapace length (M.I.) as a function of premoult carapace length (Pre M.C.L.) for female crayfish parasitized by Thelohania contejeani, those regenerating chelipeds (and/or pereiopods in a few cases) and normal animals

The regression parameters for normal females were calculated for crayfish of Pre M.C.L. $\leq$ 28 mm. and $>$ 28 mm. because of the change in growth pattern at this size (Fig. 4.2). The solid regression lines fitted to the data for normal crayfish are also shown on the plots of parasitized and limb-regenerating M.I.'s for comparison. The broken regression line on the plot of normal female M.I.'s is the one fitted to the data for normal male M.I.'s (Fig. 4.3a)

normal females $\leq$ 28 mm. Pre M.C.L.:-

$y = 0.0839x + 0.3272$ (n = 27)

SE slope = 0.0318

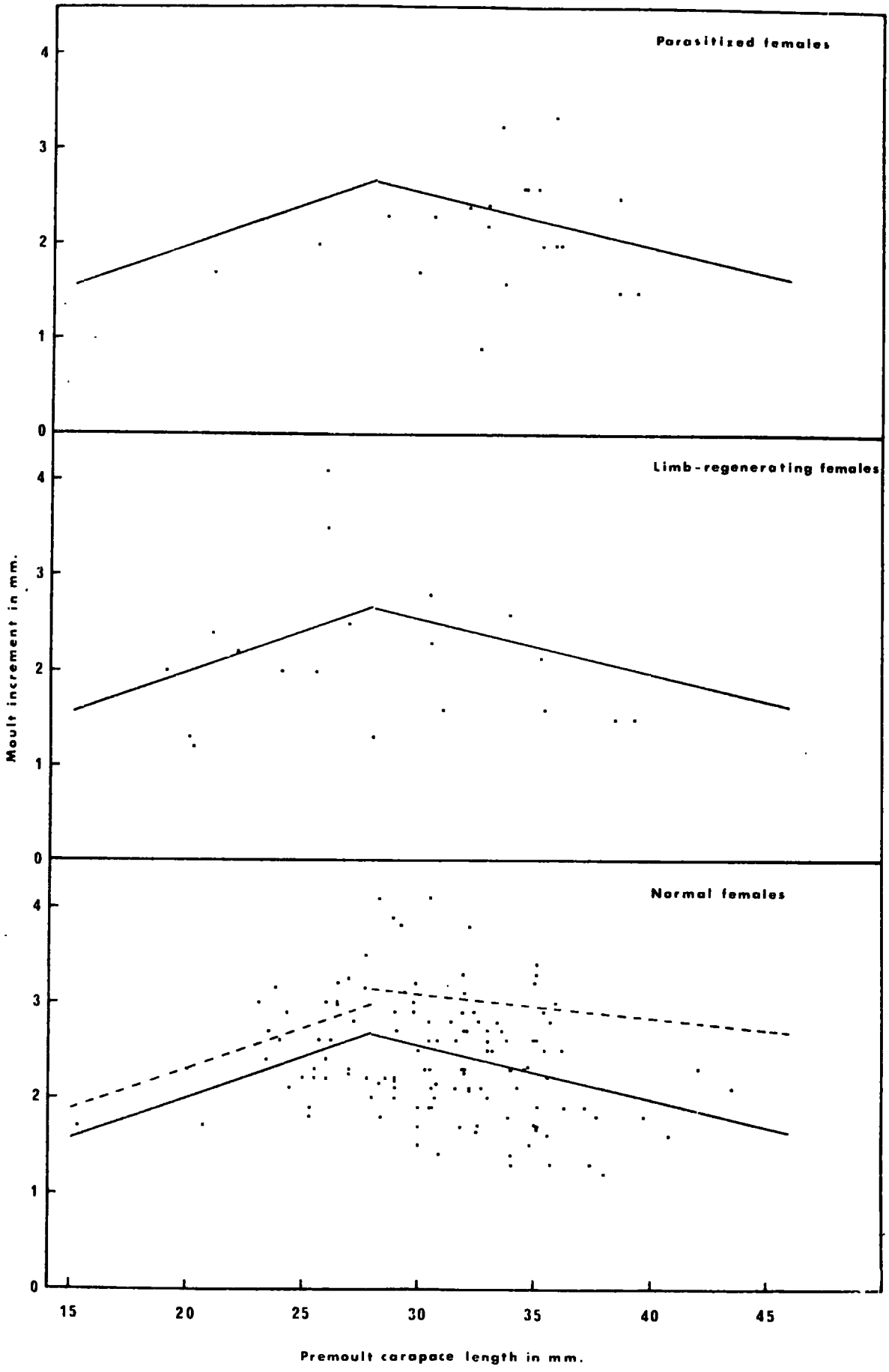
$r = 0.4671$, $t = 2.64$, $p < 0.02$

normal females $>$ 28 mm. Pre M.C.L.:-

$y = -0.0571x + 4.2575$ (n = 94)

SE slope = 0.0268

$r = -0.2216$, $t = 2.18$, $p < 0.05$


Parasitized females
Limb-regenerating females
Normal females
Moult increment in mm.
Premoult carapace length in mm.
0
1
2
3
4
15
20
25
30
35
40
45

As predicted from the previous analysis, the slope of the regression line for M.I. as a function of Pre M.C.L. was, in both sexes, positive up to 28 mm. Pre M.C.L. (equivalent to progressive geometric growth) and negative, in both sexes, above this point (equivalent to retrogressive geometric growth). However, both slopes were significantly different from zero in either sex ($p < 0.05$ - $p < 0.01$) indicating that the growth pattern of smaller females differed significantly from arithmetic growth as the method of Kurata (1962) proposed.

The relationship between M.I. expressed as a percentage of Pre M.C.L. (% M.I., y) and Pre M.C.L. (x) was plotted on Fig. 4.4. The equations for the regression lines were as follows:-

Males Pre M.C.L. $\leqslant$ 28 mm.

$y = -0.1009x + 13.4560$ ($n = 43$, $r = -0.11$)

Females Pre M.C.L. $\leqslant$ 28 mm.

$y = -0.0616x + 11.2626$ ($n = 27$, $r = -0.09$)

Males Pre M.C.L. $>$ 28 mm.

$y = -0.3125x + 19.4533$ ($n = 374$, $r = -0.55$)

Females Pre M.C.L. $>$ 28 mm.

$y = -0.3737x + 19.6304$ ($n = 94$, $r = -0.44$)

As expected from the previous two analyses, the slope of the line up to 28 mm. Pre M.C.L. was not significantly different from zero in both sexes ($p > 0.40$). However, a highly significant negative slope was

Fig. 4.4: Individual moult increments in mm. carapace length expressed as a percentage of premoult carapace length (% M.I.) as a function of premoult carapace length (Pre M.C.L.) in normal males and females respectively

All regression parameters were calculated for crayfish of Pre M.C.L. $\leq$ 28 mm. and $>$ 28 mm. due to the change in growth pattern at this size (Fig. 4.2)

normal females $\leq$ 28 mm. Pre M.C.L.:-

$y = -0.0616x + 11.2626$ (n = 27)

SE slope = 0.1310

$r = -0.0937$, $t = 0.47$, $p > 0.60$

normal females $>$ 28 mm. Pre M.C.L.:-

$y = -0.3737x + 19.6304$ (n = 94)

SE slope = 0.0817

$r = -0.4381$, $t = 4.67$, $p < 0.001$

normal males $\leq$ 28 mm. Pre M.C.L.:-

$y = -0.1009x + 13.4560$ (n = 43)

SE slope = 0.1376

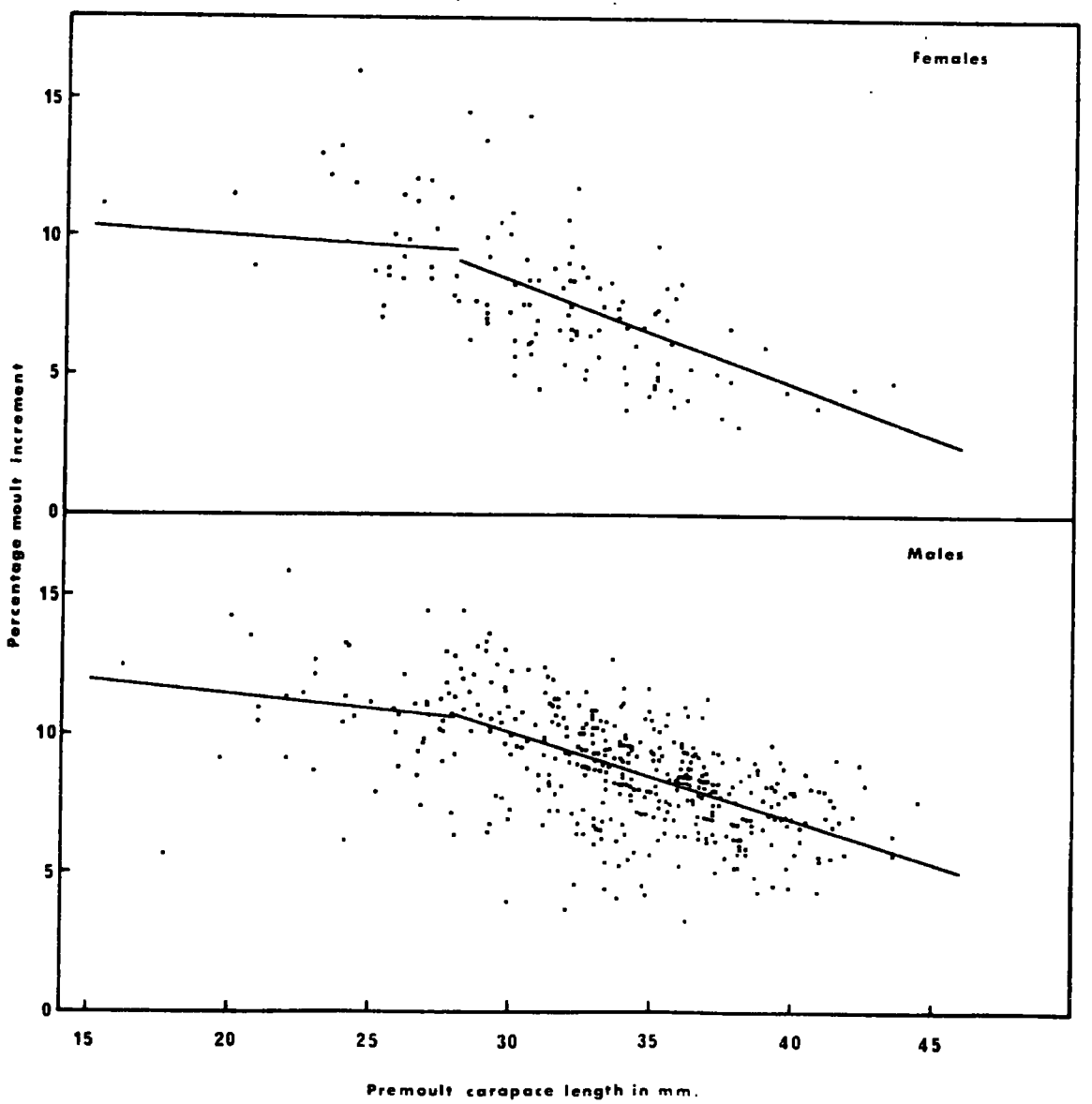
$r = -0.1138$, $t = 0.73$, $p > 0.40$

normal males $>$ 28 mm. Pre M.C.L.:-

$y = -0.3125x + 19.4533$ (n = 374)

SE slope = 0.0245

$r = -0.5515$, $t = 12.75$, $p < 0.001$


Females
Males
Percentage moult increment
0
5
10
15
15
20
25
30
35
40
45
Premoult carapace length in mm.

obtained beyond this size as M.I. decreased with increasing Pre M.C.L. in both sexes ($p < 0.001$).

These three methods of analysis revealed similar overall growth patterns when data from a wide size range was examined; the relative merits of these three methods in describing the data are considered in section 4.5.

Although the moult increments of normal crayfish were observed to follow the above growth patterns above and below 28 mm. Pre M.C.L. as a result of the considerable variation in individual moult increments there was no significant difference in the mean absolute moult increments for normal animals of $\leq$ 28 mm. and $>$ 28 mm. Pre M.C.L. of either sex:-

Sex	Pre M.C.L.	mean absolute M.I. (mm.)
Males	$\leq$ 28 mm.	2.7628 ± 0.0897
	$>$ 28 mm.	2.9415 ± 0.0290
	difference	$t = 1.90$, $p > 0.05$
Females	$\leq$ 28 mm.	2.4185 ± 0.1062
	$>$ 28 mm.	2.3856 ± 0.0823
	difference	$t = 0.24$, $p > 0.80$

This meant that the mean moult increment was a meaningful statistic with which to make comparisons between the growth of different sub-populations providing the Pre M.C. Lengths of the two data sets being compared had a similar distribution. Otherwise any differences observed between the two sub-populations may have been attributable to the overall trends between growth increment and size already described and not to any real

difference in growth rate between the sub-populations.

A comparison of the mean M.I. and mean Pre M.C.L. for adults and juveniles is shown on Table 4.1. Two points emerge from this analysis:-

(i) There were no significant differences between the mean M.I.'s for the three years 1974-76 within any sub-population of either sex.

(ii) The mean M.I. was significantly lower for the normal females than for the normal males ($p < 0.001$). That this was the case over the whole size range was clear from the broken (males) and solid (females) lines fitted to Fig. 4.3b.

A more detailed analysis of the moult increment data for normal crayfish was carried out according to the characteristics of several moult categories; Table 4.2. The date of the 12th August was used to characterise moults temporally as there were insufficient data to be more precise in the majority of cases. This date was also approximately half way through the growth season and was the latest date when females were observed with hatchlings attached to the pleopods (3.3). The following four points emerge from this analysis:-

(i) Of the females that moulted only once in a growth season the mean M.I. of those that had been berried that year (2.10 ± 0.09 mm.) was significantly less than those that had not been berried (2.52 ± 0.16 mm., $p < 0.05$). There was no significant difference in mean Pre M.C.L. between these two groups.

Table 4.1: An analysis of the moult increment (M.I. in mms. carapace length) and premoult carapace length (Pre M.C.L. in mms.) data for normal adults and juveniles from the aqueduct population throughout the study period

Males				Females			
Year	n	Mean M.I. ± SE	Mean Pre M.C.L. ± SE	Year	n	Mean M.I. ± SE	Mean Pre M.C.L. ± SE
1974	25	2.47 ± 0.28	28.55 ± 1.21	1974	23	2.25 ± 0.11	29.12 ± 0.89
1975	243	3.08 ± 0.09	33.40 ± 0.28	1975	63	2.51 ± 0.08	31.58 ± 0.50
1976	149	2.84 ± 0.05	35.33 ± 0.34	1976	35	2.23 ± 0.09	30.99 ± 0.89
Total	417	2.96 ± 0.06	33.79 ± 0.23	Total	121	2.38 ± 0.06	30.94 ± 0.41

Table 4.2: An analysis of the moult increment (M.I. in mms.) and premoult carapace length (Pre M.C.L. in mms.) data for normal crayfish with respect to the time of the moult, annual moult frequency and previous reproductive status

	Moulting before 12th August			Moulting after 12th August			Single moults the timing of which was not known		
	n	M.I. ± SE	Pre M.C.L. ± SE	n	M.I. ± SE	Pre M.C.L. ± SE	n	M.I. ± SE	Pre M.C.L. ± SE
Males moulting twice in one growth season	6	2.67 ± 0.42	31.68 ± 1.39	87	3.35 ± 0.04	29.91 ± 0.43	261	2.85 ± 0.03	34.68 ± 0.28
Males moulting once in one growth season	63	2.92 ± 0.05	35.57 ± 0.44		-			-	
Females moulting twice in one growth season		-		22	2.78 ± 0.17	26.11 ± 0.92	15	2.22 ± 0.13	32.26 ± 1.40
Females moulting once in one growth season non-post-reproductive	10	2.52 ± 0.16	31.94 ± 1.06		-		32	2.50 ± 0.07	30.64 ± 0.64
Females which had a single post-reproductive moult	42	2.10 ± 0.09	33.28 ± 0.45		-			-	

(ii) Males that moulted only once in a growth season had a significantly greater mean M.I. (2.92 ± 0.05 mm.) than females that did the same but were not berried in the previous reproductive season (2.52 ± 0.16 mm., $p < 0.02$). This indicated that the difference in mean M.I. of the total males and females (Table 4.1) was not entirely due to the energetic demands of reproduction (cf. 7.2.2).

(iii) The second moults of animals known to have moulted twice in one growth season showed the largest mean M.I. of any sub-population of either sex (males 3.35 ± 0.04 mm., females 2.78 ± 0.17 mm.). The paucity of the data mitigated against any significant difference from the M.I. at the first moult (males 2.67 ± 0.42 mm.) but such a difference would have been expected as water temperatures were highest and food most plentiful prior to the period when most second moults occurred (3.3).

(iv) Several other differences between the mean M.I.'s on Table 4.2 were calculated to be significant. However, there were also corresponding differences in mean Pre M.C.L.; this and the growth patterns already observed in Figs. 4.2-4.4 could therefore have accounted for these differences.

Moult increments of abnormal crayfish

The M.I.'s of crayfish infested by the parasite Thelohania contejeani and/or missing or regenerating limbs are shown on Figs. 4.3a & b and compared to the solid regression line fitted to the normal M.I.'s for

each sex. The mean M.I.'s of these abnormal animals are compared to the normal mean M.I.'s on Table 4.3.

The following points emerge from this analysis:-

(i) Males parasitized by T. conteieani had a significantly lower mean M.I. (2.13 ± 0.12 mm.) than normal males (2.96 ± 0.06 mm., $p < 0.001$). This could be clearly seen from Fig. 4.3a as 39 of the 45 moult increments recorded from parasitized males fell below the normal regression line.

(ii) Those males that had lost or were regenerating limbs had a significantly lower mean M.I. (2.69 ± 0.09 mm.) than normal males (2.96 ± 0.06 mm., $p < 0.02$) and a significantly higher mean M.I. than those parasitized by T. conteieani (2.13 ± 0.12 mm., $p < 0.001$). Twenty-nine of the forty-eight M.I.'s of the limbless or limb-regenerating males fell below the normal regression line.

(iii) The mean M.I. of the parasitized females (2.17 ± 0.13 mm.) was not significantly different from that of the normal females (2.38 ± 0.06, $p > 0.10$). However, fourteen of the twenty-one M.I.'s from parasitized females fell below the normal regression line.

(iv) The mean M.I. of the total limbless and limb-regenerating females (2.17 ± 0.20 mm.) was not significantly different from the normal females (2.38 ± 0.06 mm., $p > 0.30$). However, twelve of the nineteen M.I.'s for limbless and limb-regenerating females fell below the normal regression line.

The practice of pooling all animals that were

Table 4.3: An analysis of the moult increment (M.I. in mms.) and premoult carapace length (Pre M.C.L. in mms.) data with respect to parasitism by T. contejeani and limb-loss and regeneration

	Males			Females		
	n	Mean M.I. ± SE	Mean Pre M.C.L. ± SE	n	Mean M.I. ± SE	Mean Pre M.C.L. ± SE
Normal	417	2.96 ± 0.06	33.79 ± 0.23	121	2.38 ± 0.06	30.94 ± 0.41
Parasitized by T. contejeani	45	2.13 ± 0.12	34.34 ± 0.64	21	2.17 ± 0.13	33.45 ± 1.00
Limbless or limb-regenerating	48	2.69 ± 0.09	34.00 ± 0.79	19	2.17 ± 0.20	27.39 ± 0.20

observed to have limbs missing or regenerating before and/or after moulting (Table 4.3, Fig. 4.3) meant that some of these animals that had lost a limb or were in the early stages of regeneration (4.5) may have lost the limb after moulting and thus the M.I. may have been normal in this respect. Also many of these crayfish were in the late stages of regeneration when this may have had a lesser effect on overall growth (4.5). In the pooled sub-populations, limb-regeneration has already been shown to have a significant effect on male growth (ii) but not on female growth (iv). Excluding all crayfish only observed as limbless or limb-regenerating post-moult and those in the later stages of regeneration when there was a $\leqslant 20\%$ difference in size between the regenerating limb and the normal one in the premoult condition (Fig. 4.1):-

	Mean M.I. $\pm$ SE (mm.)
normal males	2.96 $\pm$ 0.06 (n = 417)
limb-regenerating males	2.39 $\pm$ 0.16 (n = 12)
normal females	2.38 $\pm$ 0.06 (n = 121)
limb-regenerating females	1.75 $\pm$ 0.17 (n = 7)

There was therefore significant evidence that the early stages of limb-regeneration had a depressive effect on overall linear growth in both sexes (males, $t = 3.24$, $p < 0.01$; females, $t = 2.27$, $p < 0.05$).

Moult increments in regenerating chelae

Twenty-seven of those animals which were numbered and had a cheliped regenerating were recaptured after

they had moulted once (Fig. 4.5). The relative length increments at the moult in the regenerating chela were always greater than those in the normal contralateral partner except in four cases where regeneration was almost complete and there was < 3 mm. size difference between the chelae; this indicated that animals of all sizes could eventually regenerate their chelipeds, although many moults would be required to achieve this in large individuals. There was also an indication that the larger the difference in size of the chelae the greater the differential in relative growth (the correlation on Fig. 4.5 was significant, $p < 0.001$) although there were too few individuals recaptured with chelae of widely different sizes to reach any definite conclusion on this point.

4.3.2 Annual moult frequency

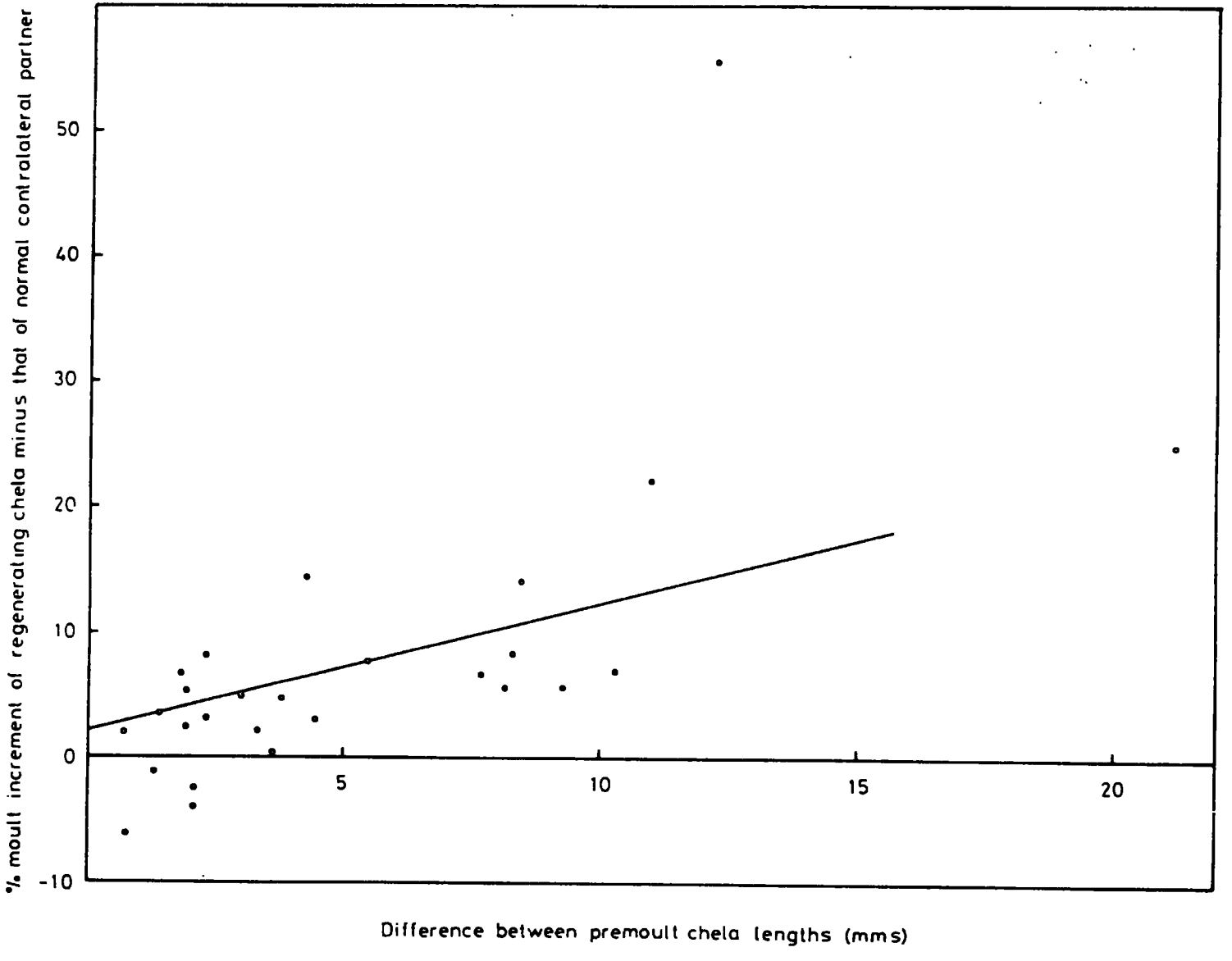
The extensive use of trapping and the individual marking of many large crayfish (> 20 mm. CL) in 1975-76 (6.3.1, Appendix 1) and the dependence on the date specific tail-marking scheme (2.3, 5.4.4) to permit the rapid processing of large hand collections resulted in the data on moult increments (4.3.1) and particularly moult frequency having been few for juveniles. Indeed, there were no moult frequency data for males < 17 mm. or for females < 19 mm. carapace length although considerable numbers of crayfish between 13 and 20 mm. carapace length were present in the hand samples (Figs. 4.7 & 4.8).

Fig. 4.5: The difference between the percentage moult increment of the regenerating chela (length increment in mms./ premoult chela length x 100) and that of its normal contralateral partner as a function of the difference between the premoult lengths of the chelae in mm

$y = 1.1246x + 2.1052$ ($n = 27$)

SE slope = 0.3023

$r = 0.5969$, $t = 3.72$, $p < 0.001$


% moult increment of regenerating chela minus that of normal contralateral partner
50
40
30
20
10
0
-10
5
10
15
20
Difference between premoult chela lengths (mms)

This was because these crayfish were only numbered when recaptured with a tail-mark and as these recaptures were relatively few (5.4.5), the odds against securing the subsequent recaptures necessary to assess annual moult frequency were large.

All data from normal crayfish of both sexes recaptured at those times of year when annual moult frequency could be assessed were plotted on Fig. 4.6 (the data from single moult increments were used to estimate annual moult frequency for those crayfish for which only the growth increment of a year or more was known, 4.2.2).

The following points emerge from an examination of the moult frequency data and Fig. 4.6:-

(i) With the exception of one female out of three, in the 24 mm. carapace length size class, all juveniles of the size range for which annual moult frequency data were available moulted twice.

(ii) Three crayfish of carapace length < 23 mm. were observed to moult twice before mid-August but were not subsequently recaptured. Due to the low numbers of juveniles known to have moulted only twice in any one year the possibility that some moulted more frequently could not, therefore, be dismissed.

(iii) There were significant negative correlations between the percentage of adults of each sex that were estimated to have moulted twice and premoult carapace length (all zero values of the percentage moulting

Fig. 4.6: The percentage of animals of each mm. size class (16.0 - 16.9 mm. etc.) that moulted twice in any one year as a function of the pre-moult carapace length (P.M.C.L.) before the first moult of that year

Regression parameters calculated for adult size classes with some crayfish that moulted twice:-

females

$y = -6.2376x + 217.35$ (n = 9)

SE slope = 2.3448

$r = -0.7356$, $p < 0.05$

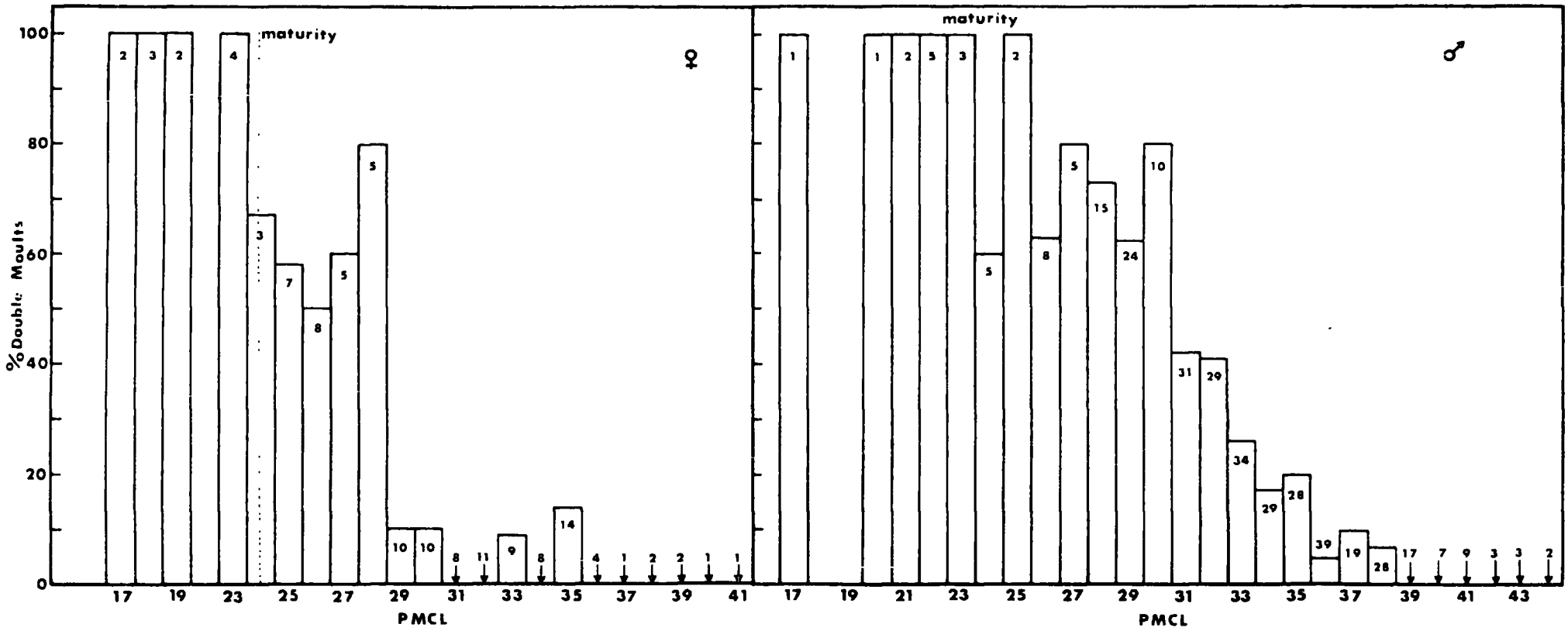
males

$y = -6.2287x + 239.66$ (n = 17)

SE slope = 0.6799

$r = -0.9211$, $p < 0.001$

Numbers above each mm. increment on the abscissa refer to the number of observations in each size class


% Double Moults
100
80
60
40
20
0
maturity
♀
2 3 2 4 3 7 8 5 5 10 10 8 11 9 8 14 4 1 2 2 1 1
17 19 23 25 27 29 31 33 35 37 39 41
PMCL
maturity
♂
1 1 2 5 3 5 2 8 5 15 24 10 31 29 34 29 28 39 19 28 17 7 9 3 3 2
17 19 21 23 25 27 29 31 33 35 37 39 41 43
PMCL

twice were excluded from this analysis; $p < 0.05$ for females, $p < 0.001$ for males).

(iv) No males of carapace length $\geqslant 39$ mm. or females of carapace length $\geqslant 36$ mm. were observed to moult twice in any one year.

4.3.3 Growth throughout the life cycle; the estimated interrelationship between size and age

The size frequency histograms for crayfish collected and measured when in an 'overwinter' condition (i.e. after the end of the growth season in one year and before the beginning of growth for that individual in the next year) in 1973-74 and 1974-75 are shown on Figs. 4.7 and 4.8. Between June and late September any sample of crayfish would contain animals in various stages of the moult cycle (3.3). As a consequence any correlation between size and age should be clearest for overwintering animals when they are all at the same moult stage.

These histograms were analysed using the method of Cassie (1954) which utilises percentage cumulative frequencies (PCF) plotted as a function of carapace length on probability paper (Figs. 4.9 & 4.10). The identification of the inflexion points (P%, ↑) was somewhat subjective and difficulties in interpretation have previously been described (e.g. Woodland 1967). Accepting these limitations it was subsequently possible to calculate the mean size of each modal group (broken lines, Figs. 4.9 & 4.10).

Fig. 4.7: Size frequency histograms of crayfish collected from the aqueduct between the dates 8.10.73 and 12. 6.74. As all crayfish had completed one years growth and none had begun the next during this period, any correlation between age and size should have been clearest during this period

Fig. 4.8: Size frequency histograms of crayfish collected from the aqueduct in the period between the 1974 and 75 growth seasons and also on 25. 6.75 and 1. 7.75. All these animals had completed a years growth in 1974 and as the first moults were observed in 1975 on the 25. 6.75 all the animals in this collection and the one on 1. 7.75 that had moulted that year (ca. 20%) were excluded so that any correlation between age and size was not obscured

All crayfish > 11 mm. carapace length were easily sexed in the field by eye (2.2.1). Crayfish 7-11 mm. carapace length in the 1974-75 overwinter period were sexed under a binocular microscope in the laboratory (Thomas 1976)

The broken lines represent the approximate sizes when crayfish first became independent from the mother and the first overwintering size, when these animals were not systematically sampled

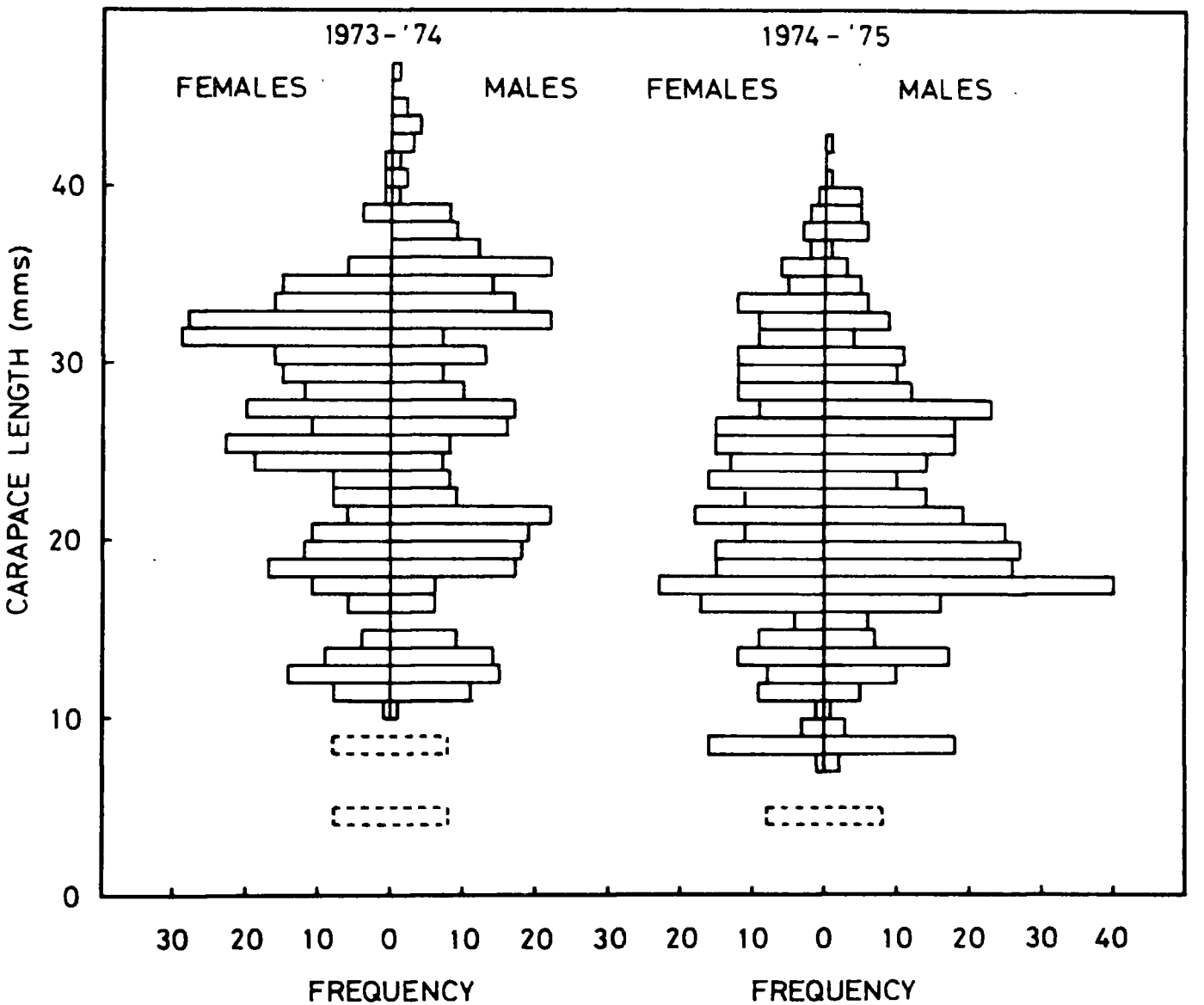

1973 - '74
1974 - '75
FEMALES
MALES
FEMALES
MALES
CARAPACE LENGTH (mms)
0
10
20
30
40
30 20 10 0 10 20 30
20 10 0 10 20 30 40
FREQUENCY
FREQUENCY

Fig. 4.9a: Carapace length as function of percentage cumulative frequency (PCF) plotted on arithmetic probability paper for males 1973-74. This was the first step in the analysis of the polymodal size frequency distribution of Fig. 4.7 using the method of Cassie (1954). The second step was to identify the inflexion points (↑), see text. The open circles (o) and broken lines represent the final step in the analysis as each mode in the distribution was separated out. Where the broken lines cross the 50% PCF this point corresponds to the mean size of that mode on the ordinate

MALES 1973-'74

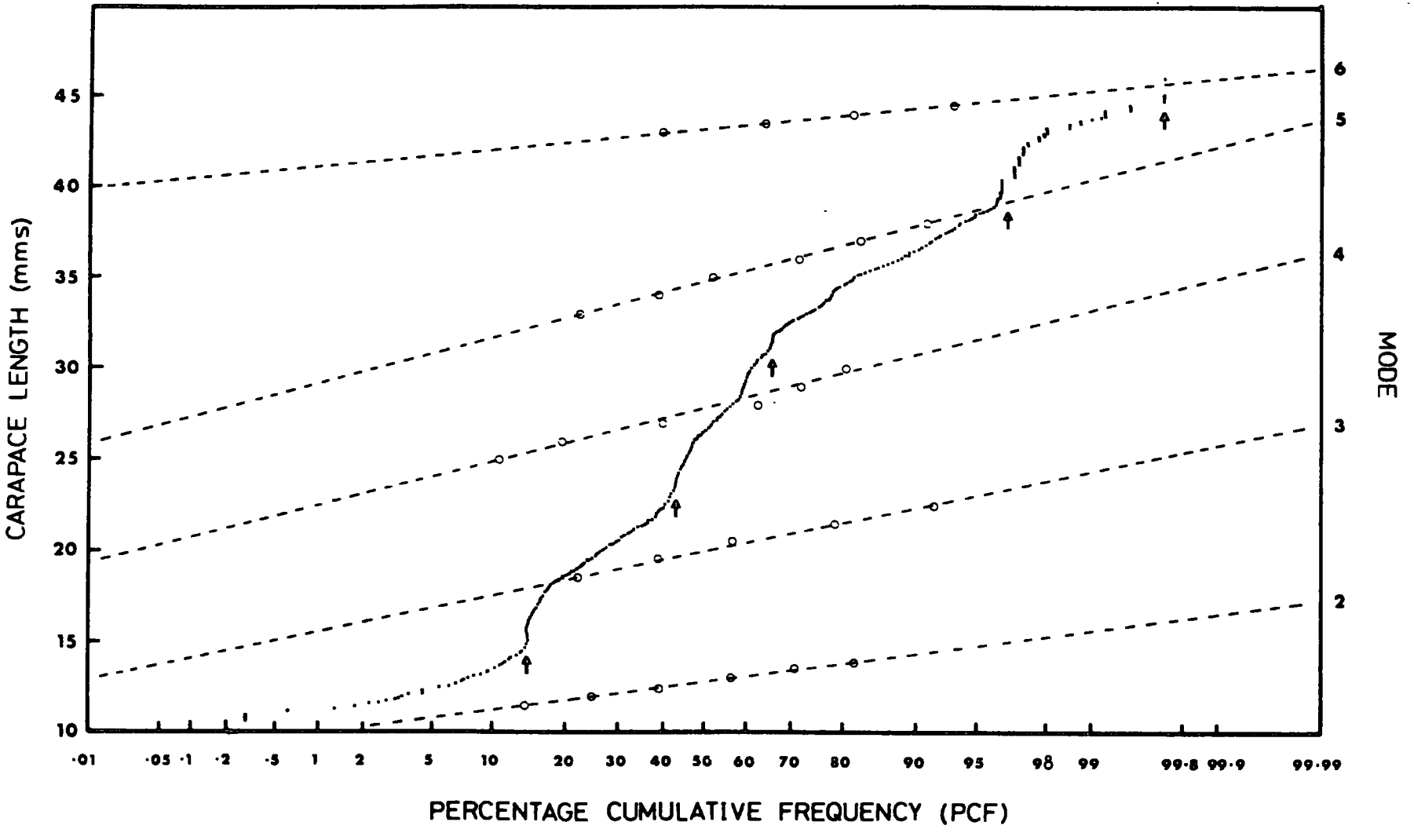


Fig. 4.9b: Carapace length as a function of percentage cumulative frequency (PCF) plotted on arithmetic probability paper for females 1973-74. This was the first step in the analysis of the polymodal size frequency distribution of Fig. 4.7 using the method of Cassie (1954). The second step was to identify the inflexion points (↑), see text. The open circles (o) and broken lines represent the final step in the analysis as each mode in the distribution was separated out. Where the broken lines cross the 50% PCF this point corresponds to the mean size of that mode on the ordinate

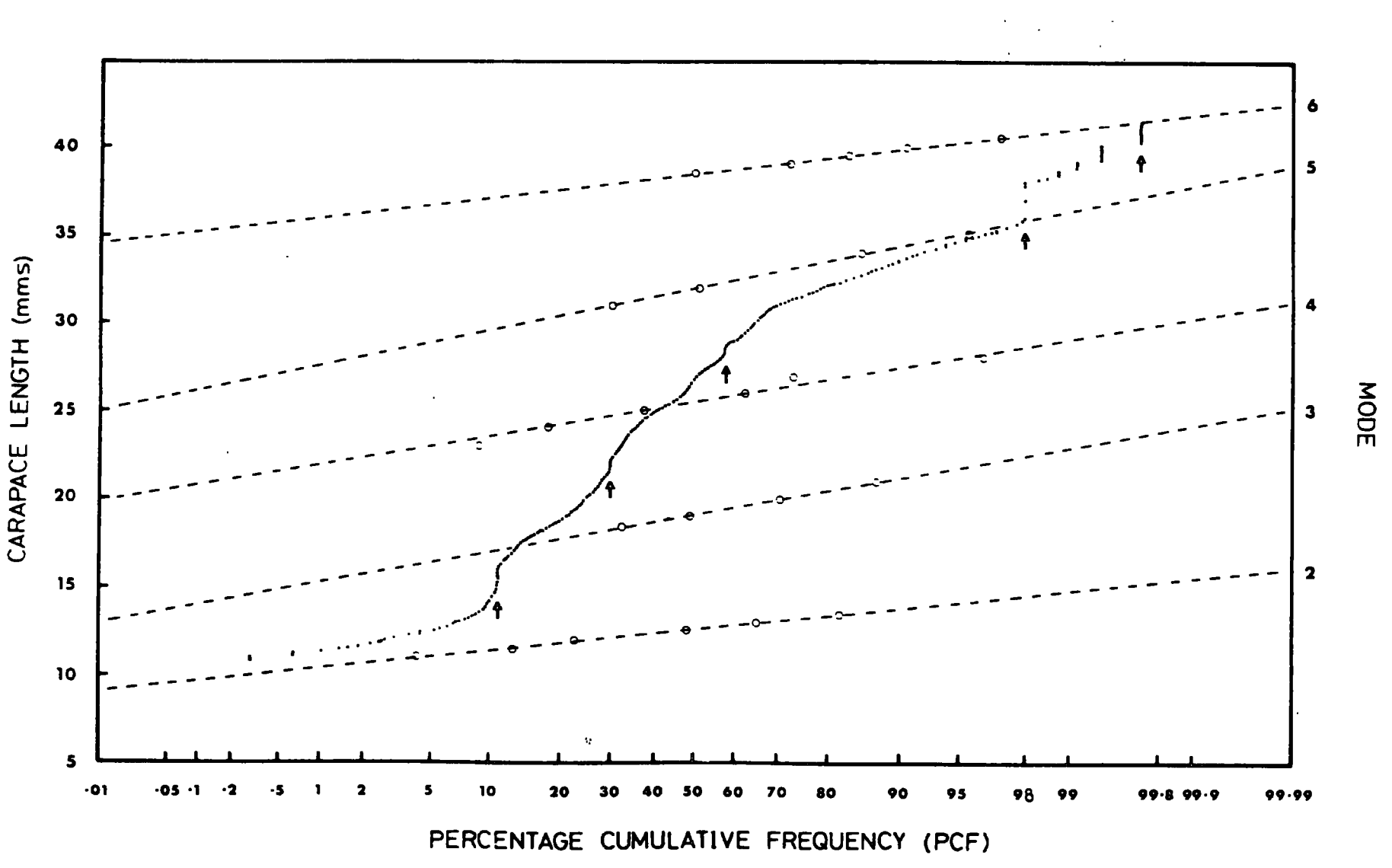

FEMALES 1973-'74
CARAPACE LENGTH (mms)
40
35
30
25
20
15
10
5
MODE
6
5
4
3
2
·01
·05
·1
·2
·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·9
99·99
PERCENTAGE CUMULATIVE FREQUENCY (PCF)

Fig. 4.10a: Carapace length as a function of percentage cumulative frequency (PCF) plotted on arithmetic probability paper for males 1974-75. This was the first step in the analysis of the polymodal size frequency distribution of Fig. 4.8 using the method of Cassie (1954). The second step was to identify the inflexion points (↑), see text. The open circles (o) and broken lines represent the final step in the analysis as each mode in the distribution was separated out. Where the broken lines cross the 50% PCF this point corresponds to the mean size of that mode on the ordinate

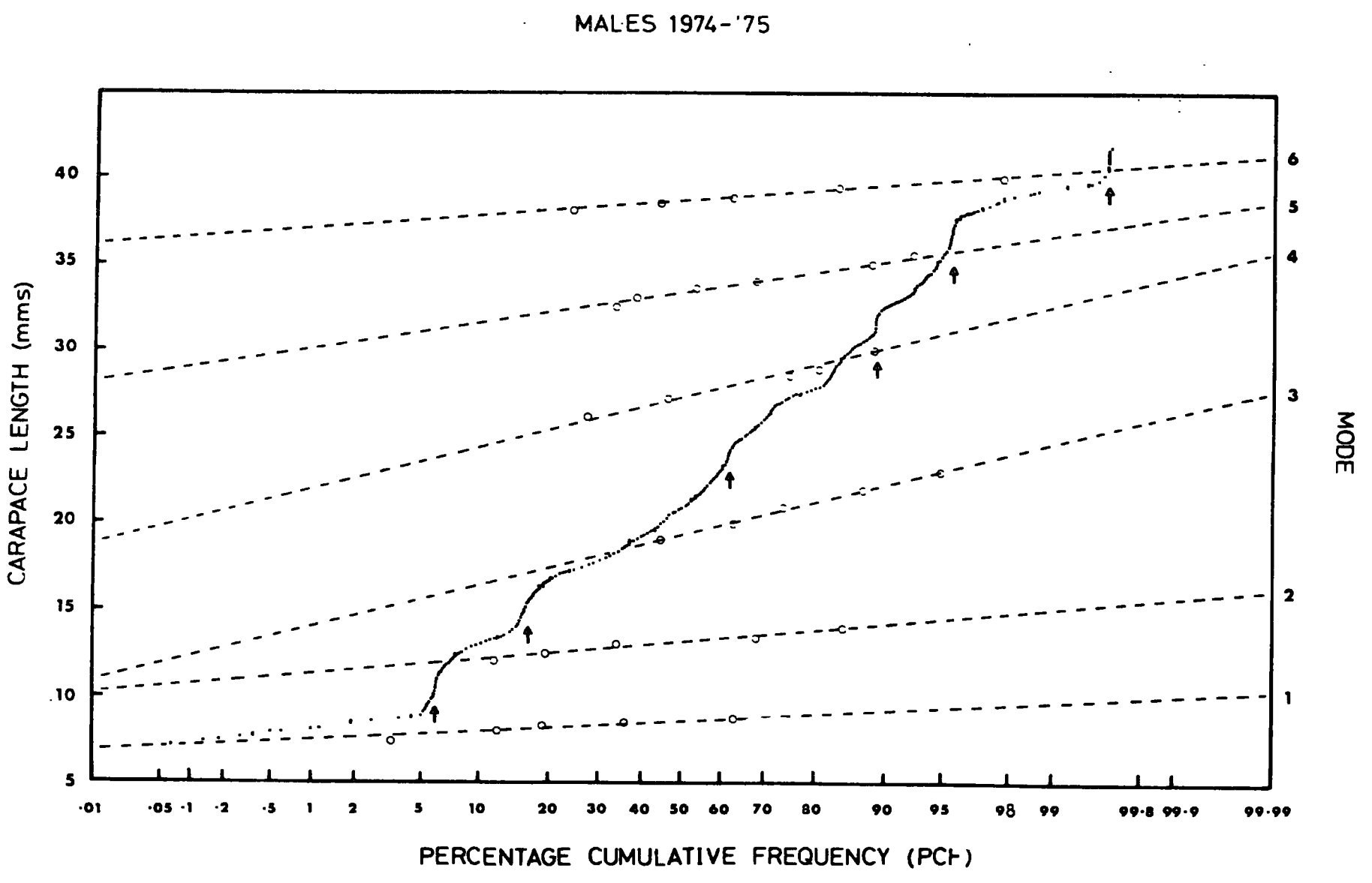
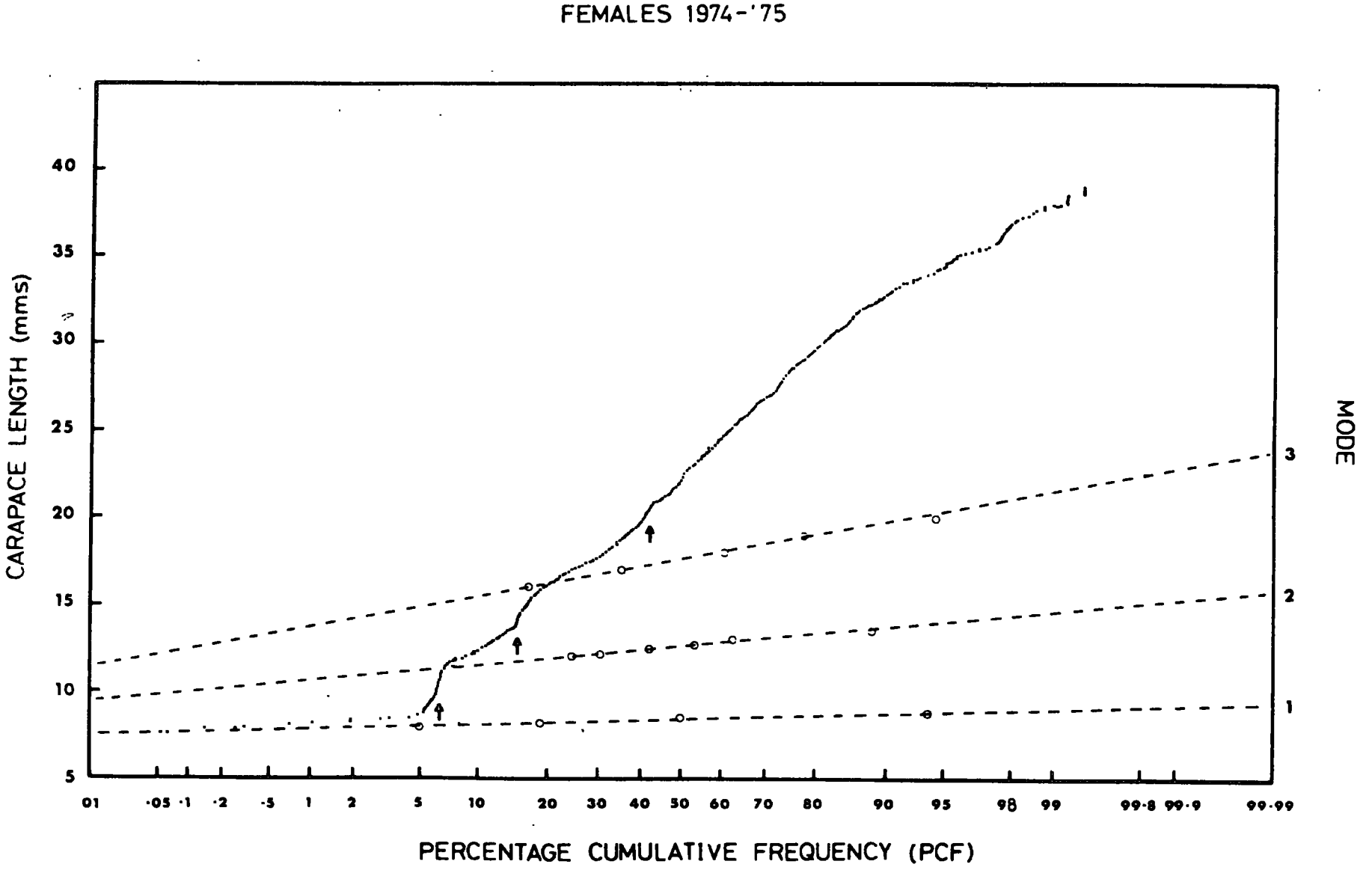

MALES 1974-'75
CARAPACE LENGTH (mms)
40
35
30
25
20
15
10
5
·01
·05
·1
·2
·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·9
99·99
PERCENTAGE CUMULATIVE FREQUENCY (PCF)
MODE
6
5
4
3
2
1

Fig. 4.10b: Carapace length as a function of percentage cumulative frequency (PCF) plotted on arithmetic probability paper for females 1974-5. This was the first step in the analysis of the polymodal size frequency distribution of Fig. 4.8 using the method of Cassie (1954). The second step was to identify the inflexion points (↑), see text. The open circles (o) and broken lines represent the final step in the analysis as each mode in the distribution was separated out. Where the broken lines cross the 50% PCF this point corresponds to the mean size of that mode on the ordinate


FEMALES 1974-'75
CARAPACE LENGTH (mms)
40
35
30
25
20
15
10
5
MODE
3
2
1
01
·05
·1
·2
·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·9
99·99
PERCENTAGE CUMULATIVE FREQUENCY (PCF)

The inflexion points chosen were those that resulted in a change of direction of the approximately linear correlation between PCF and carapace length for at least $2\frac{1}{2}$ mm. carapace length (e.g. P = 96.7%, Fig. 4.9a) or where the line became almost vertical for even quite a small increase in carapace length (e.g. P = 58%, Fig. 4.9b). There were several other 'weaker' inflexion points which were rejected on these rather subjective criteria (e.g. P = 61%, Fig. 4.9a, P = 50%, Fig. 4.9b). However, as the mean moult increments in this size range ($\simeq$ 30 mm. carapace length) were approximately 2.5 and 3.0 mm. carapace length for the females and males respectively (4.3.1) and all crayfish in this size range moulted once and some twice each year(4.3.2) it seemed unlikely that there could have been two pairs of modes as close together as the 'strong' inflexion points nearest to these latter two 'weak' ones would suggest. It was, therefore, considered reasonable in such cases to select the 'stronger' inflexion points and ignore the 'weaker' ones.

The results of the analysis of Figs. 4.7 & 4.8 on Figs. 4.9 & 4.10 are presented on Table 4.4. Comparing the mean carapace length of each mode between 1973-4 and 1974-5. For the males the means of modes 2, 3 and 4 were not significantly different (73-4, 12.8 $\pm$ 1.2, 20.0 $\pm$ 1.9 and 27.75 $\pm$ 2.4; 74-5, 13.20 $\pm$ 0.8, 19.4 $\pm$ 2.2 and 27.2 $\pm$ 2.3) but the means of modes 5 and 6 were highly significantly different (73-4, 34.75 $\pm$ 2.4 and

42.7 ± 1.2; 74-5, 33.4 ± 1.4 and 38.7 ± 0.7). In the females the means of modes 2 were the same in both years (12.6 mm.) but the means of mode 3 were highly significantly different (19.10 ± 1.7 and 17.60 ± 1.7).

Comparing the sexes in each year there was no significant difference between the means of mode 1 in 1974-5 (males 8.6 ± 0.4, females 8.5 ± 0.2) or between the means of mode 2 in either year (73-4, males 12.8 ± 1.2, females 12.6 ± 1.2 and 74-5, males 13.2 ± 0.8, females 12.6 ± 0.8). The means of modes 3 and 4 of the females in 1973-4 were both significantly lower than those for the males (males, 20.0 ± 1.9 and 27.75 ± 2.4; females 19.10 ± 1.70 and 25.50 ± 1.60) but were of a similar order. The mean of mode 3 in 1974-5 was significantly higher in the males (males 19.4 ± 2.2, females 17.6 ± 1.70).

Therefore, the two analyses produced similar results in the two years especially between the sexes in modal sizes 1 and 2. The mean sizes of modes 3 and 4 were also comparable within each sex with females increasing in size less in the 3rd and 4th growth season as expected from the smaller moult increments already described (4.3.1). The only exception to this latter point was the mean of mode 3 in 1974-5 (17.6 ± 1.7) which was much lower than that in the previous year (19.1 ± 1.7). However, the whole of the female size frequency histogram in 1974-5 was difficult to interpret above 15 mm. carapace length and it was doubtful if this mode represented a complete year class.

The principle assumptions underlying the use of size frequency distributions to estimate age are that all individuals of each year class are born a similar size and grow a similar amount each year. Where initial size and yearly growth increment are identical such an analysis could easily be made 'by eye', the use of this analysis with natural populations can only yield approximate answers at best. The similarities of the results from the analysis of Figs. 4.7 and 4.8 up to the 4th overwintering size suggested that this was a reasonably accurate description of the interrelationship between size and age in A. pallipes. A considerable amount of data concerning moult increment and frequency was available after this period and this was used to extend this interrelationship into a postulated growth pattern throughout the life span of an average crayfish of each sex.

This was carried out in the following way: Fig. 4.9 and 4.10 derived by the methods of Cassie (1954) gave overwintering sizes of the following estimated values, 8.5 mm., 13 mm. and 19.5 mm. carapace length for 0+, 1+ and 2+ aged juveniles of both sexes. It was also possible to estimate the size of the 3+ year class as 25.5 mm. carapace length in the females and 27.5 mm. carapace length in the males. Therefore some animals first became sexually mature in this year (3.4). These data are shown on Table 4.4. Young crayfish first become independent from the mother at around 4.59 mm. carapace

Table 4.4: The results of the analysis of the polymodal size frequency distributions on Figs. 4.7 and 4.8 using the method of Cassie (1954)

Sex	Mode number		Mean Carapace length (mm.)		Standard Deviation		Estimated percentage of total sample		Estimated number in modal group		p (difference between 73-4 & 74-5)
	1973-4	1974-5	1973-4	1974-5	1973-4	1974-5	1973-4	1974-5	1973-4	1974-5	
Males	0‡	0*	-	4.59	-	0.24	-	-	-	-	
	1‡	1	-	8.60	-	0.4	-	6.0	-	23.9	
	2	2	12.80	13.20	1.2	0.8	14.0	10.5	50.1	41.8	< 0.10
	3	3	20.00	19.40	1.9	2.2	29.0	45.5	103.8	181.1	< 0.10
	4	4	27.75	27.20	2.4	2.3	23.0	27.0	82.3	107.5	< 0.20
	5	5	34.75	33.40	2.4	1.4	30.7	6.5	109.9	25.9	< 0.001
	6	6	42.70	38.70	1.2	0.7	3.0	4.1	10.7	16.3	< 0.001
	7+	7+	-	-	-	-	0.3	0.4	1.1	1.6	
							100.0	100.0	358	398	
Females	0‡	0*	-	4.59	-	0.24	-	-	-	-	
	1‡	1	-	8.50	-	0.2	-	6.4	-	20.9	
	2	2	12.60	12.60	1.2	0.8	11.0	8.6	36.5	28.0	> 0.90
	3	3	19.10	17.60	1.7	1.7	19.0	27.0	63.1	88.0	< 0.001
	4	4+	25.50	-	1.6	-	28.0	58.0	93.0	189.1	
	5		32.00		1.9		39.9	100.0	132.5	326	
	6		38.50		1.1		1.8		6.0		
	7+		-		-		0.3		1.0		
							100.0		332		

Table 4.4 - Notes

I Hatchlings which had just become independent of the mother and which had survived one winter were not systematically collected in 1973-74 but were observed to have been present in large numbers and were of similar size to those measured in 1975; Fig. 4.7 and 4.8

0* The zero mode (broken lines Figs. 4.7 and 4.8) represents the mean size when the hatchlings became independent of the mother. These measurements were not included in the above analysis but are presented here for comparison; the mean size of the sixteen hatchlings measured was 4.59 ± 0.06 (SE) mms. carapace length.

'mode' number According to the selected points of inflexion shown and the subsequent analysis of Harding (1949) and Cassie (1954; Figs. 4.9 and 4.10) this describes one approximately normal distribution which may or may not represent an individual year class (Kurata 1962).

length; as they overwinter at about 8.5 mm. it is possible to estimate the number of moults in the first growth season assuming that the correlation between the percentage moult increment (% M.I.) and premoult carapace length (Pre M.C.L.) (Fig. 4.4) can be extrapolated back to yearling crayfish. As can be seen 5 or 6 moults are predicted to occur in their first growth season. The same procedure for 1+ crayfish suggests 4 moults occur in their second growth season and that 2+ juveniles moult 3 or 4 times with 3+ juveniles moulting 3 times in their 4th growth season. However, as can be seen from Fig. 4.6 the eighteen juveniles, for which moulted frequency data were obtained, all moulted only twice. In three cases the second moult was completed by August, it is therefore possible that these animals moulted again in September (4.3.2).

The projected growth pattern is shown on Table 4.5, the lower part of which is constructed on two assumptions. One, crayfish moult twice a year up to the size class at which no second moult was observed to occur in any re-captured crayfish (see Fig. 4.6) or alternatively adult crayfish moult only once a year. These two assumptions, the correlation of % M.I. and Pre M.C.L. (Fig. 4.4) and the maximum size attained by A. pallipes in the aqueduct provide an estimation of the minimum and maximum life span respectively.

The largest male caught in the aqueduct was 50.5 mm. carapace length and an animal of this size was calculated to be 10 to 12 years old. The largest female was 45.6 mm. carapace length and this was predicted to be between 10 and 13 years of age.

Table 4.5: The projected mean growth pattern throughout the life cycle. For derivation see text (4.3.3)

Overwinter	Male Carapace length mm.		Moults per annum	Year Class	Female Carapace length mm.		Moults per annum
Hatchlings	4.59				4.59		
1st	5.19 5.86 6.61 7.46 8.41		5	0+	5.09 5.65 6.27 6.95 7.70 8.51		6
2nd	9.47 10.65 11.95 13.43		4	1+	9.45 10.46 11.57 12.79		4
3rd	15.06 16.86 18.84		3	2+	14.13 15.60 17.21 18.96		4
4th	21.02 23.40 25.99		3	3+	20.88 22.96 25.22		3
	Minimum Life Span	Maximum Life Span			Minimum Life Span	Maximum Life Span	
5th	31.96	28.94		4+	30.36	27.79	
6th	37.96	31.96		5+	35.29	30.36	
7th	40.84	34.98		6+	37.57	32.88	
8th	43.58	37.96		7+	39.67	35.29	
9th	46.12	40.84		8+	41.57	37.57	
10th	48.44	43.58		9+	43.27	39.67	
11th	50.53	46.12		10+	44.77	41.57	
12th		48.44		11+	46.07	43.27	
13th		50.53		12+		44.77	
14th				13+		46.07	

There was some evidence from the recapture histories of three numbered crayfish that the interpretation of the third and fourth modes as year classes was valid.

(i) Animal number 901 (male) was caught on the 24. 7.74 and had a carapace length of 16.0 mm. and had already moulted that year; it had probably, therefore, overwintered with a carapace length of around 13 mm. It was recaptured again on the 27. 8.76 and had again already moulted that year, its carapace length was now 34.5 mm. This corresponded to the expected growth pattern from year class 1+ to 4+.

(ii) Animal number 941 (female) was caught on 13. 7.74, had moulted that year and had a carapace length of 24.1 mm.; it had probably, therefore, overwintered with a carapace length of around 21.5 mm. It was recaptured on the 11. 6.76, had not moulted that year and had a carapace length of 32.3 mm. corresponding to the expected growth pattern in year classes 3+, 4+ and 5+.

(iii) Animal number 1123 (male) was caught on the 7. 8.74, had moulted that year and had a carapace length of 25.1 mm.; it had probably overwintered with a carapace length similar to animal number 941. It was recaptured on the 27. 6.76, had not moulted that year and had a carapace length of 35.5 mm. again corresponding to a possible growth pattern in year classes 3+, 4+ and 5+.

The above three recapture histories, the distinct nature and small amount of overlap between the modes of

the year classes 0+ and 1+, the fact that recently collected information has clearly demonstrated these modes as year classes (Brewis, unpubl.) and the large amount of growth data on which the mean sizes of year classes 4+ to 11+ were based, lead to the conclusion that these postulated mean growth patterns were a valid and reasonably accurate description of the interrelationship of size and age in the aqueduct population of A. pallipes.

This projected growth pattern for both sexes and the above three recapture histories are plotted on Fig. 4.11.

4.4 Growth of A. pallipes in the laboratory

A laboratory study of growth under controlled conditions was carried out, the original intention of which was to aid in the interpretation of field growth data. As this study progressed it became clear that the information gained would be of little value in this respect but the study was continued in order to investigate the effects of limb-loss on subsequent growth in more detail than was possible in the aqueduct.

4.4.1 Laboratory methods

(i) All measurements and weighings were carried out as described in sections 2.1 and 4.2.1.

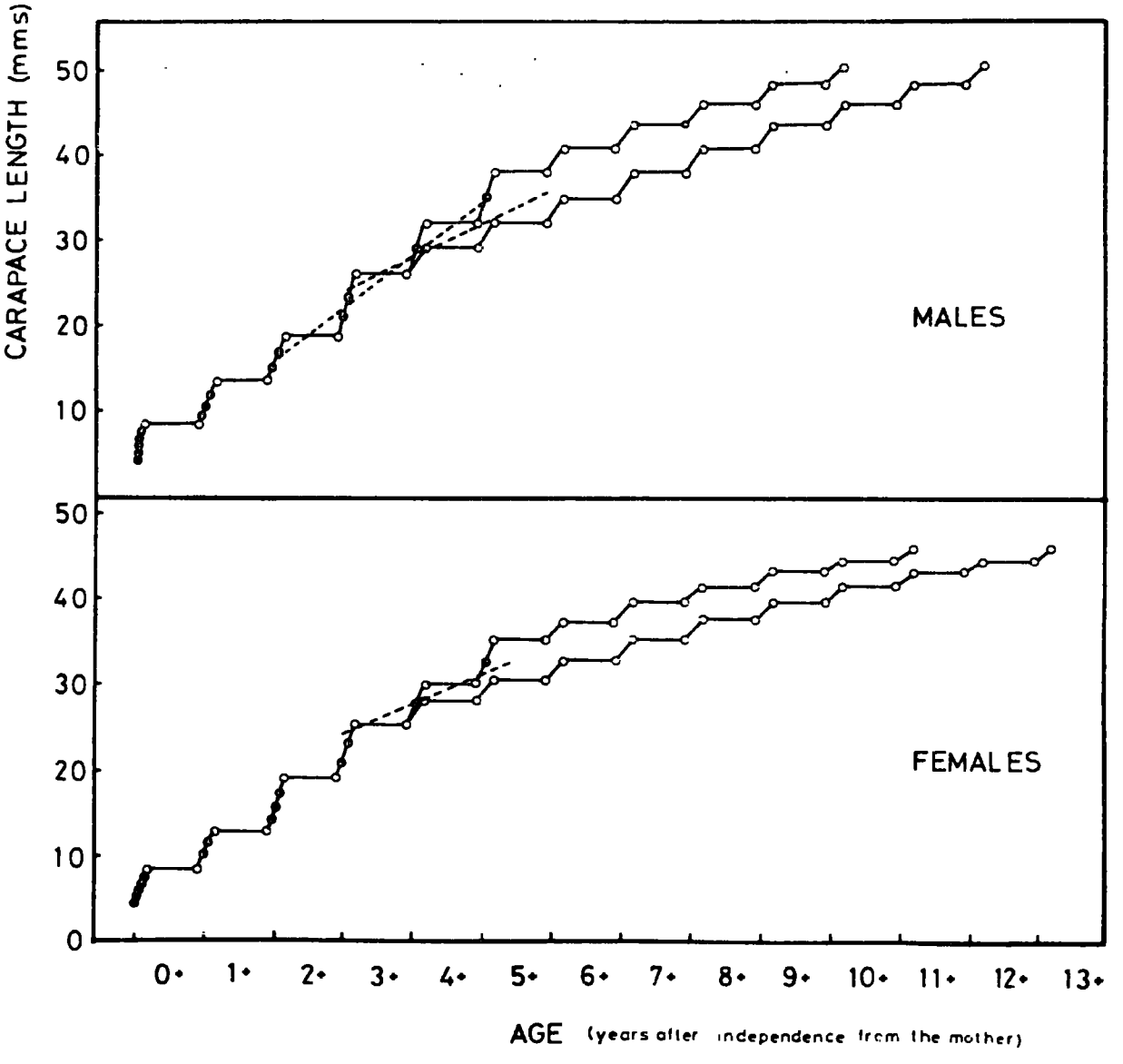
(ii) The experimental animals were collected during the months June to September from feeder streams, other than the aqueduct, situated amongst the Hallington and Whittle Dene reservoir complexes in Northumberland.

Fig. 4.11: The projected mean growth pattern throughout the life cycle (see section 4.3.3 & Table 4.5). Estimated mean carapace length as a function of age in years after independence from the mother

o - estimated over-wintering sizes

● - estimated sizes after each moult during the growth season

——— - the increase in size during the longest three known recapture histories which spanned the size range where the two methods of estimating age overlapped (see text)


CARAPACE LENGTH (mms)
50
40
30
20
10
MALES
50
40
30
20
10
0
FEMALES
0+
1+
2+
3+
4+
5+
6+
7+
8+
9+
10+
11+
12+
13+
AGE (years after independence from the mother)

(iii) All animals were individually maintained in compartments which contained a constant volume of standing, stirred and aerated tap water at a temperature of 15 ± 0.5°C under a 12L : 12D photoperiod regime. The volumes of water in the three types of compartments used were 500 ml., 1.5 litres and 6 litres.

(iv) Crayfish were fed with an excess of either 'Trouvit' or Cooper Nutrition Products 'Beta' trout pellets with an approximately fortnightly addition of Fontinalis antipyretica on every alternate day; faeces and uningested food were removed and the water changed the day following feeding.

(v) A daily examination for moults was made.

(vi) All exuviae were left in the compartment for at least six days following moulting; by which time they had always been largely ingested save for the heavily calcified structures such as the dactyl tips of the first three pairs of pereiopods.

4.4.2 Moult increments

The interrelationship between premoult carapace length (Pre M.C.L.; x) and postmoult carapace length (Post M.C.L.; y) for male and female crayfish maintained in the laboratory is shown on Fig. 4.12. The correlation was highly significant for normal and limb-regenerating animals of both sexes; the equations for the regression lines were as follows:-

Fig. 4.12: Postmoult carapace length (y) as a function of premoult carapace length (x) for normal (solid symbols) and limbless or limb-regenerating (open symbols) crayfish maintained under laboratory conditions

normal males (solid line):-

$y = 1.0374x + 0.9536$ (n = 56)
SE slope = 0.0181, r = 0.9919

significance of the slope compared to unity:-

$t = 2.07$, $p < 0.05$

Limbless or limb-regenerating males (broken line):-

$y = 1.0282x + 0.6343$ (n = 51)
SE slope = 0.0099, r = 0.9977

significance of the slope compared to unity:-

$t = 2.85$, $p < 0.01$

normal females (solid line):-

$y = 1.0708x + 0.1197$ (n = 39)
SE slope = 0.0119, r = 0.9977

significance of the slope compared to unity:-

$t = 5.95$, $p < 0.001$

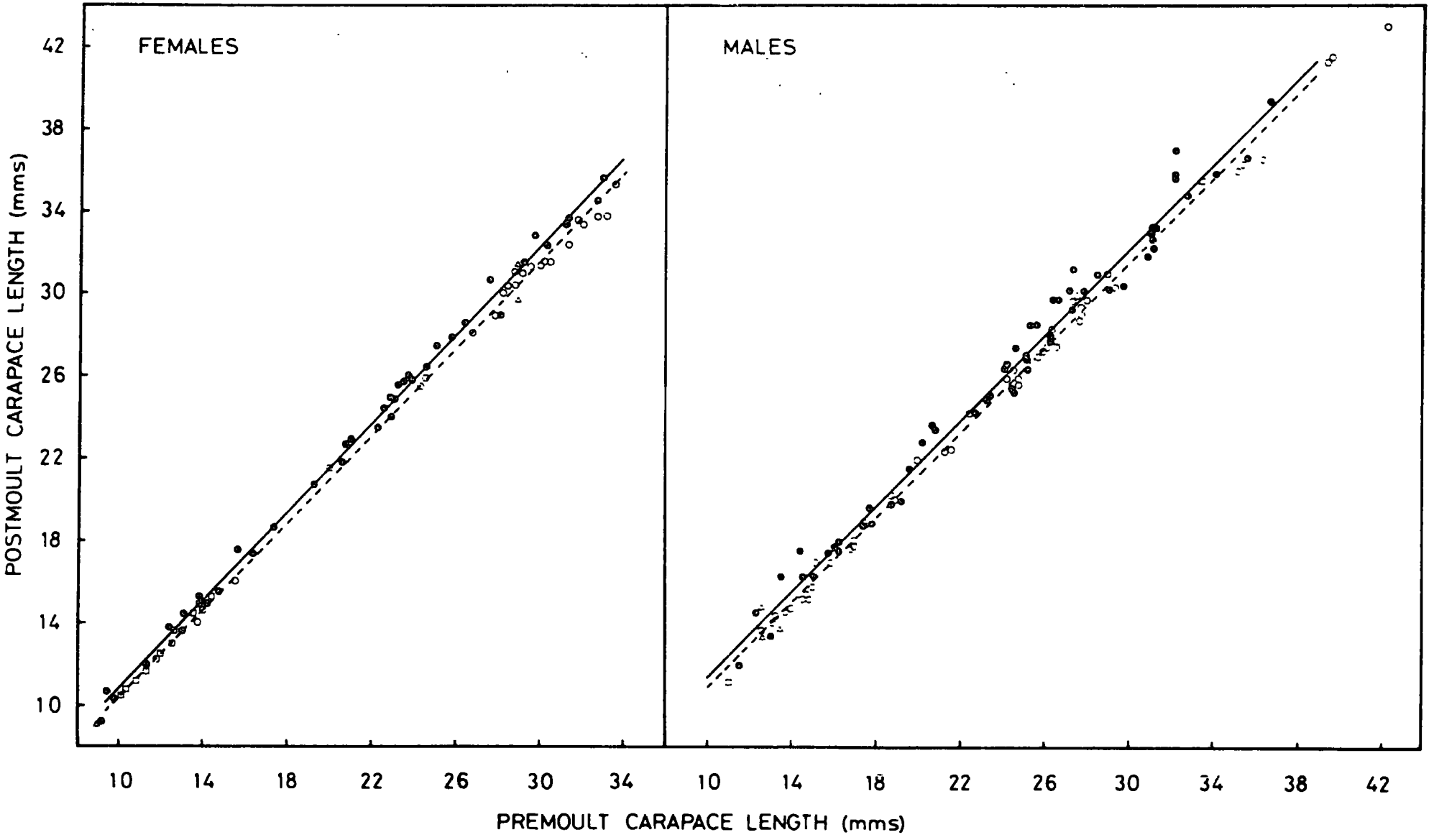
limbless or limb-regenerating females (broken line):-

$y = 1.0493x + 0.0642$ (n = 37)
SE slope = 0.0093, r = 0.9986

significance of the slope compared to unity:-

$t = 5.30$, $p < 0.001$

- ● - normal crayfish
- o - crayfish missing or regenerating a cheliped in the premoult condition
- △ - crayfish missing or regenerating both chelipeds in the premoult condition
- □ - crayfish missing or regenerating one or more walking legs (pereiopods pairs 2-5) in the premoult condition


FEMALES
MALES
POSTMOULT CARAPACE LENGTH (mms)
PREMOULT CARAPACE LENGTH (mms)
10
14
18
22
26
30
34
38
42

normal males	$y = 1.0374x + 0.9536$	$(p < 0.001)$
limb-regenerating males	$y = 1.0282x + 0.6343$	$(p < 0.001)$
normal females	$y = 1.0708x + 0.1197$	$(p < 0.001)$
limb-regenerating females	$y = 1.0493x + 0.0642$	$(p < 0.001)$

There was no indication of any change in growth pattern over the size range studied (9-39 mm. carapace length) as compared to the decrease in slope observed to occur at around 28 mm. Pre M.C.L. for the field growth data (Fig. 4.2). This may, however, have been due to the paucity of the laboratory growth data for crayfish of Pre M.C.L. > 28 mm.

The slopes of all four regression lines on Fig. 4.12 were significantly greater than unity (normal males, $p < 0.05$ and other three slopes $p < 0.001$) indicating progressive geometric growth (4.1) as observed for the juvenile males and strongly suggested for the juvenile females in the aqueduct.

There was no significant difference between the mean moult increments (M.I.'s) of normal crayfish of either sex that were maintained in the three different sizes of compartment:-

Compartment size	Males n	Males Mean M.I. ± SE(mm.)	Females n	Females Mean M.I. ± SE(mm.)
0.5 L.	35	1.76 ± 0.14	22	1.88 ± 0.11
1.5 L.	14	1.89 ± 0.19	9	1.54 ± 0.15
6.0 L.	10	1.54 ± 0.11	8	1.59 ± 0.23

The data was therefore pooled for each compartment type. An analysis of the M.I. data from normal and limbless or limb-regenerating crayfish which were maintained in the laboratory is shown on Table 4.6.

The mean M.I. for males that were missing or regenerating a cheliped in the premoult condition (1.30 ± 0.08 mm.) was significantly less than that for normal males (1.85 ± 0.13 mm., $p < 0.001$) but all other significant differences between the mean M.I.'s of crayfish in any one of the three separate classes of limb-loss and normal crayfish may have been accounted for by corresponding significant differences in mean Pre M.C.L. and the progressive geometric growth pattern rather than limb-regeneration.

When the M.I. data from all limbless and limb-regenerating crayfish of either sex was pooled (Table 4.6) there were no significant differences between mean Pre M.C. Lengths and the mean M.I.'s (males 1.28 ± 0.09 mm. and females 1.16 ± 0.11 mm.) were significantly lower than those for normal crayfish in both sexes (males 1.85 ± 0.13 mm. and females 1.63 ± 0.11 mm.; males $p < 0.001$ and females $p < 0.01$). The solid (normal) and broken (limb-regenerating) regression lines fitted to Fig. 4.12 showed that these differences were similar over the whole size range studied for both sexes.

There was no significant difference between the mean M.I. of normal males (1.85 ± 0.13 mm.) and females (1.63 ± 0.11 mm., $p < 0.20$). This was in contrast to

Table 4.6: An analysis of the moult increment (M.I.) data for crayfish maintained in the laboratory

Population	Males			Females		
	n	Mean M.I. ± SE mm.	Pre M.C.L. ± SE mm.	n	Mean M.I. ± SE mm.	Pre M.C.L. ± SE mm.
Normal crayfish	56	1.85 ± 0.13	24.04 ± 0.87	39	1.63 ± 0.11	21.29 ± 1.09
Total limbless or limb-regenerating	51	1.28 ± 0.09	24.72 ± 0.94	37	1.16 ± 0.11	22.28 ± 1.13
Crayfish with one cheliped missing or regenerating*	45	1.30 ± 0.08	25.80 ± 1.17	23	1.35 ± 0.13	26.80 ± 1.37
Crayfish with both chelipeds missing or regenerating*	3	1.23 ± 0.60	12.80 ± 0.30	3	1.20 ± 0.67	22.23 ± 2.11
Crayfish with one or more walking legs missing or regenerating	3	1.00 ± 0.56	20.47 ± 2.12	11	0.76 ± 0.11	12.85 ± 0.83

* includes some crayfish also missing or regenerating one or more walking legs (pereiopods pairs 2-5)

the difference observed in the aqueduct but again may have been due to the paucity of the M.I. data for adults.

The gravimetric growth data which were recorded for some of the laboratory moult increments was shown on Fig. 4.13. There were no significant differences between the mean absolute wet weight increments at the moult for normal and limbless or limb-regenerating animals of either sex; these increments were similar over the whole size range studied, as shown by the regression lines fitted to Fig. 4.13.

	Mean absolute weight increment at the moult	
Normal males	0.4132 ± 0.0750 gm. (n=23)	
Limb-regenerating males	0.3268 ± 0.0638 gm. (n=22)	$t = 0.88$, $p > 0.40$
Normal Females	0.4048 ± 0.0771 gm. (n=27)	
Limb-regenerating females	0.3106 ± 0.0636 gm. (n=17)	$t = 0.94$, $p > 0.30$

Therefore the only significant difference between the total growth increment per moult between normal animals and those that were limbless or limb-regenerating in the premoult condition was one of growth in terms of length not body mass.

The growth rates of the regenerating chela and its normal contralateral partner for three small animals (males 14.3, 18.8 mm., female 11.4 mm. initial carapace length) which survived in the laboratory to moult several times were compared on Fig. 4.14. In the larger male and

Fig. 4.13: Postmoult wet weight in gms. as a function of premoult wet weight in gms. for normal (solid symbols) and limbless or limb-regenerating (open symbols) crayfish maintained under laboratory conditions

normal males:-

$y = 1.1979x + 0.0619$ ($n = 23$)

SE of slope = 0.0175

$r = 0.9978$, $t = 68.97$, $p \ll 0.001$

limbless or limb-regenerating males:-

$y = 1.2241x - 0.0269$ ($n = 22$)

SE of slope = 0.0197

$r = 0.9974$, $t = 61.90$, $p \ll 0.001$

normal females:-

$y = 1.1606x + 0.0662$ ($n = 27$)

SE slope = 0.0283

$r = 0.9927$, $t = 41.15$, $p \ll 0.001$

limbless or limb-regenerating females:-

$y = 1.2135x - 0.0708$ ($n = 17$)

SE slope = 0.0133

$r = 0.9991$, $t = 91.23$, $p \ll 0.001$

- ● - normal crayfish
- o - crayfish with one cheliped missing or regenerating in the premoult condition
- △ - crayfish with both chelipeds missing or regenerating in the premoult condition
- □ - crayfish with one or more walking legs (pereiopods pairs 2-5) missing or regenerating in the premoult condition

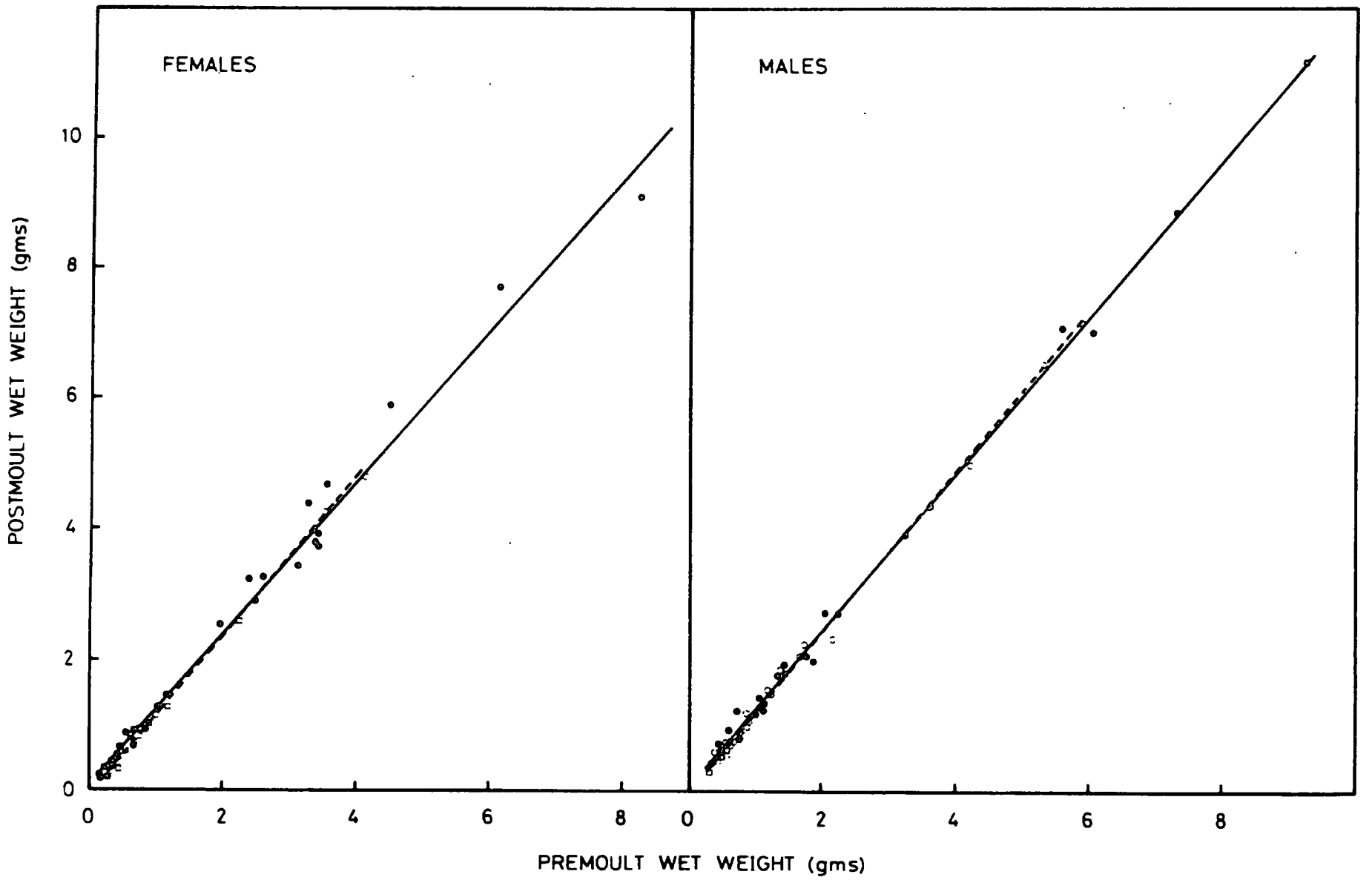
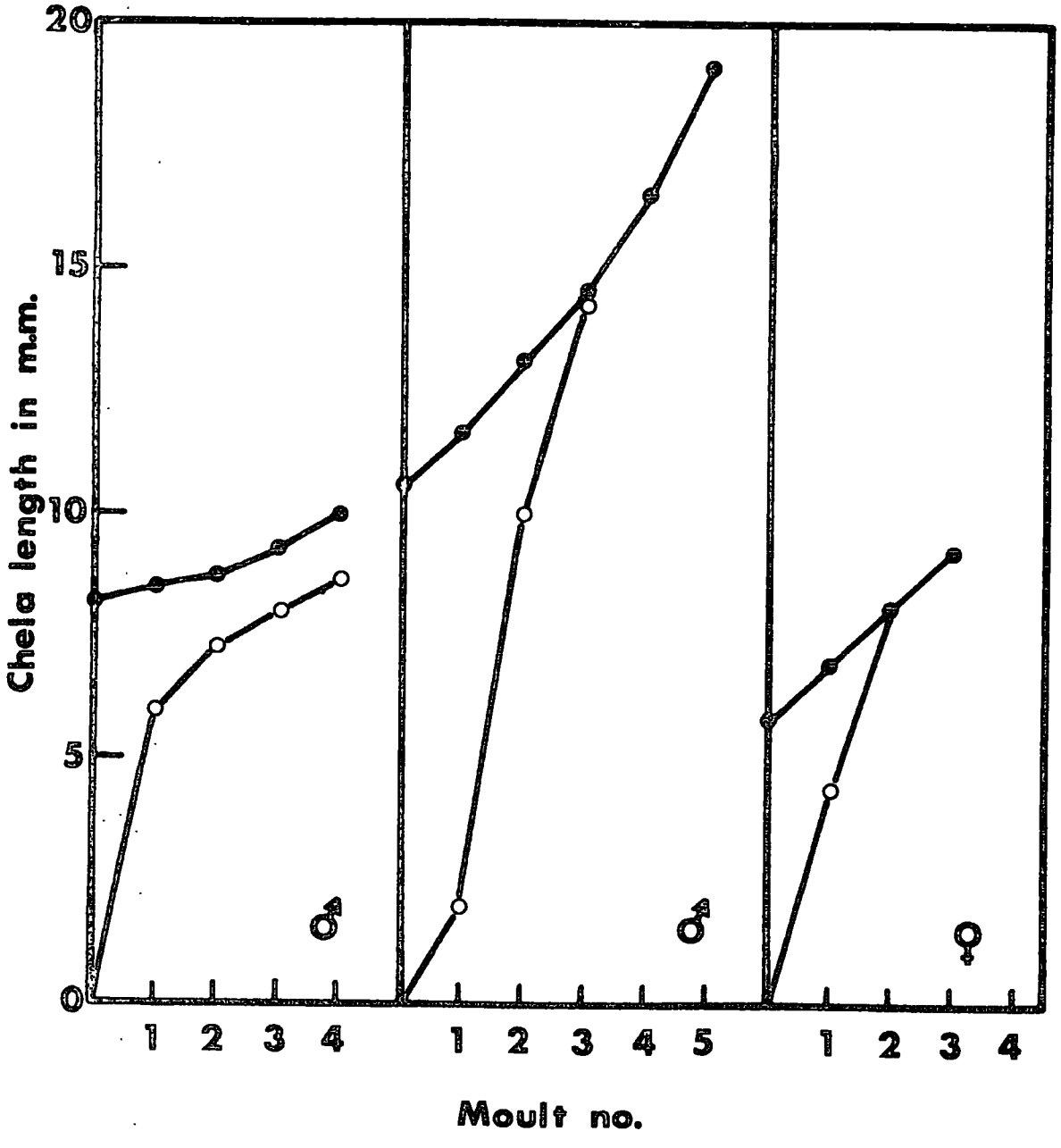

FEMALES
MALES
POSTMOULT WET WEIGHT (gms)
PREMOULT WET WEIGHT (gms)
0
2
4
6
8
10

Fig. 4.14: A comparison of the growth rate of the regenerating chela (○) and its normal contralateral partner (●) in three small crayfish maintained in the laboratory. Males 14.3 and 18.8 mm., female 11.4 mm. initial carapace length


20
15
10
5
0
Chela length in m.m.
♂
♂
♀
1 2 3 4
1 2 3 4 5
1 2 3 4
Moult no.

the female these animals regenerated the lost cheliped to the size expected from carapace length (Fig. 4.1) in three and two months respectively. The smaller male regenerated the lost cheliped to within 18% of the size of its contralateral partner after the second moult, both chelae then increased in size by similar absolute increments. These three animals were selected as they moulted several times and demonstrated that A. pallipes can regenerate chelipeds of equal and appropriate size. Larger animals also partially regenerated chelipeds in the laboratory but did not survive the greater number of moults required to regenerate it to equal the size of its contralateral partner. Many large specimens were observed to be in the late stages of regeneration in the aqueduct (Fig. 4.5) proving that complete regeneration was still possible, given sufficient time.

It was concluded, therefore, that there was some mechanism by which A. pallipes controlled the differential growth rate of lost limbs during their regeneration at the expense of overall body growth.

4.4.3 Moult frequency and survival

As all moults were recorded on the day they occurred (4.4.1) from the second moult onwards the intermoult period was known:-

(i) There was no significant difference between the mean intermoult periods of normal or injured animals of either sex:-

	intermoult period (days) ± SE	
normal males	106.25 ± 14.31	
		t = 0.28, p > 0.70
injured males	111.78 ± 13.29	
normal females	91.31 ± 10.99	
		t = 1.22, p > 0.20
injured females	120.82 ± 21.47	

(ii) There were significant positive correlations between the length of the intermoult period and for the total of normal and injured animals of both sexes ($p < 0.001$ in both cases; Fig. 4.15).

(iii) Moulting in the laboratory was not confined to a particular season as it was in the aqueduct (3.3). Indeed, there were no significant differences in the numbers of the animals which moulted in any month throughout the year.

The survival rate for all animals of both sexes decreased exponentially following each moult; 72% survived the first moult, 31% the second, 17% the third, 3% the fourth, 1% the fifth and none the sixth.

4.5 Discussion

The majority of studies of decapod growth have employed one or more of the three methods used in this chapter for the analysis of moult increments.

A decrease in slope of the relationship between premoult carapace length (Pre M.C.L.) and postmoult carapace length (Post M.C.L.) shortly after the minimum

Fig. 4.15: The length of the intermoult period in days as a function of premoult carapace length in mm. for laboratory maintained crayfish

males:-

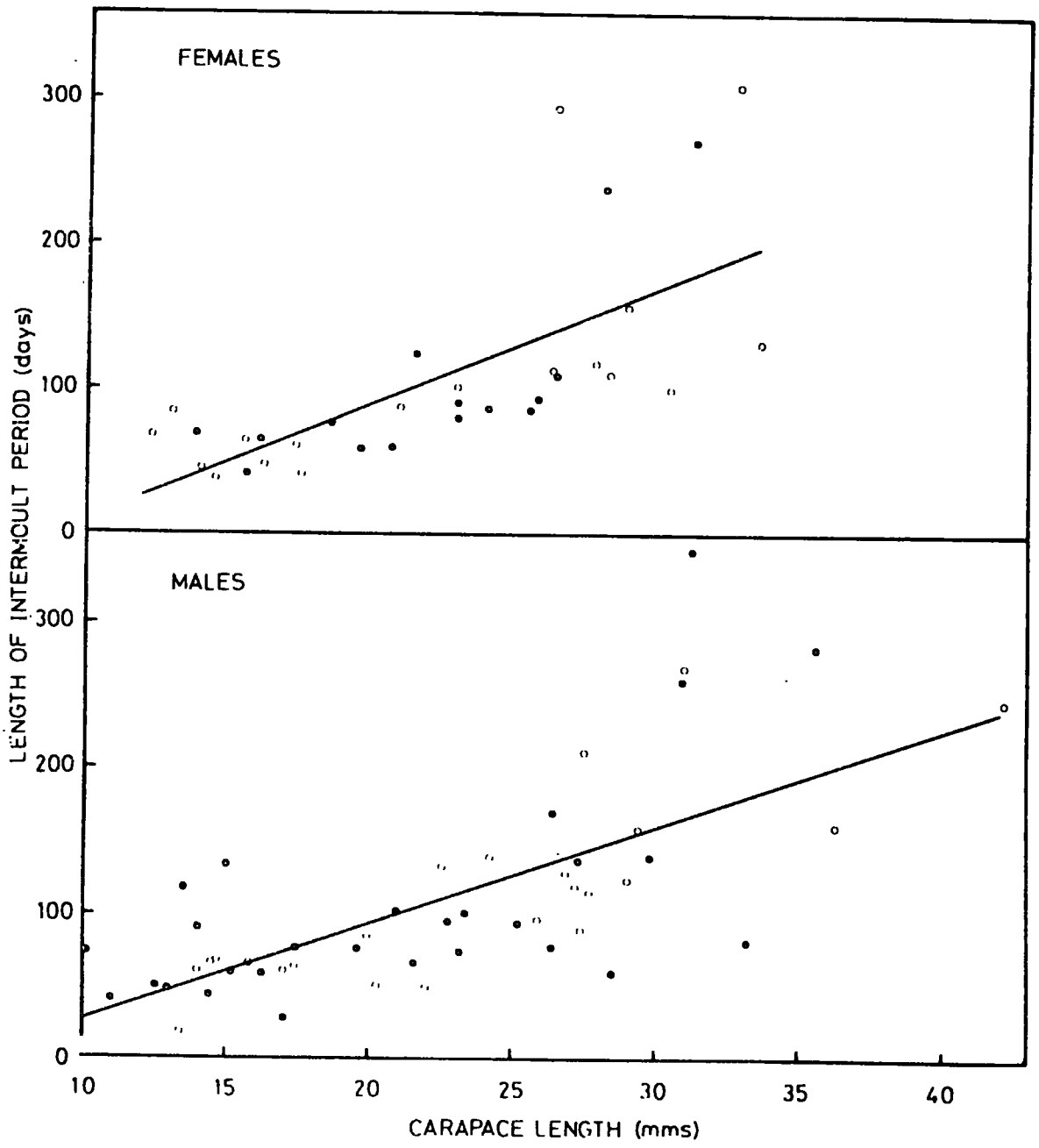
$y = 6.5945x - 38.9064$ (n = 51)
SE slope = 0.9585
$r = 0.7010$, $t = 6.88$, $p < 0.001$

females:-

$y = 7.9354x - 69.4568$ (n = 33)
SE slope = 1.4815
$r = 0.6933$, $t = 5.36$, $p < 0.001$

● - normal animals

o - limbless or limb-regenerating animals


FEMALES
MALES
LENGTH OF INTERMOULT PERIOD (days)
300
200
100
0
300
200
100
0
10
15
20
25
30
35
40
CARAPACE LENGTH (mms)

size at which sexual maturity was attained, similar to that observed in this study, has often been found to be the case in decapods (e.g. Pachygrapsus crassipes, Hiatt 1948; review, Kurata 1962; Pacifastacus leniusculus, Mason 1974). If this change was associated with the attainment of sexual maturity, as seemed likely, any alteration in overall growth pattern would not have been expected to occur abruptly at the minimum size at sexual maturity as a considerable proportion of all animals would have to be sexually mature to affect the overall growth pattern. Hopkins (1967) has interpreted this relationship to be curvilinear over the whole size range in Paranephrops planifrons.

Patterns varying between arithmetic and retrogressive geometric growth have frequently been observed for adult decapods (e.g. Nephrops norvegicus, Farmer 1973; Homarus americanus, Wilder 1963). Studies including data from a wide size range were fewer but showed that juvenile growth was normally between an arithmetic and progressive geometric pattern as was found in the present study (e.g. P. leniusculus, Flint 1975a and Mason 1974; P. crassipes, Hiatt 1948; Orconectes virilis, Momot 1964).

The correlation between the absolute moult increment (M.I.) and this increment expressed as a percentage of Pre M.C.L. (% M.I.) with Post M.C.L. has frequently been used to describe Crustacean growth. This has in many cases resulted in the observation of similar growth patterns to those already described by the inter-relationship of Pre M.C.L. and Post M.C.L. In this study,

however, the growth pattern of small females ⩽ 28 mm. Pre M.C.L. was described as arithmetic by the interrelationship of Pre M.C.L. and Post M.C.L. and progressive geometric by the interrelationship of M.I. and Pre M.C.L. This was probably due to the paucity of the data for M.I.'s of smaller females (n = 27) and the variability of these increments.

Considerable variation between individual M.I.'s has been observed in many decapod growth studies, including the present one (Cancer pagurus, Edwards 1965; P. leniusculus, Flint 1975a; Jasus lalandii, Heydorn 1969; P. crassipes, Hiatt 1948; P. planifrons, Hopkins 1967; Panulirus interruptus, Lindberg 1955; O. virilis, Momot 1967; Jasus tristani, Pollock & Roscoe 1977; P. vigil, Sather,1966; Paralithodes camtschatica, Weber & Miyahara 1962). This has often obscured any overall pattern or change in pattern with increasing size when M.I. or % M.I. has been used to describe growth. In terms of describing decapod growth the interrelationships between Pre M.C.L. and Post M.C.L. and those of M.I. and % M.I. with Pre M.C.L. had mutually exclusive advantages; the first interrelationship clearly showing the overall pattern of growth throughout the size range whereas the latter two methods of analysis illustrated the variability of the M.I.'s at the expense of any pattern.

As a result of the change in growth pattern from progressive geometric to retrogressive geometric at

about 28 mm. Pre M.C.L. there was no significant difference between the mean M.I.'s of crayfish of either sex above and below this size. The mean M.I. over the whole size range studied was, therefore, used as an overall index of growth per moult for comparisons between the various sub-populations in the aqueduct and with other decapods. This was a valid procedure providing the distribution of Pre M.C.L.'s in the two groups being compared was similar; this was tested by also comparing the mean Pre M.C.L.'s between the aqueduct sub-populations.

In the aqueduct normal female A. pallipes grew less at each moult (mean M.I. = 2.38 ± 0.06 mm.) than normal males (mean M.I. = 2.96 ± 0.06 mm.). This was not entirely due to the energetic demands of reproduction as females that did not bear eggs in the previous reproductive cycle also grew less (mean M.I. = 2.52 ± 0.16 mm.) than males. Indeed it will be calculated in Chapter 7 that the production of eggs made up only 1.4% of the total estimated annual production. Trap catches were mostly males and there was some evidence that females were even more 'trap shy' than usual at some stages of the reproductive cycle (Chapter 6 and also Momot 1964, Morrissy 1970, Woodland 1967). If trap catch composition was a reflection of a dominance order in the aqueduct population, as seemed very likely (section 6.4), females may have been less able to compete for food (or may have avoided contact with other crayfish, especially

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males, with similar results) particularly when bearing eggs. A similar suggestion has been made by Abrahamsson (1966, 1972a). The slower growth of female A. pallipes was compounded as egg-bearing females moulted only once each year following the release of the young (section 3.3). Similar trends in adult growth rates were observed in many decapod growth studies (e.g. Astacus astacus, Abrahamsson 1966, 1971b, 1972a; Pacifastacus leniusculus trowbridgii, Emadi 1974; H. vulgaris, Hepper 1972; H. vulgaris, Hewett 1974; J. lalandii, Heydorn 1969; P. planifrons, Hopkins 1967; A. astacus, Huxley 1896; Kurata 1962; O. virilis, Momot 1964, 1967; A. leptodactylus, Rumyantsev 1973), with only a few exceptions (N. norvegicus, Farmer 1973; P. leniusculus, Flint 1975a; P. L. trowbridgii, Mason 1974).

Infestation by Thelohania contejeani is a progressive disease (3.7) and consequently only M.I.'s from those crayfish which had enough muscle fibres infested to be visible could be treated as abnormal. Crayfish at this stage of the disease were few in number (6.5% of the total >13 mm. carapace length, 3.7) and M.I.'s were only recorded from forty-five parasitized males and twenty-one parasitized females. The disease did have a significant depressive effect on growth in the males (mean M.I.'s, normal 2.96 ± 0.06 mm., parasitized 2.17 ± 0.13 mm.) but not in the females (mean M.I.'s, normal 2.38 ± 0.06, parasitized 2.17 ± 0.13 mm.). However, the paucity of the data for parasitized females mitigated against

showing an overall statistical difference. Diseased females did grow less at each moult (mean M.I. = 2.17 ± 0.13 mm.) than those that had not borne eggs in the previous season (mean M.I. = 2.50 ± 0.07, $t = 2.24$, $p < 0.05$).

The lower growth per moult in parasitized crayfish may have had a nutritional basis, as suggested with respect to the comparison of male and female growth. Alternatively the way in which an increasing number of the host's muscle fibres were crammed with the spores of this parasite (Cossins 1972, Cossins & Bowler 1974) may have restricted the expansion which occurs by absorbing water into the soft tissues during early postmoult (Carlisle 1960, Needham 1965).

Annual moult frequency was inversely proportional to carapace length in adults (excluding reproductive females, 4.3.2) and there was some evidence that this was the case for juveniles also (4.3.3); this was generally true for Macruran species (e.g. Allen 1966, Emadi 1974, Farmer 1973, Flint 1975a, Kurata 1962, Mason 1974).

A projected mean growth pattern throughout the life cycle was constructed for A. pallipes on the basis of the analysis of the size frequency distributions (Figs. 4.7 and 4.8) up to year 3+, when the first crayfish became sexually mature, and from the interrelationships of mean moult frequency (Fig. 4.6) and % M.I. (Fig. 4.4) with Pre M.C.L. thereafter (Table 4.5). The similarities

between the results of the analyses (Cassie 1954, Table 4.4) of the size frequency histograms (Figs. 4.7 and 4.8) suggested that the resulting modes were a reasonably accurate description of the interrelationship between size and age in A. pallipes from the aqueduct up to the fourth overwintering size. The annual moult frequencies in the first four years of life, as estimated from interpolation between the mean overwintering sizes by assuming the interrelationship of % M.I. and Pre M.C.L. was similar for all crayfish $\leqslant$ 28 mm. Pre M.C.L., were within reasonable limits (bearing in mind the short moulting season in the aqueduct) compared to the moult frequencies which have been observed elsewhere in A. pallipes (6-7 moults in first year, sexual maturity in third or fourth year, Holdich et al. 1978; Huxley 1896) and other crayfish species (e.g. Emadi 1974, Kossakowski 1971, Mason 1974, Momot 1967). This was a further piece of evidence to support the above use of size frequency analysis over the lower part of the size range.

The facts that adults may moult once or twice annually (Fig. 4.6) and the considerable variations in individual M.I.'s, some of which were accounted for by reproduction, limb-loss and parasitism by T. contejeani, resulted in a cumulative 'smoothing out' of the size frequency distribution particularly after sexual maturity. This was most pronounced for adult females where moult frequency was dependent on previous reproductive status (e.g. Fig. 4.8). It was not, therefore, surprising that

size frequency analysis (as a method of ageing) has only been employed successfully in short lived decapods (e.g. Momot 1967, Woodland 1967) or during the first few years of life, as in this study, for longer lived species (e.g. Abrahamsson 1971b, Farmer 1973).

Considerable data concerning M.I.'s and frequency for crayfish of carapace length > 25 mm. (Figs. 4.4 and 4.6) was used to extend the projected growth pattern from the fourth overwintering size to the maximum size attained by either sex (Fig. 4.11).

Similar analyses have been carried out by Flint (1975b) and Mason (1974) on data collected from populations of Pacifastacus leniusculus. These postulated growth patterns suggested that this species had 9-12 year classes in the Lake Tahoe population (Flint 1975b) and 6-9 year classes in a coastal woodland stream (Mason 1974). Both these authors suggest that as the larger size classes were such a small proportion of sample size that they may not have represented year classes but could have been spillover products from preceding year classes that had maintained consistently high growth rates. However, as mortality would have been expected to have increased exponentially with age (this was demonstrated in Lake Tahoe, Flint 1975b) the proportion of animals in these larger size classes would have been low in any case.

These suggestions were not believed to have applied to the larger size classes of A. pallipes in the aqueduct

as the absolute moult increments at successive moults of numbered individuals often showed large variations (0-100+% difference between consecutive moults) and despite the fact that there was a considerable amount of growth data from multiple recaptures in the larger size classes no individuals grew by increments that were consistently above (or below) the average.

The projected growth pattern indicated a potential life span of between ten and thirteen years. This was not an unusually long life span for a Macruran species and compared well with some of those estimated for other relatively cold water species (e.g. A. astacus, France; P. leniusculus, Lake Tahoe, Table 4.7; Panulirus interruptus, 15+ year life span, Lindberg 1955). Temperature has often been shown to be a factor of primary importance for decapod growth rates (e.g. Abrahamsson 1972a, Adelung 1971, Aiken 1969, Emadi 1974, Kurata 1962, Momot 1964, Roberts 1957); this was also apparent from several comparisons in Table 4.7. There was a certain amount of similarity between most of the mean M.I.'s listed, in that most ranged from 2-5 mm.; some of the exceptions were from relatively warm water environments (Procambarus clarkii from swamps in Louisiana, the comparison between P. leniusculus from the sub-alpine Lake Tahoe and ponds in southern Sweden and the variations in M.I.'s of A. astacus in Swedish waters at different latitudes, Abrahamsson 1972a). The size at which hatchlings became independent of the

Table 4.7: Some growth parameters for several foreign species of freshwater crayfish and from all known sources of reference for A. pallipes

Species	C.L. at 'birth' mm.	Mean moult increment mm. C.L. ♀♀	Mean moult increment mm. C.L. ♂♂	Minimum C.L. at sexual maturity ♀♀	Minimum C.L. at sexual maturity ♂♂	First year class for sexual maturity ♀♀	First year class for sexual maturity ♂♂	Maximum C.L. ♀♀	Maximum C.L. ♂♂	Maximum life-span (years) ♀♀	Maximum life-span (years) ♂♂	Source of reference	Location
Astacus astacus		ca. 1	ca. 2.5	41	32	3+	2+	57	64	> 4	> 4	Abrahamsson 1971b*	Sweden
		2.5-5.9	2.7-10.3									Abrahamsson 1972a*	"
	ca. 5			45	45	5+	5+	100	100	15-20	15-20	Huxley 1896*	France
	ca. 4-6.5			ca. 40	ca. 40	2+	3+	100-125	100-125			Kossakowski 1971*	Poland
Astacus leptodactylus	ca. 4.5-6			48	55	2+	3+	150	150			Kossakowski 1971*	Poland
		4	5.1 ± 0.25									Rumyantsev 1973	U.S.S.R.
Austropotamobus pallipes	4.59 ± 0.06	2.36 ± 0.06	2.97 ± 0.06	25	22	3+	3+	45.6	50.5	ca. 13	ca. 13	Author	England
	ca. 5					2+-3+	2+-3+	ca. 50	ca. 50	6-7+	6-7+	Holdich et al.1978	England
		2.7(n=1)		28				46	58	> 5	> 6	Moriarty 1972	Ireland
				26	26-28	2+	2+					Pratten pers. comm.	England
				27	23			42	55			Thomas & Ingle 1971	England
				20				40	44			Watson unpubl.	Ireland
Cherax albidus	ca. 4		2.9-4.4	35	35	1+	1+	52	64	3	3	Woodland 1967	Australia
Cherax tenuimanus	2.9 ± 0.07			23		1+		100	100	> 4	> 4	Morrissy 1970	"
Faxonella clypeatus	ca. 2-3			13.1		0+	0+	19.6	19.2	2	2	Smith 1953	U.S.A.
Orconectes limosus				35	35	1+	1+	50	50	> 5	> 5	Kossakowski 1971*	Poland
				22	22	0+	0+	50	50	> 4	> 4	Kossakowski 1974	Poland
Orconectes propinquus	4-6			18	18			36	36	2	2	Capelli 1975	U.S.A.
		ca.1.5	ca.1.5									Fielder 1972	"
				18.5	18.5			40	40			Stein 1977	"
				17	17	0+	0+	35	35	2	2	Momot 1964	"
Orconectes virilis	4.5-5.1	ca. 3	ca. 3	25	25	1+	1+	38	45	3	4	Momot 1964	"
Pacifastacus leniusculus		ca. 4	ca. 5	45	35	2+	1+	60	65	> 4	> 4	Abrahamsson 1971	Sweden
				41	36	3+	2+	64	64	> 4	> 4	Abrahamsson & Goldman 1970	Lake Tahoe, U.S.A.
	3.75	ca. 2.2	ca. 2.2					57	57	8-12	8-12	Flint 1975	" " "
		1.5-4.2	1.5-4.2	30	30	2+	2+	54	54	8	8	Mason 1974	Coastal stream U.S.A.
Paranephrops planifrons	3.5	2.0-3.5	2.0-3.5	20		2+		27	30	5	5	Hopkins 1966, 1967	New Zealand
Procambarus clarkii		5.9	5.9									Huner et al 1974	U.S.A.
	4-6			31-32	31-32	0+	0+	52	57	2	2	Penn 1943	"
	4.3-4.7	ca. 5	ca. 5	36-45	36-45	0+	0+	55	55	3	3	Payne 1972	"
Procambarus pictus				22	20	0+	0+	30	28	1	1	Franz 1977	"

C.L. - carapace length in mm.

'birth' - this refers to that time at which the young become totally independent of the mother

Year class - 0+, 1+ equals 1st and 2nd years of life etc.

* - sizes quoted in source of reference as total body length; an approximation to C.L. was obtained by dividing by a factor of two (2.1, 3.8). Huxley (1896) quoted overall total length (including outstretched chelipeds), an approximation to C.L. was obtained by dividing by a factor of three (the observed ratio in a small sample of A. pallipes).

mother was similar for all species.

The minimum sizes at sexual maturity and maximum size attained were similar within each species but there were some cases where the time taken to attain these two sizes was clearly inversely correlated with the prevailing environmental temperature. A. pallipes in the aqueduct had a growth season from late June to mid-September when the maximum water temperature recorded was 17.2°C (3.3). In a population of A. pallipes in the River Ouse, Bucks. moulting began in early June and continued until late September and the maximum water temperature was 24°C in the shallows (Pratten pers. comm.). Members of both sexes first became sexually mature at a similar size in the aqueduct and the R. Ouse but this size was attained one year earlier in the southernmost population (Table 4.7). Faster growth in southern waters was also reported by Thomas and Ingle (1971); they observed the first overwintering size of A. pallipes in the River Darent, Kent to have been 12-13 mm. carapace length. A similar trend was shown by P. leniusculus between the mean minimum age at which sexually maturity was attained in both sexes (Table 4.7) and the seasonal temperature differences that would have been expected in the sub-alpine Lake Tahoe, a coastal stream in the U.S.A., and a small pond in southern Sweden. There have been no other detailed growth studies of A. pallipes and studies of other crayfish species in comparatively cold water environments

such as the aqueduct have been few. Farmer (1973) observed that the Norway lobster, Nephrops norvegicus, in the cold waters (7-13°C) off the Isle of Man grew from a carapace length of 3.3 mm. to 14 mm. in the first complete year of growth; following this, however, growth in years 1+ (14-21 mm.) and 2+ (21-26 mm.) was remarkably similar to that in years 2+ and 3+ for A. pallipes in the aqueduct.

Crayfish maintained at 15°C under controlled laboratory conditions (4.4.2) had a smaller mean M.I. than animals of a similar size range from the aqueduct (mean M.I. of normal males and females; laboratory, 1.76 ± 0.09 mm., aqueduct 2.84 ± 0.05 mm.; $t = 10.49$, $p < 0.001$). Moulting occurred all year round in the laboratory as has been found to be the case in some other studies (Adelung 1971, Westman 1972b). However, annual moult frequency was lower in the laboratory as the mean intermoult period was approximately one hundred days, the equivalent of less than one moult per annum in the aqueduct (mean length of moulting season in the aqueduct ca. 85 days, 3.3); whereas many smaller crayfish moulted two or more times each year under field conditions (4.3.2, 4.3.3). The phenomenon of slower growth in the laboratory than in the field has often been recorded in decapod growth studies despite varied attempts to optimize the holding conditions (e.g. Edwards 1965, Farmer 1973, Fielder 1964, Flint 1975, Heydorn 1969, Hiatt 1948, Hopkins 1967, Kurata 1962, Lindberg 1955, Stewart & Squires 1968). Growth in the

laboratory was further reduced in animals that were missing or regenerating limbs at premoult. This was also observed to have been the case in the early stages of regeneration in the aqueduct. Limb regeneration had no significant effect on moult frequency under laboratory or field conditions.

The reasons underlying the slower growth rate in the laboratory-maintained crayfish were not known. It is possible that crayfish must be maintained in a larger water volume or fed a more varied diet to attain growth rates comparable to those observed in the aqueduct. The trout food pellets which made up the major part of the diet of the laboratory-maintained animals were not an ideal complete diet. Crayfish fed with these, and some Fontinalis antipyretica, for over twelve months or more had very pale bluish-green exoskeletons which were almost transparent in small individuals. These animals did not turn pink when boiled and thus obviously lacked some natural pigments in the exoskeleton; whether this was a dietary deficiency or an adaptation to background colour as seen in some other crustacea (Green 1961) was not known.

That growth rates were slower in so many other related species when they were maintained in a variety of controlled environments suggested that decapods may find captivity traumatic in some way.

The ability to regenerate lost limbs is widespread within the Crustacea and although a large literature

exists describing the regenerative processes up to, and less often after, the limb-bud stage little work has been done on the possible effects of limb loss on the growth of the whole animal. Reports exist for several species of crustaceans which have shown that overall body growth was affected by limb-loss and subsequent regeneration. Emmel (1907) found that in lobsters growth was reduced after limb-loss and studies on other malacostracans by Paulian (1938), Bliss (1960), Adelung (1971) and Bennett (1973) have supported this view. Only Adelung, studying Carcinus maenas and Bennett working with Cancer pagurus, have clearly demonstrated that limb-loss reduced the overall length increment at the moult. More usually it has been shown that limb loss altered the timing of the moult (Bennett 1973, Bliss 1960, Hiatt 1948, Kurata 1962, Skinner & Graham 1970).

Almost half of the data from laboratory-held animals described the growth of limbless or limb-regenerating animals. This was largely a result of limbs having been lost during transport of the crayfish from the collection sites in Northumberland; although ca. 11% of all crayfish were already limbless or limb-regenerating in natural populations. Loss of limbs due to an autotomy reflex has been observed only with regard to the chelipeds of this species; there have been no cases observed where autotomy of the walking legs has occurred. Bliss (1960) reported that the autotomy reflex did not occur in the walking legs of the American lobster, Homarus americanus.

However, Bittner and Kopanda (1973) have reported a rather inconsistent autotomy reflex of walking legs in the crayfish Procambarus clarkii and Durand (1960) used it as a reliable method of inducing limb-loss in Orconectes limosus. In the laboratory-held animals chelipeds (and possible walking legs also) were autotomized presumably either as an escape mechanism or as a result of injury sustained during the relatively overcrowded conditions that existed in transit from the collection sites. Cheliped loss in natural conditions presumably occurs for similar reasons (although to a lesser extent) and probably also happens when animals encounter difficulty withdrawing these large limbs from the partly shed old exoskeleton at the moult (Kossakowski 1971). This made a distinction with some other similar studies where autotomy has been stimulated by crushing limbs or chela (Bennett 1973, Bittner & Kopanda 1973, Durand 1960).

The present study clearly demonstrated that overall growth in length was inhibited in those crayfish regenerating limbs and thus supported the conclusion of Emmel (1906), who showed that moult increments were smaller in autotomized H. americanus than in normal specimens, and that of Kurata (1962) who demonstrated this aspect of growth retardation in Hemigrapsus sanguineus. More detailed studies were made by Adelung (1971) on Carcinus maenas and Bennett (1973) on Cancer pagurus. Adelung (1971) showed that intermoult cycles of C. maenas were significantly shortened and growth increments much

smaller when crabs lost more than five walking legs. Bennett showed that the loss of two chelipeds or six walking legs was more effective in reducing moult increments than the loss of one cheliped or of two legs. In this study however, it was not possible to demonstrate whether a similar situation existed as too few crayfish lost both chelipeds.

Many workers have suggested that the reduction in moult increment, as a result of limb loss, may be compensated for in terms of annual growth by a stimulation of moulting. A number of studies clearly show a shortening of the intermoult period as a result of limb loss (Adelung 1971, Bittner & Kopanda 1973, Bliss 1960, Skinner & Graham 1970). However, Emmel (1906, 1907) suggested that stimulation and/or inhibition of moult may occur depending on the timing of the injury relative to the stage of the moult cycle and Bennett (1973) clearly demonstrated this point in C. pagurus. Stimulation of moult appears to have been the general case, inhibition only occurring when injury took place late in the moult cycle. Some other workers such as Needham (1965) have been unable to demonstrate any clear differences as was the case in this study.

That the crayfish in this study selectively regenerated a lost limb at the expense of overall body growth was clear from the fact that growth in terms of length was reduced whereas gravimetric growth was not significantly affected (Figs. 4.11 and 4.12). The differential

between the growth rates of normal and regenerating limbs was very marked in small crayfish (Fig. 4.13; individuals < 20 mm. carapace length) and was also significant in larger animals (Fig. 4.5). The smaller animals could regenerate a cheliped to normal size in two to three moults, larger animals required many more moults to achieve this and therefore the regenerating cheliped may never reach normal size (Kossakowski 1971). This ability to regenerate a chela to normal size by reducing overall body growth was a property of many Macruran species and was clearly of functional significance. It was obviously undesirable for cheliped loss to occur to any significant extent in a population that was being commercially exploited as the chelae were an important source of meat, particularly in large males (Kossakowski 1971). One exception to this was the Florida stone crab, Menippe mercenaria, which has a marked dimorphism between the chelae which always occurs the same way round in nature. Fishermen are in the habit of removing the large chela to sell for its meat and returning the crab; it has been claimed that such crabs harvested again in the following year have reversed the natural asymetry by regeneration and have thus regained their commercial value (Goss 1969).

Behavioural studies have shown the chelae to be of prime importance in interspecific interactions (Bovbjerg 1953, 1956) and in mating behaviour (Ingle & Thomas 1974); also Stein (1976) has clearly demonstrated that in Orconectes propinquus chela size was

the dominant factor in determining the outcome of attacks by predators, aggressive encounters and attempts to copulate. Moreover, large males with small chelae were seriously disadvantaged in the above acts compared to similar sized males with normal chelae. Stein also suggested that the primary function of chelae in the males was reproductive as would appear to have been the case in any species showing this type of sexual dimorphism as natural selection would have favoured those males with large chelae as they mated with the largest and most fecund females. The hormonal mechanism involved in ensuring that adult crayfish had, or could regenerate, chela of equal and appropriate size was not known.

The relatively small maximum size and protracted life cycle observed in the aqueduct made A. pallipes seem an unlikely candidate for commercial aquaculture; at least under these conditions of temperature and food supply. However, populations of A. pallipes are known to exist in several reservoirs with bank structures (and consequently many hides per unit area) similar to the aqueduct. If the density of crayfish in these reservoirs is comparable to the aqueduct (5.4.5) such populations must be enormous. Indeed, SCUBA divers have reported this to be the case in some reservoirs (Holdich et al. 1978, pers. communications). The cropping of natural populations may, therefore, not only satisfy the home demand but provide an excess for export. If this is the case, it would be prudent for those who wish

to market crayfish to explore the natural potential first, before contemplating the importation of foreign species and its inherent uncertainties (3.1, 5.1, Goddard & Holdich 1979, Holdich et al. 1978).

CHAPTER 5

The estimation of some of the parameters of the aqueduct population from the hand collected samples

5.1 Introduction

Austropotamobius pallipes is the only crayfish species indigenous to the British Isles and it is widely distributed and abundant in England, Ireland and Wales (Huxley 1896, Thomas & Ingle 1971, pers. communications, Aston, Bowler, Holdich, Langford and Thomas). Davies (1964) reported a density of $4/m^2$ from the River Stour, Laurent (1972) 2 adults/m^2 in France, Watson (unpubl.) 4 adults/m^2 in Northern Ireland and Pratten (pers. comm.) $7/m^2$ in the River Ouse. The density of the study population varied from 3.8-10.4 individuals of carapace length $\geqslant$ 13 mm./m^2 in the years 1975-77 (5.4.5). At such densities very large populations would be expected in extensive stretches of freshwater.

Considerable variations from time to time in the density of some populations of A. pallipes have been documented (Duffield 1933, 1936, Moriarty 1972, Pixell Goodrich 1956, Smith 1932). Indeed some reports state that A. pallipes is now generally much less common in the U.K. (Carpenter 1928, Jackman 1977, Stellan Karlsson 1978) but these reports are anecdotal and remain unsubstantiated.

There have been many speculations concerning the causes of these variations in abundance which have included fungi, bacteria, protozoan diseases and predation (Duffield 1933, Pixell Goodrich 1956, Vey & Vago 1972). There is some evidence to suggest that some of these variations may follow an approximately fourteen year cycle but the reasons underlying such a cycle, if it exists, remain obscure (Duffield 1933).

However, the factor known to have by far the most drastic effect on crayfish abundance is the fungal disease Aphanomyces astaci. The crayfish plague fungus is fatal to all members of the family Astacidae indigenous to Europe (Unestam 1972) and it has destroyed many stocks of crayfish during its spread through Europe, Scandinavia and Russia following its introduction into Italy in the mid-nineteenth century (Kossakowski 1971, Unestam 1969, Unestam and Weiss 1970). Stellan Karlsson (1978) has emphasized the necessity to keep an open mind about the possibility that crayfish plague has reached the British Isles and it has in some cases been assumed that it has already had a considerable effect on native crayfish populations (Jackman 1977, Richards and Fuke 1977) but there is no direct evidence to substantiate this assumption.

Carpenter (1928), Duffield (1936) and Smith (1932) all attribute the disappearance of certain crayfish stocks to an unspecified epidemic disease which may or may not have been A. astaci. As the fungal plague can usually only be diagnosed by microscopic examination of an

infected animal (Stellan Karlsson 1978, Unestam 1972) the cause of such disappearances is mere conjecture. The last few years have seen a considerable increase in scientific interest in the ecology of A. pallipes in the U.K. and Eire (pers. communications, Jay, Pratten, Reynolds, Rhodes) but no outbreaks of plague have been directly observed. As angling is our most popular non-spectator sport (man is probably the major vector of the plague, Söderhäll et al. 1978) and the majority of rivers, dykes and canals are interconnected especially in the North-west, East Anglia and the Midlands, had the crayfish plague reached such U.K. waters the disappearance of crayfish stocks would be expected to be so dramatic that it could scarcely be missed.

There are many factors other than plague which could account for the disappearance of crayfish populations such as pollution (Davies 1964, Hobbs and Hall 1974), drought (Thomas pers. comm.) and other diseases (Duffield 1933, Pixell Goodrich 1956).

The role of the crayfish in the energetics of fresh-water communities is also poorly understood but cannot be of small importance due to their density in some areas. It seems this role is a complex one as they are reported to belong to several trophic levels being opportunistic feeders on detritus, macrophytes, and animal material both living and dead (e.g. 3.5; Flint 1975 - Pacifastacus leniusculus; Pratten, Ph.D. thesis in prep.,). The importance of Astacus astacus in Sweden as a grazer of macrophytes has been made plain as ponds became weed-

choked following the extermination of the crayfish population by A. astaci (Abrahamsson 1966, Unestam 1972). Similarly, they are a prey item to more than one trophic level as a wide variety of predators have been either identified or are strongly suspected (e.g. 3.5, Pratten Ph.D. thesis in prep., Huxley 1896 and Lagler & Lagler 1943 - American species).

In view of the extensive literature concerning the population dynamics of many of the other major groups, it does seem surprising that there have been no studies on the population dynamics of this, one of the largest and long lived of our native freshwater invertebrates. There are, however, several reasons why A. pallipes has been neglected in this way. Collecting crayfish is not a common pastime for the British public since they are not widely appreciated gastronomically in the U.K. The situation in Scandinavia and the U.S.A. is very different and field studies of the native crayfish species have been numerous in both regions. Indeed had the British crayfish received more limelight in this way its role in freshwater communities may not have been so overlooked. There are also two further physical obstacles which are common to the study of all Macruran species: not only are most populations unmanageably large (Abrahamsson & Goldman 1970, Morgan 1974) but they are also relatively inaccessible to sampling. Of the methods available for sampling crayfish many have severe limitations:- trapping may not provide a random sample due to behavioural components (e.g. Morrissy 1973, 1975, Woodland 1967),

sampling by hand is only possible in shallow water unless SCUBA gear is used, electrofishing can have undesirable effects on any fish present and is illegal in trout waters, and seine netting is often impossible due to obstructions or ineffective due to the nature of the substratum (Capelli, 1975, Woodland 1967). Inherent in all these methods there is also a strong possibility that the resulting sample may not be representative of the whole population.

The area chosen for this study has several unique features which make it particularly suitable for the investigation of crayfish population dynamics. The study-population is situated in a man-made aqueduct which acts as a feeder stream in a Northumberland catchment reservoir complex (Fig. 1.1). The population is delimited to the part of the aqueduct lined with sandstone blocks which provide many crevices or 'hides'. Above the sluice gates which guard the inlet to this stretch, the lining is concrete and there are no hides or macrophytes causing crayfish to avoid this substratum. Immigration is thus thought to be insignificant owing to the rapid nature of the run-off at the lower end (Plate 1.2b) and the fact that the concrete lined stretch at the upper end is approximately 400 m. long before disappearing below ground to connect with the source, trapping this stretch over two years has yielded few crayfish (3.6.1). Thus the physical features of the aqueduct must have a profound effect on the crayfish population since emigration and mortality can occur but immigration must be negligible

and the population reproductively isolated. Consequently the two principal obstacles to a population study of any crayfish species are absent in this situation; first the population is delimited to a relatively small area and secondly large samples can be easily collected on lowering the water level by means of the sluice gates.

Having located a delimited population that is accessible to sampling one or more of the methods developed for the estimation of population parameters had to be selected. There are essentially only three ways of determining the number of animals in a given area. Whichever method is chosen care must be taken to ensure that the inherent assumptions are satisfied.

1(a) Absolute count This method has the obvious advantage that the result need not be an estimate. The only requirement is that all the animals must be captured or observed and counted and for this to occur the capture rate must usually be high. All crayfish with C.L. $\geqslant$ 13mm. which leave hides on lowering the water level are theoretically catchable, however it is not known how many animals do not leave hides and it is impossible to check this among the fixed blocks of the walls of the aqueduct. The method is obviously only suitable for small populations.

(b) Quadrat sampling All animals in several sub-areas must be captured or observed and counted and this number increased by an areal ratio to estimate total numbers. This method has the same disadvantages in the aqueduct as (a); it has, however, been used successfully on stony lake

bottoms using SCUBA gear, enclosing the sub-areas in a walled metal hoop and collecting all the crayfish within the hoop by gradually removing all the upper sub-stratum. (e.g. Abrahamsson & Goldman 1970, Capelli 1975, Flint 1975). The method is clearly not suitable for animals which are sufficiently mobile to leave the sub-area before sampling is complete.

2 Return per unit effort methods Successive samples are taken and the return per unit effort decreases proportionately to the decrease in population numbers. The catchability of all individuals must remain constant throughout the sampling period and the animal must be very mobile; otherwise successive samples even at random sites may yield spurious data as some areas become depleted and others remain untouched. Although often employed in fisheries investigations it is usually unsuitable in pure ecological studies as most species are insufficiently mobile and/or do not all remain equally catchable as sampling proceeds (Ricker 1958).

3 Mark-recapture methods These methods are frequently the best suited to pure ecological investigations, particularly of invertebrates, and many sophisticated models have been developed for both 'closed' and 'open' populations (reviewed by Seber 1973). All involve certain assumptions; the following five of which are common to most methods.

(i) As the marked sub-population is assumed to behave in the same way as the unmarked, it is obvious

that marking must not effect catchability or survival. The marking technique used in this study was based on that of Abrahamsson (1965) for applying numbers to the carapace and was extended to the uropods for date specific marks. Although the former were often visible to the collector before capture any bias in catchability must largely have been avoided as an attempt was made to catch every animal seen within randomly selected sections of the aqueduct irrespective of mark status. Also recaptures from all catches of > 250 individuals included $< 10\%$ bearing individual numbers. No increase in mortality amongst marked individuals was noted for laboratory held animals, indeed the method has been used and reported harmless for other decapods such as lobsters (Dybern 1965).

(ii) The number of marked animals introduced into the population and the number recaptured must obviously be accurately known. Thus marks must not be lost between samples and all the marks must be reported at each sampling. No individual numbers were lost after two moults (2.3, Abrahamsson 1966) and all date specific marks have been shown to be reliable for a similar period (5.4.4). It was thus possible to select sequences of samples during which no marks would have been lost. Errors due to marks not having been reported were believed to have been small as recaptures were always identified by the author while less experienced personnel processed the unmarked portion of the sample.

(iii) It is clearly statistically sound not to rely totally on uniform mixing of marked animals with the unmarked to produce a representative sample and to sample always at random (Seber 1973). However, perfectly random samples, although they exist in theory, are rarely achieved in practice and thorough mixing of marked individuals with the unmarked ones is an essential assumption of all mark-recapture methods (Woodland 1967). Whether the Astacidae in general possess a measurable 'home range' is not clear; they are however mobile animals and extensive movements have been reported; considerable mixing would thus be expected to occur (3.6.2, Black 1963, Camougis & Hichar 1959, Henry 1951, Merkle 1969, Mobberley & Pfrimmer 1967, Momot 1966, Momot & Gowing 1972).

(iv) It is essential that the estimate of population size is valid at a particular point in time, hence sampling must be at discrete time intervals and the time taken to release the sample must be small in relation to the total time. These conditions were satisfied as all samples were collected, processed and returned in one day and the period between samples was always greater than 15 days.

(v) In the general case it is a requirement that the population be sampled at random with respect to size, sex and mark status. That is the probability of capture must be the same for all individuals. There are, however, two situations which may modify this requirement:-

(a) If sampling is believed to be random with respect to mark status (as in this study (i)) and unequal catchability between age classes and/or the sexes is suspected; valid estimates for the size of the various sub-populations can be obtained if they are enumerated separately (Southwood 1966). This practice was followed throughout the present study.

(b) When two sampling methods are available, one or both of which show bias in catchability between age classes and/or the sexes, the use of one for marking and the other for recapture can give valid single census estimates of population size provided that the source of the selectivity which is the cause of the variations in catchability is independent in the two methods (Junge 1963). Several approximate estimates between trapped and hand-collected samples were obtained in this way (6.3.5).

Any single census estimates make the additional requirement:-

(vi) The population must be 'closed' between the two sampling occasions i.e. there must be no births or immigration (gains) and deaths or emigration (losses) over that time. Alternatively, these factors can either be estimated independently and allowed for in the estimate of population size or the two occasions may be sufficiently separate in time to allow thorough mixing of marked and unmarked animals and yet sufficiently close in time to assume that any gains or losses are negligible. The latter assumption was occasionally made during the present study for approximate estimates.

The more sophisticated 'open' population models, which estimate gains and losses, all require at least two recapture occasions and hence make the additional assumption:-

(vii) Recapture on one or more occasions does not affect the probability of subsequent recapture. This implies a learned behaviour change in response to the sampling method.

The two main aims of this study were to investigate the life history of A. pallipes in detail and to obtain reliable estimates of crayfish population parameters in one particular watercourse. The study area was the aqueduct already described, this was chosen because samples could be collected by two independent methods, hand collection when the water level was artificially lowered and trapping.

There were two factors which limited when hand samples could be taken. The aqueduct containing the study population was the main inflow into the reservoir system and on occasions when water was in short supply the Water Company could not grant permission to divert the flow by lowering the sluice gate. Also the number of animals that could be collected increased with water temperature so that it was only possible to collect more than ca. 800 crayfish during a morning (the amount of time the Water Company could usually permit the flow to be diverted) at water temperatures above about 9°C. This restricted the period during which adequate samples could be collected to between May and October. There were

no such limitations to the frequency of the trapped samples.

The preliminary study in 1974 was undertaken, by hand collection, to establish the timing of the various stages of the life history, to test the methods of collection, marking and returning crayfish to the aqueduct and to obtain an approximate estimate of the maximum number of crayfish in the population so that all future hand samples would be of such a size as to produce statistically 'accurate' results (Robson & Regier 1964).

In the summer of 1975 the volume of water which had to flow through the aqueduct to meet the requirements of the Water Company increased considerably. It was, therefore, only possible to lower the water level and hand collect on three occasions in June and July. The density of the crayfish in the aqueduct was determined at this time. Trapping was begun in June and continued at approximately fortnightly intervals until October the following year.

Although the rest of the country was suffering a drought in the summer of 1976 the rainfall in Scotland and Northumbria and the reserves held by the Water Company were sufficient to permit the water level to be lowered on five occasions in that year and three further occasions in May and June 1977. The gains to and losses from the aqueduct population and the resulting variations in crayfish density were estimated from these eight samples. A very approximate estimate of the net production over this time period was also made.

The advantage of alternative sampling methods is that when both methods are employed concurrently the validity of the mark-recapture estimates between samples collected by the same method can be checked by calculating a comparable estimate between samples collected by different methods over the same time period. The latter estimate should be free from any bias due to unequal catchability providing the source of the bias is independent in the two methods (Junge 1963, Seber 1973). There was no significant difference between estimates of adult population size obtained between adjacent hand samples and adjacent hand and trap samples taken over the same time period. However, it will be shown that adjacent trapped samples produced a threefold underestimation of the number of adults (6.3.5). This confirmed my original suspicion that trapped samples were biased as the crayfish play a very 'active' role in their own trap capture whereas their role in hand collection is much more 'passive'.

The trapping program was continued as a methodological study after this bias was observed in order to demonstrate clearly the severe shortcomings of trapping when it is used as the sole sampling method in a mark-recapture study. Many mark-recapture studies on other species of freshwater crayfish have depended solely on trapping as a sampling method and this bias brings the accuracy of some estimates of crayfish population parameters into question (Chapter 6).

Trap returns also provided much information on growth (Chapter 4) and the general biology of A. pallipes

(Chapter 3) as trapping was continued at fairly regular intervals throughout the year.

5.2 General methods

(i) The water flow into the aqueduct was diverted into the West pond by means of the sluice gates (1.1). After about half an hour, when most of the water had drained from the aqueduct, sampling was begun with the water at < 10 cm. average depth.

(ii) Stretches of the aqueduct selected at random from the 117 six meter sections from section 6 to section 122 were sampled by one or more persons experienced in handling crayfish. Many animals left their hides in the stone block walls of the aqueduct when the water level had been lowered (1.1), and large numbers of animals of carapace length ⩾13 mm. were easily collected from exposed positions on the walls and floor of the aqueduct. Smaller crayfish of carapace length < 13 mm. tended to remain in their 'hides' in the growths of Fontinalis antipyretica and were thus not readily accessible to hand-sampling in situ; these crayfish were excluded from all estimates of population parameters.

(iii) Catches from all sections were kept separately in cool, well-oxygenated water until they were returned to the aqueduct.

(iv) All unmarked crayfish in samples of less than 250 animals were sexed, measured, given an individual number and several other factors noted as described in 2.1 and 2.3.

(v) All unmarked crayfish in samples of 250 or more animals were sexed and divided into two size classes; adults and juveniles (adult males > 22 mm. carapace length, adult females > 25 mm. carapace length, 2.1). All were then given a coded mark particular to one sampling occasion (a 'Day' mark) by cauterising one or two areas ca. 1.5 mm. diameter on the uropods and telson (2.3).

(vi) All crayfish with previous 'Day' marks were treated as described in (iv). Therefore the complete recapture history of all marked crayfish was known.

(vii) All crayfish with individual numbers were treated as described in (iv) and their marks reinforced if they had moulted since last capture.

(viii) All crayfish collected from the sections sampled were kept separate and returned in random sequence to the sections collected from.

(ix) The catches from each section sampled were returned in one of two ways:-

(a) When the water level was still lowered crayfish were emptied onto the aqueduct floor in the middle of the section.

(b) When the water level had been restored to its original level catches were introduced to the water one section above that to which it was wished to return them to allow them to find bottom in the current. Observations when the water was especially clear, the surface unbroken and in direct sunlight indicated that this was successful.

5.3 The preliminary study 1973-74

5.3.1 Introduction

The original aims of the field study involved in this project were somewhat limited and it was supposed, with considerable naivete in retrospect, that the population would be of such a size and movements along the aqueduct small enough to allow the majority of individuals large enough to be given individual numbers ($\geqslant$ 13 mm. C.L.) to be captured and marked. This must be borne in mind during the interpretation of the 1973-74 field data since the approach taken, which was based on the above supposition, gave rise to inconclusive results. These results are, however, presented here as they clearly show the extent of, and the problems inherent in, the task undertaken and may thus be considered a useful preliminary study.

All but two samples were collected from and returned to a limited stretch between sections 42 and 51, the other two samples were of marked crayfish only and were collected from section 17 to section 96 (Fig. 1.1).

Results

5.3.2 Movements of marked crayfish

As it was originally intended either to mark all the crayfish in the aqueduct or at least in one restricted stretch it was obviously important to know how much crayfish moved in the aqueduct. This was investigated on two occasions as follows:-

It was possible, when the water level was lowered to its full extent (depth $<$ 10 cm.) and many animals had

left their hides, to see marked individuals on the aqueduct floor from a standing position as the marks appeared as red dots (ca. 1.5 mm. diameter) or slightly larger pale patches after a moult (2.3). Two persons collected all the marked animals they found in this way from sections 17-96 inclusive on 27. 5.74 and 7. 8.74. The number for each animal and section in which it was found were recorded. Of the 363 and 666 animals which had been marked before each date 42 and 94 were recaptured on respective occasions. The results of these collections re presented on Fig. 5.1.

The net movements out of the stretch being studied (sections 42-51) were clearly extensive and appeared to increase the longer it was since a sample of crayfish had been released into the aqueduct. That some of the net movements were progressive was shown by the significant positive correlations between the mean number of sections moved for all individuals from section 43-50 in an upstream (as far as section 96) and a downstream (as far as section 17) direction for each sample excluding the one taken on 8.10.73 and the number of days between the return of each sample and the collection of marked individuals on 27. 5.74 and 7. 8.74 (Fig. 5.2, $r = 0.81$, $t = 4.80$, $p < 0.001$). Eventually the marked animals would become randomly distributed along the aqueduct (broken line, Fig. 5.2).

These considerable displacements suggested that A. pallipes was a vagrant animal (as shown in a detailed analysis of displacements in 3.6) and any estimates of

Fig. 5.1: Position of individuals marked on previous dates*, and returned between sections 43 & 50, when recaptured on 27. 5.74 and 7. 8.74 by collecting only previously marked crayfish between sections 17 & 96

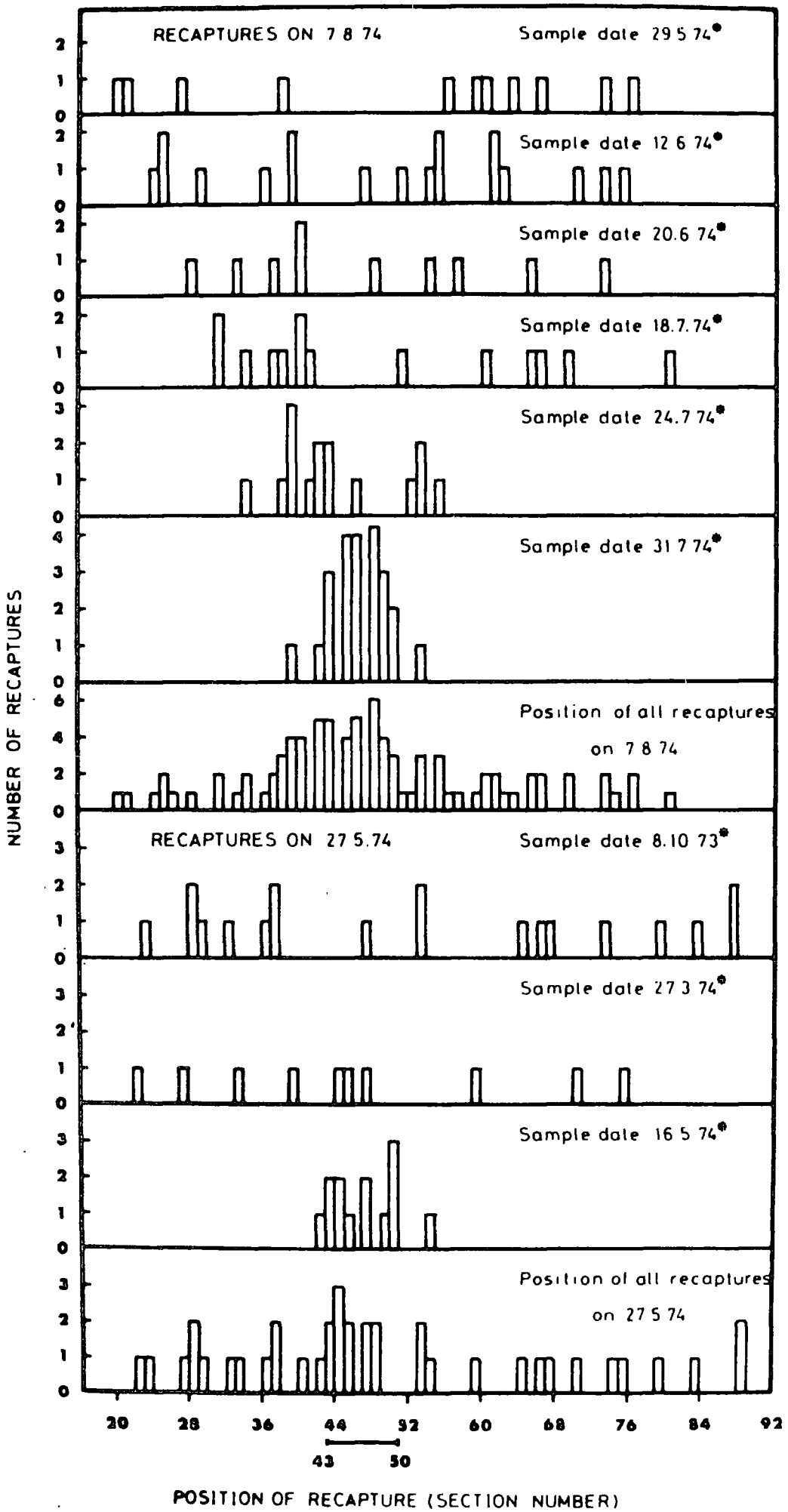

RECAPTURES ON 7 8 74
Sample date 29 5 74*
Sample date 12 6 74*
Sample date 20.6 74*
Sample date 18.7.74*
Sample date 24.7 74*
Sample date 31 7 74*
Position of all recaptures on 7 8 74
RECAPTURES ON 27 5.74
Sample date 8.10 73*
Sample date 27 3 74*
Sample date 16 5 74*
Position of all recaptures on 27 5 74
NUMBER OF RECAPTURES
20
28
36
44
52
60
68
76
84
92
43
50
POSITION OF RECAPTURE (SECTION NUMBER)

Fig. 5.2: Mean number of sections moved per individual, from sections 43-50 for each sample, in an upstream (as far as section 96), a downstream (as far as section 17), or both directions (for 27. 5.74 data) as a function of the number of days since that sample was marked and released in sections 43-50

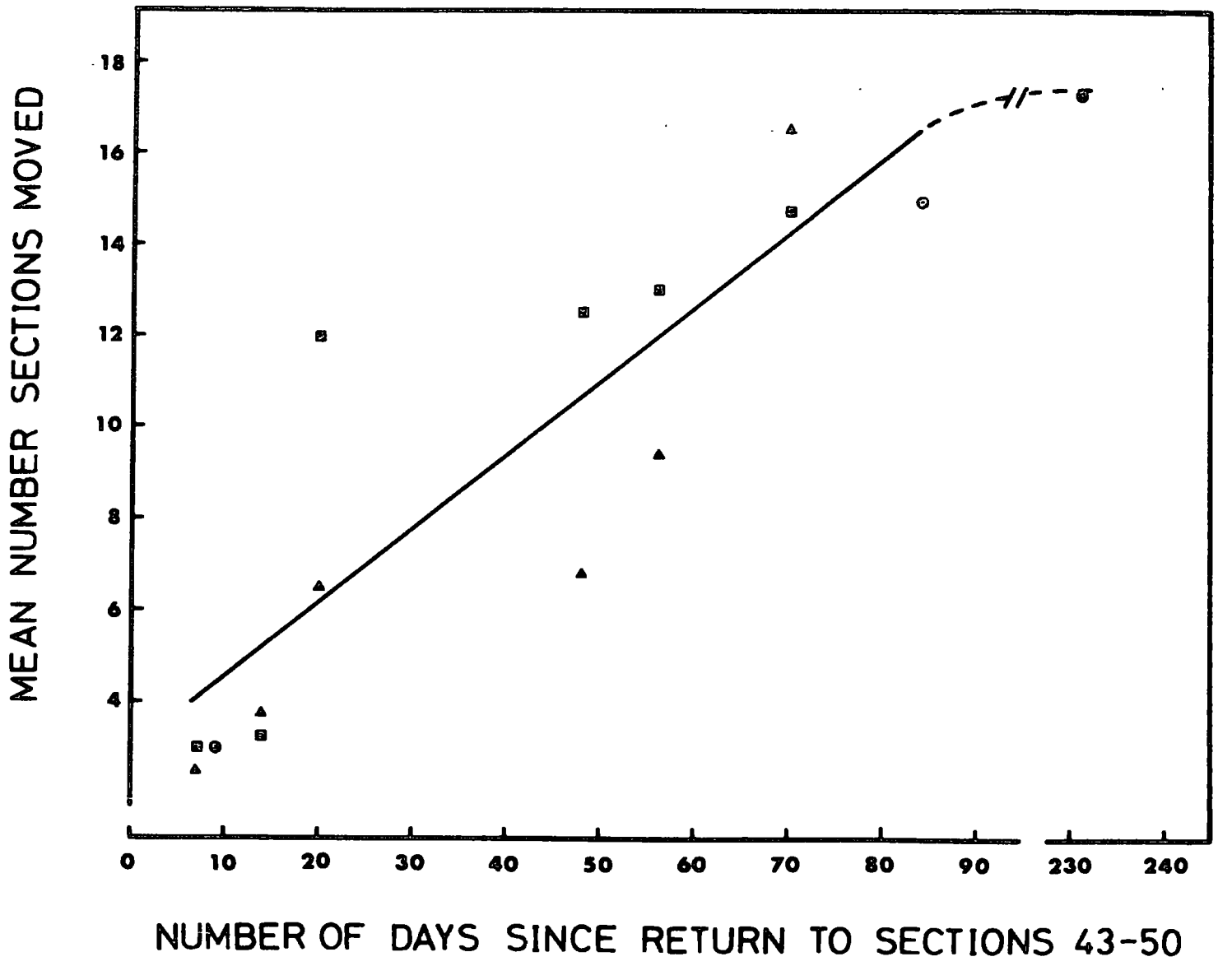
- ● - upstream and downstream movements before 27. 5.74
- ■ - upstream movements before 7. 8.74
- ▲ - downstream movements before 7. 8.74

Excluding the sample taken on 8.10.73:-

$y = 0.1610x + 2.9219$

SE slope = 0.0336

$r = 0.8107$, $t = 4.7968$, $p < 0.001$


MEAN NUMBER SECTIONS MOVED
18
16
14
12
10
8
6
4
0
10
20
30
40
50
60
70
80
90
230
240
NUMBER OF DAYS SINCE RETURN TO SECTIONS 43-50

population size obtained from studying a limited stretch of the aqueduct would be very approximate.

5.3.3 The size and structure of the hand collected samples

(i) The logarithm of the potential catchable population, assuming equal distribution and catchability along the aqueduct (Table 5.1; catch/section x 117 as most of the study population was between sections 6 and 122; 3.6, 5.2) was positively correlated with water temperature (Fig. 5.3, $r = 0.76$, $t = 3.08$, $p < 0.02$). The aqueduct was the most important inflow to this reservoir complex (1.1) and the time available for hand collection was limited by the Water Company to around four hours. As the number of persons experienced in collecting crayfish was also limited this suggested that hand collections from randomly selected sections along the whole aqueduct that were large enough to produce statistically accurate results (Robson and Regier 1964) would be limited to when water temperatures were above a certain level (5.1). This was later shown to be the case (5.4.2).

(ii) Neither the mean sex ratio nor the mean adult: juvenile ratio in the 1973-74 hand collections was significantly different from one ($t = 0.67$, $p > 0.50$ and $t = 1.55$, $p > 0.10$ respectively).

5.3.4 Approximate population size estimates

(i) The potential catchable population (Table 5.1) could be considered as a quadrat sampling type estimate of population size. The estimates would then have ranged

Table 5.1: Sample size, structure and associated parameters 1973-74

Date	Sections sampled	Water temp °C	Total marked & returned	Sex ratio ♀♀:♂♂	Adult: Juvenile ratio	Potential catchable population*	Cumulative total of marked animals from 16. 5.74 onwards	Total recaptures marked on any previous occasion from 16. 5.74 onwards	% of r/c
8.10.73	42-51	-	203	0.95	4.21	2,375			
27. 3.74	43-50	4.3	65	0.97	1.51	951			
16. 5.74	43-50	7.2	115	0.69	1.13	1,682			
29. 5.74	43-50	10.7	90	1.20	2.00	1,316	115	7	7.78
12. 6.74	43-50	13.6	160	0.84	0.42	2,340	205	10	6.25
20. 6.74	43-50	-	154	0.83	1.37	2,252	365	13	8.44
18. 7.74	43-44	13.3	104	1.42	1.31	6,084	519	10	9.62
24. 7.74	49-50	12.7	117	0.80	0.95	6,845	623	11	9.40
31. 7.74	43-46	13.8	141	1.04	1.05	4,124	740	17	12.06
7. 8.74	43-50	13.8	204	0.98	0.62	2,984	881	30	14.71
11. 9.74	43-48	11.6	170	0.83	1.74	3,315	1,085	32	18.82
				0.96 ± 0.06	1.48 ± 0.31				

* Potential catchable population, at this sampling intensity, assuming equal distribution and catchability along the aqueduct

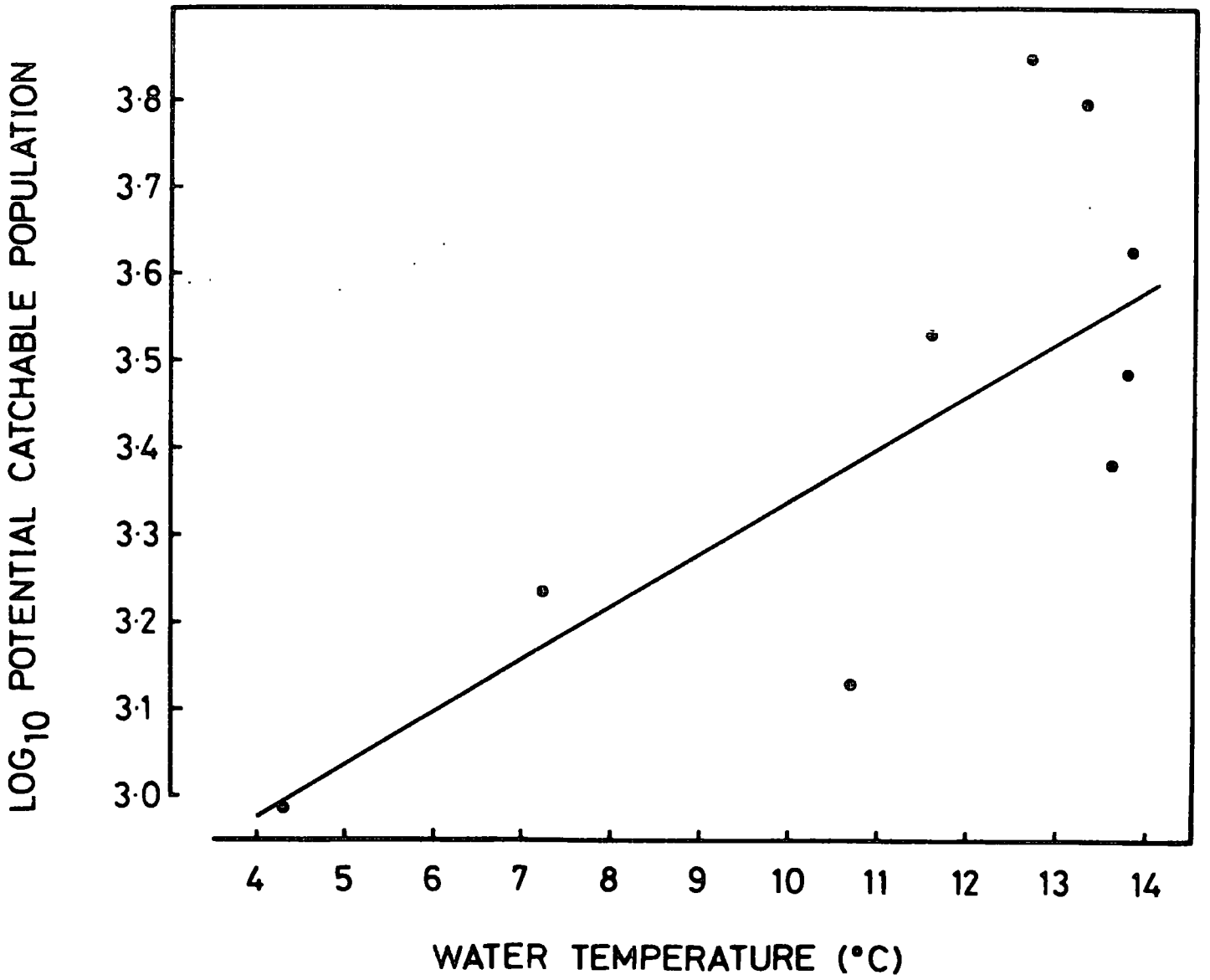
r/c - recaptures of crayfish marked from 16. 5.74 onwards

Fig. 5.3: Logarithm of the potential catchable population (catch/section x 117) at this sampling intensity, assuming equal distribution and catchability along the aqueduct, as a function of water temperature (^{o}C)

$y = 0.0659x + 2.7070$

SE slope = 0.0214

$r = 0.7580$, $t = 3.0747$, $p < 0.02$


LOG10 POTENTIAL CATCHABLE POPULATION
3·8
3·7
3·6
3·5
3·4
3·3
3·2
3·1
3·0
4
5
6
7
8
9
10
11
12
13
14
WATER TEMPERATURE (°C)

from 951-6,845; these were only real estimates if all animals were prone to capture, every animal in every section was caught and the population was evenly distributed and equally catchable all along the aqueduct. Therefore even the highest value of 6,845 must have been a considerable underestimate as it was unlikely that all crayfish left their hides on lowering the water level or that all that did so were seen, also some that were seen evaded capture and the population was much less dense at the upper end (5.4.3).

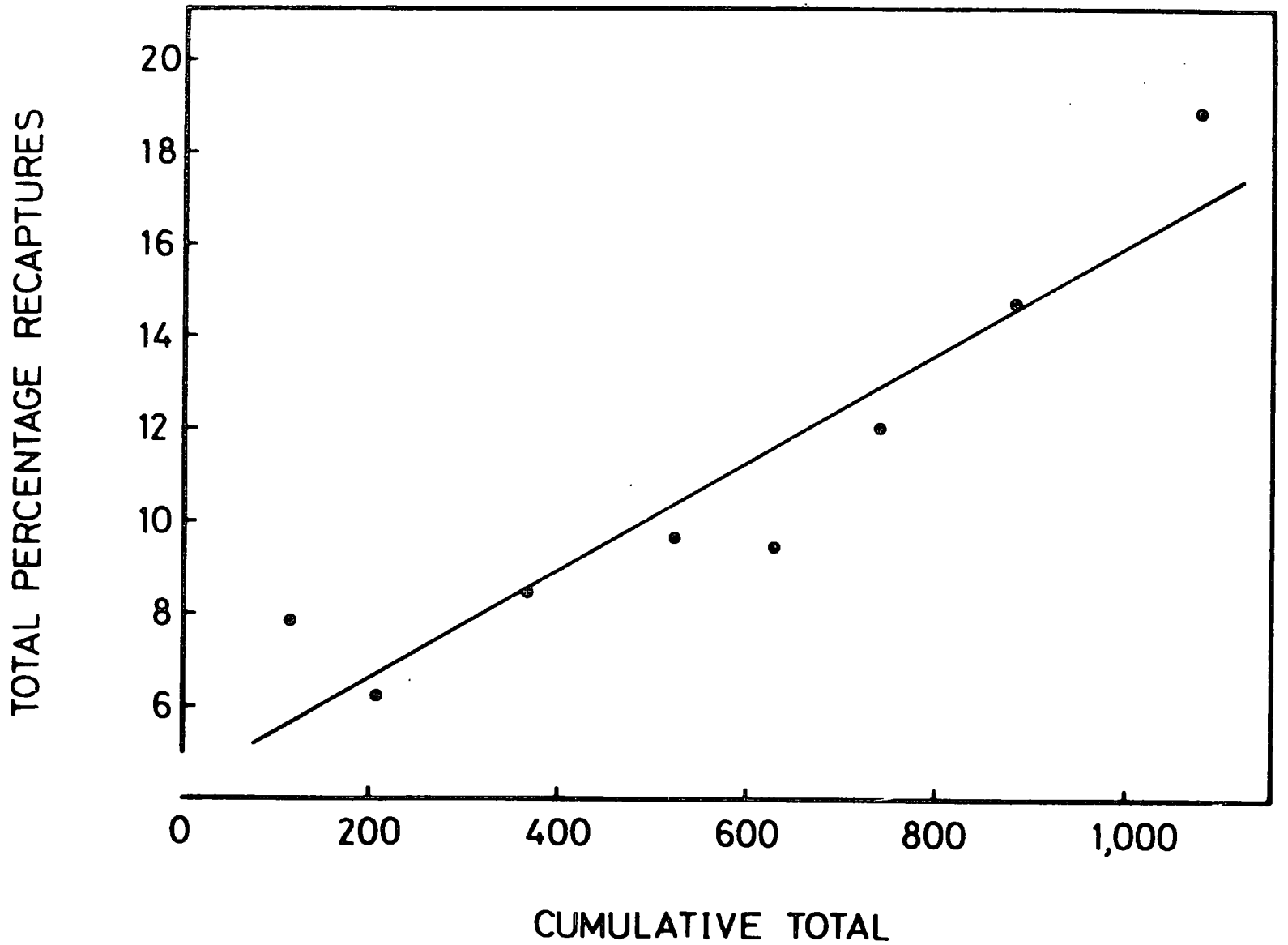
(ii) Another approximate estimate of population numbers was obtained by assuming 'closed' population conditions over four months and using a regression method (Eberhardt 1969, Hayne 1949, Marten 1970, Schumacher and Eschmeyer 1943). Considering the samples 16. 5.74 onwards the total percentage of all recaptures in each sample was positively correlated with the cumulative total of marked animals as shown in Fig. 5.4 ($r = 0.94$, $t = 6.66$, $p < 0.001$). Extrapolation of this correlation to 100% recapture rate produced a predicted cumulative total of 8,217. If movements out of sections 42-51 were small this represents an estimate of the number of crayfish in that stretch of aqueduct. Theoretically, however, as movement out of sections 42-51 increases and the distribution of the marked animals along the aqueduct tends to random so 8,217 tends to an estimate of total population size. Although movements were known to be extensive (Fig. 5.2) sufficient movement to produce a random distribution within a four month period was unlikely from such a

Fig. 5.4: Total percentage recaptures in each sample as a function of the cumulative total of individuals marked before that sample was taken (Table 5.1, considering samples 16. 5.74 onwards only)

$y = 0.0116x + 4.2848$

SE slope $= 0.1748 \times 10^{-3}$

$r = 0.9386$, $t = 6.6639$, $p < 0.001$


TOTAL PERCENTAGE RECAPTURES
20
18
16
14
12
10
8
6
0
200
400
600
800
1,000
CUMULATIVE TOTAL

restricted sampling area and 8,217 was thus another underestimation; since percentage recaptures must have been overestimated.

(iii) It was possible to estimate the approximate population size from the two samples of marked animals taken on 27. 5.74 and 7. 8.74 by making the assumptions that had the collectors sampled for unmarked as well as marked animals their efficiency would have been the same in every section from 17-96 as it was in sections 43-50 on the same or the closest sampling date. The population also had to be assumed to have been 'closed' over the entire sampling period. Thus total sample size on 27. 5.74 (as predicted from 29. 5.74) was estimated as:-

$$90/(50 - 43) \times (96 - 17) = 1,016$$

Total sample size on 7. 8.74 (as predicted from the sample from sections 43-50 on the same day) was estimated as:-

$$204/(50 - 43) \times (96 - 17) = 2,302$$

The following Lincoln Index estimates (Lincoln 1930) were then possible; standard errors were calculated as recommended by Robson and Regier (1971).

Date	n_1	n_2	m_2	$\hat{N}$	SE
29. 5.74	363	1,016	42	8,781	1,248
7. 8.74	666	2,302	94	16,310	1,527

The much larger second estimate was probably due to the recruitment into the catchable population following the beginning of the growth season in late June (3.3).

(iv) Several more Lincoln index type estimates were possible by assuming the movements of marked animals out of the sections sampled to have been negligible between adjacent samples and that 'closed' population conditions applied over the same period (Table 5.2).

The following steps were taken to allow for the different numbers of samples taken on some consecutive visits. When more sections were sampled on the second occasion n_2 was reduced by dividing by the number of sections sampled on the first occasion/the number of sections sampled on the second occasion, m_2 was not altered as there was assumed to have been no movement between sections and although this was not so (Fig. 5.1) this would compensate for some movement. When less samples were taken on the second occasion this did not affect the n_2/m_2 ratio and no adjustment was necessary. The resulting estimate therefore applied to the sections sampled on the first occasion and was multiplied up to 117 sections assuming equal distribution along the aqueduct.

These estimates ranged from 30,030 ± 9,935 to 18,290 ± 3,149. As some movements out of the sections sampled did occur, although these were few between adjacent samples (Fig. 5.1), these may have been overestimates.

In summary the preliminary study showed that large samples could be collected by hand (indeed the size limit was determined by the time spent processing the catch rather than collecting it) and also that lowering the water level and later returning marked individuals must

Table 5.2

Approximate Lincoln index type estimates assuming no movement from stretch sampled between adjacent samples (see text, 5.3.4 (iv))

Date	No. sections sampled	No. crayfish caught & returned	No. recaptures from previous occasion	Population estimate ± SE
16.5.74	8	115		
29.5.74	8	90	7	21,624 ± 7,807
12.6.74	8	160	9	23,400 ± 7,375
20.6.74	8	154	12	30,030 ± 9,935
18.7.74	2	104	8	
24.7.74	2*	117	8	
31.7.74	4*	141	11	
7.8.74	8	204	23	18,290 ± 3,149
11.9.74	6	170	27	18,795 ± 3,219

Standard errors calculated by the method of Robson and Regier 1971.

*no population estimate was possible as there were no sections common to the adjacent samples (Table 5.1)

have been a considerable disturbance to the population and was probably responsible, at least in part, for the large displacements of animals observed over quite short time periods. It was also possible to state, with reasonable certainty, that population numbers had been within the limits 10^4 - 3 x 10^4.

5.4 The estimation of population parameters 1975-77

5.4.1 Introduction

One of the primary objectives of this project was to estimate population parameters with sufficient accuracy for a study to have been made of the dynamics of this population. It was, therefore, essential not only that sample size be increased but also that the sampling was carried out in such a way that the basic assumptions underlying mark-recapture methods were satisfied (5.1). In order to achieve this increased sampling intensity it was necessary to stop the flow of water through the aqueduct for up to four hours (usual flow $\simeq$ 54 x 10^6 l./ day).

As the aqueduct was the most important inflow of water into the catchment reservoir complex (1.1) it was only possible to obtain permission from the Water Company to stop the water flow for a limited period on three occasions in 1975.

In 1976-77 it was proposed to increase sample size to around one thousand individuals by collecting from twenty to thirty randomly selected sections (as mean catch/section in 1975 was ca. forty crayfish). Say

population size was around fourteen thousand at most times of year this should have produced an estimate with negligible bias at the 95% level of probability (as $n_1 n_2 \gg 4N$) with an accuracy < 0.25 (estimate $\pm$ 1.96 SE) for a Lincoln Index estimate (Robson & Regier 1964). Permission was obtained from the Water Company to make five such visits in 1976 and a further three visits in the first half of 1977.

5.4.2 The size and structure of the hand collected samples

The full details of the composition of all samples are listed in Appendix 1.

(i) The potential catchable population was highest on 7. 7.75 at 9,529 (Table 5.3). This indicated that the maximum efficiency of hand collection was approximately 50% (5.4.5). The half that evaded collection were either missed by the collector or did not leave their hides (Fig. 1.2).

(ii) The mean sex ratio in the hand collections was not significantly different from unity (Table 5.3; $t = 1.75$, $p > 0.10$).

(iii) The mean adult:juvenile ratio in the hand collections in 1975-77 (Table 5.3) was not significantly different from the ratio in 1973-74 (Table 5.1, 1.48 $\pm$ 0.31; $t = 1.46$, $p > 0.10$). This indicated that there was no significant variation in the relative hand collection efficiency of adults and juveniles throughout the study.

Table 5.3

Sample size, structure and associated parameters 1975-77

Date	Water temp. °C	No. sections sampled	Total marked & returned	Sex ratio ♀♀:♂♂	Adult: Juvenile ratio	Potential catchable population *
25. 6.75	11.1	19	445	0.79	0.77	2,740
1. 7.75	11.6	15	529	0.83	1.32	4,126
7. 7.75	11.3	9	733	0.79	1.42	9,529
26. 5.76	9.9	21	972	1.07	1.68	5,415
11. 6.76	10.9	18	1,017	0.91	1.46	6,611
27. 8.76	16.7	20	951	1.43	3.88	5,563
8.10.76	10.4	20	885	1.42	2.67	5,177
26.10.76	9.3	24	1,018	1.44	2.34	4,963
12. 5.77	8.6	21	778	1.32	2.52	4,335
27. 5.77	9.1	26	677	1.15	2.22	3,047
17. 6.77	9.5	29	703	1.34	2.45	2,836
			means	1.14±0.08	2.07±0.26	

* Potential catchable population, at this sampling intensity, assuming equal distribution and catchability along the aqueduct.

(iv) There was no positive correlation between potential catchable population and water temperature in 1975-77 unlike that observed in 1974. Indeed the potential catchable population decreased as water temperature increased in 1977. Observations when collecting indicated the possibility that this may have been due to the traps no longer having been in the aqueduct at this time. In this case the increased activity at higher water temperatures not only would have meant that more animals left their hides in the walls of the aqueduct but also could have led to more individuals finding 'secure' alternative hides after the water had been drained away rather than the many previously found around and under the traps many of which were captured.

(v) Every person who collected crayfish from the aqueduct attempted to catch every crayfish they saw, irrespective of size. It was, therefore, unlikely that any bias in catchability existed within the four sub-populations (with the possible exception of those females in berry in the adult female sub-population) as all members of each one on the aqueduct floor were easily seen and would have been equally exposed to an attempted capture. It was possible that some bias was present due to larger animals having been easier to handle but it was considered to have been insignificant as attempted capture was almost always successful with animals > ca. 25 mm. carapace length.

5.4.3 Catch distribution along the aqueduct

The variations in numbers caught from randomly selected sections (with the exception of stratified sampling on 12. 5.77 and 27. 5.77) along the length of the aqueduct is shown on Fig. 5.5.

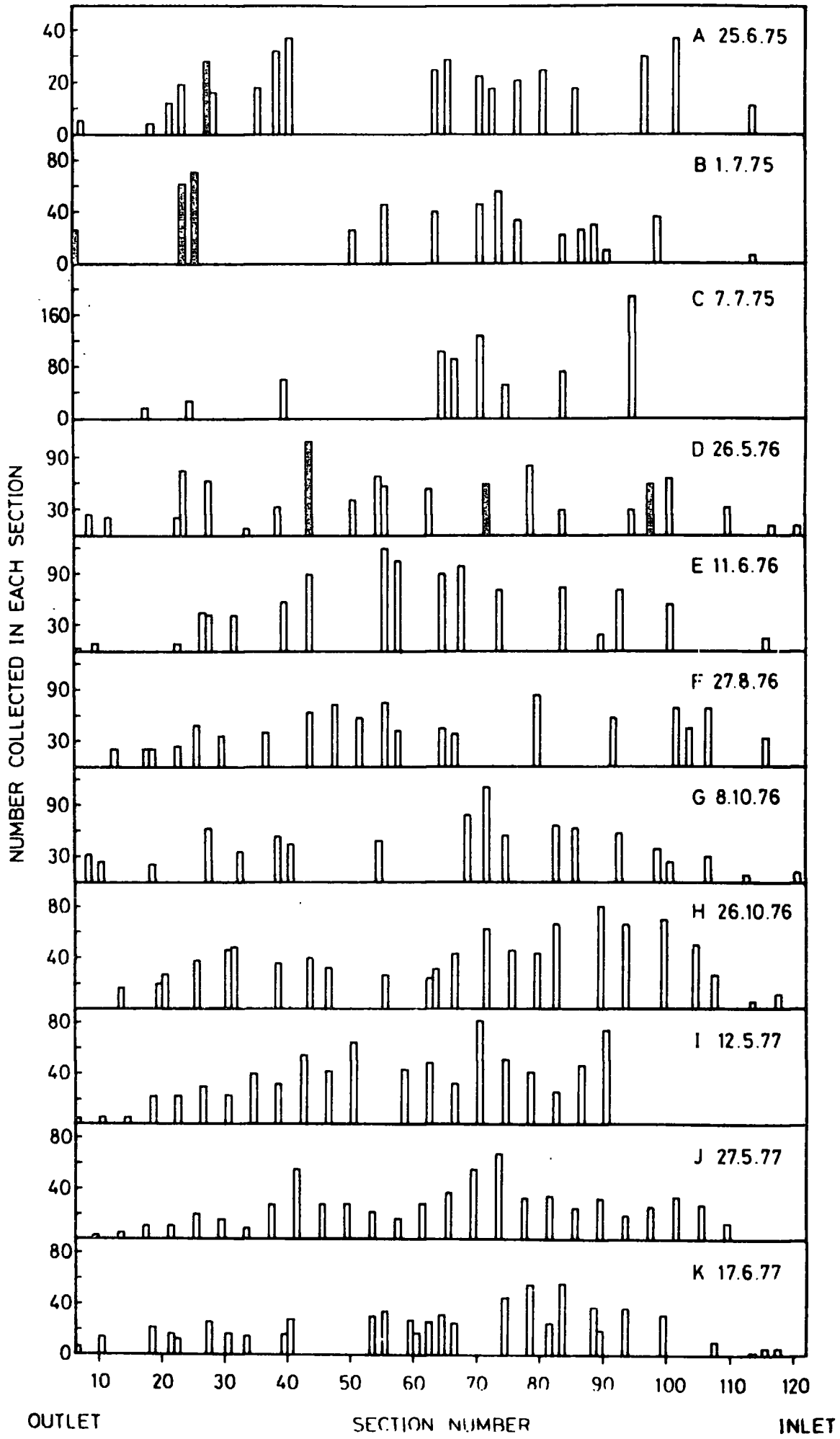
The selected sections (1.1, 5.2) were, as a general rule, collected from in ascending numerical order for convenience to the collector. It was anticipated that such an approach would result in fairly consistent variations in sample size along the aqueduct as observations on lowering the water level in 1974 showed that it took some time for many individuals to vacate their hides and become available for capture. There were, however, believed to have been several effects which contributed to the catch distributions shown on Fig. 5.5.

(i) Catches from the sections at either end of the aqueduct (below section 22, above section 110) were always relatively low.

(ii) The largest catches were always obtained from the region sections 45 to 101. The only exception to this were those sections that were collected from after the first sampling sequence, going from the lowest to the highest number sections in ascending numerical order, had been completed (Fig. 5.5B, sections 23 & 25; Fig. 5.5D, section 43).

(iii) When the water level was down to ca. 20 cm. before collecting was begun, it was always observed that there were many more animals on the aqueduct floor in sections between 30 and 100 than above or below this region.

Fig. 5.5: Catch per section by hand collection along the aqueduct 1975-77 ■ - sections collected from after the first sampling sequence (going from the lowest to the highest number sections in ascending numerical order) had been completed


A 25.6.75
B 1.7.75
C 7.7.75
D 26.5.76
E 11.6.76
F 27.8.76
G 8.10.76
H 26.10.76
I 12.5.77
J 27.5.77
K 17.6.77
NUMBER COLLECTED IN EACH SECTION
SECTION NUMBER
OUTLET
INLET

If the catch distribution were determined solely by the rate at which animals vacated their hides catches from the highest numbered sections would be expected to be the largest. This was not the case as sections 97 and above were brick lined and crayfish density was low due to a lack of hides in the walls of the aqueduct. The fact that some relatively large collections came from sections slightly above section 97 was probably due to movements since the water level had been lowered.

However those samples taken after the completion of the usual numerical sequence on 25. 6.75 and 1. 7.75 confirmed that the amount of time since the water was down was correlated with the number of animals available for collection. Indeed, the catches from the lower sections showed a tendency to follow the expected situation, especially on 7. 7.75.

The only observation available when the time since the water was down was the same for all sections was that there were many more animals on the aqueduct floor (the area where capture was most likely) in the middle sections when the water level had dropped to < 20 cm. This may have been due to hides having been vacated more rapidly in mid-aqueduct and/or that the greater growths of F. antipyretica in the lower sections (1.3.2) may have supported and concealed animals as they left their hides in the aqueduct wall; such animals would then have taken some time to appear on the aqueduct floor.

There was, therefore, no reliable evidence to suggest any marked variations in density below section 97.

It was because it was expected that there would be considerable variability in catch/section, despite the apparently even distribution below section 97, that catches from each section were returned to the sections originally collected from, but in random sequence. Returning samples to the same section as they were collected from would have led to a situation comparable to inherent unequal catchability; animals from mid-aqueduct having been more catchable than those in the lower sections. Extensive movements of marked individuals would have tended to remove any bias this might have introduced but it was considered a worthwhile precaution against unequal catchability and consequent underestimation of population numbers (Robson and Regier 1971, Bohlin and Sundström 1977). It was decided to return the animals to the same sections in random sequence to avoid depleting any sections. It was also possible that displacing animals increased the disturbance to the population which was caused by lowering the water level and was, at least in part, responsible for the considerable movements already demonstrated (3.6, 5.3.2). These movements were, of course, essential to ensure adequate mixing of marked and unmarked animals.

5.4.4 The history of the tail-marks

In order that a complete capture history was available for every individual marked all tail marked ('Day' marked) recaptures were given an individual number before release. One other advantage of this was that it was

possible to investigate the reliability of the tail marks under field conditions by following these 'double-marked' individuals when they occurred in hand and trap samples. Some of the larger trap samples were also 'Day' marked and thus the 'Day' numbers of the hand samples were not always sequential.

Tail marks 'Day' 1 to 'Day' 7 (25. 6.75 to 1.10.75) were followed from 'Day' 5 to 'Day' 3A (7. 7.75 to 17. 6.77) and tail marks 'Day' 8 and 'Day' 9 (26. 5.75 and 11. 6.76 were followed to 'Day' 3A (17. 6.77, Fig.5.6).

The following observations were made from Fig. 5.6 and the rest of the recapture data from 'Day' 11 to 'Day' 3A (27. 8.76 to 17. 6.77):-

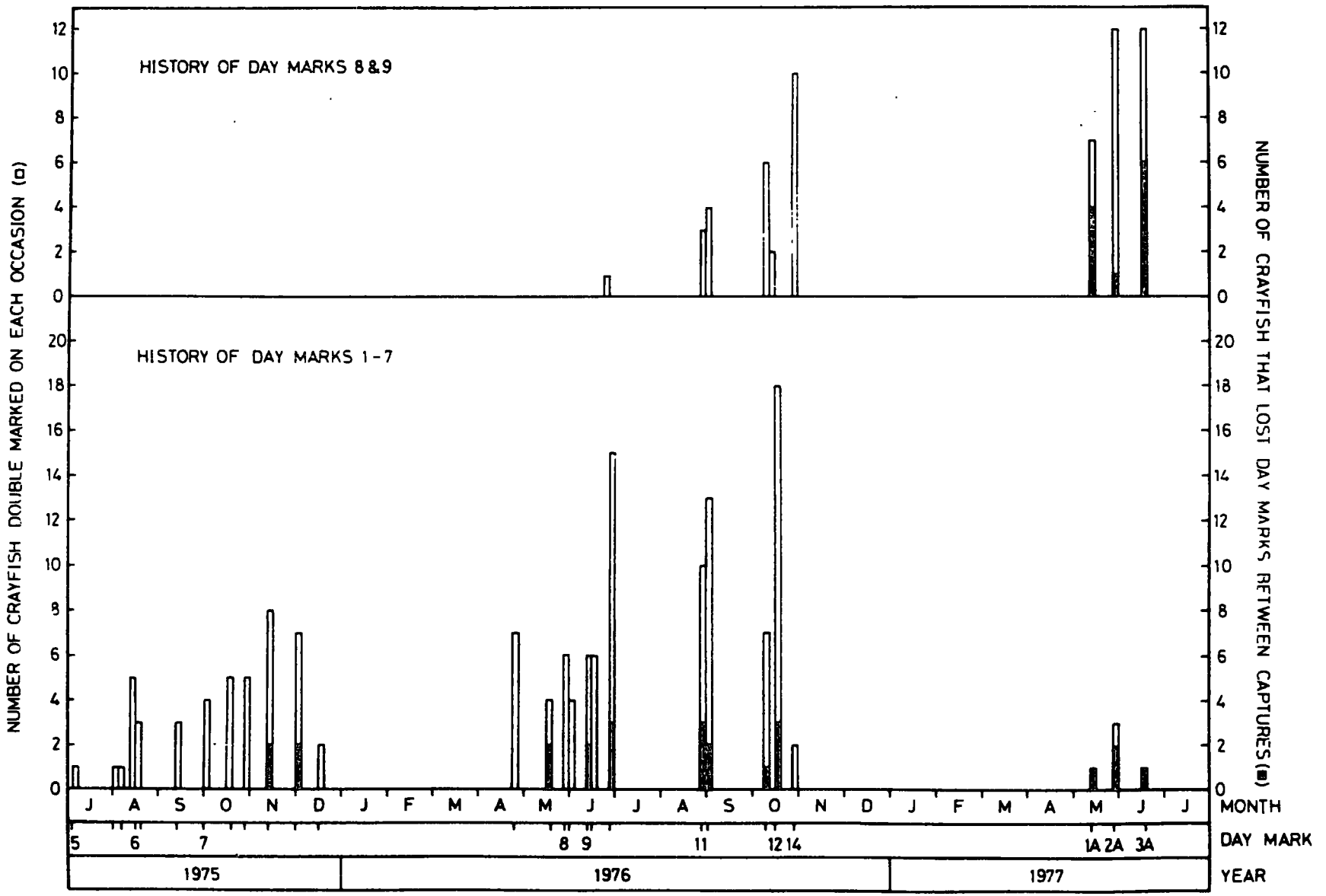
(i) The period over which tail marks 'Day' 1 to 'Day' 7 were followed was almost two years and thus exceeded the time for which the numbering system was 100% effective (2.3); however this should not have altered the proportion of tail marks lost on those animals re-captured that still bore a recognizable number.

(ii) None of the tail marks 'Day' 1 to 'Day' 7 were lost within that period but they began to disappear in November 1975.

(iii) Of the tail marks 'Day' 8 to 'Day' 3A only some of those marked 'Day' 8 and 'Day' 9 (Fig. 5.6) were lost over this period although there were 23 recaptures from 'Day' 12 to 'Day' 3A where the loss of a 'Day' 11 or 'Day' 12 mark was a possibility. On 'Day' 14 the whole sample was examined for previous marks but no 'Day' 14 marks were applied.

Fig. 5.6: The history of 'Day' marks 1-7 from 'Day' 5 to 'Day' 3A and of 'Day' marks 8 and 9 from 'Day' 9 to 'Day' 3A

The number of crayfish that were 'double marked' (i.e. given both tail marks and individual numbers) caught on each trapping and hand-collecting visit from 1975-77 (□) and the number of these that no longer had a recognizable 'Day' mark (i.e. those that had lost a 'Day' mark between last capture and recapture, ■); as a function of date


HISTORY OF DAY MARKS 8&9
HISTORY OF DAY MARKS 1-7
NUMBER OF CRAYFISH DOUBLE MARKED ON EACH OCCASION (a)
NUMBER OF CRAYFISH THAT LOST DAY MARKS BETWEEN CAPTURES (m)
J A S O N D J F M A M J J A S O N D J F M A M J J
MONTH
5 6 7 8 9 11 12 14 1A 2A 3A
DAY MARK
1975 1976 1977
YEAR

(iv) Losses of 'Day' marks 1-7, 8 and 9 were considerable after one winter (7% - 86%) and almost total after two overwinterings ('Days' 1-7 only, 67% - 100%).

(v) No 'Days' 6, 7 or 11 marks were lost overwinter up to the beginning of the next growth season although there were 21 ('Days' 6 and 7) and 9 ('Day' 11) recaptures where this was a possibility ('Day' 3A - 17. 6.77 - was before the start of the growth season in 1977).

The above observations led to the conclusion that 'Day' marks were a reliable means of recognition for a complete growth season or overwinter but probably not for both. It also seemed probable that more than one moult plus the overwinter period was necessary to obliterate a 'Day' mark.

'Day' marks applied to laboratory held animals were clearly recognizable when observed for up to four months after a second moult following the application of the mark. It therefore seemed likely that the loss of 'Day' marks in the field was caused by the paler more diffuse marks which followed a moult having been obscured by the dark epizootic growths which occurred on the exoskeleton overwinter (2.3).

There was thus considerable evidence to support the contention that 'Day' marks were a reliable means of recognition for the sample sequences 'Day' 1 to 'Day' 5 (25. 6.75 - 7. 7.75), 'Day' 8 to 'Day' 14 (26. 5.76 - 26.10.76) and 'Day' 11 to 'Day' 3A (27. 8.76 - 17. 6.77).

5.4.5 Mark-recapture analysis

There was a considerable amount of evidence (3.6, 5.3.2, 5.4.4, 6.3.5) to support the premise that the assumptions involved in the estimation of population parameters by mark and recapture (5.1) had been valid for this sampling method on the aqueduct population. It was not possible to test whether marked and unmarked animals were equally catchable in a population of unknown size but this was assumed to have been the case within each sub-population due to the 'passive' nature of the sampling method and the fact that an attempt was made to collect every animal that was seen (5.4.2(v)). Reproductive females may have had a lowered catchability due to the possibility that their 'retiring' habit may have resulted in them not appearing on the aqueduct floor in representative numbers; this assumption would then not have been valid for the total adult female sub-population (6.3.4, Capelli 1975, Woodland 1967).

As the 'Day' marks applied in 1975 did not persist through the winter into 1976 (5.4.4) and the three samples were taken within a fortnight 'closed' population conditions were assumed over the sampling period.

Several estimates of population and sub-population size which met with the criterion that $m_2 \geqslant 7$ (with the exception of 'Day' 1 - 'Day' 3 males) as suggested by Robson and Regier (1964), so that with 95% confidence limits these represented unbiased estimates, were listed on Tables 5.4a and b. There were no significant differences between corresponding estimates on the two tables or the

Table 5.4a

Lincoln Index Estimates 1975
Standard errors calculated as
proposed by Robson & Regier (1971)

Days & dates of mark and recapture	Population	n_1	n_2	m_2	Estimate	S.E.
Day 1 - Day 3	Total	445	529	18	13,078	2,968
25. 6.75 -	Adults	193	301	9	6,455	2,069
1. 7.75	Juveniles	252	228	9	6,384	2,048
	Males	249	289	6	11,994	4,787
	Females	196	240	12	3,920	1,069
Day 3 - Day 5	Total	529	733	30	12,925	2,245
1. 7.75 -	Adults	301	430	11	11,766	3,473
7. 7.75	Juveniles	228	303	19	3,636	773
	Males	289	410	15	7,899	1,949
	Females	240	323	15	5,168	1,262
Day 1 - Day 5	Adults	193	430	7	11,856	4,371
25. 6.75 - 7. 7.75						

Table 5.4b

Schnabel's binomial model (1938)
Total population

Date	Day	n_i	m_i	M_i	$n_i M_i$
25. 6.75	1	445	-	-	-
1. 7.75	3	529	18	445	235405
7. 7.75	5	733	37	956	700748
Total			55		936153

$\hat{N}/\lambda$ = (0.01475 - 0.02625), m_2 = 50
$\hat{N}$ = 16,717 (13,808 - 24,574), 95% Confidence limits

$\hat{N}$, n_1, n_2, m_2 see Glossary. n_i, m_i, M_i & λ as Seber (1973)

three possible pairings of 'Days' on Table 5.4a. There was, also, no significant evidence for any population structure other than ratios of unity between adults and juveniles, males and females. Considering 'Day' 1 and 'Day' 5 the only possible estimate was for the adult sub-population due to the absence of juvenile recaptures.

The estimates obtained in 1975 indicated that the density of the study population was approximately 6 crayfish/m^2 in June and July.

Several methods of testing whether marked individuals were recaptured at random have been developed (e.g. Carothers 1971, Cormack 1966, Eberhardt 1969, Keith & Meslow 1968, Leslie 1958, Phillips & Campbell 1970, Seber 1962, 1965). The only one of these which could be applied to the two sequences of five hand samples in 1976-77 was that of Leslie (1958). This was either because of the relatively low sampling intensity (ca. 5-10%) or that the sample sequence spanned too long a period in time to have made the assumption that deviations from closed population conditions were negligible. The data were examined using Leslie's method:-

Sample sequence 'Day' 8 - 'Day' 14 (26. 5.76 - 26.10.76). There were three possible recapture occasions between these two 'Days'.

(i) Twenty-nine of the animals marked and released on 'Day' 8 were recaptured on 'Day' 14. The following notation and method of calculation are those of Southwood (1963).

i	n_i	x	f(x)
'Day' 9	1	0	26
'Day' 11	2	1	3
'Day' 12	0	2	0
total	3	total	29

Sum of squares = 2.6897, expected variance = 0.0975, χ^2 = 27.59. Thus the hypothesis of random recapture was disproven (28 d.f., p = 0.50 - 0.30).

(ii) Twenty-five of the adults marked and released on 'Day' 8 were recaptured on 'Day' 14.

i	n_i	x	f(x)
'Day' 9	1	0	22
'Day' 11	2	1	3
'Day' 12	0	2	0
total	3	total	25

Sum of squares = 2.6400, expected variance = 0.1120, χ^2 = 23.57. Thus the hypothesis of random recapture was disproven (24 d.f., p = 0.50 - 0.30).

Sample sequence 'Day' 11 - 'Day' 3A (27. 8.76 - 17. 6.77). There were three possible recapture occasions between these two 'Days'.

(iii) Thirty three of the animals marked and released on 'Day' 11 were recaptured on 'Day' 3A.

i	n_i	x	f(x)
'Day' 12	1	0	28
'Day' 1A	0	1	5
'Day' 2A	4	2	0
total	5	total	33

Sum of squares = 4.2424, expected variance = 0.1478, χ^2 = 28.19. Thus the hypothesis of random recapture was not disproven (32 d.f., p = 0.50 - 0.70).

(iv) Thirty of the adults marked and released on 'Day' 11 were recaptured on 'Day' 3A.

i	n_i	x	f(x)
'Day' 12	1	0	25
'Day' 1A	0	1	5
'Day' 2A	4	2	0
total	5	total	30

Sum of squares = 4.1667, expected variance = 0.1478, χ^2 = 28.19. Thus the hypothesis of random recapture was not disproven (29 d.f., p = 0.50 - 0.70).

The capture of the marked animals known to have been alive throughout the sampling period was thus shown, on the basis of Leslie's test (1958), to have been non-random during the first sample sequence and random during the second sample sequence for both the total and adult populations in each case. In all four cases the data were only just outside the limits suggested by Leslie (1958) of more than twenty recaptures and at least three possible recapture occasions. As these suggestions appeared in an appendix to a study in which mean sample size was $> 3{,}000$ from a shearwater population of mean size ca. 15,000 individuals (sampling intensity $\simeq$22%) it was presumably implied that these limits would usually result in relatively large values of n_i and f(x). This was not the case in the present study as $n_i < 5$ and f(x) < 29 due to the relatively low sampling intensity (ca. 5 - 10%). The test must, therefore, have been operating at low sensitivity; further evidence for this was that

all the calculated values of χ^2 were very close to the level of probability above which the hypothesis was not disproven ($p = 0.50$, Southwood 1966). Computer simulation studies have clearly proven the insensitivity of this test (Roff 1973b). In the absence of any more sophisticated tests which could be applied to these data it was assumed that deviations from equal catchability were negligible due to the 'passive' nature of the sampling method and further supported by the fact that all values of χ^2 calculated by Leslie's test lay above or very close to the acceptable probability level.

The two five sample sequences for which the marking technique was shown to have been reliable (5.4.4) spanned five and nine months respectively. This was so that the dynamic parameters of the aqueduct population (gains and losses) could be estimated as well as population size at several points in time. All previous estimates had been from samples taken within relatively short periods of time when an approximation to 'closed' population conditions could reasonably have been assumed; the Lincoln Index, binomial models (Schnabel 1938) and regression methods were therefore adequate. Of the 'open' population models it is widely accepted that those of Jolly (1965) and Manly and Parr (1968) are the most powerful and generally applicable (e.g. Bishop & Sheppard 1973, Emmel 1976, Southwood 1966, Woodland 1967).

The mark-recapture data was listed as trellis diagrams on Tables 5.5a and b according to the notation of Jolly's stochastic model (1965); that is only dates

Table 5.5a: The mark-recapture data 1976 (trellis diagrams as Jolly 1965)

Adult females

Date	Day	n_i				
26. 5.76	8	259				
11. 6.76	9	233	15			
27. 8.76	11	433	11	13		
8.10.76	12	383	6	14	17	
26.10.76	14	403	15	17	20	30

Adult males

Date	Day	n_i				
26. 5.76	8	350				
11. 6.76	9	371	25			
27. 8.76	11	323	15	20		
8.10.76	12	261	4	11	7	
26.10.76	14	310	10	23	12	20

Juvenile females

Date	Day	n_i				
26. 5.76	8	244				
11. 6.76	9	251	12			
27. 8.76	11	126	2	4		
8.10.76	12	136	3	6	3	
26.10.76	14	197	2	4	3	6

Juvenile males

Date	Day	n_i				
26. 5.76	8	119				
11. 6.76	9	162	8			
27. 8.76	11	69	2	2		
8.10.76	12	105	0	3	0	
26.10.76	14	108	2	0	1	2

Total recognizable as having been parasitized by T. contejeani

Date	Day	n_i				
26. 5.76	8	75				
11. 6.76	9	81	5			
27. 8.76	11	82	2	3		
8.10.76	12	57	1	2	4	
26.10.76	14	80	3	1	3	10

$n_i = s_i$ as Jolly (1965), i.e. there were no losses on marking

Table 5.5b: The mark-recapture data 1976-77 (trellis diagrams as Jolly 1965)

Adult females

Date	Day	n_i				
27. 8.76	11	433				
8.10.76	12	383	17			
12. 5.77	1A	317	18	19		
27. 5.77	2A	244	12	17	31	
17. 6.77	3A	280	17	18	13	28

Adult males

Date	Day	n_i				
27. 8.76	11	323				
8.10.76	12	261	7			
12. 5.77	1A	240	9	8		
27. 5.77	2A	223	9	9	12	
17. 6.77	3A	219	8	21	14	21

Juvenile females

Date	Day	n_i				
27. 8.76	11	126				
8.10.76	12	136	3			
12. 5.76	1A	125	3	4		
27. 5.77	2A	118	4	1	1	
17. 6.77	3A	122	1	4	6	3

Juvenile males

Date	Day	n_i				
27. 8.76	11	69				
8.10.76	12	105	0			
12. 5.77	1A	96	1	1		
27. 5.77	2A	92	2	1	4	
17. 6.77	3A	82	1	1	1	2

Total recognizable as having been parasitized by T. contejeani

Date	Day	n_i				
27. 8.76	11	82				
8.10.76	12	57	4			
12. 5.77	1A	31	0	0		
27. 5.77	2A	32	1	2	0	
17. 6.77	3A	35	1	2	5	2

$n_i = s_i$ as Jolly (1965), i.e. there were no losses on marking

of last capture were considered, previous captures were ignored. It was not possible to use the Manly and Parr model (1968) due to the relatively low sampling intensity (ca. 5 - 10%), the result of this was that all but one of the values of c_i were less than 10 ($m._{hi}$ = the number of each value of the m_{hi} on the trellis diagrams that occurred earlier in the sample sequence, $c_i = \sum m._{hi}$ for all recaptures from each date originally marked, Seber 1973); $c_i > 10$ is essential for this model to estimate population size even to an order of magnitude (Seber 1973).

Analysis of the recapture data listed on Tables 5.5a and b using the Jolly model was computerised (Davies 1971) and the resulting parameter estimates (N, Phi, B) and their standard errors were listed on Tables 5.6a-d. The sub-samples into which the unmarked portion of each sample were divided (5.2) were, as far as was possible, treated separately to avoid any bias due to unequal catchability which may have existed between the sub-populations (5.4.2, Southwood 1966, Seber 1973). It was not possible to estimate the number of males and females separately for the juveniles or to estimate the recognizable parasitized population in the 1976-77 sample sequence as in all cases one or more of the n_{ij} values between adjacent samples was zero.

The parameter estimates on Tables 5.6 a-d provided two types of information about the aqueduct population; its size and structure at several points in time (N_i for the sub-populations) and its dynamics over various periods of time (Phi = loss rate, B = gains).

Table 5.6a: Population size estimates 1976 (Jolly's method)

Date	Day	Alpha	M	$\hat{N}$	$\hat{Phi}$	$\hat{B}$	SE($\hat{N}$)	SE($\hat{Phi}$)	SE($\hat{B}$)
Total population									
26. 5.76	8		0		0.7056*			0.0919	
11. 6.76	9	0.0590	686	11,625	1.1446	12,611*	2,044	0.1765	3,943
27. 8.76	11	0.0726	1,880	25,917	0.6289*	4,477	4,776	0.1135	3,103
8.10.76	12	0.0836	1,737	20,776			3,861		
26.10.76	14	0.1640							
Adult population									
26. 5.76	8		0		0.6830*			0.0941	
11. 6.76	9	0.0662	416	6,281	1.4378	9,023*	1,247	0.2347	3,000
27. 8.76	11	0.0780	1,409	18,054	0.6213*	3,065	3,552	0.1185	2,341
8.10.76	12	0.0916	1,308	14,281			2,866		
26.10.76	14	0.2062							
Adult female population									
26. 5.76	8		0		0.7122*			0.1398	
11. 6.76	9	0.0644	184	2,865	1.5717	6,909*	881	0.3371	2,858
27. 8.76	11	0.0554	633	11,412	0.6729*	-424	3,169	0.1626	1,959
8.10.76	12	0.0966	701	7,254			1,874		
26.10.76	14	0.2035							

Alpha = proportion marked, M = total marked, N = total number, Phi = probability of survival until t+1, B = number joining between t and t+1.

* = significant parameter at $p < 0.05$ or less: Phi < 1, B > 0.

Table 5.6b: Population size estimates 1976 (Jolly's method)

Date	Day	Alpha	M	$\hat{N}$	Phi	$\hat{B}$	SE($\hat{N}$)	SE(Phi)	SE($\hat{B}$)
Adult male population									
26. 5.76	8		0		0.6407*			0.1238	
11. 6.76	9	0.0674	224	3,328	1.4924	2,887	875	0.3907	1,780
27. 8.76	11	0.1084	851	7,854	0.5349*	3,027	2,331	0.1676	1,783
8.10.76	12	0.0843	609	7,728			2,311		
26.10.76	14	0.2097							
Juvenile population									
26. 5.76	8		0		0.7133			0.2449	
11. 6.76	9	0.0484	259	5,351	0.8697	6,406	2,145	0.3871	4,543
27. 8.76	11	0.0513	567	11,059	0.5006	513	5,776	0.2691	2,339
8.10.76	12	0.0622	377	6,049			3,000		
26.10.76	14	0.0656							
Population of animals recognized as parasitized by T. contejeani									
26. 5.76	8		0		1.1467			0.5981	
11. 6.76	9	0.0617	86	1,393	0.5370	679	936	0.3012	776
27. 8.76	11	0.0610	87	1,427	0.2860*	-26	914	0.1358	236
8.10.76	12	0.1228	47	382			193		
26.10.76	14	0.2125							

Alpha = proportion marked, M = total marked, N = total number, Phi = probability of survival until t+1, B = number joining between t and t+1

* = significant parameter at $p < 0.05$ or less: Phi < 1, B > 0

Table 5.6c: Population size estimates 1976-77 (Jolly's method)

Date	Day	Alpha	M	$\hat{N}$	Phi	$\hat{B}$	SE($\hat{N}$)	SE(Phi)	SE($\hat{B}$)
Total population									
27. 8.76	11		0		0.7817*			0.1041	
8.10.76	12	0.0305	743	24,367	0.7865	-3,854	5,559	0.1116	4,247
12. 5.77	1A	0.0823	1,259	15,310	0.7192*	-1,682	2,646	0.1225	1,630
27. 5.77	2A	0.1521	1,419	9,329			1,613		
17. 6.77	3A	0.2262							
Adult population									
27. 8.76	11		0		0.7077*			0.0995	
8.10.76	12	0.0373	535	14,356	0.8115	-1,982	3,444	0.1215	2,742
12. 5.77	1A	0.0969	937	9,667	0.6647*	-1,458	1,730	0.1172	1,002
27. 5.77	2A	0.1927	957	4,967			879		
17. 6.77	3A	0.2806							
Adult female population									
27. 8.76	11		0		0.8091			0.1436	
8.10.76	12	0.0444	350	7,893	0.6953*	-1,221	2,294	0.1325	1,522
12. 5.77	1A	0.1167	498	4,267	0.6147*	-678	959	0.1384	490
27. 5.77	2A	0.2459	478	1,945			433		
17. 6.77	3A	0.2714							

Alpha = proportion marked, M = total marked, N = total number, Phi = probability of survival until t+1, B = number joining between t and t+1.

* = significant parameter at $p < 0.05$ or less; Phi < 1, B > 0.

Table 5.6d: Population size estimates 1976-77 (Jolly's method)

Date	Day	Alpha	M	$\hat{N}$	$\hat{Phi}$	$\hat{B}$	SE($\hat{N}$)	SE($\hat{Phi}$)	SE($\hat{B}$)
Adult male population									
27. 8.76	11		0		0.5745*			0.1329	
8.10.76	12	0.0268	186	6,919	1.0256	-732	2,977	0.2479	3,123
12. 5.77	1A	0.0708	451	6,365	0.7222	-979	2,032	0.2032	1,282
27. 5.77	2A	0.1345	486	3,617			1,046		
17. 6.77	3A	0.2922							
Juvenile population									
27. 8.76	11		0		1.2513			0.4902	
8.10.76	12	0.0214	244	19,601	0.5918	-4,596	13,575	0.2469	7,542
12. 5.77	1A	0.0407	285	7,004	1.2086	1,243	3,405	0.6588	4,019
27. 5.77	2A	0.0619	601	9,708			5,529		
17. 6.77	3A	0.0931							

Alpha = proportion marked, M = total marked, N = total number, Phi = probability of survival until t+1, B = number joining between t and t+1.

* = significant parameter at $p < 0.05$ or less; Phi < 1, B > 0.

The structure of the population

There was no significant evidence for an unequal sex ratio for the adults nor was there any significant difference between the numbers of adults and juveniles at any one time.

The proportion of the population recognized as parasitized by T. contejeani as estimated by the Jolly model or the proportion of parasitized animals recognized in each sample lay between 2 and 12% in 1976-77 (3.7). The probability of survival between Days 11 and 12 (27. 8. - 8.10.76) indicated significant mortality over this period (Phi = 0.2860 ± 0.1358, $p < 0.001$) and was the lowest value calculated for any sub-population. Although recaptures were too few for any Jolly estimates in 1977 the proportion of parasitized individuals recognized in the three samples, Day 1A - Day 3A, indicated a further overwinter decrease in numbers.

It was not possible to obtain any Jolly estimates for the sub-population of egg-bearing females as Days 11 and 12 (27. 8.76 and 8.10.76) were during the non-reproductive part of the year and egg-laying and attachment was not completed by Day 14 (26.10.76; 3.3). However three Lincoln Index estimates between adjacent samples were possible ('closed' population conditions were assumed as the samples were taken within a period of no more than 21 days; Table 5.7a). For two of these estimates (Days 1A & 2A) there was a corresponding Jolly estimate for the total adult female sub-population and for the other (Day 8) a corresponding Lincoln Index

Table 5.7a: The size of the sub-population of egg-bearing females in the 1975-76 and 1976-77 breeding seasons. Lincoln index estimates, standard errors calculated as proposed by Robson & Regier (1971)

Dates*	Days*	n_1	n_2	m_2	N	SE
26. 5. - 11. 6.76	8 - 9	83	107	9	987	297
12. 5. - 27. 5.77	1A - 2A	146	123	12	1,497	394
27. 5. - 17. 6.77	2A - 3A	123	136	13	1,288	321

* = sampling occasions when n_1 and n_2 collected. Estimates apply to the date of the initial sample as recruitment was unlikely to have been significant (1. 1): Ricker (1958), Seber (1973)

Table 5.7b: Estimates of the proportion of the adult female population that bore eggs in the 1975-76 and 1976-77 breeding seasons

Season	Date	Day	Adult female population	SE	Egg-bearing population	SE	%*	Adult female sample	Egg-bearing female sample	%*
75-76	26. 5.76	8	4,023	975	987	297	24.5	259	83	32.0
75-76	11. 6.76	9	2,865	881				233	107	45.9
76-77	12. 5.77	1A	4,267	959	1,497	394	35.1	317	146	46.1
76-77	27. 5.77	2A	1,945	433	1,288	321	66.2	244	123	50.4
76-77	17. 6.77	3A						280	136	48.6

%* = Estimated percentage of adult females that bore eggs.
Days 11 and 12 were in the non-reproductive part of the year and egg-laying was not completed by Day 14 (3.2).

estimate between Days 8 and 9 (26. 5. - 11. 6.76, deviations from 'closed' population conditions were assumed negligible due to the samples having been relatively close in time; because gains were unlikely to have been important outside the growth season, even over long periods, this estimate was assumed valid on Day 8 - 26. 5.76). The proportion of the adult female sub-population which bore eggs in the 1975-76 and 1976-77 breeding seasons as estimated by mark-recapture or the egg-bearing proportion of the adult female sub-sample lay between 35 and 66% (3.4, Table 5.7b).

The dynamics of the population

The estimates of the dynamic population parameters Phi and B (survival rate and number joining) and their significance levels (for Phi < 1, B > 0) were summarised on Tables 5.8a and b. There were no significant differences in the estimates of Phi and B between the sub-populations for any one time period or over several time periods for the same sub-population; this reflected the large standard errors of the estimates of these parameters (mean SE as a % of mean Phi = 27%, mean SE as a % of mean B = 82%). There were also no significant differences between the sum of the sizes of the sub-populations and the total population estimated together at any one time. Any differences in catchability between the sub-populations were thus not affecting the total population estimates significantly at this sampling intensity and they were therefore considered together.

Table 5.8a: Summary of population parameters: probability of survival (Phi) and number joining (B), with significance levels 1976

Dates	Days	Population	$\hat{Phi}$	p	$(\hat{B})$	p
26. 5. - 11. 6.76	8 - 9	Adult ♀♀	0.7122	0.05		
		Adult ♂♂	0.6407	0.01		
		Adult ♀♀ + ♂♂	0.6830	0.01		
		Juvenile ♀♀ + ♂♂	0.7138	-		
		Parasitized*	1.1467	-		
		Total	0.7056	0.01		
11. 6. - 27. 8.76	9 - 11	Adult ♀♀	1.5717	-	6909	0.05
		Adult ♂♂	1.4924	-	2887	-
		Adult ♀♀ + ♂♂	1.4378	-	9023	0.01
		Juvenile ♀♀ + ♂♂	0.8697	-	6406	-
		Parasitized*	0.5370	-	679	-
		Total	1.4476	-	12611	0.01
27. 8. - 8.10.76	11 - 12	Adult ♀♀	0.6729	0.05	-424	-
		Adult ♂♂	0.5349	0.01	3027	-
		Adult ♀♀ + ♂♂	0.6213	0.01	3065	-
		Juvenile ♀♀ + ♂♂	0.5006	-	513	-
		Parasitized*	0.2860	0.001	-26	-
		Total	0.6289	0.01	4477	-

Parasitized* - the total animals recognized as having been parasitized by T. contejeani

Table 5.8b: Summary of population parameters, probability of survival (Phi) and number joining (B), with significance levels 1976-77

Dates	Days	Population	$(\hat{Phi})$	p	$(\hat{B})$	p
27. 8. - 8.10.76	11 - 12	Adult ♀♀	0.8091	-		
		Adult ♂♂	0.5745	0.002		
		Adult ♀♀ + ♂♂	0.7077	0.01		
		Juvenile ♀♀ + ♂♂	1.2513	-		
		Total	0.7817	0.05		
8.10. - 12. 5.77	12 - 1A	Adult ♀♀	0.6953	0.05	-1221	-
		Adult ♂♂	1.0256	-	-732	-
		Adult ♀♀ + ♂♂	0.8115	-	-1982	-
		Juvenile ♀♀ + ♂♂	0.5918	-	-4596	-
		Total	0.7865	-	-3854	-
12. 5. - 27. 5.77	1A - 2A	Adult ♀♀	0.6147	0.01	-678	-
		Adult ♂♂	0.7222	-	-979	-
		Adult ♀♀ + ♂♂	0.6647	0.01	-1458	-
		Juvenile ♀♀ + ♂♂	1.2086	-	1243	-
		Total	0.7192	0.05	-1682	-

As N_{i+1} must obviously equal $N_i Phi_i + B_i$ the inter-relationship of these three parameters was crucial to the description of the dynamics of the population (Fig. 5.7). A significant estimate of Phi or B ($Phi < 1$, $B > 0$) from the total population and/or one or more of the sub-populations was interpreted as evidence that mortality (all emigration was almost certainly permanent and thus regarded as equivalent to mortality; 1.1, 3.6.1) or recruitment (as birth or immigration) was occurring at that time in at least part of the population and may also have been occurring in other parts but remained undetected. There was significant evidence of recruitment between Days 9 and 11 (11. 6. - 27. 8.76) and significant evidence of mortality amongst one or more of the sub-populations at all other times. It seemed probable therefore that recruitment occurred mainly from within the sub-populations of unsampled juveniles (< 13 mm. C.L.) to juveniles and from juveniles to adults over the growth season and mortality caused population size to fall throughout the rest of the year.

5.5 Discussion

The uses of mark-recapture methods in the study of the dynamics of animal populations of species from all the major phyla have been extensively reviewed (e.g. invertebrates, especially insects, Morris 1960, Sheppard & Bishop 1973, Southwood 1966; crayfish, Woodland 1967; fish, Beverton & Holt 1957, Regier & Robson 1967, Ricker 1958; birds, Taylor 1966; small mammals, Edwards &

Fig. 5.7: Total population parameters vs date 1976-77

Day 12 - two estimates of population size (●) are available on Day 12, one from each sequence of five samples

-·-·-· - Growth season:-

Moulting first observed 20. 6.74

Moulting first observed 27. 6.76

Moulting last observed 11. 9.74

Moulting last observed 13. 9.75

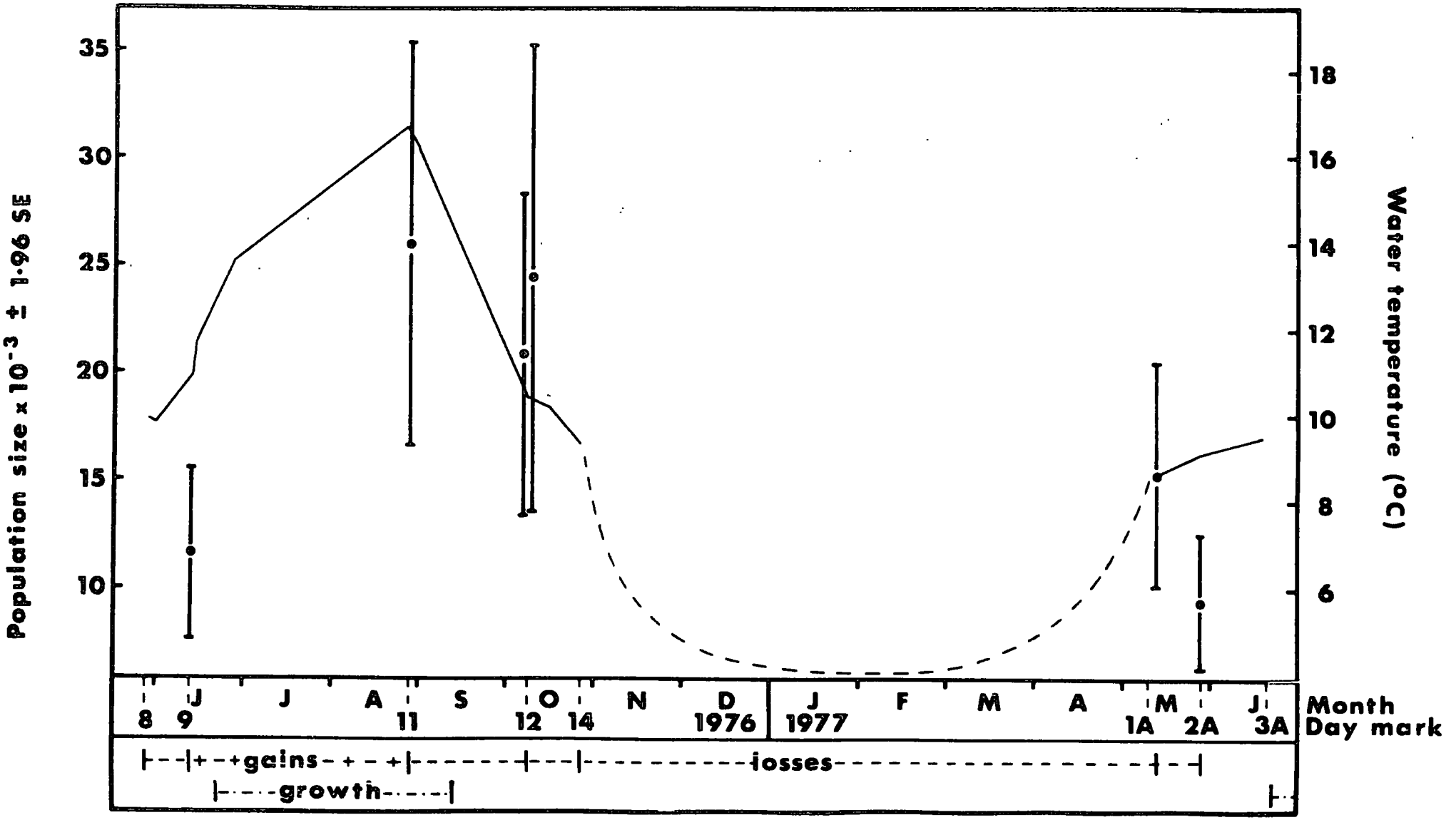
In other years trips were not frequent enough over the necessary periods to make any accurate observations. On the basis of this information the longest possible growth season was from 20th June to 13th September

– – – – - Significant mortality (Phi) amongst the total population and/or one or more of the sub-populations (Tables 5.6 a-d)

–+–+ - Significant recruitment (B) into the total population and several of the sub-populations (Tables 5.6 a-d)

——— - Water temperature (^{o}C)

— — - Water temperature was not recorded over-winter 1976-77. Seasonal variations in water temperature were similar from year to year (1.2.5, 3.3) and ranged from 3.4 - 5.0^{o}C between the end of November and the end of March 1974-75, 1975-76


Population size x 10⁻³ ± 1·96 SE
35
30
25
20
15
10
Water temperature (°C)
18
16
14
12
10
8
6
8
9
J
J
A
S
O
N
D
J
F
M
A
M
J
11
12
14
1976
1977
1A
2A
3A
Month
Day mark
gains
losses
growth

Eberhardt 1967, Flowerdew 1976; a comprehensive review, Seber 1973). Many of these reviews (especially that of Cormack 1973) were written specifically for biologists and thus avoided as much mathematical notation and statistical derivation as was possible, however they have all stressed the importance of the animals behaving in such a way that the underlying assumptions of the model were valid; as Cormack (1969) stated "In all cases every iota of information, both biological and statistical, must be gathered in order to check and counter-check the unavoidable assumptions." Despite this certain authors have shown no criticism of the models they have used or examined their data with respect to these assumptions (e.g. Manga 1972) and others have criticised the model for producing erroneous estimates when their data has plainly not satisfied the inherent assumptions (e.g. Eisenberg 1972). Violations of these assumptions can lead to considerable errors, particularly with respect to the conditions of equal catchability required by most models (e.g. Bishop & Bradley 1972, Emmel 1976, Ayre 1962, Seber 1973).

The methods used in this study for the collection, processing and return of the hand samples were such that, in all aspects over which any control could be exercised, these assumptions would not have been violated. The resulting mark-recapture data was analysed in several ways and these analyses produced a considerable amount of evidence to support the view that there were no significant deviations from the assumed behaviour of the animals

considered as the study population (i.e. all individuals $\geqslant$ 13 mm. C.L.); at least within the adult and juvenile sub-populations of each sex.

Another possible source of error in mark-recapture estimates may result from any bias intrinsic of whatever mathematical model has been used. This aspect of some of the available models has been investigated using the technique of computer simulation (Bishop & Sheppard 1973, Manly 1970, 1971, and Roff 1973a). The consensus of these studies has confirmed the advantages of estimating population size and recruitment using Jolly's open population model that have also been predicted on the grounds that it gives a more realistic representation of the natural situation (Emmel 1976, Southwood 1966); provided that sampling intensity was at least 10%. Sampling intensity in this study varied between 12.54 and 3.79% for the adult females, 11.15 and 3.38% for the adult males and 7.72 and 1.22% for the total juveniles. Thus most of the estimates of sub-population size and recruitment for the adult male and female sub-populations satisfied or fell slightly below this criterion and should therefore have been relatively free of any such bias and those for the juveniles somewhat more approximate. Bishop and Sheppard (1973) found that Jolly's model consistently overestimated survival rate and this may have accounted for the unexpectedly high value of this parameter during the 1976 growth season. An estimate made at an increased sampling intensity over the same period in the following year did however indicate significant mortality (Brewis unpubl.).

The formulae used to estimate the standard errors of the parameters which result from Jolly's model have also been criticised as they involve terms that are also used to obtain the parameter estimate itself. Hence the two are not independent; indeed Manly (1971) showed that the estimates of population size were positively correlated with their standard errors thus making underestimates seem more accurate than was actually the case.

The results of two recent studies have suggested that the models currently available are of rather limited use for determining population size (Roff 1973a, 1973b, Rose & Armentrout 1974); indeed this was considered intuitively obvious since as Cormack has pointed out "... the most general mathematical model is a plaything relative to the complexities of an animal population." Roff (1973a & b) has proposed that the coefficient of variation (SE N/N) should be less than 0.05 for population size estimates to have any meanings; the coefficient of variation never fell below 0.22 in this study and reached 0.69 for the juveniles on one occasion. The sampling intensity required to reduce the coefficient of variation to less than 0.05 has rarely been achieved in studies of invertebrate populations; high sampling intensities may not be possible due to purely practical reasons but may also destroy portions of the habitat and have such a profound influence on the population parameters that these do not represent the natural situation.

It was considered unduly pessimistic to dismiss these results because they did not meet this latter

criterion; indeed answers, the majority of which, met or were on the borderline of all but one of the criteria suggested by the computer simulation studies were better than no answers at all.

The size of the aqueduct population was estimated to have been always in the region of ca. 20,000 individuals during the summer months of 1974, 1975 and 1976, recruitment into the 0+ age class was not significantly different in 1975, 1976 and 1977 (3.4) and age structure was also similar in 1974 and 1975 (4.3.3). This lack of significant variation in biomass has been observed in unexploited populations of other crayfish species (Cukerzis 1974, Momot 1967, Momot & Gowing 1977 and Woodland 1967) and fish (Chapman 1971).

The variations in size of the aqueduct population observed between May 1976 and May 1977 were a result of losses due to death or emigration (mortality) and gains due to birth or immigration (recruitment). There was significant evidence of mortality at all times during this twelve month period, with the exception of the growth season. Cannibalism of recently moulted individuals was widely recognized as an important source of mortality in all crayfish species (e.g. Huxley 1896, Momot 1967, Woodland 1967). The remains of recently moulted A. pallipes which had been cannibalised were found in the aqueduct during the 1976 growth season, although the gaps between the sandstone blocks making up the walls of the aqueduct did provide numerous hides and it was widely acknowledged that cannibalism was less

likely when adequate cover was available; it was not therefore believed to have been an insignificant factor in the dynamics of the aqueduct population. A continuation of the present study into the 1977 growth season at an increased sampling intensity demonstrated significant mortality at this time (Brewis unpubl.); thus supporting the view that mortality was acting on the population all year round.

Several pieces of evidence showed that locomotor activity was strongly temperature dependent and emigration would thus have been expected to be important only during the warmer months. Momot (1967) observed "quite severe" overwinter mortality in all ages of both sexes in a population of O. virilis and yet concluded that population size was probably regulated by cannibalism and natural mortality at moulting, which occurred only between June and September! Huxley has observed that many crayfish were in "poor condition" early in the year and in the absence of any predators that could have had a significant effect it seemed probable that overwinter mortality had a physiological basis such as depleted energy reserves or low temperature stresses. Several of the A. pallipes hand collected between September and March had vegetable matter in the gut (3.5) and it would seem therefore that they feed, at least sporadically, over the winter months as has been observed in other species (e.g. Capelli 1975, Flint 1975). There was a considerable decrease in the amount of F. antipyretica in the aqueduct during the winter months and assuming this was the major food item

for this population this would support the above explanation. Also the second largest population estimate was obtained after the growth season in October (ca. 21,000) and this high density (8.5/m^2) would have resulted in increased competition for a decreasing food supply; Dye and Jones (1974) report lowered survival of juvenile O. virilis at higher densities which they attribute to reduced food availability.

As immigration was believed to have been insignificant (1.1, 3.6.1) the substantial recruitment during the growth season must have been largely a result of animals < 13 mm. C.L. moulting and increasing the size of the juvenile population and juveniles growing and increaseing the size of the adult populations. Similar life cycles have been reported by Woodland (1967) for C. albidus and Flint (1975) for P. leniusculus, and many others. All crayfish are relatively long lived and the majority breed only once a year and would thus have been predicted to have a simple, slow univoltine seasonal cycle of abundance (Hynes 1972). Environmental conditions peculiar to some populations may modify this situation as with the massive mortalities in Lake Tahoe caused by storms in the summer and early autumn (Flint 1975).

Seasonal cycles of this type are not restricted to the Astacidae and an analogous situation has been reported for the Western Rock Lobster, Panulirus cygnus, where recruitment to the main population occurs only during a specific period when younger "white" lobsters migrate from shallower water, population size then

gradually falls due to death and emigration until the next annual period of recruitment (Morgan 1974).

CHAPTER 6

A methodological investigation of trapping as a sampling technique for A. pallipes in the aqueduct

6.1 Introduction

The majority of populations of freshwater crayfish are not as accessible to direct sampling by hand collection as A. pallipes is in the aqueduct. In some lakes where the water is clear and macrophytes are not abundant direct quantitative sampling is possible using SCUBA equipment (e.g. Abrahamsson & Goldman 1970, Flint 1975), hand collection is also sometimes possible in lake or river shallows without special equipment. Seine and dip netting have also been used (5.1) but these are not possible in many cases due to snags and weed growth. However, watercourses where extensive direct collections can be made are rare.

The only crayfish sampling method which is universally applicable is the use of funnel traps (Capelli 1975). Indeed many studies of the population dynamics of freshwater crayfish have used trapping as one of the sampling methods and in some cases the only one (e.g. Abrahamsson 1971b, Abrahamsson & Goldman 1970, Cukerzis 1959, Flint 1975, Mason 1974, Momot 1967, 1977, Tack 1941, Watson unpubl., Woodland 1967).

Trapping was carried out in the aqueduct from June 1975 to October 1976 for several reasons:-

(i) Several mark-recapture estimates from hand collected samples were available over this period and these were considered to be reliable (5.5). A direct comparison between estimates using either method was therefore possible.

(ii) The use of two independent sampling methods in a Lincoln index type mark-recapture estimate gives an estimate which is independent of any bias inherent of either sampling method, providing the sources of any such bias in the two methods were unrelated (Junge 1963, Seber 1973).

(iii) The composition of the continuously trapped samples, the frequency of the multiple recaptures and the positions in the aqueduct at which these recaptures were taken provided data on the responses of crayfish to the traps with respect to size, sex and recapture status.

(iv) The number of times the water level could be lowered each year was limited (5.1) and the continuous trapping records provided more complete information on growth and life history (Chapters 3 & 4) than was available solely from the hand collections.

6.2 General methods

6.2.1 Trap construction

Thirty-three traps were constructed of cylindrical, opaque plastic-ducting with detachable funnel entrances

fitted to both ends. Each trap was weighted with two house bricks to ensure they held bottom in the current (section 1.1).

6.2.2 Trap placement

Traps were spaced at four section (24m) intervals along the aqueduct (Fig. 1.1). The highest trap position was section 134 and the lowest position was section 6; it was not possible to set traps below this point due to the increased strength of the current (Plate 1.2b). Within the stone lined section of the aqueduct traps were reset one section upstream of their original position on each occasion. Following a setting in section 121 at the sluice gates that trap would complete the cycle of rotation and be reset in section 6; and so on. The four traps in the concrete lined stretch above the sluice gates were outside the area containing most of the study population (3.6.1) and were not moved.

The traps in the stone lined section were moved to ensure that all animals were equally exposed to trap-capture. Moving the traps in this cyclical fashion also avoided any possible effects due to the small differences in dimensions of some of the traps which may have led to a sequence of spurious catches from any one position.

6.2.3 Processing trapped animals

Details of the marking technique used to apply individual numbers to the carapace and abdominal tergites, measurements taken and other characteristics recorded

during the processing are described in Chapter 2. After processing, the contents of each trap were released in the aqueduct one section above the section from which they had been trapped to allow them to find bottom with the current in the latter section. Observations when conditions were favourable (direct sunlight, unbroken water surface) indicated that this was successful.

6.2.4 Variations in the trapping method

The traps were emptied, moved and reset at approximately fortnightly intervals from June 1975 to October 1976. During this time there were three distinct types of trap sample:-

(i) It was originally supposed that the traps would provide samples of one hundred or more crayfish by providing an artificial hide. This was, however, shown not to be the case (Appendix, Table 6.1), but several of the initial trappings did fall into the category where the traps had not been baited and the water level had not been lowered between setting and emptying (category n.b. ↘ '75).

(ii) In both 1975 and 1976 the water level was lowered several times and sizeable trap samples were always taken following these occasions (Appendix, Table 6.1). These trappings were in the category n.b. ↓ '75, '76 where the traps had not been baited and the water level had been lowered between setting and emptying.

Table 6.1: The size, structure & associated parameters of the trapped samples 1975, 76

Sample category	Number of samples	Mean no. days* ± SE	Mean sex ratio ♀♀:♂♂ ± SE	Mean A:J ratio ± SE	Mean sample size ± SE
n.b. ↯ '75	5	4.80 ± 0.80	0.65 ± 0.07	7.94 ± 2.02	47.00 ± 9.44
n.b. ↓ '75	6	5.50 ± 1.67	0.56 ± 0.10	9.64 ± 4.17	67.50 ± 14.09
b. ↯ '75,'76	15	12.60 ± 1.80	0.27 ± 0.05	85.87 ± 21.09**	124.53 ± 8.01
n.b. ↓ '76	4	4.25 ± 1.03	0.58 ± 0.07	58.08 ± 20.64	196.75 ± 15.32

b. = traps baited (n.b. = not b.), ↓ = water level lowered between setting & emptying (↯ = not)

* Mean no. days ± SE - either:- n.b. ↯ 75, b. ↯ 75, 76 no. days since traps set

n.b. ↓ 75, 76 no. days since water level lowered

** No. samples = 5, in remaining 10 samples A:J ratio =

(iii) As the water level could only be lowered with the permission of Newcastle and Gateshead Water Company Ltd., and since it was not always possible for the Company to grant this permission (5.1), another means of increasing sample size was required. A considerable increase was achieved by baiting the traps with approximately 40 gms of fresh ox-liver, which has been shown to be one of the most effective baits for this species (Moriarty 1972). These trappings were thus in the category where the traps had been baited and the water level had not been lowered between setting and emptying (b. ↓ '75, '76).

The fourth possible permutation involving baiting and adjustments to the water level was not carried out as acceptable sample sizes could be predicted when it was planned to lower the water level.

6.3 Results

6.3.1 The size and structure of the trapped samples

The full details of the composition of all samples are listed in Appendix 1. The parameters relevant to the assessment of trapping as a sampling technique are shown on Table 6.1:-

(i) The mean sex ratio (♀♀:♂♂) in all sample categories was significantly less than unity ($p < 0.01$ in all cases). The overall mean sex ratio in the trapped samples was 0.44 ± 0.05; therefore the traps caught more than twice as many males as females.

(ii) The mean A:J ratio in all sample categories showed that traps caught many more adults than juveniles

(adult males > 22 mm.C.L, adult females > 25 mm.C.L., 3.4). The overall mean A:J ratio in all the trapped samples which caught any juveniles at all (ten of the baited trap samples caught no juveniles) was 37.96 ± 9.63.

(iii) The sample size in the n.b. ↓ '75 category was significantly greater than that in the n.b. ↓↓ '75 category (Appendix 1, excluding the largest sample from the n.b. ↓ '75 category to form a 5 x 2 c.t., 4 d.f., χ^2 = 16.99, $p < 0.001$). The mean sample size in the baited traps was significantly greater than that in the n.b. ↓ '75 category ($t = 3.46$, $p < 0.01$) and the mean catch in the n.b. ↓ '76 category was significantly greater than that in the baited traps ($t = 4.18$, $p < 0.001$). There was thus a significant trend of increasing sample size in each category:- n.b. ↓↓ '75 < n.b. ↓ '75 < b. ↓↓ '75,'76 < n.b. ↓ '76.

These observations led to the following conclusions:-

The considerable excess of adults in the trapped samples and the twofold excess of males amongst the adults strongly suggests that the probability of entering a trap is dependent on the position of the individual in any dominance order that may have existed. Such an order has been demonstrated by Bovbjerg (1956) for Procambarus alleni:- amongst adults, males were dominant to females of similar size, adults were dominant to juveniles and there was no sexual dominance amongst the juveniles. It thus seems likely that the lowest numbers of juveniles

having been recorded from samples in the n.b. ↓ '76 and b. ↓ '75,'76 groups reflected the more intense behavioural interactions that would have been expected in the larger samples.

The fact that the samples from the unbaited traps in 1976 were the largest was probably due to the considerable disturbance caused to the aqueduct population by lowering the water level and collecting around one thousand crayfish (5.4.2) whilst the traps were in the aqueduct.

This did not necessarily invalidate trapping as a sampling method in mark-recapture studies as the size of those sub-populations which were sampled in representative numbers can be estimated provided the inherent assumptions (5.1) are satisfied <u>within</u> each resulting sub-population (Junge 1963, Seber 1973). As it seemed very likely that the probability of trap capture was dependent on the status of the individual in a dominance order and since this status depended on such factors as sex, body size and cheliped length in many crayfish species (6.4) the prospect of obtaining reliable estimates by considering adult males and females separately seemed poor. Any such bias could not be avoided by further subdivision into size classes as there were not enough recaptures (6.3.4).

6.3.2 Trap entry and escape

Some indirect evidence for behavioural interactions having influenced sample size and structure (as proposed

in 6.3.1) was obtained from two analyses of the trapping data with respect to trap entry and escape.

(a) The number of days traps were left in the aqueduct was varied (n.b. ↘ '75), as was the period for which the water level was left lowered and the number of days the traps were in the aqueduct before and after this (n.b. ↓ '75, '76, Appendix 1). The correlation between these parameters and sample size was investigated as follows:-

(i) There was a significant positive correlation between sample size and the number of days the traps had been in the aqueduct for the n.b. ↘ '75 group of samples (Fig. 6.1, $r = 0.8934$, $t = 3.44$, $p < 0.05$).

(ii) A significant negative correlation existed between sample size and the number of days since the water level had been lowered before the traps were emptied for the n.b. ↓ '75 group of samples (Fig. 6.2, $r = -0.9266$, $t = 4.93$, $p < 0.01$). There was no significant correlation between these two parameters for the n.b. ↓ '76 group of samples.

(iii) The period for which the water level was lowered varied from one to five hours; this did not, however, have any significant correlation with sample size in any category.

(b) Five traps were used to investigate trap entry and escape as follows:-

(i) All traps were baited and set on 25. 4.76.

(ii) All traps were emptied on 18. 5.76 and the contents of five traps with fairly large catches were

Fig. 6.1: Total sample sizes from non-baited traps when the water level was not lowered between setting and emptying in 1975 (n.b. ↓ 75) as a function of the number of days the traps were in the aqueduct

$y = 10.55x - 3.62$ ($n = 5$)

SE slope = 3.06

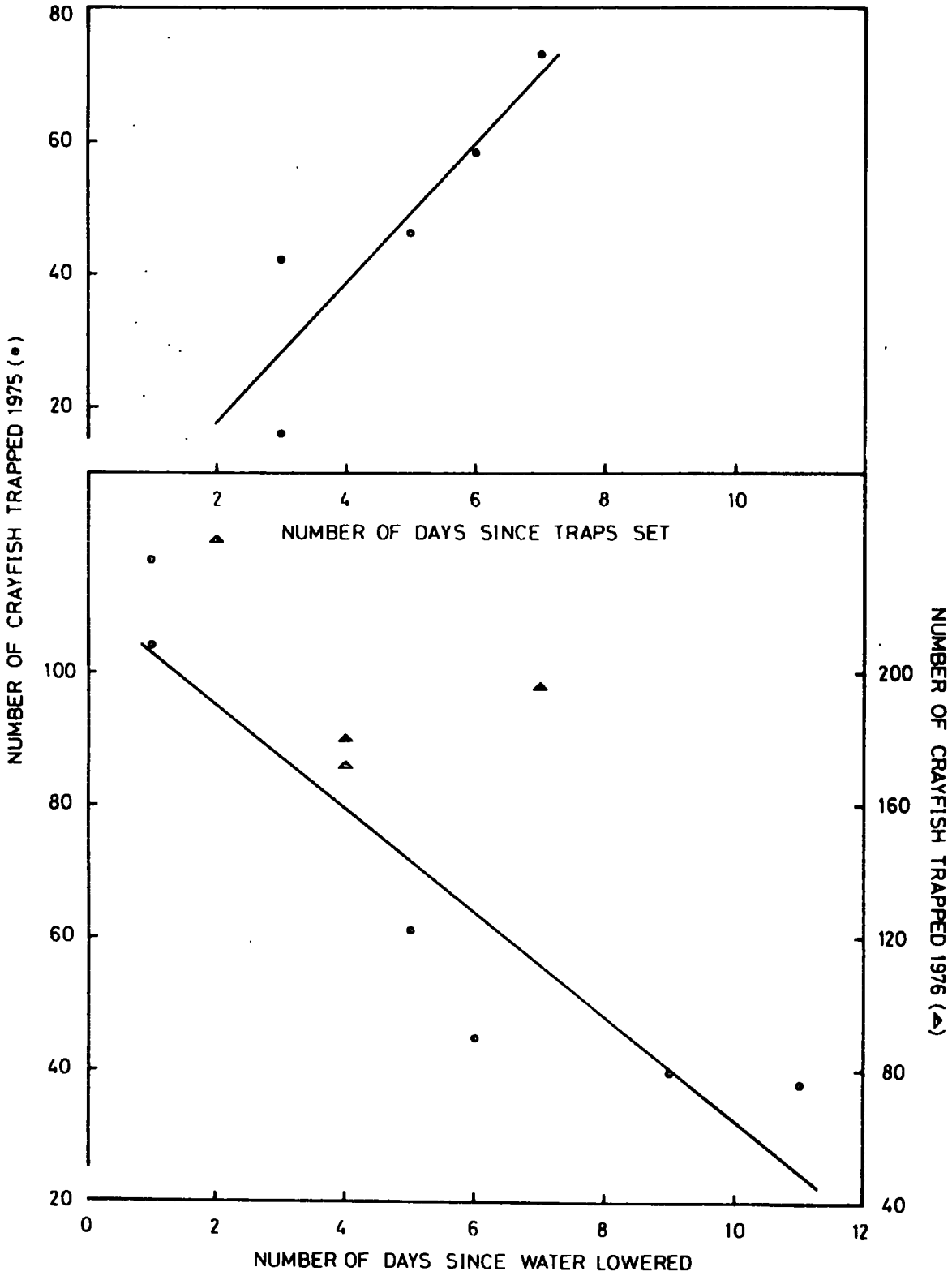
$r = 0.89$, $t = 3.44$, $p < 0.05$

Fig. 6.2: Total sample sizes from non-baited traps when the water level was lowered between setting and emptying in 1975 (●) and 1976 (▲) (n.b. ↓ 75, 76) as a function of the number of days traps were in the aqueduct following the restoration of the normal water level. The regression line was fitted to the 1975 (●) data only:-

$y = -7.83x + 110.54$ ($n = 6$)

SE slope = 1.59

$r = -0.93$, $t = 4.93$, $p < 0.01$


NUMBER OF CRAYFISH TRAPPED 1975 (●)
NUMBER OF CRAYFISH TRAPPED 1976 (▲)
NUMBER OF DAYS SINCE TRAPS SET
NUMBER OF DAYS SINCE WATER LOWERED
80
60
40
20
100
80
60
40
20
200
160
120
80
40
0
2
4
6
8
10
12

marked, measured and returned to the same traps. The traps were not rebaited.

(iii) It was incidental to this experiment that the water level was lowered on 26. 5.76.

(iv) All traps were emptied on 30. 5.76.

The results obtained from the five experimental traps re listed in Table 6.2. The contents of all the traps were predominantly male (mean 79%, 18. 5.76; 66%, 30. 5.76) but as the sexes appeared to behave similarly with respect to trap entry and escape the data w pooled.

These results clearly showed that both trap entry and escape were important in determining sample size in this experiment. Of the 38 individuals returned to the traps on 18. 5.76, 20 escaped (53%) and of the 44 individuals removed from the traps on 30. 5.76, 26 were new entries since 18. 5.76 (59%). There was, however, an unknown factor during this experiment; namely how many individuals did the traps contain immediately after the water level had been lowered on 26. 5.76. It was known that lowering the water level caused the traps to catch relatively large samples (6.3.1). Since the traps were not baited on 18. 5.76 and non-baited traps catch relatively few individuals (6.3.1) it was reasonable to conclude that most of the trap entry had occurred during or soon after the period for which the water level had been lowered. It was therefore possible that these results do not reflect the normal incidence of trap

Table 6.2: Trap entry and escape (For details see text 6.3.2)

Trap	1		2		3		4		5	
	No.	Mean C.L. ± SE	No.	Mean C.L. ± SE	No.	Mean C.L. ± SE	No.	Mean C.L. ± SE	No.	Mean C.L. ± SE
Total contents 18.5.76 (a)	8	37.4 ± 1.54	12	34.38 ± 1.12	5	34.54 ± 0.95	9	35.52 ± 1.03	4	35.85 ± 1.42
Total contents 30.5.76 (b)	5	36.08 ± 2.36	10	31.16 ± 1.69	14	31.52 ± 1.01	7	38.83 ± 1.52	8	32.75 ± 1.11
Present since 18.5.76 (c)	5	36.66 ± 1.00	2	35.05 ± 1.15	3	36.80 ± 0.20	6	36.59 ± 0.65	2	37.15 ± 2.75
New entries since 18.5.76 (d)	0		8	30.06 ± 1.84	11	30.60 ± 0.96	1	39.8	6	33.17 ± 1.46
Escapes since 18.5.76 (e)	3	38.63 ± 3.53	10	34.25 ± 1.34	2	33.65 ± 0.55	3	33.03 ± 2.69	2	34.55 ± 1.05

entry and particularly of trap escape as it may have been that escape was only a common occurrence when the traps were full i.e. soon after the water level was restored to normal. Indeed it is common practice in some countries to lift traps the same night that they are set in order to secure optimum catches before escapes can lead to appreciable losses (Lindqvist, pers. comm.).

The mean carapace lengths (C.L. $\pm$ S.E. mm.) of each group of individuals which made up the five components (a) - (e) of each trap contents during the experiment (Table 6.2) did not differ significantly from each other for traps 1, 2, 4 and 5. There was, however, some evidence from Trap 3 that smaller individuals had a greater probability of escape in these circumstances (mean C.L. $\pm$ SE; individuals present since 18. 5.76 36.80 $\pm$ 0.20, escapees between 18. 5.76 and 30. 5.76 33.65 $\pm$ 0.55; difference, $t = 5.38$, 3 d.f., $p < 0.02$). Due to the construction of the traps (6.2.1) and the fact that the diameter of the entrances at the end of the funnels was ca. 35mm. it would be expected that the physical constraints placed on larger individuals would be greater even in relatively full traps. Also in Trap 3, those individuals that were caught in baited traps previous to 18. 5.76, were returned to the same traps without bait on 18. 5.76 and remained in those traps until 30. 5.76 were significantly larger than new entries over that period (mean C.L. $\pm$ SE; individuals present since 18. 5.76 36.80 $\pm$ 0.20 new entries between 18. 5.76 and 30. 5.76 30.60 $\pm$ 0.96; difference, $t = 6.32$, 12 d.f.,

$p < 0.001$). This may have been attributable to two factors; that some of the individuals caught in the baited traps were too large to escape and/or that the new entries, although on average smaller, were so much more numerous following the lowering of the water level on 26. 5.76 that only a proportion had escaped by 30. 5.76.

The following conclusions were drawn from the previous analyses:-

Non-baited traps were shown to catch larger samples the longer they were left in the aqueduct (Fig. 6.1). This implied that the probability of trap entry was greater than that of trap escape up to the maximum time period for which the traps were left. There must obviously have been a point in time at which sample size ceased to increase; this point would have arisen when no more new entries could occur or entry and escape were in equilibrium. Further evidence for this gradual growth in sample size for n.b.↓ '75 samples came from two 24 hour trapping sessions on 15-16. 8.75 and 18-19. 8.75. Fourteen traps were emptied at 4 hourly intervals on each occasion and mean total catches per 4 hours were 4.29 and 4.33 respectively.

Lowering the water level whilst non-baited traps were in the aqueduct produced large samples provided the traps were emptied soon after the water level was restored to normal (Fig. 6.2). This was further evidence that the probability of trap escape increased with sample size (cf. Table 6.2). As sample size decreased trap

escape would have become less important and eventually equal to trap entry when some residual catch would have been expected to remain.

6.3.3 The variations in the number of crayfish trapped in different stretches of the aqueduct

Several conclusions concerning the distribution of the crayfish population along the aqueduct have already been drawn from the hand collected samples (5.4.3). A comparison of the distribution of the trapped and hand collected samples was therefore made to identify any variations in trappability along the aqueduct. As trap catches were returned to the section they were caught from any such variations would introduce a bias into any mark-recapture estimates made from the trapping data.

The twenty-nine traps set within the stone and brick lined sections of the aqueduct (Chapter 1) were moved after each catch in an attempt to expose all individuals to traps and to avoid any effects due to the small differences which existed in the dimensions of the traps (6.2.1). These traps were placed in every fourth six metre section (Fig. 1.1) starting not lower than Section 6 and ending not higher than Section 121 on each occasion; movement of each trap was one section upstream after each setting with the exception that a setting in section 121 was followed by a setting in Section 6 to complete the cycle (6.2.2). This manner of trap placement resulted in several of the thirty trapped samples having been taken from each six metre section of the aqueduct.

The following results were obtained:-

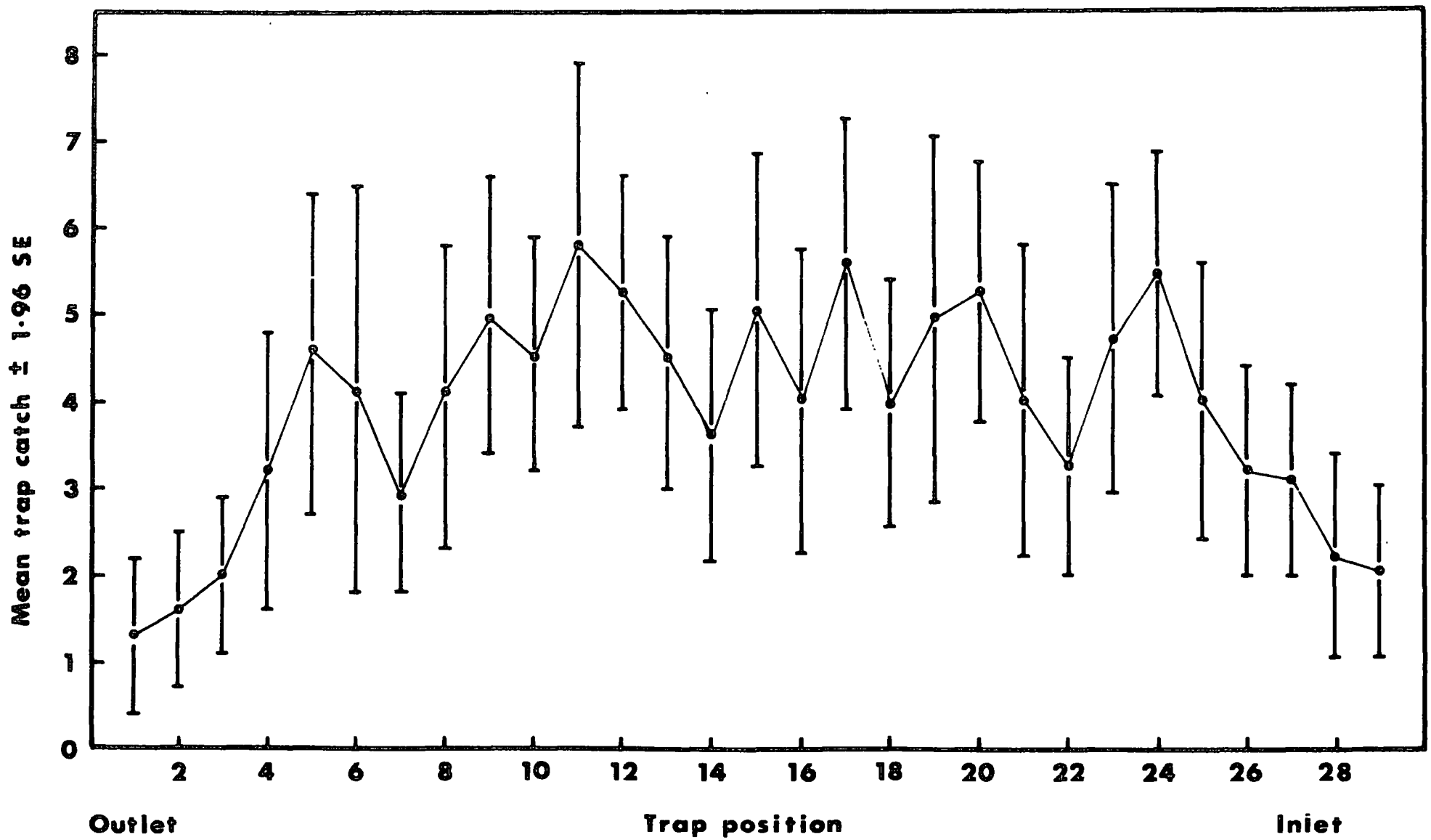
(i) There was no reason to suspect any variation in effectiveness between the twenty-nine traps as none produced catches that were consistently smaller or larger than the mean catch.

(ii) On each sampling occasions there was a trap set in all 29 of the 24 metre stretches ($\equiv 4$ sections) of aqueduct starting from section 6. Considering each 24 metre stretch as a trap position for all thirty trapped samples and the mean catch $\pm$ 2SE from each position produced Fig. 6.3. Mean catches from trap positions 1-3, 28 and 29 were significantly lower than several of the mean catches at intermediate positions ($p < 0.05$). There was considerable variation in mean catch from trap positions 4 to 27 but none of these were shown to have been significant.

The substratum, construction of the stone block walls, associated flora and current speed all showed little obvious variations from trap position 4 to trap position 24. Below trap position 4 there was a progressive increase in current speed due to the gradually increasing incline, which culminated in the torrential outflow into the East pond (Plate 1.2b). Above trap position 24 the walls of the aqueduct were constructed of brick and there were far fewer potential hides than in the stone lined section (1.1).

There were three possible reasons for the lower mean catches below section 20:-

Fig. 6.3: Mean trap catch ± 1.96 SE as a function of trap position. Twenty-nine traps were spaced out at 24 m. intervals along the aqueduct and moved 6 m. upstream after each setting (see section 6.6.2)


Mean trap catch ± 1·96 SE
0
1
2
3
4
5
6
7
8
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Outlet
Trap position
Inlet

In the case of the baited traps it was clear that the major reason for trap entry was the ox-liver bait (3.5, 3.6.3, 6.3.1). Chemoreception has been shown to play an important role in decapod feeding behaviour (Mackie and Shelton 1972) and it may have been that the increased current speed in the lower sections reduced the concentration of attractants from the bait and thus lowered baited trap efficiency.

In the case of the non-baited traps taken when the water level had been lowered between setting and emptying the smaller catches in the lower sections may have been due to a temporary low density in these sections caused by some individuals showing a positive rheotactic response during or soon after the drop in water level.

The smaller catches may, of course, reflect a real and permanent lower crayfish density in these sections. The evidence available from the hand samples did, however, suggest that this was not the case.

The lower mean trap catches in the two highest trap positions were almost certainly due to a lower crayfish density in the brick lined sections of the aqueduct resulting from the low numbers of suitable hides. The evidence available from the hand samples confirmed this observation (5.4.3). Such an area of low density must have further delimited the aqueduct population; thus increasing the likelihood that immigration along the concrete lined stretches leading from the source and feeding the West pond was negligible (3.6.1).

There was therefore some evidence to suggest that crayfish may have been less trappable in the lower trap positions and this was a possible source of bias to any mark-recapture estimate involving trap catches.

6.3.4 Seasonal variations in the proportion of females in the trapped samples

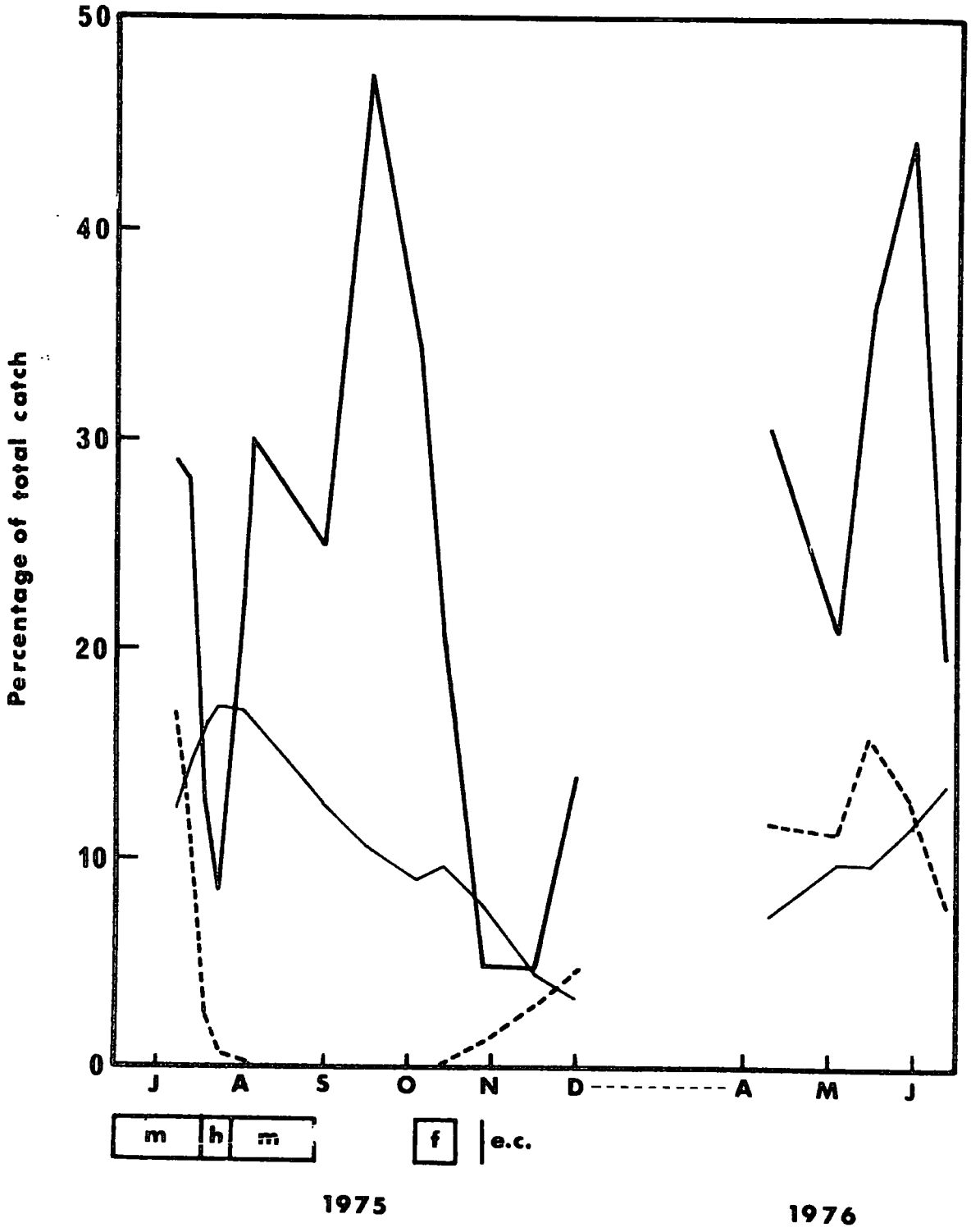
In a study where it is intended to estimate population parameters by mark and recapture methods over a prolonged period all groups within the population must be captured in adequate numbers (Robson & Regier 1964) throughout the study period for the estimates to have any validity. Trapping was not a suitable sampling method for such a study as not only were very few juveniles trapped (6.3.1) but females represented less than 10% of the total catch (usually < 15 individuals) at some times of year (Appendix 1, Fig. 6.4).

The seasonal variations in the proportion of females and egg-bearing females in the trapped samples is shown on Fig. 6.4. With the exception of one trapping occasion in 1976 the only period during which the sex ratio approached unity in the trapped samples was when no females were carrying eggs; that is after hatching in early August and before fertilization in October. There was a marked decrease in the proportion of both total females and berried females prior to hatching and of total females following fertilization. The proportion of females increased following the completion of egg-laying but did not usually approach 50%.

The fact that these variations in the proportion of

Fig. 6.4: Catch composition for trap samples 1975-76

m	= moulting season
h	= hatching of young
f	= fertilization of females
e.c.	= completion of egg-laying
————	= % females in total catch
— — — —	= % berried females in total catch
————	= water temperature in °C on same scale as above


50
40
30
20
10
0
Percentage of total catch
J
A
S
O
N
D
A
M
J
m
h
m
f
e.c.
1975
1976

females in the trapped samples coincided with several stages in the reproductive cycle suggested that there may have been a change in the behaviour of females in response to the traps and/or any crayfish within them.

Such behaviour would have the obvious survival values of limiting cannibalism of the young before they became independent of the mother and ensuring that the female was not disturbed whilst spawning, thus reducing the chances of egg-loss at this stage. The period when disturbance is most likely to lead to egg loss is when the eggs have been extruded and are suspended in the glair but are not yet attached to the pleopods (Ingle & Thomas 1974). Laboratory observations have indicated that fertilized females were only able to spawn and attach the eggs to the pleopods successfully when isolated and left undisturbed. If females were secretive at this stage in the aqueduct this would account for the low numbers trapped from the time of fertilization until the completion of egg-laying.

6.3.5 Mark-recapture analysis of the trapping data

The application of any of the mark-recapture models can only produce valid estimates of population parameters when certain assumptions hold; these assumptions have already been discussed (5.1). Several are quite 'strong' assumptions and mark-recapture methods are thus not generally considered to be particularly 'robust' to departures from these assumptions (with the exception of regression methods for 'closed' populations, Hayne

1949, Marten 1970, Schumacher and Eschmeyer 1943, Seber 1973). Hence, although several of the models now available are quite sophisticated departures from the basic assumptions can still lead to considerable errors; indeed care must be taken when applying all models since as Cormack (1969) has pointed out "an approximately right answer is always preferred to a highly precise but wrong answer".

The marking technique used has been shown not to affect survival and to be a reliable means of recognition over two growth seasons (2.3, 5.1, 5.4.4). The accuracy of any mark-recapture estimations was therefore dependent on the behavioural responses of all individuals in the population, with respect to the sampling technique, meeting a number of requirements. Of these requirements the one concerning equal catchability of all individuals irrespective of size, sex and mark-status is crucial to this method of estimation (Bishop & Bradley 1972, Emmel 1976, Seber 1973).

Of all the methods available for sampling crayfish populations (5.1) only trapping and hand-sampling were possible in the aqueduct. These methods were employed concurrently in an attempt to obtain independent estimates or, failing this, unbiased estimates using one method for capture and marking and the other for recapture (Junge 1963).

It was clear that the animals themselves must have played a considerably more active role in their own trap capture than in their capture by hand. Behavioural

responses to the sampling method were thus expected to have been a more important influence on the composition of the trapped samples. All behavioural responses can classified as learned or innate and, since decapods have been shown to have a limited capacity for learned responses, both may have been important in trap behaviour (Schöne 1961). When learned and innate behavioural variations in response to the sampling method have both been suspected it has often been found difficult to distinguish their effects on sample composition (Carothers 1971, Seber 1973).

The terms trap addiction and trap avoidance were defined as learned behavioural tendencies, as both terms imply trap experience; trap proneness and trap shyness were defined as innate responses.

(i) Leslie's test for random sampling of marked individuals

A test which compares the actual and expected frequences of a series of recaptures of individuals known to have been alive throughout the sampling period has been devised by Leslie (1958). The test can detect departures from the assumption of equal catchability but does not distinguish between innate and learned unequal catchability (Cormack 1966).

Leslie (1958) suggested that the number of individuals known to be alive throughout the sampling period should be greater than twenty and the number of occasions on which recapture was possible at least three. Of the 529 adult individuals marked during the trapping session

when the traps were baited and emptied continually for 24 hours on 15-16. 8.75, 21 were recaptured on 30.11.75. Between these dates there were six trapping occasions when recapture was possible. The recapture frequencies were listed and the test statistics calculated on Table 6.3. The calculated value of χ^2 was 62.16 and thus the hypotheses of random recapture was disproven ($p < 0.001$).

It was not possible to test whether the assumption of random recapture held for the adult male and female sub-populations as there were no cases where more than twenty individuals from either group were known to have been alive during three recapture occasions.

(ii) Unequal catchability due to learned and/or innate behavioural responses

The fact that any breakdown of the assumption of random recapture may have been due to innate and/or learned unequal catchability has been stressed by Cormack (1966, 1969). Application of the test of Leslie (1958) has demonstrated that the hypotheses of random recapture of marked individuals was disproven for trapped samples when all adults were considered. This non-randomness may, therefore, have been due entirely to the trap proneness of the adult males (6.3.1) but learned behavioural responses (trap addiction and trap avoidance) may also have contributed. There is no generally applicable test which can distinguish between learned and innate responses when both are suspected to have been important (Carothers 1971).

When an estimate of population size by a reliable

Table 6.3: Leslie's test for random recapture of marked individuals

Recapture occasion	No. recaptured at each i	No. recaptures of each individual	Frequency of recapture
i	n_i	x	f(x)
18. 8.75	3	0	13
13. 9.	7	1	4
1.10.	2	2	1
17.10.	2	3	1
28.10.	1	4	1
12.11.	3	5	1
Total	18	Total	21

Sum of squares = 42.57

Expected variance = 0.68

$\chi^2 = 62.16$

20 degrees of freedom

$p < 0.001$

sampling method exists departures from the assumption of random recapture in another sampling method can easily be tested by comparing the observed number of recaptures to the number expected, as predicted from sampling intensity. Several estimates of the size of this population were obtained in the years 1975-77 by hand collection and these were believed to have been reliable (5.4.5). Further evidence for this was obtained by an analysis of animals in hand samples that were recaptured in the repeated trappings of 15-16. 8.75 (Table 6.4). There were no significant differences between the estimates made by the two methods on comparable dates and those from the trap recaptures of hand collected crayfish should have been relatively free from any sampling bias (Junge 1963, Seber 1973).

During the period when the twenty-one largest trap samples were taken (20. 7.75 - 15.10.76) nine reliable estimates of the total adult sub-population (mean 9743 - 2407, range 18054 - 5265), six estimates of the adult male sub-population (mean 4563 ± 1268, range 7854 - 2392) and six estimates of the adult female sub-population (mean 5260 - 1320, range 11412 - 2865) were made (5.4.5, Table 6.4). These estimates were used in a method devised from first principles to calculate the approximate number of multiple captures expected, on the basis of random recapture of marked individuals, between the twenty-one largest trap samples by making four assumptions:-

(a) All members of the adult male sub-population were assumed to have been equally trappable. All members

Table 6.4: A comparison of mark-recapture estimates from paired hand collections and from hand collection and trap recapture

	Mark-recapture estimates			
	Hand collected, hand recaptured		Hand collected, trap recaptured	
Sub-population	Dates of collections	Estimate ± SE	Dates of collections	Estimate ± SE
Total Adults	25.6.-1.7.75	6,455 ± 2,069	25.6.-16.8.75	6,806 ± 1,664
	1.7.-7.7.75	11,766 ± 3,473	1.7.-16.8.75	6,923 ± 1,357
			7.7.-16.8.75	5,265 ± 1,068
Adult Males	25.6.-1.7.75	4,532 ± 2,198	25.6.-16.8.75	3,496 ± 939
	1.7.-7.7.75	4,258 ± 1,397	1.7.-16.8.75	3,080 ± 646
			7.7.-16.8.75	2,392 ± 506

of the adult female sub-population were also assumed to have been equally trappable.

(b) There was assumed to have been no mortality, emigration or recruitment occurring in either of the above two aqueduct sub-populations throughout the trapping period under consideration. This was known not to be the case in the aqueduct (1.1, 3.6.1, 5.4.5) but none of these factors could have increased the probability of multiple capture and could not therefore have contributed to any underestimation of population numbers; which is the usual result of non-random responses to the sampling equipment (Bohlin & Sundström 1977, Ricker 1958).

(c) Mean sub-sample sizes for the twenty-one largest trapped samples were calculated as 96.58 ± 19.13 adult males and 43.05 ± 8.36 adult females. It was assumed that all sub-samples were 120 adult males and 50 adult females. As most of the adult male sub-samples were less than 120 individuals (15 out of 21) and most of the adult female sub-samples were less than 50 individuals (14 out of 21) this assumption must have overestimated the expected number of recaptures.

Assumption (b) and the fact that the assumed sub-sample sizes were set this much higher than the mean sub-sample size ensured that the expected number of recaptures was too high. Therefore any variations in trappability which resulted in more recaptures being observed than the calculated expected value (the usual result of sampling bias, see (b)) must have been real.

(d) The adult male and female sub-populations were both assumed to have numbered 5,000 individuals throughout the trapping period under consideration. Although, the numbers of each sub-populations were known to have varied on either side of this figure during the trapping period such variations must, to a large extent, have cancelled each other out in terms of their effects on the expected frequencies of multiple captures.

Defining n_i = size of the ith sub-sample

m_{ij} = numbers of recaptures from the ith sample in the jth sample

N = constant population size

Then if N and n_i are always known the expected frequencies of multiple capture from any one sample (m_{ij}) are easily calculated:-

$m_{12} = n_1 n_2/N$ = double capture from sample one

$m_{13} = m_{12} n_3/N$ = treble capture from sample one

$m_{14} = m_{13} n_4/N$ = quadruple capture from sample one

In order to estimate the total expected frequencies of multiple capture in a twenty-one sample sequence where n_i was assumed constant the number of combinations of the twenty-one samples where each capture frequency could have occurred must be calculated e.g.:-

Defining (20) = (20+19+18+ ..... +1)

(19) = (19+18+17+ ..... +1)

(a) The number of sample combinations in a twenty-one sample sequence where double captures (single recaptures) could have occurred must equal (20) = 210:-

i.e. Individuals from sample 1 were recaptured in samples 2-21 = 20 combinations

Individuals from sample 2 were recaptured in samples 3-21 = 19 combinations etc.

Finally individuals from sample 20 were recaptured in sample 21 = 1 combination

The total of all combinations = (20) = 210.

(b) The number of sample combinations in a twenty-one sample sequence where triple captures (double recaptures) could have occurred must equal (19) + (18) + (17) ... + (1) = 1,330 from similar reasoning to that stated in (a).

By continuing to summate successive lists of cumulative totals it was possible to estimate the number of sample combinations where all recapture frequencies could have occurred.

Thus the expected frequency of double capture over a twenty-one sample sequence where n_i and N are known constants = m_{12} x 210. Similarly, the expected frequencies of triple capture = m_{13} x 1,330 etc.

However, when analysing data for the observed frequencies of multiple capture it seemed logical and was more meaningful to consider an individual that had been caught, say five times, as only a quintuple capture and not also 3 quadruple captures, 6 treble captures and 10 double captures; which it must also have been if all sample combinations were considered. The observed multiple capture frequencies were thus recorded only as the largest number of times captured for each individual

and the expected values had to be adjusted to fit this convention. This was because all sample combinations were considered in the estimation of the expected values and every sample from number one to number twenty-one was assumed to consist of n_i unmarked individuals which had not previously been captured. The expected values were adjusted to meet the above convention by subtracting, say for every individual expected to have been caught five times, three from the expected quadruple recapture frequency, six from the expected triple recapture frequency and ten from the expected double recapture frequency. This procedure was applied to all expected multiple capture frequencies in ascending numerical order.

The observed and expected multiple capture frequencies for the adult male sub-population were compared on Table 6.5. The number of individuals caught twice was close to the number expected (Obs/Exp = 0.92). At higher capture frequencies there were significantly more recaptures than expected (comparing observed and expected values for capture frequency 3 and total values for frequencies 4-10, 2x2 c.t., 1 d.f., $\chi^2 = 19.15$, $p < 0.001$). There were very few multiple captures from the adult female sub-population (Table 6.6). Those adult females captured on two and three occasions were considerably fewer in number than the expected values (Obs/Exp = 0.48 and 0.53 respectively); the numbers were, however, too low for this difference to be statistically tested.

Table 6.5: Observed and expected multiple capture frequencies for the adult male sub-population

Capture frequency	Sample combinations*	Expected frequency from one sample**	Calculated expected no. recaptures‡	Adjusted expected no. recaptures‡	Observed no. recaptures	Observed / Expected
2	210	2.88	604.80	260.52	240	0.92
3	1,330	6.91×10^{-2}	91.90	56.66	97	1.71
4	5,986	1.66×10^{-3}	9.94	7.17	45	6.28
5	20,355	3.98×10^{-5}	0.81	0.63	17	26.98
6	54,279	9.56×10^{-7}	5.19×10^{-2}	4.32×10^{-2}	5	115.74
7	116,300	2.29×10^{-8}	2.66×10^{-3}	2.30×10^{-3}	2	869.57
8	204,045	5.50×10^{-10}	1.12×10^{-4}	9.93×10^{-5}	2	20×10^{3}
9	294,476	1.32×10^{-11}	3.89×10^{-6}	3.55×10^{-6}	0	
10	352,717	3.17×10^{-13}	1.12×10^{-7}	1.12×10^{-7}	1	89×10^{5}
11	352,716	7.61×10^{-15}	2.68×10^{-9}	2.68×10^{-9}	0	
12	293,930	1.83×10^{-16}	5.38×10^{-11}	5.38×10^{-11}	0	

* - All possible sample combinations at which each capture frequency could have occurred in a twenty-one sample sequence

** - Expected number of recaptures from one sample in one multiple capture sequence only

‡ - See text (6.2.6.) for details

Table 6.6: Observed and expected multiple capture frequencies for the adult female sub-population

Capture frequency	Sample combinations*	Expected frequency from one sample **	Calculated expected no. recaptures‡	Adjusted expected no. recaptures‡	Observed no. recaptures	Observed / Expected
2	210	0.50	105	83.15	40	0.48
3	1,330	5.0×10^{-3}	6.65	5.69	3	0.53
4	5,986	5.0×10^{-5}	0.30	0.27	0	
5	20,355	5.0×10^{-7}	1.02×10^{-2}	1.02×10^{-2}	0	

* - All possible sample combinations at which each capture frequency could have occurred in a twenty-one sample sequence
** - Expected number of recaptures from one sample in one multiple capture sequence only
‡ - See text (6.2.6) for details

The trapping technique (as described in 6.2.2-6.2.4) involved emptying the traps, returning the contents and re-setting all traps on each trapping visit. Although carrying out all three operations on one day had the obvious advantage that an additional visit was not necessary to reset the traps it may also have had one major disadvantage. Animals were returned to the section one above that which they were caught from to allow them to find bottom in the current and traps were usually emptied during the daylight hours when this species has been shown to be relatively inactive (3.6.3). Thus the contents of the traps were returned to the aqueduct at a time when they would have normally been in a hide and were immediately exposed to the same stimuli that had prompted trap-capture i.e. an empty, suitable hide and the scent of fresh ox-liver. It was, therefore, possible that some multiple captures on consecutive trapping occasions were a direct result of this disadvantage of the trapping method. As the intention was to investigate the response of the crayfish to the baited traps in situ and not to this aspect of the trapping method all captures on consecutive trapping occasions were ignored. This practice must also have eliminated some captures which were not a result of this aspect of the trapping method but a normal trap response.

The trapping program was intended as a generally applicable methodological investigation of traps as a means of sampling crayfish populations. A further analysis was therefore carried out to demonstrate whether

or not there was appreciable bias in crayfish behaviour in response to traps irrespective of traps being reset on the same day the previous sample was returned. Comparing the observed number of captures on non-consecutive trapping occasions to the calculated number expected showed a very similar situation to that when all captures were considered (Table 6.7). The number of observed double captures of adult males was similar to the expected (Obs/Exp = 0.87); there were, however, significantly more captures than expected at higher capture frequencies (comparing observed and expected values for capture frequency 3 and pooled capture frequencies 4 - 7 to form a 2x2 c.t., 1 d.f., $\chi^2 = 5.05$, $p < 0.05$) and adult females were caught in considerably fewer numbers than expected at capture frequencies 2 and 3 (Obs/Exp = 0.37 and 0.35 respectively). All of the non-random responses to the traps so far demonstrated, however, could have been due to learned and/or innate behaviour patterns.

The relative positions of the traps in the aqueduct which caught individuals that were consecutive and non-consecutive multiple captures were summarized on Tables 6.8 and 6.9 and the following observations made:-

(a) Most of the male recaptures that were consecutive double captures occurred in the same trap as initial capture or its nearest neighbour (57%) while the remainder were displaced by between 2 and 15 inter-trap distances. This indicated that the previously described

Table 6.7: Observed non-consecutive multiple capture frequencies and expected multiple capture frequencies for the adult male and adult female sub-population

Sex	Capture frequency	Total observed number recaptures	Observed no. non-consecutive recaptures*	Adjusted expected no. recaptures‡	Observed* / Expected
Male	2	240	227	260.52	0.87
	3	97	80	56.66	1.41
	4	45	20	7.17	2.79
	5	17	6	0.63	9.52
	6	5	2	4.32×10^{-2}	46.30
	7	2	1	2.30×10^{-3}	434.78
	8	2	0	9.93×10^{-5}	
	9	0	0	3.55×10^{-6}	
	10	1	0	1.12×10^{-7}	
Female	2	40	31	83.15	0.37
	3	3	2	5.69	0.35
	4	0	0	0.27	

* - Number recaptures excluding capture on consecutive trapping occasions
‡ - See text for details

Table 6.8: Relative trap positions of all consecutive multiple captures

			Movements																						
Sex	ccf	S	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	...	26
Male	2	90	25	26	9	7	5	2	1	2	2		1	4	4		1	1							
	3	23	1	4	2	3	1	2	2		1		1	1		2						1	1		1
	4	11	2	4	2	1				1											1				
	5	2	2	1																					
	6	12	6	5	1																				
Female	2	6	3	1		2																			

ccf - consecutive capture frequency

S - number of recaptures for which both trap catch positions were known (trap position not recorded on 24 hour trapping sessions 15-16. 8.75 and 18-19. 8.75)

Movements - total number inter-trap distances moved between successive trappings (one inter-trap distance = 4 sections or 24 meters)

Table 6.9

Relative trap positions of all non-consecutive multiple captures

Sex	nccf	N	Mean* ± SE	Range*	R
Male	2	191	25.53 ± 1.76	1 - 106	37
	3	130	22.00 ± 1.87	0 - 81	28
	4	48	22.29 ± 2.52	2 - 93	6
	5	16	10.88 ± 2.99	0 - 51	4
	6	8	1.63 ± 0.50	0 - 4	8
	7	5	2.20 ± 1.02	0 - 6	4
Female	2	27	23.74 ± 3.77	1 - 70	5
	3	2	2.00		2

nccf - non-consecutive capture frequency

* - mean number sections between trap positions for recaptures for which both traps catch positions were known (trap positions not recorded on 24 hour trapping sessions 15-16. 8.75 and 18-19. 8.75)

N - number of non-consecutive pairs of known trap catch positions

R - number of known pairs of trap positions that represented return to the same trap or its nearest neighbour

disadvantage, in emptying and setting the traps on the same day may have been important at lower capture frequencies.

(b) The higher consecutive multiple capture frequencies were more equally distributed between those that entered the same trap as initial capture or its nearest neighbour and those that were displaced between 2 and 26 inter-trap distances.

(c) There was no significant correlation between the mean number of inter-trap distances by which the males at each consecutive capture frequency were displaced and their capture frequency (Fig. 6.5, $r = -0.74$, $t = 1.89$, 3 d.f. $p > 0.10$).

(d) There was a significant negative correlation between the mean number sections by which the males at each non-consecutive capture frequency were displaced and their capture frequency (Fig. 6.5, $r = -0.95$, $t = 6.02$, 4 d.f., $p < 0.01$).

(e) The range of the number of sections by which the males that were non-consecutive multiple captures were displaced also decreased from 1 - 106 to 0 - 4 with increasing capture frequency.

(f) The percentage of the number of non-consecutive pairs of known trap catch positions that represented return to the same trap or its nearest neighbour (R/N x 100, Table 6.9) increased from 19 - 100% with increasing capture frequency.

(g) The three males that were caught on six and seven non-consecutive trapping occasions had mean

Fig. 6.5: Mean number sections moved ± 1.96 SE between all non-consecutive captures and mean number inter-trap distances moved ± 1.96 SE (one inter-trap distance was four sections) between all consecutive captures as a function of non-consecutive and consecutive capture frequency

o - male consecutive capture

△ - female consecutive capture

● - male non-consecutive capture

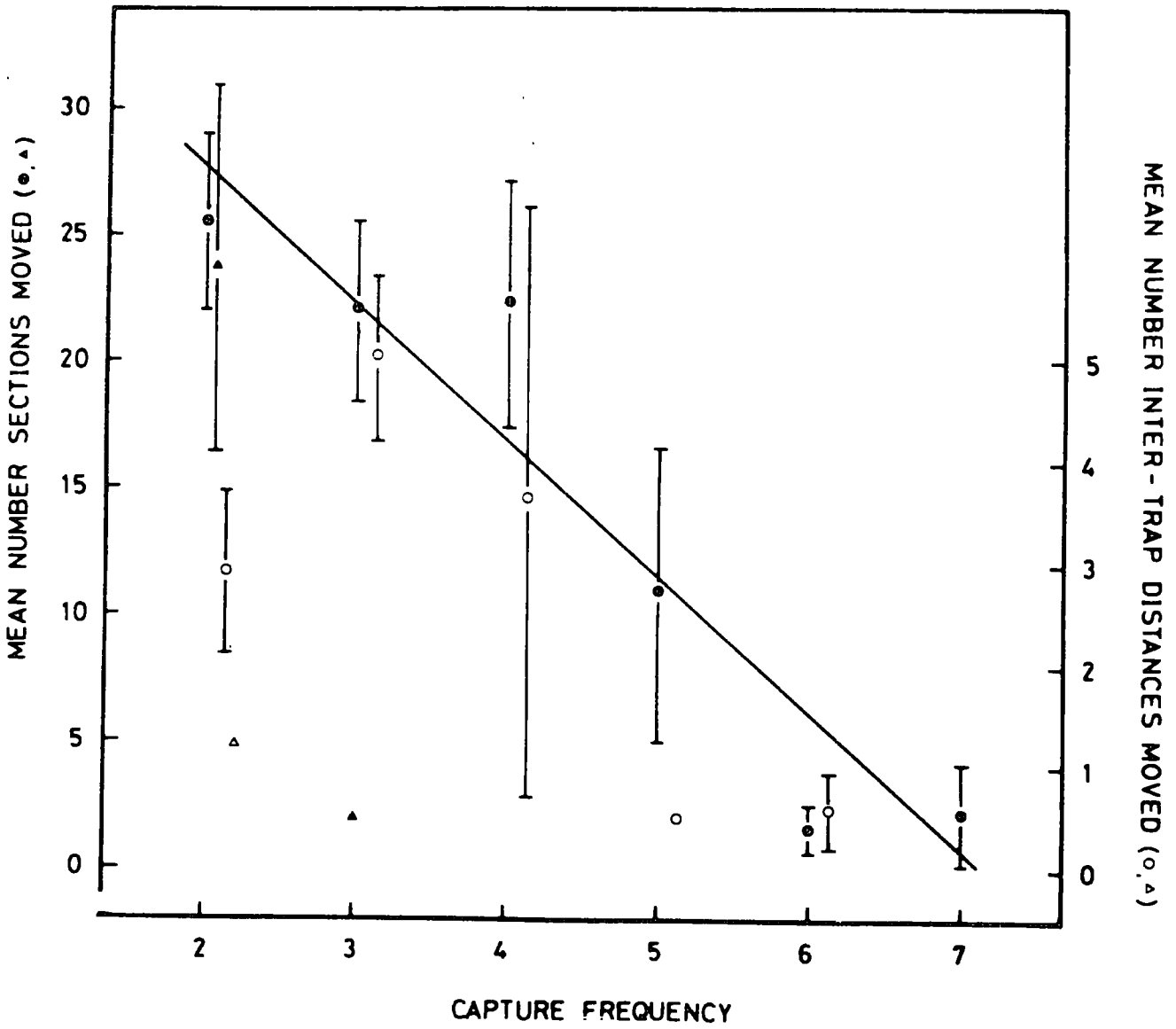
▲ - female non-consecutive capture

No regression line was fitted to the male consecutive captures (o):-

$y = -0.9200x + 6.2140$ ($n = 5$)
SE slope = 0.4877
$r = -0.7366$, $t = 1.8864$, 3 d.f.,
$p > 0.10$

Solid regression line fitted to the male non-consecutive captures (●):-

$y = -5.4049x + 38.4102$ ($n = 6$)
SE slope = 0.8975
$r = -0.9490$, $t = 6.0201$, 4 d.f.,
$p < 0.01$


MEAN NUMBER SECTIONS MOVED (●, ▲)
MEAN NUMBER INTER-TRAP DISTANCES MOVED (○, △)
CAPTURE FREQUENCY
0
5
10
15
20
25
30
0
1
2
3
4
5
2
3
4
5
6
7

carapace lengths over this trapping period of 42.8, 41.6 and 40.6 mm.

(h) The female that was caught on three non-consecutive trapping occasions had a mean carapace length over this trapping period of 36.8 mm. This female was caught at the same trap position on all three occasions.

The analyses of the recapture data from the trapping program presented in sections (i) and (ii) made it clear that the crayfish in the aqueduct were not equally trappable. However, juveniles could be seen to have been present in large numbers on lowering the water level and there was no reliable evidence to suggest an unequal sex ratio in this population (5.4.5, Table 6.4). Therefore some of the bias in the number of recaptures in the trapped samples must have been a result of innate behavioural responses to the traps; as all trapped samples, including the initial ones, contained a large excess of adults (mean proportion adults = 96.12%) and a large excess of males amongst the adults (mean proportion adults that were male = 74.01%). The estimated bias in the number of male trap recaptures at the higher capture frequencies was considerable (Tables 6.5, 6.6); such non-random responses could have been the result of innate and/or learned behaviour patterns (Robson & Regier 1971). It did, however, seem improbable that a bias of the magnitude estimated for the non-consecutive captures (Obs/Exp > 400),

in an adult male sub-population of approximately 5,000 individuals at a sampling intensity of around 2½%, could have been due solely to innate catchability being unevenly distributed in this sub-population. Females were caught less frequently than expected (Obs/Exp = 0.50 - 0.30) and this negative bias may also have been due to either trap shyness or trap avoidance.

There was also some definite evidence to support the contention that a learned component existed in this biased behaviour to traps. Non-consecutive captures at higher capture frequencies were displaced over significantly smaller distances between trappings, thus indicating that repeated capture by trap had caused an abnormal response. All animals thus suspected of trap addiction were quite large (♂♂ > 40 mm. C.L., ♀♀ > 36 mm. C.L.) and it would thus be predicted that it would have been possible for them to enter many traps even if they were already occupied. These individuals, and others which may have become trap addicted, would therefore have had every opportunity to manifest this response. This evidence was by no means conclusive, however, as the large size of these individuals may merely have reflected a strongly size dependent innate catchability distribution within the adult male and female sub-populations.

(iii) <u>A comparison between the mark-recapture estimates from the trapping and hand-sampling data</u>

The trapping data from the 15 baited trappings, the 2 twenty-four hour repeated trappings and the four largest

non-baited trappings were listed in two trellis diagrams, one for all adults and one for all adult males alone (Tables 6.10 and 6.11 respectively), according to the stochastic model of Jolly (1965). Too few adult females were recaptured for this sub-population to have been estimated separately. The stochastic model was computerised (Davies 1971) and the estimated total number (N) and associated parameters (alpha, M, SE(N)) for the total adult and adult male sub-populations were listed on Tables 6.12 and 6.13.

As stated in section (ii) several mark-recapture estimates were made by hand-sampling over the same period that the above trap samples were taken. The mean estimates over this period were compared:-

Sub-population	(a) Mean trapping estimates	(b) Mean hand-sampling estimates	b/a
Total adults	2,878	9,743	3.4
Total males	1,721	4,563	2.7

The reliability of the estimates from the hand collected samples has already been demonstrated (5.4.5, Table 6.4). However, even if this were not the case the methods which produce the larger estimates are generally more reliable in mark-recapture studies as variations in catchability invariably result in underestimation of population size (Bohlin & Sundström 1977, Seber 1973).

6.4 Discussion

That the structure of trapped samples was a large majority of adults that were mostly male has also been

Table 6.10: Mark re-capture trellis diagram. All trapped adults

Date	n_i	s_i																			
20. 7.75	121	121																			
25. 7.75	156	156	3																		
2. 8.75	116	116	2	8																	
6. 8.75	116	116	2	7	8																
12. 8.75	118	118	6	3	4	5															
15. 8.75	529	529	11	4	7	15	32														
18. 8.75	267	267	5	7	3	0	6	98													
13. 9.75	147	147	6	5	0	0	3	28	11												
1.10.75	122	122	0	1	0	1	0	11	1	17											
17.10.75	119	119	3	0	0	0	1	9	4	9	12										
28.10.75	123	123	2	1	2	1	3	6	5	6	2	8									
12.11.75	163	163	1	4	1	2	1	18	7	7	7	5	7								
30.11.75	105	105	3	0	0	4	4	13	2	4	3	3	3	13							
15.12.75	65	65	0	1	0	2	2	5	1	2	1	1	2	5	5						
25. 4.76	75	30	0	1	3	1	0	1	0	1	1	1	0	6	7	1					
18. 5.76	185	185	2	2	0	2	0	7	1	5	1	4	4	8	7	7	5				
30. 5.76	166	166	0	3	1	1	1	9	1	2	2	0	1	1	7	0	1	11			
13. 6.76	223	223	1	1	1	1	0	10	3	0	2	2	5	6	6	2	0	11	6		
27. 6.76	127	127	1	1	1	0	1	7	0	3	1	2	3	2	3	3	2	10	3	13	
31. 8.76	178	178	1	0	0	0	0	3	0	3	1	1	1	7	5	3	2	4	4	5	13
15.10.76	194	194	0	0	0	0	1	1	0	1	0	1	0	3	4	3	0	11	2	9	6	16

Notation as Jolly (1965):- n_i - number caught
s_i - number released with marks

Table 6.11: Mark-recapture trellis diagram. Trapped adult males

Date	n_i	s_i																			
20. 7.75	87	87																			
25. 7.75	112	112	3																		
2. 8.75	102	102	2	7																	
6. 8.75	107	107	2	7	8																
12. 8.75	107	107	5	3	5	5															
15. 8.75	368	368	9	3	7	15	30														
18. 8.75	163	163	5	6	2	0	6	84													
13. 9.75	111	111	6	2	1	0	2	24	11												
1.10.75	69	69	2	0	0	1	0	12	1	17											
17.10.75	78	78	4	0	0	0	1	9	4	9	6										
28.10.75	98	98	2	0	2	1	3	6	5	5	2	9									
12.11.75	155	155	1	4	1	2	1	18	7	7	7	5	7								
30.11.75	100	100	3	0	0	4	4	10	2	4	2	3	3	13							
15.12.75	56	56	0	0	0	2	2	4	1	2	1	1	2	5	4						
25. 4.76	59	27	0	1	3	1	0	1	0	1	1	1	0	6	7	1					
18. 5.76	146	146	2	2	0	2	0	7	1	4	1	1	4	8	7	7	5				
30. 5.76	109	109	0	2	1	1	1	9	0	2	2	1	0	1	1	7	1	11			
13. 6.76	131	131	1	0	1	1	0	9	3	0	2	2	4	5	6	2	0	10	4		
27. 6.76	102	102	1	1	1	0	1	6	0	3	1	1	3	2	3	3	2	10	3	11	
31. 8.76	119	119	0	0	0	0	0	3	0	1	1	1	1	7	5	3	2	4	3	3	13
15.10.76	132	132	0	0	0	0	1	1	0	1	0	1	0	3	4	3	0	10	2	9	6	16

Notation as Jolly (1965):- n_i - number caught
s_i - number released with marks

Table 6.12

Total adult sub-population size estimates
Jolly's stochastic model (1965)

Date	Proportion marked (alpha)	Total marked ($\hat{M}$)	Total number ($\hat{N}$)	S.E.($\hat{N}$)
20. 7.75		0.0		
25. 7.75	0.0192	149.45	7771.34	4585.76
2. 8.75	0.0862	328.06	3805.55	1312.49
6. 8.75	0.1466	387.45	2643.79	730.63
12. 8.75	0.1525	258.29	1693.24	403.04
15. 8.75	0.1304	299.41	2295.47	281.32
18. 8.75	0.4457	1632.00	3661.71	620.46
13. 9.75	0.3605	511.15	1417.72	209.74
1.10.75	0.2541	829.55	3264.66	708.12
17.10.75	0.3193	934.75	2927.24	627.50
28.10.75	0.2927	996.35	3404.18	768.68
12.11.75	0.3681	600.14	1630.37	253.92
30.11.75	0.4476	459.84	1027.30	161.87
15.12.75	0.4154	677.00	1629.81	396.35
25. 4.76	0.3067	581.00	1894.57	581.67
18. 5.76	0.2973	610.00	2051.82	353.10
30. 5.76	0.2470	1667.80	6752.55	1929.40
13. 6.76	0.2556	993.60	3887.24	883.30
27. 6.76	0.4409	550.63	1248.75	293.25
31. 8.76	0.2978	498.00	1672.53	461.14
15.10.76	0.2887			

Table 6.13

Adult male sub-population size estimates
Jolly's stochastic model (1965)

Date Code	Proportion marked (alpha)	Total marked ($\hat{M}$)	Total number ($\hat{N}$)	S.E.($\hat{N}$)
20. 7.75		0.0		
25. 7.75	0.0268	135.63	5063.58	2987.16
2. 8.75	0.0882	244.87	2775.25	985.88
6. 8.75	0.1589	289.09	1819.54	482.83
12. 8.75	0.1682	236.12	1403.57	331.23
15. 8.75	0.1739	234.40	1347.82	157.50
18. 8.75	0.6319	1006.49	1592.79	250.73
13. 9.75	0.4144	408.73	986.29	143.81
1.10.75	0.4783	579.69	1212.08	241.18
17.10.75	0.4231	630.00	1489.09	309.38
28.10.75	0.3571	810.83	2270.33	509.66
12.11.75	0.3871	537.40	1388.28	214.59
30.11.75	0.4800	469.62	978.38	162.70
15.12.75	0.4286	388.00	905.33	190.59
25. 4.76	0.3898	487.40	1250.29	367.78
18. 5.76	0.3493	476.02	1362.73	230.32
30. 5.76	0.3670	1275.33	3475.28	1050.19
13. 6.76	0.3817	661.33	1732.69	400.70
27. 6.76	0.5098	411.68	807.53	183.10
31. 8.76	0.3950	337.06	853.41	223.74
15.10.76	0.4167			

demonstrated in lake populations of this species of freshwater crayfish (Moriarty 1972, Watson - unpubl.) and those of many other species (e.g. Astacus astacus, Abrhamsson 1966, 1971; Cherax albidus, Woodland 1967; Orconectes propinquus, Capelli 1975; Orconectes virilis, Aiken 1965, Momot & Gowing 1972, Threinen 1958; Pacifastacus leniusculus trowbridgii, Mason 1963). Baited funnel-type traps have been used to sample populations of many decapod species and it has often been the case that larger individuals were caught in greater numbers (e.g. the spiny lobster, Panulirus interruptus, Lindberg 1955; the river crab, Potamon perlatus, Turnbull-Kemp 1960).

The relative abundance of the main sub-divisions of sample structure corresponded to the dominance order of Bovbjerg (1953, 1956; amongst adults, males were always dominant to females of similar size, there was no sexual dominance in juveniles, size was directly related to position in the dominance order in both sexes). Infestation by the parasite Thelohania contejeani did not appear to have modified this hierarchy in the aqueduct. It has been suggested (Woodland 1967) that females and juveniles were poorly represented in trap catches due to their smaller size (females grow more slowly after maturity, 4.3.1, Woodland 1967). It was considered more likely, however, that chelae size was the most important factor as males had been shown to dominate similar sized heterosexual groups of P.l. trowbridgii due to positive

allometric growth of the chelae after sexual maturity (Mason 1974). Chelae size has also been shown to have been the deciding factor in both aggressive and sexual encounters in O. propinquus (Stein 1976). It does, therefore, seem most likely that A. pallipes was responding to the other crayfish in the traps or attracted to their vicinity by the scent of the bait (chemoreception is well known to be important in the location of foods by decapods, Mackie & Shelton 1972) and not to the traps themselves. There was considerable direct evidence that this was the case in other crayfish species (Capelli 1975, Flint 1975, Woodland 1967).

Seasonal variations in the sex ratio of the adults similar to those observed in the aqueduct have also been documented in lake populations of this species (Moriarty 1972, Watson - unpubl.) and in several other species (A. astacus, Abrahamsson 1971; C. albidus, Woodland 1967; O. propinquus, Capelli 1975; O. virilis, Momot 1967; Pacifastacus leniusculus, Flint 1975; P.l. trowbridgii, Mason 1974). Momot (1967) has suggested that such variations were the result of reproductive females migrating into deeper water. However, as Capelli (1975) has stated, variations in behavioural response to the traps associated with breeding (and also probably moulting) were a more likely explanation; indeed, of the two explanations, this was the only possible one in the aqueduct.

The 'retiring' behaviour of reproductive female crayfish is well known (Mason 1970, Merkle 1969, Stephens

1955) and their low numbers in traps (6.3.1, Capelli 1975, Morrissy 1970) or complete absence from them (Woodland 1967) has in two species been shown not to have been due to their avoiding traps *per se* but to the fact that they sequester themselves over much of this period (*O. propinquus*, Capelli 1975; *C. albidus*, Woodland 1967). This does not appear to have been generally the case for decapods however, breeding females of the lined shore crab *Pachygrapsus crassipes* have been observed to become more abundant in catches whilst reproductive (Hiatt 1948). Females of all crayfish species documented were most abundant in trapped samples during the non-reproductive part of the year (*A. pallipes* females represented up to almost 50% of some samples at this time, 6.3.4). A similar situation has been reported for the lobster *Homarus americanus* (Templeman & Tibbo 1945) where the increased proportion of females in catches was shown to have been due to the large females feeding intensively following the hatching of their eggs in preparation for the summer moult; the same explanation may also have accounted for the increase in *A. pallipes* females in the baited traps at this time.

Other crayfish species were also known to escape from funnel traps (Lindqvist, pers. comm.) and spiny lobsters, *P. interruptus*, have been reported to escape from traps which had several funnels (Lindberg 1955). Indeed they escaped even when left in traps which had been re-baited but were, to some extent at least, replaced by new entries; as was observed in this study of *A. pallipes*.

Crayfish behaviour in response to traps has been reviewed by Woodland (1967). He suspected that trap-addiction (i.e. a learned behavioural response cf. trap proneness) was a component of the trap behaviour of C. albidus but did not demonstrate this. That previous capture did influence future catchability, with respect to baited drop-nets, has been demonstrated for Cherax tenuimanus (Morrissy 1975). That this was the case for A. pallipes, in response to baited funnel traps in the aqueduct, seemed to have been likely. It was not possible to prove this conclusively however, as has often been observed to be the case when both innate and learned behavioural responses were believed to have been involved (Carothers 1971, Seber 1973).

Whether A. pallipes showed learned behavioural responses to the traps or not the bias in estimating the total adult and adult male sub-populations by mark and recapture from the trapping data was of the order of a threefold under-estimation. Although it has often been assumed that when catchability was dependent on size and/or sex any bias in the resulting mark-recapture estimates could be avoided by enumerating adult and juvenile sub-populations of each sex separately, this is only the case when the original assumption is valid for the resulting sub-populations; all members of each sub-population must be equally catchable (Junge 1963, Seber 1973). It was known that this was not the case when trapping the adult male and female sub-populations of

A. pallipes, irrespective of whether this was due to learned responses and/or a size dependent innate catchability distribution, and was also strongly suspected in other species of freshwater crayfish due to the apparently universal tendency for traps to catch larger animals. This was particularly significant because, as has been stated in the introduction (6.1), many studies of the population dynamics of freshwater crayfish have involved trapping as one of the sampling methods or the only one.

There have been several attempts to avoid biased mark-recapture estimates when trapping was used as a sampling method. Woodland (1967) trapped repeatedly to obtain each sample and multiple captures were only counted once; this would have removed some but not necessarily all of the bias.

Momot (1967, 1977) used trapping only to sample the largest animals and supplemented this with other methods to obtain each sample. He claimed (Momot 1977) that he had successfully enumerated a population of known size by the mark-recapture method (Momot 1967). The mark-recapture model he selected for this test and the subsequent study was that of Schumacher (Schumacher & Eschmeyer 1943); however the 95% confidence limits (203-240) he placed either side of the estimate (222) did not include the known size of the population (284)! He also stated that estimates of a 'population' of unknown size obtained by trapping and seine netting were not significantly different. His data shows this to have been the case

but it had previously been stated that traps sampled crayfish < 24 mm. C.L. and seine netting was used to supplement the trapping by taking smaller crayfish (and presumably some bigger ones also); the resulting estimates, therefore, must almost certainly apply to different or possibly overlapping portions of the whole population and may well have been similar. It was most unlikely that this was because the trapping estimate was a reliable estimate of the size of the whole population.

Estimations of population density using trapping returns as an index of density and converting this to real units by intensive hand or SCUBA collections from a known area have been attempted several times (Abrahamsson & Goldman 1970, Cukerzis 1959, Flint 1975). The catch per trap (c) was compared to an intensive collection (quadrat-sampling type) estimate of density (D) at a point reasonably close in time and the area from which the trap attracted animals estimated as c/D. Subsequent trappings provided further values of catch per trap (c_2) and these were converted to density estimates by multiplying by c/D. There were several disadvantages in such a method. Catch per trap was usually reduced at low water temperatures (traps emptied on 30.11.75, 15.12.75 and 25. 4.76 when water temperature was at its lowest produced the smallest catches, Appendix 1; also Capelli 1975, Morrissy 1970) and also showed other variations which were not acccounted for (Appendix 1); thus for accurate results the density estimate (D) must have been

continually re-estimated and if density was already known there was little point in estimating it using a trapping index! In the author's opinion crayfish behaviour in response to traps was too complex and unpredictable for all the variation in catch per trap to have been ascribed to changes in population density. Another assumption, inherent in this method of estimation, was that all crayfish within a certain radius of the trap were captured; there was no evidence to support this and there seemed no reason why crayfish from further afield should not have been captured whilst ones within the radius may not have been, these two classes of recapture would then have been present in some unknown proportion and the calculation impossible. Also, as Flint (1975) has pointed out, this radius must vary considerably with substrate type. Indeed there seemed little to recommend this method of estimation.

Bias in trapped samples of many species of freshwater crayfish and other decapod species was, therefore, so extensive as to preclude most mark-recapture methods of population estimation. The only ways to obtain reliable estimates using traps seemed to have been regression methods, which do not rely on the assumption of equal catchability (Eberhardt 1969, Marten 1970, Seber 1973), or trapping out 'fenced off' sections of water (e.g. Turnbull-Kemp 1960).

CHAPTER 7

The estimation of the annual production of the crayfish population in the aqueduct in 1976

7.1 Introduction

It was possible to obtain an approximate estimate of annual production for the total aqueduct population in 1976 by making certain assumptions regarding the age structure of this population and its variations from year to year. It has often been necessary to make such assumptions when estimating production and the accuracy of most of these estimates is heavily dependent on how realistic these assumptions were (Chapman 1971, Hamilton 1969, Hynes and Coleman 1968 & Woodland 1967). Most of the assumptions made in this chapter are relatively 'weak' and departures from them would have resulted in fairly small errors; some, however, are quite 'strong' assumptions and although there was some evidence to support their validity in some cases the approximate nature of these estimations is stressed.

The estimate of annual production to be made, albeit an approximate one, is considered to have been of value as it is the only estimate for any population of this species; the importance of this became apparent from the following points. In the author's opinion there

is an urgent need for direct comparisons between A. pallipes and foreign crayfish species owing to the increasingly popular trend amongst fish farmers and aquaculturists to import exotic species as stock (Bowler pers. comm., Fuke 1978, Jackman 1977, Pratten pers. comm., Richards & Fuke 1977). This has been stimulated by the increase in demand for imported crayfish as a food item in many European countries and the consequent high prices (£8-£12/Kg., ca. 50-70p/individual; Fuke 1978) which have resulted largely from the effects of the fungal plague A. astaci in their home waters (Abrahamsson 1972a, Brinck 1974, Laurent 1972, Westman 1972, 1974). These introductions have usually been juvenile P. lenuisculus from the A B Simontorps Akvatiska Avelslaboratorium in southern Sweden (Abrahamsson 1972c, Fuke 1978, Pratten pers. comm.) but A. leptodactylus and Procambarus sp. are also known to have been introduced in small numbers (Bowler pers. comm.). This has been done by commercial aquaculturists attempting to rear crayfish as a monoculture, by fish farmers wishing to increase the efficiency of their salmoniid monocultures by adding a benthic opportunistic feeder (3.5) or occasionally by somewhat optimistic landowners who have introduced sometimes less than a hundred juveniles to a watercourse (often containing known crayfish predators such as trout) in an attempt to establish a breeding population. The dangers inherent in the introduction of non-indigenous species have been well documented (e.g. Elton 1958, Udvardy 1969)

and several items in the crayfish literature have recently added to this (Lahser 1974, Unestam 1972b, 1974, Westman 1972). Regarding the introduction of foreign species into the U.K. there exist not only the results of interspecific competition, interbreeding, differences in reproductive and grazing potential which are at present intangible but also the very real possibility of bringing crayfish infected with the crayfish plague into the U.K. This disease is fatal to A. pallipes (Unestam 1972b) and as there is no evidence that this disease has reached the U.K. to date (5.1) there is the danger of establishing a reservoir of fungal spores from which the plague could proliferate. P. leniusculus and other North American species can tolerate the disease but may harbour spores (Unestam 1972b) as may other aquatic invertebrates (Hastein and Gladhaug 1974); indeed so little is known of the life history and vectors of the plague that prophylactic measures often have only a temporary effect and the spread of the disease to many crayfish waters is inevitable (Hastein and Gladhaug 1974, Svensson et al.1976, Unestam 1972b, Westman 1972).

In view of these possibilities any introductions of foreign species must be made only to closed water bodies and then only for very sound reasons. A. pallipes grows relatively slowly (4.3.3) but can exist at high densities under ideal conditions (Pratten pers. comm.) and may therefore be equally suitable as stock for natural water bodies and salmonid monocultures. The

relatively rapid growth and large final size of P. leniusculus (Abrahamsson 1971b, Fuke 1978) may make this a more suitable animal for commercial aquaculture where turnover and capital outlay are paramount but these systems are easily isolated from our native stocks and indeed the need for them is questioned as large native stocks of A. pallipes exist which could be cropped with minimum outlay. Such uncertainties would be clarified if the potential production of A. pallipes were known and it might then be possible to convince importers of foreign crayfish species that the advantage of these over A. pallipes are vastly outweighed by the risks they present to the whole of our native crayfish population.

7.2 Results

All the assumptions which had to be made to arrive at an approximate value for annual production were due either to the relatively low sampling frequency (five hand samples in 1976, only one of which was within the growth season) or the limited information available for the juveniles, especially those of CL < 13 mm. which were not included in the hand-samples (5.2).

7.2.1 The estimation of annual production for animals of carapace length < 13 mm.

The maximum potential recruitment into the aqueduct population (i.e. the total number of eggs carried prior to hatching) in 1976 has already been estimated as 47,142 ± 12,700 (3.4).

The age structure and sex ratio of the aqueduct

population were assumed to have been approximately constant from year to year. This was probably the case, within the limits of accuracy of the available data. A comparison of the size frequency histograms of the hand samples taken in 1974 and 1975 (4.3.3) and the estimated recruitment in the three years 1974-76 (3.4) supported this assumption. A similar situation was assumed to have existed in the population studied by Woodland (1967).

The number of crayfish in the 13 mm. carapace length size class at the end of the growth season was estimated by assuming that the size frequency distributions shown in Figs. 4.7 and 4.8 were a realistic estimate of the proportions of each size class in the juvenile population. An approximate estimate of the size of the total juvenile sub-population at the end of the growth season was obtained as the mean value of the mark-recapture estimates on 27. 8.76 (11,059) and 8.10.76 (6,049; 5.4.5) as moulting ended in mid-September (3.3) but no estimate was available at this time:-

Mean estimate of juvenile sub-population = 8,554

Estimated number in 13 mm. carapace length size class = 590

Two patterns of mortality were considered between hatching (carapace length ca. 4.5 mm., 4.3.3) and reaching 13 mm. carapace length; i.e. linear and exponential mortality between mm. size classes. The vast majority of studies of fish and invertebrates have shown mortality patterns in the young stages that lay somewhere between these two extremes (Chapman 1971, Waters 1969).

The estimate of maximum potential recruitment was interpolated to the estimated size of the 13 mm. size class following both these mortality patterns (Fig. 7.1) to produce two plots with carapace length as the index of size on the abscissae but otherwise analogous to those of Allen (1951). Production was equivalent to the area beneath the curves (exponential mortality) or the lines (linear mortality). This method was similar to one suggested by Chapman (1971).

The abundance of each mm. size class was estimated from each plot.

The correlation between $\log_{10}$ carapace length and $\log_{10}$ wet weight was assumed to have been linear over the whole size range. For size ranges 12-54 mm. (males) and 11-46 mm. (females; 3.8):-

w = wet weight (gms)

l = carapace length (mms.)

$$w = (1.1803 \times 10^{-4})l^{3.2768} \text{ males } (r = 0.9961) \quad \ldots\ (1)$$

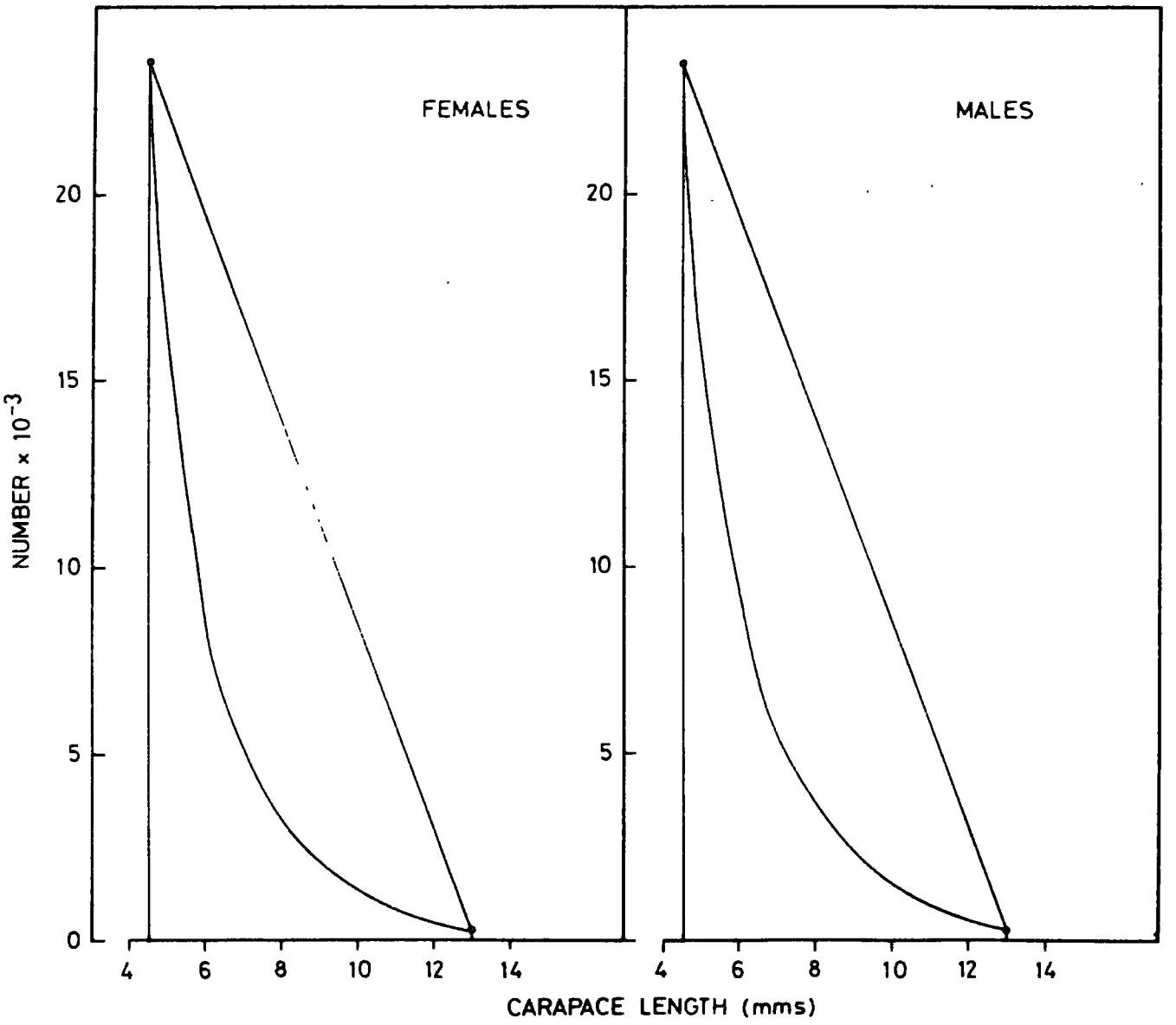
$$w = (1.7480 \times 10^{-4})l^{3.1548} \text{ females } (r = 0.9971) \quad \ldots\ (2)$$

The sex ratio of the juveniles was assumed to have been unity (as was the case for the adults, within the limits of accuracy, 5.4.5) and the weight of the animals estimated to have been in each mm. size class was calculated as above.[1] The totals of these weights were the

1 This method of converting the mean length of size classes into weights was not strictly accurate and tends to underestimate weight by around 5% as the weight of an individual whose length is L is always less than the mean weight of a group of individuals whose mean length is L (Ricker 1958).

Fig. 7.1: Allen curves resulting from the interpolation of the estimated maximum potential recruitment of hatchlings (4.5 mm. carapace length) of each sex in 1976 to the estimated size of the 13 mm. carapace length size class (see text). A sex ratio of unity and a pattern of mortality that lay somewhere between a linear and an exponential one were assumed

The relationship between length and weight for each sex (equations 1 and 2) were used to calculate the area beneath these interpolations in terms of gms. wet weight


FEMALES
MALES
NUMBER x 10^{-3}
0
5
10
15
20
4
6
8
10
12
14
CARAPACE LENGTH (mms)

estimated production ($\hat{P}$) for each mortality pattern:-

Linear mortality - $\hat{P}_A = 20,778 \pm 5,598$ gms. wet weight

Exponential mortality - $\hat{P}_B = 7,698 \pm 2,074$ gms. wet weight

As it was not known which mortality pattern was nearest to the actual one these estimates were considered as upper and lower confidence limits and an approximate estimate of production for the juveniles < 13 mm. CL(P_1) was given by:-

$$\hat{P}_1 = \left[(\hat{P}_A + 2SE) - (\hat{P}_B - 2SE)\right] \tfrac{1}{2} + (\hat{P}_B - 2SE)$$

$$\hat{P}_1 = 17,762 \pm 7,106$$

The two major errors involved in these estimates of recruitment and the number in the 13 mm. carapace length size class tended to cancel each other out in terms of estimating production. All the eggs carried did not hatch (3.4) so recruitment was overestimated but small crayfish (< 20 mm. carapace length) were not equally catchable by hand collection (5.2, Figs. 4.7 and 4.8) and the number at 13 mm. carapace length was therefore underestimated.

The accuracy with which P_1 was estimated would have been considerably increased by greater knowledge of the variations in abundance of the size classes < 13 mm. carapace length during the moulting season. This was not possible in this study due to the difficulty in sampling the smaller crayfish in representative numbers and the limitations on the number of times the aqueduct could be drained for hand collection (5.1 and 6.1).

7.2.2 The estimation of annual production for animals of carapace length ⩾ 13 mm.

The mark-recapture estimates for the sizes of the three main sub-populations at the sampling occasion immediately before the start of the growth season (Day 9 - 11. 6.76; earliest moulting 20th June, 3.3) were as follows:-

Adult females 2,865 ± 881

Adult males 3,328 ± 875

Total juveniles ⩾ 13 mm. CL: 5,351 ± 2,145

The proportional age structures of these sub-populations was estimated from the pooled data on Figs. 4.7 and 4.8 and the weight of each mm. size class calculated from formulae (1) and (2).

The moult frequency of juveniles ⩾ 13 mm. carapace length has already been estimated as 3-4 moults <u>per annum</u> (Table 4.5); all juveniles of this size were assumed to have moulted four times in 1976. The proportion of adults of each sex that moulted once or twice was estimated from the regression line fitted to Fig. 4.6.

As a result of the relatively low sampling intensity (ca. 5-10%) and sampling frequency (five hand-samples in 1976) no significant mortality was detected during the 1976 growth season (5.4.5). Some mortality did occur however (dead animals were seen on the floor of the aqueduct) as expected since animals of all sizes were very vulnerable to cannibalism when the exoskeleton was soft for a few days immediately following postmoult (e.g. Huxley 1896, Momot 1967); significant mortality

during the growth season has since been demonstrated in the aqueduct with an intensified sampling program (Phi = 0.55, 17. 6.-12. 8.77; Brewis, unpubl.). Due to this deficiency in the data describing the aqueduct population in the 1976 growth season there was no alternative but to 'assume' that all animals present on Day 9 (11. 6.76) survived and moulted. This was undoubtedly the 'strongest' of all the assumptions made and would have resulted in an overestimation of annual production for animals of carapace length $\geqslant$ 13 mm. of the order of 1.8 x actual value; if mortality was of a similar magnitude in the 1976 and 1977 growth seasons (if cannibalism and natural mortality at the moult were the major causes of mortality at this time of year this would be predicted to have been the case as population density was not significantly different for the two growth seasons, Brewis, unpubl.). Indeed it has been stated that in unexploited populations with relatively stable environmental conditions production may be similar from year to year (Chapman 1971).

The mean moult increments for the total data for each sex (therefore allowing for the effects of egg-production, infestation by T. contejeani and/or limb-regeneration; 4.5) as calculated in 4.3.1 were:-

Males 2.8815 ± 0.0489 mm. n = 510

Females 2.3847 ± 0.0829 mm. n = 161

These increments, the percentage of animals of each mm. size class estimated to have moulted twice and formulae (1) and (2) were used to calculate the total growth in weight of the juveniles of carapace length

$\geqslant$ 13 mm. ($\hat{P}_2$), adult females ($\hat{P}_{3a}$) and adult males ($\hat{P}_4$):-

$\hat{P}_2$ = 21,842 ± 8,736 gms. wet weight

$\hat{P}_{3a}$ = 7,670 ± 2,363 " " "

$\hat{P}_4$ = 13,648 ± 3,588 " " "

Total = 43,160 ± 14,687

It was known that this was a considerable over-estimate; assuming a similar level of mortality in the 1976 and 1977 growth seasons (see above), and that growth and mortality occur at random at this time, an approximate estimate for crayfish which survived long enough to moult and grow could be obtained:-

$(\hat{P}_2 + \hat{P}_{3a} + \hat{P}_4) \div 1.8$ = 23,978 ± 8,159 gms. wet weight

One aspect of annual production which has not so far been considered was egg production ($\hat{P}_{3b}$). Crayfish eggs had a mean wet weight (2.1) of 12.36 ± 0.51 mg. (n = 14) each. The total biomass of eggs produced in 1976 was therefore estimated as 47,142 x 12.36 = 582,675 mg. wet weight (3.4).

The difference between estimated annual production in terms of wet weight between adult males ($\hat{P}_4$ = 13,648 gms.) and adult females ($\hat{P}_{3a} + \hat{P}_{3b}$ = 8,253 gms.) was not therefore accounted for by the energetic demands of egg production.

$\therefore \quad \left[(\hat{P}_2 + \hat{P}_{3a} + \hat{P}_4) \div 1.8\right] + \hat{P}_{3b}$ = 24,561 ± 8,159 gms. wet weight

Adding to this $\hat{P}_1$ = 17,762 ± 7,106 gms wet weight for the juveniles of carapace length < 13 mm. to produce an overall approximation to annual production ($\hat{P}a$):-

$\hat{P}a$ 42,323 ± 15,265 gms. wet weight.

The use of arithmetic means for growth increments and assuming all mortality to occur at the mid-point of a time interval tends to overestimate production as compared to the method of Ricker (1958) which employs instantaneous rates. As mortality was not accurately known in 1976 the former method was employed here. This overestimation may be as high as 30% (Momot 1967).

The assumption that all juveniles $\geqslant 13$ mm. carapace length moulted four times would also have tended to overestimate annual production as the analysis of the growth data suggested these animals may moult three or four times (4.3.3).

The total area of the walls and floor of the aqueduct has been estimated as 2,482 m^2 (1.1). An approximate estimate of annual production ($\hat{P}a$) per unit area was therefore:-

$\hat{P}a = 17.05 \pm 6.15$ gms. wet weight/m^2

The ratio of production to biomass (P/B or 'turnover ratio' of Waters 1969 and other American authors) has been used in attempts to characterize species' populations and the associated set of environmental conditions. This ratio can be calculated in several ways according to the period of time to which the estimates of P and B apply and will then have various magnitudes; a fact which has often been overlooked (Winberg 1971). However calculated this ratio is a relative measurement and two populations may have the same P/B ratio and very different values for P and B; it therefore has no value as a

characteristic for comparing populations unless P or B is also known in each case.

An approximate measurement of the annual mean biomass ($\bar{B}$) in the aqueduct in 1976 was calculated so that $\hat{P}_a$ (annual production) and $\bar{B}$ could be compared with estimates for other crayfish species. The estimate of $\bar{B}$ for the juveniles of CL < 13 mm. was estimated as suggested by Chapman (1971) from Figs. 4.7 and 4.8 and this was added to $\bar{B}$ calculated from the three population size estimates in 1976 (11.6, 27.8, 8.10.76; 5.4.5), the size frequency distributions (Figs. 4.7 and 4.8) and formulae (1) and (2):-

Mean biomass $\simeq$ 101, 686 gms. wet weight

$\hat{P}_a/\bar{B} = 0.42$

7.2.3 The conversion of the estimate of production into energy units

The calorific value of whole specimens of A. pallipes was determined with a Gallenkamp 'macro-bomb' calorimeter. It was decided not to attempt to homogenise the crayfish tissues as this would have presented obvious problems (Woodland 1967); small crayfish were burnt whole and larger ones piece by piece after drying to constant weight at 40°C in a vacuum oven. Determinations of the calorific value (CV) of whole individuals of carapace length 13-42 mm. (females) and 16-49 mm. (males) were plotted against wet weight; Fig. 7.2 (crayfish were dried with filter paper until no more wet spots appeared on the paper before weighing, 2.1).

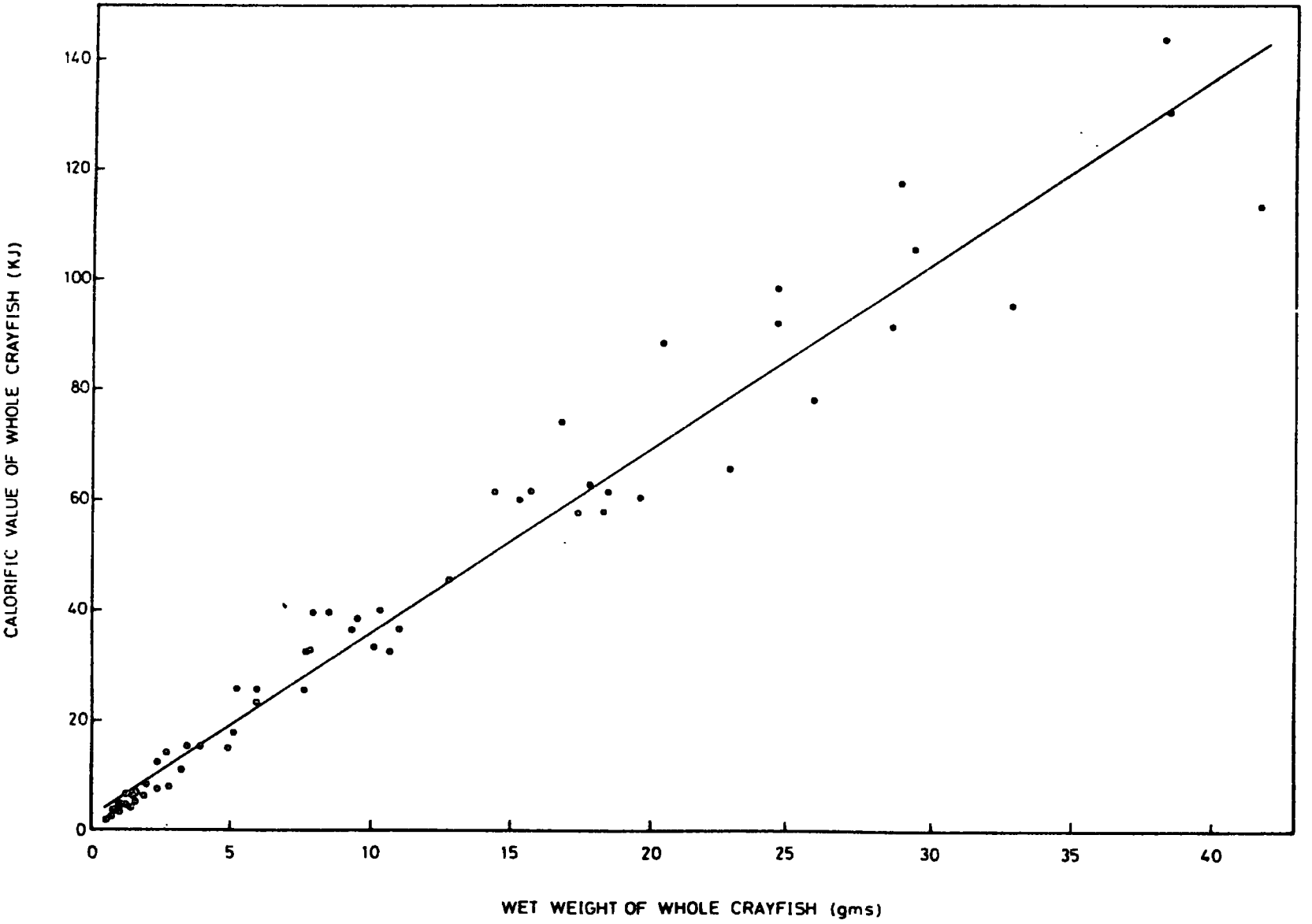
Samples were collected, dried and burnt in June, August and September of 1975; there was no significant

Fig. 7.2: The total calorific value of whole crayfish as a function of total wet weight in grams (7.2.3)

$y = 3.3036x + 3.261$ ($n = 59$)

SE slope = 0.0934

$r = 0.9780$, $t = 35.40$, $p \ll 0.001$


CALORIFIC VALUE OF WHOLE CRAYFISH (KJ)
0
20
40
60
80
100
120
140
0
5
10
15
20
25
30
35
40
WET WEIGHT OF WHOLE CRAYFISH (gms)

difference between the CV of one gram of crayfish tissue in these three months or between the sexes:-

	Males KJ/gm w.wt.	Females KJ/gm w.wt.
June	3.69 ± 0.20 (n=15)	3.73 ± 0.22 (n= 5)
August	4.14 ± 0.21 (n=12)	3.74 ± 0.13 (n=12)
September	3.73 ± 0.27 (n= 9)	3.86 ± 0.16 (n= 6)
Total	3.85 ± 0.13 (n=36)	3.77 ± 0.09 (n=23)

Fig. 7.2: x = wet weight (w.wt.) grams, y = CV (KJ):-

$y = 3.3036x + 3.2610$ ($r = 0.9780$, $t = 35.40$, $p < 0.001$)

Therefore mean CV of crayfish tissue in the summer of 1975 was 3.30 ± 0.09 KJ/gm w.wt. Seasonal variations would have been expected (as observed for Calanus finmarchicus by Comita & Schindler 1963); particularly in view of the short growing season and low water temperatures during the winter (minimum 3.4°C, 1.2.5, 3.3) but sample size and frequency were too low to demonstrate this. For the purposes of the conversion of the approximate estimate of P_a into energy units CV was assumed constant throughout the life cycle and from year to year (CV for eggs and adults, Table 7.1).

Production in energy units for 1976 was estimated as:-

$$\hat{P}_a = 56.27 \pm 21.05 \text{ KJ/m}^2\text{/annum}$$

Calorific value per gram dry weight was also calculated so that comparisons could be made with estimates for other species. Dry weight was a mean proportion of 24.16 ± 2.44% of wet weight ∴ CV = 13.66 ± 1.74 KJ/gm dry weight.

Table 7.1: A comparison of the calorific values of several Crustacean orders

Order	Species	n	KJ/gm a.f.d.w. ± SE	Reference
Anostraca	*Artemia* sp (nauplii)		28.295 ± 1.849	Slobodkin & Richman 1961
"	*Streptocephalus seali*		20.714 ± 0.773 (SD)	Comita & Schindler 1963
Calanoida	*Calanus finmarchicus*	5	26.750 ± 0.546	Phillipson 1964
"	*Calanus helgolandicus*		22.680 ± 0.414	Slobodkin & Richman 1961
"	*Diaptomus arcticus*		23.087 ± 1.300 (SD)	Comita & Schindler 1963
Cladocera	*Daphnia pulex*		18.808 ± 1.562 (SD)	" "
"	*Daphnia* sp	18	18.560 ± 2.134 (SD)	Golley 1961
"	*Leptodora kindtii*		23.541 ± 1.226	Slobodkin & Richman 1961
Concostraca	Concostracan *		21.861 ± 0.487 (SD)	Comita & Schindler 1963
Cyclopoida	*Mesocyclops edax*		23.008 ± 0.407 (SD)	" "
Euphausiacea	*Euphausia krohni*	3	22.054 ± 0.550	Phillipson 1964
Decapoda	*Cherax albidus*	5	21.168 ± 0.472	Woodland 1967
"	*C. albidus* (eggs)	1	26.977	"
"	Crayfish, immature*		18.593 ± 1.554 (SD)	Comita & Schindler 1963
"	*Orconectes virilis*	25	20.148 ± 2.439 (SD)	Kelso 1973
"	*Uca* sp & other crabs*	8	19.270 ± 3.623 (SD)	Golley 1961
"	*A. pallipes*	59	22.04 ± 3.29	Author
"	*A. pallipes* (eggs)	3	27.38 ± 4.01	Author

n = number of determinations, where stated
* = unknown genus

The conversion of this value to ash free dry weight (a.f.d.w.) using ash weights after bomb calorimetry would have tended to overestimate CV as when material is burnt in the bomb at temperatures of around 1,000°C $CaCO_3$ starts to break down to CaO thus reducing the weight of the remaining ash. However, a more important point is that this breakdown is endothermic, all determinations of CV by bomb calorimetry are therefore underestimates (Winberg 1971, Paine 1966).

In order that these determinations were comparable to other species where ash content was determined separately a small sample of crayfish (10) were burnt in a muffle furnace at ca. 450°C for 48 hours following drying and the proportion of dry weight that was ash was estimated as 38.02 ± 0.83%; this was some 8% higher than that after burning in the bomb (30.55 ± 0.97%). Therefore assuming that this mean percentage ash was representative over the whole size range (% ash may increase in larger individuals due to the positive allometric growth of the chelae with their heavily ossified cuticle, 3.8; Woodland 1967):-

$$CV = 22.04 \pm 3.29 \text{ KJ/gm. a.f.d.w.}$$

The estimated CV of A. pallipes in the summer of 1975 was comparable to all available estimates of other crustacean species and those of many other species (references Table 7.1) as predicted by the hypothesis of Slobodkin and Richman (1961) that CV of many different species would have a skewed distribution with the modal frequency at or near the lower range limit. The

relatively large SE for this estimate of CV for A. pallipes resulted from the fact that dry weight was not recorded in all cases and KJ/gm. a.f.d.w. had to be calculated indirectly from KJ/gm w.wt. using estimates of percentage water and ash both based on relatively small samples ($n < 20$) i.e. three steps were required and errors accumulated at each step.

7.3 Discussion

A representative cross-section of the available estimates of some population parameters, including all estimates of annual production ($\hat{P}_a$) and mean annual biomass ($\bar{B}$), for several foreign species and all estimated parameters available for A. pallipes were listed on Table 7.2. The 'population' of animals to which these estimates apply has not always been clearly defined and it was strongly suspected that some authors who claimed to have estimated total population size had been more able to make certain that this was in fact what they were doing than others; this could have resulted from variations in sampling methods, substratum and growth rates e.g. Flint (1975) estimated ca. 10 P. leniusculus/m^2 in some transects of the littoral zone of Lake Tahoe using SCUBA equipment and metal hoops to contain the quadrat being sampled, this was the highest estimate in the literature for this species (cf. Mason 1974, Goldman & Rundquist 1978, Niemi 1978) and came from an oligotrophic lake (Abrahamsson & Goldman 1970).

Table 7.2: Estimates of population parameters for several crayfish species

Species	Population	Sampling methods	Environment	Substratum	Method of Estimation	Population size ± SE or seasonal range**	Density/m^2	Biomass (B) Kg. w.wt./ha	Production (P) Kg. w.wt./ha	Reference
Astacus astacus	Total	Trapping and electro-fishing	Artificial pond Sweden	Littoral zone mainly largish stones	Lincoln Index	ca. 50,000 ± 2,345*	ca. 2.0			Abrahamsson (1966)
A. astacus	Total	Trapping and SCUBA collection	Berziukas Lake, Trakai District U.S.S.R.	Not stated	Cukerzis (1959)	18,000	ca. 1.5	$\hat{B}$ (October)=60	$\hat{P}_a$ = 42	Cukerzis (1974)
Austropotamobius pallipes	All ≥ 13 mm. C.L.	Hand collection at lowered water level	The aqueduct (1.1) Northumberland U.K.	Sandstone block walls, some loose stones	Jolly (1965)	9,945 - 25,917**	3.8-10.4	$\bar{B} \simeq 409.7$	$\hat{P}_a$ 170.5	Author
A. pallipes	Not stated but unlikely that small individuals included	Hand collection and bottom samplers	One hundred m^2 of the River Brett, Suffolk U.K.	Not stated	Quadrat sampling	Not stated	ca. 4			Davies (1964)
A. pallipes	Mostly adults	Hand collection at lowered water level	540 m^2 of a small stream, Geneva basin, France	Clay banks, nature of bottom not stated	Quadrat sampling but some animals were missed ∴ an underestimate of $\hat{N}$ = 920		At least 1.7 adults			Laurent (1972)
A. pallipes	All ≥ 13 mm. C.L.	Hand collection at lowered water level	Section of the River Ouse, Bucks. U.K.	Many large stones > 25 cm. across	Quadrat sampling	Not stated	ca. 7			Pratten pers. comm.
Cherax albidus	Total	Trapping	Agricultural dam, N.S.W., Australia	Clay with many fallen trees	Lincoln Index	1,189 - 4,077**	1.2-4.3	$\bar{B}$ 340	$\hat{P}_a$ 672	Woodland (1967)
Orconectes virilis	Unstated, probably adults only	Trapping	Small pond. Massachusetts U.S.A.	Boulders on sand or mud	Schumacher & Eschmeyer (1943)	ca. 3,066	ca. 2.0			Camangis and Hichar (1959)
O. virilis	Total	Trapping and some netting	A marl lake, Michigan, U.S.A.	Sandy, many logs in littoral zone	"	28,010 - 214,004**	1.9-14.3	$\hat{B}$max 119.5	$\hat{P}_a$ 205.3	Momot (1967)
O. virilis	Total	Trapping and dip nets	Three lakes in Michigan, U.S.A.	"	"	Ranges over 3 years: 1. 29,696 - 91,194 2. 35,165 - 67,785 3. 40,161 - 60,279	 2.1-6.5 1.9-3.6 2.5-3.8	$\bar{B}$ 58.6-212.7 45.9-116.0 64.4-126.8	$\hat{P}_a$ 86.9-133.4 60.2- 84.6 110.3-141.8	Momot and Gowing (1977)

Table 7.2 (Continued)

Species	Population	Sampling methods	Environment	Substratum	Method of Estimation	Population size ± SE or seasonal range	Density/m^2	Biomass (B) Kg. w.wt./ha	Production (P) Kg. w.wt./ha	Reference
Pacifastacus leniusculus	Adults in littoral zone (< 40 m. deep)	Trapping and SCUBA collection	Lake Tahoe, California, U.S.A.	Variable in littoral zone sand to boulders	Cukerzis (1959)	ca. 55.5×10^6	ca.0.9			Abrahamsson and Goldman (1970)
P. leniusculus	Adults	"	Artificial pond, Sweden As Abrahamsson (1966)	Littoral zone, mainly largish stones	Lincoln Index	ca. 9,000 ± 1,300	ca. 0.4			Abrahamsson (1971b)
P. leniusculus	Total	"	Three transects of Lake Tahoe, California, U.S.A.	Varied from small boulder to sand	Schnabel (1938)	16,561 - 192,448	mean 10.04	$\overline{B}$ = 998	$\hat{P}_a$ = 306	Flint (1975)
Pacifastacus leniusculus trowbridgii	Total	Trapping, benthos sampler and minnow seine netting	Berry Creek, Western Oregon, U.S.A.	Boulders on gravel with some silt	"	926 - 1,608‡‡	1.0 - 1.7	$\overline{B}$ = 124.6	$\hat{P}_a$ = 133	Mason (1974)
Procambarus acutus) Orconectes propinquus) Orconectes rusticus)	Various combinations of 1-3 species; excluding young of the year	Trapping and SCUBA collection	Forty-one lakes in Northern Wisconsin U.S.A.	Variable	Quadrat sampling	Not stated	0-15			Capelli (1975)

ca. = approximate estimate

‡ = SE calculated from authors data

‡‡ = seasonal range of N

$\overline{B}$ = mean annual biomass

$\hat{B}$ = biomass at one time of year e.g. B(October) or maximum biomass, Bmax

$\hat{P}_a$ = annual production

All crayfish species show marked substrate preferences (e.g. Aiken 1968, Kossakowski 1971) and although these vary from species to species they all involve either ready made 'hides' amongst stones, aquatic plants, roots and/or fallen trees or a substratum into which some species excavate burrows which range in form from a simple depression to elaborate chambered cavities with 'chimnies' as an insurance against a fall in water level (3.3). One of the major factors determining crayfish density was widely acknowledged to be substrate type (Capelli 1975, Flint 1975, Niemi 1978) and A. pallipes was no exception as demonstrated by the much higher densities found over stony substrates (1.1, 3.6.1, Pratten pers. comm.) than over stream or river beds which contained more silt (Davies 1964, Laurent 1972).

An approximate estimate of Pa for A. pallipes in the aqueduct was calculated by making several assumptions concerning the mortality patterns of crayfish < 13 mm. carapace length and the variations in age structure and mortality of the total population from year to year. One interesting observation resulting from these calculations was that the ratio of total estimated growth per annum between adult males and females was 1.78. When egg production was taken into account the ratio of total estimated annual production between the sexes was 1.65 (7.2.2). As the total biomass of eggs produced in 1976 was estimated as 583 gms. (only 7.1% of $\hat{P}a$ for the adult females, 7.2.2) and the calorific value of crayfish eggs was found to be only 24% higher than that of post-

hatching crayfish (7.2.3) the much lower $\hat{P}a$ in the adult females compared to the adult males was not accounted for by the direct energetic demands of reproduction. This difference may have been due to adult females feeding less particularly when they bore eggs overwinter from November to August (3.3). This would have been consistent with the evidence from trap catches that females tended to avoid behavioural interactions with other crayfish at some stages of the reproductive cycle (6.3.4).

Woodland (1967) estimated that 1.4% of the net annual production of Cherax albidus was accounted for by egg production; this compared well to the estimated 1.38% ($\hat{P}_{3b}/\hat{P}a$ = 583/43,323, 7.2.2) in this study. The adult females of C. albidus were also observed to grow much more slowly than the adult males and Woodland (1967) attributed this to the energy "cost of rearing the young".

The estimated mean annual biomass ($\bar{B}$) for A. pallipes in the aqueduct was the second highest listed on Table 7.2 as expected from the high mean density; both P. leniusculus and C. albidus had high values of $\bar{B}$ due mainly to their high maximum weights (Table 7.3). The estimated annual production ($\hat{P}_a$) was however in the middle of the range in absolute terms and second to the lowest value relative to $\bar{B}$ (Fig. 7.3). Net annual production for A. pallipes in energetic terms was estimated as 56.27 KJ/m^2/year, this was considerably less than the 284 KJ/m^2/year estimated for C. albidus by Woodland and the 147 KJ/m^2/year of a mixed population

Table 7.3: Estimated annual production ($\hat{P}a$) per unit of mean annual biomass ($\bar{B}$) and some aspects of the life history at the end of the year to which these estimates refer of five species of freshwater crayfish

Species	Males		Females		'gms/year'	$\hat{P}_a/\bar{B}$	Reference
	Maximum weight	Maximum life span (years)	Maximum weight	Maximum life span (years)			
Astacus astacus	88.5	7	29.3	5	9.3	0.70	Cukerzis (1974)
Austropotamobius pallipes	38	11	18	9	2.7	0.42	Author
Cherax albidus	87	3	44	3	21.8	1.98	Woodland (1967)
Orconectes virilis	21	3	15	3	6.0	1.72	Momot (1967)
O. virilis	17.3	3	11.5	3	4.8	0.94	Momot & Gowing (1977)
	21.0	3	13.1	3	5.7	1.33	
	21.6	3	14.7	3	6.1	1.32	
	17.5	3	14.9	3	5.4	1.00	
	18.5	3	14.2	3	5.5	1.19	
	24.4	3	15.0	3	6.6	1.23	
	19.1	3	15.2	3	5.7	1.17	
Pacifastacus leniusculus	60.9	11	60.9	11	5.5	0.31	Flint (1975)
Pacifastacus leniusculus trowbridgii	54.8	8	54.8	8	6.9	1.07	Mason (1974)

'gms/year' - mean of the maximum wet weight divided by the maximum life span in years of both sexes

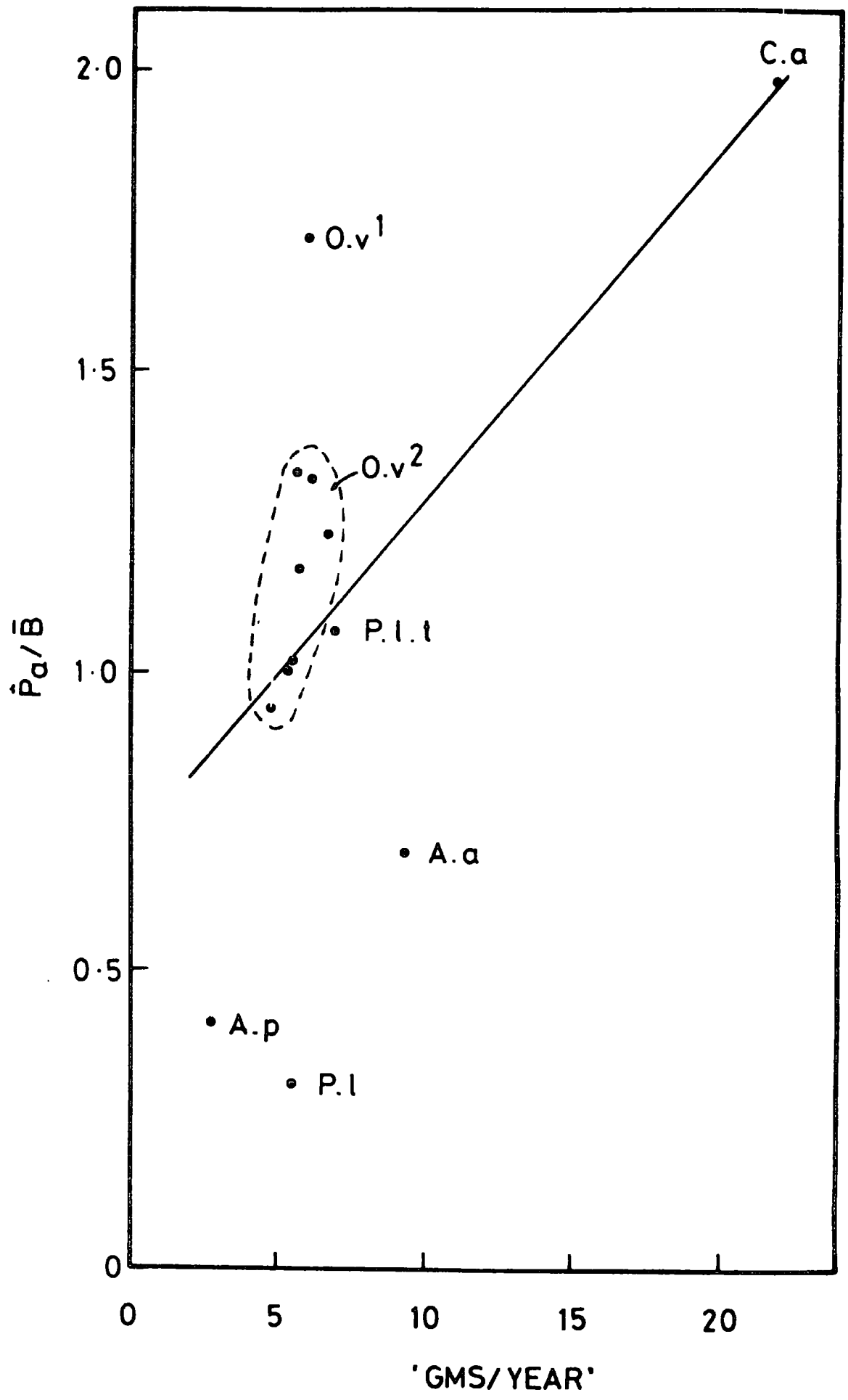
Fig. 7.3: The estimated annual production ($\hat{P}_a$) per unit of mean annual biomass ($\bar{B}$) as a function of the mean of the maximum wet weights attained by any individual of both sexes divided by the maximum life span in years ('gms./year') in five species of freshwater crayfish

$y = 0.0584x + 0.6950$

SE of slope = 0.0240

$r = 0.5922$, $t = 2.44$, 11 d.f., $p < 0.05$

A.a	- Astacus astacus	Cukerzis (1974)
A.p	- Austropotamobius pallipes	Author
C.a	- Cherax albidus	Woodland (1967)
O.v^1	- Orconectes virilis	Momot (1967)
O.v^2	- Orconectes virilis	Momot & Gowing (1977)
P.l	- Pacifastacus leniusculus	Flint (1975)
P.l.t.	- Pacifastacus leniusculus trowbridgii	Mason (1974)


2·0
1·5
1·0
0·5
0
$\hat{P}_\alpha/\bar{B}$
C.a
O.v 1
O.v 2
P.l.t
A.a
A.p
P.l
0
5
10
15
20
'GMS/YEAR'

of Uca pugilator, Uca pugnax and Sesarma reticulatum by Teal (1962). This low estimate of net production was probably a reflection of the relatively short growth season (ca. 13 weeks, 3.3). A comparable level of production (45 KJ/m^2/year) was observed in the short-lived, herbivorous grasshopper, Orchelium fidicinium by Smalley (1960).

The theoretical inter-relationship between production, growth and biomass has been examined in detail by Momot and Jones (1976); for th s data there was a significant positive correlation between the annual turnover ratio ($\hat{P}_a/\bar{B}$) and an index of annual growth ('gms/year'; Fig. 7.3, $p < 0.05$). This was predicted as higher productivity was usually explained by faster growth not lower mortality, as pointed out by Woodland (1967). In order to select a suitable animal for intensive culture, on theoretical grounds one of the most important priorities would be that the $\hat{P}_a/\bar{B}$ ratio be high, providing that this animal could maintain itself at a high biomass in the intended environment and produce a high absolute value of $\hat{P}_a$ and therefore a high sustained yield (a more rigorous approach would be to compare the $\hat{P}_a/\bar{B}_o$ - initial biomass - ratio as this accounts for all the effects of mortality and growth throughout the life cycle but this ratio has rarely been computed; Winberg 1971).

On this basis C. albidus is the best choice as although the Lake Tahoe population of P. leniusculus

had a higher mean annual biomass the rapid growth rate of C. albidus (Table 7.3) results in its $\hat{P}_a$ having been more than twice as large. However, it seems very likely that all crayfish species non-indigenous to the North American continent are susceptible to A. astaci and this makes it a poor choice for most purposes (Unestam 1972). The densest and most productive populations of a resistant crayfish species that were known to the author were of the Louisiana red swamp crayfish, Procambarus clarkii; $B \simeq 2{,}000$ Kg. w.wt/ha (Huner 1978) and $P_a \simeq 1{,}000$ Kg.w.wt/ha (de la Bretonne and Avault 1978). This would seem to make it the ideal species with which to rapidly repopulate crayfish waters affected by A. astaci; however, this species is considered a pest in many areas due to its burrowing habits (Lowery & Mendes 1977, Momot 1978a, Penn 1954). By far the most popular species for introduction into Europe has proved to be P. leniusculus (e.g. Abrahamsson 1972c, Brinck 1974, Fuke 1978). This species is resistant to the plague and has a high $\hat{P}_a$ value at high biomass (Flint 1975) but had a $\hat{P}_a$ very similar to A. pallipes in a woodland stream (Mason 1974). These differences may have been related to substrate type in which case P. leniusculus in a stony bottomed watercourse relatively free from silt and yet with a high input of aquatic or terrestial primary production would have been expected to produce high yields. There is, as yet, little direct evidence that this is the case; Abrahamsson (1971b) found that P. leniusculus in an artificial pond from which A. astacus

had disappeared due to plague had a moult increment more than twice that of the latter species, the P. leniusculus population was, however, much less dense than that of A. astacus which had previously existed there and indeed this population had grown slowly even relative to other contemporary stocks of A. astacus. A comparison of the mean annual standing crop of P. lenuisculus in Lake Tahoe (1.1×10^6 Kg) and the annual harvest of A. astacus from Lake Hjälmaren in Sweden, which is similar in area, before A. astaci reached this population (ca. 1.06×10^5 Kg) suggests that these two species could provide similar yields but does not necessarily mean that P. leniusculus would do equally well in the latter environment (Abrahamsson & Goldman 1970). In the case of a long-lived invertebrate such as P. leniusculus, however, it will obviously be some time before there are any answers to such questions; recently Brinck (1978) has stated that P. leniusculus seems a satisfactory replacement for A. astacus in some Swedish waters.

As stated in the introduction to this section there were not, in the author's opinion, any sound reasons for introducing foreign crayfish species into the U.K. as our native stocks probably remain unaffected by A. astaci (5.1). There is good evidence to suggest that these stocks are extensive (5.1, Table 7.2, Thomas & Ingle 1971) and present an as yet largely untapped source which is available at negligible cost to anyone wishing to exploit the European demand and high market prices for crayfish.

GENERAL DISCUSSION

The main aims of this study were; first, to make detailed observations of the life cycle and biomonics of a population of A. pallipes in Northumbria and, secondly, to estimate the abundance and investigate the population dynamics of A. pallipes at this location (the aqueduct, Chapter 1). The achievement of the first main aim is an essential preliminary to any attempt to tackle the second in all population studies (Varley & Gradwell 1970).

A considerable amount of data describing several of the major aspects of the life cycle and bionomics of A. pallipes was collected by sampling the aqueduct, on seventy-two occasions, with traps and by hand-collection (Chapter 3 & 4). The timing of the beginning and end of the growth season, fertilization, the extrusion and attachment of the eggs to the pleopods, the hatching of the eggs and release of the young were all remarkably consistent from year to year (section 3.3). Seasonal trends in water temperature were also quite similar, although some relatively small differences corresponded to slight differences in the timing (up to one week) of

some of the above stages in the life cycle. These observations and comparisons with other reports for A. pallipes populations, all of which were at least 120 km. south of the aqueduct, led to the conclusion that water temperature was one of the most important environmental factors controlling the timing of the life cycle; as has been observed for many invertebrates in running-water (Hynes 1972). It is possible that changes in the annual trend of water temperature were merely modifying an endogenous circannual rhythm, as demonstrated in Orconectes pellucidus inermis by Jegla & Poulson (1970). Annual cycles of reproduction and growth, with growth being much slower in the winter months and the females carrying one brood of eggs for long periods each year, similar to that observed for A. pallipes in the aqueduct, appear to be the general pattern in many species of freshwater crayfish (with the exceptions of some members of the Cambarine sub-families and a few members of the family Parastacidae, see Discussion of section 3.3) and in almost all reptant, marine decapods (Allen 1966, Kaestner 1970). Hynes (1972) has observed that "animals with more than one generation a year are, as far as we know, relatively scarce in the running-water habitat".

The selective advantages, if any, of female decapods carrying their eggs attached to the pleopods for most of the year, in terms of reproductive tactics (Pianka 1978), appear to be obscure. Embryonic

development of the eggs overwinter is slow (Mason 1976b, pers. observations) and losses due to physical damage and disease are often considerable (section 3.4). It would, perhaps, be more efficient in terms of number of progeny produced, to mate and spawn after the overwinter period when water temperatures have begun to increase; however, the females may not have the energetic resources to produce eggs at this time, egg attachment may be less efficient at higher temperatures (pers. observations) or there may not be a sufficient number of 'day degrees' after spawning at this time to allow hatching and growth to a size at which survival of the young overwinter is maximized (Abrahamsson 1972a). As this pattern of reproduction is so widespread amongst decapods it may be that this was the most 'efficient' tactic for some very early common ancestor to the present day decapods and that the majority of these have since experienced insufficiently keen selective pressure to have further evolved. This would be consistent with the fact that the number of instances where there would be expected to be intense competition, for food or any other natural resource, between a decapod species and that of another group or between decapod species, appear to be few (sections 3.2 and 3.3). Indeed, where competition would be expected to be more intense, between the many crayfish species identified from Australia (Riek 1969) and North America (Hobbs 1972, 1974a), some species produce several generations

each year and a few have been shown to store sperm for considerable periods (sections 3.3 & 3.4). However, these species may experience higher water temperatures than the four European species and this alone may make repeated reproduction and a short period of egg-attachment physiologically possible (e.g. Albaugh 1973, de la Brettone & Avault 1976, Caldwell & Bovbjerg 1969, Capelli 1975, Franz 1977, Goellner 1943, Kaestner 1970, Morrissy 1970, Penn 1943, Weagle & Ozburn 1972, Woodland 1967).

The internal and external factors controlling the reproductive cycles of freshwater crayfish are poorly understood but are, to some extent, clearly open to experimental investigation. It is known that these cycles can be artificially manipulated, within limits, and this may be important in producing the maximum number of offspring at the optimum time for restocking and aquaculture programs (Mason 1976a & b).

A. pallipes grew relatively slowly in the aqueduct taking an estimated ten to thirteen years to reach a maximum size of 50 mm. carapace length (Chapter 4). This was probably mainly owing to the low water temperatures (recorded water temperatures only exceeded 12°C during ca. two months of each year from 1974-76, Chapter 1) which resulted in the moulting season being a short one (ca. 12 weeks, Chapter 3). Despite the paucity of the literature on A. pallipes there are several indications that growth is considerably faster

in more southerly populations (see sections 3.3 & 4.5). Food availability may also limit the growth rate of A. pallipes in the aqueduct, although this was not investigated in this study. A comparison of the nutritional status (e.g. as calorific value of whole animals or the hepatopancreas) of crayfish from several locations with similar temperature regimes but with obvious differences in the quantity of food available, or the comparison of growth rates (and reproductive rates) before and after cropping a proportion of the aqueduct population would both be informative concerning the relative importance of water temperature and food availability as regards growth and reproduction.

The loss of limbs and infestation by the parasite Thelohania contejeani both resulted in smaller growth increments at the moult (section 4.3.1) but had no apparent effect on moult frequency (sections 4.3.2 and 4.4.3). However, by far the largest difference in mean moult increments (M.I.'s) was between normal males and females (mean female M.I. 20% < mean male M.I., 4.3.1). That this was not entirely due to the energetic demands of egg-production was apparent from two of the results obtained: the mean M.I.of females that had borne eggs in the previous reproductive cycle was significantly lower (by 17%) than those which had not, but these latter non-reproductive females also grew less than males (by 15%); also the energy content of the estimated number of eggs produced was only 1.4% of

the total estimated annual production (Chapter 7). There was some evidence from trap returns (Chapter 6) that these differences in growth rates were a result of animals lower down the proposed dominance order being disadvantaged when competing for food; a similar tentative conclusion was drawn by Abrahamsson (1966, 1972a). Dominance orders, and the associated intra-specific behaviour patterns, are common amongst the Decapoda (Allen 1966).

Differences in growth rate after maturity have often been observed in the decapod Crustacea, particularly in reproductive females which cannot moult whilst bearing eggs. In species with a short life span (< 5 years), such as the Natantia and smaller Reptantia, the lower moult frequency of the female does not result in a slower growth rate as the females grow rapidly in the non-reproductive season. However, in the longer-lived forms (including A. pallipes) the male and female are similar in size at sexual maturity but thereafter the growth rate of the female is slower than the male (Allen 1966).

Many adult female crayfish in the aqueduct population did not carry eggs each year; this was particularly so in the smaller size classes (section 3.4). In terms of reproductive tactics it would be predicted that natural selection would favour early breeding as, although these smaller crayfish carry fewer eggs, they are many times more numerous than the larger size

classes and would therefore leave the maximum number of progeny (Pianka 1978). In some populations of A. pallipes almost all adult females do bear eggs every year (96%, Thomas & Ingle 1971; Pratten pers. comm.) as expected from the evolutionary hypothesis. However, these populations were in the south of England; it would appear, therefore, that reproduction is limited by temperature and/or food availability in the aqueduct and females breed as soon as they are physiologically capable. This would be consistent with the contention that A. pallipes in the aqueduct is near to its natural, northern limit of distribution (section 3.2, c f. Abrahamsson 1972a).

Individual A. pallipes were often displaced over considerable distances between trap captures (section 3.6.2). These displacements, or net movements, appeared to be random and implied that A. pallipes did not have a recognizable home range in the aqueduct. Both natant (Allen 1966) and reptant decapods (Herrnkind 1969, see also section 3.6.2) are very mobile arthropods and have often been reported to undertake mass migrations which are usually associated with reproduction. The function of the apparently random 'movements' of A. pallipes in the aqueduct was not known. However, the evidence from continuous round-the-clock trapping indicated that there was considerable 'activity' by day, as well as by night (section 3.6.3); such observations have been attributed to

obligate feeding by day, despite the increased threat of predation, in other dense crayfish populations (Abrahamsson 1971a, Capelli 1975, Flint 1975, 1977). The following five pieces of evidence indicated that intraspecific competition, particularly for food, may be intense in the aqueduct population: A. pallipes seemed to be an opportunistic feeder (section 3.5); the aqueduct was relatively homogeneous throughout most of its length with respect to the many available hides; most of the available food had a clumped distribution (mainly Fontinalis antipyretica, Chapter 1); population density was relatively high (density of crayfish $\geq$ 13 mm. carapace length 3.8 - 10.4/m^2, maximum potential recruitment at hatching $\simeq$ 18/m^2; Chapters 3 & 5) and a dominance order was strongly suspected on the basis of trap catch composition (Chapter 6). The ability to move long distances may, therefore, be an important behavioural tactic for finding sites at which to feed (i.e. where the individual is not ousted by a dominant animal), or finding a hide, and may account for the apparently random movements observed.

It had been hoped to follow the movements of individuals by tagging them with a radioactive cobalt source but as the recovery of the tag could not be absolutely guaranteed the Water Company was unable to grant permission to carry this out. Continuous records of the position of individuals, rather than displacements

between captures, would be of considerable value in the interpretation of crayfish behaviour under natural conditions.

As hand-collection was the only method by which reliable mark-recapture estimates of population parameters could be obtained, it was only possible to obtain reasonably accurate estimates for these parameters over one twelve month period from May 1976 to June 1977. Approximate density estimates were also obtained during the summer months of 1974 and 1975 (Chapters 5 & 6). An attempt was also made to calculate a rough estimate of the annual production and mean annual biomass in 1976 (Ricker 1971, Winberg 1971; Chapter 7).

The setting of baited funnel traps is a common method of catching reptant decapods (e.g. Hiatt 1948, Kaestner 1970); indeed, it is the only universally applicable one (Capelli 1975). It was obvious from the first few trap samples taken from the aqueduct that the composition of these samples was not equally representative of all components of the population. Any population size estimates, using mark-recapture methods, from data collected by any sampling method to which all members of the population are not equally prone are invariably negatively biased (Bohlin & Sundström 1977, Ricker 1971, Seber 1973). As traps have often been used in mark-recapture studies of the population dynamics of freshwater crayfish trapping was continued in the aqueduct as a methodological

examination of this technique (Chapter 6). It was calculated that this method produced a threefold underestimation of the size of the total adult and adult male sub-populations by mark and recapture. There was a considerable amount of evidence that this bias was, to a large extent, due to innate behaviour patterns; there was also some indication that a learned component may have contributed as demonstrated by Morrissy for Cherax tenuimanus (1973, 1975). Similar behaviour patterns have been reported for fish (Ricker 1958, 1971) and small mammals (e.g. Keith & Meslow 1968, Kikkawa 1964). It is, therefore, strongly recommended that trapping be used only for capture or recapture, in a Lincoln index type estimate of the size of populations of reptant decapods, and not for both operations; a completely independent method being used to collect the other sample in the pair (as suggested by Junge 1963 and Seber 1973). Such estimates should then be relatively free of any sampling bias; the accuracy of the estimates obtained by hand-collection from the aqueduct was confirmed by pairing hand and trap samples in this way. The mean estimates from the hand-collected, hand-recaptured samples and hand-collected, trap-recaptured samples were as follows: total adults 9,111 $\pm$ 2,771 and 6,331 $\pm$ 1,363 respectively and adult males 4,395 $\pm$ 1,798 and 3,787 $\pm$ 697 respectively, see Chapter 6.

The seasonal cycle of abundance of A. pallipes appeared to be a simple univoltine one (Chapter 5; i.e. population numbers increased dramatically, at birth, once each year and decreased at all other times, Hynes 1972). The density of A. pallipes of carapace length $\geqslant$ 13 mm., as estimated by mark and recapture, was at its highest of 10.4/m^2 in August 1976, following 'recruitment' from the smaller sized crayfish during the first two months of the growth season. This fell to 3.8/m^2 the following May after losses due to emigration and deaths. The main causes of death in the population were believed to be cannibalism and difficulty in withdrawing from the old exoskeleton (or other physiological trauma) at the moult and low temperature stresses over-winter (Chapter 5). As hatching of the eggs occurred in early August (recruitment into the total population) and growth occurred from late June to mid-September (recruitment into the population studied by mark and recapture) the seasonal cycle of abundance of the population of consistently catchable size probably reflected that of the total population.

This seasonal cycle of abundance was similar to that of many insects, which are either wholly or partially aquatic, as these are often univoltine; the exception being that, in many cases, these die out completely each year and are then present only as eggs until hatching (Hynes 1972). The many overlapping generations of crayfish present at any one time is a

feature more commonly found amongst vertebrate populations; crabs and crayfish being one of the few invertebrate groups in which this is found in freshwater (Hynes 1972).

The possible causes and effects underlying the cycles of abundance of natural populations have been reviewed by Pianka (1978). The two extreme types of variations in abundance are illustrated by "opportunistic" populations (usually at low density or in a "competitive vacuum", these populations vary in size in erratic, or regular, bursts) and "equilibrium" populations (environment is "saturated"; populations exist at "stable" sizes, provided resources do not change, with relatively small, often regular, seasonal cycles of density). "Clearly these two sorts of populations represent endpoints of a continuum; however, the dichotomy is useful in comparing different populations." (Pianka 1978) The selective forces which operate under these very different conditions have been designated as the two opposing forces of r selection and K selection. In terms of natural populations these are usually neither completely r selected or K selected but lie somewhere between the two; therefore, when comparing different species one species can only be termed an "r-strategist" or a "K-strategist" relative to another species (Pianka 1978). Brinck (1976) has considered Pacifastacus leniusculus introduced into crayfish-free waters in Sweden as an r-species relative to the

populations of Astacus astacus which were native to those waters, before being exterminated by the plague, and has stated that this is advantageous in terms of recolonization.

Pianka (1978) has listed some of the correlates of r and K selection and on the basis of these A. pallipes in the aqueduct would appear to be a K-strategist relative to most other invertebrates and the majority of other species of freshwater crayfish (see Tables 4.7 and 7.2). Some of these correlates were as follows: environmental conditions fairly "predictable" (sections 1.2 and 3.3); mortality more "directed", rather than "catastrophic", probably density dependent (e.g. cannibalism and infestation by Thelohania contejeani, Chapter 5); population size "fairly constant in time, equilibrium, at or near carrying capacity of the environment; saturated communities; no re-colonization necessary" (density, animals $\geq$ 13 mm. carapace length, similar in summer months 1974-76 at ca. 8+ crayfish/m^2; density varied from 10.4 - 3.8/m^2 from August 1976 to May 1977; also Brewis unpubl.); intraspecific competition "usually keen" (predicted from relatively high density of crayfish $\geq$ 13 mm. carapace length; maximum recruitment at hatching $\simeq$ 18/m^2, section 3.4; limited amount of food and number of hides available). Under these conditions "selection favours": "slower development" (maturity in 3+ year class, maximum life span 10-13 years, section 4.3.3);

"delayed reproduction" (first breeding at age 3+ years, many females do not bear eggs until several years later, section 3.4); "repeated reproduction" (see section 3.4); "fewer, larger progeny" (crayfish hatchlings of different species are usually of similar sizes, Chapter 4; but as A. pallipes is a small species its progeny are relatively large). The longer length of life "leads to efficiency" and suggests a "stage in succession" from "late" to "climax" (Pianka 1978).

It was considered possible that this relatively simple ecosystem could be approaching climax as although the aqueduct was not constructed until 1871 (Newcastle & Gateshead Water Company 1969) crayfish were reported from Whittle Dene in 1909 (these reservoirs were constructed in the mid-nineteenth century and interconnect with the aqueduct, Newcastle & Gateshead Water Company 1969; Norman & Brady 1909) and the aqueduct population may, therefore, be sixty or more years old.

Growth has often been demonstrated to be a key factor in determining net annual production (e.g. Chapter 7, Momot & Jones 1976, Woodland 1967); although under certain circumstances mortality may be of primary importance (e.g. Flint 1975). Despite the slow growth and relatively small maximum size of A. pallipes in the aqueduct, the high density resulted in an estimated net annual production of 171 Kg. wet weight/ ha. which was comparable to some faster growing species

(see Table 7.2); the estimated mean annual biomass was also relatively high (410 Kg. wet weight/ha.) resulting in a low "turnover ratio" of 0.42 (Waters 1969; see section 7.3). The enormous populations of A. pallipes which must be present in some reservoirs (Holdich et al. 1978, pers. observations) would, therefore, be expected to withstand cropping on a commercial scale.

The protozoan parasite Thelohania contejeani has been present in populations of A. pallipes in Northumberland for at least the past eleven years at below the 10% level (section 3.7). The majority of reports indicate that it is usually only a relatively small proportion of individuals ($< 10\%$) that are sufficiently infested to be diagnosed by external examination (Cossins & Bowler 1974, Holdich et al. 1978, Pixell Goodrich 1956, Mazylis 1978 and mean 6.6% in the aqueduct from 1974-77, section 3.7). There are reports of this disease reaching 'plague' proportions on the European continent (Calman 1911, Kossakowski 1971, Kudo 1924, Schäperclaus 1954) and one report that this may have occurred in Oxfordshire (Calman 1911, Pixell Goodrich 1956). Both Duffield (1933) and Pixell Goodrich (1956) suggest this disease may have been responsible for some isolated, but considerable, fluctuations in numbers of A. pallipes in the U.K.

However, the majority of the evidence would suggest that the normal interrelationship between this parasite

and its host is a balanced one; the extermination of populations of the natural host, the crayfish, are probably associated with unusual environmental circumstances or due to some other agency such as pollution or drought. A similar relationship is usually observed between the crayfish 'plague' fungus, Aphanomyces astaci, and indigenous populations of North American crayfish species which are the natural hosts to this parasite (Unestam 1969, 1972a; Unestam & Weiss 1970); although an exceptionally virulent infection, usually in laboratory cultures or dense populations, may be fatal to P. leniusculus (e.g. Fürst 1977, Unestam et al. 1976).

A classic example of the dangers inherent in the introduction of exotic species is provided by the effects of A. astaci on European crayfish stocks following its importation into Italy, probably on chronically diseased Orconectes limosus, in the late nineteenth century (Kossakowski 1971, Schweng 1972, Spitzy 1972, Unestam 1969, Unestam & Weiss 1970). Many crayfish populations, particularly of A. astacus and A. leptodactylus, have been wiped out as these species (and also A. pallipes and A. torrentium) have no resistance to, or more precisely are "over-susceptible" to (Unestam 1969, 1972b), this parasite (e.g. Abrahamsson 1972a, Brinck 1974, Fürst 1977, Hynes 1972, Laurent 1972, Spitzy 1972, Westman 1972, 1974). This is a totally unbalanced, unnatural host-parasite interrelationship where both host and parasite do not

survive for long in the same water body. All of the "tolerant" (Unestam 1969, 1972b) North American species of crayfish and the over-susceptible European ones belong to the family Astacidae and the tolerant P. leniusculus belongs to the same subfamily, the Astacinae, as the four native European species. It has been suggested that there may be sufficient "hidden" resistance in A. astacus (and presumably other astacin species also) that, with an increased knowledge of the host-parasite relationship, it might be possible to rear highly resistant strains of A. astacus (Unestam 1972b). Although this may be theoretically possible the state of knowledge in the field of arthropod mycopathology and the complexity of the natural, balanced host-parasite relationship make this seem unlikely in the foreseeable future (Unestam et al. 1976).

The effects of A. astaci in Europe and Scandinavia have been considered already but are reiterated here for emphasis as, despite these effects and the many other examples of planned and accidental introductions of organisms from almost all the phyla which have had rather less than beneficial effects, such introductions are still made (Elton 1958, Huner 1976, Lowery & Mendes 1977, Momot 1978, Penn 1954, Udvardy 1969, Unestam 1972b, 1974). The number of such introductions which prove to have been beneficial in overall terms are very few indeed (e.g. Momot 1978) and the possible

negative effects are no less than catastrophic (e.g. A. astaci and IPN, a fish disease, which could cause great damage to salmoniid stocks, Fürst 1976).

Crayfish are widely appreciated gastronomically in Europe and Scandinavia and the plague has caused considerable economic and recreational losses there (see General Introduction, sections 5.1 and 7.1). There is no direct evidence that crayfish plague has affected the abundance of our native stocks of A. pallipes, or even been introduced into the U.K., despite some suggestions which vary from the assumption that it must have crossed the English channel (e.g. Stellan Karlsson 1978, Stott pers. comm.) to crayfish being virtually extinct in the U.K. (see Holdich et al. 1978, sections 5.1 and 7.1). Although the extent of interest in eating A. pallipes in the U.K. is limited to a few isolated localities (Holdich et al. 1978, pers. observations) there are several good reasons why it would be most undesirable for the plague to come into the U.K.or to establish populations of introduced crayfish species such as P. leniusculus. These reasons are based on what is already known; past experience of faunal introductions would suggest there may be many more, perhaps even more serious, consequences.

These reasons are that the loss of crayfish from some water bodies results in weed-growth proceeding unchecked and the flow being 'choked' (Abrahamsson 1966, Unestam & Ajaxon 1978) and that the establishment

of populations of P. leniusculus, which is 'tolerant' of the plague and can carry spores, produces a potential reservoir of plague spores where this fungus could survive indefinitely and from which it could proliferate into our native stocks of A. pallipes. Without a 'tolerant' host to act as a carrier neither the plague nor the 'over-susceptible' crayfish survive long in any one water body and so an outbreak might be contained. Most lakes to which P. leniusculus has been introduced in Sweden contain infected crayfish (Fürst 1977, Fürst & Boström 1978, Unestam et al. 1976).

The importation of foreign crayfish species into the U.K. (see General Introduction, sections 5.1 and 7.1) has not been restricted to P. leniusculus juveniles produced under controlled conditions at the hatchery at Simontorps, Sweden (Abrahamsson 1972c) but has included some adult A. leptodactylus and Procambarus sp. (Bowler pers. comm.). Such uncontrolled introductions may bring not only crayfish plague but other diseases which may affect animals which are commercially important, such as fish (Fürst 1976).

In view of the undesirability of having crayfish plague, P. leniusculus (or any other foreign crayfish species), other diseases and possible ecological effects in the U.K. it would appear to be a matter of some urgency to pass legislation controlling importation of crayfish, and other invertebrates (in the author's opinion), into this country.

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Note

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APPENDIX 1

The composition of those samples of crayfish taken from the aqueduct which were included in the analyses presented in Chapters 5 and 6.

For an analysis of the sample size and structure of the hand-collections taken during the preliminary study in 1973-74 (Table 1) see section 5.3.3.

For an analysis of the sample size and structure of the hand-collections taken during the study of the population dynamics of A. pallipes in the aqueduct from 1975-77 (Table 2) see section 5.4.2.

For an analysis of the sample size and structure of the trapped samples taken during the methodological study of trapping as a sampling method for freshwater crayfish in 1975-76 (Tables 3 & 4) see section 6.3.1.

Table 1: Sample size, structure and associated parameters of the hand-collections taken in 1973-74

Date	No. of sections sampled	Water Temp.	Adults ♀♀	Adults ♂♂	Juveniles ♀♀	Juveniles ♂♂	Total marked & returned	Berried ♀♀
8.10.73	10	-	83	81	16	23	203	0
27. 3.74	8	4.3	9	13	23	20	65	5*
16. 5.74	8	7.2	21	40	26	28	115	8*
29. 5.74	8	10.7	35	25	14	16	90	12*
12. 6.74	8	13.6	14	33	59	54	160	3*
20. 6.74	8	-	41	48	29	36	154	8*
18. 7.74	2	13.3	23	36	38	7	104	7*
24. 7.74	2	12.7	18	39	34	26	117	2
31. 7.74	4	13.8	31	36	41	33	141	1
7. 8.74	8	13.8	37	41	64	62	204	0
11. 9.74	6	11.6	51	57	26	36	170	0

* - samples taken when all reproductive females bore eggs (i.e. excluding periods of fertilization and egg-laying)

Infestation by the parasite Thelohania contejeani was not systematically recorded in 1973-74.

Table 2: Sample size, structure and associated parameters of the hand-collections taken in 1975-77

Date	'Day'	Water Temp. (°C)	No. of sections sampled	Adults ♀♀	Adults ♂♂	Juveniles ♀♀	Juveniles ♂♂	Total marked & returned	Total Parasitized[‡] ♀♀	Total Parasitized[‡] ♂♂	Berried ♀♀
25. 6.75	1	11.1	19	79	114	117	135	445	-	-	-
1. 7.75	3	11.6	15	142	159	98	130	529	-	-	-
7. 7.75	5	11.3	9	189	241	134	169	733	-	-	-
26. 5.76	8	9.9	21	259	350	244	119	972	50	25	83*
11. 6.76	9	10.9	18	233	371	251	162	1,017	47	34	107*
27. 8.76	11	16.7	20	433	323	126	69	951	53	29	0
8.10.76	12	10.4	20	383	261	136	105	885	35	22	0
26.10.76	14	9.3	24	403	310	197	108	1,018	53	27	49
12. 5.77	1A	8.6	21	317	240	125	96	778	16	15	146*
27. 5.77	2A	9.1	26	244	223	118	92	677	22	10	123*
17. 6.77	3A	9.5	29	280	219	122	82	703	22	13	136*

* - samples taken when all reproductive females bore eggs (i.e. excluding periods of fertilization and egg-laying).

Infestation by the parasite Thelohania contejeani[‡] and the presence of eggs were not systematically recorded in the 1975 hand samples.

Table 3: Sample size, structure and associated parameters of the non-baited trap samples taken in 1975-76

Date	'Day'	Water Temp. (°C)	Days (↓ or ↓)	Hours (↓)	Adults ♀♀	Adults ♂♂	Juveniles ♀♀	Juveniles ♂♂	Total marked & returned	Total parasitized‡ ♀♀	Total parasitized‡ ♂♂	Berried ♀♀
Water level not lowered between setting & emptying (↓)												
6. 6.75		10.0	7	-	27	39	4	3	73	0	2	6*
11. 6.75		10.2	5	-	13	30	3	0	46	0	2	5*
19. 6.75		10.7	6	-	23	29	2	4	58	3	7	8*
18. 7.75		12.4	3	-	4	8	3	1	16	0	0	1*
23. 7.75		12.6	3	-	7	27	6	2	42	1	3	1*
Water level lowered between setting & emptying (↓)												
12. 6.75		10.2	1	4	31	51	15	7	104	1	2	13*
13. 6.75		10.6	1	4	41	57	12	7	117	8	3	10*
28. 6.75	2	11.1	9	5	9	24	4	3	40	2	2	3*
4. 7.75	4	11.3	6	5	11	23	8	3	45	1	0	3*
15. 7.75		12.4	11	5	9	26	1	2	38	1	0	1*
30. 7.75		16.1	5	1	9	50	1	1	61	0	4	3*
30. 5.76		9.8	4	5	57	109	5	0	171	5	5	27*
13. 6.76	10	11.7	2	5	92	131	14	3	240	16	10	32*
31. 8.76		16.2	4	5	59	119	1	1	180	1	9	0
15.10.76	13	10.2	7	5	62	132	1	1	196	3	4	0

Days (↓ or ↓) - no. days since traps set (↓) or since water level lowered (↓)
Hours (↓) - no. hours for which the water level was lowered
parasitized‡ - infested by Thelohania contejeani
* - samples taken when all reproductive females bore eggs (i.e. excluding periods of fertilization and egg-laying)

Table 4: Sample size, structure and associated parameters of the baited trap samples taken in 1975-76

Date	Water Temp. (°C)	Days	Adults ♀♀	Adults ♂♂	Juveniles ♀♀	Juveniles ♂♂	Total marked & returned	Adults parasitized‡ ♀♀	Adults parasitized‡ ♂♂	Berried ♀♀
20. 7.75	12.2	2	34	87	2	1	124	3	13	20*
25. 7.75	14.4	2	44	112	1	3	160	9	10	20*
2. 8.75	16.5	8	14	102	1	0	117	0	6	3
6. 8.75	17.0	4	9	107	1	0	117	0	10	1
12. 8.75	17.2	6	11	107	0	1	119	1	6	0
13. 9.75	12.6	24	36	111	0	0	147	4	26	0
1.10.75	10.7	17	53	69	0	0	122	4	10	0
17.10.75	8.9	16	41	78	0	0	119	4	11	3
28.10.75	9.6	11	25	98	0	0	123	9	11	7*
12.11.75	7.8	14	8	155	0	0	163	1	15	2*
30.11.75	4.6	18	5	100	0	0	105	1	8	5*
15.12.75	3.4	15	9	56	0	0	65	1	10	3*
25. 4.76	7.4	15	16	59	0	0	75	0	1	12*
18. 5.76	9.8	23	39	146	0	0	185	7	9	21*
27. 6.76	13.6	14	25	102	0	0	127	4	10	11*

Days since traps baited and set in the aqueduct

parasitized‡ - infested by Thelohania contejeani

* - samples taken when all reproductive females bore eggs (i.e. excluding periods of fertilization and egg-laying)