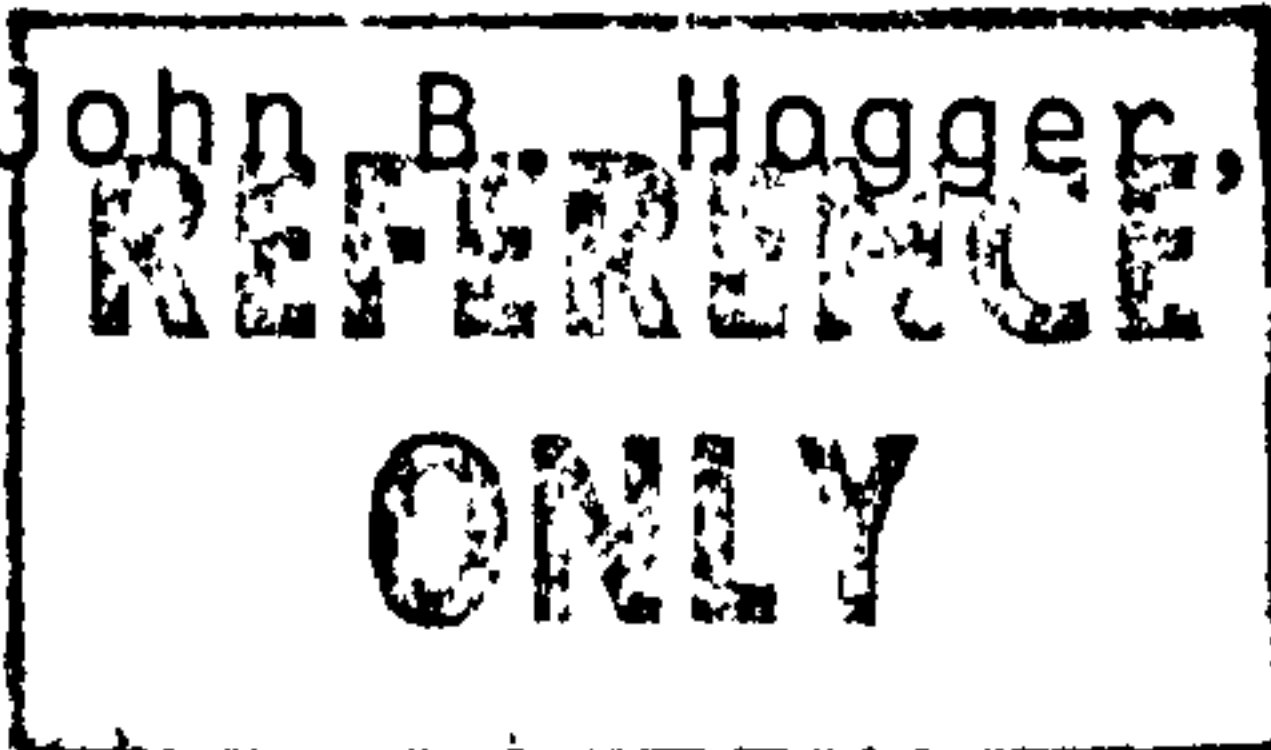


A STUDY OF
ASPECTS OF THE BIOLOGY AND
DISTRIBUTION OF FRESHWATER CRAYFISH
IN THE THAMES CATCHMENT.

by

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Being a thesis submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy.
(C.N.A.A.).

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A statement of the advanced studies undertaken in connection with the programme of research in fulfilment of the requirements of the degree.

(1). Participation in relevant seminars at the City of London Polytechnic.

(2). Attendance at meetings of the following professional societies:- Freshwater Biological Association; London Freshwater Group; British Microscopical Society; Institute of Fisheries Management; Institute of Biology.

(3). Membership of the International Association of Astacology; Institute of Biology and Freshwater Biological Association.

(4). Publication of a paper in the Journal of the Institute of Water Engineers and Scientists. (see Appendix 6.)

(5). Lectures given to:- 13th Fishery Management Course, Two Lakes, Hampshire. 1981. (proceedings published); Plymouth Polytechnic Piscatorial Society. 1982. (unpublished); 1st and 2nd Crayfish Workshops, Hampshire College of Agriculture, Sparsholt, Hampshire. 1982 and 1983. (unpublished).

(6). Liason with biological and fisheries staff within Thames Water and in other Regional Water Authorities; with the Ministry of Agriculture Fisheries and Food and Zoology departments at Reading and Nottingham Universities.

.....

I declare that whilst registered as a candidate for the degree for which submission is made I have not been a registered candidate for any other award of the C.N.A.A. or of a University.

J.B. HOGGER.

ABSTRACT.

The results presented in this thesis concern an examination of the biology and distribution of freshwater crayfish in the Thames Catchment. Studies of the distribution of both the native (Austropotamobius pallipes. Lereb.), and an introduced (Pacifastacus leniusculus. Dana.) species have been undertaken and attempts to evaluate some of the factors controlling distribution have been made. The specific influences of river engineering works on populations of A.pallipes have been studied in more detail.

Data concerning A.pallipes at the population level has been obtained by sampling a single lacustrine population. A comparison has been made with crayfish from a riverine population. Information concerning life-history, growth, density and trophic position is discussed and is related to similar information from elsewhere in the Thames Catchment and the U.K. The morphology of A.pallipes in this area has been quantified and an assessment made of sexually dimorphic features and hence the size at maturity of A.pallipes in southern England. The collection of information regarding diseases and parasites of A.pallipes in the Thames Catchment has been undertaken throughout the study and the incidence and importance of these is discussed.

Comparable information has been obtained from a population of the introduced P.leniusculus. Survival of implants, growth and life-history of this alien species in a single population are discussed in detail and compared with information collected from other introduced populations in the Thames Catchment. The morphometry of P.leniusculus has been investigated and their size at maturity calculated. The data collected concerning P.leniusculus forms the only known study of this species in the U.K., to date, and the results are compared with information from Scandinavia and North America.

The results from both parts of this thesis are discussed in terms of the ecological and economic importance of crayfish populations and the effects that introductions of alien species may have on native populations. It is intended that this thesis should provide a full and accurate assessment of the status of freshwater crayfish in the Thames Catchment at a time when increasing pressures may result in serious alterations to stocks of both species.

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INDEX

Abstract.		(i)
Acknowledgements.		(ii)
Index.		(iii)
Index - Tables.		(ix)
Index - Figures.		(x)
<u>Chapter 1.</u>	<u>General Introduction.</u>	1.
<u>Chapter 2.</u>	<u>Methods.</u>	
2.1	Introduction.	14.
2.2	Sampling methods.	14.
2.3	Hand collection.	15.
2.4	S.C.U.B.A. collection.	15.
2.5	Trapping.	16.
	(i) Trap construction.	16.
	(ii) Mode of operation.	17.
	(iii) Processing of crayfish samples.	17.
2.6	Reasons for sampling.	18.
2.7	Marking techniques.	18.
2.8	Measurements.	20.
2.9	Condition recording.	23.
	(i) Life-history.	23.
	(ii) Parasitism and disease.	24.
	(iii) Injuries.	24.
2.10	Statistical methods.	25.
	(i) Length-frequency analysis.	25.
	(ii) Morphometric data.	28.
	(iii) Estimation of population size.	30.
<u>SECTION A.</u>	<u>The biology and distribution of</u> <u>A.pallipes in the Thames Catchment.</u>	
	Section Introduction.	32.
A.1	General considerations.	32.
A.2	Aims of study (Section A).	32.
	(iii)	

A.3	Species description.	34.
A.4	Life-cycle.	35.
A.5	Taxonomy.	36.
A.6	Distribution.	36.
A.7	Biology.	37.
A.8	Economic importance.	39.

Chapter 3. The distribution of A.pallipes in the Thames Catchment.

3.1	Introduction.	40.
3.2	Methods.	43.
3.3	Results.	44.
3.4	Discussion.	47.
	(i) Geology.	48.
	(ii) River management - water quality.	50.
	(iii) River management - land drainage.	53.
	(iv) Biological quality.	54.
	(v) Disease.	55.
	(vi) Fishing.	55.

Chapter 4. A study of the biology of a population of the native freshwater crayfish, A.pallipes, in a lacustrine environment.

4.1	Introduction.	57.
	(i) Study site.	58.
4.2	Methods.	65.
	(i) Sampling.	65.
	(ii) Statistical analysis.	67.
	(iii) Trophic position.	68.
	(iv) Life History.	69.
4.3	Results.	70.
	(i) Comparison of sampling methods.	70.
	(ii) Population estimates.	74.
	(iii) Length-frequency analysis.	74.
	(iv) Morphometric data.	75.

	(v) Trophic position.	75.
	(vi) Life-history.	92.
	(vii) Parasites, damage and disease.	92.
4.4	Discussion.	96.
	(i) Study site.	96.
	(ii) Sampling methods.	99.
	(iii) Population estimates.	107.
	(iv) Catchability.	109.
	(v) Length-frequency data and growth.	111.
	(vi) Morphometric analysis.	113.
	(vii) Adult productivity.	114.
	(viii) Trophic position.	115.
	(ix) Incubation time and life-history.	117.
	(x) Parasites, diseases and damage.	120.

Chapter 5. An investigation to assess the impact of river engineering works on populations of the freshwater crayfish A.pallipes.

5.1	Introduction.	123.
	(i) General considerations.	123.
	(ii) Study site - Ware Lock.	127.
	(iii) Study site - R. Beane at Hertford.	128.
5.2	Methods.	132.
	(i) Ware Lock.	132.
	(ii) R. Beane at Hertford.	135.
5.3	Results.	137.
	(i) Ware Lock.	137.
	(ii) R. Beane at Hertford.	141.
5.4	Discussion.	141.
	(i) General considerations.	141.
	(ii) Colonisation of basin.	148.
	(iii) Population estimation at Ware.	149.
	(iv) Dredging.	151.
	(v) Conclusions.	153.

<u>Chapter 6.</u>	<u>Miscellaneous observations regarding the biology of <u>A.pallipes</u> in the Thames Catchment.</u>	
6.1	Introduction.	156.
6.2	Observations on the biology of a riverine population of <u>A.pallipes</u> .	
	(i) Introduction.	157.
	(ii) Study site.	157.
	(iii) Methods.	160.
	(iv) Results.	160.
	(v) Discussion.	160.
6.3	The morphology and sexual dimorphism of <u>A.pallipes</u> in the Thames Catchment.	
	(i) Introduction.	171.
	(ii) Methods.	172.
	(iii) Results.	172.
	(iv) Discussion.	173.
6.4	Observations on diseases and parasites of <u>A.pallipes</u> in the Thames Catchment.	
6.4a.	The occurrence of the crayfish parasite <u>Thelohania contejeani</u> .	
	(i) Introduction.	187.
	(ii) Methods.	188.
	(iii) Results.	189.
	(iv) Discussion.	189.
6.4b.	The occurrence of the crayfish parasite <u>Branchiobdella astaci</u> in the Thames Catchment.	
	(i) Introduction.	195.
	(ii) Methods.	197.
	(iii) Results.	199.
	(iv) Discussion.	199.
6.4c.	Observations concerning certain crayfish diseases in the Thames Catchment.	
	(i) Introduction.	205.
	(ii) Methods.	205.
	(iii) Results.	205.
	(iv) Discussion.	207.

SECTION B. The biology and distribution of P.leniusculus in the Thames Catchment.

	Section Introduction.	211.
B.1	General considerations.	211.
B.2	Aims of study (Section B).	211.
B.3	Species description.	212.
B.4	Life-cycle.	213.
B.5	Taxonomy.	213.
B.6	Distribution.	214.
B.7	Biology.	215.
B.8	Economic importance.	216.

Chapter 7. The distribution of crayfish introductions in the Thames Catchment.

7.1	Introduction.	218.
7.2	Methods.	219.
7.3	Results.	220.
7.4	Discussion.	220.

Chapter 8. An investigation into the biology of a population of the 'Signal Crayfish', P.leniusculus, introduced into an isolated lake.

8.1	Introduction.	226.
	(i) Study site.	227.
	(ii) Chemical water quality.	229.
8.2	Methods.	229.
	(i) Sampling.	229.
	(ii) Statistical analysis.	233.
8.3	Results.	234.
	(i) Population estimation.	235.
	(ii) Catchability.	235.
	(iii) Length-frequency data.	235.
	(iv) Morphometric data.	244.
8.4	Discussion.	257.
	(i) Water quality.	258.
	(ii) Methods.	260.

	(iii) Population estimates.	263.
	(iv) Catchability.	267.
	(v) Length-frequency data and growth.	268.
	(vi) Morphometric analysis.	275.
	(vii) Adult productivity.	279.
	(viii) Miscellaneous information.	280.
	(ix) Biological and economic importance of <u>P.leniusculus</u> .	284.
<u>Chapter 9.</u>	<u>An investigation into the success of introductions of P.leniusculus into the Thames Catchment.</u>	
9.1	Introduction.	289.
9.2	Methods.	290.
9.3	Results.	291.
9.4	Discussion.	291.
	(i) Success of introductions.	291.
	(ii) Predators.	294.
	(iii) Water quality.	296.
	(iv) Stocking rate.	296.
	(v) Habitat suitability.	297.
	(vi) Other considerations.	297.
<u>Chapter 10.</u>	<u>General Discussion.</u>	
10.1	Aims of study.	301.
10.2	Distribution of <u>A.pallipes</u> .	302.
10.3	Introductions.	303.
10.4	Aquaculture potential.	305.
10.5	Life-history.	306.
10.6	Growth.	307.
10.7	Economic considerations.	307.
10.8	Ecological considerations.	309.
10.9	Water Authority considerations.	311.
10.10	Future studies.	312.
Bibliography.		313.
Appendices.		340.

Index - Tables.

<u>Table No.</u>	<u>Page.</u>	<u>Table No.</u>	<u>Page.</u>
A.1	38.	6.1	158.
4.1	63.	6.2	161.
4.2	71.	6.3	174-175.
4.3	72.	6.4	179.
4.4	78.	6.5	191.
4.5	80.	6.6	196.
4.6	81.	6.7	201.
4.7	88.	6.8	206.
4.8	89-90.	8.1	230-231.
4.9	91.	8.2	236.
4.10	94.	8.3	237.
4.11	97.	8.4	248-249.
4.12	98.	8.5	250.
4.13	103.	8.6	251.
4.14	106.	8.7	256.
4.15	119.	8.8	265.
5.1	131.	8.9	273.
5.2	134.	8.10	278.
5.3	136.	8.11	281.
5.4	139.	8.12	282.
5.5	139.	8.13	285.
5.6	140.	9.1	292.
5.7	143.	9.2	293.
5.8	143.		
5.9	144.		
5.10	145.		
5.11	145.		
5.12	145.		

Index - Figures.

<u>Figure No.</u>	<u>Page</u>	<u>Figure No.</u>	<u>Page</u>
2.1	22.	6.1	162.
3.1	41.	6.2	163.
3.2	45.	6.3	164.
3.3	46.	6.4	166.
3.4	49.	6.5	169.
3.5	52.	6.6	176-178.
4.1	59.	6.7	190.
4.2	60.	6.8	198.
4.3	62.	6.9	200.
4.4	73.	7.1	221.
4.5	76.	7.2	222.
4.6	77.	7.3	224.
4.7	79.	8.1	228.
4.8	82.	8.2	232.
4.9	83-84.	8.3	238-239.
4.10	85.	8.4	240.
4.11	86.	8.5	241.
4.12	87.	8.6	242.
4.13	93.	8.7	243.
4.14	95.	8.8	245.
5.1	129.	8.9	246-247.
5.2	130.	8.10	252.
5.3	133.	8.11	253-254.
5.4	142.	8.12	255.
5.5	146.		
5.6	147.		

CHAPTER 1. GENERAL INTRODUCTION.

There is only one indigenous species of freshwater crayfish in the British Isles: Austropotamobius pallipes (Lereboullet, 1858) (Huxley, 1880; Thomas & Ingle, 1971; Gledhill, et al, 1976). There are, however, in excess of 500 species of freshwater crayfish to be found worldwide and they are distributed in the temperate latitudes of the northern hemisphere, north of 20° north, and the temperate and tropical latitudes of the southern hemisphere, south of 2° south (Huxley, 1880; Arrignon, 1981). All species of freshwater crayfish belong to one of only two families (Hobbs, 1972) the Astacidae and the Parastacidae, which are distributed in the northern and southern hemispheres respectively (Huxley, 1880; Hobbs, 1972). Other reports include a further family, the Cambaridae, comprising species from both eastern North America and Asia (André, 1960 in Arrignon, 1981; Vigneux, 1981).

The Astacidae are divided into two major sub-families, the Astacinae and the Cambarinae. The former includes the four native European species in two genera (Gledhill et al, 1976) and the North American genus Pacifastacus containing five species (Pennak, 1978). The latter includes the seven other North American genera except the minor sub-families Cambaroidinae and Cambarellinae (Hobbs, 1972).

There are four species of the Astacinae which are native to Europe (Gledhill, et al., 1976). The 'European' or 'Noble' Crayfish Astacus astacus (L. 1758) (Syn. A. fluviatilis Fab. and A. nobilis Huxley.) is indigenous to northern Europe, including Russia, Scandinavia, Poland, Germany and northern France (Laurent & Suscillon, 1962; Abrahamsson, 1972; Laurent, 1973; Cukerzis, 1975; Laurent & Forest, 1979). The 'Turkish' Crayfish or 'Slender - Clawed' Crayfish, Astacus leptodactylus (Escholz, 1823), is found in southwest Europe, including Greece, Turkey, Russia, Afghanistan and Iran (Cukerzis, 1975; Erençin & Köksal, 1977 a,b; Laurent & Forest, 1979).

The 'Torrent Crayfish', Austropotamobius torrentium (Schrank, 1803) (Syn. Astacus torrentium Schrank), is limited to the alpine regions of France, Austria, Switzerland and northern Italy (Vigneux in Arrignon, 1975; Laurent & Forest, 1979; Büttiger, in Westman and Pursainen, 1982). Austropotamobius pallipes (Lereboullet, 1858) (Syn. Astacus pallipes, Lereb.) is widely distributed throughout western Europe, including France, Italy, Greece, Spain, Holland, the U.K. and Eire (Laurent & Suscillon, 1962; Holthuis, 1967; Gledhill et al, 1976; Arrignon, 1979; Laurent & Forest, 1979; Jay & Holdich, 1981) (see Chapter 3).

The four indigenous European species comprising the classification generally adopted (Laurent & Forest, 1979; Arrignon, 1981) have also been taxonomically ordered as follows (Holthuis, 1967):- Astacus astacus (2 subspecies); A.colchicus; A.pachypus; A.leptodactylus (4 subspecies); Austropotamobius pallipes (4 subspecies); and A.torrentium (2 subspecies). An alternative revised classification that has been proposed (Albrecht, 1982) lists five European species within a single genus: Astacus astacus; A.leptodactylus; A.pallipes; A.torrentium and A.pachypus. This system is based on a phylogenetic analysis (Kraus, 1976) which includes morphological weighting and biochemical, biological and zoogeographical criteria. Only three subspecies of A.astacus; i.e. A.a.astacus; A.a.bavaricus and A.a.colchicus are considered to be warranted in this system, all other forms being classed as variations.

In addition to these native species some North American species of crayfish have also been introduced to mainland Europe. These are Orconectes limosus (Rafinesque, 1817) (Syn. Cambarus affinis, Say) and more recently Pacifastacus leniusculus (Dana, 1852) and Procambarus clarkii (Girard, 1852). Breeding populations of all three species occur in the wild where suitable habitat is available (Laurent & Forest, 1979).

That A.pallipes is the only member of the Astacidae to be native to the U.K. is thought to be attributable to the effects of the Pleistocene Ice Ages (Huxley, 1880; Hynes, 1972). As a result of this isolation A.pallipes apparently has a wider ecological range in the U.K. than on the mainland of Europe (Reynolds, 1979). In this country it is found in water-bodies of all types, including streams and large rivers, lakes and reservoirs (Lilley, et al, 1979; Jay & Holdich, 1981; pers obsn.) whereas on mainland Europe it is largely confined to small streams whilst A.astacus and A.leptodactylus occupy lakes and the larger streams and rivers (Hynes, 1972; Laurent & Forest, 1979).

There is now considerable evidence to suggest that A.pallipes is widely distributed and may be abundant in suitable locations in England, Ireland and Wales (Huxley, 1880; Thomas & Ingle, 1971; Moriarty, 1973; Lilley et al, 1979; Reynolds, 1979; Jay & Holdich, 1981; O'Keefe, in press, see Chapter 3). Some anecdotal reports, however, imply that this species is extinct in the U.K. (Carpenter, 1928; Anon, 1976; Jackman, 1977; Conran 1975; Karlsson, 1978).

The life-history of A.pallipes is typical of that of all the Astacinae, differing only in timing. Moulting, by which means growth is achieved, is restricted to the warmer summer months when feeding can occur. Fertilisation and egg-laying take place in the late autumn and the eggs are carried over winter, by the female, until they hatch early the following summer. A.pallipes are not generally sexually mature until at least three years old (Brown, 1979).

The reproductive cycle of the Cambarinae, e.g. P.clarkii, differs in several respects to that of the Astacinae as they are generally a 'warm-water' species. The adult males undergo a change of form from the sexually competent Form 1 to the sexually incompetent Form 2 when their post-reproductive moult occurs (Momot, 1964). Their reproductive cycle is usually less synchronous than that of the Astacinae but still shows a peak of mating activity in the autumn.

The eggs, however, are not normally laid until the next spring and hatching occurs within two months. There is considerable variability, however, and some populations of the genus *Procambarus* have year-round recruitment (de la Brettonne & Avault, 1977).

There is apparently no common, overall pattern to the reproductive cycle of the ninety-seven species belonging to the Parastacidae. Some species mate and hatch out eggs during the summer, sometimes in as little as six weeks, e.g. *Cherax tenuimanus* (Morrissey, 1970, 1979; Carroll, 1980) whereas others carry eggs through the winter, e.g. *Paranephrops planifrons* (Jones, 1981).

In the U.K, with only one species of freshwater crayfish to consider, it would be thought that the majority of the features of its biology and life-history would have been fully elucidated. This is, however, not the case and until the last ten years research on the biology of the native crayfish was scant. It has been pertinently pointed out (Brown & Bowler, 1977) that the most quoted reference regarding this species is "The Crayfish" (Huxley, 1880). This scarcity of information is in contrast to the wealth of data available for some other crayfish species, e.g. *A. astacus* (e.g. Abrahamsson, 1966, 1971a, 1971b, 1972; Cukerzis, 1968, 1973; Kossakowski, 1965, 1967, 1971); *C. tenuimanus* (Morrissey, 1970, 1973, 1975; Carroll, 1980) and many of the North American species (e.g. Momot, 1964, 1966, 1967a; Abrahamsson & Goldman, 1970; Momot & Gowing, 1972, 1977a,b; Emadi, 1974; Avault, 1975; Mason, 1975; Flint, 1975a,b, 1977) which are recognised as being ecologically and sometimes commercially important. There is no comprehensive body of ecological knowledge for any species of freshwater crayfish, however, a deficiency which the International Association of Astacology, formed in 1972, is attempting to remedy by organising regular symposia devoted to all aspects of the study of freshwater crayfish (Abrahamsson, 1973; Avault, 1975; Lindqvist, 1977; Laurent, 1979)

This paucity of information is principally due to the inaccessibility to direct sampling of these benthic, largely nocturnal and in many cases burrowing freshwater invertebrates (Brown, 1979).

There are several reasons, apart from esoteric ones, why a much greater knowledge of the ecology of A.pallipes is desirable. These reasons, all concerning the ultimate fate of our native species with possible far-reaching effects on the trophic condition of our waterways, are directly or indirectly linked with the appearance of an epidemic crayfish disease in Europe in the late nineteenth century (Kossakowski, 1971; Spitzzy, 1973). This disease, known as the 'Crayfish Plague', was thought to have been introduced into Italy on imported North American crayfish of the species Orconectes limosus (Unestam, 1969; Schweng, 1973). The causative organism of the plague, since identified as the parasitic fungus Aphanomyces astaci (Schikora, 1903) (Schaperclaus, 1954), is endemic among North American crayfish which all show a high but not complete resistance (Unestam, 1969, 1972, 1973; Unestam & Weiss, 1970; Fürst & Bostrom, 1978). A.astaci has spread through Europe and Scandinavia and destroyed many crayfish populations which were formerly of local economic importance. (Abrahamsson, 1973; Laurent, 1973; Westman, 1973; Brinck, 1975; Fürst, 1977).

Efforts to restore European crayfisheries devastated by the plague have concentrated on the introduction and farming of A.leptodactylus in France (Arrignon, 1981; Massé, 1981) and the importation of the plague-resistant North American species Pacifastacus leniusculus, to Sweden in particular (see Section B). This latter species is now widely available throughout Europe, for stocking purposes, in the form of 'hatchlings' produced in Sweden (Abrahamsson, 1973b; Goldman, 1973; Spitzzy, 1973; Brinck, 1975; Karlsson, 1978).

There is some evidence to indicate that stocking can be successful and that some waters can be restored to their former productivity (Brinck, 1975; Fürst, 1977). Most populations of P.leniusculus established in Scandinavia have, however, been found to contain individuals infected with the plague (Fürst, 1977; Unestam, et al, 1977; Fürst & Bostrom, 1978) and recent reports suggest that as many as 60% of introduced juveniles may carry the fungus (Söderhäll, pers comm). As the four native European crayfish species are susceptible to the plague the establishment of populations of an alien species, that may act as a reservoir for the disease, should be carefully considered and carried out in a controlled manner in order to preserve native stocks (Brown, 1979).

There is, as yet, no scientific evidence that crayfish plague has had any effect on populations of A.pallipes in the U.K. (Holdich, et al, 1978) and little research has been carried out on the susceptibility of A.pallipes to A.astaci (Unestam, 1969). Reports of large-scale crayfish mortalities in the past (Cornish, 1902; Duffield, 1933, 1936; Pixell-Goodrich, 1956) failed to identify a definite cause and although studies of recent mortalities (see Chapter 6) suggest that they are caused by disease, rather than pollution, no causative organism has yet been positively identified (Alderman, pers comm). * See page 209.

The increase in interest in freshwater crayfish during the last decade, and the current availability of material for stocking, has resulted in considerable aquacultural interest in crayfish in the U.K. (Richards & Fuke, 1977; Holdich, et al, 1978; Goddard & Holdich, 1979). The large maximum size and rapid growth rates reported for P.leniusculus (Abrahamsson, 1971b; Richards & Fuke, 1977; Fuke, 1978; Karlsson, 1978) has resulted in the importation of this species into this country (Richards & Fuke, 1977; Fuke, 1978; Behrendt, 1980; Richards, pers comm). The threat of such introductions to our native species is

obvious and populations of this alien species could act as reservoir of fungal spores from which the plague could spread to populations of A.pallipes. In addition information concerning the ecology of both the native and introduced species is still scant and no research has yet been carried out on interspecific competition. Until recently there has been no legislation governing the introduction of foreign crayfish species. A recent Act of Parliament, however, makes licencing introductions to the wild, by M.A.F.F. in conjunction with the Nature Conservancy Council, obligatory. There remains no control over introductions to 'closed' systems, e.g. fish-farms, and in any case there are already large breeding populations of P.leniusculus in various parts of the country (see Chapters 7 & 9).

It is clear, then, that our native crayfish is considerably threatened by the importation of alien species. Although only consumed on a local basis in the U.K. (Holdich, et al, 1978) the abundance of A.pallipes at some locations could prove a valuable export (Brown, 1979). As there is no existing trade in A.pallipes their devastation by A.astaci could also have serious ecological consequences as there would be no economic incentive to restock. Evidence has suggested that populations of crayfish can have a considerable effect on the abundance of aquatic macrophytes and macroinvertebrates. Ponds in Sweden are reported as becoming "choked" with excessive plant growth following the extermination of the resident population of A.astacus (Abrahamsson, 1966). Other species of crayfish have also been used successfully for the control of macrophytes in the U.S.A. (Dean, 1969; Magnusson, et al, 1975; Lorman & Magnusson, 1978) and zebra mussels, Dreissena polymorpha, in Poland (Piesik, 1974).

Aspects of the biology of the native British freshwater crayfish, A.pallipes, in the U.K. have recently been reviewed (Bowler & Brown, 1977, 1979; Holdich, et al, 1978; Rhodes & Holdich, 1979, 1982; Jay & Holdich, 1981; Pratten, 1980) but no similar studies have, so far, been

carried out on P.leniusculus in this country despite the threat to our native species and its potential economic importance. It is clear, therefore, that crayfish biology in the U.K. requires much more attention from both the ecological and potential commercial points of view. An assessment of existing published information has shown that several aspects of crayfish biology can be considered to require urgent investigation and the present study is directed at obtaining detailed information concerning these.

Initially three main areas of investigation were thought to be relevant for inclusion in this study; subsequently a fourth, related, but new, topic was added. In consideration of the involvement of Thames Water the field of research was restricted, geographically, to the Thames Catchment. From a detailed review of the literature available at the commencement of this study (1978) it was clear that two contrasting opinions were held regarding the occurrence of A.pallipes in the U.K. On the one hand there was a small amount of published information containing positive distribution records (Duffield, 1933, 1936; Thomas & Ingle, 1971) although many of the published records were more than ten years old. On the other hand there were published implications that A.pallipes was extinct in the U.K.(Anon, 1976; Richards & Fuke, 1977; Karlsson, 1978). It was clear, therefore, that a concerted attempt was required to collate and update existing records of crayfish occurrence in the Thames Catchment, to improve knowledge of the distribution of A.pallipes and to use these records for the compilation of a distribution map. At that time it was also learnt that researchers at Nottingham University were carrying out a similar exercise, collating records on a national basis, (Holdich, pers comm) and subsequently a number of records obtained during the current study were included in their published survey results (Jay & Holdich, 1981)

Further, as stated previously, little published information was available regarding aspects of the general

biology and ecology of A.pallipes. Several research projects were currently being carried out at Universities, however, the results of which have subsequently been presented as unpublished theses (Brown, 1979; Rhodes, 1980) and published papers (Bowler & Brown, 1977, 1979; Brown & Bowler, 1977; Brown & Brewis, 1979; Rhodes & Holdich, 1979, 1982; Pratten, 1980; Jay & Holdich, 1981). From the published information available in 1978 (Thomas & Ingle, 1971; Bowler & Brown, 1977; Brown & Bowler, 1977) it was evident that data concerning the life-cycle and growth rate of A.pallipes would only be applicable to crayfish in the locality or type of water-body in which the research was conducted as both geological and climatic differences would play a large part in controlling the timing and duration of various aspects of the life-cycle. For example, data concerning the fecundity of A.pallipes has usually been derived from single collection sites by making simple counts of pleopod eggs and may vary according to season and location as well as the size of the female (Rhodes, 1980; Rhodes & Holdich, 1982). This is despite the fact that details regarding the fecundity of crayfish are important in terms of potential population recruitment (Brown, 1979) and from the potential commercial point of view (Rhodes & Holdich, 1979). Indeed, studies concerning the reproduction and subsequent growth of crayfish are considered to be of the greatest importance amongst the biological criteria necessary for the commercial evaluation of any particular species (Webber & Riordan, 1976).

In order to obtain information regarding crayfish in the Thames Water area, i.e. the Thames Catchment, and the south of England generally, it was therefore considered of value to undertake a study of the basic population biology and life-history of a population of A.pallipes in this area. Initially it was intended to study both lacustrine and riverine populations and to compare and contrast data from the two but for reasons outlined elsewhere (see Chapter 6) the study finally concentrated on obtaining information regarding a lacustrine population.

Having elicited some basic facts concerning such a population it was considered important to attempt an assessment of a population management strategy, whereby simulated cropping would enable the maximum sustainable yield to be determined. Again, due to problems described elsewhere (see Chapter 4) this section of the study was not carried out in detail and a longer-term but simpler population study was carried out.

One of the main factors surmised to have resulted in the reputed decline in the abundance and distribution of A.pallipes in recent years is the greater impact man has had on the management of watercourses in the last thirty years (Reynolds, 1979; Wells, et al, 1983). This impact could affect crayfish in two ways. Use of the water by man, necessitating abstraction and effluent discharge, could drastically alter both water quality and quantity to the detriment of crayfish. These aspects of human influence will be considered in relation to crayfish distribution (see Chapter 3).

In addition man has altered the physical characteristics of most lowland waterways for the purposes of flow management, and hence navigation, and flood alleviation. Schemes that involve dredging and the construction of barriers to impound and control rivers often result in channels of uniform cross-section and depth with carefully graded banks and a bed devoid of large obstructions. Such management schemes are generally carried out by, or with approval from, the Regional Water Authority so it was considered to be of direct relevance to assess the impact of such schemes on crayfish populations. The detailed investigations that were carried out to this end are described (see Chapter 5) and have been reported elsewhere (Hogger & Lowery, 1982).

Finally, although not included in the original proposals, it was decided to broaden the field of study to include the introductions of 'alien' crayfish to the Thames Catchment.

Only in recent years, i.e. since 1976, have large-scale introductions of crayfish been made to the U.K. although reports have been received of introductions made in the past (Jay & Holdich, 1980; Chapter 7). A.astacus is reputed to occur in some rivers (Davies, 1964; Gledhill, et al, 1976), including the Thames (Anon., 1973; Clegg, 1974), but this has not been confirmed during this study or a national distribution survey (Jay & Holdich, 1981). A.leptodactylus is also reputed to have been introduced to several watercourses and fish-farms and is frequently imported from France, through Billingsgate Fish Market, for wholesale distribution (Pearson, per comm). No positive record is available of the survival of A.leptodactylus introduced into the wild in the Thames Catchment. Similarly, although there are reports of an experimental introduction of P.clarkii to a fish-farm in the U.K. the results have not been published and it is reported that investigations were terminated and all the stock destroyed (Goddard, pers comm).

Interest in crayfish 'farming' in the U.K. is currently very high (Richards & Fuke, 1977; Holdich, et al, 1978; Behrendt, 1980; Rhodes & Holdich, 1979). In view of the dangers of importing alien animals it is essential not only to investigate the potential of the native A.pallipes (Rhodes, 1980) but also that of the introduced P.leniusculus. Indeed introductions of other crayfish species elsewhere have been shown to be both ecologically and economically damaging (Goldman, 1973; Lowery & Mendes, 1977). From the commercial aspect one of the major considerations is the potential size of the organism being evaluated and in the case of the freshwater crayfish the size of the abdomen and claws is of the greatest importance. Such factors may influence the determination of a legal cropping size limit, for nutritional purposes. Hence, as morphometric studies of species intended for culture are desirable, it was decided to examine these parameters in both the native and introduced species of crayfish obtained from their natural environment.

The one species of freshwater crayfish currently being imported to the U.K. in large numbers is the 'Signal Crayfish', Pacifastacus leniusculus (Dana, 1852) (see Section B: Introduction). Native to the west coast of North America this species is bred in a commercial hatchery in Sweden and juveniles are being introduced, by prospective aquaculturists, throughout Europe (Abrahamsson, 1973b; Karlsson, 1977). It is apparent that virtually no research has been carried out regarding the effects of the introduction of this species to the U.K. Such research as has been undertaken elsewhere in Europe, particularly in Sweden, may not be directly applicable to this country, with only one native species and no proven record of mortalities caused by the crayfish plague. It is hoped that the present study (Section B) will remedy this situation and perhaps encourage further research to be carried out on P.leniusculus in the U.K.

As it is both of potential ecological and commercial importance the biology and distribution of P.leniusculus in the Thames Catchment is considered to be within the scope of this study. Consequently Section B is devoted to this species and describes a detailed investigation into the population dynamics and life-history of a single population. This is then related to data obtained from other sites within the Thames Catchment and to information regarding the native crayfish A.pallipes discussed in Section A.

Incidental to the main topics considered during this study a considerable quantity of miscellaneous information has been collected regarding both the native A.pallipes and the introduced P.leniusculus. This information is discussed in Chapter 6 and in the general discussion (Chapter 10) and includes data on fecundity, survival, timing of the reproductive cycle, parasitism and disease incidence. Such data was collected from both field and laboratory studies and has been included to provide as complete a record as possible of relevant information obtained during the course of this study.

In order to accomplish the aims of this study information has been obtained in the following ways. Distribution records have been collated, supplemented and verified (see Chapters 3 & 7). For the purpose of studying population dynamics, ecology and general life-history a detailed study was made of A.pallipes in a single location (see Chapter 4). To obtain similar information regarding introduced P.leniusculus a population in a lake near Reading was studied (see Chapter 8) and twelve other introduced populations in the Thames Catchment were sampled to obtain data for comparison (see Chapter 9). Data concerning the potential effects of the engineering aspects of river management schemes on A.pallipes was collected from sites on the River Lee and River Beane in Hertfordshire (see Chapter 5).

As can be seen the data obtained during these investigations is organised into two sections, regarding the native and introduced species, for ease of presentation. An attempt has been made to present the information from such a wide variety of topics as logically as possible. Methods which are generally applicable to more than one chapter are described separately (see Chapter 2) and a general discussion (see Chapter 10) and bibliography conclude the thesis. Each section is preceded by a Section Introduction which includes a full species description and presents background information relevant to that section.

CHAPTER 2. METHODS.

2.1 Introduction.

Throughout the course of this study the same methods of sampling and treatment of data have been applied wherever possible. This chapter outlines the methods applicable to more than one investigation and any variations in method, or unique methods used, according to the individual site characteristics will be considered in the relevant chapter. The means by which the various populations of crayfish were sampled is the subject of the first part of this chapter. Then the methods by which data was collected from individual crayfish in the samples is described. Finally the statistical treatment of the data thus collected will be outlined.

2.2 Sampling Methods.

Some of the populations of freshwater crayfish investigated during this study were accessible to direct sampling by hand collection. In lacustrine situations when the water is clear direct, qualitative sampling is possible, using S.C.U.B.A. (Capelli & Magnusson, 1975), and this method was used extensively at one site (see Chapter 4). Seine netting, used in the Ukraine for harvesting A. leptodactylus (Brodsky, 1975), was also used to sample a population of P. leniusculus, incidental to the removal of coarse fish. It is not a generally applicable method for sampling benthic organisms due to snags and weed growth fouling the net. Electric fishing (Westman, et al, 1979b) was not evaluated as a sampling method.

The only method of sampling crayfish populations which is almost universal in application is the use of 'funnel traps' (Capelli, 1975) and this was the method most often used during the course of this study. Most other studies of the population dynamics of freshwater crayfish populations have used trapping as one, or the only, method of sampling (e.g. Moriarty, 1973; Arrignon & Magne, 1979; Brown, 1979; Pratten, 198

2.3 Hand Collection.

The collection of crayfish by hand was widely used throughout this study for determining the presence or absence of crayfish at many sites and for the purpose of accumulating and verifying distribution records. A fuller description of this method, as used for that purpose, is presented elsewhere (see Chapter 3).

Hand collection was frequently used at some sites for obtaining data on the size distribution of juvenile crayfish that were not satisfactorily sampled by other methods; particularly at Clattercote Reservoir (see Chapter 4) a considerable quantity of data was collected in this way. Such collections simply consisted of wading in the shallows overturning rocks and stones to reveal the crayfish which were then caught manually or by using a small hand-held net (Demars, 1979). At night torchlight was used to collect crayfish in the open. Juveniles were also collected in this way from a small number of sites to which P.leniusculus had been introduced (see Chapter 9).

Collection of crayfish by hand was also carried out when individual site circumstances permitted. For example, when a pound of the Oxford Canal (South) was dewatered for maintenance purposes (see Chapter 6) and whilst investigating the effects of dredging on populations of A.pallipes (see Chapter 5).

2.4 S.C.U.B.A. Collection.

The collection of A.pallipes by divers using S.C.U.B.A. and snorkels was carried out extensively at one site, Clattercote Reservoir, (see Chapter 4). Groups of 2 to 6 divers collected crayfish both in daylight and at night. During the former operation crayfish were located by stone turning whereas at night they could be collected whilst foraging in the open. To reduce disturbance of the habitat

as much as possible collections were made at night whenever practicable.

Each diver carried a small, cylindrical wire basket, approximately 30 cm. long and 15 cm. in diameter (modified crayfish traps) on his or her wrist. Crayfish, when caught, were placed in the basket 'tail first' through the funnel entrance. The baskets were periodically emptied into buckets on the shore. Divers collected for an average of 1 hour, range 0.3 to 2.5 hours, depending on the water temperature and overall success rate of the collectors. Comparative analysis of the samples collected by the divers and by the following method, trapping, is described in Chapter 4.

2.5 Trapping

2.5(i) - Trap Construction.

The type of traps generally used was based on a traditional Swedish design (Westman, et al, 1979) and they were either home-made or commercially obtained. A coil of 10 swg. (13 mm.) wire, approximately 25 cm. in diameter was covered in $\frac{1}{2}$ " mesh knotless nylon netting. At each end the netting was drawn into the trap body to form an inscale, a 'funnel entrance'. Modification of the trap entrances, as has been recommended (Westman, et al, 1979), was not attempted. The approximate final dimensions of the traps were: 50 cm. long and 25 cm. in diameter. All were made to be collapsible on their longitudinal axis. The commercial traps were constructed with a flap at one end to facilitate emptying; the home-made traps had an opening in the long seam for the same purpose. Various rigid traps were also used on several occasions. These were constructed to the above pattern using 'Chicken wire,' (2.0 cm. mesh), 'Weldmesh' (1.25 cm. mesh) or plastic (1.5 cm. mesh). Wire or plastic clips were provided in the centre of the trap body for affixing the bait. 'Pillow' traps, used to

harvest P.clarkii in North America (Bean & Huner, 1979), were not utilised during the present study.

2.5(ii) - Mode of Operation.

Traps were generally operated during darkness either overnight or for a shorter period during the evening. Crayfish have been shown to be most active shortly after dark and again just before dawn (Abrahamsson, 1971b; Westman, et al, 1979) so trapping is most effective during these periods (see Chapter 4). For general use the traps were always baited, usually with portions of frozen, fresh coarse fish or liver as these were found to be the most effective baits (see Chapters 4 & 8) and such fish was readily available. Traps were normally set from the bank, on individual lines, at approximately five metre intervals (Westman, et al, 1979) shortly before or after dusk (except at one site, see Chapter 4). The actual time of setting was dependent on the time of year. For comparative purposes the total time the traps were in operation during any one sampling occasion was recorded.

2.5(iii) - Processing of Crayfish Samples.

Generally the catches from individual traps were pooled and the total catch treated as a sample from that population. At certain sites data from individual traps was collected either in order to ascertain the localised distribution of crayfish, for example in relation to sex, or to determine the efficiency of different styles of trap or baits. Descriptions of such procedures are outlined in the relevant sections.

Details of the marking techniques used, measurements taken and other characteristics recorded are described elsewhere (2.7). After processing the sample was released at random within the sampling area. On some occasions specimens were removed to the laboratory for detailed

examination.

2.6 Reasons for Sampling.

Samples were collected for a number of reasons:

- (i) For the collection of morphometrical data from both A.pallipes and P.leniusculus.
- (ii) To obtain life-history information
- (iii) To enable mark-recapture experiments to be carried out for the purpose of estimating population size.
- (iv) For the collection of specimens for disease and parasitological investigations.
- (v) To evaluate the success of introductions of the alien species P.leniusculus.
- (vi) To provide data for the construction of length-frequency histograms for use in identifying discrete size-groups of crayfish within the population.

2.7 Marking Techniques.

All arthropods are notoriously difficult to mark permanently as any mark applied or attached to the outer exoskeleton will be lost when the animal moults. Coded mutilations, for example partial leg amputation, may be regenerated (Brown, 1979). The method of cauterisation of small areas of integument was adopted for use in this study (Abrahamsson, 1965, 1973) as it most nearly fulfils the following criteria for a practicable marking technique for use in the field:

- (i) The marks must not be lost through moulting.
- (ii) Marking must not directly or indirectly affect survival, including predation.
- (iii) Marks should be distinguishable from natural injuries and abnormalities.
- (iv) Moulting, growth and reproduction should all be unaffected.

- (v) No abnormal behaviour should be produced by marking; for example, tags may hinder locomotion.
- (vi) The method used must be applicable to all stages of the moult cycle.
- (vii) Marking quickly and effectively in field conditions must be possible.
- (viii) The system used must be able to cope with large numbers of individual crayfish.

The majority of methods described in the literature appear to have some drawbacks in relation to these requirements. Limb removal is obviously numerically limited in scope, liable to confusion with natural injuries and autotomy, may possibly disappear through regeneration and may result in behavioural abnormalities and increased mortality. Similarly other mutilation techniques have disadvantages although cutting or punching holes in the telson and pleural clipping (Chien & Avault, 1979) may last through several moults (Goellner, in Momot, 1967). Staining and dye injection methods do not allow large-scale individual recognition and may be difficult to apply in the field (Niemi, 1977). Tags have been developed that will remain in position through the moult but it has been demonstrated that growth may be adversely affected and some post-marking mortalities occurred when tagging was carried out in early post-moult (Cooper, 1970). A recently developed tagging system (Weingartner, 1982) involves the insertion of sub-cutaneous, nylon, colour-coded tags which are reputed to last the lifetime of the crayfish and to be harmless. This method would appear to have some advantages over hot-branding and may be preferable for use in a long-term study of crayfish populations.

Cauterisation, 'hot-branding', was used for marking crayfish in the current study (see Chapters 4, 5 & 8). Marks were created using a small soldering iron, 12v. for field use and 240v. for laboratory use, or an electrically

heated red-hot wire (12v.). The marks thus applied to the exoskeleton appeared as small red/orange spots with black centres. They were easily visible as paler areas after two to three moults but no assessment of their longevity was attempted as, wherever necessary, recaptured crayfish had their marks re-branded.

A marking scheme (Abrahamsson, 1965) was used to apply individual numbers to the cephalothorax or date-specific marks to the cephalothorax or abdominal terga. Such a scheme provided ample numerical scope as a maximum of 850 individuals could be marked, with the possibility of increasing this to 25,500 (Brown, 1979).

This method of marking fulfils most of the criteria listed previously and has been widely used by other workers in this field (Abrahamsson, 1965; Moriarty, 1973; Flint, 1975; Brown, 1979). It has been compared to two tagging techniques (Cooper, 1970) and the durability of the marks was questioned. In that study reduced durability of the marks was probably due to the fact that relatively large areas of the carapace were being marked. Other applications of this method have proved successful and the use of high temperatures applied to discrete areas not only ensures that the hypodermal cells, beneath the integument, are cauterised but also that marking is achieved before a significant amount of heat is conducted to the surrounding tissues. An absence of marking mortalities and the persistence of marks through several moults has been demonstrated (Brown, 1979).

2.8 Measurements.

Measurements of body size were made to the nearest 0.5 mm or 0.1mm. using vernier callipers; except for total body length (T.L.) which was measured on a standard fish measuring board (Lagler, in Ricker, 1971) to the nearest 1.0 mm. For reasons outlined below the standard measurement taken throughout this study was carapace length (C.L.) (see

Figure 2.1) being the minimum distance from the tip of the rostral spine to the posteriomedial rim of the cephalothorax. This distance was measured on all individuals in most samples of crayfish and on randomly selected subsamples from very large ($n > 250$) samples.

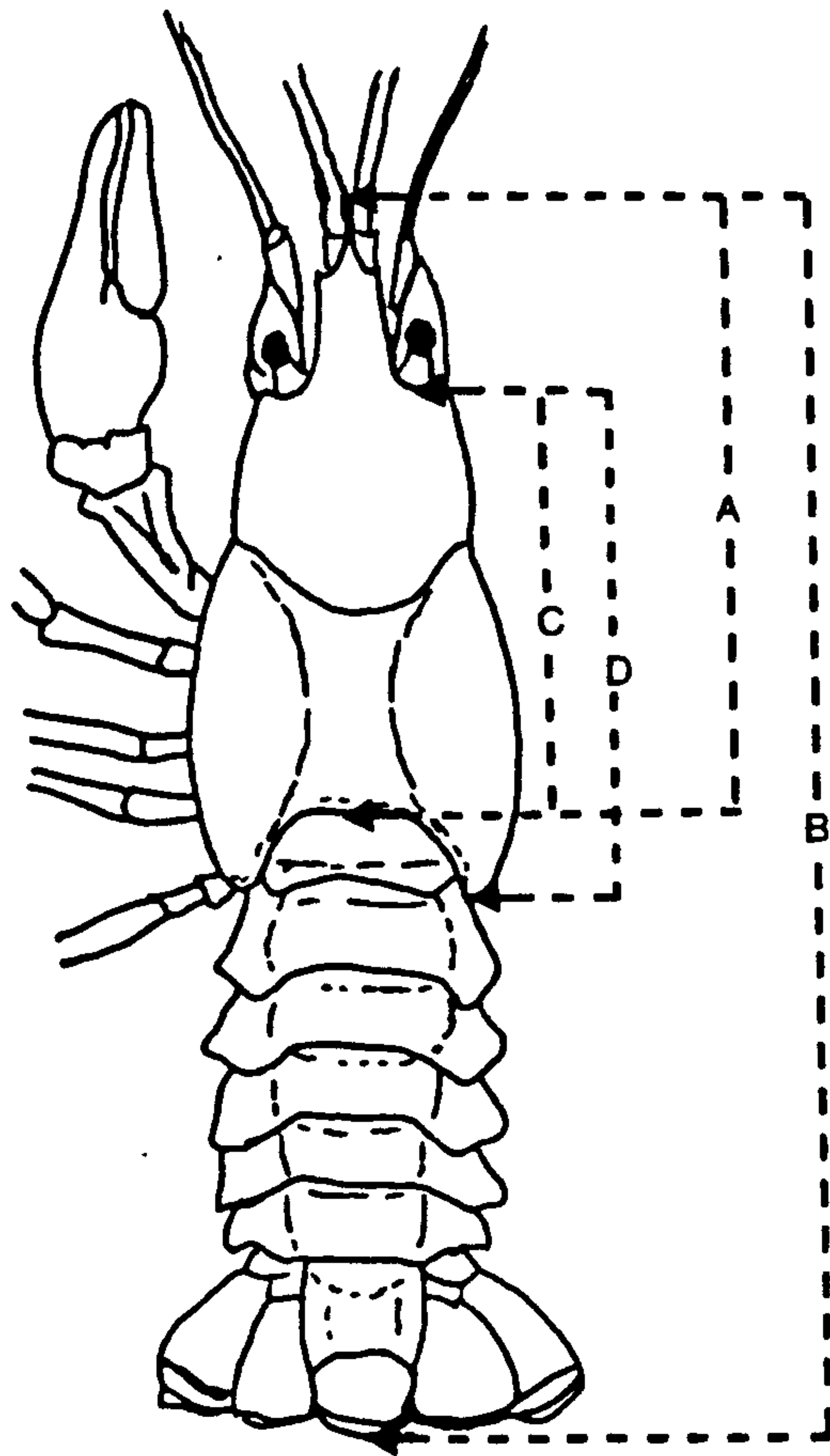
In addition, in order to characterise the morphometry of the two species of crayfish being investigated, a quantity of other morphometrical data was collected as follows (see Figure 2.1):

- (i) Carapace Width (C.W.) at the widest point.
- (ii) Postorbital carapace length (P.O.C.L.), being the minimum distance from the posterior rim of the eye socket to the posterior rim of the carapace.
- (iii) Total body length (T.L.), being the minimum distance from the tip of the rostral spine to the posterior margin of the telson.
- (iv) The width of the second abdominal segment (2A.W.), being the minimum width of somite XVI (Huxley, 1880).
- (v) Chela length (Ch.L.), being the maximum distance from the tip of the propodite to the hardened rim adjacent to the hinge with the carpopodite.
Ch.L.L. relates to the left chela, Ch.L.R. relates to the right chela and $\bar{\text{Ch.L.}}$ corresponds to the mean of measurements from both chelae.
- (vi) A record was also kept of all damaged, diseased or parasitised crayfish caught.

Carapace length was selected as the standard characteristic for measurement as the cephalothorax is a rigid part of the exoskeleton, the size of which the crayfish is unable to alter. This results in a considerable reduction in measuring errors when compared with total length or weight (Brown, 1979). C.L. rather than C.W. was used as it is much easier to quickly and accurately locate the longitudinal limits of the cephalothorax than the transverse limits. In addition it is the morphological character most frequently used by other workers studying crayfish in the U.K. (e.g. Brown, 1979; Pratten, 1980; Rhodes, 1980) thus assisting the comparison

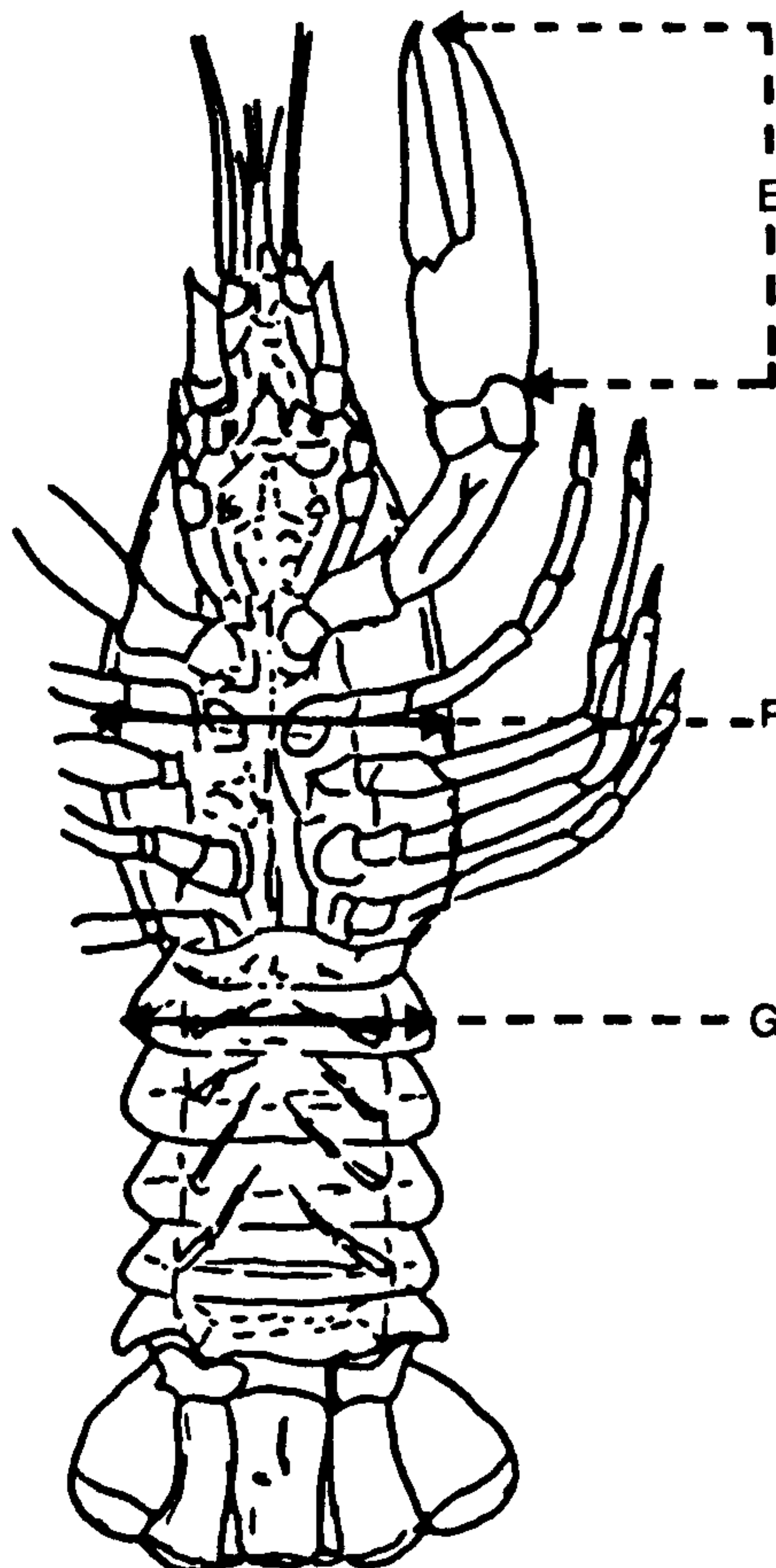
Figure 2.1 Location of measurements collected from
crayfish during this study.

Dorsal



- A Carapace Length
- B Total Length
- C Postorbital Carapace Length
- D Maximum (French) POCL

Ventral



- E Chela Length
- F Carapace Width
- G Abdomen Width

of the results of the present study with published data.

The live (fresh) weight of crayfish in certain samples was determined in the field using 'Pesola' spring balances. Laboratory weighing was carried out on a 'Sartorius' 1364 MP top-pan balance. Each crayfish was dried with filter or tissue paper (Brown, 1979) until as much water as possible was removed from the external surface and the branchial cavity, prior to being weighed to the nearest 0.5g. (field) or 0.1g. (laboratory). Drying was carried out until no more moisture appeared on the filter paper; each crayfish was also shaken to remove water from the branchial chambers.

2.9 Condition Recording.

Observations on the condition of each crayfish examined were made in accordance with pre-determined criteria, and the results recorded, as part of the routine processing of all crayfish samples. The criteria considered worth recording and the abbreviations used were as follows:

2.9(i) Life-History

(a) Sex. All individuals of C.L. > 11mm were sexed by eye through the presence of the fully developed first two pairs of pleopods (gonopods) in the male and the absence of the first pair and lack of modification of the second pair in the female (Huxley, 1880; Thomas, 1977). (b) Moulting condition. Newly moulted (N.M.) crayfish were those that had not fully hardened their new exoskeleton after moulting. Crayfish are reported to remain soft for up to about 100 hours post-moult (Stevenson, 1975) so the time of individual moults could be established to within a week. Those crayfish judged to be ready to moult (R.T.M.) or with a moult imminent were also recorded. In this case the old exoskeleton was observed to be becoming free from the new one forming underneath. This condition was recognised by an increase in the flexibility of the soft cuticle between the posterior

rim of the cephalothorax and the first abdominal tergum. (c) Maturity. The reproductive condition of the females was established, at relevant times of the year, by the presence of eggs (Q̇B) or young (Q̇Y) or the visible development of glair glands on the ventral surface of the abdomen (Thomas & Crawley, 1975a, b; Rhodes, 1980).

2.9(ii) - Parasitism and Disease.

(a) Thelohanosis. Crayfish that were infested by the microsporidian parasite Thelohania contejeani, as determined by visual examination, were recorded (Th) (see Chapter 6). (b) Branchiobdellids. Small sub-samples of A.pallipes collected from certain sites, were sacrificed, dissected and examined for the presence of the parasitic annelid Branchiobdella astaci. Presence (B+) or absence (B-) of this parasite was recorded (see Chapter 6). (c) Others. The occurrence of crayfish showing the external symptoms of other diseases was also recorded. For example, 'burn-spot' disease was recorded (B.S.) when rust coloured patches were visible on otherwise undamaged dorsal areas of the exoskeleton, usually on the carapace. Presumed tumours were also recorded from a very small number of individuals.

2.9(iii) - Injuries.

(a) Chela loss. The loss of chelae which are used for sexual display and aggression (Thomas, 1979), through fighting and autotomy, and their subsequent regeneration is a fairly common feature in all decapods (Brown, 1979). It may significantly reduce overall growth rates in A.pallipes (Brewis & Bowler, 1982). The occurrence of missing or regenerating chelae was always noted, therefore, even if chela measurements were not being collected on that occasion. (b) Body damage. Any damage to the rostrum was readily apparent and always recorded. The C.L. and T.L. of crayfish thus damaged were estimated. Damage to any other area of the body, particularly the cephalothorax,

was also recorded.

2.10 Statistical Methods.

The more common methods of data analysis and statistical tests of significance have been taken from standard texts (Bishop, 1966; Snedecor & Cochran, 1967) (The m-r formulae used are tabulated in Appendix 1.) Some more detailed and specialised analyses have also been carried out and the methods utilised are outlined below. Basic data handling was achieved using a Casio 602P programmable calculator. More complex analysis was carried out using the University of London (City of London Polytechnic) computer facility.

2.10(i) - Length-Frequency Data.

As part of the investigation into the population biology of the two species of freshwater crayfish included in this study it was considered essential to acquire data regarding both growth rates and density. The stepped increases in size which occur as arthropods moult, by shedding their hardened exoskeleton, has been well studied in decapod Crustacea (Kurata, 1962; Allen, 1966). Such studies have concerned growth in the laboratory (e.g. Emadi, 1974; Pratten, 1980) and in the field (e.g. Hiatt, 1948; Kossakowski, 1971; Abrahamsson, 1972a; Hepper, 1972; Pratten, 1980). As a result of the nature of decapod growth all of these studies have described linear or gravimetric growth.

Methods of study elsewhere have fallen into two categories. Moulting-increment data, such as the relationship between premoult and postmoult size (Hiatt, 1948; Mason, 1974); moulting-increment relationship with premoult carapace length (Abrahamsson, 1971b); and moulting-increment expressed as a percentage of premoult size (Hopkins, 1967). Analysis of the regression line of postmoult C.L. as a function of premoult C.L. has also been used to characterise growth

patterns (Kurata, 1962; Brown, 1979).

For reasons which will be explained elsewhere (Chapters 4 & 8) such methods were not employed during this study which, instead, has concentrated on using the second method of assessing growth in field populations, i.e. the relationship between size and age. The periodic shedding of all parts of the hardened exoskeleton, at ecdysis, eliminates the possibility of any such parts showing annual growth rings such as are found in the scales and otoliths of fish (Tesch, 1971). Successful methods of instar determination, based on the number and arrangement of aesthetascs on the antennules of some Isopoda (Holdich, 1968) are unadaptable for use in ageing Decapoda (Farmer, 1973; Brown, 1979). There are, so far as is known, no structures by which the accurate ageing of any decapod species can be accomplished. One of the methods of assessing growth used in this study is based on the analysis of the polymodal size-frequency distribution by means of cumulative probability curves (Harding, 1949; Cassie, 1954). The mean of each modal group, thus separated, is usually considered to constitute the mean size of a year class (Brown, 1979) but as both species of crayfish studied moult more frequently early in life (Emadi, 1974; Pratten, 1980) each modal group has been considered to form a size-class, during this study, and this has been related to age using a knowledge of moult frequency (Brown, 1979; Pratten, 1980).

The three methods of analysis length-frequency data that have been considered for use during this study have been fully described elsewhere (Cassie, 1954; Tanaka, 1962; Bhattacharya, 1967) and will only be briefly outlined here. The 'probability paper' method (Harding, 1949; Cassie, 1954) involves the dissection of a length-frequency distribution, at the point of inflexion, followed by a correction for the overlap of components. Attempts have been made to utilise this method in the present study for the analysis of crayfish populations of known age (see Chapter 8). Some

success was achieved but the major problem encountered was with the identification, by eye, of inflexion points on the probability curves (e.g. Figure 4.10).

The other method that was attempted, unsuccessfully, depends on equating the class-frequency to the ordinate at the mid-point of the class in a region where the effect of all but one component is negligible (Tanaka, 1962). This method was tried but was considered too cumbersome for general application throughout this study. Both this and the previous method were therefore abandoned in favour of the following method (Bhattacharya, 1967) which was found to be simpler in operation and probably just as accurate in respect of the current investigation. Consequently it was felt to be more readily applicable to the large amount of data available and provided at least as accurate an analysis of the data as the two methods already outlined.

The method of analysis of length-frequency data adopted for use in this investigation has been fully described elsewhere (Bhattacharya, 1967). This method considers that the frequency distributions of components of the distribution of a morphometric characteristic in a biological population are Normal. Hence the problem is one of the resolution of a distribution into its Gaussian components. In fish populations, for which this method was devised, the frequency distribution is usually skew and polymodal, with modes corresponding to individual age groups. This is not the case with crayfish, however, where moult frequency governs the size of individuals in an age class or cohort. Ideally samples of crayfish for length-frequency analysis should have been collected during the intermoult period, i.e. November to March (Brown, 1979) but this was not practicable, for reasons discussed elsewhere (see Chapter 4).

This method of analysis considers a cubic approximation to density within a class but approximates the logarithm of class-frequency by a quadratic. Simple differencing

reduces this to a straight line. If $y(x)$ is the observed frequency in the class with midpoint x and λ is the class interval then $\Delta \log y$ (i.e. $\log y(x-\lambda) - \log y(x)$) is plotted against x . The number of regions of this line which are straight and with a negative slope are, subject to certain conditions, equivalent to the number of components comprising the distribution. The mean and standard deviation of each component can then be calculated and overlapping components identified.

The length-frequency distributions of crayfish from both native and introduced populations have been analysed using this latter method. (see Chapters 4 & 8). In both cases the component size classes identified have been used to construct generalised growth curves. In the former case, involving A.pallipes, published data (Brown, 1979; Pratten, 1980) has provided estimates of moult frequency for each age group so that size classes could be converted to age classes. In the latter case, involving P.leniusculus, as the exact age of the population was known from the recorded dates of introduction of the crayfish interpretation of the analysis is simpler and size groups may be more readily converted to age groups. It is clear that this method of analysis only provides an approximate solution to the problem of analysing the age distribution within a crayfish population. It does, however, enable direct comparison to be made between, for example, the growth of crayfish in different parts of the country (see Chapter 4) or in different latitudes (see Chapter 8).

2.10(ii) - Morphometric Data

Data concerning the morphometry of both species of crayfish investigated during this study has been collected in order to characterise and define the body form of each species and to obtain comparative data regarding, for example, growth in populations from different locations and habitat types. Measurements were collected, as described

previously, and used to establish the relationships between the following parameters:

- (i) Length - Weight. The relationship between C.L. and fresh weight has been established for each species by means of exponential regression analysis. Data collected concerning this relationship has also been used to calculate a 'Condition Factor' (Ricker, 1975) for individual crayfish in selected samples. In this case C.L. was converted to T.L. using equations [1] and [2] Table 6.3(a) for A.pallipes and equations [1] and [2] Table 8.6(a) for P.leniusculus.
- (ii) C.L. x T.L. The relationship of C.L. to T.L. was established to afford comparability with published data concerning A.pallipes, P.leniusculus and other crayfish species (Demars, 1979).
- (iii) C.L. x C.W. The ratio of C.L. to C.W. was established for both male and female A.pallipes to enable a complete morphometric analysis to be carried out.
- (iv) C.L. x P.O.C.L. This relationship has been examined to enable comparisons to be made with published data concerning A.pallipes in France (Anon., 1980).
- (v) C.L. x 2 A.W. The width of a female crayfish abdomen is reported to be proportionally greater in mature females than in males and immature females (Wenner, et al, 1974; Stein, 1976; Brown, 1979; Rhodes & Holdich, 1979; Rhodes, 1980). The size at which maturity commences, in females, has been established by multiple regression analysis of C.L. x 2 A.W. in both species.
- (vi) C.L. x Ch.L. As with (v) the size of the chelae in mature crayfish is proportionally greater than in females or immature males (Rhodes & Holdich, 1979; Rhodes, 1980). The size at which maturity commences in the males has been established by the multiple regression analysis of C.L. x $\overline{\text{Ch.L.}}$.

2.10(iii) - Estimation of Population Size.

A number of methods of mark and recapture analysis have been developed for estimating population size and several of these have been considered for use in the current study. A basic prerequisite to the use of these methods is a marking technique which enables the animals to be released unharmed and unaffected whilst also being recognisable upon subsequent recapture (Southwood, 1966). The method of marking used throughout this study (Abrahamsson, 1965) is described elsewhere.

Individual marking has been carried out in some instances in order to obtain additional information of life-span, dispersal, moult-frequency, etc. The low recovery rates achieved, (see Chapters 4 & 8) however, suggested that the additional time involved was unjustified.

The assumptions that are made concerning the use of mark - recapture methods have been reviewed elsewhere (Seber, 1973) but may be briefly summarised as follows:-

- (a) Random mixing occurs after the release of marked animals.
- (b) Sampling is random with respect to marked and unmarked animals.
- (c) Size groups and sexes are sampled in proportion to their abundance.
- (d) All individuals are equally available for capture.
- (e) The duration of sampling is small in relation to total time.

The extent of remixing has been checked in selected instances, by comparing the ratio of marked and unmarked individuals in samples from different locations within the same site. The significance of the difference has been checked by using a χ^2 test (Southwood, 1966; Iwao, 1963).

The following methods of estimating population size have been utilised at one or more of the sites investigated:-

- (i) Lincoln Index/Petersen Method (Ricker, 1971, 1975) uses data from two or more sampling occasions. A modification of the basic formula (Ricker, 1975) has been applied if data is from small samples of crayfish.
- (ii) Schnabel and Schumacher (Ricker, 1975) approximates the maximum likelihood estimate from multiple census data.
- (iii) Bailey (Bailey, 1951, 1952; Ricker, 1975) also utilises maximum likelihood techniques, using data from only three sampling occasions, and enables accurate variances of the estimate to be calculated. As it is based on a deterministic model of survival the method is most valuable when large numbers are marked and recaptured (Ricker, 1975).
- (iv) Jolly (Jolly, 1965; Ricker, 1975) uses three or more successive samples and allows for migration, mortality, etc. As it is a stochastic model the survival rate can be calculated.

The formulae for the calculation of these estimates are listed in Appendix 1.

SECTION A. THE BIOLOGY AND DISTRIBUTION OF A.PALLIPES IN THE THAMES CATCHMENT.

SECTION INTRODUCTION.

A.1. General Considerations.

Few detailed studies of Britain's largest freshwater crustacean and only native crayfish, A.pallipes, have been undertaken and information on its biology and distribution is incomplete (Brown, 1979; Rhodes, 1980; Jay & Holdich, 1981). Until recently such studies were limited to a single published account (Duffield, 1933) but in recent years more information has been published (e.g. Thomas & Ingle, 1971; Brown, 1979; Pratten, 1980; Rhodes, 1980; Jay & Holdich, 1981). Crayfish have, however, long been used as laboratory animals for, for example, studies on temperature acclimation (Bowler, 1963a, b), calcium metabolism (Greenaway, 1974a, b & c) and metal ion metabolism (Adams, et al, 1982). There is still only one standard English text on crayfish biology and physiology (Huxley, 1880).

As previously stated this lack of information concerning crayfish in the U.K., and in the Thames Catchment in particular, was highlighted in 1976 by the introduction of a byelaw by the Thames Water Authority under powers granted to them by the Salmon and Freshwater Fisheries Act, 1975. Byelaw 14 states that "Except with the previous consent of the Authority in writing no person shall remove crayfish from non-tidal waters." (T.W.A. Fishery Byelaws, 1978). In addition permission is also required from the riparian owner.

A.2. Aims of Study. (Section A).

This section of the study aims to provide information which will enable an assessment to be made of the distribution and economic importance of the native crayfish, A.pallipes, in the Thames Catchment and the factors controlling these.

In order to facilitate such an assessment attempts have been made to collate existing records of crayfish occurrence and further determine the distribution of the native crayfish in the area under consideration. This distribution has been related to factors considered to be of importance in governing the suitability of a waterbody or watercourse for occupation by A.pallipes (see Chapter 3).

It was then envisaged that the population dynamics of an enclosed lacustrine population would be studied, both before and after simulated cropping, to provide information necessary for the construction of a management policy for such a population. In fact no such cropping was carried out (see Chapter 4). The study did permit, however, a mean growth pattern for A.pallipes throughout its lifecycle to be postulated for the study population, based on the analysis of size-frequency distributions, together with the assimilation of a considerable amount of ecological and life-history information.

In addition data on the general biology and growth-rate of this population were to be compared and contrasted with similar data obtained from a riverine population. It has been established that closely related species of crayfish may be subject to environmental control of aspects of their life-cycle. Orconectes virilis, in a region of North America where it is sympatric with, and has a similar range to, O.immunis exhibits relatively fixed timing of its life-cycle. Conversely O.immunis is more flexible in the yearly timing of its life-cycle. This difference has been 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 water level would be more likely to interfere with reproduction (Caldwell & Bovbjerg, 1969). The variability in the pattern of life-history of the Cambarinae, compared to the Astacinae, may reflect the wide variety of habitat types inhabited by the former (Momot, 1964; Albaugh, 1973). A.pallipes in the

U.K. occupies a much wider range of habitat types than do other species of crayfish elsewhere in Europe (Laurent & Forest, 1979) and one of the reasons for this could be a greater ability to adapt to a wider range of environmental conditions than, for example, A.astacus. Investigation of two geographically close but hydrologically dissimilar populations could provide information relevant to explaining this aspect of the biology of A.pallipes.

Finally, it has been suggested that increased pressure on waterways, by man, in the form of pollution and flood regulation/flow management schemes, could be accountable for a reputed decline in the abundance and distribution of the native crayfish (Reynolds, 1979). Direct effects of pollutants on crayfish were to be studied elsewhere (Holdich, pers comm) so in this study only the gross effects of pollution on crayfish distribution have been investigated (see Chapter 3). A more detailed investigation has been carried out, however, into the ways in which engineering schemes for flood-alleviation and flow-management can directly affect crayfish populations (see Chapter 5).

A.3 Species Description.

AUSTROPOTAMOBIUS PALLIPES (Lereboullet, 1858)

Order: Decapoda.

Family: Astacidae.

Sub family: Astacinae.

Genus: Austropotamobius.

Species: pallipes.

Synonym: *Astacus pallipes* (Lereboullet, 1858).

Common names: 'White-Clawed Crayfish.' (Laurent & Forest.
1979; Westman &
Pursainen, 1982)

'Atlantic Stream Crayfish.' (Wells, 1982)

'River Crayfish.' (Westman & Pursainen, 1982)

This species is characterised by its rostrum which is

triangular in form, expanding from the apex to the ocular region, with an ill-defined, toothless median dorsal ridge (Laurent, 1960; Laurent & Forest, 1979). A single post-orbital ridge and only a single row of spines, posterior to the vertical groove, occur on the cephalothorax. Colour is very variable, from dark brown through greenish and chestnut brown to almost blue. Size is generally small with few individuals exceeding 10 cms. T.L. and 70g. live weight (Laurent & Forest, 1979). Males, as with other crayfish species, grow larger and heavier than the females.

Growth is relatively slow, it takes two years to attain 4.0 cm. T.L., three years to reach 5.0 - 5.5. cm.T.L., four years to reach 6.0. - 7.0 cm. T.L. and by six years old may be 7.0 - 8.0 cm. T.L. (Pratten, 1980). The minimum size of ovigerous females has been reported as 6.0 cm.T.L. (Moriarty, 1973) and 25.3 mm.C.L. (equivalent to approximately 5.4 cms. T.L.) (Rhodes, 1979) with an average brood of 85 eggs at 40 mm.C.L. (Rhodes & Holdich, 1982).

A.4, Life - Cycle.

The main features of the life-history of A.pallipes are identical to those of other members of the Astacidae (see Chapter 1). Differences in timing do, however, occur largely as a result of climatic variations. Mating takes place in late - September or October when the male deposits a spermatophore mass on the female. The eggs, laid 14 - 20 days later, are attached to hairs and ventral appendages on the female abdomen and are carried through to the next spring. Hatching occurs in May or June (see Chapter 4) through to August (Brown, 1979) depending on winter and spring water temperatures. The young remain with the mother until at least after their second moult when they leave the female and become free - living. Sexual maturity is reached at 3+; the natural life span of A.pallipes is not known (Wells, 1983) but is at least 10 - 13 years (Brown & Bowler, 1979).

A.5. Taxonomy.

Although generally treated as a single species there are several systems of classification that recognise from two to five subspecies of A.pallipes (for review see Albrecht, 1982). A.pallipes italicus (Faxon, 1914) and A.pallipes lusitanicus (Ninni, 1886) form the simplest subspecies division (Holthuis, 1967). A more commonly accepted classification is Atlantoastacus pallipes pallipes (Lereboullet, 1858), A.pallipes italicus (Faxon, 1914) and A.pallipes lusitanicus (Mateus, 1934) (Bott, 1950). The most complex classification system lists five subspecies: A.pallipes carsicus (Karaman, 1962), A.pallipes bispinosus (Karaman, 1962), A.pallipes pallipes (Lereboullet, 1858), A.pallipes italicus (Faxon, 1914), A.pallipes lusitanicus (Mateus, 1934) (Karaman, 1962). Using the criteria on which the three subspecies system is based (Bott, 1950; Laurent & Suscillon, 1962) all of the specimens examined during this study were identified as A.pallipes pallipes (Lereboullet, 1858) and will be referred to as A.pallipes (Gledhill, et al, 1976) in this report.

A.6. Distribution

The only species of freshwater crayfish indigenous to the British Isles is Austropotamobius pallipes (Lereboullet, 1858) (Thomas & Ingle, 1971; Gledhill, et al, 1976; Brown, 1979). It is widely distributed and locally abundant in waters in England (Huxley, 1880; Thomas & Ingle, 1971; Jay & Holdich, 1977, 1981; Brown, 1979), Wales (Lilley, 1977; Jay & Holdich, 1981) and Ireland (Moriarty, 1973; Gledhill, et al, 1976; Reynolds, 1979) but apparently does not occur naturally in Scotland (Jay & Holdich, 1981).

A.pallipes is also the most common species of crayfish in France where it can be found in all the major catchments and also in Corsica (Laurent & Suscillon, 1962; Laurent & Forest, 1979; Albrecht, 1982). It is also reported to occur in Spain (Cervignon & Marques, 1964; Albrecht, 1982),

Switzerland and the Dalmatian region of Yugoslavia (Ingle, 1979; Albrecht, 1982) and Italy (Albrecht, 1982). It is also suggested that A.pallipes may be found in Germany (Thomas & Ingle, 1971) but it is not included in species found during a recent survey of crayfish distribution in that country (Hofmann, 1980).

That A.pallipes is the only freshwater crayfish species native to the U.K. has been attributed to the effects of the Pleistocene Ice Age (Hynes, 1972) and the fact that it was the only crayfish species in most of western Europe when the English Channel was formed (Huxley, 1880). Other species, it is suggested, later colonised Europe from the east, with A.astacus spreading into northern Europe and A.leptodactylus migrating into eastern Europe from Asia Minor (Huxley, 1880; Cukerzis, 1968).

A.7, Biology.

A.pallipes inhabits, in the U.K., calcium - rich waters of all types; rivers, lakes, streams, canals and reservoirs. (Jay & Holdich, 1981). By contrast over the rest of its range it is more limited to streams and small rivers (Laurent & Forest, 1979).

Physiological studies have estimated oxygen consumption (Sutcliffe, et al, 1975) but not the minimum oxygen requirements (Laurent & Forest, 1979). The minimum calcium concentration required is reported to be $2.8 \text{ mg.l.}^{-1} \text{Ca}$. (Laurent & Forest, 1979).

Generally A.pallipes are omnivorous, feeding on algae, diatoms, etc. as juveniles and being far more scavenging in nature as adults, subsisting on plant food and detrital material and supplementing this with fresh carrion when available (Brown, 1979). Cannibalism is prevalent in dense populations. There have been numerous predators of A.pallipes reported and these are listed in Table A.1

TABLE A.1. PREDATORS OF EUROPEAN FRESHWATER CRAYFISH

N.B. Compiled from published information. Predators of possible importance in the Thames Catchment are marked *.

Species	Common name	Prey	Reference(s)
<i>Barbus barbus</i>	Barbel	<i>A.pallipes</i>	Taverner, 1957
* <i>Cottus gobio</i>	Bullhead	" " "	Green, 1975
<i>Lota lota</i>	Burbot	<i>A.astacus</i>	Dehli, 1981
<i>Cyprinus carpio</i>	Carp	<i>A.leptodactylus</i>	Erençin & Koksäl, 1977
<i>Leuciscus cephalus</i>	Chub	<i>A.pallipes</i>	Mann, 1976
" "	"	<i>A.astacus</i>	Kossakowski, 1973, 1975
<i>Leuciscus leuciscus</i>	Dace	<i>A.pallipes</i>	Taverner, 1957
* <i>Anguilla anguilla</i>	Eel	" "	Watson in Brown 1979
" "	"	<i>A.astacus</i>	Svårdsson, 1972; Dehli, 1981
" "	"	<i>A.leptodactylus</i>	Knoeppfler, 1979
" "	"	<i>O.limosus</i>	Kossakowski, 1973, 1975
* <i>Perca fluviatilis</i>	Perch	<i>A.pallipes</i>	Mann, 1978
" "	"	<i>A.astacus</i>	Dehli, 1981
" "	"	<i>O.limosus</i>	Kossakowski, 1973, 1975
" "	"	<i>P.leniusculus</i>	Fürst, 1977; Westman, 1973, 1975
(" "	"	<i>C.tenuimanus</i>	Morrissey, 1978b)
* <i>Esox lucius</i>	Pike	<i>A.pallipes</i>	Mann, 1976; Taverner 1957; Moriarty, 1973
* <i>Esox lucius</i>	Pike	<i>A.astacus</i>	Dehli, 1981
" "	"	<i>O.limosus</i>	Kossakowski, 1973, 1975
" "	"	<i>P.leniusculus</i>	Westman, 1973
<i>Rutilus rutilus</i>	Roach	" "	Westman, 1973
<i>Tinca tinca</i>	Tench	<i>A.astacus</i>	Spitzzy, 1973
(<i>Salmo fontinalis</i>	Trout (Brook)	<i>O.virilis</i>	Momot, 1967)
" "	" "	<i>A.pallipes</i>	Brown, 1979
<i>Salmo trutta fario</i>	" (Brown)	" "	Towner-Coston, 1936; Frost & Brown, 1967
" <i>clarkii</i>	" (Cutthroat)	<i>P.leniusculus</i>	Mason, 1975
* <i>Salmo gairdneri</i>	" (Rainbow)	<i>A.pallipes</i>	Watson, in Brown, 1979
<i>Silurus glanis</i>	Wels	<i>A.leptodactylus</i>	Erençin & Koksäl, 1977; Arrignon, 1981
<i>Corvus corone</i>	Crow	<i>A.pallipes</i>	Laurent, 1973; Pratten in Brown, 1979
* <i>Ardea cinerea</i>	Heron	" "	Macan & Worthington, 1972
" "	"	<i>A.astacus</i>	Dehli, 1979
<i>Alcedo atthis</i>	Kingfisher	<i>A.pallipes</i>	Eastman, 1979
<i>Strix aluco</i>	Tawny Owl	" "	Fryer, 1976
<i>Vulpes vulpes</i>	Fox	<i>A.pallipes</i>	Laurent, 1973
* <i>Mustela vison</i>	Mink	<i>A.astacus</i>	Erlinge, 1972; Dehli, 1981
<i>Lutra lutra</i>	Otter	<i>A.pallipes</i>	Harris, 1968; Macan & Worthington, 1972
" "	"	<i>A.astacus</i>	Erlinge, 1972; Dehli, 1981
<i>Rattus norvegicus</i>	Rat	<i>A.pallipes</i>	Lowe, 1920; Laurent, 1973
† <i>Arvicola amphibius</i>	Water Vole	" "	Southern, 1964; Lawrence & Brown, 1967
" "	" "	<i>A.astacus</i>	Dehli, 1981
(<i>Aeshna</i> sp.	Dragonfly	<i>O.virilis</i>	Dye & Jones, 1975)
" "	Cannibalism	<i>A.astacus</i>	e.g. Cukerzis, et al, 1976
" "	"	<i>A.pallipes</i>	e.g. Brewis, 1979
" "	"	<i>P.leniusculus</i>	e.g. Mason, 1977, 1979
" "	("	<i>C.tenuimanus</i>	e.g. Morrissey, 1978)

†(Vegetarian according to Macan & Worthington, 1972.)

together with known predators of other crayfish species which may also affect A.pallipes in the U.K. Those considered as potentially important predators in the Thames Catchment are indicated in the table.

A.8. Economic Importance.

Crayfish were formerly of considerable local importance in certain areas of the U.K., particularly in parts of southern England and including the Thames Catchment (Cornish, 1902). Anecdotal reports recount how special trains were arranged to transport watercress and crayfish to the London markets from parts of the Kennet valley (Van Moppes, pers comm; Anon, 1975) in the nineteenth century. Currently, however, there is little apparent interest in A.pallipes from an economic viewpoint as it is slower growing and generally smaller than the P.leniusculus currently being produced for the table market. A.pallipes that have been offered for sale in retail outlets attract a price of about £3.50 kg.⁻¹ (Goddard & Holdich, 1979) which is comparable with the retail price of imported A.leptodactylus and P.clarkii (Moore, pers comm) but considerably less than the £11 kg.⁻¹ (Richards, pers comm) paid for home produced P.leniusculus. Those A.pallipes that are harvested from natural populations are generally for individual consumption with few reaching the market. Accurate records of cropping and marketing activities are seldom kept so there is no information available regarding the scale or extent of such activities in the U.K.

CHAPTER 3. THE DISTRIBUTION OF A.PALLIPES IN THE THAMES CATCHMENT

3.1. Introduction.

The general dearth of information that has been published regarding national crayfish distribution (Jay & Holdich, 1981) is also true of the Thames Catchment. This area, by definition the area drained by the River Thames and its tributaries, covers some 13,000 square km. and includes more than 4,000 km. of rivers. It extends from northwest Kent and southwest Essex in the east to Cirencester in the west; from Haslemere and Alton in the south to Banbury and Luton in the north (Figure 3.1). The Thames Water Authority is responsible for water supply, sewerage, drainage and fisheries within this area and caters for a population of more than twelve million (Anon., 1978).

The factors that have been reported as controlling the natural distribution of freshwater crayfish are water quality, particularly with respect to pH and calcium content, and temperature (Brown, 1979; Laurent, 1980; Jay & Holdich, 1981). It appears, however, that A.pallipes is relatively eurytopic with respect to calcium content as it thrives in the fairly soft waters of an aqueduct in Co. Durham, with a mean calcium concentration of 18.6 mg. l^{-1} (Brown, 1979), and in Lough Lea, in Northern Ireland, with a mean calcium concentration of 11.5 mg. l^{-1} (Watson, unpubl.). It has been reported to naturally occur in waters, in Wales, with a mean concentration of 6.1 mg. l^{-1} of calcium (Lilley, et al, 1979) but is unable to moult successfully in water from Lake Windermere, Cumbria, with a calcium concentration of only 5.0 mg. l^{-1} (Sutcliffe & Carrick, 1975). These figures contrast with the minimum calcium requirement of 2.8 mg. l^{-1} reported from France (Laurent & Forest, 1979). Clearly, then, the lower acceptable limit of calcium concentration in the water is well to the 'soft' end of the scale.

A.pallipes is not restricted to totally unpolluted waters, as is often assumed, and is no more susceptible to heavy metal pollution than other aquatic invertebrates (Chaisemartin, 1976). Temperature is thought to be a factor limiting distribution nationally. Populations in Northumberland are considered to be at the northern limit of its range in the U.K. (Brown & Bowler, 1977) due to the short growing season.

The distribution of A.pallipes in the Thames Catchment in the late nineteenth and early twentieth centuries has been partially established from the available literature (Thomas & Ingle, 1971). A limited survey that was carried out in the 1930's (Duffield, 1933) concentrated on the River Ock but also included records from the Rivers Thame, Windrush and Cherwell. The tentative conclusion drawn from this latter study, which relied largely on anecdotal information, was that crayfish populations although widely distributed suffer dramatic periodic declines. It was not confirmed whether this was due to disease, pollution or as a result of excessive population densities. A small number of more recent published records of crayfish distribution in Kent (Thomas & Ingle, 1971), Oxfordshire (Pixell-Goodrich, 1956) and Berkshire (Leeke & Price, 1965) also exist. Recent records from the main River Thames are limited to the upper reaches and unsubstantiated reports of crayfish at North Stoke and Weybridge. This is in direct contrast to the situation at the turn of the century when they were reported to be "plentiful from Staines upstream to the source" (Cornish, 1902).

A full survey of crayfish distribution in the Thames Catchment has never been carried out and a national survey of their distribution was only attempted in the late 1970's (Jay & Holdich, 1981). Clearly a survey of distribution on a more local scale, concentrating, for example, on a single river basin, must form an essential part of any study of crayfish ecology within that area and will supplement

distribution information collected nationally.

3.2. Methods.

The records collated were obtained from a variety of sources, principally:

- (i) Water Authority biological sample records;
- (ii) County Biological Recording Schemes;
- (iii) Published data;
- (iv) Personal observation and personal communication with, for example, landowners, fishery bailiffs, anglers and research institutes such as Reading University and the Freshwater Biological Association.

Those records collected from sources (i) to (iii) were considered 'reliable' whereas those obtained through personal communication were often of a vague nature and of doubtful reliability. Wherever possible such doubtful records were personally verified before inclusion as definite records.

In order to determine whether or not crayfish were present at a site hand searching was carried out. A brief visual assessment was made before commencing such a search and in some cases this resulted in no search being carried out. Unsuitable sites were considered to be those with a very soft substratum, little suitable cover and a depth too great for hand collection (i.e. >0.75m). Hand collection involved methodically working upstream, in the water, turning over suitable refugia whilst holding a collecting net (standard F.B.A. or 'Antox' pond-net, with 0.04m² opening) at their downstream side (Lilley, et al, 1979). In order to ensure some degree of comparability between sites searches were timed and ranged from 0.25 to 1.0 hours in length depending on the amount of available cover and crayfish abundance. The majority of sites searched in this way were located adjacent to roadbridges, for ease of access. This frequently contributed to the suitability of the site in respect of shade and an abundance of refugia in the form of

stone, brick rubble and eroded masonry.

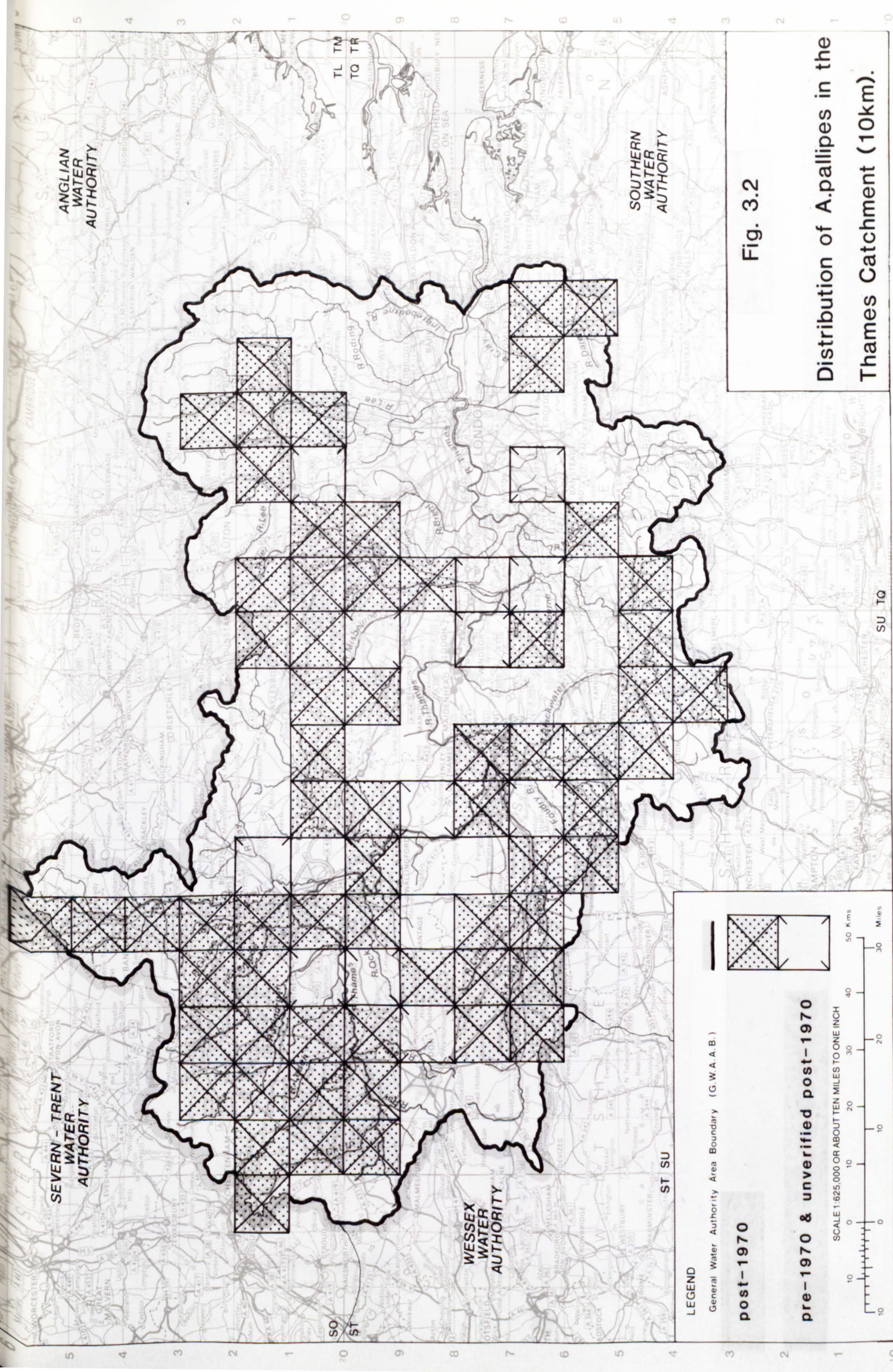
At certain sites, which were unsuitable for hand collection as they were too deep, overnight trapping using baited 'lobster pot' type traps was carried out but always proved unsuccessful. Sites where trapping was attempted included the Kennet and Avon Canal, the River Loddon at Sindlesham, Reading and Hambridge Lake, Newbury. To check trap effectiveness trapping was also carried out at one shallow site, known to be inhabited by A.pallipes, but the trap design proved to be unsuitable for use in fast flowing water, as the traps tended to collapse in situ. This method was abandoned in favour of hand collection. Subsequently successful trapping was carried out in a river situation, although of a population of P.leniusculus (see Chapter 9).

3.3. Results.

The distribution of A.pallipes in the Thames Catchment is illustrated in Figures 3.2 and 3.3. A list of distribution records is presented in Appendix 2.

Figure 3.2 shows distribution plotted according to the method and scale adopted by the I.T.E. Biological Records Centre at Monkswood (Heath & Perring, 1978). Each solid 100 km² square, based on the Ordnance Survey 'National Grid' system corresponds to one in which crayfish have been recorded since 1970.

Figure 3.3 illustrates the distribution of A.pallipes according to the method and scale used by the county biological recording schemes (Campbell, pers comm). Each 100 km² square on Figure 3.2 is subdivided into 25 squares 4 km² in area with sides 2 km. long, known as tetrads. Again each square relates to one, or more than one, record from within that square. All the solid squares correspond to confirmed or reliable post-1970 records; open



SEVERN - TRENT
WATER
AUTHORITY

WESSEX
WATER
AUTHORITY

ANGLIAN
WATER
AUTHORITY

SOUTHERN
WATER
AUTHORITY

LEGEND

General Water Authority Area Boundary (G.W.A.A.B.)

post-1970

pre-1970 & unverified post-1970

SCALE 1:625,000 OR ABOUT TEN MILES TO ONE INCH



Fig. 3.2

Distribution of A.pallipes in the Thames Catchment (10km).

squares either relate to pre-1970 records or unverified and doubtful post-1970 records.

3.4. Discussion.

In order to try and account for the distribution of A.pallipes in the Thames Catchment, as illustrated in Figures 3.2 and 3.3, a number of factors have to be taken into consideration. It is appreciated that crayfish may occur where there is no record of them so only their presence and not their absence will be considered here.

The factors that apparently govern distribution can be separated into the natural and artificial characteristics of a water body. In lowland Britain virtually all rivers and lakes are managed to a greater or lesser degree (Swales, 1981) and such management may considerably alter the natural condition of the site. Indeed habitat alteration and urban growth are reputed to have caused the disappearance of A.pallipes from some areas (Reynolds, 1979). The characteristics of a water body that are reported to determine its suitability for crayfish are as follows:

- (i) Water quality, both natural and artificially managed;
- (ii) The physical nature of the river or lake;
- (iii) The biological community living within or around the water body. (Daguerre de Hureaux & Roqueplo, 1980; Jay & Holdich, 1981).

Clearly all three factors are inter-related.

As it would be impossible to totally separate the three factors, listed above, the relationship between them and crayfish distribution will be examined by considering their component parts. Those that have been evaluated in most detail in the current study are solid geology and pollution status. The effects of physical alteration of the habitat and the biological community on crayfish distribution will be discussed in less detail here but the

former aspect is considered at length elsewhere (see Chapter 5).

3.4(i) - Geology

Figure 3.4 shows the distribution of A.pallipes, transposed from Figure 3.3, in relation to the solid geology of the Thames Catchment. It can be seen that most of the areas that support extensive crayfish populations are those based on chalk and limestone substrata and sandstone areas that are influenced by these.

The solid geology of an area will dictate the natural quality of the water flowing over it, particularly those factors known to be of importance to crayfish, namely pH and calcium concentration (Laurent, 1980; Jay & Holdich, 1981). Those areas with base rich, easily weathered substrata tend to have soils rich in calcium and hence are primarily 'hard-water' areas (Jay & Holdich, 1981). Almost all of the water bodies in the Thames Catchment can be classed as having hard water; water analysis data supplied by Thames Water shows that pH is normally in the range 7.0 to 8.5 + and hardness ranges from 100 to 350 + mg.l^{-1} CaCO_3 . Published distribution information states that crayfish occur, on a national scale, within a pH range of 7.0 to 9.0 (Jay & Holdich, 1981). Clearly, the pH and calcium concentration are unlikely to be a major factor controlling crayfish distribution in the Thames Catchment, although they may do so nationally.

The other main effect that the geology of an area will have on waterbodies in that area is to determine the physical nature of the bed. Rivers flowing through alluvial deposits, consisting largely of 'river gravels' and clays, are generally slower flowing and of a more silty nature than those flowing across less easily weathered strata (Lewin, 1981). In the Thames Catchment the former tend to be the lower reaches of most of the tributaries, together with some

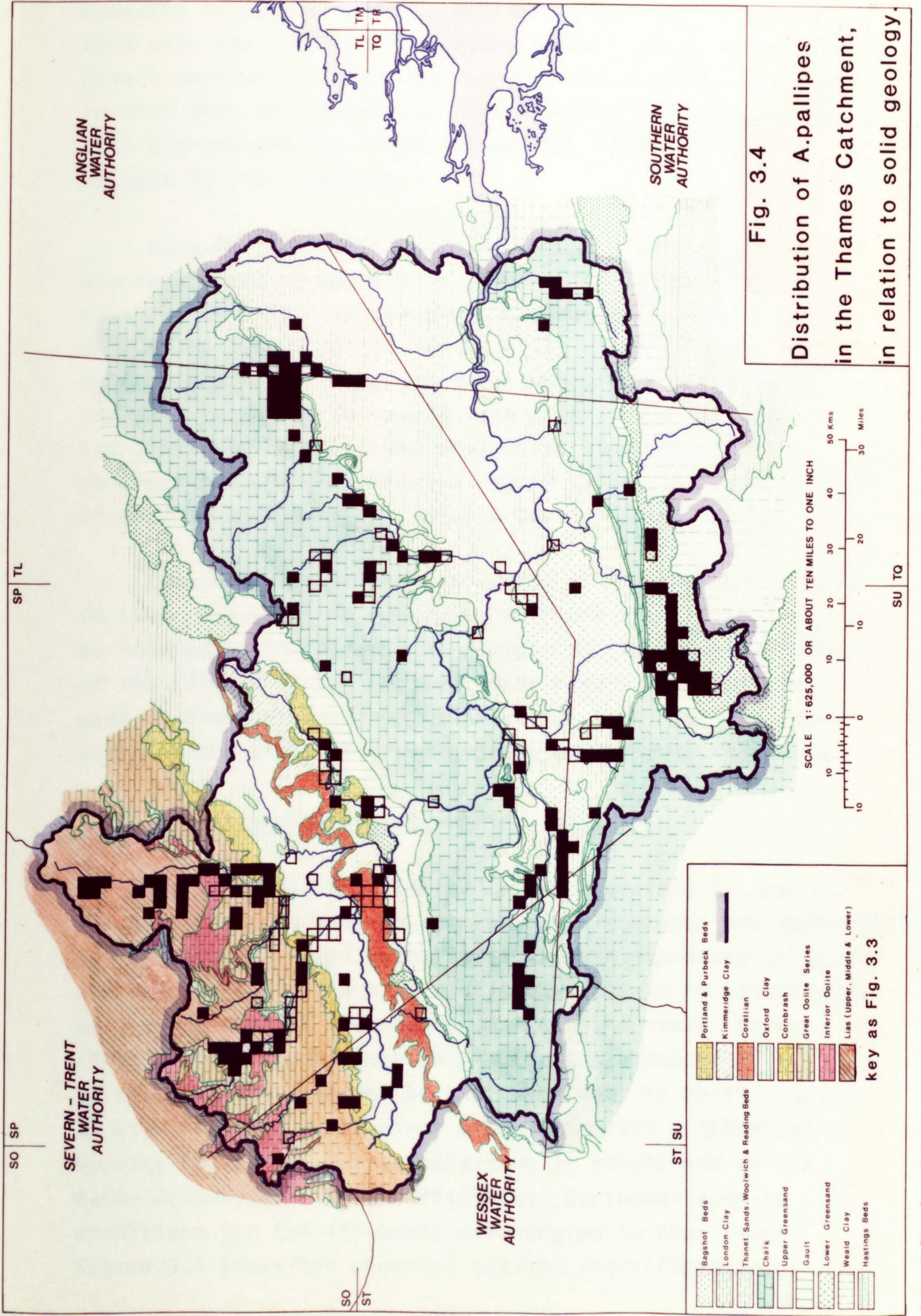


Fig. 3.4
Distribution of *A. pallipes*
in the Thames Catchment,
in relation to solid geology.

Based upon the Ordnance Survey 1:625 000 map with the permission of the Controller of Her Majesty's Stationery Office.

complete tributary systems, and the latter are rivers that flow over the chalk and limestone areas. These latter rivers more often fulfil the habitat requirements of crayfish in that they are frequently fast flowing, well aerated rivers with a predominantly stony substratum, offering ample refugia for the crayfish.

Such factors could explain, in part, why A.pallipes are restricted to the middle reaches of the River Mole (see Figure 3.3). In the Dorking and Leatherhead region (N.G.R. TQ 180500 to TQ 165550) this river crosses the chalk scarp that forms the North Downs and this results in the river changing in nature from a slow-flowing, deep and silty channel upstream of Dorking to a shallower, well-aerated and fast flowing one in this area. Downstream of Leatherhead the river reverts to its former type.

Similarly the downstream extent of crayfish occurrence in such rivers as the Windrush, Evenlode and Cherwell may be related to the effects of geology on the physical nature of the river. It can be seen, from Figure 3.4, that in each of these rivers crayfish have not been recorded from sites in the areas of river gravels and alluvial deposits.

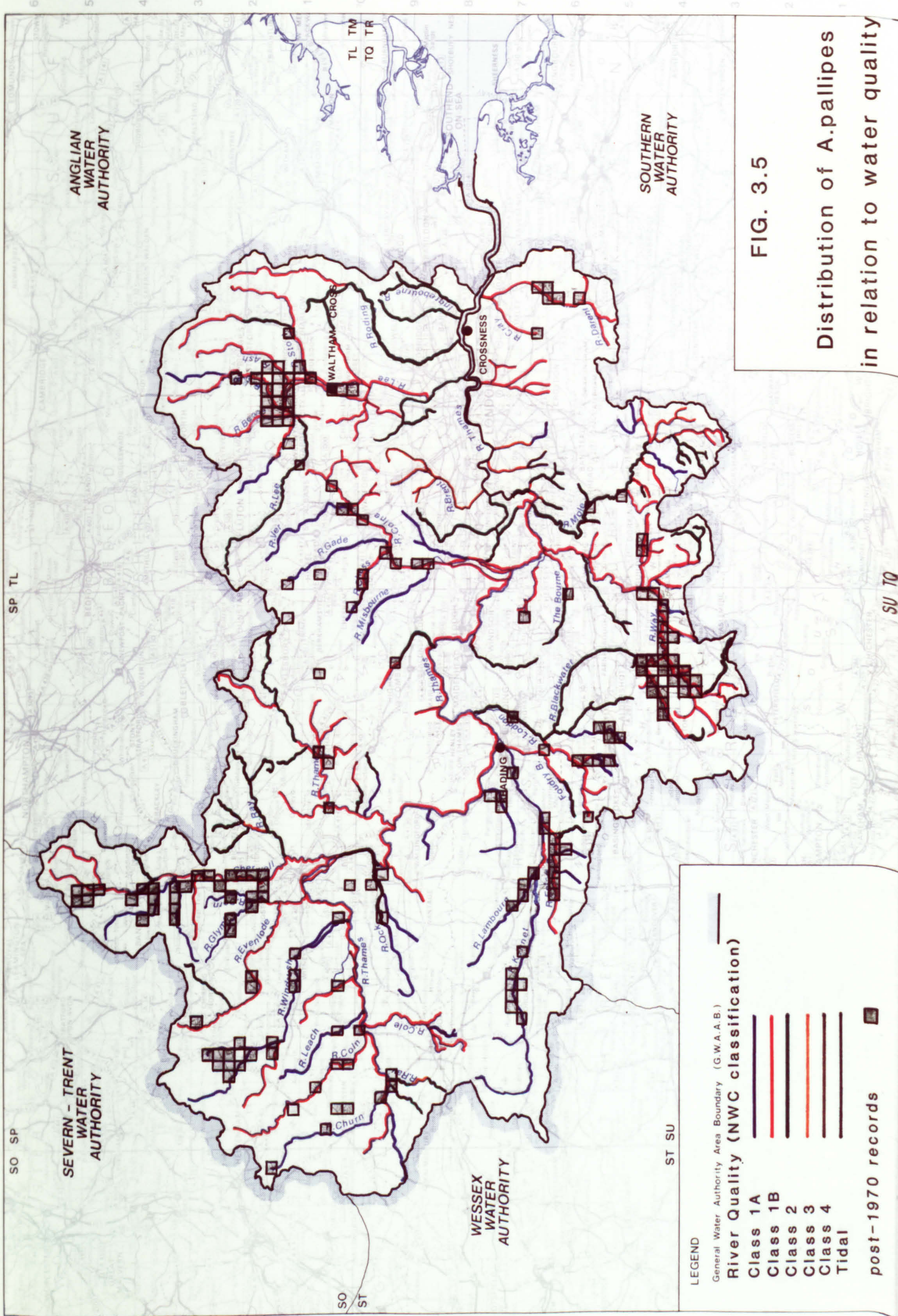
3.4(ii) - River Management - Water Quality

The other major influence on water quality is man. All discharges to watercourses within their area are controlled by the Regional Water Authorities who are empowered to limit the concentration and nature of substances to be discharged by issuing consent 'standards' for each effluent (Porter, 1978). These limits take into account the degree of dilution of the effluent by the river and, in fact, result in each reach of every river being allocated a 'Chemical Quality Objective'. This objective is maintained by the Water Authority setting sufficiently stringent consent conditions for the effluents discharging to that reach. Figure 3.5 shows the chemical quality classification,

according to the National Water Council scheme (see Appendix 3), for the River Thames and its tributaries in 1980 (N.W.C., 1981).

The relationship between crayfish distribution and the chemical classification of rivers is shown in Figure 3.5. As can be seen the majority of crayfish records are from Class IA and IB rivers, with few records from rivers with a lower quality classification. There are exceptions, such as the middle reaches of the River Mole, Class 2. As explained previously this is a region where the river crosses a band of chalk strata and it is thought that, in addition to physical improvements in the habitat, local improvements in water quality may occur adjacent to springs in the river bed. Similarly the records from the upper River Lee are from an area where there are a number of spring-fed watercress beds which may effect a local improvement in water quality. The chemical quality of the water may, to some extent, explain why crayfish have only been recorded from the upper River Wandle (an unverified record) and the middle reaches of the Rivers Lee and Thame. Such local variations in water quality do not however explain, for example, the occurrence of A.pallipes in the lower River Loddon. Temporary pollution factors, either short term or intermittent, may also have a long term effect on the distribution of A.pallipes by reducing or totally eliminating populations and this is known to have occurred in the Kingsclere Brook (NGR S.U.530610) and possibly the River Ash (NGR T.L.400155).

The suggested relationship between crayfish distribution and water quality implies that domestic and agricultural effluent as well as industrial pollution determines the suitability of a river as crayfish habitat (Davies, 1964; Bowler, in Westman & Pursainen, 1982). This may take place through a lowering of water quality, for example, reduced dissolved oxygen, increased suspended solids, increased nitrate levels, etc., or by an alteration of the physical



LEGEND

General Water Authority Area Boundary (G.W.A.A.B.)

River Quality (NWC classification)

- Class 1A
- Class 1B
- Class 2
- Class 3
- Class 4
- Tidal

post-1970 records

FIG. 3.5
 Distribution of *A.pallipes*
 in relation to water quality

environment by, for example, siltation caused by the settling out of excess suspended solids.

3.4(iii) - River Management - Land Drainage

The other major influence that man can have on a watercourse is by physical alteration of its nature. This may either be for the improvement of drainage and flood alleviation or to enable the watercourse to be used for navigation (see Chapter 5). This type of river management usually takes place at the downstream end of lowland rivers where the risk of flooding is maximal as the tributary meanders across the floodplain prior to its confluence with other rivers. Rivers in the Thames Catchment that are managed in this way tend to be those crossing relatively flat areas of land, e.g. the River Thame, River Ock, River Cole. Management for navigation purposes usually concerns first order rivers, e.g. River Thames, and the lower reaches of second order rivers, e.g. Rivers Lee, Loddon, Mole and Wey; flood alleviation schemes, in the form of maintenance dredging, etc., have their most serious impact on higher order rivers.

The principal form that routine land-drainage schemes take is the periodic dredging of a section of river with the removal of bankside trees, etc., every twenty years or so, accompanied by a more regular perhaps biennial, clearance of bankside and emergent vegetation (Wood, in Lewin, 1981). Such operations often result in straightened channels of uniform cross-section and substrata type with neatly graded but denuded banks. The type of habitat required by crayfish in lowland rivers is that which is usually regarded as an impediment to water flow by the drainage engineer so is removed (Ferguson, in Lewin, 1981).

Such engineering schemes can obviously have a devastating effect on crayfish distribution in three main ways. Firstly crayfish may be bodily removed from the

water during the dredging operations and then be unsuccessful in their attempts to return to the water. Secondly suitable crayfish habitat may be devastated as suggested above. Thirdly, although not directly affected, such operations may induce deleterious effects on populations of crayfish further downstream by reducing the suitability of otherwise unmanaged areas of crayfish habitat, for example by increased siltation due to excessive suspended solids. It is, however, difficult to accurately assess the effect of engineering schemes on crayfish distribution on a regional basis as such management generally takes the form of a 'rolling programme' and is often dependent on the availability of manpower and machinery and the suitability of the weather. Consequently it is difficult to coordinate fieldwork to coincide with engineering operations. No attempt at such an assessment has been made, therefore, other than on a very local scale and which will be more fully discussed in Chapter 5.

Coupled with the routine maintenance schemes is the construction or modification of flow-regulating mechanisms such as weirs and flood-relief channels. As will be more fully discussed in Chapter 5 such areas can be constructed to provide suitable habitat for crayfish and will contain a base population from which recolonisation of other areas could take place.

3.4(iv) - Biological Quality

Another characteristic of river quality that was assessed in the 1980 D.O.E survey (N.W.C. 1981), was their biological quality. Every river was subdivided into reaches for the assessment of chemical water quality and a site was selected within each reach for biological sampling. A collection of benthic macroinvertebrates was made at each site and the species composition and abundance was used to calculate a biological 'score' (B.M.W.P. Score - Appendix 4) and diversity index (T.W.A.B.I. - Appendix 5).

The score enables biological quality of a site to be compared and correlated with the chemical quality.

Within the Thames Catchment a total of 160 sites were assessed in this way and the B.M.W.P. Scores subsequently calculated ranged from 18 to 220. Of these sites only 24 (15%) correspond to those from which crayfish had previously been recorded. The sampling method utilised for this survey was, however, not designed for collecting crayfish and consequently these were only found at 6 (3.75%) sites. 20 (83%) of the 24 sites at which crayfish had previously been recorded were allocated B.M.W.P. Scores in excess of 100; the other 4 (17%) sites scored between 50 and 100. It would appear, therefore, that there is a correlation between biological diversity, as measured by the B.M.W.P. Score, and the occurrence of A.pallipes. Crayfish generally appear to inhabit sites where the physical and chemical environment are such that macroinvertebrate diversity results in a B.M.W.P. Score >100.

3.4(v) - Disease

Populations of A.pallipes may also be eradicated or seriously depleted by other influences, both natural and human. Disease has been reputed, in the past, to have caused the decline of crayfish populations. Stocks in the River Ock (Duffield, 1933) and River Thames (Cornish, 1902) are reported to have diminished or disappeared earlier this century but no proof that disease was the cause is offered. Similar large scale mortalities that have occurred in the Rivers Lee and Whitewater during the current study are thought to be due to disease, pollution has been ruled out, but proof has yet to be obtained (see Chapter 6).

3.4(vi) - Fishing

In addition the extent to which populations of A.pallipes in the Thames Catchment are fished is unknown.

The Thames Water fishery byelaw (see Section A: Introduction) should enable catch statistics to be collated but few licences have been issued and the return of catch data is scant. Unsubstantiated reports suggest that in some areas considerable numbers of crayfish may be taken for local use, e.g. from Clattercote Reservoir (Webber & Smith, pers comm); the Rivers Glyme and Dorn (Snell, pers comm); River Lee (Lowery, pers comm). In the Woodstock, Oxon., area 'crayfish suppers' are a tradition (Snell, pers comm) that still take place annually and presumably necessitate the cropping of large numbers of A.pallipes from local streams. In the U.S.A. cropping has been shown to be the most important factor influencing the distribution of commercially exploited species, such as Orconectes rusticus. For other species natural factors, such as calcium content, substrata and depth regulate distribution (Capelli & Magnusson, 1980).

Due to the informal but fairly widespread interest in crayfish populations, particularly amongst anglers, natural distribution may be confused by random and uncoordinated stocking of waterbodies that may or may not have contained crayfish previously. Reports of movements bear this out and it is known that A.pallipes have been introduced to the River Ash from the River Mimram, the River Lee from the River Rib (Lowery, pers comm) and to the Sor Brook from Clattercote Reservoir (Smith, pers comm). The extent to which such introductions take place is unknown but their occurrence will not only confuse attempts to explain the natural distribution of crayfish but also aid the spread of parasites and diseases and complicate attempts to account for their distribution as well (see Chapter 6).

CHAPTER 4. A STUDY OF THE BIOLOGY OF A POPULATION OF THE
NATIVE FRESHWATER CRAYFISH, AUSTROPOTAMOBIOUS
PALLIPES, IN A LACUSTRINE ENVIRONMENT.

4.1. Introduction.

Knowledge of the population biology of the crayfish Austropotamobius pallipes (Lereboullet, 1858), is scant (Chapter 1) but is essential for a greater understanding of the role of the crayfish in freshwater ecosystems in the U.K. Such knowledge is also desirable if such systems are to be modified, either accidentally (Chapter 3), or deliberately (Chapter 5), and if crayfish populations are to be managed for economic purposes.

Initially it was intended that this study would encompass the population biology of A.pallipes in both lacustrine and riverine systems, in the Thames Catchment, in order to identify and quantify differences between such populations. To achieve this aim the study of the population of A.pallipes in the River Loddon at Sherfield-on-Loddon, Hampshire, (NGR:SU682583) was initiated and a full years data obtained. However, due to constraints on time, the problem involved with representative sampling from a river site (see Chapter 6) and the availability of data from a similar study being carried out on the River Great Ouse, near Buckingham, (Pratten, 1980) it was decided to limit the sampling programme and concentrate on obtaining more detailed information regarding a lacustrine population. No such information is available regarding A.pallipes in the U.K., although quarry and reservoir populations in the Midlands have been included in recent studies of crayfish biology (Rhodes & Holdich, 1979, 1982; Rhodes, 1980), previous accounts only describing riverine populations (e.g. Thomas & Ingle, 1971). The data that was collected from the River Loddon during 1979 is discussed elsewhere (see Chapter 6).

In order to obtain information concerning population dynamics and the ecology of A.pallipes in a lacustrine habitat the population of crayfish inhabiting Clattercote Reservoir near Banbury, Oxfordshire, was studied from 1979 to 1982. The criteria considered to be of importance in selecting a suitable study site were:-

- (i) The presence of a long-established crayfish population;
- (ii) Accessibility;
- (iii) The relative security of the site against crayfish migration;
- (iv) Minimal human interference.

The first three of these criteria were met by the study site but the fourth was, and remains, a largely unknown factor.

The information collected during this investigation, together with data collected from other sites (Chapter 6) and published results (e.g. Brewis, 1979; Brown & Bowler, 1979; Rhodes & Holdich, 1979; Pratten, 1980), provide the basis for an assessment of the ecological and economic importance of A.pallipes in the Thames Catchment.

4.1(i) - Study Site

Clattercote Reservoir (NGR:SP450485) is owned by the British Waterways Board and is used as a replenishment reservoir for the Oxford Canal (South). The reservoir, built in 1787, is located approximately 8 km. north of Banbury, Figure 4.1, and consists of a 9ha. lake retained by a dam. The dam, 206 m. in length, is constructed with a clay core faced with earth on the east side and limestone rubble on the west side, Figure 4.2. The crest of the dam is topped with 2 m. concrete piles and a further 1 m. high concrete wall was added in 1962 to increase the holding capacity of the reservoir (Peppiatt, pers. comm). The inward facing (west) side of the retaining wall, originally faced with limestone, now consists of a steep slope of loose limestone rubble formed by the collapse of the original

Figure 4.1 Map showing the location of
Clattercote Reservoir.

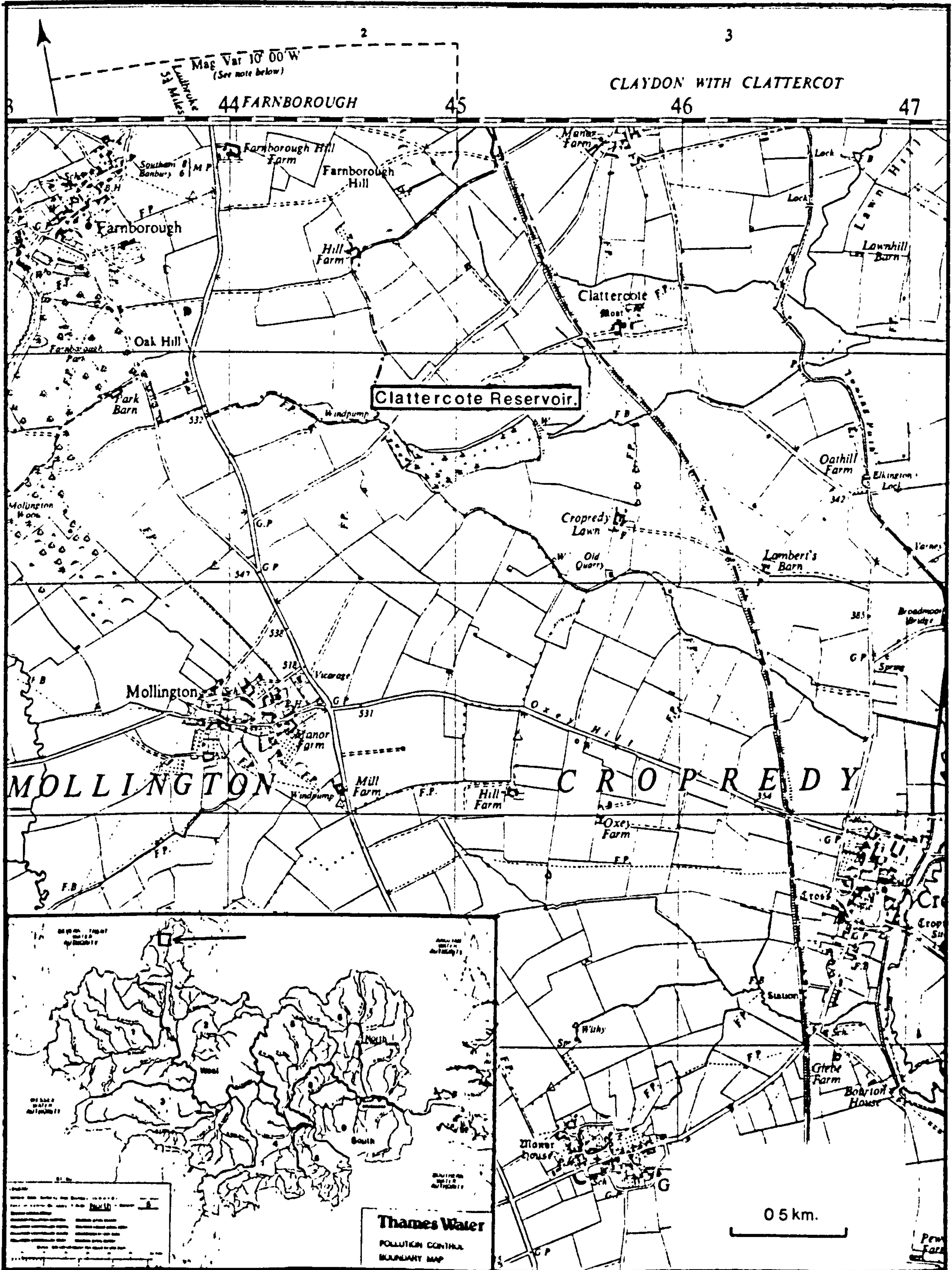
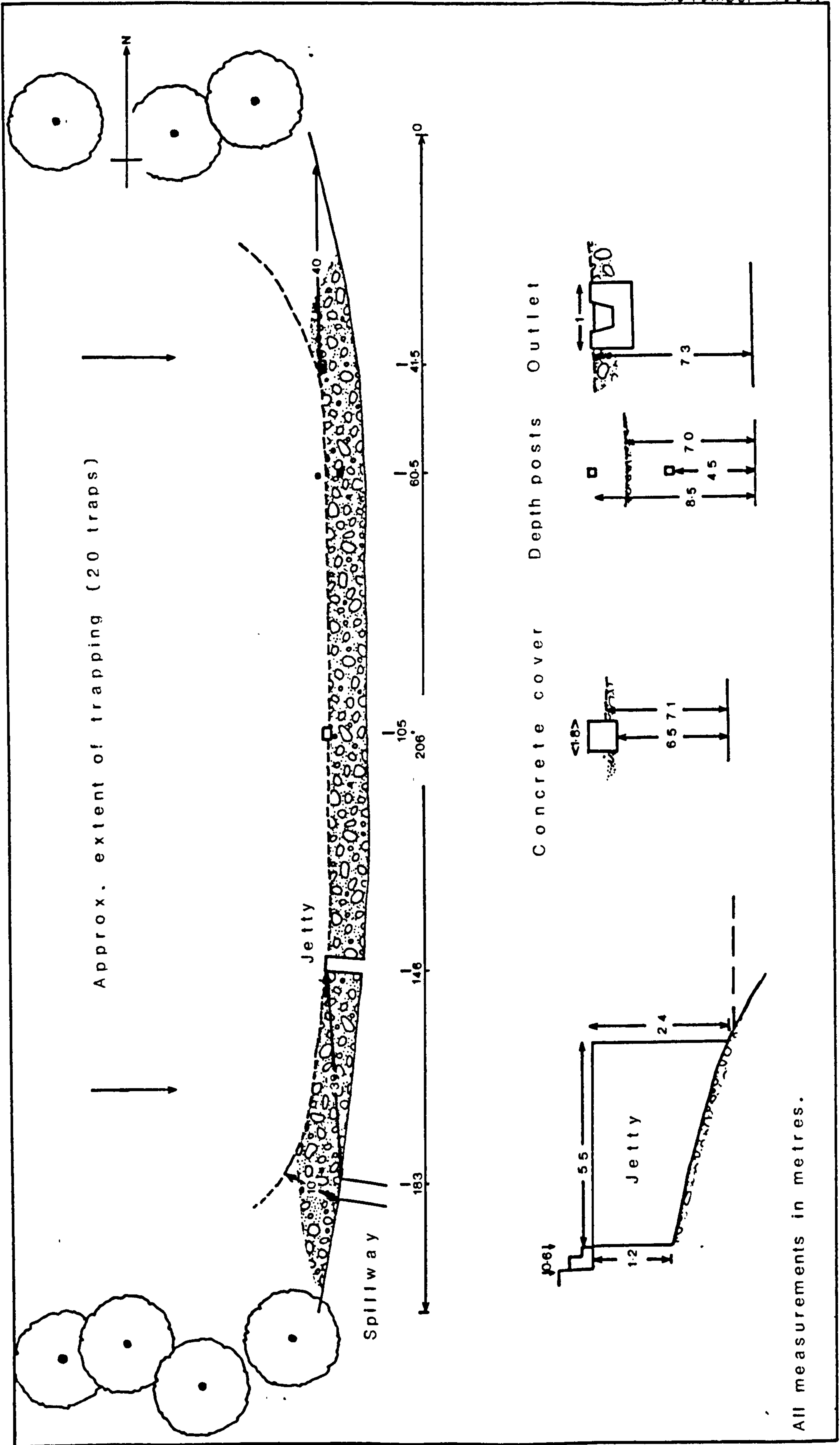


Figure 4.2 Sketch diagram of dam area, Clattercote Reservoir.

November 1981.



dam facing and subsequently modified by wave action.

The surrounding land is agricultural, the majority being used for cereal growing. The reservoir inflow consists of two small streams, fed by field drainage, and a number of small springs at the head (west) end of the reservoir. The outflow consists of the Clattercote Brook, which takes water from the overflow spillway, when water levels are at a maximum, and an artificial canal feeder channel which links the reservoir with the Oxford Canal (South) approximately 1 km. distant. Water is drawn from the reservoir at 4.0 m. depth, through manually operated sluices and a 20 cm. diameter pipe, to maintain levels in the canal during periods of maximum use. Consequently marked seasonal differences in water level occur and maximum capacity, nominally $250 \times 10^3 \text{ m}^3$, is normally retained in late winter and spring. Maximum depth, originally 7.5 m., is currently approximately 6.0 m., due to siltation, and drawdown does not exceed 4.0 m. (Bodsworth, pers comm) leaving $1.14 \times 10^3 \text{ m}^3$. The water level, measured on each sampling visit in 1979 and 1980, is illustrated in Figure 4.3.

Chemical water quality data has been obtained through the analysis of water samples collected periodically during the study. The results show that those parameters considered to be of primary importance to crayfish (Laurent, 1980) gave the following values:-

Mean pH = 8.25 (n = 14)

Mean Hardness = 261 mg. l^{-1} CaCO₃, (n = 14)

Mean Alkalinity = 153 mg. l^{-1} CaCO₃, (n = 14)

The full results are tabulated (Table 4.1) and discussed elsewhere (see 4.4(i)).

Clattercote Reservoir is considered to be a moderately successful coarse fishery, with tench, Tinca tinca, carp, Cyprinus carpio, pike, Esox lucius, and perch, Perca fluviatilis, being the most abundant species (Handley, pers comm).

Figure 4.3 Graph showing measured water levels,
Clattercote Reservoir. 1979 - 1982

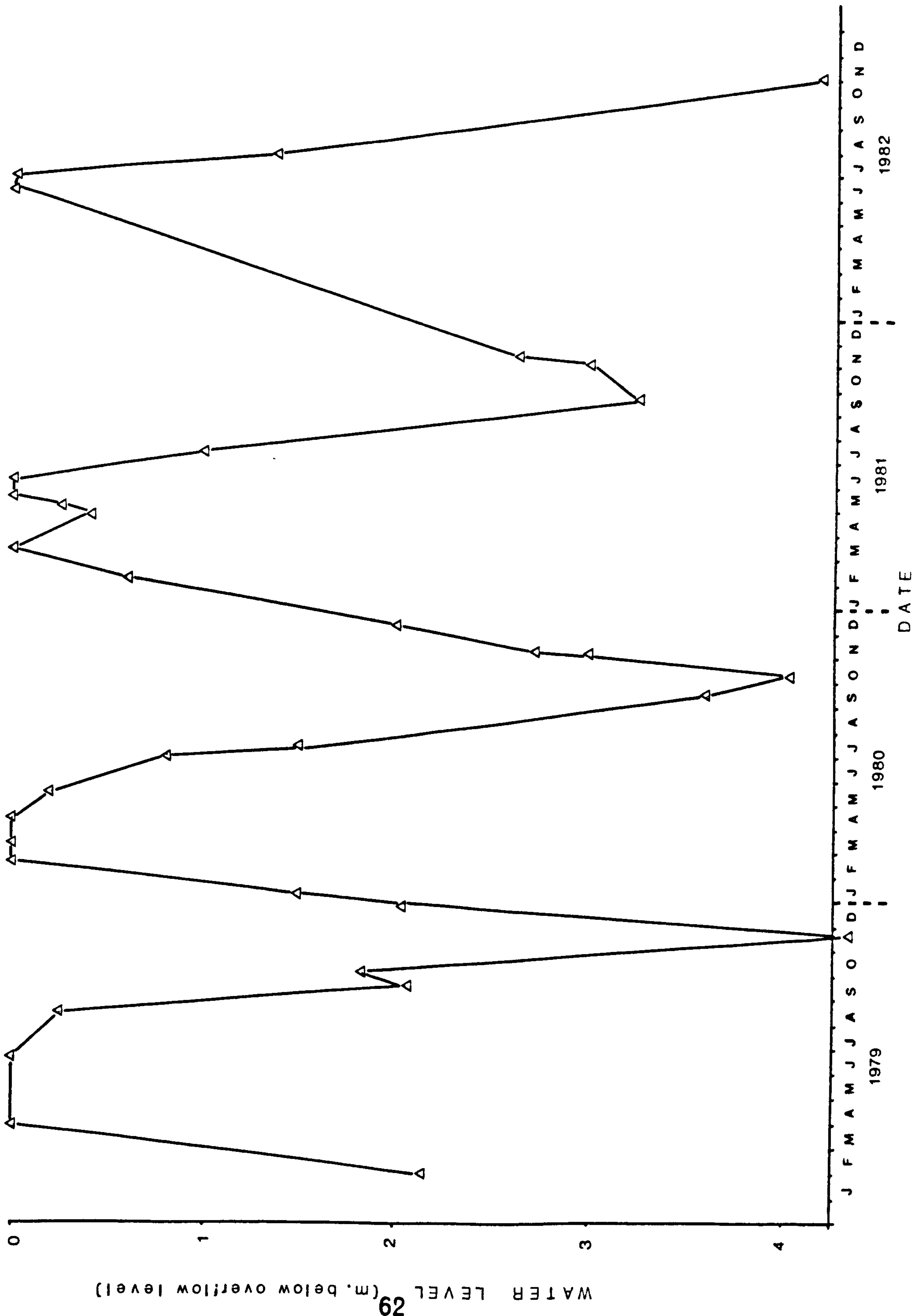


TABLE 4.1 : RESULTS OF CHEMICAL ANALYSIS OF WATER FROM CLATTERCOTE RESERVOIR 1980 - 1982

DATE	15.80	29.5.80	3.6.80	3.7.80	4.11.80	10.12.80	4.2.81	17.3.81	29.4.81	13.7.81	5.4.82	12.5.82	8.6.82	27.7.82
TIME	15.00	21.00	22.00	22.00.	23.30	13.00	11.00	16.30	16.30	21.00	18.00	14.00	18.00	21.20
pH.	8.08	8.27	8.42	8.08	8.12	8.38	8.38	8.34	8.39	8.20	8.23	8.39	8.15	8.04
Susp. Solids (105°C)	-	-	3.0	-	4.4	-	-	8.0	5.0	7.0	9.5	5.5	10.5	3.2
B.O.D. (A.T.U.)	-	-	1.9	-	1.7	-	-	2.0	2.3	3.2	3.6	3.7	7.5	2.3
C.O.D.	-	-	-	-	-	-	-	15.9	-	-	15.3	20.4	25.8	21.0
Temp. (°C)	10.0	-	16.5	18.0	6.0	3.0	5.0	7.5	8.5	19.5	9.5	15.5	21.0	18.0
D.O.	-	-	10.35	-	-	12.95	-	10.21	10.85	10.3	12.7	13.95	12.0	8.75
† Saturation	-	-	106	-	-	96.2	-	85.1	92.8	111	111	140	135	92.5
Ammoniacal nitrogen	-	-	0.03	-	0.07	< 0.01	< 0.01	0.01	0.02	0.01	< 0.01	< 0.01	< 0.01	0.04
Unionised Ammonia	-	-	0.001	-	0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Oxidised N.	-	-	2.5	-	1.5	2.3	3.7	3.8	3.1	1.8	5.4	2.8	0.9	0.4
Chloride (Cl)	-	-	22	-	25	26	27	25	22	26	27	32	25	27
Silica (SiO ₂)	-	-	0.1	-	8.9	6.5	5.7	4.0	2.2	2.5	7.3	5.4	3.4	3.0
-Phosphate (P)	-	-	0.01	-	< 0.01	< 0.01	0.05	< 0.01	< 0.01	< 0.01	< 0.01	0.08	0.02	< 0.01
Hardness (as Ca CO ₃)	268	252	276	218	278	292	281	270	280	258	312	274	188	201
† Alkalinity (as Ca CO ₃)	159	145	171	126	171	166	172.	169	170	153	175	151	91	117
Chlorophyll (Methanol) (µg.l ⁻¹)	-	-	1.46	-	-	-	-	13.6	5.32	3.3	17.3	16.3	45.1	6.26
Chromium (Cr)	-	-	-	-	-	-	-	-	-	-	< 0.01	< 0.01	< 0.01	< 0.01
Zinc (Zn)	-	-	-	-	-	-	-	-	-	-	0.01	0.01	0.02	0.01
Nickel (Ni)	-	-	-	-	-	-	-	-	-	-	< 0.01	< 0.01	< 0.01	< 0.01
Copper (Cu)	-	-	-	-	-	-	-	-	-	-	< 0.01	< 0.01	< 0.01	< 0.01
Cadmium (Cd)	-	-	-	-	-	-	-	-	-	-	< 0.001	< 0.001	< 0.001	< 0.001

† NB. Values in µg.l⁻¹ except †

Eels, Anguilla anguilla, reputed to be serious crayfish predators (Svårdsson, 1972), are not commonly caught by anglers but it is improbable that they are totally absent.

Utilisation of the reservoir by wildfowl is relatively limited and it only achieves a class 5 (sites holding <100 wildfowl) in a Water Space Amenity Commission research report on wildfowl in reservoirs (Tanner, 1979). It is not classified by the R.S.P.B. Heron, Ardea cinerea, coot, Fulica atra, great-crested grebe, Podiceps cristata, and mallard, Anas platyrhynchos, were observed to be common residents and flocks of tufted duck, Aythya fuligula, were regular winter visitors. Of these only heron is reputed to be a potential crayfish predator (Macan & Worthington, 1951; Brown, 1979).

During periods of maximum water retention aquatic macrophytes are abundant. Marginal plants include sedges, Carex sp., rushes, Juncus sp., and reedmace, Typha latifolia; along with water mint, Mentha aquatica, brooklime, Veronica beccabunga, and water speedwell, Myosotis scorpioides. Submerged macrophytes in the shallower areas of the lake are dominated by M.aquatica, V.beccabunga, and Amphibious persicaria, Polygonum amphibium. In the principal area inhabited by A.pallipes, i.e. the area of loose limestone rubble, macrophytes are limited by wave action and substrate instability and include few emergent or marginal species, such as Carex sp., M.aquatica and V.beccabunga. The growth and abundance of submerged macrophytes in this area also appears to be greatly influenced by the large annual fluctuations in water level, but this was not tested quantitatively. During periods of low water they tend to be dominated by growths of P.amphibium, Ranunculus peltatus and Chara sp., with extensive growths of the filamentous green alga Spirogyra sp., in spring and early summer if weather conditions are favourable. The aquatic moss Fontinalis antipyretica is present. The margins of the reservoir, with the exception of the dam area, are lined

with deciduous trees; mainly ash, Fraxinus excelsior, elder, Sambucus nigra, elm, Ulmus procera, hawthorn, Crataegus monogyna, and oak, Quercus robur.

The occurrence of a thriving population of A.pallipes at this site was reported during the initial collation of existing crayfish distribution records (Chapter 3). The origins of this crayfish population are unknown and there is no record of them having been introduced although it is possible that some have been introduced by anglers to boost the existing population. It could be assumed, therefore, that A.pallipes was present in the existing streams prior to the reservoir construction in 1787; indeed they are abundant in adjacent watercourses and the Oxford Canal (South) itself (Chapter 3). In either case it seems probable that Clattercote Reservoir holds a long-established and 'mature' population of A.pallipes.

Initial investigations revealed that the crayfish population is located along the dam wall in the area of collapsed limestone rubble, consequently sampling has been restricted to this area. Few individuals have been observed elsewhere in the reservoir.

4.2. Methods.

4.2(i) - Sampling.

The general methods of sampling crayfish populations used in this study have been described elsewhere (Chapter 2). In order to obtain maximum information regarding the population of A.pallipes in Clattercote Reservoir samples of crayfish were collected throughout the three-year period 1979 - 1982. Three sampling methods, namely trapping, hand collection by divers using S.C.U.B.A. and hand collection in shallow marginal areas, were used at this site. One or a combination of these methods was used on each sampling occasion. A list of sampling occasions and methods used is

presented in Table 4.2.

Sampling was always restricted to the dam wall area although crayfish were also observed elsewhere in the lake, in small numbers, where suitable cover was available. During periods of low water, in September - November, crayfish were frequently observed, at night, at considerable distances from the nearest refugia and were presumed to be foraging. Trapping was always carried out along the dam wall area.

All crayfish caught, or a random subsample, were measured as previously described (see Chapter 2); carapace length (C.L.) being the standard measurement taken with other parameters being measured on selected occasions. Morphometric analysis was carried out on combined data from all three sampling methods and using only specimens showing no visible signs of limb regeneration as this has been demonstrated to inhibit moult increment (Bowler & Brown, 1977).

Estimation of population size was attempted by means of mark-recapture procedures (see Chapter 2) carried out in 1980 and 1981. A small number of crayfish were individually marked to obtain growth data but recaptures were too few to warrant the continuation of this incidental investigation. The method of marking used (Abrahamsson, 1965) is described in Chapter 2. An assessment of 'catchability' was made using data from trap catches only.

Small numbers of individuals were returned to the laboratory for more accurate morphometric analysis than could be achieved in the field, primarily the collection of fresh weight data. Gut analysis and parasitological examination was also carried out on these crayfish.

4.2(ii) - Statistical Analysis.

- (a) Mark-recapture data has been used to calculate estimates of the catchable population size (C.L. >30 mm) using the following methods: Petersen, Schnabel, Bailey and Jolly (Ricker, 1975) which are described elsewhere (see Chapter 2). Some of the assumptions made in the use of such methods are clearly not fully met during the current investigations, e.g. non-selectivity of sampling methods, and hence the figures obtained must be considered as very approximate estimates.
- (b) Catchability has been calculated, by expressing the results of trapping success in terms of catch per trap per unit time, in order to establish the seasonality of activity and trapping potential and to monitor changes in the structure of the trappable population. Traps were considered, for this purpose, to be standard catching units affected by constant variability in comparison with hand collection methods.
- (c) Length-frequency data, consisting of combined size data using measurements of crayfish collected by all three sampling methods, has been used for the construction of length-frequency histograms for each sampling occasion. The method of analysis of such distributions selected for use (see Chapter 2) was the separation of the distributions into their Gaussian components (Bhattacharya, 1967). The resulting separation of each set of sample data into its component size-groups has been plotted. Then, using knowledge of the age-size relationships for populations of A.pallipes in other areas (Brown, 1979; Demars, 1979; Pratten, 1980; Brewis & Bowler, 1983) and the size of hand caught (0+) juveniles from Clattercote Reservoir, the data has been used to construct 'average growth curves' for each sex.

(d) Morphometric Data. A considerable quantity of data has been collected concerning the morphometry of A.pallipes, as described in Chapter 2, in order that body form could be biometrically defined. This data has been included in the establishment of the relationship between the various characteristics of A.pallipes throughout the Thames Catchment that have been measured (see Chapter 6). A comparison of morphometric relations of A.pallipes in Clattercote Reservoir with data from populations elsewhere has also been carried out in Chapter 6. Condition factors (C.F.) for individual crayfish (see Chapter 2) have been calculated for comparison with C.F. values obtained from A.pallipes from other sites (Chapter 6) and P.leniusculus (Chapter 8).

4.2(iii) - Trophic position.

Samples of benthic macroinvertebrates were collected on three occasions to aid identification of gut contents and to establish the availability of suitable food items in the study site. These samples were collected using a standard pond-net (mesh size = < 1.0 mm.) from the area considered to be the major crayfish habitat, i.e. the area of limestone rubble adjacent to the dam wall. The samples were preserved in Industrial Methylated Spirits, sorted in the laboratory and the organisms identified using standard keys. A single macroinvertebrate sample was collected from the head (west end) of the reservoir on 2.12.81 for comparative purposes.

A small number of A.pallipes (n = 23), from hand collected samples, were returned to the laboratory for gut contents analysis. These crayfish were sacrificed as soon as possible after collection by injection with chloroform into the thoracic cavity (Mahoney, 1973) dissected and the digestive tract removed and preserved in 10% formalin. Gut contents were subsequently examined using Wild M8 binocular and M12 high power microscopes.

In addition attempts were made, in the laboratory, to

obtain samples of stomach contents from living A.pallipes using 1.14 mm. external diameter catheter tubing (Brown, 1979). A syringe was attached to one end of the tubing and the free end was inserted into the crayfish stomach, via the mouth. In theory suction could then be applied to remove the gut contents. In practice the only material thus removed was too finely disintegrated or too well digested to enable satisfactory identification; larger food items blocked the tubing.

4.2(iv) - Life-History.

Life-history information was collected throughout the study. In addition to the calculation of size at the onset of sexual maturity, in both males and females, it was considered important to evaluate the time required for the incubation of A.pallipes eggs in the wild. Other studies have estimated fecundity (Brown, 1979; Rhodes, 1980; Rhodes & Holdich, 1982) and calculated temperature requirements for artificially reducing incubation time (Rhodes & Holdich, 1982) but no published values are available for natural incubation times. To obtain this information an automatic temperature recorder, 'Thermoscript' (supplied by Channel Electronics, Hove, Sussex), was located on the bed of the reservoir, approximately in the centre to avoid interference by fishermen, from November, 1981 to June, 1982. Temperature was recorded on a clockwork driven, pressure-sensitive chart which was changed monthly. The timing of egg-laying and hatching was obtained by observation at the study site and elsewhere in the Thames Catchment.

Incidental to the morphometric data collected from individual A.pallipes, as described previously, various aspects of life-history and biology were recorded throughout the period of study. These were:-

- (i) The moult condition of crayfish examined, e.g. soft, recently moulted, etc.,
- (ii) The frequency of occurrence of damaged crayfish,

i.e. those showing signs of chela loss or regeneration.

- (iii) The occurrence of the parasite Thelohania contejeani (see also Chapter 6).
- (iv) The occurrence of the parasite Branchiobdella astaci (see Chapter 6) and manifestations of other disease conditions such as 'burn spot' and assumed tumorous growths (Unestam, 1973; Vey & Vago, 1973).

4.3. Results.

4.3(i) - Comparison of Sampling Methods

During the course of this study samples of A.pallipes were obtained from Clattercote Reservoir using three collection methods, see Table 4.2. The mean C.L. of crayfish of each sex from each sample, calculated from the raw data is illustrated in Figure 4.4. Comparisons of the total mean C.L. of crayfish of each sex, caught by each sampling method, and yearly means, Table 4.3, have been made using Students t-tests to give the following results:-

Sampling Method(s)	Date	♂ t	♀ t
Trapped	1979 v 1982	0.36	0.68
Subaqua	1979 v 1982	0.32	1.03
Trapped v Subaqua	1979	0.25	0.82
Trapped v Subaqua	1980	0.24	1.72
Trapped v Subaqua	1981	0.50	1.37
Trapped v Subaqua	1982	1.47	0.78

NB: For $p = 0.05$ limit of $t = 1.96$ (d.f. >100)

These results show that both the apparent decline in C.L. during the period of study and the apparently higher mean C.L. for trapped samples were not statistically significant ($p > 0.05$).

TABLE 4.2 : CATCH COMPOSITION: ALL SAMPLING METHODS. CLATTERCOTE RESERVOIR. 1979 - 1982.

Date	Sampling Method *		Time **	No. of Traps	♂	♀	(♀B)	J	Total	Catch. Trap ⁻¹ Night ⁻¹	Sex Ratio (%♀)	
											Traps	Hand
22. 6.79	Hand	s/a	d	-	26	32	(21)	-	58	-	-	55
16. 8.79	"	"	d	-	92	52		-	144	-	-	36
21. 9.79	"	"	d	-	195	226		-	421	-	-	54
3.10.79	Traps		n	13	30	39		-	69	3.0	56	-
1. 5.80	Hand	s/a	d	-	110	118	(76)	-	228	-	-	52
19. 5.80	Traps		n	10	16	17	(11)	-	33	3.3	51	-
20. 5.80	Hand	s/a	d	-	233	181	(119)	-	414	-	-	44
29. 5.80	Hand	"	n	-	61	60	(42)	-	121	-	-	50
3. 7.80	"	"	n	-	191	226		-	417	-	-	54
11. 7.80	Traps + Hand	o/s	n	25	92	119		-	211	3.92	43	68
17. 7.80	"	"	n	25	69	74		-	143	1.36	25	58
11. 9.80	"	"	n	30	567	506		38	1111	17.33	45	56
16. 9.80	Hand	s/a	d	-	150	267		19	436	-	-	61
25. 9.80	Traps + Hand	o/s	n	26	157	230		4	387	11.81	59	60
4.11.80	Traps		n	20	46	1	(1)	4	47	2.35	2	-
10.12.80	Hand	s/a	d	-	19	15	(12)	-	34	-	-	44
17. 3.81	Traps		n	10	5	4	(4)	-	9	0.90	44	-
22. 4.81	"		n	33	14	10	(10)	-	24	0.73	42	-
29. 4.81	Hand	s/a	n	-	21	57	(7)	-	78	-	-	73
6. 5.81	Traps		n	40	N/D	N/D		-	8	0.20	-	-
13. 5.81	Hand	s/a	n	-	77	107	(94)	-	184	-	-	58
3. 6.81	"	"	n	-	218	172	(57)	-	390	-	-	44
13. 7.81	Traps		n	22	23	26		-	49	2.23	53	-
9. 9.81	"		n	20	71	161		-	332	15.00	48	-
21. 9.81	" + Hand	o/s	n	20	124	124		7	255	10.75	51	45
30. 9.81	Traps		n	20	98	112		-	257	15.00	37	-
12.11.81	Hand	s/a	d	-	n o d a t a a v a i l a b l e				-	-	-	-
2.12.81	Traps		d	3	1	0		-	1	-	0	-
8. 6.82	Traps		n	17	130	42	(2)	-	174	7.09	24	-
16. 6.82	Hand	s/a	n	-	10	10		-	20	-	-	50
28. 7.82	Traps		n	-	48	22		-	70	-	31	-
1.11.82	Hand	s/a	d	-	46	40	(20)	-	86	-	-	46

* s/a = subaqua. o/s = onshore.
 ** n = nighttime. d = daytime.

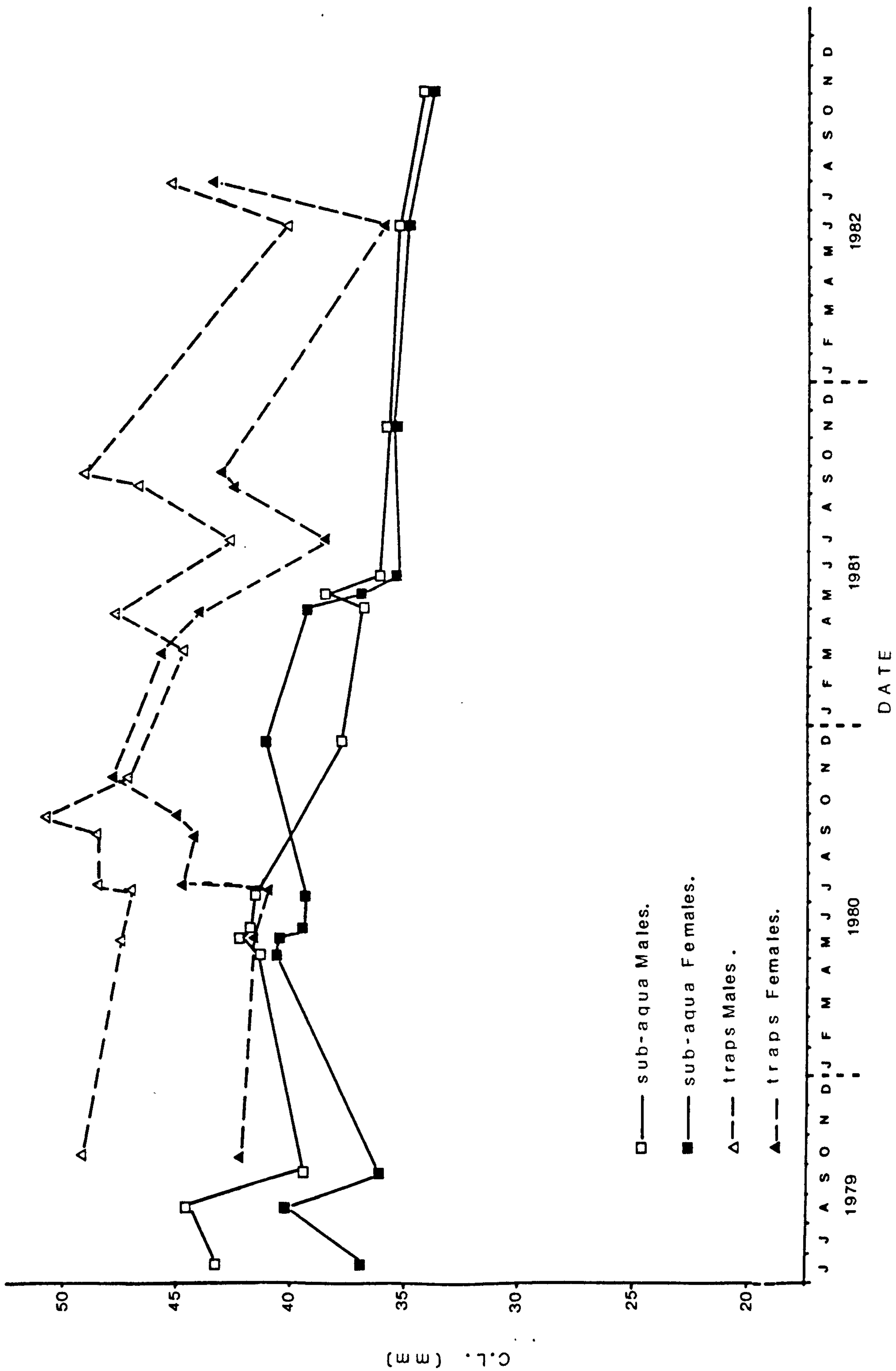
TABLE 4.3 : ANNUAL MEAN C.L. VALUES FOR CRAYFISH SAMPLES.
CLATTERCOTE RESERVOIR, 1979 - 1982.

Year + Method	MALE				FEMALE			
	CL. (mm)	S.D.	Range (mm)	n	CL. (mm)	S.D.	Range (mm)	n
<u>Trapped</u>								
1979	44.1	10.6	11.0 - 55.0	30	37.2	4.3	30.0 - 46.0	39
1980	44.5	24.2	29.5 - 54.0	331	38.5	4.6	22.0 - 52.0	219
1981	42.3	7.0	19.0 - 54.5	136	36.9	5.1	18.0 - 47.5	122
1982	36.6	5.8	25.0 - 54.0	178	33.6	5.9	23.0 - 52.0	64
<u>Hand (subaqua)</u>								
1979	38.9	7.7	14.7 - 59.5	286	33.9	6.7	17.0 - 48.7	279
1980	36.7	6.8	18.0 - 54.5	719	34.4	7.5	17.0 - 51.0	869
1981	32.9	17.9	17.0 - 50.0	305	32.1	6.9	17.0 - 47.0	333
1982	29.6	5.5	19.0 - 45.5	56	29.1	5.2	19.0 - 50.0	50

Figure 4.4

Mean C.L. of *A. pallipes*,

Clattercote Reservoir. 1979 - 1982



The size ranges of A.pallipes obtained by trapping and hand collection throughout the period of study are illustrated by the histograms, Figure 4.5, and the overall size distribution of crayfish caught, in all samples, is shown in the histogram Figure 4.6. The ratio of males to females in all samples and caught by each method are listed in Table 4.4 and illustrated by Figure 4.7.

4.3(ii) - Population Estimates.

Population estimates calculated by various mark-recapture formulae have provided estimates of the catchable population; defined as the population of markable adults (C.L. >30 mm). These estimates are listed in Table 4.5. In addition the total trap catch, on any one occasion when this method of sampling was used, has been expressed in terms of catch trap⁻¹. night⁻¹. The trapping results are listed in Table 4.6 and catchability is illustrated graphically in Figure 4.8.

The extent of remixing of marked individuals was checked by comparing the ratio of marked to unmarked crayfish in subsequent samples in May, July and September, 1980, and May and September 1981 using χ^2 (see Chapter 2). Satisfactory mixing ($p > 0.1$) was shown to have occurred.

4.3(iii) - Length-frequency data.

A generalised 'growth curve' has been constructed using data obtained by the analysis of the length-frequency distribution of crayfish within the samples collected by all three methods. Length-frequency histograms which have been drawn, Figure 4.9, illustrate the size distribution of crayfish in each sample. Analysis of the length-frequency data (see Chapter 2), e.g. Figure 4.10, has permitted a generalised growth curve, Figure 4.11, with males and females shown separately, to be drawn. For comparative purposes published information concerning

the growth of A.pallipes elsewhere in the U.K. (Thomas & Ingle, 1971; Brown, 1979; Pratten, 1980; Brewis & Bowler, 1982) and in France (Demars, 1979) are shown in Figure 4.12. Similar graphs for Pacifastacus leniusculus, Astacus astacus, Astacus leptodactylus and (Orconectes limosus) are included in Chapter 8 (Figure 8.8 and 8.9).

4.3(iv) - Morphometric data.

The data, collected during this investigation, concerning selected morphometric characteristics of A.pallipes in the Clattercote population are included in analyses described in Chapter 6. Where sufficient data has been obtained from this population of A.pallipes the analysis of a given pair of characteristics has been carried out. Otherwise that information has been incorporated into the analysis of data from all populations of A.pallipes that were sampled (Chapter 6).

A 'condition factor' (C.F.) has been calculated for each individual for which length-weight data is available. The mean values of this factor for each season and each sex are listed in Table 4.7. Comparisons of C.F. values for each sex and ovigerous and non-ovigerous females have been carried out using t-tests. The overall C.F. values for males and females are significantly different ($p < 0.01$) as are those for ovigerous and non-ovigerous females ($p < 0.01$).

4.3(v) - Trophic position.

The qualitative macro-invertebrate samples collected from the main area inhabited by A.pallipes in the reservoir, i.e. the dam wall, and the head of the reservoir have been used to compile a species list, Table 4.8.

The results obtained from the few gut contents analyses that were attempted are listed in Table 4.9. Crayfish of both sexes, in the size range 29.0 mm.C.L. to 42.5 mm.C.L., were examined.

Figure 4.5 Size ranges of *A. pallipes* caught by each

sampling method, Clattercote Reservoir. 1979 - 1982

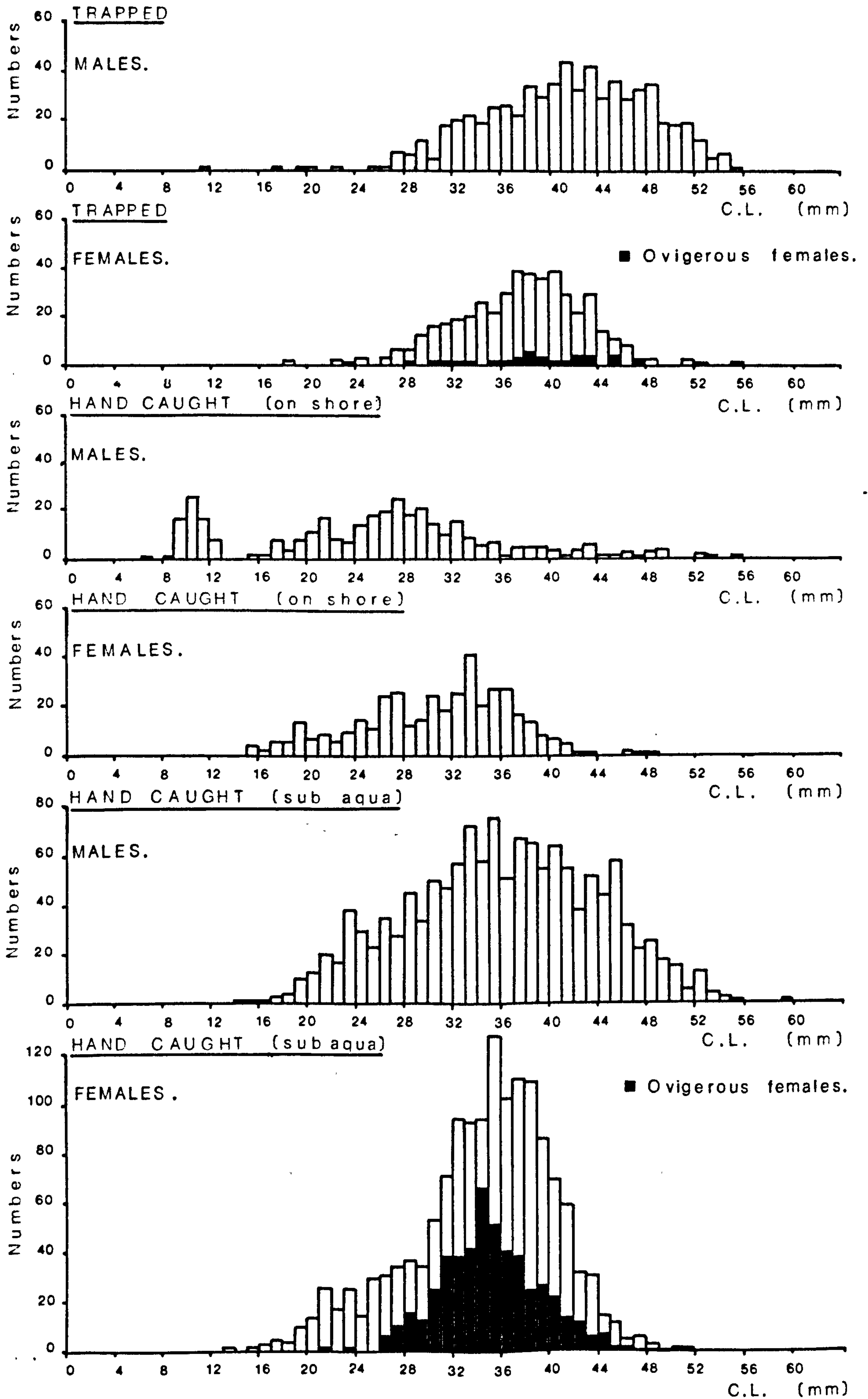


Figure 4.6 Overall size range of *A. pallipes*

in all samples from Clattercote Reservoir, 1979 - 1982

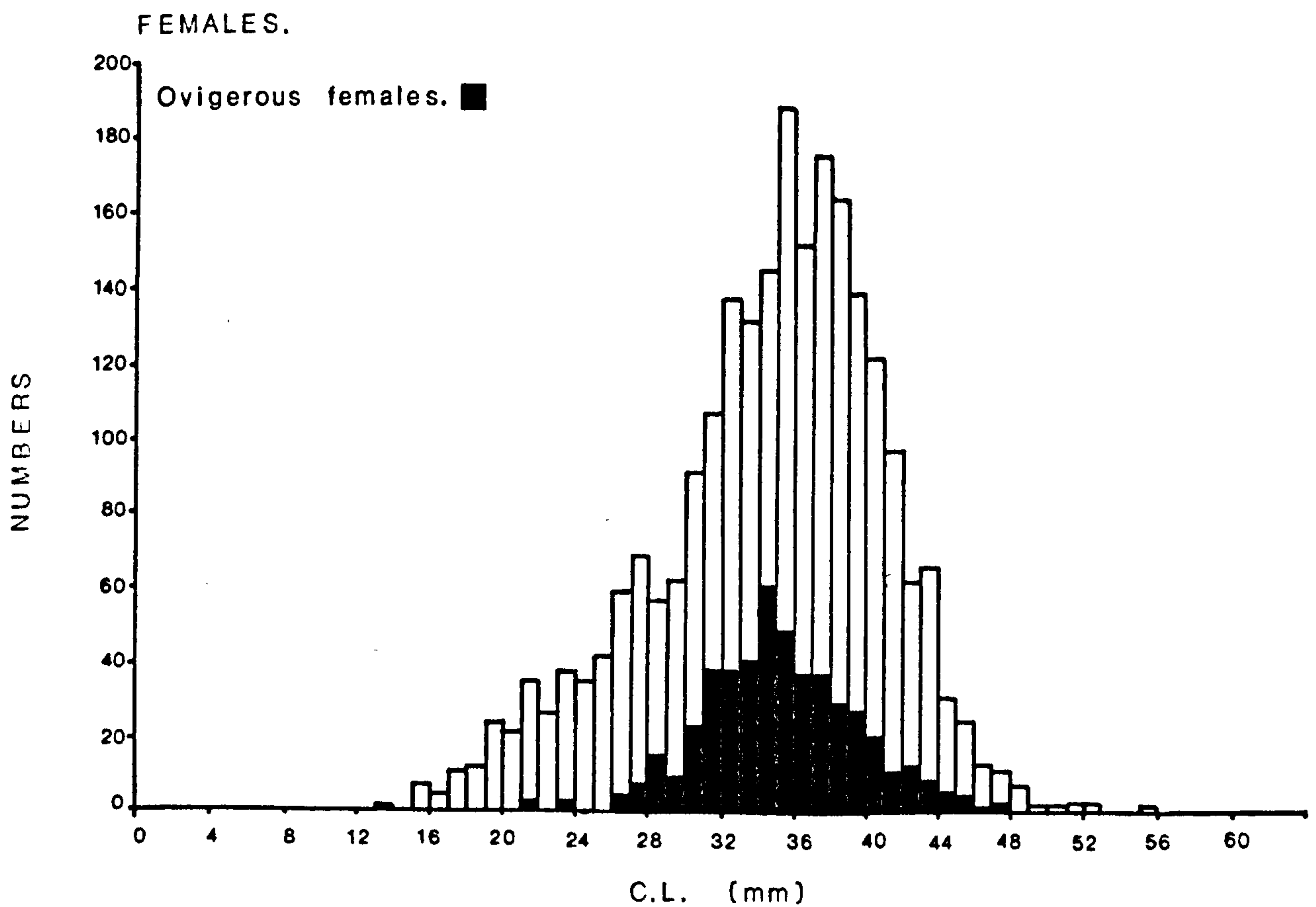
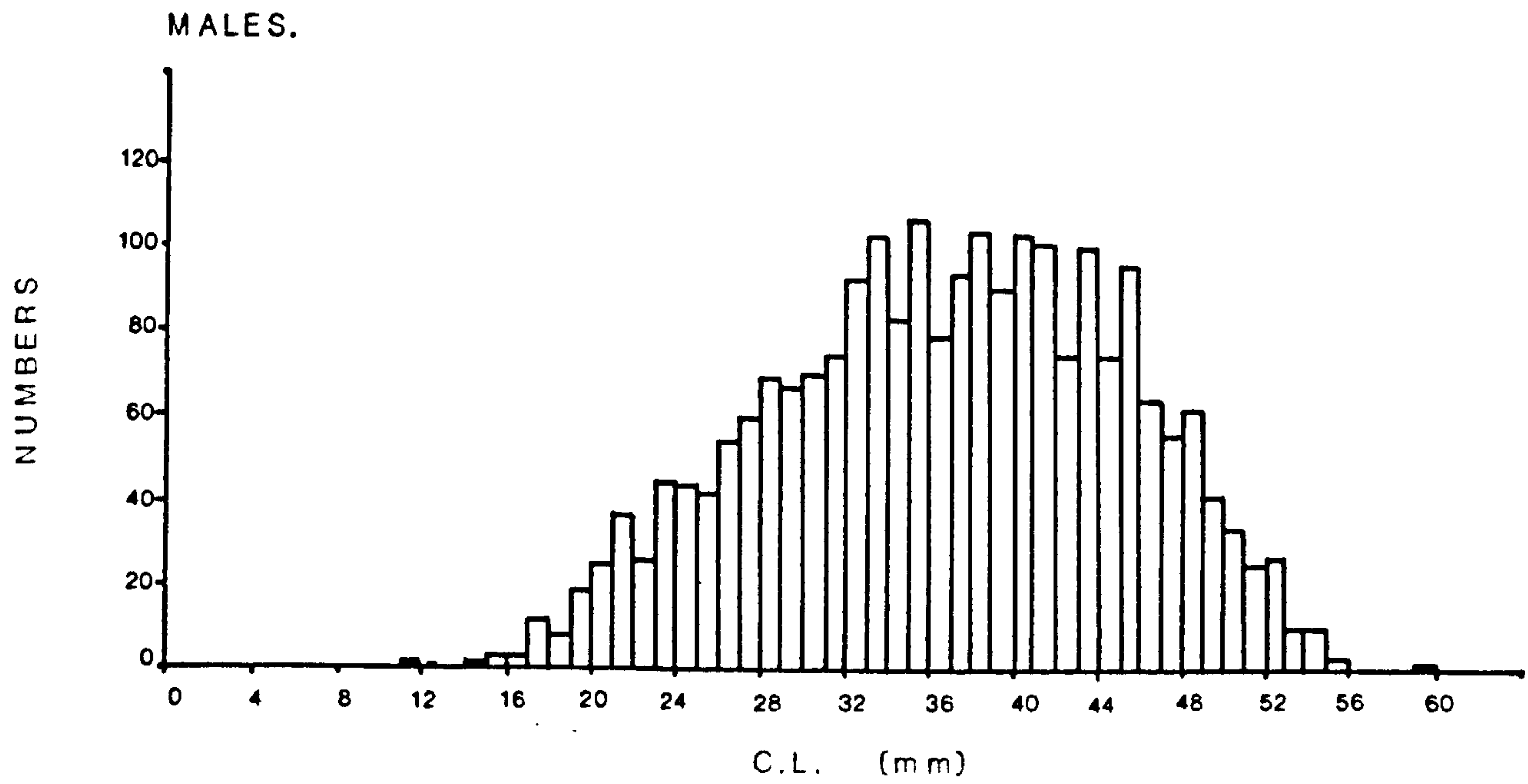


TABLE 4.4 : SEX RATIO OF A.PALLIPES IN ALL SAMPLES.
CLATTERCOTE RESERVOIR. 1979 - 1982.

Date	Males	Females	%♀	Date	Males	Females	%♀
<u>TRAPPED SAMPLES.</u>				<u>HAND-CAUGHT SAMPLES (SUB-AQUA).</u>			
3.10.79	30	40	57	22. 6.79	26	32	55
19. 5.80	16	17	51	16. 8.79	92	52	36
11. 7.80	56	42	43	21. 9.79	195	135	41
17. 7.80	23	11	32	1. 5.80	110	119	52
11. 9.80	288	232	45	20. 5.80	233	181	44
25. 9.80	125	182	59	29. 5.80	61	60	50
4.11.80	46	1	2	3. 7.80	191	226	54
17. 3.81	5	4	44	16. 9.80	150	270	64
22. 4.81	16	10	38	10.12.80	19	15	44
13. 7.81	15	19	56	29. 4.81	21	57	73
9. 9.81	157	143	36	13. 5.81	80	110	58
21. 9.81	106	109	51	3. 6.81	218	172	44
30. 9.81	98	112	53	1.11.82	46	40	46
8. 6.82	130	42	24				
28. 7.82	48	28	37	Total	1442	1469	50
Total	1159	992	46				
<u>HAND-CAUGHT SAMPLES.</u> <u>(WADING)</u>				<u>SAMPLES USING >1 METHOD.</u>			
11. 7.80	36	77	68	11. 7.80	92	119	56
17. 7.80	46	63	58	17. 7.80	69	74	52
11. 9.80	129	215	62	11. 9.80	417	447	52
25. 9.80	32	48	60	25. 9.80	157	230	59
21. 9.81	18	15	45	21. 9.81	124	124	50
30. 9.81	21	26	55	30. 9.81	119	138	54
Total	282	444	61	Total	978	1132	54

Figure 4.7

Sex ratio in samples of *A. pallipes*

from Clattercote Reservoir. 1979 - 1982

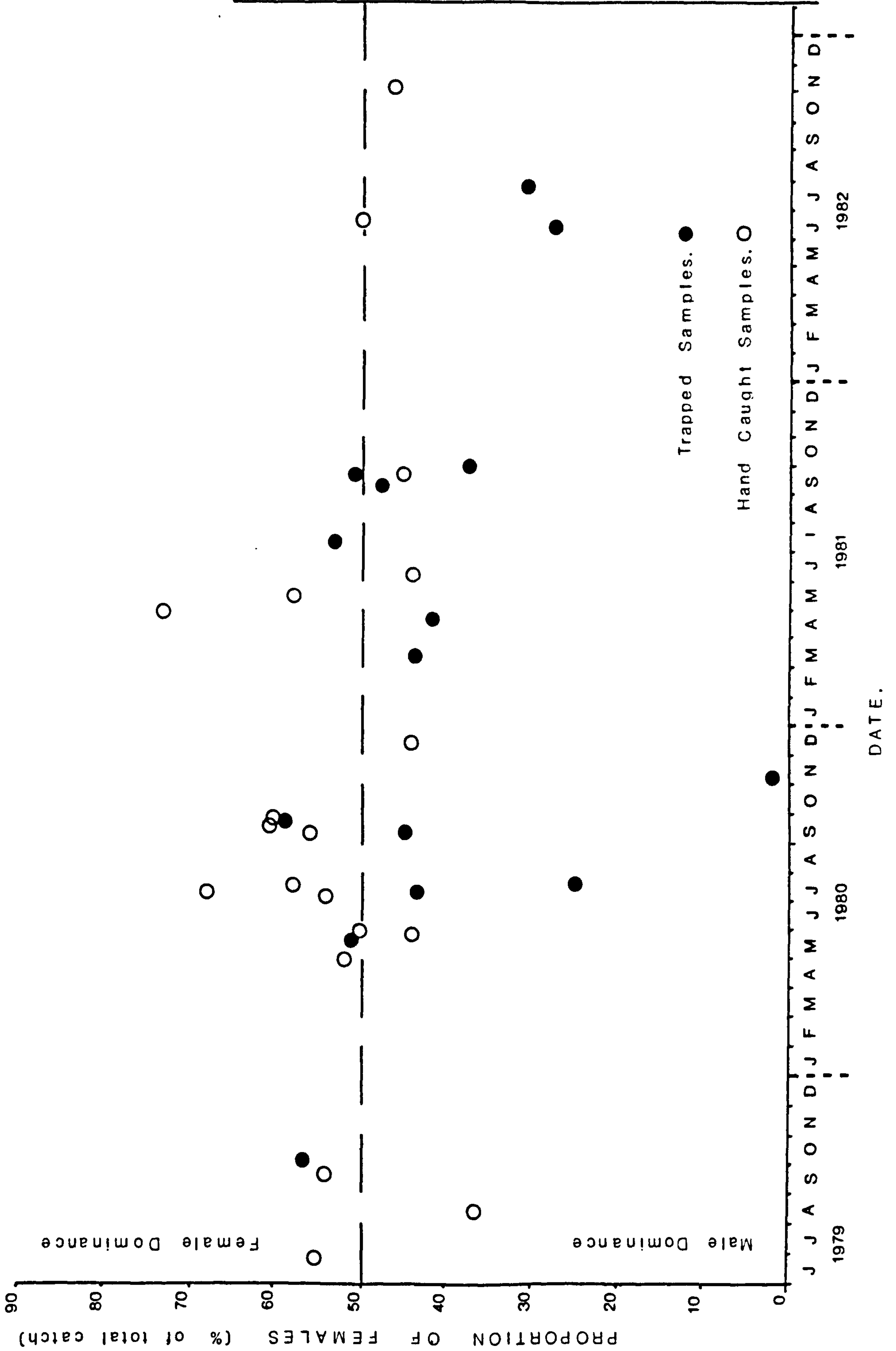


TABLE 4.5 : POPULATION ESTIMATES FOR A.PALLIPES IN
CLATTERCOTE RESERVOIR. 1980 + 1981.
(METHODS FROM RICKER, 1975)

Method	Petersen	Schumacher*	Schnabel*	Bailey*	Jolly
Date					
<u>1980</u>					
May	7299	26236±20605	8823±7219	3143±1430	-
July	6464	-	-	1958±1298	-
September	3656	-	-	10158±3686	-
<u>1981</u>					
May	3002I	-	-	1460±1038	5252
September	1096	-	-	721± 208	-

* ± 95% confidence limits

TABLE 4.6 : TRAPPING RESULTS. CLATTERCOTE RESERVOIR.

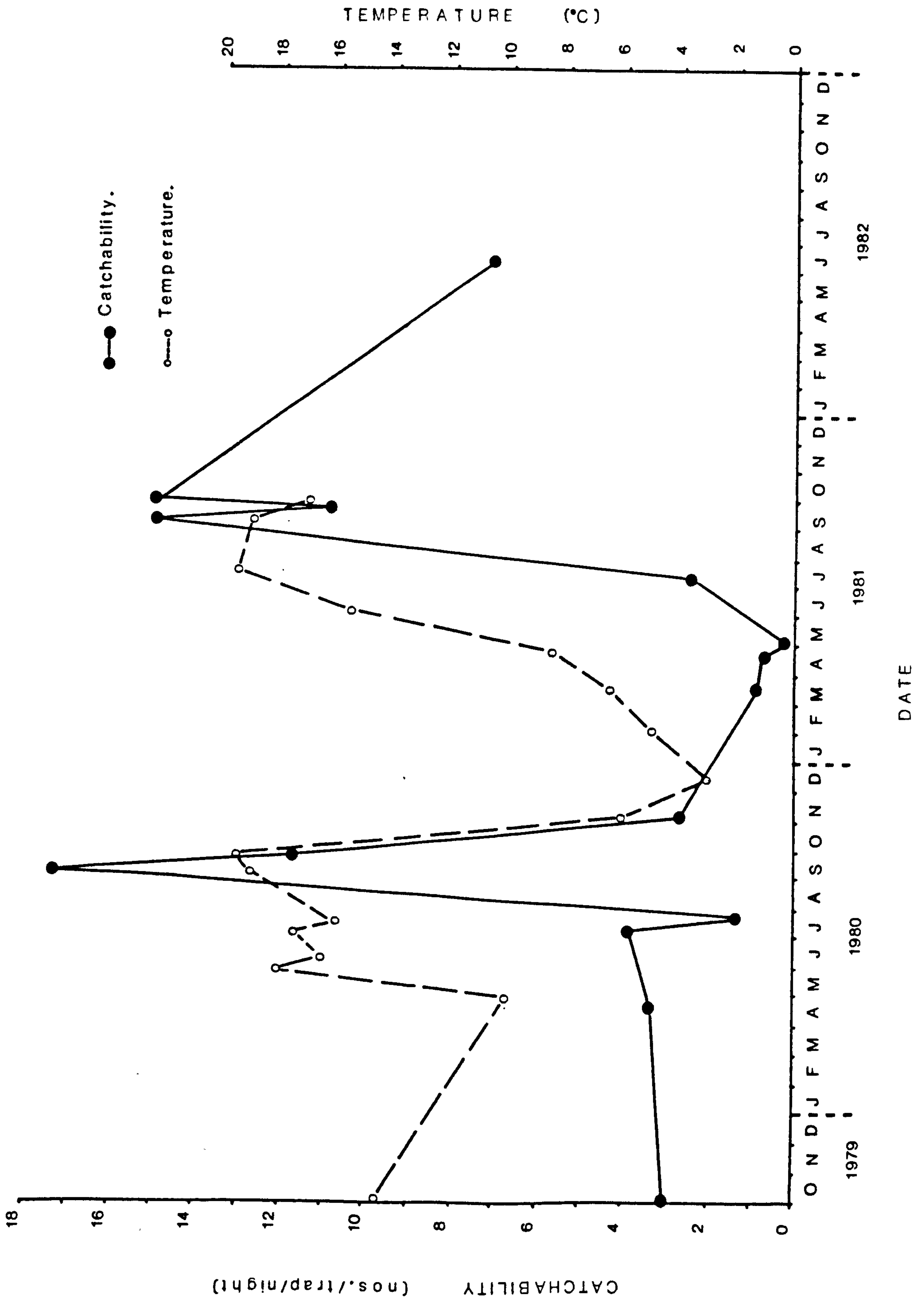
1979 - 1982.

Date	No. of Traps	MALE			FEMALE			Total Catch	Catch. trap ⁻¹ night ⁻¹
		Mean C.L. (mm)	Range	n	Mean C.L. (mm)	Range	n		
3.10.79	13	44.15	11 -55.5	30	37.23	30 -46	40	70	5.38
19. 5.80	10	42.52	31 -50.7	16	36.82	22.6-47.5	17	33	3.3
11. 7.80	25	42.01	29.5-52	56	35.97	22 -45.5	42	98	3.92
17. 7.80	N/R	43.39	32 -54	23	39.91	31 -55.5	11	34	-
11. 9.80	30	43.97	31.5-53	288	39.80	29.5-51.5	232	520	17.33
25. 9.80	26	45.65	34 -54	125	39.49	29 -48.5	182	307	11.81
4.11.80	20	42.10	32 -53	46	43.00	-	1	47	2.35
17. 3.81	10	39.76	36 -45.3	5	40.72	38.5-43	4	9	0.9
22. 4.81	33	42.69	33.3-54.2	16	37.20	18.3-45.2	10	26	0.79
6. 5.81	40	-	-	-	-	-	-	8	0.20
13. 7.81	22	37.83	22.5-49.5	15	33.56	27 -45	19	34	1.54
9. 9.81	20	41.79	19 -54.5	157	37.63	18 -46.5	143	400	20.0
21. 9.81	20	44.25	28.5-54.5	106	38.14	27 -47.5	109	215	10.75
30. 9.81	20	32.38	17.5-50	98	32.31	15 -42.5	112	210	10.5
8. 6.82	23	35.14	25 -54	130	27.00	22 -45	42	172	7.48
28. 7.82	N/R	40.14	33 -50	48	37.61	32 -45	22	70	-

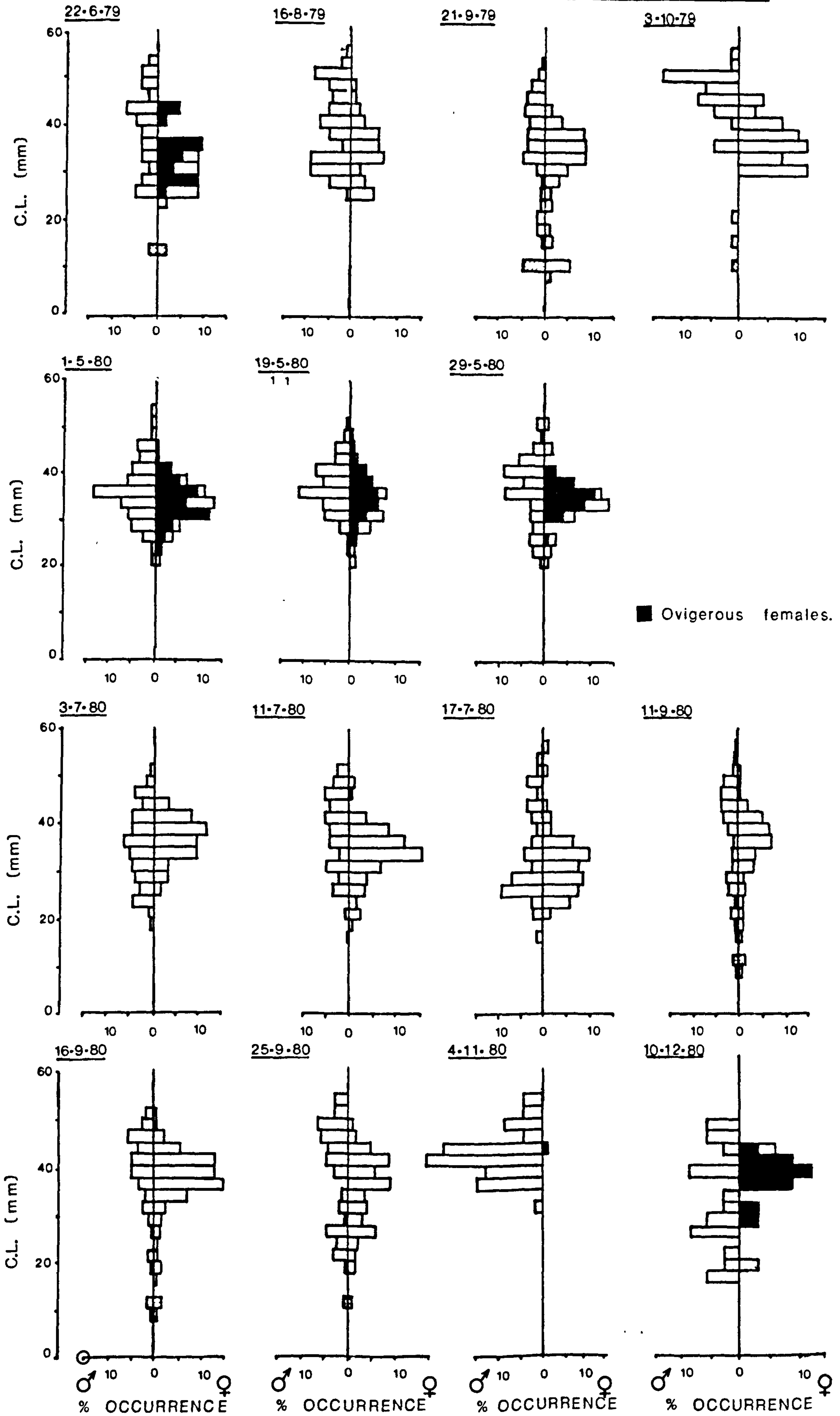
* 6.5.81 - no size data available.

Figure 4.8 Catchability of *A. pallipes*,

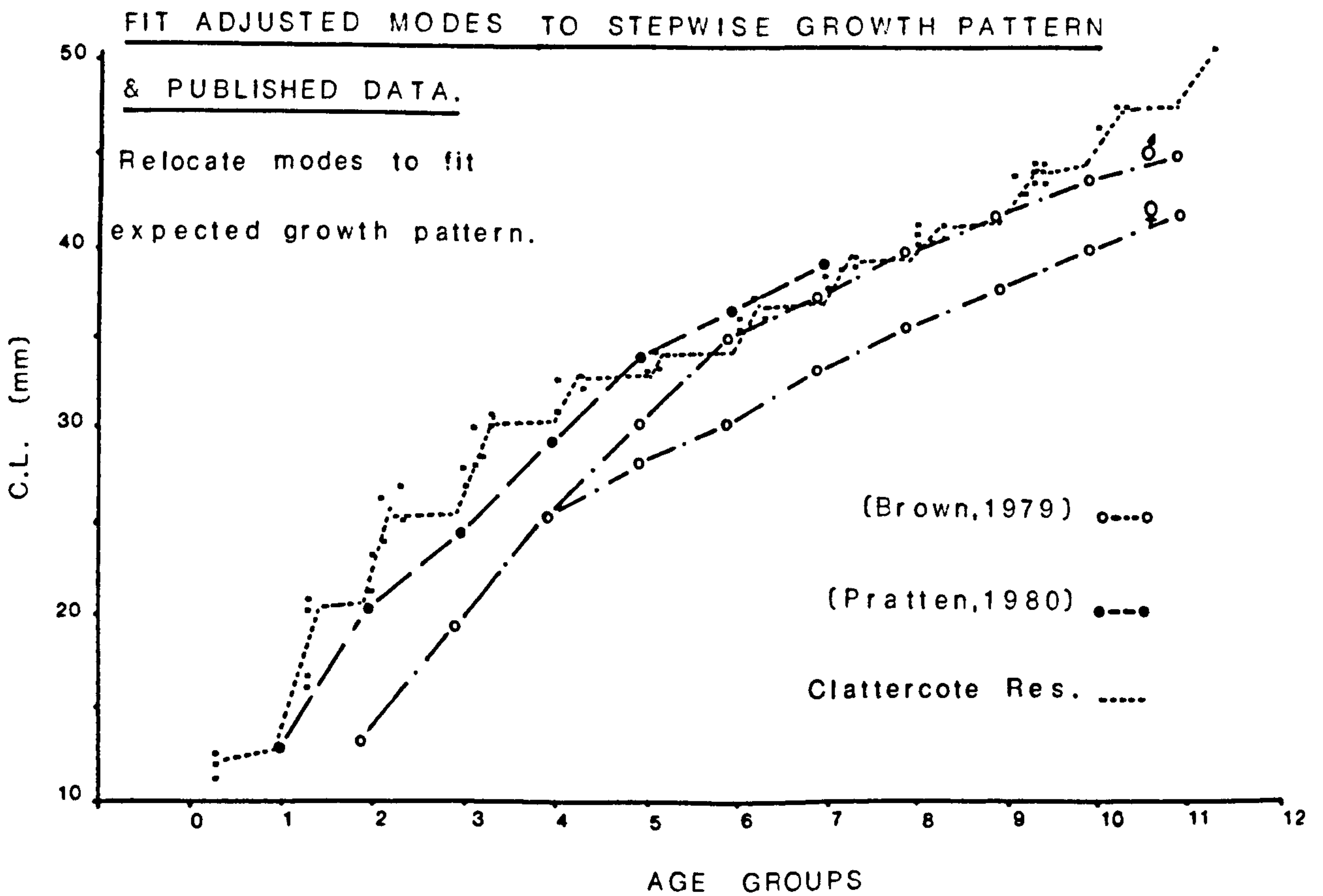
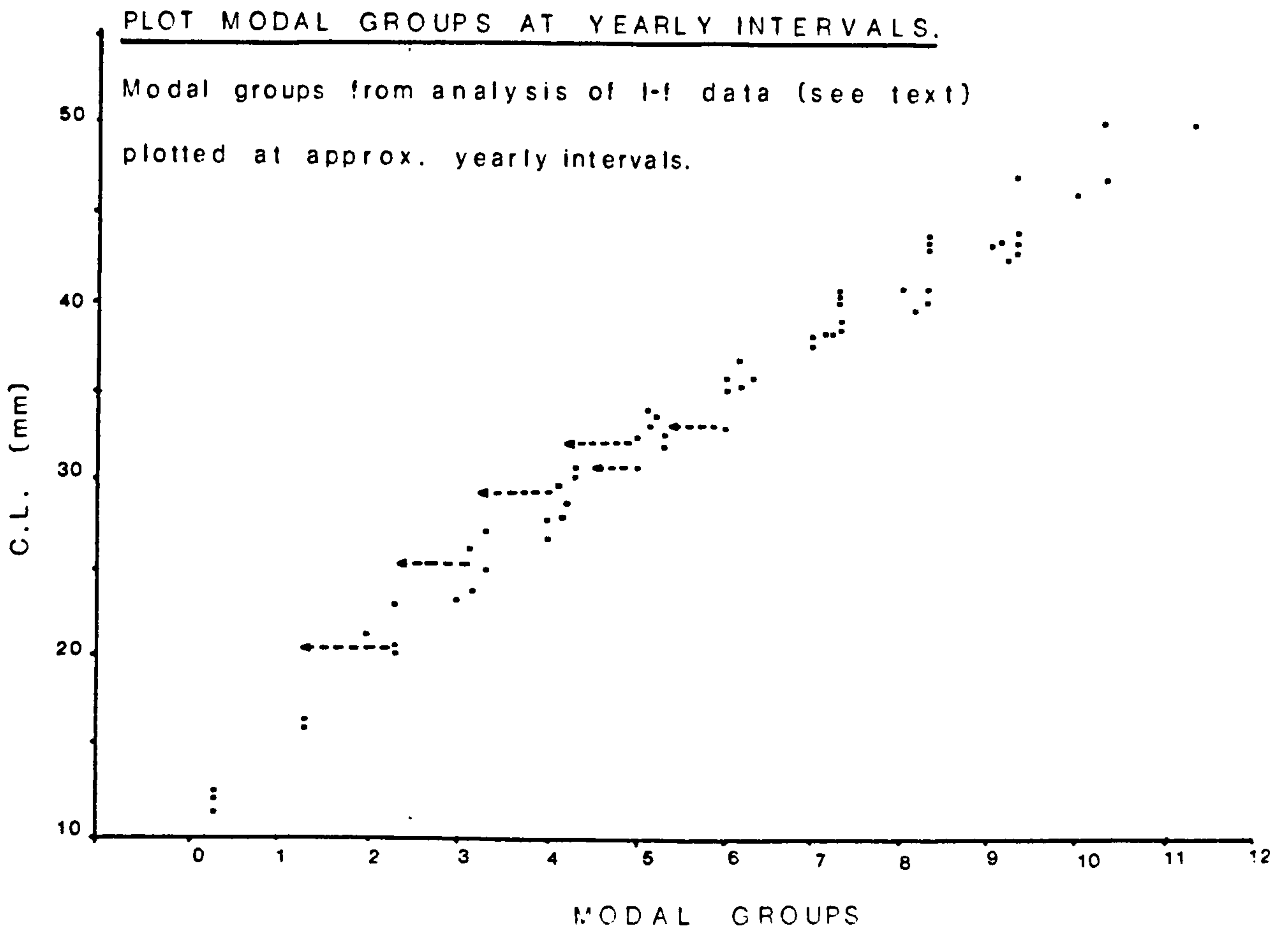
Clattercote Reservoir. 1979 - 1982



A. pallipes, Clattercote Reservoir.



of length - frequency histograms (Fig. 4.9).



Clattercote Reservoir.

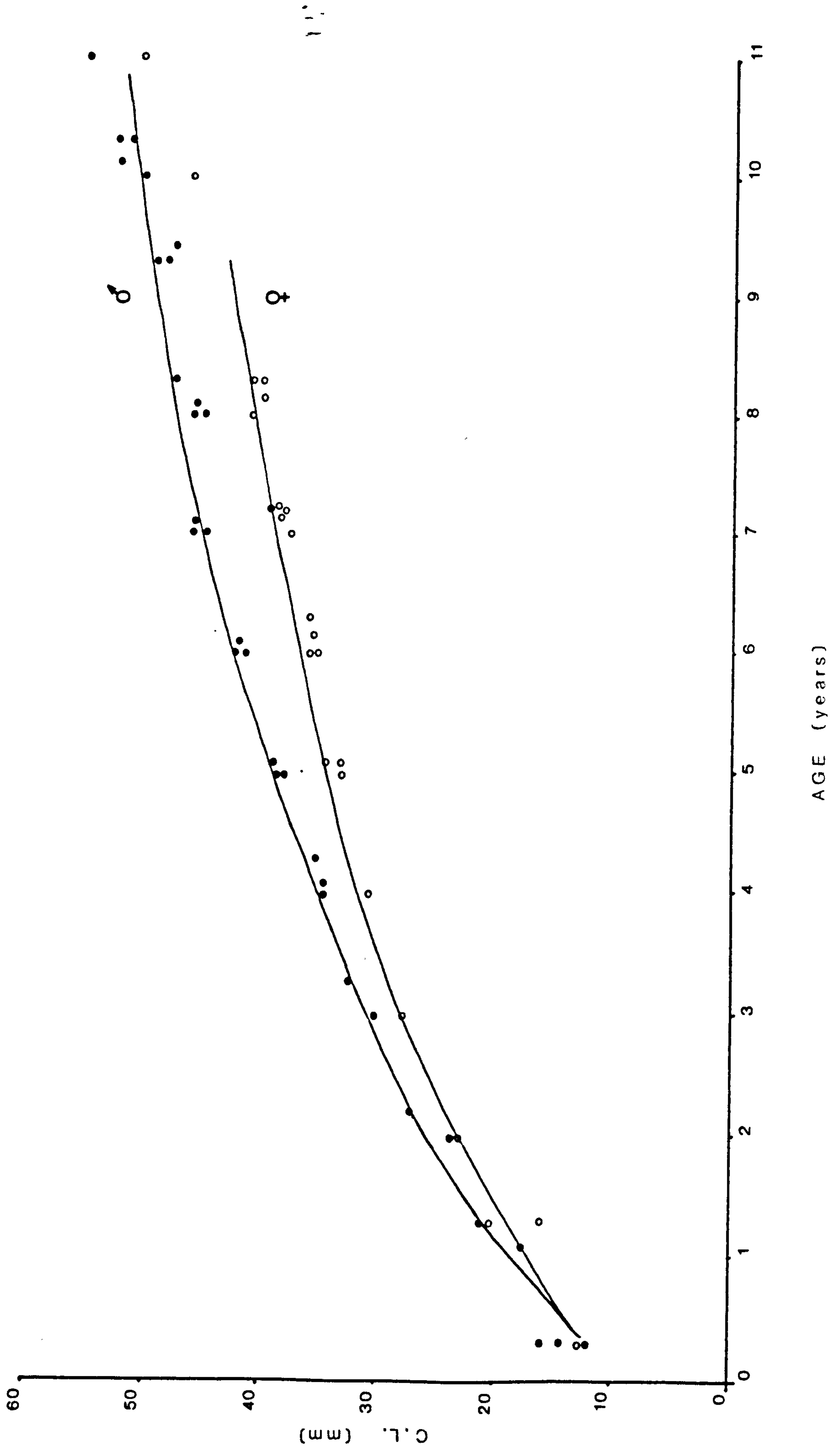


Figure 4.12

Growth curves for *A. pallipes*

- published data.

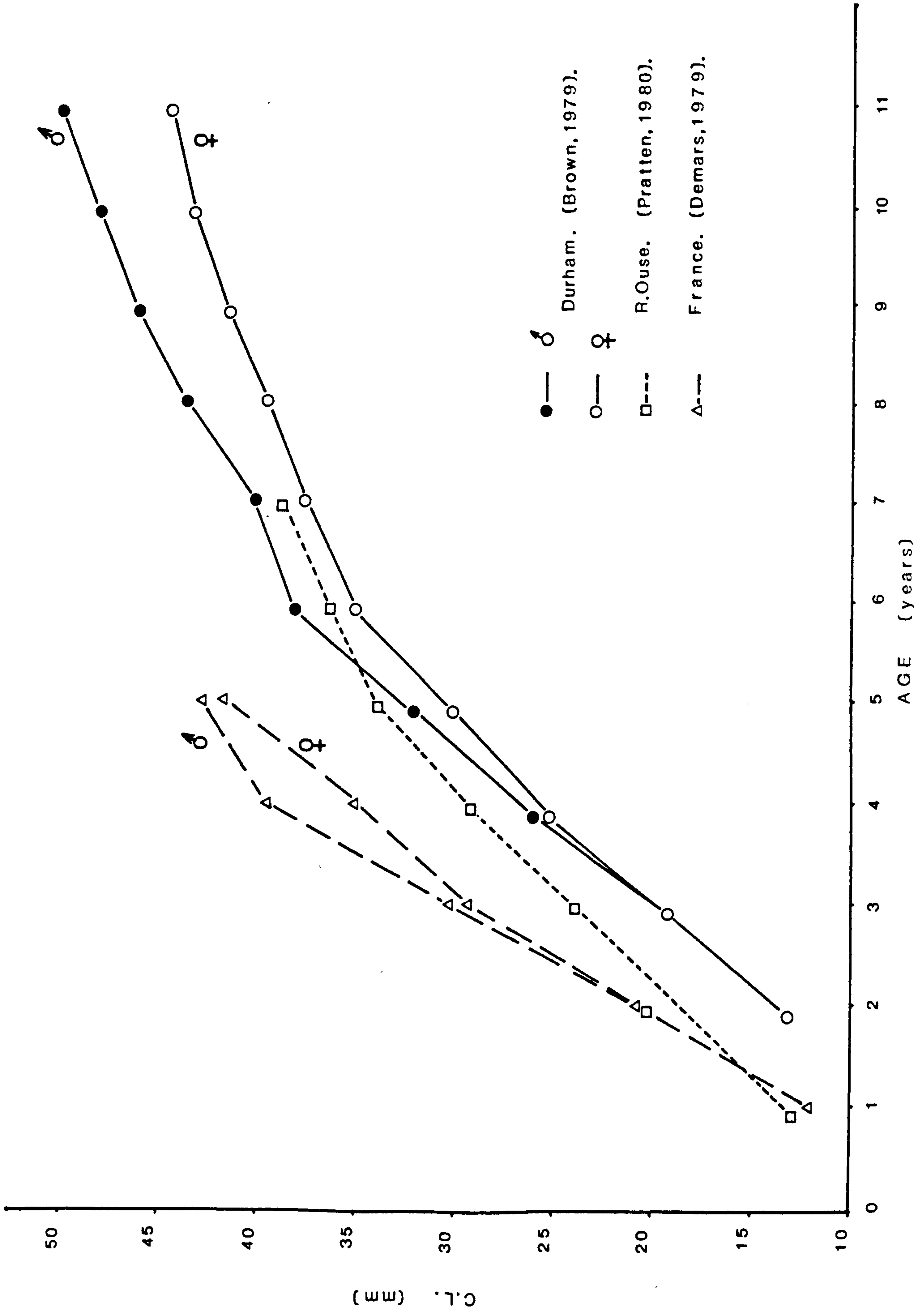


TABLE 4.7 : CONDITION FACTORS CALCULATED FOR A.PALLIPES:
CLATTERCOTE RESERVOIR. 1979 - 1982.

Date	Male			Female			Female (B)		
	C.F.** ($\times 10^{-5}$)	S.D.	n	C.F.** ($\times 10^{-5}$)	S.D.	n	C.F.** ($\times 10^{-5}$)	S.D.	n
6.79	2.43	0.45	21	1.54	0.26	10	1.48	0.27	17
8.79	1.82	0.22	83	0.94	0.06	49	-	-	-
9.79	2.15	0.27	177	1.21	0.06	203	-	-	-
10.79	2.22	0.20	6	-	-	-	-	-	-
5.80	2.06	0.14	15	0.83	0.17	5	1.09	0.26	12
7.80	1.96	0.13	70	0.92	0.08	42	-	-	-
9.80	2.14	0.16	30	0.89	0.02	8	-	-	-
7.82	2.02	0.19	4	0.95	0.12	4	-	-	-
11.82	1.90	0.13	12	0.96	0.03	3	0.95	-	1

* Pooled data if > 1 sample per month

** Mean C.F. per month where $C.F. = K = W/l^b$ (Ricker, 1971)

Where W = Weight

l = total length

b = constant ($wt = a.TL.^b$)

TABLE 4.8 : MACROINVERTEBRATE SPECIES LIST. CLATTERCOTE

RESERVOIR. 1979 - 1982.

Date Location	4.2.81 Dam	13.6.81 Dam	2.12.81 Dam	2.12.81 Head
PLANARIIDAE				
<i>Polycelis nigra/tenuis</i>				+
DENDROCOELIDAE				
<i>Denrocoeleum lacteum</i>		+		+
GASTROPODA				
<i>Bithynia tentaculata</i>		+		
<i>Lymnea peregra</i>		+	+	+
<i>Lymnaea stagnalis</i>	+	+		
OLIGOCHAETA				
<i>Nais elinguis</i>			+	
<i>Ophidonais serpentina</i>	+		+	
<i>Stylaria lacustris</i>	+			
Enchytraeidae		+		
<i>Limnodrilus</i> sp. (imature)	+		+	+
<i>Limnodrilus hoffmeisteri</i>				+
<i>Psammoryctides barbatus</i>		+	+	+
<i>Tubifex tubifex</i>				+
<i>Lumbriculus variegatus</i>	+		+	+
<i>Eiseniella tetraedra</i>	+			
HIRUDINEA				
<i>Glossiphonia complanata</i>		+		+
<i>Helobdella stagnalis</i>		+		+
<i>Theromyzon tessulatum</i>				+
<i>Erpobdella octoculata</i>		+	+	+
Ostracoda				+
EUCARIDA				
<i>A. pallipes</i>		+		
ISOPODA				
<i>Asellus meridianus</i>				+
AMPHIPODA				
<i>Gammarus pulex</i>		+	+	+
EPHEMEROPTERA				
<i>Caenis moesta</i>		+		
<i>Centroptilum luteolum</i>				+
<i>Cloeon dipterum</i>		+		
PLECOPTERA				
<i>Nemoura cinerea</i>	+			
HETEROPTERA				
<i>Notonecta</i> sp.N.			+	
<i>Notonecta viridis</i>				+
Corixidae N.		+		
<i>Sigara dorsalis</i>	+	+	+	+
<i>Sigara falleni</i>	+			
<i>Callicorixa praeusta</i>		+		
COLEOPTERA				
Colymbetini	+			+
Hydroporini	+	+		
<i>Halipus</i> sp.	+	+	+	+
<i>Halipus confinus</i>		+		
<i>Deronectes depressus</i>			+	

TABLE 4.8 : Continued

Date Location	4.2.81 Dam	13.6.81. Dam	2.12.81 Dam	2.12.81 Head
MEGALOPTERA <i>Sialis lutaria</i> TRICHOPTERA Limnephilidae L. DIPTERA Chironomidae Tipulidae Chaoboridae Limoniidae	 + + + + +	 + + 	 + + 	 +
TOTAL NO. OF TAXA.	16	21	14	21

TABLE 4.9 : IDENTIFIABLE GUT CONTENTS A.PALLIPES.
CLATTERCOTE RESERVOIR.

Food Item	% occurrence*
<u>Animal origin:-</u>	
Oligochaeta: Tubificidae	35
Lumbriculidae	17
Amphipoda: Gammarus pulex	30
Arthropoda: poss. Ephemeroptera	9
Diptera: Chironomidae	13
Fish Scales	4
<u>Plant origin:-</u>	
Chlorophyta: Spirogyra	13
Zygnema	4
Diatoms: e.g. Cymbella	22
Unidentified, presumed aquatic	26
Leaf material, presumed allochthonous	13
Detritus	39
<u>Inorganic origin:-</u>	49
No food contents:-	9

*TOTAL No. of guts examined = 23

4.3(vi) - Life-History.

The continuous temperature recordings, measured on the reservoir bed during 1981 - 1982 to establish the in-situ incubation time, are reproduced as Figure 4.13. This data has been analysed to provide the approximate number of degree-days required for the incubation of A.pallipes eggs over winter 1981 - 1982. Egg laying was observed to occur between 21.10.81 and 3.11.81 in Thames Valley A.pallipes and it is assumed that the Clattercote population laid eggs during this time. The first berried females were observed in Clattercote Reservoir on 3rd November, 1981. Hatching was first observed on 2nd June, 1982 in a Thames Valley population of A.pallipes; females with young were first observed on 8th June, 1982 in Clattercote Reservoir. The number of degree-days measured by the temperature recorder was calculated by weighing the sections of the recording between the measured temperature and zero (i.e. the shaded area Figure 4.13). Ten additional sections, each of ten degree-days, were also weighed and used to convert the total trace weight to degree days (Table 4.10).

It is estimated that laying took place over a period of 14 days and that hatching occurred between 2.6.82 and 8.6.82. Consequently the measured minimum number of degree-days, 1121°d., could be extended by as much as 176°d. Overall these results show that, for 1981 - 1982 at least incubation of the eggs of A.pallipes in Clattercote Reservoir required 1209 ± 88 °d.

Observations on the life-cycle of A.pallipes in the reservoir in the period 1979 - 1981 has enabled the timing of aspects of their life-cycle to be established. These findings are depicted in Figure 4.14.

4.3(vii) - Parasites, Disease and Damage.

The macroscopic presence of the parasitic microsporidian

Figure 4.13

Temperature recorded on bed of

Clattercote Reservoir, 1981 - 1982.

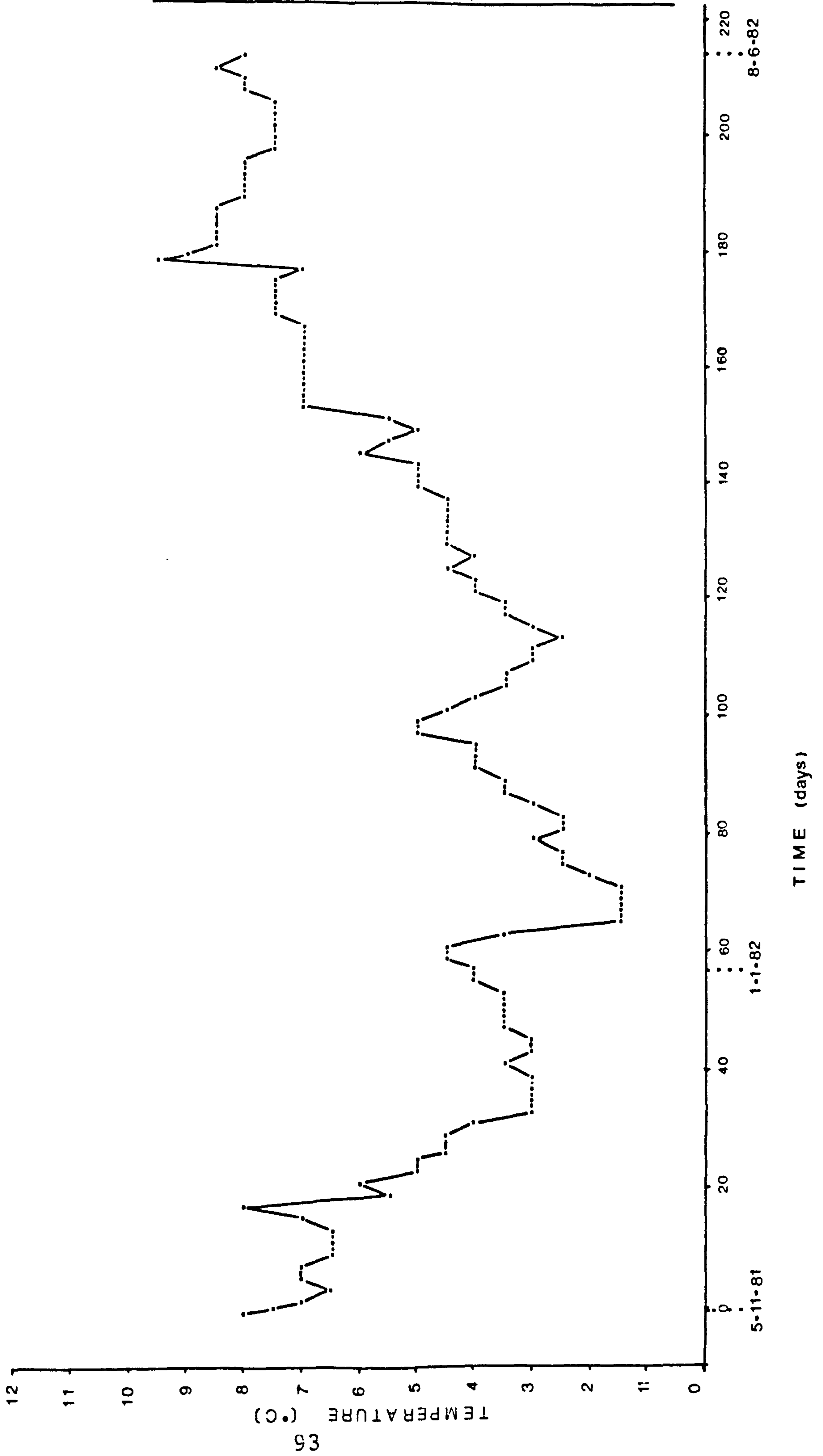
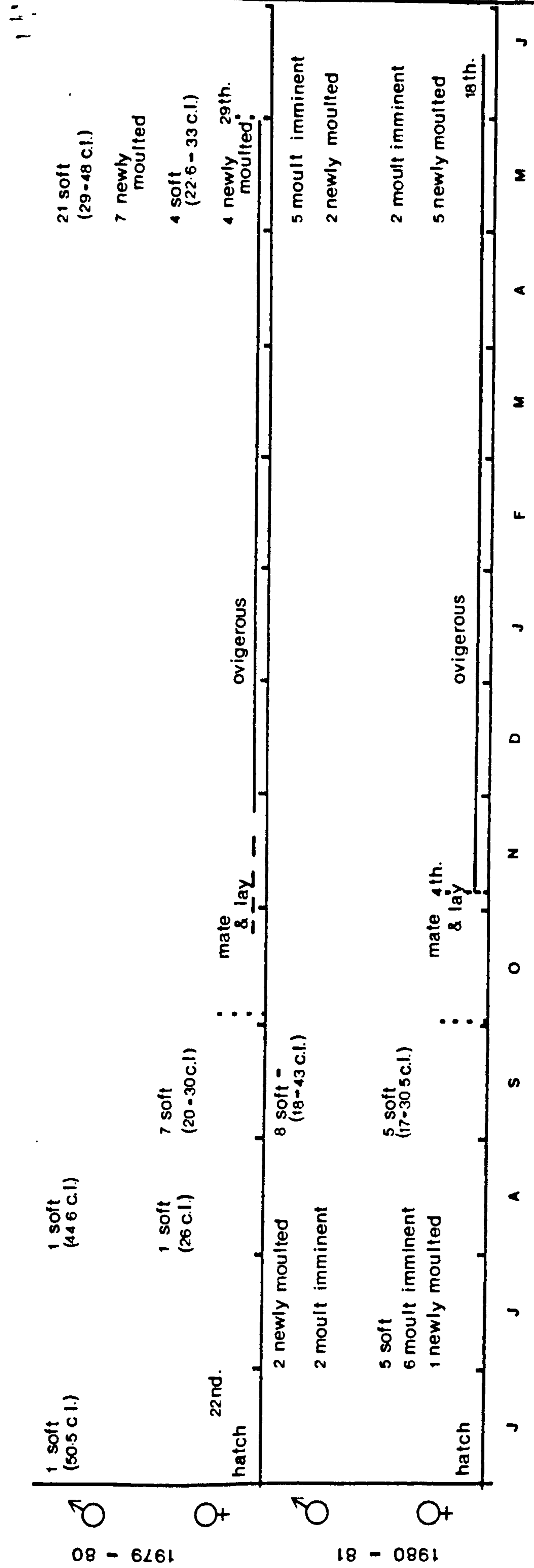


TABLE 4.10 : CALCULATION OF INCUBATION TIME FOR A.PALLIPES.
CLATTERCOTE RESERVOIR. 1981-1982

Weight of total trace (incl. hatching period)	=	2.3821g.
Weight of hatching period	=	0.1009g.
Mean of 10 x 10°d.	=	0.02035g.
Total period 4.11.81. to 8.6.82.	=	1170.6°d. (i.e. 2.3821/0.02035)
Hatching period 2.6.82. to 8.6.82.	=	49.6°d. (i.e. 0.1009/0.02035)
Minimum incubation period	=	1121°d.
Estimated laying period (21.10.81. - 4.11.81.)	=	14 days x 9°C. (mean temp.) = 126°d.
Max. incubation period (21.10.81. - 8.6.82.)	=	1170.6 + 126°d. = 1296.6°d.
Incubation period	=	1121°d. to 1296.6°d.
	=	<u>1209 ± 88°d.</u>

of *A. pallipes* in Clattercote Reservoir. 1979 - 1981



Thelohania contejeani (see Chapter 6) has been recorded, Table 4.11. Overall it appears to occur in a low proportion, < 2.1%, of adult crayfish (C.L. > 25.0 mm.) in Clattercote Reservoir, is apparently seasonal to some extent and may have declined in incidence during the period of study.

In addition some 68 individual A.pallipes of both sexes (C.L. > 28.0 mm.) were dissected and examined for evidence of parasitism or disease. No evidence was found to suggest that the parasitic annelid Branchiobdella astaci (see Chapter 6) is present in this population of A.pallipes. Similarly no evidence of fungal disease, apparent elsewhere in the Thames Catchment (see Chapter 6) was found.

The incidence of crayfish with missing or regenerating chelae, in samples collected by all methods, was recorded on 21 sampling occasions and is listed in Table 4.12. Overall mean values of 6.5% and 4.9% were calculated for males and females respectively.

4.4. Discussion.

This investigation into the biology, life-history and population dynamics of a lacustrine population of the freshwater crayfish, A.pallipes, has resulted in the acquisition of a large quantity of 'raw' data. This has been analysed to allow an assessment of both crayfish biology and crayfish fishery methods to be made.

4.4(i) - Study Site.

Parts of Clattercote Reservoir form an excellent lacustrine habitat for A.pallipes. There is ample cover in the form of limestone rubble in part of the lake and abundant food in the form of aquatic macrophytes, allochthonous plant material and aquatic macroinvertebrates (Table 4.8). Water quality is satisfactory, particularly with respect to pH and calcium content (Table 4.1).

TABLE 4.11 : OCCURRENCE OF THELOHANIA CONTEJEANI IN A.PALLIPES.
CLATTERCOTE RESERVOIR. 1979 - 1982.

Date	Male				Female				Total			
	Hand		Traps		Hand		Traps		Hand		Traps	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
22. 6.79	0	0	-	-	0	0	-	-	0	0	-	-
16. 8.79	3	3.3	-	-	3	5.8	-	-	6	4.2	-	-
21. 9.79	5	2.6	-	-	4	1.8	-	-	9	2.1	-	-
3.10.79	-	-	1	3.3	-	-	0	0	-	-	1	1.4
1. 5.80	0	0	-	-	0	0	-	-	0	0	-	-
19. 5.80	-	-	0	0	-	-	0	0	-	-	0	0
20. 5.80	2	0.9	-	-	0	0	-	-	2	0.5	-	-
29. 5.80	1	1.6	-	-	0	0	-	-	1	0.8	-	-
3. 7.80	3	1.6	-	-	2	0.9	-	-	5	1.2	-	-
11. 7.80	5	13.9	0	0	5	6.5	0	0	10	8.8	0	0
17. 7.80	2	4.3	2	8.7	1	1.6	1	9.1	3	2.7	3	8.8
11. 9.80	2	1.5	1	0.7	3	1.4	0	0	5	1.4	1.	0.4
16. 9.80	2	1.3	-	-	2	0.7	-	-	4	0.9	-	-
25. 9.80	1	3.1	0	0	2	4.2	0	0	3	3.7	0	0
4.11.80	-	-	1	2.2	-	-	0	0	-	-	1	2.1
10.12.80	0	0	-	-	0	0	-	-	0	0	-	-
17. 3.81	-	-	0	0	-	-	0	0	-	-	0	0
22. 4.81	-	-	0	0	-	-	0	0	-	-	0	0
29. 4.81	0	0	-	-	0	0	-	-	0	0	-	-
6. 5.81	-	-	0	0	-	-	0	0	-	-	0	0
13. 5.81	1	1.3	-	-	0	0	-	-	1	0.5	-	-
3. 6.81	1	0.5	-	-	0	0	-	-	1	0.3	-	-
13. 7.81	-	-	0	0	-	-	0	0	-	-	0	0
9. 9.81	-	-	0	0	-	-	0	0	-	-	0	0
21. 9.81	0	0	0	0	0	0	0	0	0	0	0	0
30. 9.81	0	0	N/R	N/R	1	3.8	N/R	N/R	1	2.1	N/R	N/R
12.11.81	0	0	-	-	0	0	-	-	0	0	-	-
2.12.81	-	-	0	0	-	-	0	0	-	-	0	0
8. 6.82	-	-	0	0	-	-	0	0	-	-	0	0
16. 6.82	0	0	-	-	0	0	-	-	0	0	-	-
28. 7.82	-	-	1	2.1	-	-	1	4.5	-	-	2	2.9
1.11.82	0	0	-	-	0	0	-	-	0	0	-	-

**TABLE 4.12 : INCIDENCE OF A.PALLIPES WITH DAMAGED OR
REGENERATING CHELAE. CLATTERCOTE RESERVOIR.
1979 - 1982.**

Date	Male			Female		
	n	Sample size	%	n	Sample size	%
22. 6.79	2	26	7.7	2	32	6.25
16. 8.79	14	92	15.2	4	52	7.7
21. 9.79	15	195	7.7	17	226	7.5
3.10.79	1	30	3.3	0	39	0
1. 5.80	4	110	3.6	0	119	0
19. 5.80	1	16	6.25	5	17	29.4
29. 5.80	3	61	4.9	3	60	5
3. 7.80	1	29	3.4	0	14	0
11. 7.80	9	92	9.8	5	119	4.2
17. 7.80	0	89	0	10	74	13.5
25. 9.80	4	42	9.5	0	68	0
4.11.80	2	46	4.3	0	1	0
10.12.80	1	19	5.2	2	15	13.3
17. 3.80	1	5	20.0	0	5	0
22. 4.81	2	16	12.5	0	11	0
29. 4.81	1	21	4.7	1	57	1.7
3. 6.81	6	204	2.9	3	172	1.7
13. 7.81	0	23	0	2	26	7.7
30. 9.81	1	21	4.8	0	26	0
8. 6.82	4	130	3.1	0	42	0
27. 7.82	3	44	6.8	1	18	5.5
Mean (n = 21)			6.5			4.9

The reservoir apparently receives no pollution and nutrients remain low throughout the year. Algal blooms typically occur in spring and early summer (Fogg, 1975) although in Clattercote Reservoir, even then, phytoplankton chlorophyll values are low in comparison to other similar water bodies in the Thames Catchment.

4.4(ii) - Sampling Methods.

The methods of sampling used throughout the study were selected for three main reasons:-

- (i) To provide as wide a range of crayfish sizes in the samples as possible.
- (ii) To provide a mixed sampling method for use in estimation of population size by mark-recapture methods.
- (iii) To enable samples to be collected, for example, in winter when trapping is least successful, see Figure 4.8.

The principal advantage of alternative sampling methods is that when two methods are utilised concurrently the validity of mark-recapture estimates between samples collected by the same method can be checked by calculating a comparable estimate from samples collected by different methods over the same period. This latter estimate should be free from bias due to unequal catchability, provided that the source of bias is independent in the two methods (Seber, 1973). In practice, in this study, recapture of marked individuals was too low to permit separate estimates to be calculated according to sampling method. Even so it is felt that a combination of sampling methods should reduce any bias inherent in single method mark-recapture estimates.

Each sampling method collected crayfish over a different overall size range, Figure 4.5. The mean and range of C.L. values caught by each method are shown in Table 4.3 and Figure 4.4. Trapping consistently resulted in samples with a large mean C.L. and crayfish less than 28.0 mm.C.L. were

seldom caught in traps. This approximates to the minimum trappable size of 25.0 mm.C.L. reported from Ireland (Moriarty, 1973) and substantiates published reports that juvenile crayfish seldom enter traps (Brown & Bowler, 1977). In effect this means that traps only sample the sexually mature sub-population.

Trapping was found to be most effective in late summer, Figure 4.8, when water levels were at a minimum, Figure 4.3, and water temperatures highest. This sampling method was used to collect samples requiring a standardised method for comparative purposes. The problems associated with trapping as an effective sampling method are brought about by the fact that the animal is an 'active agent'. Its capture depends not only on the density of sampling units (traps) and the percentage of the population sampled but also on the physiological state of the individual crayfish (Brown & Bowler, 1977).

Hand sampling is generally thought to be less biased (Brown & Bowler, 1977) in respect of the size and physiological state of the crayfish but is difficult to standardise. Hand catching by divers, either collecting crayfish by turning over the stones in the daytime or by torchlight at night, did not significantly reduce the mean C.L. of samples ($p < 0.05$) when compared with trapping. However, a wider size range of A.pallipes was caught by this method, Figure 4.5, with a minimum size of 19.0 mm.C.L., so it could be concluded that hand sampling is less biased in favour of larger individuals, than trapping.

Hand collection in the shallow marginal areas (<1.0 m. deep) was the only sampling method that consistently provided specimens of 0+ and 1+ crayfish, Figure 4.5, and was generally used in conjunction with another method. This method of sampling was not used as part of the mark-recapture investigations as small crayfish may be permanently damaged by the marking method (Cooper, 1970). The major

drawback in using this sampling method is that it is difficult to standardise, as is hand collection by divers, and could only be used effectively when water levels in the reservoir were reduced, i.e. in late summer and autumn.

By using a combination of the three sampling methods throughout the study it is considered that all size groups within the population are represented in the samples, although numerically not in proportion to their abundance, i.e. 0+ crayfish are presumably most abundant but are poorly represented in all but the hand-collected samples from the margins. The juvenile to adult ratio has been calculated to be 3 to 1 for other populations of A.pallipes (Brown & Bowler, 1977). The wide size range of individuals sampled greatly aids attempts to analyse the length-frequency data for the purpose of calculating growth rates. Such a combination of sampling methods should also improve the accuracy of the population estimates. Indeed a review of crayfish behaviour in response to trapping emphasised their selective nature, with only mature, active individuals being caught (Woodland, 1967). Elsewhere it has been concluded that direct hand capture provides the least biased sample as all size classes and conditions are collected (Pratten, 1980).

From a management point of view the results suggest that cropping of crayfish, assuming that only the largest individuals are required, for example for the table market, would most effectively be achieved by trapping. This method would have little short-term effect on recruitment as juveniles are not sampled and may not have a great effect on recruitment in the longer term as female crayfish in their first year of maturity (i.e. C.L. 24-30 mm.) are only caught in relatively small numbers by this method. In addition it would be reasonable to apply a minimum size limit for crayfish to be harvested commercially to ensure adequate recruitment. Such size limits for A.pallipes removal are in force in some European countries, e.g. 9.0 cm.T.L.

in France (Laurent, 1973; Laurent & Forest, 1979); 10.0 cm.T.L. in Switzerland (Büttiger, in Westman & Pursainen, 1982) and 8.0 cm.POTL in Spain (Habsburgo-Lorena, in Westman & Pursainen, 1982), together with 'close' seasons of varying duration (Westman & Pursainen, 1982). For monitoring the progress of a population from maturity to marketable size a combination of collecting methods would be preferable.

Monitoring changes in gross population structure, during this study, was achieved by calculating mean C.L. for each sampling method for each year, Table 4.3. It can be seen that the mean C.L. of both trapped and hand-caught (sub-aqua) samples has apparently declined throughout the period 1979 to 1982, Figure 4.4. Statistical analysis has been used to compare these mean C.L. values and has shown, however, that the observed decline in these values is not statistically significant ($p > 0.05$). This is due to the large sample variances attached to each mean. The reason for the apparent decline, it is suggested, is that numerous large crayfish have been removed. The sizes and number removed for experimental use at Reading University has been recorded, see Table 4.13, but it is not known how many have been removed each year by local anglers, etc., and this information remains unrecorded. Elsewhere it has been shown that the mean C.L. of hand-caught A.pallipes increased from 24.3 mm. to 31.3 mm. over a three year period, (Brown, 1979). The reason for this increase was postulated to be the removal of several hundred large crayfish (>40 mm. C.L.) "some years" previously and growth during the study period resulting in large crayfish being caught more frequently in successive years. A similar increase in mean C.L. could occur in the Clattercote population of A.pallipes over the next three or four years if the known removals have reduced the population significantly. The current study only documents the decline in mean C.L. presumed to be due to the known recent (1979 - 1981) removals of crayfish.

TABLE 4.13 : SUMMARY OF DATA CONCERNING A.PALLIPES
REMOVED FROM CLATTERCOTE RESERVOIR.
1979 - 1982.

Date	Males			Females			Total
	C.L.	Range	n	C.L.	Range	n	
22. 6.79	38.2	14.7 - 52.9	26	28.1	13.7 - 42.9	11	37
16. 8.79	39.3	25.1 - 55.7	92	35.1	26.0 - 48.7	50	142
21. 9.79	34.6	10.0 - 59.5	192	31.1	9.5 - 48.0	134	326
1. 5.80	37.8	28.7 - 54.5	82	34.6	27.5 - 46.5	21	103
29. 5.80	39.6	32.0 - 50.0	16	33.7	33.5 - 34.0	2	18
3. 7.80	42.5	23.5 - 50.0	29	39.1	37.0 - 41.0	14	43
11. 7.80	44.9	38.6 - 51.7	31	40.7	35.8 - 49.9	16	47
17. 7.80	45.6	34.8 - 52.6	13	39.5	33.2 - 52.1	7	20
16. 9.80	39.2	29.5 - 53.0	63	39.2	33.0 - 48.0	62	125
25. 9.80	47.3	38.0 - 53.5	52	45.4	42.5 - 48.5	8	60
10.12.80	21.4	19.0 - 25.0	5	20.0	-	1	6
9. 9.81	17.2	10.0 - 26.5	14	14.8	9.0 - 31.5	18	32
27. 7.82	40.1	33.0 - 50.0	48	37.6	32.0 - 45.0	22	70
1.11.82	29.4	19.0 - 40.0	46	28.9	19.0 - 37.0	40	86
<u>Mean</u> <u>Total</u>	36.9	10.0 - 59.5	709	33.4	9.0 - 52.1	366	1075

The mean C.L. of the hand-caught crayfish tended to increase during each year, Figure 4.4, although a decline was recorded from year to year. This seasonal increase was due to the mature females not being sampled so readily earlier in the year, as they were ovigerous until June. A similar seasonal increase in the mean C.L. of samples of A.pallipes has been reported from the River Darent in Kent (Thomas & Ingle, 1971). Long-term fluctuations in mean C.L., in an Irish population of A.pallipes, have been attributed to variations in breeding success caused by fluctuations in water level (Moriarty, 1973). There is no evidence to suggest that this was the case in Clattercote Reservoir.

The ratio of males to females, expressed as the number of females as a percentage of the total catch, in all samples has also been calculated. This information has been used to evaluate reports that females do not readily enter traps (Brown, 1979) and are very seasonal in their catchability (Brown & Bowler, 1977). Figure 4.7 clearly shows that males, on average, outnumber females in trap catches but some catches, e.g. 25 males and 22 females in a single trap on 9.9.81, show that females are not prevented from entering traps by males. Male dominance was exhibited in 67% of samples obtained by trapping and was greatest during the winter months and June/July. The reason for this variability in sample sex ratio is probably that females are ovigerous throughout the winter (November to June), so are less catchable, and either have newly hatched juveniles attached to them in June/July or are undergoing a post-hatching moult as is reported to occur for adult female A.pallipes in the River Ouse in July and August (Pratten, 1980). Similar reductions in the proportion of females collected in winter, and a mid-September moult period, have been reported from Durham (Brown & Bowler, 1977).

It is quite clear, however, that female A.pallipes do enter traps contrary to reports that all females avoid traps irrespective of their reproductive state (Brown & Bowler,

1977). They are, on occasions, the dominant sex. It has also been reported by the same authors that adult females respond to traps in a similar way to males irrespective of their reproductive status (Brown, 1979). The current results confirm that the reproductive cycle plays a major role in determining female catchability.

In order to determine the diel activity of A.pallipes in Clattercote Reservoir, in relation to trapping, traps were lifted four hourly over a twenty hour period on a single sampling occasion (19.5.80), when darkness occurred at approximately 21.00 hours. The results, Table 4.14, suggested that maximum catches, 79% of the total, could be obtained in the period 21.00 hours to 01.00 hours but that numbers caught declined after this time. Trapping by day on 1.5.80 and 19.5.80 resulted in no success. These findings agree with those reported elsewhere (Brown, 1979) although some success with daytime trapping has also been reported (Brown, 1979).

The collection of samples by hand, either by divers or along the shore, produced different results to the trapped samples. Female dominance occurred in 69% of these samples and was most evident in the summer. This concords with similar findings from hand-collected samples from the River Wye, Gwent (Lilley, 1977) and River Darent, Kent (Thomas & Ingle, 1971).

No clear seasonal pattern emerges from these results except that in winter males tended to be dominant. Little of both types of sampling was, however, carried out in the winter as catches at this time were always low (see Figure 4.8) and were considered to be unsatisfactory in terms of time and effort expended. Such behavioural differences in activity would aid survival by limiting cannibalism of the attached young by other crayfish and ensure that female was not disturbed whilst egg-laying, reducing the chances of egg loss at this stage (Brown, 1979). The period during

TABLE 4.14 : RESULTS OF TRAPPING DURING 20 HOUR PERIOD.
CLATTERCOTE RESERVOIR. 19.5.80.

Traps Set (time : hours)	Traps Emptied (hours)	No. of Traps	Catch			No. trap. ⁻¹ hour. ⁻¹
			♂	♀	Total	
21.00	01.00	5	10	16	26	1.30
01.00	06.00	5	3	1	4	0.16
21.00	06.00	5	3	0	3	0.06

which egg loss is most probable is after extrusion but prior to pleopodal attachment (Ingle & Thomas, 1974). This has been borne out by laboratory observations during the current study. Elsewhere the mean sex ratio in all trapped samples has been reported as 30% females (Brown, 1979) and 43% females (Moriarity, 1973) but in other studies females have been reported as being dominant overall (Thomas & Ingle, 1971; Demars, 1979; Lilley, 1977).

4.4(iii) - Population Estimates.

The size of the catchable population has been estimated using mark and recapture methods (Ricker, 1975). Where it is intended to employ such methods of population estimation all groups within the population should be sampled in adequate numbers throughout the study period for the estimates to be really reliable (Robson & Reiger, 1964). It is clear that the sampling methods used in this study were not ideal and that sampling efficiency with respect to all size groups was seasonally variable. Variations in sex-ratio and numbers of juveniles caught have been discussed elsewhere (see 4.4(ii)). Consequently the estimates of population size calculated by mark-recapture methods during this study are approximations of the size of the catchable adult population. These estimates, Table 4.5, vary widely and range from 3,143 to 26,236 for May, 1980; 3,656 to 10,158 for September, 1980 and 1,460 to 5,252 for May, 1981. A number of formulae were used to try and arrive at credible estimates (see Chapter 2). The simplest method used, the Petersen estimate, implies that a decline in adult population occurred between May and September, 1980 and between May and September, 1981. A decline may, in fact, have occurred as a number of adult crayfish are known to have been removed in both years, Table 4.13, but the known numbers removed are not comparable with the decline in estimated population size.

Conversely the Bailey estimate, using a three-catch

sampling method, suggests that the adult population in 1980 increased from 3,143 in May to 10,158 in September. Such an increase could be explained, in the absence of any other estimates, by the influx of crayfish into the catchable population. It is, however, a large increase and would imply that mortality would have to be in excess of 80% over winter to result in the May 1981 estimate of 1,460. Elsewhere over-winter mortality has been calculated to be $2\% \text{ week}^{-1}$, in a northern population of A.pallipes (Brewis, 1979). A similar increase in population estimates does not occur during 1981 and the estimated adult population declines from 1,460 to 721. This decline affords more consistency with the Petersen estimates, although not in scale, than with the 1980 Bailey estimates.

The estimates of population size calculated using the Schumacher and Schnabel methods, used in 1980, result in figures that are widely different and have very large confidence limits attached to them. This feature of estimating crayfish population size using those methods has also been reported previously (Lilley, 1977). The estimate calculated using Jolly's stochastic model in 1981, provided an estimate in excess of that calculated by both the Petersen and Bailey methods.

Overall, it is considered that the unreliable nature of population estimates calculated in this way renders them to be of little practical use. The results obtained during this study suggest that the probable maximum size of the adult population of A.pallipes in Clattercote Reservoir during 1980 and 1981 does not exceed 10,000 and is more probably within the range 1,000 to 6,000. If the published juvenile to adult ratio of 3:1 (Brown & Bowler, 1977) is applied to these figures the total population of A.pallipes in the study area would be within the range 4,000 to 24,000. (If, then, the population estimates calculated from trapping results are considered to be threefold underestimates, as has been reported, (Brown & Brewis, 1979), the

population size could potentially be very large indeed).

It is probable, in view of the numbers of crayfish known to have been removed, Table 4.13, that population size did decline in any one year but to what extent is not known. The results obtained during this study call into doubt the validity and usefulness of population estimates calculated by mark-recapture methods and agree with similar conclusions from other such studies (Brown, 1979; Brown & Brewis, 1979). Reliable estimates of decapod population size are, elsewhere, reported to be only available from regression methods on a closed population (Eberhardt, 1969). The low percentage of individually marked crayfish that were recaptured subsequently (i.e. mean 3.7%) compares favourably with the 1.3% recapture recorded from an Irish lake (Moriarty, 1973), but confirms that one of the major problems in studies of this type is obtaining and processing sufficiently large samples (Brown & Bowler, 1977).

4.4(iv) - Catchability.

As a consequence of the poor reliability of the population estimates calculated by mark-recapture methods an alternative approach to assessing relative abundance has been used. By expressing catches using standard sampling units, i.e. traps, in terms of catch per trap per unit time the success of trapping throughout the study period can be assessed. According to some reports catchability can be considered as an indirect index of activity (Brown, 1979) and differentiation between feeding and hide-seeking activity should be carried out using baited and unbaited traps. In this study however, it is felt that this difference is unimportant as open-mesh traps were used throughout compared with the rigid and partially enclosed traps used in the reported study (Brown, 1979).

Figure 4.8 illustrates the catchability of adult

A. pallipes in Clattercote Reservoir from 1979 to 1982 and shows a maximum catch of $4.33 \text{ trap}^{-1} \text{ hour}^{-1}$ i.e. $17.33 \text{ trap}^{-1} \text{ night}^{-1}$ (where night = 4 hour sampling period from dusk) which compares very favourably with the $2.12 \text{ trap}^{-1} \text{ hour}^{-1}$ reported from Durham (Brown, 1979).

It can be seen that, in general, catchability was lowest in winter and spring, from about November to July, and was at a maximum in August and September. Lowest catchability was recorded in February and March in an Irish lake (Moriarty, 1973). This relationship only permits an assessment of relative abundance to be made through comparison of results from the same period each year, to discount seasonal variations. It is only a crude measurement of abundance and assumes that catchability at the same time of year is only density dependent. On this basis there appears to be only a slight decline in catchability and, by implication, abundance during the period of study. It could be that catchability in the same season is not density dependent and that the study site was so heavily trapped on each occasion that the maximum number of trappable crayfish was caught on each visit. This seems improbable, however, as catches in individual traps ranged from 0 to 47 on the same occasion (9.9.81). This also illustrates the clumped distribution of adults in this population and an average of only 20% of 'batch' marked individuals were ever recaptured.

In order to quantify trappability a population of crayfish of known size would have to be trapped in the standard way and catch per trap related to total population size. Thus the efficiency of trapping, at that time, could be quantified. This approach has been experimentally carried out in Australia to estimate the size of marron, Cherax tenuimanus, populations (Morrissey, 1975; Morrissey & Caputi, 1981) and has been used, in combination with quadrat sampling, to estimate numbers of P. leniusculus in Lake Tahoe, California (Abrahamsson & Goldman, 1970;

Flint, 1975). In this latter case catch per trap (c) was compared with intensive hand collection by divers, considered to be an estimate of density (d), in a similar area and time to the trap samples; to give the ratio c/d . Subsequent trapping yielded further values of catch per trap (c_2) which were converted to density estimates by multiplying by c/d . This method would, however, be of little use at times of low trap efficiency and would have to be frequently repeated. In addition the method assumes that all crayfish within a certain radius of the trap are captured, which is certainly not the case, and must vary with substrata type and the physiological condition of the crayfish (Flint 1975). Consequently there seems little to recommend this method of estimation of population size.

The relationship between catchability and temperature, in Clattercote Reservoir, is shown in Figure 4.8. Although an increase in catchability is partially related to a temperature increase in summer there is a time lag before it increases significantly. This is primarily due to the crayfish moult and reproductive cycles. Females are ovigerous until June and less readily enter traps in this condition. After the young have left the female these may then moult (Pratten, 1980) and so are less trappable. Similarly one of the two main moult periods for adult males in southern England is in May/June (Pratten, 1980) and so these individuals only become more freely available for trapping after this time. Consequently the population as a whole remains relatively untrappable until August. In addition there may be some physiological mechanisms that require a certain temperature threshold, in terms of degree-days, to be reached before the major feeding period commences.

4.4(v) - Length-Frequency Data and Growth.

The collection of a large quantity of C.L. - frequency data was undertaken to facilitate an attempt to identify

age-groups within this natural population of A.pallipes. Decapods are notoriously difficult to age due to their periodic moulting and the shedding of all hard skeletal structures. This difficulty is particularly apparent in long-lived species, such as A.pallipes. This species may have a life-span of 10 - 13 years (Brown & Bowler, 1979), compared with, for example, the 2.5 - 3 year life-span of Orconectes neglectus (Price & Payne, 1979). The analysis of length-frequency data has been attempted in several studies of crayfish populations (Abrahamsson & Goldman, 1970; Abrahamsson, 1971, 1973a; Lilley, 1977; Brown, 1979; Brewis & Bowler, 1982) with varying degrees of success. Where juvenile crayfish have been sampled the method has successfully identified age-groups up to age 3+ (Brown, 1979). Preliminary analysis involves the construction of length-frequency histograms and the selection of size classes is critical for clear separation of the data into size groups. In the present study crayfish were grouped into 2.5 mm C.L. size groups as this is less than the mean moult increment reported for this species (Brown, 1979). The method of analysis described in Chapter 2 (Bhattacharya, 1967) was then used to distinguish distinct size groups within each sample. Only data from crayfish with a complete complement of limbs was used for this analysis as it has been shown that limb regeneration has a depressive effect on linear growth in both sexes (Brown, 1979).

Some of the data thus obtained was plotted against known age (i.e. 0+ and 1+), Figure 4.10, and compared with published growth data for A.pallipes (Thomas & Ingle, 1971; Moriarty, 1973; Demars, 1979; Pratten, 1980). It was then possible to construct a 'growth curve' of C.L. against age for A.pallipes in Clattercote Reservoir, Figure 4.11. This curve, it must be stressed, has been fitted by eye and variations in growth rate will occur due to the effects of disease, individual variations in successive moult increments and reproduction in females (Brewis & Bowler, 1982).

This estimated growth rate is similar to that measured in the River Ouse, Buckinghamshire (Pratten, 1980) and White Lake, Ireland (Moriarty, 1973) but is markedly faster than that reported from Durham (Brown, 1977; Brewis & Bowler, 1982), Figure 4.12. Elsewhere it has been reported that lake populations grow more rapidly than stream populations (Reynolds, 1979) but the current data is insufficient to test this theory. When compared with the growth of the introduced P.leniusculus, however, (see Figure 8.7) the growth of A.pallipes is clearly much slower.

Other researchers have measured growth rate in terms of moult increments for individuals but this could not be attempted in the current study due to the poor recapture rate of individually marked crayfish. According to these studies the absolute moult increment of males increases with increasing body size, until sexual maturity, and then declines (Brown, 1979). However, individual growth increments, in the larger size classes at least, have been shown not to be consistently above or below average in any one individual (Brown, 1979). The relationship of moult-increment to C.L. has been reported to be:-

$$\begin{array}{l} \text{PoMCL} = 0.974 \text{ Pre MCL} + 3.85 \\ \text{PoMCL} = 0.917 \text{ Pre MCL} + 5.06 \\ \% \text{ GICL} = 19.08 - 0.296 \text{ Pre MCL} \\ \% \text{ GICL} = 17.89 - 0.316 \text{ Pre MCL} \end{array} \left. \begin{array}{l}) \\) \\) \\) \end{array} \right\} \begin{array}{l} \text{Brown \& Bowler, 1979} \\ \text{Brown \& Bowler, 1977} \end{array}$$

and $\log_{10}(\% \text{ GICL}) = 1.259 - 0.1174 \cdot \text{PreMCL}$ (Pratten, 1980)

Where PoMCL = Post-moult C.L.

PreMCL = Pre-moult C.L.

GICL = Moult increment as a % of PreMCL

No comparable data is available from the Clattercote population of A.pallipes.

4.4(vi) - Morphometric Analysis.

Selected morphometric data has been collected from A.pallipes obtained by all three sampling methods in order

to establish the relationship between several body characteristics. This information is of use for:-

- (i) Comparison with published work utilising measurements other than C.L;
- (ii) Comparison with similar data from other sites;
- (iii) Assessment of the size at which A.pallipes mature;
- (iv) The calculation of estimates of standing crop and yield;
- (v) The biometric definition of the body-form of A.pallipes.

Results of the analysis of this data are listed and discussed fully elsewhere (see Chapter 6).

A common method for determining the success of fish populations, in terms of body size, is the condition factor (Ricker, 1975). This relationship appears not to have been used for the comparison of geographically separate populations of crayfish or crayfish populations in dissimilar habitats. Changes in condition factor (C.F.) within the same population reflect seasonal and life-history variations so, for example, ovigerous females have C.F. values that differ significantly from those of non-ovigerous females ($p < 0.01$). The C.F. values for males and females are also significantly different ($p < 0.01$) within this population at the same time of year. This confirms that males are heavier for their length than females due to the possession of proportionally larger chelae.

4.4(vii) - Adult productivity.

By converting the mean C.L. of trappable crayfish to wet weight, using equations (18) and (19) Table 6.3, and then multiplying this by the annual catch of crayfish, used to calculate the mean, an estimate of potential yield can be calculated. These figures are tabulated below:-

		Mean C.L.	Calculated mean wet weight (g.)	Catch	Yield (kg)	Popn estimate	Biomass estimate
1979	♂	44.1	26.9	30	0.81	-	-
	♀	37.2	15.2	39	0.59	-	-
1980	♂	44.5	27.7	331	9.2)	-	80 Kg.
	♀	28.5	17.0	219	3.7)	5,806	49 Kg.
1981	♂	42.3	23.6	136	3.2)	-	24 Kg.
	♀	36.9	14.8	122	1.8)	2,049	15 Kg.
1982	♂	36.6	14.96	178	2.7	-	-
	♀	33.6	10.9	64	0.7	-	-

As little reliance can be placed on the calculated population estimates extrapolation to approximate standing crop figures are equally unreliable and range from 39.0 kg, 1981, to 129 kg, 1980. As no accurate estimate of the data to which these estimates relate can be made comparison with published values, such as 176.6 kg.ha⁻¹. (Brown & Bowler, 1979) and 350 - 400 kg.ha⁻¹. (Arrignon & Magne, 1979) is not possible. As it is not possible to calculate productivity from the data available no comparison can be made with published production : biomass ratios of 0.42 for A.pallipes (Brown & Bowler, 1979) or 0.79 for A.astacus (Cukerzis, 1973).

4.4(viii) - Trophic position.

Information concerning the position of A.pallipes in the food web is scant. It is reported to be preyed upon by a range of fish, animals and birds (see Introduction: Section A) and is omnivorous in its own feeding habits (Moriarty, 1973; Brown, 1979; Pratten, 1980; Rhodes, 1980). The trophic position of A.pallipes was not systematically studied during the course of this project but as so much of the reported information concerning the biology of A.pallipes is anecdotal the small amount of data that has been collected in this study has been reported. That

crayfish are omnivorous, taking macrophytes and detritus but with a preference for animal material, has also been found in other studies (Moriarty, 1973; Brown, 1979; Pratten, 1980; Rhodes, 1980; Watson, unpubld).

An assessment of the trophic position of crayfish should play an important part in the evaluation of a management strategy for A.pallipes and the potential of crayfish as environmental controlling agents is poorly understood. Trophic studies should go some way towards elucidating this role (Reynolds, 1979). Results from the macroinvertebrate samples collected during this study provide an indication of potential food sources and suggest that a wide variety of organisms are available for consumption by crayfish in Clattercote Reservoir. Only invertebrate diversity can be considered in this instance as no attempt was made to assess abundance. Diversity was greatest in June, 1981, see Table 4.8, at a time when water levels were greatly reduced, Figure 4.3, and lowest in December, 1981, when the water level was at a maximum. This suggests that the macroinvertebrate fauna along the dam wall is affected by the periodic reductions in water level and may be partly restricted to the areas permanently covered by water. It may also reflect sampling efficiency.

The examination of a small number of stomachs and identification of their contents suggests that the adult A.pallipes in Clattercote Reservoir are largely detritus and macrophyte consumers, with few identifiable invertebrate remains being found. Reports listing the stomach contents of A.pallipes in Durham include the aquatic moss Fontinalis antipyretica, diatoms, terrestrial leaf litter, Potamogeton crispus, arthropod limbs and inorganic material in the form of sand or silt (Brown, 1979). Elsewhere reports suggest that they are predominantly carnivorous (Hynes, 1970; Clegg, 1974) mostly consuming gastropods but this was found not to be so in Irish investigations (Reynolds, 1979) where Hydrobia sp. and Planorbis sp. were never accepted by

A.pallipes in laboratory tests. Laboratory investigations have shown A.pallipes to readily consume various macrophyte species, such as Fontinalis antipyretica, Elodea canadensis, Myriophyllum spicatum, Potamogeton crispus and Rorippa sp. (Brown, 1979) and the majority of forty-six food items offered in another study were consumed (Reynolds, 1979). This latter study showed that of deciduous leaf matter beech, Fagus sylvatica, was rarely taken, in contrast to elm, Ulmus procera, and maple/sycamore, Acer sp. and concluded that immunological identification would be the most satisfactory way of analysing gut contents. The current results confirm these published findings and further consolidate the suggestion that A.pallipes are largely omnivorous and consume large quantities of detrital material.

4.4(ix) - Incubation Time and Life-History.

Further information of potential use in the management of freshwater crayfish stocks is the data presented regarding incubation time. This period is known to be eight to nine months in duration in Midland populations of A.pallipes, with hatching occurring in May or June (Rhodes, 1981) and nine to ten months in duration in Durham, near to the recorded northern limit of this species in the U.K., with hatching taking place early in August (Brown & Brewis, 1979). If crayfish populations are to be managed or 'farmed' it seems likely that a reduction of the natural incubation time will be desirable (Rhodes, 1981). Information concerning this time span in their natural environment will enable the calculation of temperature requirements for artificial incubation to be made. Indeed water temperature is a major factor, together with day length, influencing the timing of the life-cycle (Brown, 1979) and growth of A.pallipes is generally limited to the period May to October when water temperatures are in excess of 10°C. (Pratten, 1980). In Durham the maximum temperature recorded was 17.2°C, in mid-September (Brown, 1979), and in the River Ouse, Bucks., it was 24.0°C, in late September

(Pratten, 1980). The highest surface temperature recorded in Clattercote Reservoir during this study was 21.0°C. on 8.6.82. (in < 1.0 m. of water).

Incubation time, in terms of degree-days, was estimated to be $1209 \pm 88^\circ\text{d}$ for A.pallipes in Clattercote Reservoir. This figure is very low compared to the 1538°d. reported for the incubation of P.leniusculus eggs at 7°C in an experimental system (Mason, 1974, 1977) although at 18°C only 900°d were required for incubation. No comparable data is available for other natural populations of A.pallipes. The low estimate calculated during this study is thought to be due either to the location of the recording device, in the bottom sediment, or to thermal stratification of the water-body in spring, 1982. Recorded bottom temperature, on the chart recorder, did not rise above 10°C, Figure 4.13, during the period 4.11.81 to 13.6.82 whereas surface temperatures during this time reached a measured maximum of 21.0°C, (see Table 4.1). Further investigation would be required to confirm the estimate obtained or to determine the reason for it being an underestimate.

The life-history information collected from Clattercote Reservoir, Figure 4.14, shows that A.pallipes in this population mate and lay eggs earlier than those in Durham (Brown, 1979) but at a similar time to other populations in the U.K., Ireland and Spain (Thomas & Ingle, 1971; Moriarty, 1973; Ingle, 1977; Cuellar & Coll, 1979; Pratten, 1980; Rhodes, 1980). The eggs hatch significantly earlier than those in Durham (Brown, 1979), at similar times to those elsewhere in the southern U.K. and Ireland (Thomas & Ingle, 1971; Moriarty, 1973; Ingle, 1977; Pratten, 1980; Rhodes, 1980) but later than those in Spain (Cuellar & Coll, 1979). Published laying and hatching times are listed in Table 4.15 for comparison. The eggs of P.leniusculus in the Thames Catchment have been observed to hatch in early May (Chapter 8) giving this species a longer first growing season than A.pallipes in this region.

TABLE 4.15 : INFORMATION CONCERNING THE INCUBATION PERIOD OF CRAYFISH
IN THE U.K. (PUBLISHED DATA).

Species	Location	Mate	Lay	Hatch	Incubation Time (approx.)	Reference
<u>A.pallipes</u>	Thames Catchment	Late Sept.	Mid Oct.	1-3 to 18-20 June	7-8 months	This study
"	Midlands (Notts. + Leics.)	Late Sept.	Mid Oct.	May to June	9 months	Rhodes + Holdich, 1982
"	Durham	12 Oct. to 7 Nov.	12-20 Nov.	24 July to 12 August	9 months	Brown, 1979
"	Bucks.	10 to 14 Oct.		9 to 26 June	7 months	Pratten, 1980
"	Kent	24 Sept. to 31 Oct.	by 8 Nov.	8 to 21 June	7 months	Ingle + Thomas, 1974
"	L. Lea, Ireland	October	November	June/July	7-8 months	Watson, unpubl.
"	White Lake, Ireland	18 Sept.	November	June	7 months	Moriarty, 1973
<u>P.leniusculus</u>	Thames Catchment	Late Sept.	3 Oct.	Early May	7 months	This study. (Chapter 9)

Variations in the timing of the stages of the moult and reproductive cycles have been shown to be small over a three year period (Brown, 1979). In Durham moulting extended from late June to mid-September, 80 - 96 days (Brown & Bowler, 1977), in the River Ouse from June to late September, 120 days (Pratten, 1980) and in Clattercote Reservoir from at least May to September. A similar growth season has been reported from the River Darent, Kent, where moulting commenced in Early May and extended to October (Thomas & Ingle, 1971).

4.4(x) - Parasites, Diseases and Damage.

Overall 1.8% of A.pallipes of both sexes in Clattercote Reservoir were found by visual inspection to be infected with the microsporidian endoparasite Thelohania contejeani and this ranged seasonally from 0% to 8.8% (see Table 4.11). The occurrence of this parasite, which is density dependent and has a direct life-cycle (Brown & Bowler, 1977), is discussed more fully in Chapter 6. It has been shown however that although only a small percentage of an A.pallipes population are past the stage at which infection can be diagnosed by eye (Brown, 1979), that is age 3+ and upwards (O'Keefe, in press), a further 1.3% can be diagnosed as infected by microscopic examination of muscle tissue (O'Keefe, in press).

The occurrence of T.contejeani in Clattercote Reservoir crayfish is low compared with that reported from some other populations, as listed below:-

Durham - overall	6.54% (♂); 6.59% (♀)	(Brown, 1979)
River Wye, Gwent	3.4%	(Lilley, 1977)
White Lake, Ireland	0.7%) (O'Keefe, in press)
Brittas River, Ireland	1.2%	
E.Germany	30%	(Schäperclaus, 1954)
Clattercote Reservoir - overall	1.8%	(This study)
Thames Catchment - overall	0.64% - 8.8%	(This study)

although no account was taken of seasonality in these other studies.

Trap catches probably underestimate the incidence of this parasite as affected individuals are generally less mobile. Conversely hand-caught samples are likely to overestimate its abundance, although it has been reported that there is no major bias in the catchability, by hand, of parasitised crayfish, (Brown, 1979). Reports that parasitism may influence the likelihood of crayfish entering traps (Bowler in Unestam, 1973) are borne out by this and another study (O'Keefe, in press) and significantly more diseased crayfish ($p < 0.05$) were taken by hand collection than by other methods. This is due to crayfish having an 'active' role in trap capture but a more 'passive' one in hand collection (Brown, 1979). The mean figure for the incidence of T.contejeani in hand caught A.pallipes in Clattercote Reservoir, 1.4% overall, compares well with the 3.4% reported elsewhere for hand caught samples of crayfish (Lilley, 1977). The apparently seasonal nature of visible parasitism in the current study is contrary to reports that incidence of the parasite is not seasonal in a Durham population (Brown, 1979). Annual variations in incidence of T.contejeani may also occur, see Table 4.11, although this may be more closely correlated with sampling methods than levels of the disease.

No evidence was found for the occurrence of systemic fungal diseases or the parasitic annelid Branchiobdella astaci in specimens of A.pallipes obtained from Clattercote Reservoir (see Chapter 6). Assumed 'burn-spot' disease, caused by the fungus Fusarium sp. (Vey & Vago, 1973; Vey, et al, 1975), was intermittently recorded and ranged from 0% to 4% in incidence in samples of crayfish collected by all three sampling methods. No confirmation of the causative organism was attempted.

The incidence of A.pallipes with damaged or regenerating chelae, of importance if crayfish populations are to be managed with a view to harvesting for the table market, was recorded on 21 sampling occasions, see Table 4.12. There was no apparent seasonal variation in numbers of damaged crayfish of either sex or between crayfish collected by the three sampling methods; although this was not tested statistically. The overall mean number of damaged males (6.5%) was greater than the overall number of damaged females (4.9%) although this difference is not statistically significant ($p > 0.05$).

CHAPTER 5. AN INVESTIGATION TO ASSESS THE IMPACT OF RIVER
ENGINEERING WORKS ON POPULATIONS OF THE FRESHWATER
CRAYFISH A.PALLIPES.

5.1 Introduction.

5.1(i) - General Considerations.

In England and Wales an estimated 100,000 hectares of land were drained during 1978-1979 compared with 51,000 hectares in 1968-1969 (Mason, 1981). In fact most of the lowland river systems in the U.K. have been affected in some way by engineering and river management works intended to increase their efficiency as drainage channels. Modifications include the dredging and widening of streams and rivers to decrease water levels, weed cutting, channel straightening and the clearance of bankside vegetation. All of these 'improvements' may cause severe long-term changes in aquatic and bankside communities (Swales, 1981).

Regional Water Authorities in England and Wales have a statutory duty generally to supervise all matters relating to drainage in their areas and have control powers under the Land Drainage Act, 1976. They are also responsible for the enforcement and administration of fisheries and water quality regulations under the Salmon and Freshwater Fisheries Act, 1975, the Water Act, 1973 and the Control of Pollution Act, 1974, and must have due regard for nature conservation interests under the Wildlife and Countryside Act, 1981 (W.S.A.C. 1978).

Drainage schemes are primarily carried out in order to control and maintain the water table in agricultural land and to effect the disposal of surface water runoff and effluents without the creation of flooding problems in agricultural or urban areas. Increased quantities of runoff, from more efficient field drainage and the expansion of built-up areas, have necessitated major river modifications

to improve the ability of the channel to contain increased flows of water (W.S.A.C. 1978). The progressive urbanisation of the lower Lee Valley (see Figure 3.1), with the consequent increased runoff, combined with extensive development of parts of the river flood-plain, has created an area with typical urban flooding problems. The major land drainage improvement works in recent years have concentrated on the improvement of the trunk flood route of the River Lee system downstream of Hertford. These have effected an improved land drainage system upstream to the confluences of the major tributaries (Anon., 1978).

The majority of investigations into long-term changes in aquatic ecosystems, caused by river engineering schemes, have been concerned with the impact that such schemes have on the fish community (Swales, 1981). This is principally due to the economic and social importance of angling; in addition fish are generally considered to be good indicators of river quality as they are dependent on both the physical and chemical characteristics of the environment. The physical alteration of rivers can therefore be used as a fishery management tool with the purpose of providing environmental conditions which are more favourable for the survival, growth and reproduction of fish. Such work is usually carried out to mitigate the adverse effects of human disturbances on fish communities (Swales & O'Hara, 1980) and, as will be shown, could equally be applied to habitat enhancement for other organisms, such as freshwater crayfish.

The preferred habitat for crayfish, such as A.pallipes, also contains specific physical characteristics concerning the availability of refugia and these benthic organisms are perhaps more dependent on the physical nature of the habitat than are the majority of freshwater fish species. Few studies, however, have examined the effects of land drainage programmes on aquatic macroinvertebrate communities (e.g. Pearson & Jones, 1975) and there is scant published information concerning the effects of engineering or drainage

works on A.pallipes (e.g. McCarthy, 1977). The reduced distribution of the crayfish A.astacus in Finland, Hungary, Poland and Holland and of A.leptodactylus and O.limosus in Poland (Kossakowski, 1973; Westman, 1973, 1975; Geelen, 1975; Westman & Pursainen, 1982) has been attributed to disease and pollution and to physical effects such as canalisation, dredging and flow regulation and the consequent deterioration or destruction of suitable habitat (Kossakowski, 1973). Similarly the diminished distribution of A.pallipes in Spain has been attributed to pollution, river regulation and canalisation (Westman & Pursainen, 1982) and to overfishing, pollution, river regulation and fungal disease (Habsburgo-Lorena, 1979).

Studies aimed specifically at evaluating the impact of engineering works on crayfish are few and generalisations such as "the decrease and in some cases the total disappearance of crayfish is due, in part, to dredging" (Cuellar & Coll, 1979) are common. Those studies that offer more detailed evidence for the effects of land drainage schemes concentrate on examining the impact of dredging. In Finland it was concluded that the disappearance of A.astacus from the River Siikajoki was as a result of dredging (Niemi, 1977) and in Eire A.pallipes did not recolonise the Trimblestown River up to 20 months after dredging despite being abundant previously (McCarthy, 1977). Conversely arterial drainage of the Shannon and Boyne systems, also in Eire, has not eradicated the crayfish, although there is no information on pre-drainage stock levels (Reynolds, 1979). The regulation of river discharges in the Ukraine, e.g. the Kakhova Dam, have been reported to have resulted in increased stocks of A.leptodactylus (Brodsky, 1975). In the past most attention has been directed towards assessing the impact of river pollution on aquatic communities. However, as an increase in scale during recent years of not only land drainage works but also river regulation, abstraction and impoundment (Swales, 1981), the importance to river communities of the physical aspects of the environment such as flow, depth,

substrate type, etc., is now being studied more intensively.

In addition to the construction of new flood alleviation structures Water Authorities undertake programmes of routine maintenance to ensure that watercourses remain efficient as drainage channels, free from obstructions and impediments to the flow. Such routine maintenance, in addition to the removal of isolated obstructions such as fallen trees, generally consists of the periodic removal of silt deposits ('sludging') and excessive aquatic or bankside plant growth. It may or may not follow guidelines produced by the relevant Water Authority (e.g. Thames Water, 1974, 1983; Wessex Water, 1974). Weed control programmes, carried out by the Water Authority, land owner or local fishery interests, may often be indiscriminate and perhaps excessive, frequently removing all vegetation from a large area of river (Swales, 1981). The impact of such large scale weed clearances on the animal life may be severe; macroinvertebrates, including A.pallipes (Ellis, pers comm), may be removed in large numbers along with the cut weed, whilst both fish and invertebrates may be affected by the loss of cover and food organisms moving away.

A.pallipes is one of the organisms that is likely to be particularly affected by the creation of smooth banks and river beds. Generally being a nocturnal, benthic animal A.pallipes is little seen but is now known to be quite abundant in many British water bodies where the water is hard and unpolluted and where there is a suitable physical habitat (Jay & Holdich, 1981; see Chapter 3). In the Thames Catchment A.pallipes has been recorded from all the major subcatchments (see Chapter 3). Their requirement for an excess of refugia results in crayfish being most commonly found in situations containing ample cover in the form of stones, rocks, eroded masonry, macrophytes, tree roots and even rubbish.

It is clear, then, that certain engineering procedures when carried out in areas inhabited by A.pallipes have the

potential for devastating crayfish populations either directly or by altering the environment to render an area uninhabitable. The recovery of rivers damaged by drainage works can be a very long process, often measured in decades, although the process can be artificially accelerated using habitat improvement structures (Swales & O'Hara, 1980).

This study aims firstly to investigate the rate of colonisation of a new weir basin by A.pallipes from adjacent areas. Secondly an attempt has been made to assess the impact of routine maintenance dredging on a population of A.pallipes. Although the site investigated during the second part of this study was not considered to be typical crayfish habitat (see Chapter 3) A.pallipes were found to be very abundant when dredging commenced. A preliminary evaluation was also made of a method by which the direct impact of dredging, in terms of numbers of individual crayfish removed from the watercourse, could be alleviated.

5.1(ii) - Study Site - Ware Lock.

The principal site investigated during this study of the impact of river engineering works on populations of A.pallipes was Ware Lock on the River Lee at Ware in Hertfordshire (NGR : TL352143), see Figure 5.1. The River Lee at this point, some 45.57 km. from its confluence with the River Thames, is an average of 16.0 m. wide and 2.45m. deep, although prior to dredging approximately 1.0 m. of this was silt. Maximum daily flow (1 : 10 years) is 30 - 40 cumecs (Haunt, pers comm). Major flooding occurred in the area in 1947 and 1968, with minor floods occurring in other years (Anon., 1978) so in 1977 a new relief channel and weir was constructed to bypass the lock and existing weirs at 'Allenbury's' (NGR : TL353143) and the river both upstream and downstream of Ware Lock was widened and regraded. Some 50% of the mean dry weather flow of $2.0 - 2.5 \text{ m}^3 \text{ sec}^{-1}$ (July) is estimated to pass through the new weir system (Haunt, pers comm). This increases to 95 - 100% in times of

high flow.

The weir itself consists of a syphon and a conventional spillway, see Figures 5.1 & 5.2. The stilling basin, also newly constructed, has a surface area of approximately 1,220 m² (see 5.2(i)) and a minimum designed depth of 2.31 m. The floor of the basin is protected from scour by a minimum of 225 mm. of crushed granite; the north bank consists of 9.0 m. concrete piles whilst the south bank is protected by 'Weldmesh' gabions filled with granite rubble. A plan of the lock area, together with cross-sections and a longitudinal section, are shown in Figure 5.2 (TWA., Lea Division, 1982).

Chemical water quality data for the River Lee at this point (TWA Lea and Northern Divisions) are listed in Table 5.1 and result in a N.W.C. Classification of IB (see Appendix 3). Those parameters considered to be of major importance to crayfish (Laurent, 1980) gave the following mean values:

pH	= 7.98	n = 333
Total Hardness	= 322.87 mg.l ⁻¹ CaCO ₃	n = 19
Alkalinity	= 210.79 mg.l ⁻¹ CaCO ₃	n = 23

5.1(iii) - Study Site - River Beane at Hertford.

In order to assess the impact of routine maintenance dredging on a population of A.pallipes a site on the River Beane at Hertford was investigated. During the overall period of this study (i.e 1979 - 1982) this site was the only one found at which crayfish were present in consistently large numbers and which could be investigated whilst dredging was in progress.

The site comprises a short (c. 50 m.) reach of the River Beane on the northern outskirts of Hertford (NGR : TL317133), see Figure 5.3. The river at this point, 1.75 km. upstream of the confluence with the River Lee, was some 7.0 m. wide and an average of 1.0 m. deep prior to dredging. The substratum consists of fine silt and sand overlying clay.

Figure 5.1 Plan of Ware Lock area - showing location
of the new flood relief weir, etc.

Showing outline of new weir, syphon & stilling basin in relation to previous features.

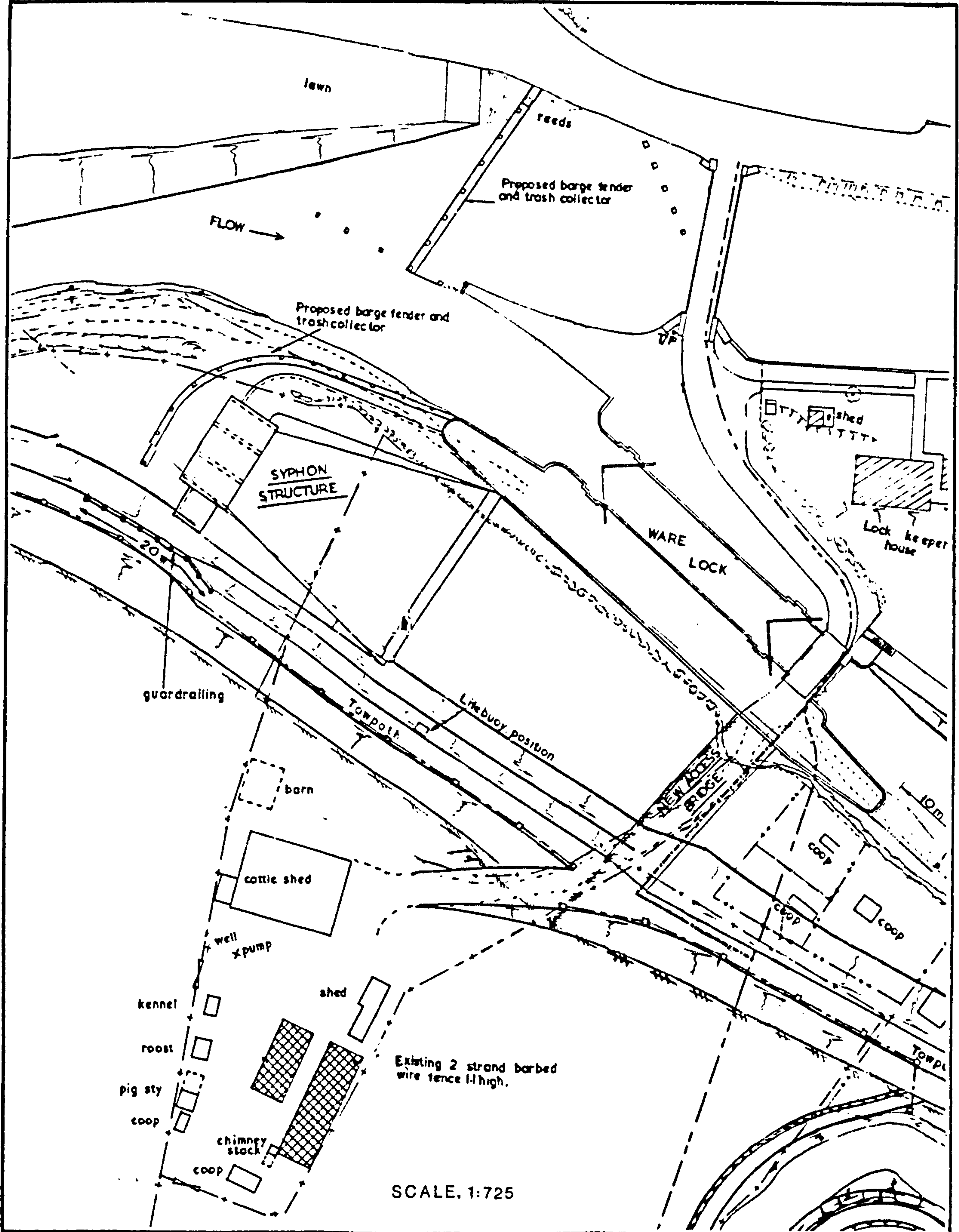
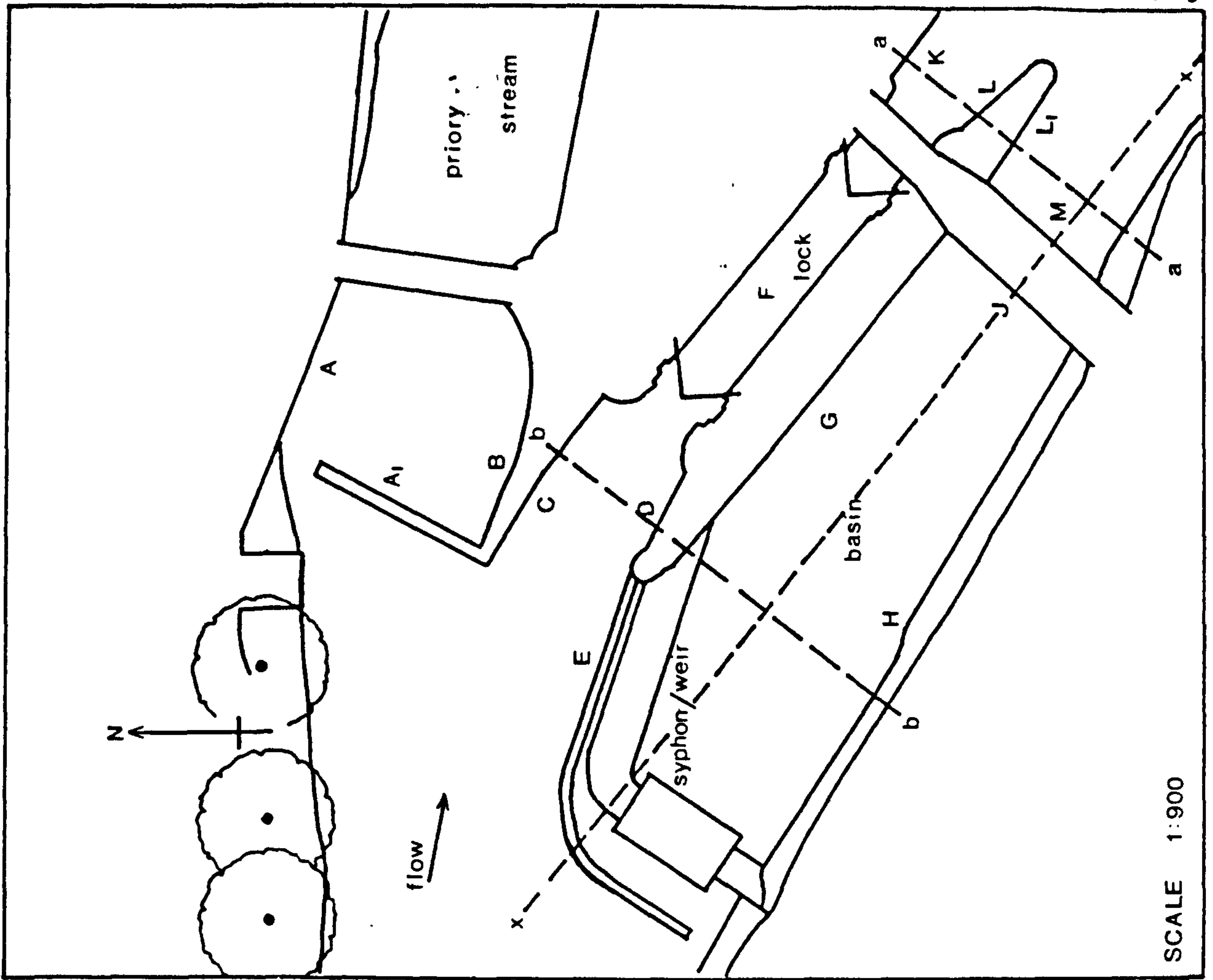


Figure 5.2

(i) Plan of Ware Lock showing trapping zones, and location of sections (Fig.5.2ii)



(ii) Transverse and longitudinal sections of Ware Lock after construction of relief weir, etc.

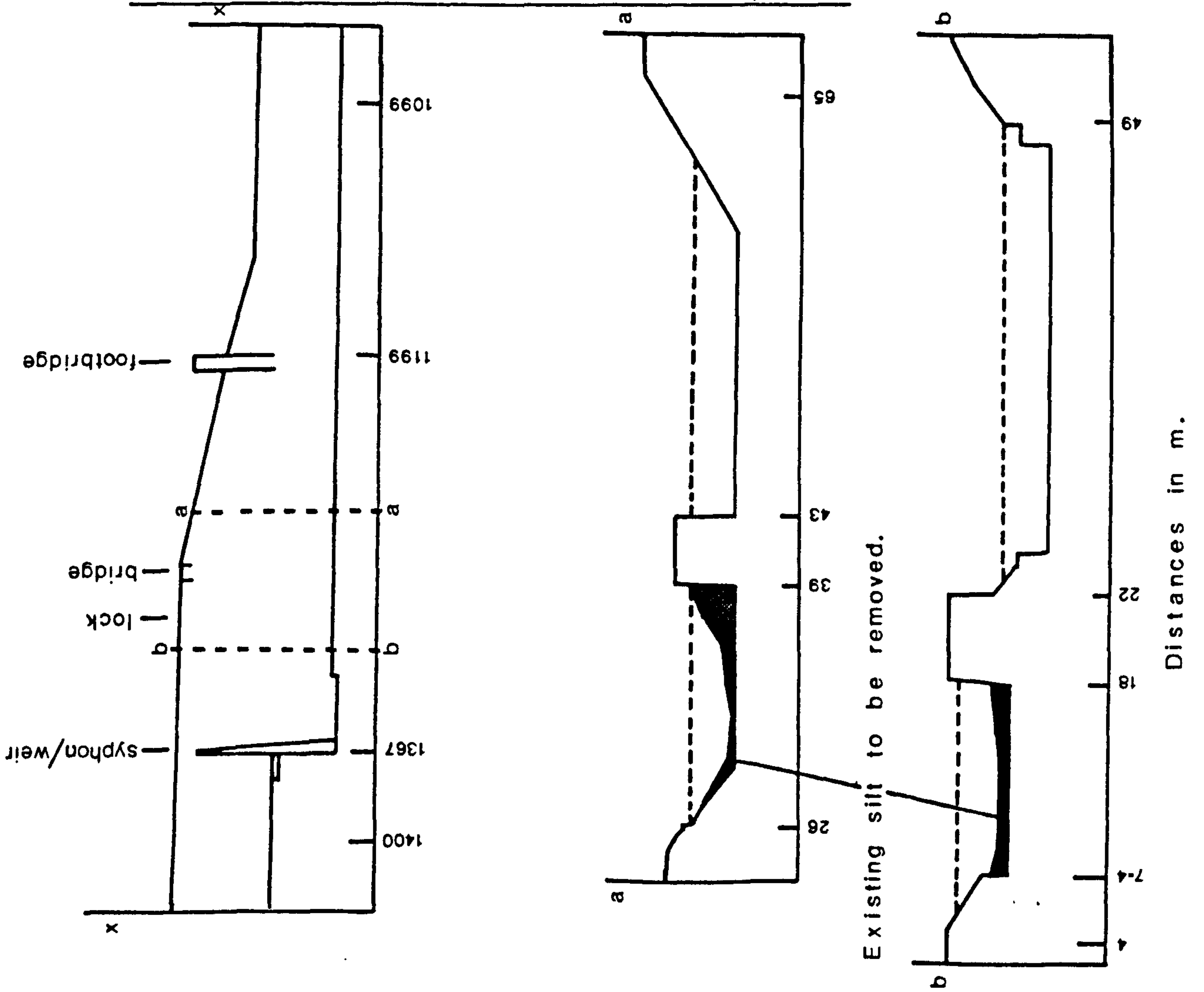


TABLE 5.1 : CHEMICAL DATA. R. LEE, WARE LOCK: 1978 - 1982.

	Mean	Range	n.
pH	7.98	6.8 - 8.54	333
S.S.	31.05	1.2 - 148	23
B.O.D. (ATU)	2.07	1.0 - 10	320
Temp (° C.)	11.18	1.0 - 22.0	322
D.O.	10.39	5.9 - 16.8	314
% Satn.	94.29	60 - 190	313
Amm.N.	0.136	0.05 - 1.39	333
Unionised Amm.	0.001	0.001 - 0.017	329
Oxidised N.	8.32	45 - 13.7	326
Cl.	42.60	14 - 125	319
SO ₄ .	44.79	10 - 85	155
SiO ₂ .	11.36	2 - 17.2	154
P.	0.84	0.07 - 7.66	319
Hardness (as CaCO ₃ .)	322.9	295.4 - 389.4	19
Alkalinity (as CaCO ₃ .)	210.8	146 - 294	23
Ca.	122.4	112 - 150	20
Mg.	3.71	1.9 - 5.0	20
Na.	26.99	18 - 38	20
K.	4.11	3.4 - 5.7	20
Zn.	0.05	0.01 - 0.24	20
Ni. **	0.02	0.03 - 0.09	20
Cu. *	0.001	0.01 - 0.01	20
Cd.	0.001	0.001 - 0.01	16
γB.H.C.	0.015	0.005 - 0.027	19
Chlorophyll a (Methanol. µgl. ⁻¹)	4.38	0.2 - 22.84	44

N.B. Values in mg.l.⁻¹ except γ.

* 31.3.78 - 26.9.80 only.

** 31.3.81 - 18.6.82 only.

Chemical water quality data from the nearest regular sampling point on the River Beane, some 50 m. downstream of the study site (NGR : TL313130) are listed in Table 5.2 (TWA Northern Division) and result in a N.W.C. Classification of IB (see Appendix 3). pH, the parameter considered to be of primary importance to crayfish (Laurent, 1980), gave the following mean value:

$$\text{pH} = 7.79 \quad n = 29$$

The surrounding land is typically agricultural, primarily coarse grazing, but with increasing urban influences. Aquatic macrophytes consist of both submerged and emergent types; the former being dominated by starwort, Callitriche sp., with some water crowfoot, Ranunculus sp. also present; the latter group consists mainly of reed sweet grass, Glyceria maxima, on the east bank and extensive stands of sedges, Carex sp., and the common reed, Phragmites communis, on the west bank.

5.2. Methods.

5.2(i) - Ware Lock.

In order to monitor the movement of A. pallipes into the new stilling basin on the River Lee, downstream of Ware weir, overnight trapping was carried out during 1979 and 1980 (see Chapter 2). Only crayfish of C.L. >30 mm. (approx.) were sampled by this method. Crayfish were marked according to the position (zone) in the basin, lock and adjacent areas from which they were captured, see Figure 5.2, using a hot branding technique (Abrahamsson, 1965; Chapter 2). Marked individuals were sexed, measured (C.L. in mm.) and their reproductive condition recorded, if possible, before being returned to their zone of capture. Patterns of movement were established upon subsequent recapture by examination of the zone/date specific marks.

Thus it was determined that a large and apparently

TABLE 5.2 : CHEMICAL DATA. R. BEANE, HERTFORD.
30.4.80 - 1.5.81.

	Mean	Range		n.
∞ pH	7.80	7.62	- 8.14	29
B.O.D. (ATU)	1.4	1.0	- 2.7	29
∞ Temp. (°C.)	9.39	4.0	- 15.5	29
D.O.	8.92	6.6	- 11.2	29
∞ % satn. -	77.09	60	- 96	29
Ammoniacal N.	0.052	0.05	- 0.3	29
Unionised Ammonia	0	0.002	- 0.002	29
Oxidised Nitrate	5.196	4.0	- 7.3	29
Nitrite	0.003	0.005	- 0.05	29
Chloride (Cl.)	32.45	14	- 115	29
Sulphate (SO ₄ .)	27.35	12	- 90	23
Silica (SiO ₂ .)	12.82	7.5	- 17.8	23
Orthophosphate (P.)	0.062	0.07	- 0.56	29
Nitrate	5.19	4.0	- 7.3	29

N.B. Values as mg.l.⁻¹ except ∞.

stable population of A.pallipes had become established in the basin. The size of the crayfish population in the stilling basin was subsequently estimated, in 1980 and 1981, using mark-recapture techniques (see Chapter 2), employing the formulae of Petersen and Bailey (Ricker, 1975). All sampling occasions, together with the number of traps used and the catch per trap per night, are listed in Table 5.3.

Recording of the recapture zone of marked individuals permitted the degree of movement of marked crayfish, from their zone of original capture, to be established. Traps were set in zones A to M (see Figure 5.2) on 5 occasions during the period August, 1979 to June, 1980 to monitor crayfish movements.

The area of the basin and the theoretical area trapped, assuming that the traps acted as effective sampling units within a radius of <2.5m. (Westman, et al, 1979) were calculated. A plan of the basin (b) and ten 1.0 cm.² squares (s) of the same grade paper, each corresponding to an area of 1.0 m.², were weighed on an 'Oertling V20' analytical balance. The surface area of the basin was calculated as $b/(\bar{s})$ m.².

5.2(ii) - River Beane at Hertford.

A single investigation has been carried out to assess the impact of routine dredging operations on a natural population of the native crayfish A.pallipes. At the study site the maintenance operation being carried out consisted of the removal of the marginal macrophytes from the east bank and the soft silt, detritus and plant material from the whole width of the river bed using a 'Hymac' excavator located on the east bank. The principal species comprising the affected marginal macrophyte community were G.maxima, Myosotis scorpioides and Mentha aquatica. The sludging operation was being carried out by a single bankside

TABLE 5.3 : CATCH DATA: WARE LOCK. 1979 - 1981.

Date	No. of Traps	♂	♀	Total	Catch. trap. ⁻¹ night. ⁻¹	Zones*
1. 8.79	28	26	30	56	2.00	A1,B,D,E,G,H,K
12.10.79	31	51	36	113	3.64	A1,B,D,E,G,H,K,J
24. 1.80	22	61	15	76	3.45	A1,B,D,G,H,J,K
3. 4.80	25	88	10	98	4.08	A1,B,D,G,H,J,K
18. 6.80	39	456	57	513	13.15	A1,B,C,D,F,G,H,J,K,L,L1,M
14. 9.80	40	200	162	362	9.05	G,H,J,M
16. 9.80	40	299	295	594	14.85	G,H,J,M
18. 9.80	40	222	236	458	11.45	G,H,J,M
3.10.80	6	79	93	172	28.67	G,H,J,M
2. 5.81	40	368	104	472	11.80	G,H,J,M
5. 5.81	40	210	69	279	6.97	G,H,J,M
8. 5.81	40	232	110	342	8.55	G,H,J,M

* see Figure 5.2

excavator with a bucket capacity of approximately 0.5 m.³ (i.e. 1.50m. x 0.6m. x 0.6m.).

The normal practice of the workman carrying out the maintenance dredging was to 'rinse' the material being removed by repeatedly dunking it in the water, thereby returning some of the crayfish to the river. To assess the efficacy of this procedure for preventing crayfish from being removed, and for reducing the number of crayfish removed from the river, single samples of 'rinsed' and 'unrinsed' material were examined, on 6.5.81, and all crayfish removed and sexed.

Subsequently three samples, each consisting of a single bucket load of 'unrinsed', dredged material were examined on 8.5.81. The material removed, comprising plant root masses, stems and detritus, was placed on a large plastic sheet by the excavator driver. Approximately thirty minutes was then spent, by two investigators, searching for and removing all crayfish by hand. A.pallipes from the three samples were retained separately and were subsequently counted, sexed and measured (C.L. in mm).

5.3. Results.

5.3(i) - Ware Lock.

During the initial stages of this study, i.e. in 1979 and early 1980, trapping was carried out in all zones (see Figure 5.2) at Ware Lock, and the zone in which marked crayfish were recaptured was recorded. The results from this initial survey are summarised in Table 5.4. After June 1980 trapping was restricted to the weir basin, zones G, H, J and M (Figure 5.2). The results obtained from this part of the investigation are summarised in Table 5.3.

Once it had been established that the majority of A.pallipes in the stilling basin were resident there and that

migrations into the basin were few, the size of the population in the basin was estimated using mark-recapture techniques, in September 1980 and May 1981. The mark-recapture data is listed in Table 5.5, and has been used to estimate the population size using the methods of Petersen and Bailey (Ricker, 1975) with the following results:

	September 1980	May 1981
Mean adjusted Petersen estimate (\pm S.E.)	1575 \pm 122	1833 \pm 217
Bailey's deterministic model (\pm S.E.)	1389 \pm 205	1579 \pm 342

The extent of remixing of marked individuals was checked by comparing the ratio of marked to unmarked crayfish in subsequent samples in 1980 and 1981 using χ^2 (see Chapter 2). Satisfactory mixing ($p > 0.1$) was shown to have occurred.

The figures used in the calculation of the area of the stilling basin are shown in Table 5.6. The forty traps used were estimated to sample crayfish from 46% of the total area of the basin, assuming an effective trap radius of $< 2.5\text{m}$. (Westman, et al, 1979). The physical characteristics of the basin did not permit the even distribution of traps, which were concentrated at the margins. The above population estimates are considered to refer to the crayfish inhabiting an area of approximately 566 m^2 and figures for the trappable population of A.pallipes (C.L. $> 30\text{mm}$) adjusted for the whole area of the basin would be:

	September 1980	May 1981
Petersen Method	3424	3985
Bailey Method:	3020	3433

These estimates suggest an overall density of adult A.pallipes of 2.5 to 3.3 m^{-2} , assuming that the adult crayfish are randomly distributed throughout the basin. To test this assumption three pairs of baited traps were

TABLE 5.4 : SUMMARY OF CATCH DATA FOR A.PALLIPES. WARE LOCK.

1979 - 1980

Date	Total Catch	Recaptures Same Zone	Moved to Adjacent Zone	Moved more than one Zone	No.Traps	Catch.trap ⁻¹ night ⁻¹
1. 8.79	56	0	0	0	28	2.00
12.10.79	113	2	0	0	28	9.03
24. 1.80	76	2	-	-	23	3.0
3. 4.80	98	7	-	-	25	4.08
18. 6.80	513	18	8	3	39	13.15

TABLE 5.5 : SUMMARY OF MARK-RECAPTURE DATA: WARE LOCK. 1980-1981.

Date		Male	Female	Total
14.9.80	New marks (A)	200	162	362
16.9.80	New marks (B)	215	237	452
	Recaptures (A)	84	58	142
	Total caught	299	295	594
18.9.80	Recaptures (A)	52	47	99
	Recaptures (B)	64	69	133
	Total caught	222	236	458
2.5.81	New marks (A)	358	114	472
5.5.81	New marks (B)	149	52	201
	Recaptures (A)	61	17	78
	Total caught	210	69	279
8.5.81	Recaptures (A)	56	26	82
	Recaptures (B)	28	8	36
	Total caught	232	110	342

TABLE 5.6 : CALCULATION OF AREA OF STILLING BASIN, WARE LOCK.

Area determined using the weight of plan relevant parts,
Figure 5.2.

Scale 1:500, hence 1cm. \equiv 5.0m.

Mean weight of known area, 10 x 1 cm. sq. = 0.00819g. (n = 10)
 \equiv 25m²

Whole basin = 0.4003g.

$$\text{Basin Area} = \frac{0.4003 \times 25}{0.00819} = \underline{1221.9\text{m}^2}$$

Zones trapped = 0.1857g.

(Assumes trap radius = 5m.)

$$\text{Trap area} = \frac{0.1857 \times 25}{0.00819} = \underline{566.8\text{m}^2}$$

Area trapped = 46% of total basin area.

set on a transect across the basin on October 1st, 1980. The results, listed in Table 5.7, clearly show that crayfish distribution within the basin is not random.

The frequency and sex distribution of A.pallipes in all trap catches, are summarised in Table 5.3 and illustrated in Figure 5.4. Mean C.L. values for all samples are listed in Table 5.8.

5.3(ii) - River Beane at Hertford.

The numbers of A.pallipes removed from samples of material dredged from the river Beane, and hence directly affected by the dredging, are listed in Table 5.10. Size-frequency data for crayfish removed from the River Beane has been used to construct length-frequency histograms, Figure 5.5. The mean C.L. of each sex in each sample is listed in Table 5.11.

The length-weight and C.L. to total length information has been used to calculate the regression equations listed in Table 5.12 and illustrated in Figure 5.6.

5.4. Discussion.

5.4(i) - General Considerations.

In an attempt to assess the impact of river engineering works on populations of freshwater crayfish two aspects of such modifications to natural watercourses have been investigated. The rate of colonisation and habitat suitability of a new flow regulating structure have been examined and that this type of modification could prove to be of considerable positive benefit to crayfish populations has been shown. Conversely the effects of routine dredging on a site inhabited by A.pallipes has been assessed and shown to be potentially devastating to the crayfish population. The increasing pressure that is being placed on natural watercourses to act

Figure 5.4 Size distribution of *A. pallipes*
in all samples from Ware Lock.

1979 - 1981.

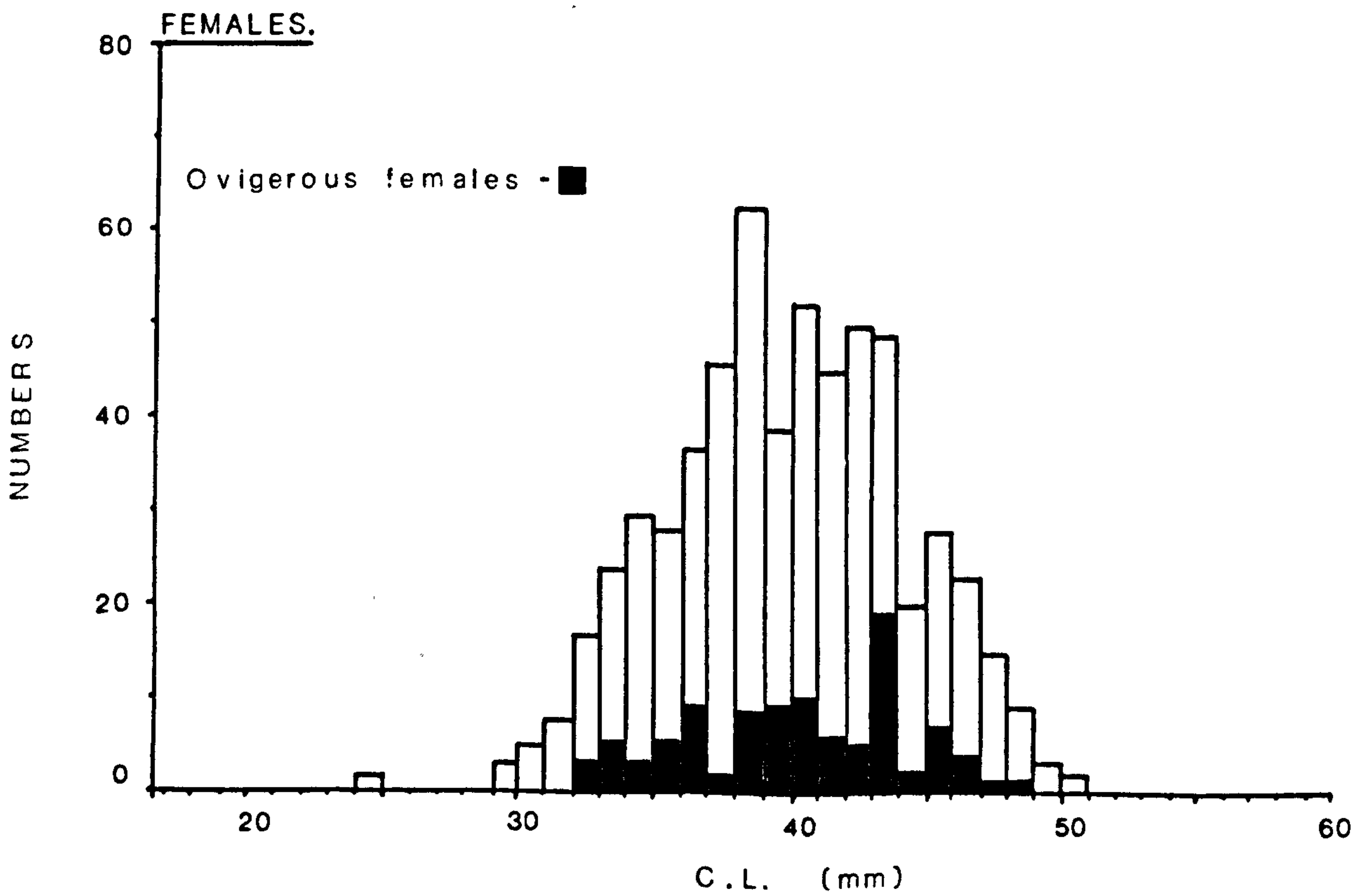
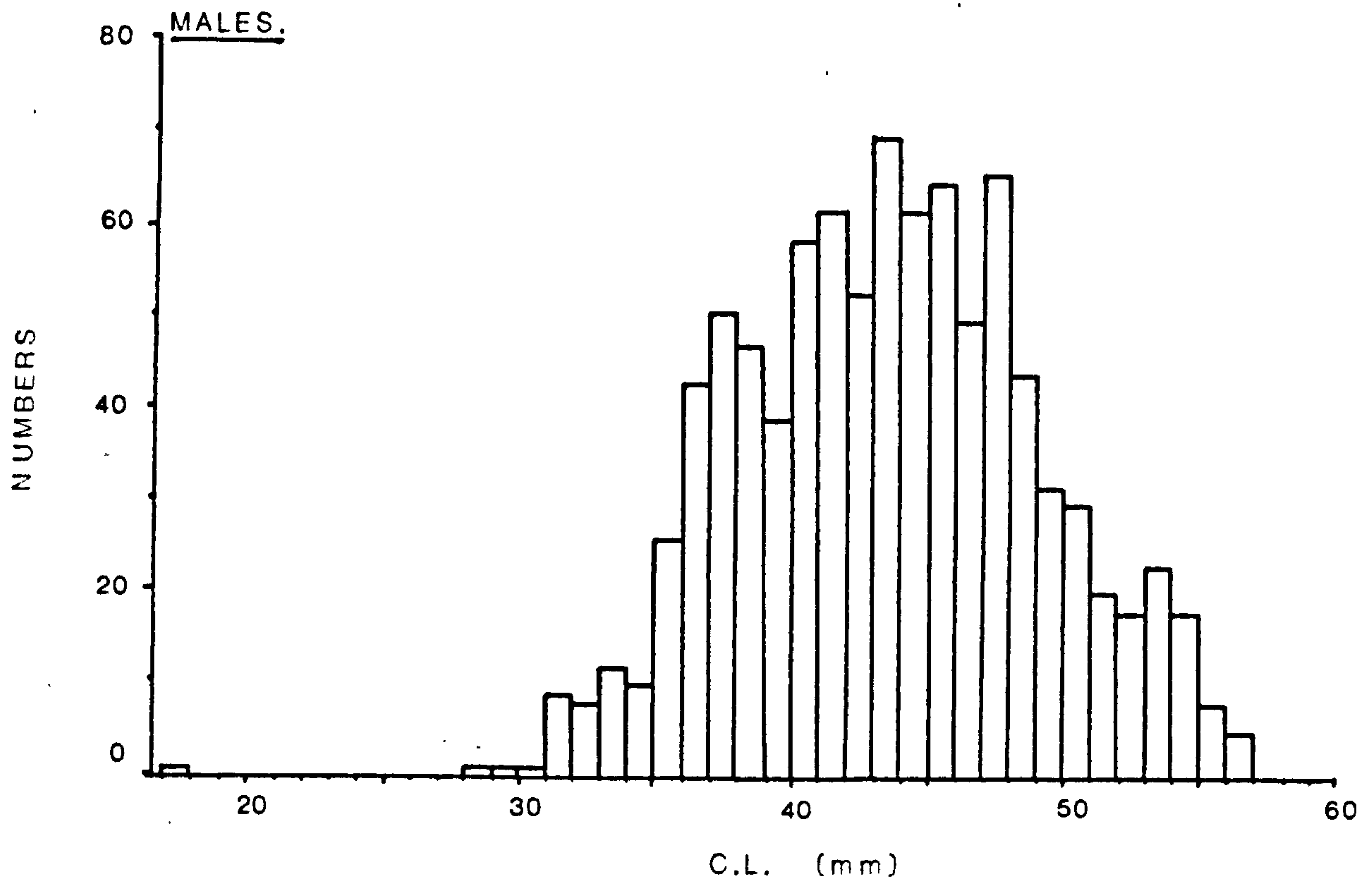


TABLE 5.7 : ASSESSMENT OF THE DISTRIBUTION OF A.PALLIPES IN THE STILLING BASIN AT WARE LOCK.

Location	Sex	Unmarked	Mark A	Mark B	Mark AB	Total
South Bank		18	5	7	4	34)
		21	4	8	3	36) 70
Centre		7	0	0	0	7)
		0	0	0	0	0) 7
North Bank		31	2	4	1	38)
		39	6	9	3	57) 95
Centre (Repeat)		15	1	5	1	22)
3.10.80		11	0	1	0	12) 34

TABLE 5.8 : MEAN C.L. VALUES FOR ALL SAMPLES. WARE LOCK. 1979 - 1981.

Date	Males				Females			
	Mean	S.D.	Range	n	Mean	S.D.	Range	n
8.79	44.9	8.47	17.5 - 55.3	26	41.3	5.07	31.8 - 50.0	30
10.79	47.5	5.72	28.0 - 56.5	51	41.9	3.12	33.0 - 48.0	62
1.80	46.1	4.43	37.0 - 56.0	61	41.0	3.11	35.0 - 48.0	15
4.80	44.6	4.87	31.0 - 55.0	88	41.1	6.21	24.0 - 47.5	10
6.80*	44.0	4.76	35.0 - 55.0	80	37.1	4.89	29.5 - 46.5	24
9.80*	43.2	4.90	29.0 - 55.0	330	39.2	3.86	29.0 - 50.0	307
5.81*	40.6	5.34	30.0 - 56.0	301	38.3	4.78	24.0 - 49.0	149

All C.L. values in (mm)

* subsample only measured.

N.B. Where >1 sample has been collected within 1 month total mean values have been calculated for that month: see Table 5.3.

TABLE 5.9 : INCIDENCE OF T.CONTEJEANI IN R. LEE AT WARE.
1979 - 1981.

Date	MALE			FEMALE			TOTAL	
	Total exd*	no. +ve	%	Total exd*	no. +ve	%	Total exd*	%
1. 8.79	26	0	0	30	0	0	56	0
12.10.79	51	0	0	62	0	0	113	0
24. 1.80	61	0	0	15	0	0	76	0
3. 4.80	88	0	0	10	0	0	98	0
18 .6.80	456	6	1.32	57	0	0	513	1.17
14. 9.80	200	2	1.00	162	0	0	362	0.55
16. 9.80	215	0	0	237	0	0	452	0
18. 9.80	106	0	0	120	0	0	226	0
2. 5.81	368	1	0.30	104	0	0	472	0.21
5. 5.81	210	0	0	69	1	1.45	279	0.36
8. 5.81	232	1	0.43	110	0	0	342	0.29

* Excluding recaptures

TABLE 5.10 : CRAYFISH REMOVED BY DREDGING . R. BEANE, HERTFORD.

Date		Male	Female	Juvenile*	Total	Mean
6.5.81	Unwashed sample	-	-	-	44	-
	Washed sample	-	-	-	28	-
8.5.81	Sample 1	36	48	3	87)	92
	Sample 2	54	74	9	137)	
	Sample 3	19	24	8	51)	

*The sex of juveniles can not easily be determined.

TABLE 5.11 : MEAN CL. OF A.PALLIPES DREDGED FROM R. BEANE

(8.5.81)

	Mean C.L. (mm)	S.D.	Range C.L. (mm)	n.
<u>SAMPLE I</u>				
♂	28.1	8.72	15.0 - 51.0	36
♀	26.5	7.27	17.0 - 47.5	26
♀B	39.0	3.91	31.0 - 46.0	22
All	32.2	8.62	17.0 - 47.5	48
Juveniles	12.8	0.85	12.0 - 14.0	3
Total Removed				87
<u>SAMPLE II</u>				
♂	31.4	9.44	14.0 - 49.0	54
♀	24.2	6.59	16.5 - 42.0	38
♀B	38.9	2.96	33.0 - 44.0	36
All	31.4	8.96	16.5 - 44.0	74
Juveniles	11.3	0.88	10.0 - 13.0	9
Total Removed				137
<u>SAMPLE III</u>				
♂	27.2	6.60	19.0 - 44.5	19
♀	24.9	5.35	18.0 - 34.5	14
♀B	36.3	2.70	32.0 - 41.0	10
All	29.7	7.17	18.0 - 41.0	24
Juveniles	11.4	1.88	8.5 - 15.0	8
Total Removed				51
Mean no. removed				92

TABLE 5.12 : MORPHOMETRY OF A.PALLIPES DREDGED FROM R. BEANE

(8.5.81.)

C.L. x Wet weight	♂ $\log_{10} \text{wt.} = 3.299 \cdot \log_{10} \text{C.L.} - 2.65$	$n = 76$	$r = 0.994$
	♀ $\log_{10} \text{wt.} = 3.285 \cdot \log_{10} \text{C.L.} - 2.99$	$n = 56$	$r = 0.989$
C.L. x T.L.	♂ $\text{T.L.} = 1.99\text{C.L.} + 1.257$	$n = 53$	$r = 0.987$
	♀ $\text{T.L.} = 2.17\text{C.L.} - 2.165$	$n = 37$	$r = 0.991$

Figure 5.5

Length - frequency distribution of *A. pallipes*

dredged from the R. Beane at Hertford.

May, 1981.

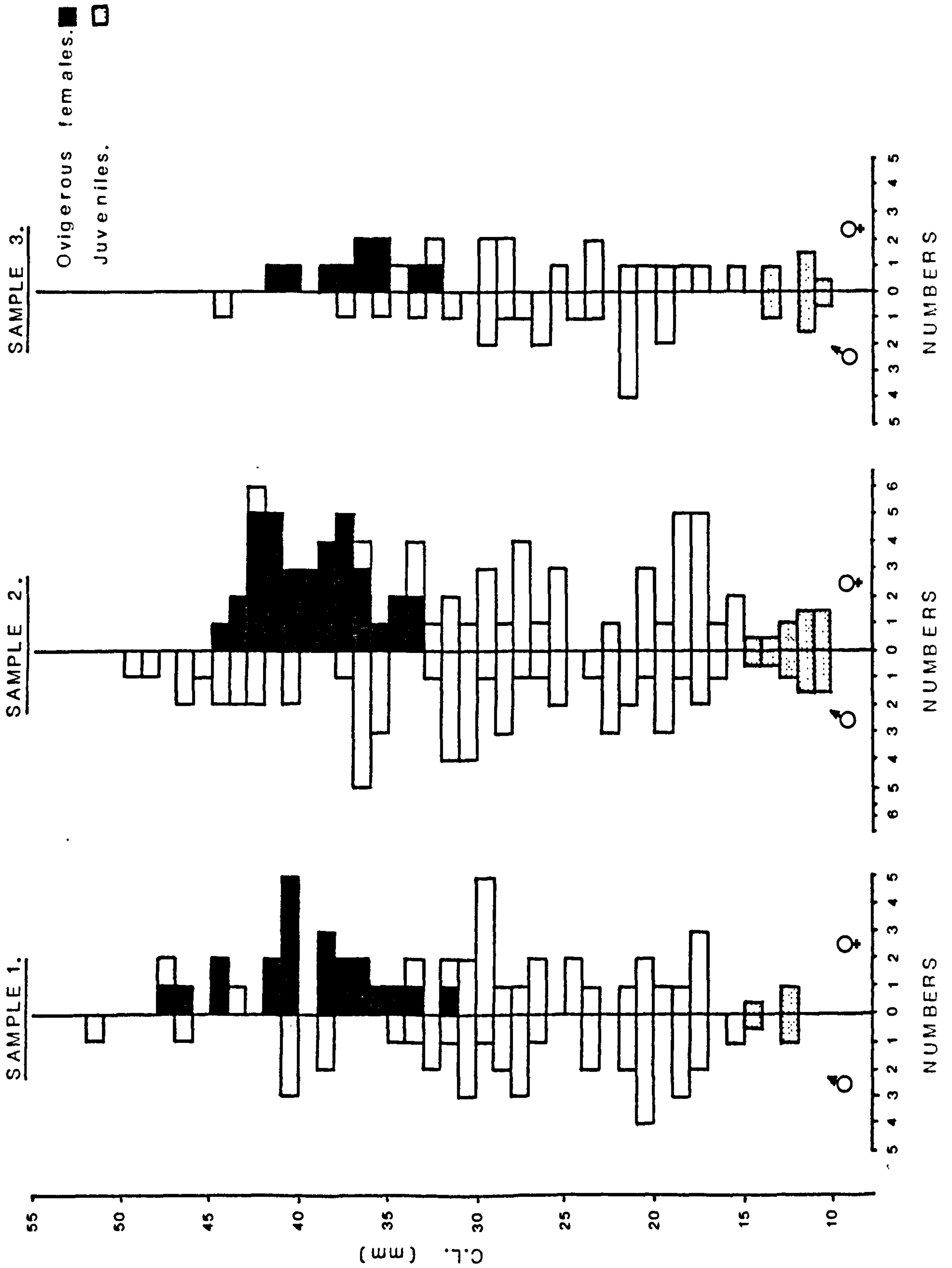
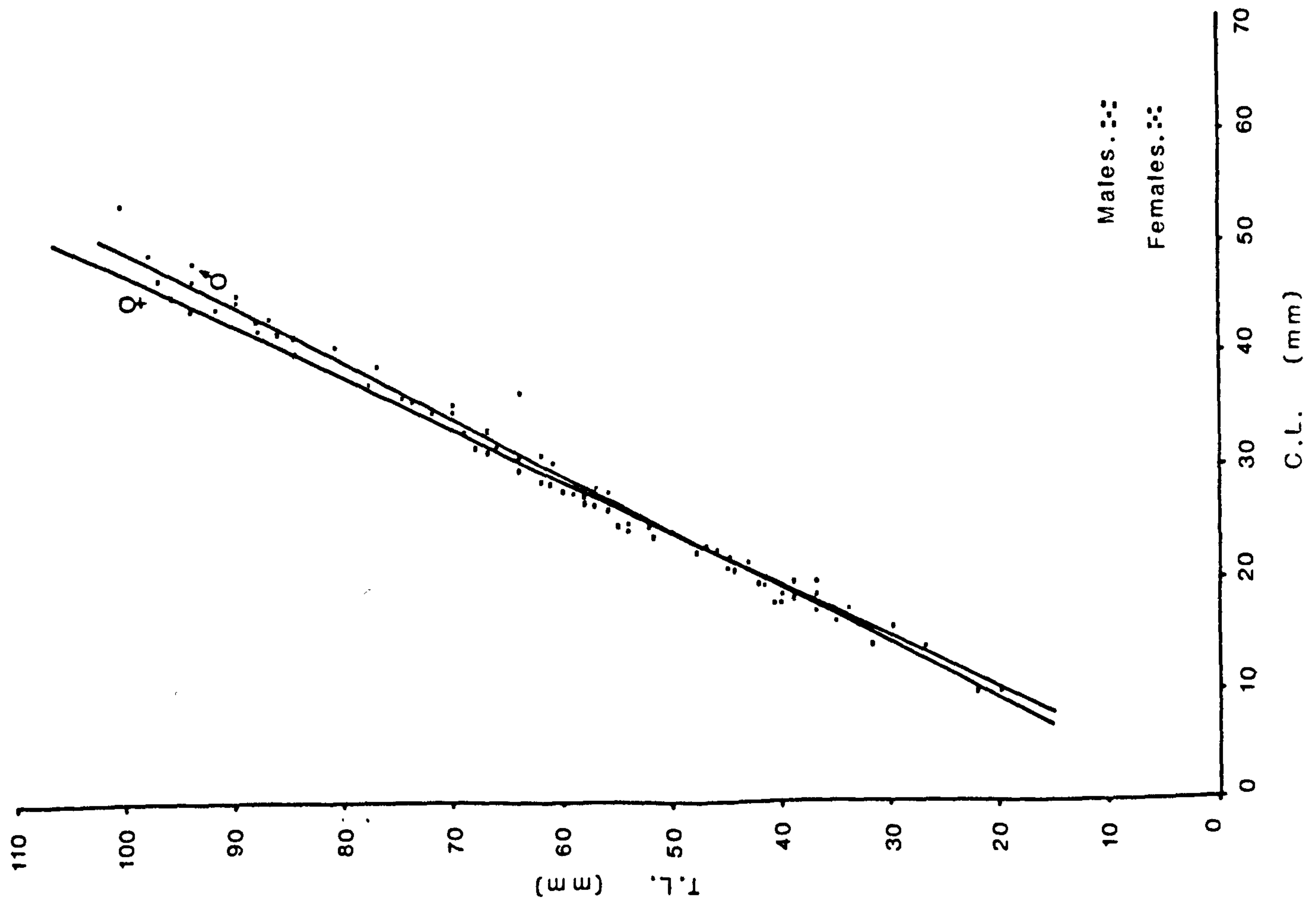
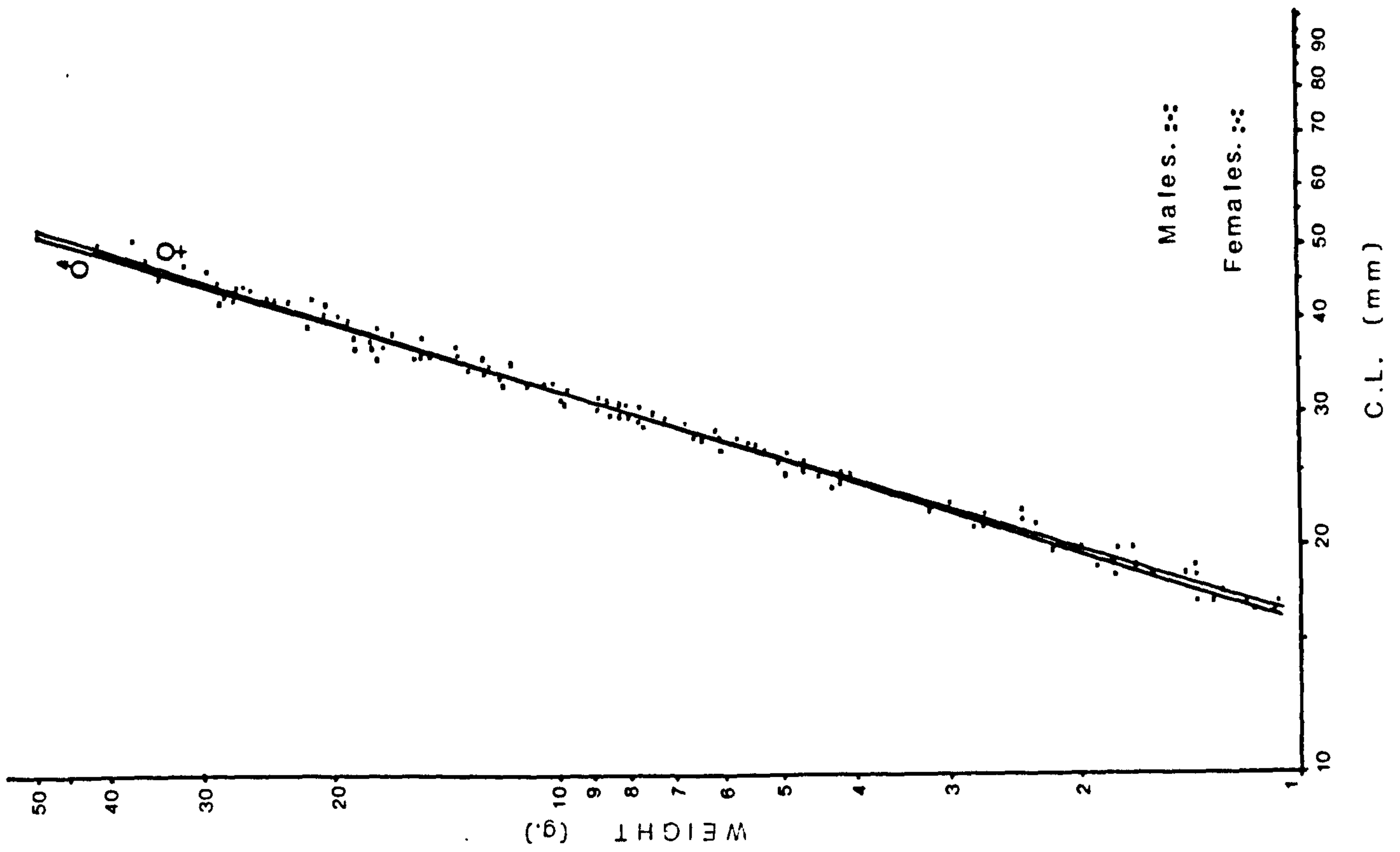


Figure 5.6

Regression lines of C.L.: T.L. and C.L.: Weight

for *A. pallipes* from the R.Beane at Hertford.



as efficient land drainage channels suggests that 'improvement' schemes will have an increased importance for aquatic communities in the future.

The River Lee in the Hertford and Ware region of Hertfordshire, where most of the major tributaries join it, has been subject to periodic flooding for many years (Anon., 1978). By modifying the existing channel and providing relief channels, to bypass major obstructions to the flow, the capacity of the River Lee in this area to cope with increased surface water runoff and land drainage has been greatly improved.

A.pallipes has long been known to inhabit the vicinity of Ware Lock, as well as occurring elsewhere in the Lee Catchment (Duffield, 1933; Thomas & Ingle, 1971; Bryce, et al, 1978; Lowery, pers.comm; see Chapter 3). The construction of a major new basin adjacent to Ware Lock therefore provided an opportunity to monitor the rate and mode of colonisation by crayfish.

5.4(ii) - Colonisation of basin.

The syphon/weir and stilling basin, constructed in 1977, was operational by 1978. At the time the current investigation commenced, in 1979 some 18 months after opening, it is clear that A.pallipes had already colonised the basin and was apparently present in large numbers. Initial studies, using crayfish marked according to the location of their capture, suggested that a stable population existed and that movements of crayfish around the whole of the Ware Lock area, and particularly into the new basin, were few in number. The number of marked crayfish subsequently recaptured in a different zone to their original capture, Table 5.4, showed that only 17% of recaptures had moved one zone between sampling occasions; 13% of recaptures had moved two zones and none had moved more than two zones away.

From the small number of movements recorded, Table 5.4, it is apparent that such movements as did occur were not all in the same direction, although there is insufficient data to permit statistical analysis of this observation. There is little published evidence concerning the territoriality of range of any crayfish species. Upstream migrations of Orconectes nais (Momot, 1966) and Pacifastacus klamathiensis (Black, 1963) have been reported but not explained and terrestrial migrations, such as the inter-pond migrations of Cambarus argillicola (Cummins, 1921), have been reported. Other reports of migrations document the movement of Orconectes virilis into deeper water in winter (Momot & Gowing, 1977). This was thought to be associated with gonadal maturation rather than winter survival (Aiken, 1968) although others (Fast & Momot, 1973) concluded that the social aggression of the larger males forces the females into deeper, colder water and that this aggression is temperature related. A similar conclusion was reached concerning the dispersal of Cambarus alleni (Bovbjerg, 1959) which increased at greater densities because of the consequent rise in aggressive behaviour.

5.4(iii) - Population estimation at Ware.

Once the presence of a relatively stable population of A.pallipes in the stilling basin at Ware Lock had been established attempts were made to estimate population numbers within the basin. Using mark-recapture methods, despite their limitations and drawbacks (see Chapter 2), the size of the adult (C.L. >30 mm.) population of crayfish inhabiting the basin was estimated. The data used to calculate these estimates were collected from three trapping sessions carried out at intervals of two days in September 1980 and three days in May 1981 to permit full remixing of marked crayfish into the population (see 5.3(i)). Each method used provided estimates of a similar order of magnitude and suggest that the adult population in the area sampled was in the range 1184 to 1679

in September 1980 and 1237 to 2050 in May 1981. There is no significant difference between the September and May estimates ($p < 0.01$).

It has been calculated that only 566 m^2 of the total area of the basin, being the marginal areas, is effectively sampled using traps in the way described (see Chapter 2); based on the assumption that each trap attracts crayfish from an area of approximately 15.0 m^2 (Abrahamsson, 1971). The mean population estimate can then be adjusted to relate to the whole area of the basin, i.e. 1220 m^2 , to give a figure of 3210 adults, at 2.6 m^{-2} (see 5.3(i)). Such a figure compares well with the 0.13 to 1.65 m^{-2} and 0.7 to 4.1 m^{-2} for river populations of A. astacus in Finland (Niemi, 1977; Westman & Pursainen, 1979) and the 2.0 m^{-2} for a pond population of A. astacus in Sweden (Abrahamsson, 1966, 1971). Density estimates for A. pallipes populations are few and range from 0.4 to 14.0 m^{-2} in France (Daguerre de Hureaux & Roqueplo, 1980) to 4.45 m^{-2} in Co. Durham (Brown, 1979).

The assumption that adult A. pallipes are randomly distributed around the basin is, however, erroneous, as implied previously. An investigation carried out in October 1980 showed that only 17% of the total number of crayfish caught on that occasion ($n = 199$) were trapped in the centre of the basin; some 55% and 41% being caught along the north and south banks respectively. Initially only 4% were caught in the centre traps but it is thought that this was due to the traps being improperly set. Subsequent trapping in the central area yielded 34 A. pallipes but no traps were set in the marginal areas on this latter occasion. It is possible, therefore, that some of those captured in the centre of the basin on 3.10.80 had previously been caught in the bankside traps on 1.10.80. The number of such possible recaptures is unknown, no marking was carried out on this occasion, but nevertheless 50% fewer adults were trapped in the centre of the basin, compared with

the marginal traps, on subsequent occasions. The true distribution of A.pallipesⁱⁿ the basin could only be established by large-scale trapping on a stratified random system (Southwood, 1966) but this was not attempted. The results suggest, however, that the distribution of A.pallipes in the basin is contagious, or clumped, in nature (Southwood, 1966).

The mark and recapture method of estimating crayfish numbers is far from ideal, as stated previously (see Chapter 4), and independent tests of the method have shown that the figures obtained may be as much as threefold underestimates (Brown, 1979). If this is the case then the stilling basin at Ware Lock may contain between 2500 and 4000 A.pallipes, in the area trapped, at a density of 2.08 to 3.33 m⁻². The only accurate means of calculating population size involves draining the waterbody and collecting the crayfish by hand (Brown & Brewis, 1979) which was obviously not possible at this site.

5.4(iv) - Dredging.

Dredging of natural watercourses has been cited as one of the two main factors supposedly reducing the distribution of A.pallipes in the U.K. (Reynolds, 1979) and most crayfish species throughout Europe (Westman, 1973, 1975; Westman & Pursainen, 1982). Dredging has been shown to cause temporary changes in the water quality downstream, with, for example, changes in suspended solids, iron, chemical oxygen demand and dissolved oxygen (Niemi, 1977). High levels of suspended solids, for example, have been shown to reduce the number of eggs laid by up to 20% and to delay the time of laying (Vey, 1977). In addition to such temporary changes in water quality serious damage to the crayfish habitat may be caused. The quantitative effect of such operations on a population of A.pallipes, in terms of the number of individuals removed, should therefore form an important part of this study. Elsewhere a study of the effect of

dredging on stream benthos has shown that although A.pallipes were "formerly abundant" they had not returned to the site up to 20 months after dredging (McCarthy, 1977). Similarly the population of A.astacus in the River Siikajoki, in Finland, disappeared as a result of dredging (Niemi, 1977).

During May 1981 part of the River Beane on the outskirts of Hertford, was dredged as part of the routine maintenance dredging programme carried out by Thames Water. The usual, unofficial, practice of the workman carrying out the dredging was to rinse the spoil as it was removed from the river, by repeatedly dunking it in the water, thereby washing some of the crayfish back into the river. In a preliminary investigation samples of rinsed and unrinsed material were examined and the numbers of A.pallipes removed was established. It was clear that large numbers of crayfish were being removed but that a reduction of some 35% of those removed could be achieved by modifying the dredging method to incorporate a rinsing process.

Subsequent investigation aimed to more accurately quantify the numbers being removed during dredging and three samples of dredged, unrinsed material were thoroughly examined and all the crayfish removed. An average of 92 crayfish per unrinsed sample were collected; clearly if a 35% reduction of the number removed could also be effected in this case then this figure would be reduced to 50.

The fact that unexpectedly large numbers of A.pallipes were found to be inhabiting the plant beds along this reach of the River Beane implies that crayfish may be more widespread than is currently thought and occur in what would often be considered to be unsuitable habitats. Typical crayfish habitat is generally thought to include 'hard' refugia, in the form of brick rubble, rocks, etc. (Daguerre de Hureaux & Roqueplo, 1980) and not the 'soft' refugia provided by the root mass of emergent plants such as G.maxima. The size range of the crayfish removed, see Figure 5.5, was similar in each sample and mean C.L. values

for each sex in successive samples were not significantly different ($p < 0.01$). The large number of berried females being removed means that not only are adults and juveniles being affected by dredging but also that recruitment into the population in that year would be drastically reduced. The relatively small number of juveniles in the spoil is thought to be due to the increased likelihood of small crayfish being washed out during the removal of the dredged material from the water and the difficulty of locating small crayfish in the samples of dredged material. In addition it may imply that juveniles (C.L. < 15.0 mm.) do not inhabit stands of marginal macrophytes, such as G.maxima. to the same extent as adults.

The periodic dredging of sites inhabited by A.pallipes will not only result in the removal of large numbers of crayfish but will also devastate their habitat. The effects of this operation on the A.pallipes population in the River Beane was alleviated, to some extent, by the rinsing process and the fact that only one bank of the river was being dredged, at that time. This ensured that an area of marginal macrophytes, Carex sp and P.communis, remained on the west bank that could be utilised by those crayfish that survived the dredging operation. The practice of carrying out routine maintenance on only one bank of a river at a time could be adopted, where appropriate, by the relevant authorities, to minimise damage to both aquatic and bankside communities. During dredging operations the immediate crayfish population will be removed from the river and if all favourable environmental factors disappear the recovery of the crayfish population will be very slow and the new population supported by the dredged area will be small compared to the situation prior to dredging (Niemi, 1977).

5.4(v) - Conclusions.

The mode of construction of the new stilling basin at

Ware Lock is clearly a factor contributing to the successful colonisation of the site by A.pallipes. The nature of the artificially provided substrate, with its many and various sized crevices, clearly provides an excellent habitat for freshwater crayfish. In fact when some species of crayfish are being commercially cultured they must be provided with an analagous substrate (Karlsson, 1977). For the new weir and basin at Ware Lock this method of construction was not selected with the object of improving the environment for crayfish, or any other aquatic organism, but was intended to protect the bed from the scouring action created by the new syphon/weir. However, when appropriate, the use of construction techniques which provide a similar creviced substrate or bank lining could be adopted to alleviate, to some extent, the impact of new engineering structures on the aquatic environment. Provision of such areas would go some way towards compensating for the detrimental effects of land drainage operations elsewhere. Indeed such areas could be actively stocked with A.pallipes, to aid natural colonisation, as was apparently a common practice in the past (Thomas & Ingle, 1971).

The examination of dredged plant material from the River Beane showed that large numbers of crayfish may be removed during maintenance dredging. The destruction of their habitat must also have a drastic effect on the crayfish population and recolonisation of such areas will be slow. If, whenever possible, the washing of dredged material containing crayfish can be carried out in the way described the numbers removed can be greatly reduced. Those animals returned to the river in this way then at least have the option of migrating to find new areas of suitable habitat. If only one bank of the river is affected, as in this case, their journey may only need to be across the river. In addition any new structures built during the course of a flood alleviation scheme, or for routine bank maintenance, could be designed to cater for the needs of crayfish at no extra cost. Indeed maximum benefit of such schemes to all aquatic organisms could be achieved if

ecologists are involved with or by the design engineer at an early stage (Toms, 1975). In the case of Ware Lock artificial habitat improvement appears to have been achieved unintentionally.

Such a policy of constructing and maintaining waterways to accommodate the needs of animals is not without precedent, particularly when economic factors are involved. Current examples range from the replacement of salmonid spawning grounds after dredging (Webster, 1962), the recent reconstruction of the River Roding to provide fish habitats in an area where angling is important (Weeks, 1982) and the provision of fish passes and ladders to enable migratory salmonids to bypass artificial flow regulating structures (Clay, 1961). There is currently considerable interest in crayfish as food (Goddard & Holdich, 1979) so perhaps, in the long term, there might be some economic as well as the ecological arguments for encouraging the survival and growth of crayfish populations and reducing the impact of river engineering schemes on existing crayfish populations.

CHAPTER 6. MISCELLANEOUS OBSERVATIONS REGARDING THE BIOLOGY OF A.PALLIPES IN THE THAMES CATCHMENT.

6.1. Introduction.

During the course of the current investigation a considerable quantity of information has been acquired concerning several aspects of the biology of A.pallipes in the Thames Catchment. Some of this information is incidental to the main topics studied and which are discussed in Section A, Chapters 3, 4 & 5. The subjects considered here provide additional information regarding the biology of A.pallipes and thus add to the body of such information available on both a local and a national scale. The paucity of factual, rather than anecdotal, information concerning the biology of A.pallipes (Brown, 1979) until recent years, is perhaps highlighted by the existence of only one English text on the subject: "The Crayfish - an introduction to the study of zoology." (Huxley, 1880) and attests that the accurate recording of such observations is of importance.

Data from a range of sites throughout the Thames Catchment will be described in sections of this chapter, under the following headings:

- 6.2. The biology of a riverine population of A.pallipes.
- 6.3. Morphological characterisation of A.pallipes.
- 6.4. Disease and parasites of A.pallipes.

6.2. Observations on the biology of a riverine population of A.pallipes in the Thames Catchment.

6.2(i) - Introduction.

Originally one of the primary aims of this study of the biology of A.pallipes was to compare aspects of the life-history and population dynamics of crayfish in both riverine and lacustrine situations. As was previously stated (see Chapter 4) the simultaneous detailed comparison of two such populations was discontinued after twelve months and efforts were concentrated on obtaining maximum information from the lacustrine population. This part of Chapter 6 presents the data acquired from the study of the population of A.pallipes inhabiting the River Loddon in north Hampshire.

6.2(ii) - Study Site.

The riverine population of A.pallipes that was studied for a period of more than twelve months (June 1979 to September 1980) inhabits a 30m reach of the River Loddon at Sherfield-on-Loddon, Hampshire (N.G.R. SU683583). The site, downstream from the A33 roadbridge, consists of a shallow, fast run leading into the upstream section of a deeper, slow-flowing reach. The substrate in the shallower area comprises coarse gravel with abundant rocks (principally brick rubble and cement blocks) and this merges into sand and fine gravel at the downstream limits of the site.

Chemical water quality, from samples collected routinely by Thames Water, gave the mean values recorded in Table 6.1. One of the parameters considered to be of major importance to crayfish, i.e. pH (Laurent, 1980; Jay & Holdich, 1981) gave the following mean values for the period 1.4.78 to 31.7.79:

mean pH = 8.04 n = 64

No data was collected regarding the hardness or calcium

TABLE 6.1 : CHEMICAL WATER QUALITY DATA . R. LODDON, SHERFIELD.
1.4.78 - 31.7.79.

	Mean	Range	n.
‡ pH	8.04	7.11 - 8.46	64
Susp. Solids (105°C)	10.036	3.7 - 47.5	62
BOD (ATU)	1.530	0.3 - 4.75	64
C.O.D.	13.737	3.95 - 47.10	50
‡ Temp. (°c)	12.5	2.5 - 18.5	54
D.O.	11.129	8.3 - 13.55	31
‡ % saturation	104.71	85 - 135	31
Ammoniacal Nitrogen	0.153	0.01 - 0.76	65
Unionised Ammonia (as N)	0.003	0.001 - 0.02	47
Total oxidised Nit (as N)	7.301	5.3 - 11.2	32
Nitrite (as N)	0.081	0.01 - 0.22	33
Chloride (as Cl)	30.736	22.0 - 59.0	63
Silica (as SiO ₂)	11.307	9.4 - 13.7	19
Orthophosphate (as P)	1.173	0.4 - 2.76	23
Syndets (Anionic)	0.054	0.05 - 0.1	23

N.B. values in mg.l.⁻¹ except ‡.

content of the water. Chemically the water quality results in a N.W.C. classification of 1B (see Appendix 3). Routine macroinvertebrate monitoring, carried out by Thames Water, has resulted in the following B.M.W.P. scores and T.W.A.B.I. classifications (see Appendices 4 & 5) in recent years:-

Year	B.M.W.P. Score	T.W.A.B.I.
1979	n/d	IA
1980	n/d	IA-
1981	159	IA-
1981	154	IA
1982	152	IA-

These results suggest that fluctuations in biological diversity have occurred and that, overall, the diversity has declined. Whether or not this apparent decline is significant, in the long term, cannot be concluded from these results and it may be that short term fluctuations of this order are a normal occurrence or a feature of the classification systems used. There is no explanation for these fluctuations in the chemical water quality data for 1979 to 1982.

The study site is located at the upstream limit of a locally important trout fishery and it is likely that both wild and introduced brown trout, Salmo trutta, are present together with introduced rainbow trout, S.gairdneri, and wild populations of chub, Leuciscus cephalus, bullhead, Cottus gobio, and stone loach, Noemacheilus barbatulus. Aquatic macrophytes comprise water-crowfoot, Ranunculus sp. and bulrush, Schoenoplectus lacustris, in approximately equal proportions. No estimates of macrophyte cover or abundance were made as all the aquatic macrophytes are cut at least once annually as part of the fishery management programme (Ellis, pers comm).

6.2(iii) - Methods.

A.pallipes were collected by hand, using a standard pond net, on eight occasions during the period June 1979 to September 1980, see Table 6.2. The collection technique has been described elsewhere (see Chapter 3). All crayfish were sexed, measured (C.L. being the standard measurement used) and those of C.L. >20mm. were individually marked by hot branding (Abrahamsson, 1965; Chapter 2). The reproductive and disease status of all crayfish in the samples was also recorded (see Chapter 2).

6.2(iv) - Results.

Catch and size data, calculated from the raw data, are summarised in Table 6.2. The size distribution of crayfish of each sex in all samples is illustrated in Figure 6.1 and the mean C.L. of crayfish in all samples is plotted in Figure 6.2. The catch data has been used to construct the length-frequency histograms in Figure 6.3. For this purpose the number of crayfish in each 2.5 mm. C.L. size class has been expressed as a percentage of the total sample. All crayfish <15mm.C.L. have been considered to be immature and termed juvenile; their occurrence is divided equally between the sexes in the histograms, Figure 6.3.

Data concerning the morphology and the incidence of diseased and damaged individuals from this site is included in an analysis of figures collected from all sites in the Thames Catchment (see 6.3 and 6.4(c)).

6.2(v) - Discussion.

The primary aim of obtaining data concerning the population of A.pallipes inhabiting the River Loddon was to enable comparisons to be made with similar data from Clattercote Reservoir (see Chapter 4) and published

TABLE 6.2 : CATCH DATA. R. LODDON SHERFIELD. 1979 - 1980.

Date	MALE				FEMALE				JUVENILE (15mm C.L.)			TOTAL
	C.L.	S.D.	Range	n	C.L.	S.D.	Range	n	C.L.	S.D.	n	
25. 6.79	33.5	7.2	12.8-44.1	23	26.3	7.9	11.5-44.4	19	13.18	0.82	18	60
26. 7.79	26.7	8.5	12.7-45.9	44	27.6	6.9	12.4-42.1	39	13.82	0.82	24	107
5. 9.79	23.9	7.8	14.9-42.2	19	24.2	7.3	12.3-44.2	23	9.53	2.71	20	62
17.10.79	31.6	12.7	17.0-53.7	15	27.4	6.5	17.0-40.5	24	10.22	0.94	12.	51
3. 2.80	30.0	9.7	10.5-52.4	29	27.5	7.6	12.0-43.0	36	10.46	1.17	19.	84
17. 3.80	27.3	8.8	16.4-47.9	22	26.4	7.8	19.3-37.0	24	9.97	0.84	16	62
27. 6.80	33.7	7.9	22.0-52.0	31	31.2	6.5	13.5-47.5	27	13.54	0.98	23	81
9. 9.80	32.9	11.2	15.0-49.0	21	25.5	8.9	16.0-46.0	19	8.97	0.46	15	55

Where: C.L. = mean C.L.

S.D. = standard deviation

n = sample size

Figure 6.1 Size distribution of *A. pallipes*

in samples collected from the R. Loddon.

1979 - 1980

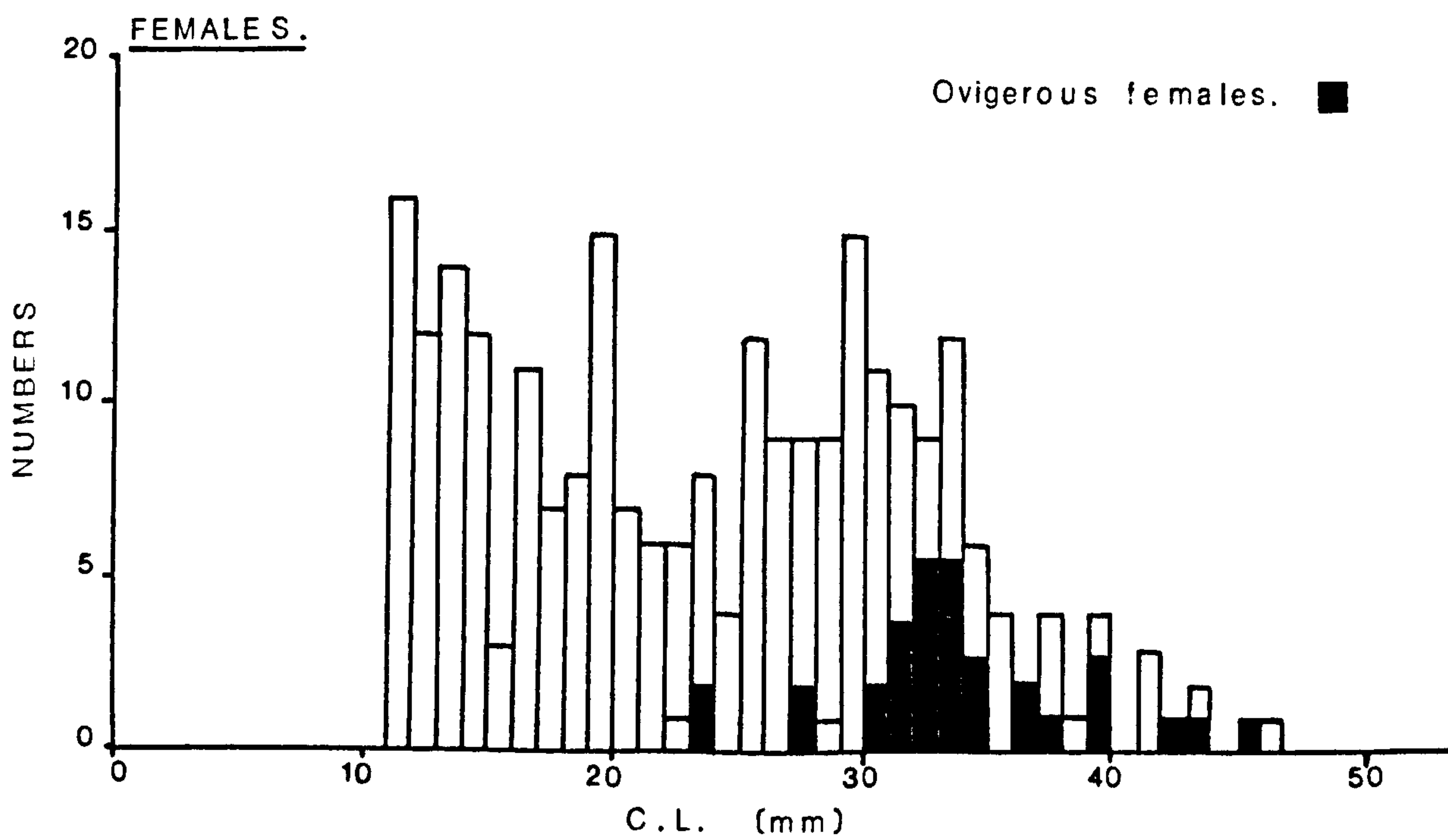
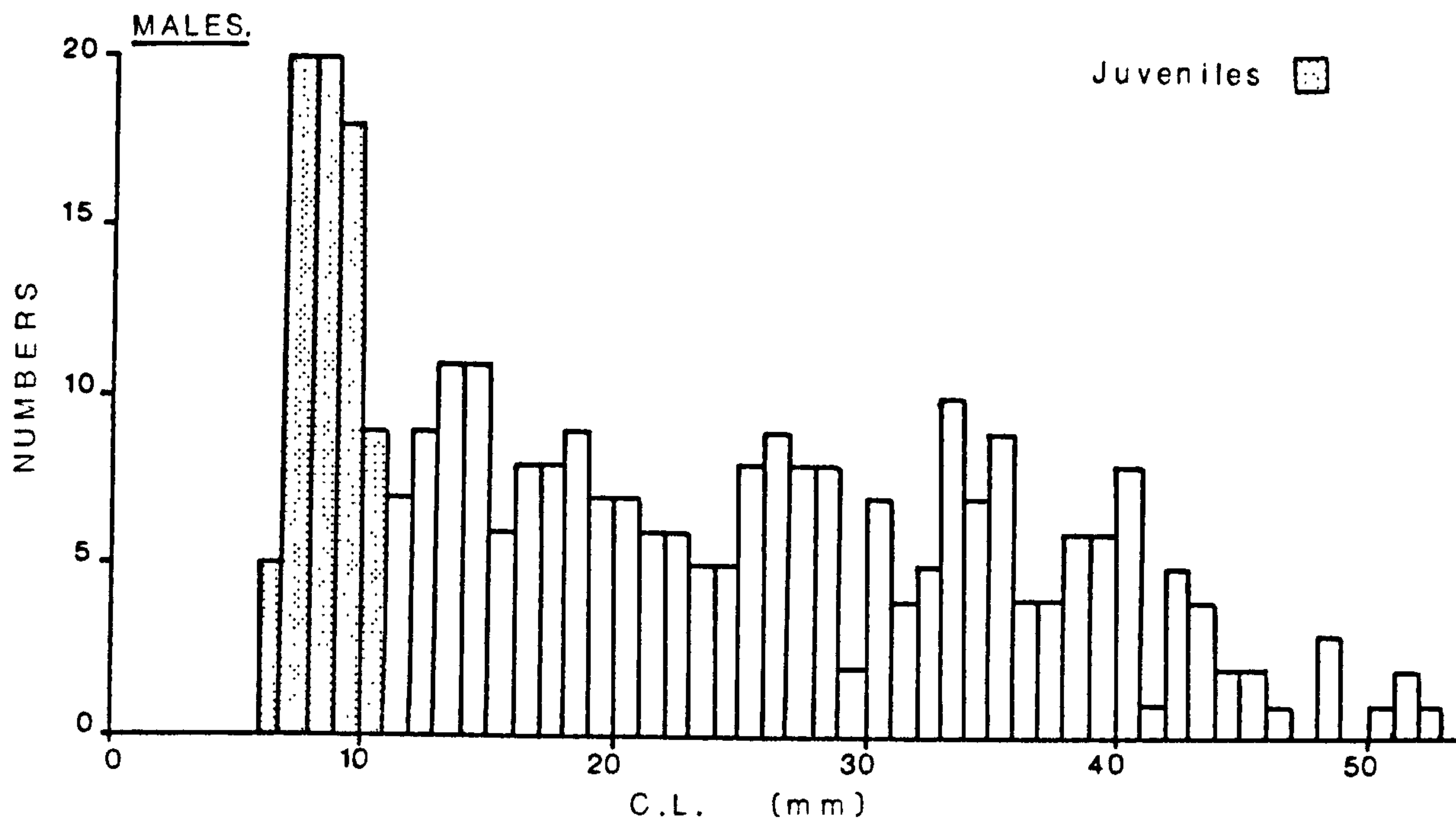


Figure 6.2 Mean C.L. of *A. pallipes*, R. Loddon.

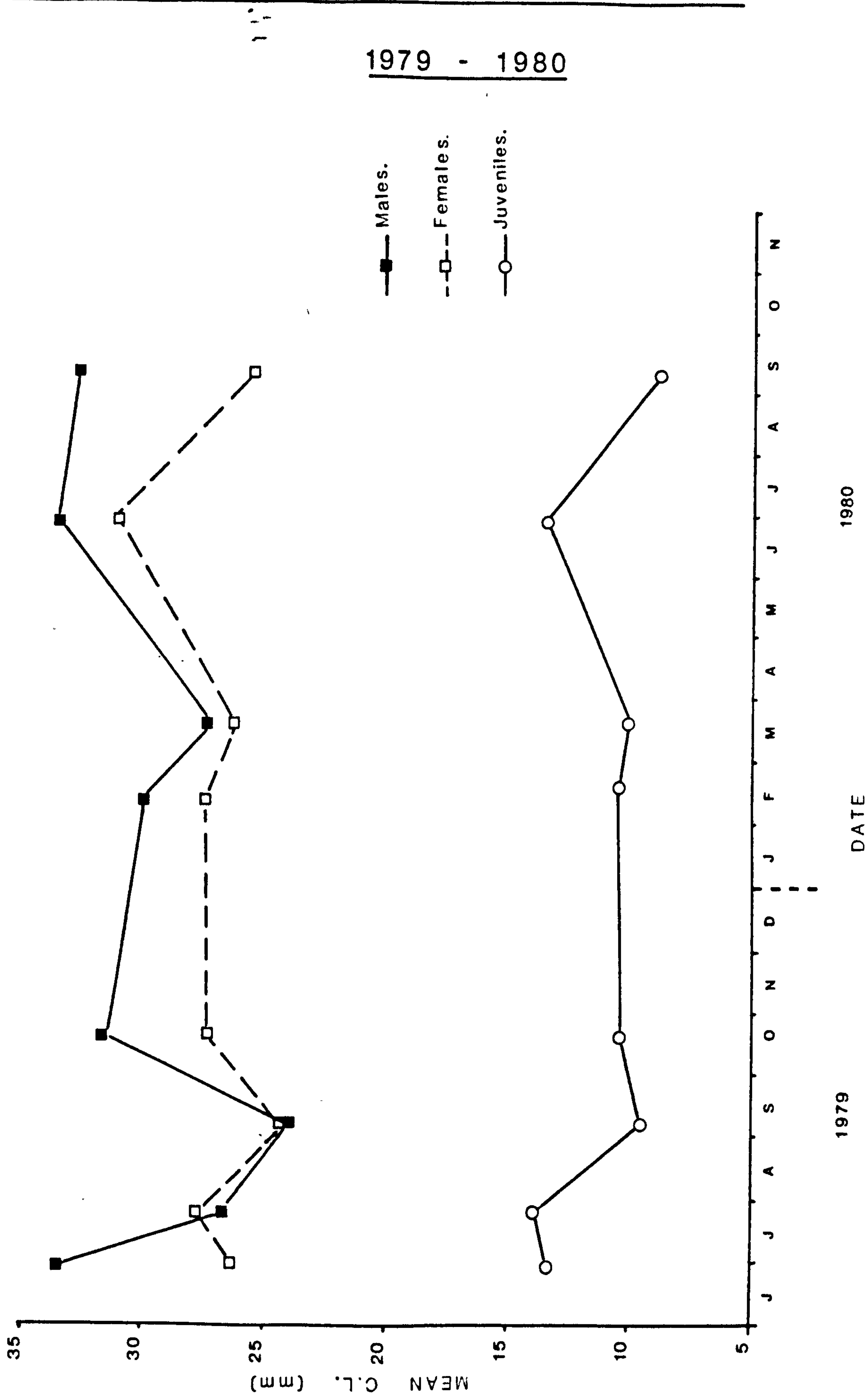
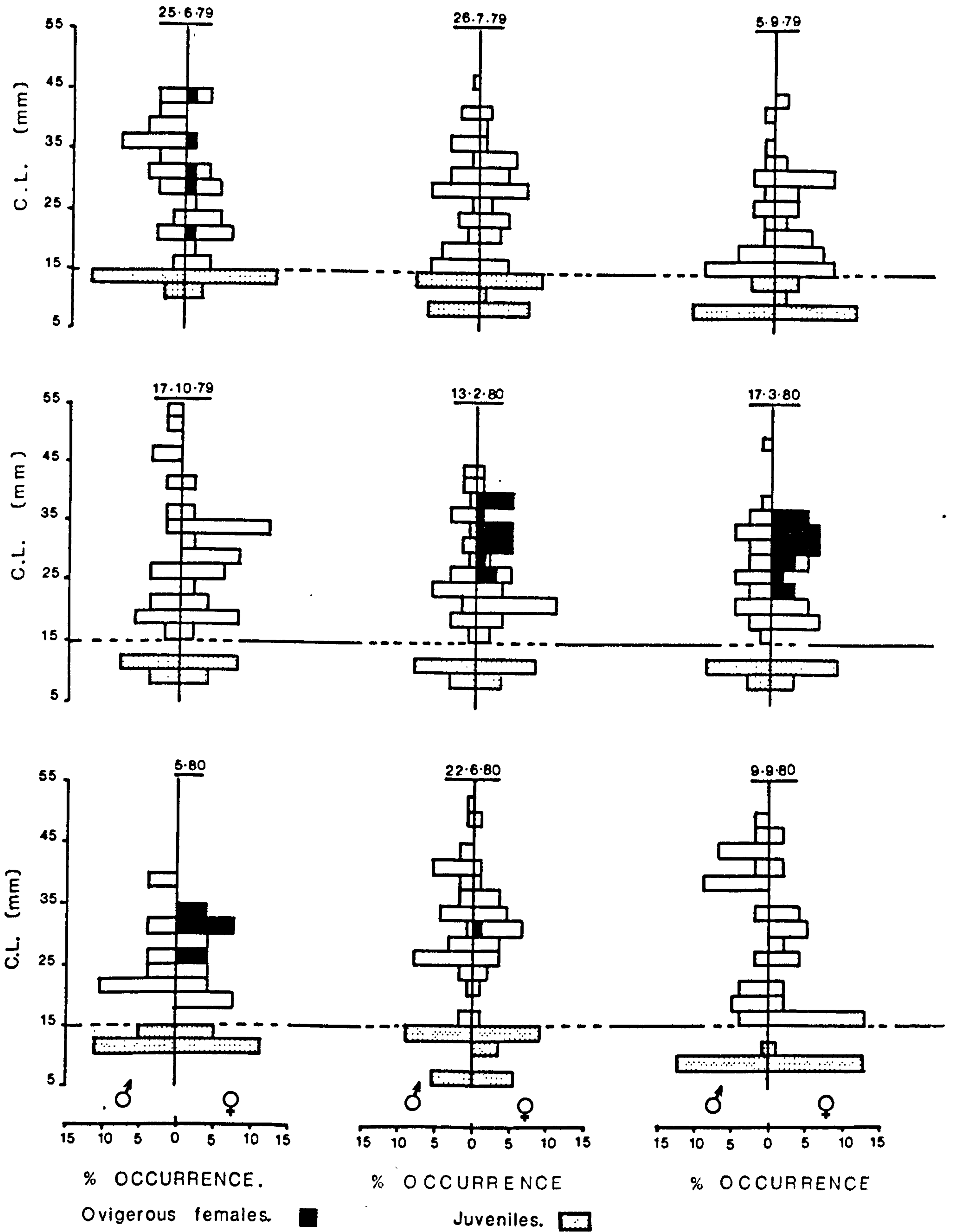


Figure 6.3 Length - frequency histograms.

A.pallipes, R. Loddon. 1979 - 1980.



The % of juveniles is shared equally between males & females.

Histograms show the number in each 2.5 mm size class as a % of the total sample size.

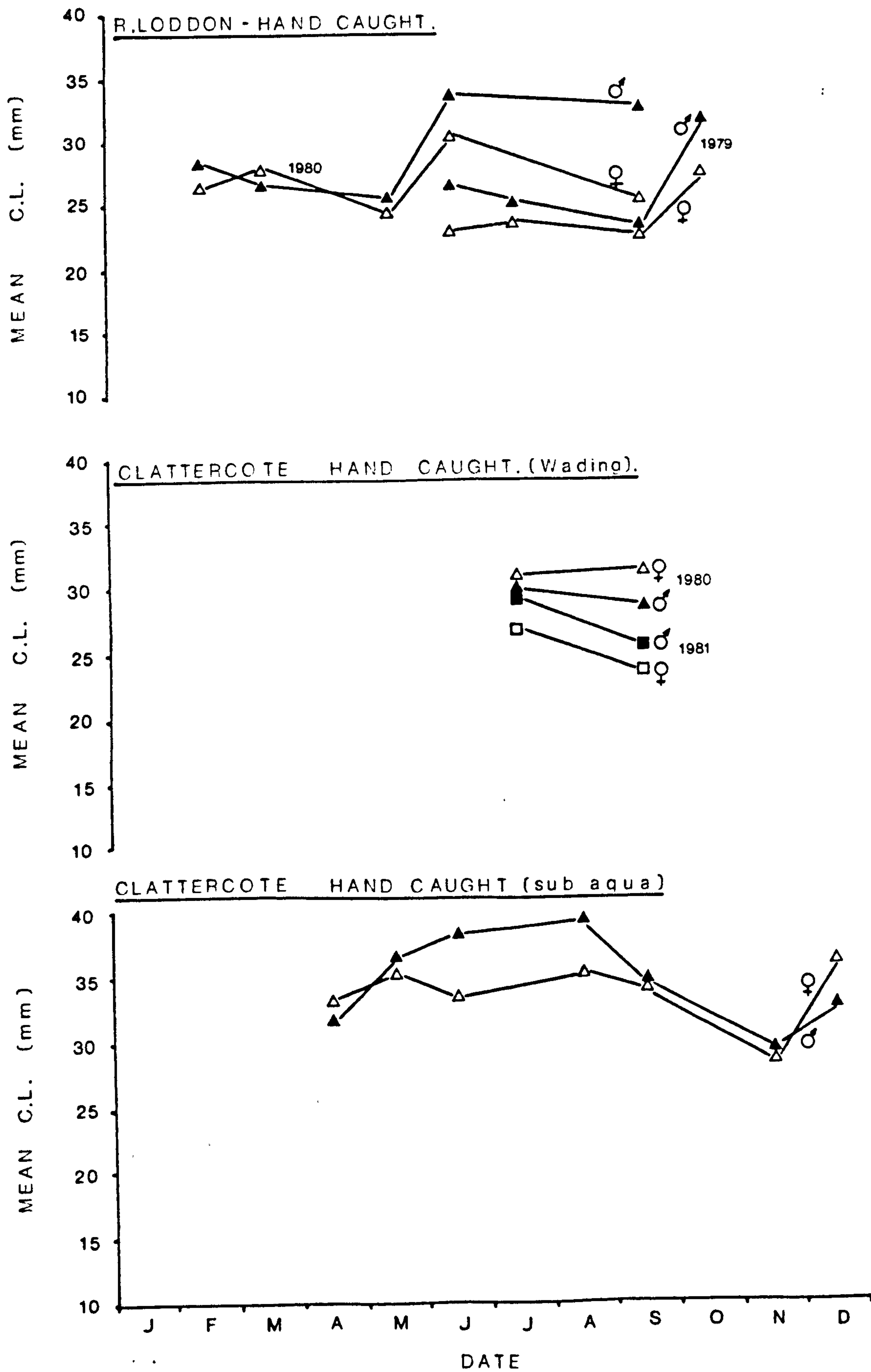
information (e.g. Brown & Bowler, 1977; Brown, 1979; Pratten, 1980). Only a single years data was obtained, for reasons discussed elsewhere, but this is sufficient to enable certain comparisons to be made and is worthy of inclusion for this reason.

The size of A.pallipes caught by hand from the River Loddon can be compared with the size of those caught by hand from Clattercote Reservoir, Figure 6.4. As can be seen the mean C.L. of male crayfish caught by the same method (i.e. hand collection whilst wading) was considerably smaller from Clattercote whereas those caught by hand by divers were of an almost identical mean size. Conversely the female crayfish caught by hand were significantly larger in samples from Clattercote than the River Loddon. The size ranges of both male and female A.pallipes were similar from both sites although a considerably wider size range of males than females was collected. These results are inconclusive in respect of the suggestion that lacustrine populations of A.pallipes would grow larger and faster than riverine populations, although the mean C.L. of crayfish in samples collected from the river is significantly smaller ($p < 0.05$).

Comparisons of the sample size from the two sites are invalid since crayfish were collected from the River Loddon for a fixed period of time (1 hour) or until at least 50 animals had been obtained. Consequently any influence that season or the moult/reproductive cycle may have had on catchability would be masked. In addition hand collections, by wading, in Clattercote Reservoir could only be carried out during periods of low water (see Chapter 4) and were therefore restricted to the period July to late September.

Another parameter by which the success of the A.pallipes populations in the two sites could be assessed is by comparing the percentage and size of berried females collected (Huner & Romaine, 1979). As no hand collected (wading)

Figure 6.4 Comparison of the mean C.L. values of A. pallipes in hand caught samples from Clattercote Reservoir and the R. Loddon.



samples could be obtained from Clattercote whilst females were ovigerous (i.e. October to June) only data from samples collected by divers can be compared with the information from the River Loddon. The mean size and percentage incidence of berried females in hand collected samples from the two sites is tabulated below:-

Month	<u>River Loddon</u>		
	% ♀ B	Mean C.L.(mm.)	Range (mm.)
Nov	-	n/s	-
Dec	-	n/s	-
Jan	-	n/s	-
Feb	35	36.4	30.5 - 43.0
March	37	32.1	23.4 - 36.4
April	-	n/s	-
May	-	n/s	-
June	23	34.1	22.5 - 44.4
Month	<u>Clattercote Reservoir</u>		
	% ♀ B	Mean C.L.(mm.)	Range (mm.)
Nov	74	32.0	27.0 - 43.0
Dec	80	27.6	31.5 - 42.5
Jan	-	n/s	-
Feb	-	n/s	-
March	-	n/s	-
April	12	35.9	31.0 - 41.5
May	72	24.4	21.0 - 47.0
June	49	33.5	26.0 - 46.5

These results, except April when the sample only contained 15 females, suggest that a greater proportion of females in the Clattercote population of A.pallipes were ovigerous, during the period of study, than in the River Loddon population. However, the mean size of the berried females in the Clattercote samples was not significantly different to that in the samples from the River Loddon. ($p < 0.05$).

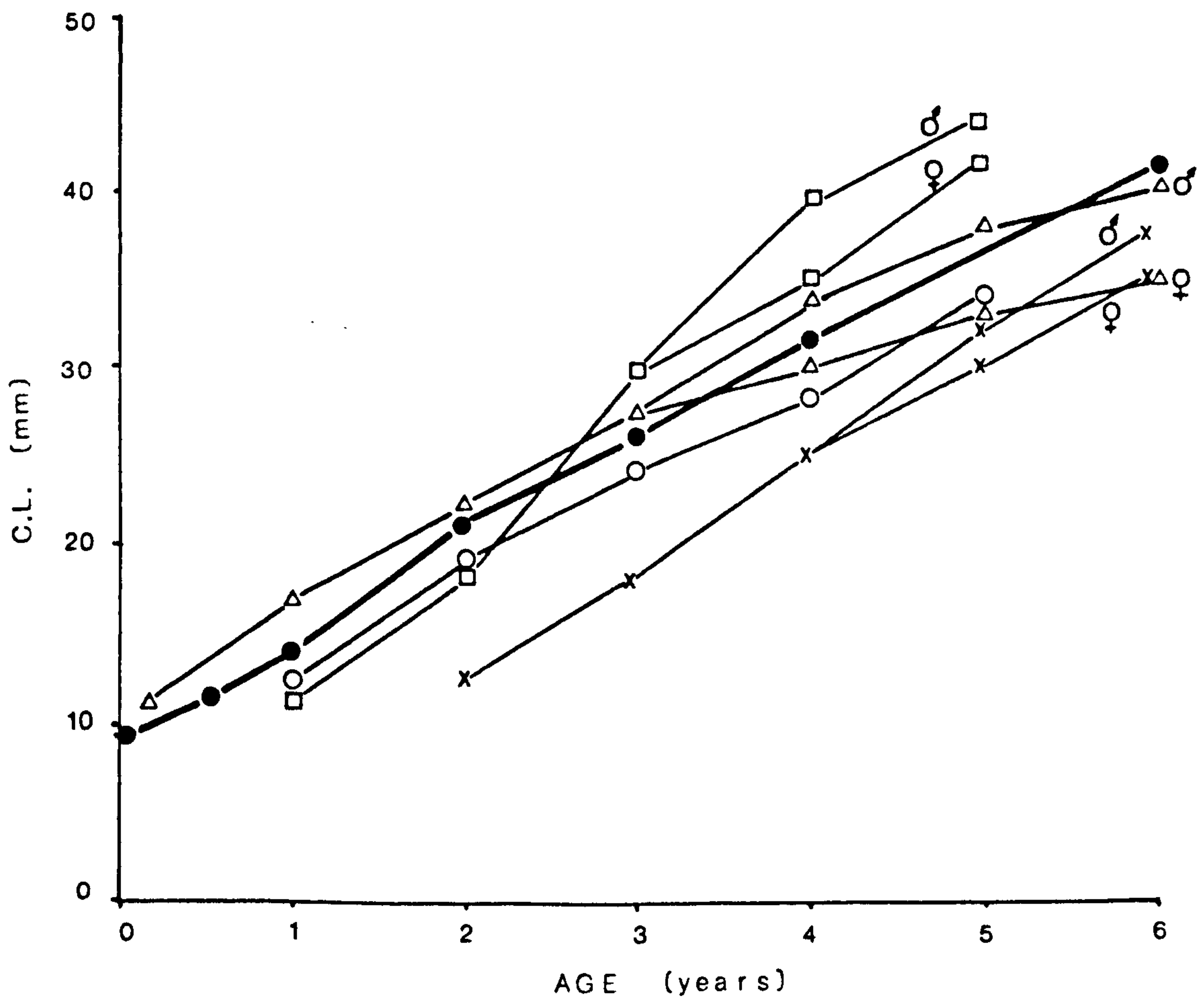
If it is assumed that sampling bias is the same in each instance then clearly many adult females in the River Loddon population did not carry eggs in any one year, particularly in the smaller size classes. It could be surmised that natural selection would favour early breeding as despite the fact that smaller crayfish carry fewer eggs (Rhodes & Holdich, 1982), they are more numerous than the larger size classes and their young have a higher survival rate (Mason, 1977a). Females in some populations of A.pallipes are reported to almost all bear eggs each year (Thomas & Ingle, 1971; Pratten, 1980). It would appear, therefore, that reproduction may be limited by temperature and/or environmental pressure such as food and refugia availability in the River Loddon when compared with Clattercote Reservoir. No comparable data is available from the River Loddon regarding the temperature that is available during incubation (see Chapter 4) and no assessment has been made concerning habitat suitability at either site.

The proportion of marked A.pallipes that were subsequently recaptured by hand sampling from the River Loddon was very low, 5% overall. This is not really surprising, however, as the proportion of recaptures during other parts of this study (see Chapters 4 & 8) was also very low. Also as the River Loddon site is 'open' considerable movements of crayfish could take place in both upstream and downstream directions. Such low numbers of recaptures prohibit the calculation of reasonable population estimates so none have been calculated for the River Loddon population of A.pallipes.

Length-frequency data collected from A.pallipes in the River Loddon (see Figure 6.3) has been analysed (Chapter 2) and can be compared with similar data collected from Clattercote Reservoir and with published information. This comparison is illustrated in Figure 6.5. As can be seen the proposed growth rate and pattern of A.pallipes in the

Figure 6.5 Growth of *A. pallipes* in the R. Loddon

- compared with some published data.



KEY

- R. Loddon - this study.
- Pratten, 1980.
- Demars, 1979.
- △—△ Clattercote Res. Fig. 4.11
- x—x Brown, 1979.

River Loddon is apparently initially slower than that in Clattercote, is similar to that reported for a population of A.pallipes in France (Demars, 1979) and is initially similar to that measured in the River Ouse, Bucks (Pratten, 1980). The initial faster growth of A.pallipes in Clattercote could be due to seasonal differences in growth rate, due to warmer than average temperatures in a particular year, or is the result of earlier hatching and faster initial growth in a waterbody which would warm up more quickly in spring and have an ample food supply for juvenile crayfish at that time of the year (see Chapter 4). That growth in the River Ouse population tails off with age (Pratten, 1980) when compared with the River Loddon population is probably a result of the interpretation of length-frequency histograms in the current study. Growth is markedly faster in the River Loddon than that reported for crayfish inhabiting an aqueduct system in Durham (Brown, 1979; Brewis & Bowler, 1982). This is due to the influence of a longer first growing season at the former site, approximately 5 months compared with 3 months, and has also been observed for populations of introduced P.leniusculus in southern England compared with those in Sweden (see Chapter 8).

6.3. The morphology and sexual dimorphism of the crayfish A.pallipes in the Thames Catchment.

6.3(i) - Introduction.

Whenever possible during the course of this study measurements of various important morphological characteristics of A.pallipes have been recorded. This information, collected from crayfish living in a wide range of habitat types, can be used for three main purposes.

- (i) The conversion of body size measurements to a standard form for comparisons of observations made during the current study, which has used C.L. as the standard measurement (see Chapter 2), with published information which reports size in other terms, e.g. total body length (Demars, 1979); wet weight (Pratten, 1980; Brewis & Bowler, 1982). Also such data will facilitate comparisons with other crayfish species the dimensions of which have already been evaluated (e.g. Weagle & Ozburn, 1972; Stein, et al, 1977).
- (ii) The evaluation of the size at which sexual dimorphisms occur in geographically separated populations as a means of comparing the relative biological success of populations in dissimilar habitats.
- (iii) The provision of information that could be beneficial in the assessment of the economic importance of populations of A.pallipes.
The size potential of an organism is of major importance from the commercial aspect (Rhodes & Holdich, 1979). In addition if crayfish are to be successfully harvested from natural populations, as has been suggested (Goddard & Holdich, 1979), then a worthwhile cropping size limit will be essential to guarantee that over-fishing does not occur.

6.3(ii) - Methods.

The data concerning body size that has been collected from the crayfish, A.pallipes, from all sites sampled during the course of this study has enabled the relationships between the following parameters to be calculated:

- (i) C.L. : T.L.
- (ii) C.L. : Post-orbital C.L.
- (iii) C.L. : 'French' P.O.C.L.
- (iv) C.L. : Carapace width.
- (v) C.L. : Abdomen width (2nd. segment)
- (vi) C.L. : Mean chela length.
- (vii) C.L. : Fresh weight.

The location of these measurements is illustrated in Figure 2.1.

Standard linear regression has been carried out on (i) to (iv); multiple regression analysis has permitted analysis of (v) and (vi) and exponential regression analysis of (vii) has been carried out (see Chapter 2).

By using multiple regression analysis (see Chapter 2) the size at which certain secondary sexual characteristics become apparent has been determined. This information could be used to compare the assumed size at the onset of sexual maturity in geographically separate populations (Wenner, et al, 1974; Stein, et al, 1977; Rhodes & Holdich, 1979; Rhodes, 1980).

No attempt has been made to investigate the occurrence of heterochely, which has been demonstrated for P.leniusculus elsewhere (Grünberg & Havelec, 1981), in A.pallipes in the Thames Catchment. Similarly no assessment of chelar abnormalities (Shelton, et al, 1981) has been made.

6.3(iii) - Results.

The regression equations calculated for (i) to (iv)

(see 6.3(ii)) are listed in Table 6.3(a) and illustrated in Figure 6.6(a). The sizes at which relationships (v) and (vi) alter, listed in Table 6.3(b), are compared with similar data from elsewhere in the U.K. in Table 6.4. All these relationships have, wherever possible, been compared with information obtained solely from Clattercote Reservoir (see Chapter 4) and with published data from elsewhere in the U.K. and mainland Europe.

The relationship of C.L. to fresh weight is curvilinear in nature, Figure 6.6(c), and has therefore been described by a regression equation of the form $y = ax^b$. All the other relationships were found to be essentially linear and best described by equations of the form $y = ax + b$ (Ricker, 1975).

6.3(iv) - Discussion.

The acquisition of data concerning the morphometry of A.pallipes during the course of this study has enabled the body-form of this species of freshwater crayfish to be defined. Other crayfish population studies have used P.O.C.L. (e.g. Flint, 1975a); maximum ('French') P.O.C.L. (Demars, 1979), (Anon, 1980), T.L. and weight (e.g. Pratten, 1980). Establishment of the relationship of these measurements to C.L. permits the comparison of such published data with the present results. C.L. was used as the standard index of body size for reasons discussed elsewhere (see Chapter 2; Brown, 1979). The calculation of C.F. values for individual crayfish has also necessitated the conversion of C.L. to T.L. values.

The relationship of C.L. to T.L. has been calculated for both male and female A.pallipes in the Thames Catchment and Clattercote Reservoir. The regression equations, see Table 6.3(a), are comparable with those reported elsewhere:-

T.L. = 1.954 C.L. + 2.131	T.L. = 2.046 C.L. + 0.962	*1
T.L. = 1.64 C.L. + 16.9	(for C.L. >35.0 mm. only)	*2
T.L. = 1.879 C.L. + 5.743	T.L. = 1.876 C.L. + 7.362	*3
T.L. = 2.012 C.L. + 1.673	T.L. = 2.168 C.L. - 0.791	*4

* 1(Brown, 1979) 2(Moriarty, 1973) 3(Lilley, 1977) 4(Rhodes, 1980)

TABLE 6.3(a) : MORPHOMETRIC RELATIONSHIPS OF A.PALLIPES IN
THE THAMES CATCHMENT.

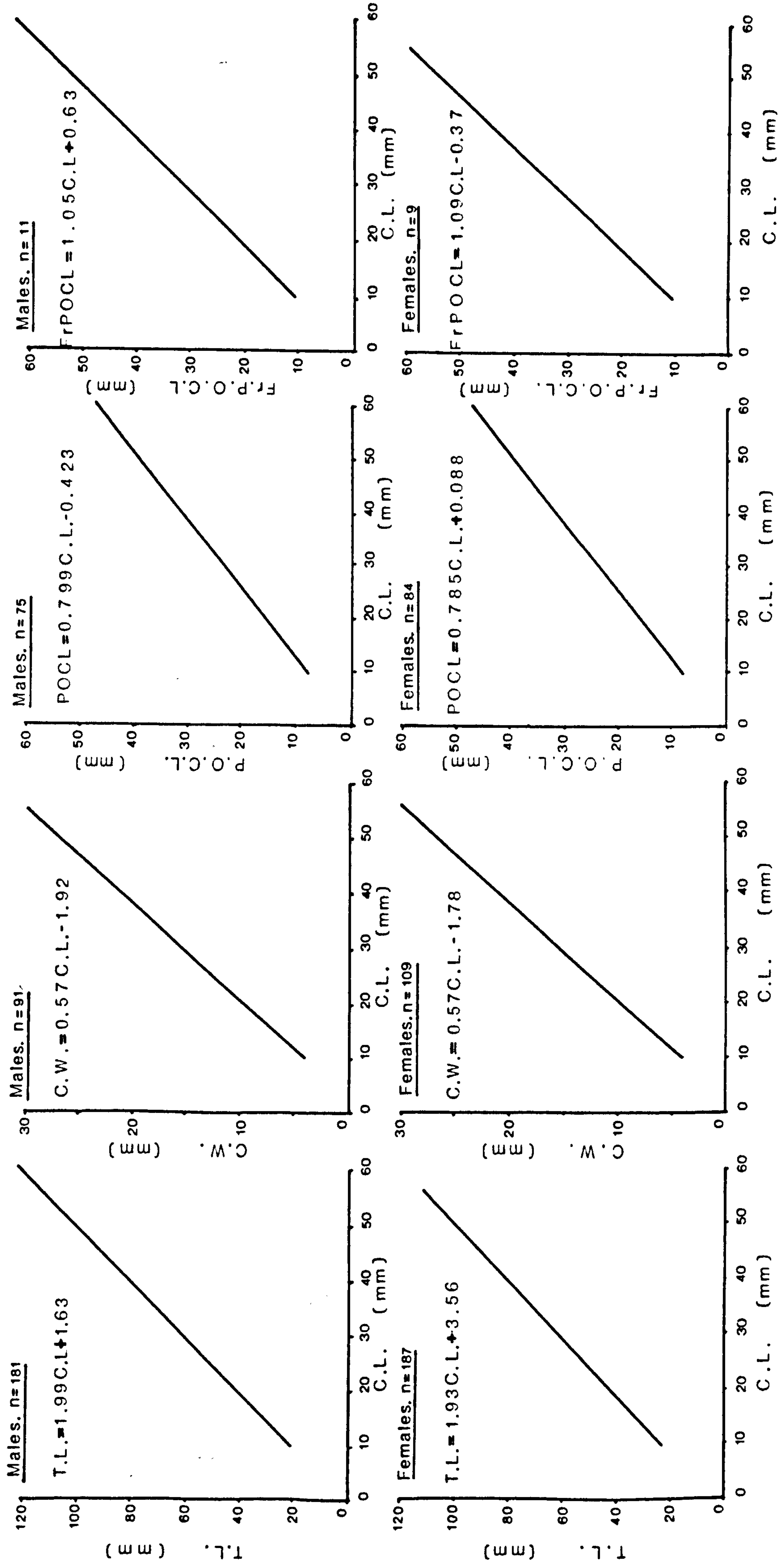
Location	Sex	Regression Equation	r	n.	Eqn. No.
<u>C.L. X T.L.</u>					
All sites	♂	T.L. = 1.996.C.L. + 1.63	0.985	181	[1]
	♀	T.L. = 1.927.C.L. + 3.56	0.910	187	[2]
Clattercote	♂	T.L. = 2.023.C.L. + 0.738	0.996	98	[3]
	♀	T.L. = 2.082.C.L. + 0.719	0.946	56	[4]
	Both	T.L. = 2.036.C.L. + 0.717	0.996	161	[5]
<u>C.L. x C.W.</u>					
All sites	♂	C.W. = 0.575.C.L. - 1.92	0.983	91	[6]
	♀	C.W. = 0.568.C.L. - 1.78	0.965	109	[7]
Clattercote	♂	C.W. = 0.645.C.L. - 3.593	0.745	130	[8]
	♀	C.W. = 0.637.C.L. - 3.424	0.974	58	[9]
<u>C.L. x P.O.C.L.</u>					
All sites	♂	P.O.C.L. = 0.799.C.L. - 0.423	0.981	75	[10]
	♀	P.O.C.L. = 0.785.C.L. + 0.088	0.988	84	[11]
Clattercote	♂	P.O.C.L. = 0.818.C.L. - 1.676	0.935	119	[12]
	♀	P.O.C.L. = 0.781.C.L. - 0.44	0.984	59	[13]
<u>C.L. x Max. P.O.C.L.</u>					
All sites	♂	Max. P.O.C.L. = 1.05.C.L. + 0.63	0.997	11	[14]
	♀	Max. P.O.C.L. = 1.09.C.L. - 0.37	0.999	9	[15]
<u>C.L. X Freshweight</u>					
All sites	♂	$\log_{10} \text{wt.} = 2.986 \cdot \log_{10} \text{C.L.} - 2.026$	0.978	50	[16]
	♀	$\log_{10} \text{wt.} = 3.069 \cdot \log_{10} \text{C.L.} - 1.457$	0.917	70	[17]
Clattercote	♂	$\log_{10} \text{wt.} = 3.15 \cdot \log_{10} \text{C.L.} - 3.75$	0.968	299	[18]
	♀	$\log_{10} \text{wt.} = 3.28 \cdot \log_{10} \text{C.L.} - 3.97$	0.990	287	[19]

TABLE 6.3(b) : MORPHOMETRIC RELATIONSHIPS OF A.PALLIPES, IN THE THAMES

CATCHMENT, SHOWING SEXUAL DIMORPHISM.

Location	Sex	Size Group	Regression Equation	t-test t	details df	p	Eqn. No.
<u>C.L. x 2A.W.</u>							
All sites	♂	C.L.<26.0mm	2A.W.= 0.494C.L.-0.513	3.167	182	<0.001	[20]
	♂	C.L.>26.0mm	2A.W.= 0.445C.L.+1.272				[21]
Clattercote	♂	C.L.<30.0mm	too little data	-	-	-	-
	♂	C.L.>30.0mm	2A.W.=0.439C.L.+1.617				[22]
All sites	♀	C.L.<23.0mm	2A.W.=0.530C.L.-1.008	9.54	149	<0.001	[23]
	♀	C.L.>23.0mm	2A.W.=0.677C.L.-4.254				[24]
Clattercote	♀	C.L.<29.0mm	too little data	-	-	-	-
	♀	C.L.>29.0mm	2A.W.=0.687C.L.-4.622				[25]
<u>C.L. x Ch.L.</u>							
All sites	♂	C.L.<32.0mm	Ch.L.=0.727C.L.-2.359	16.91	365	<0.001	[26]
	♂	C.L.>32.0mm	Ch.L.=1.455C.L.-26.221				[27]
Clattercote	♂	C.L.<32.0mm	Ch.L.=0.810C.L.-4.983	5.89	224	<0.001	[28]
	♂	C.L.>32.0mm	Ch.L.=1.465C.L.-26.582				[29]
All sites	♀	C.L.<32.0mm	Ch.L.=0.627C.L.-0.959	9.33	269	<0.001	[30]
	♀	C.L.>32.0mm	Ch.L.=0.921C.L.-10.541				[31]
Clattercote	♀	C.L.<30.0mm	too little data	-	-	-	-
	♀	C.L.>30.0mm	Ch.L.=0.862C.L.-7.929				[32]

morphometric relationships for *A. pallipes* in the Thames Catchment.



C.L. : 2A.W. and C.L.:Ch.L for A. pallipes

in the Thames Catchment.

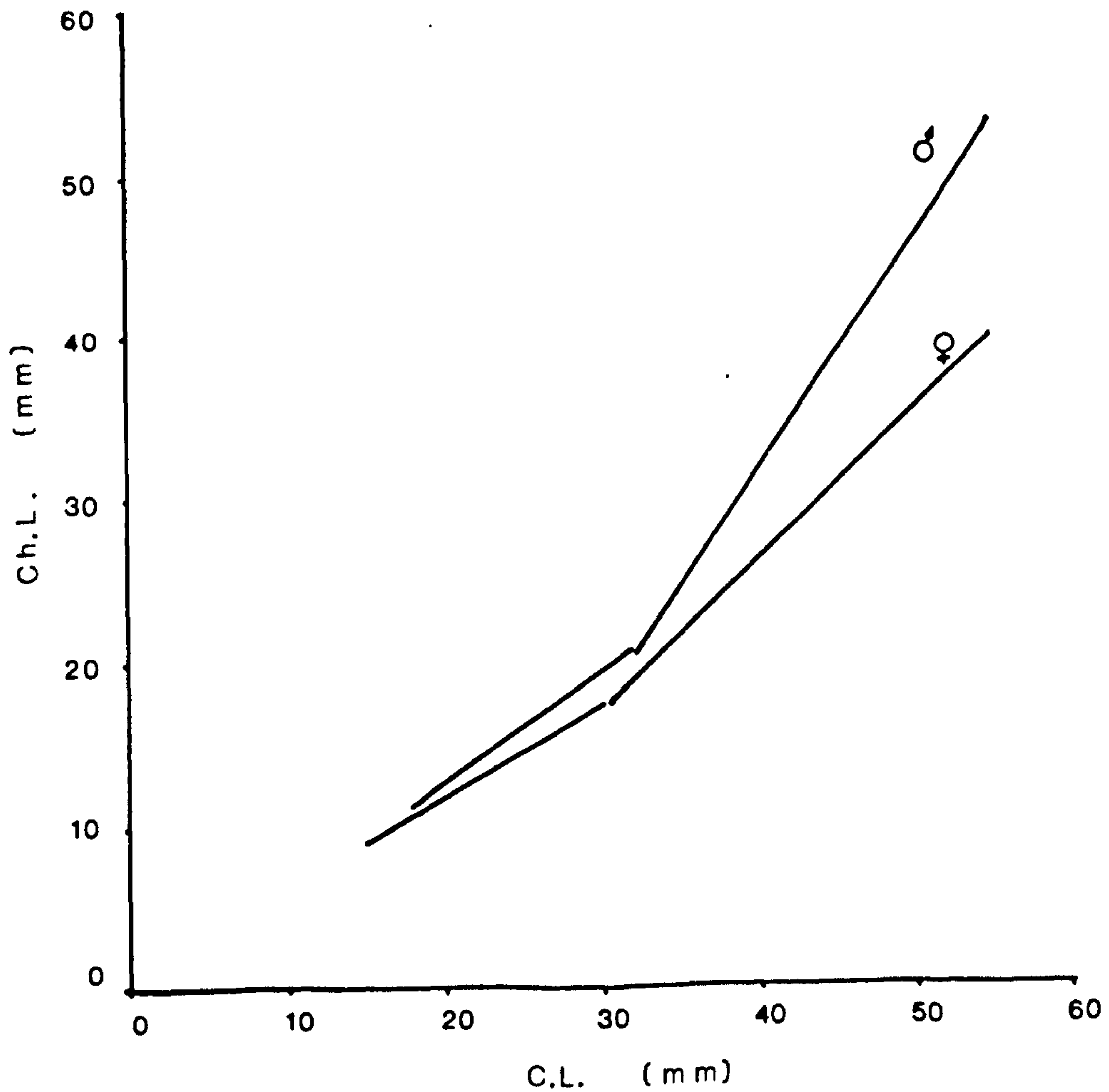
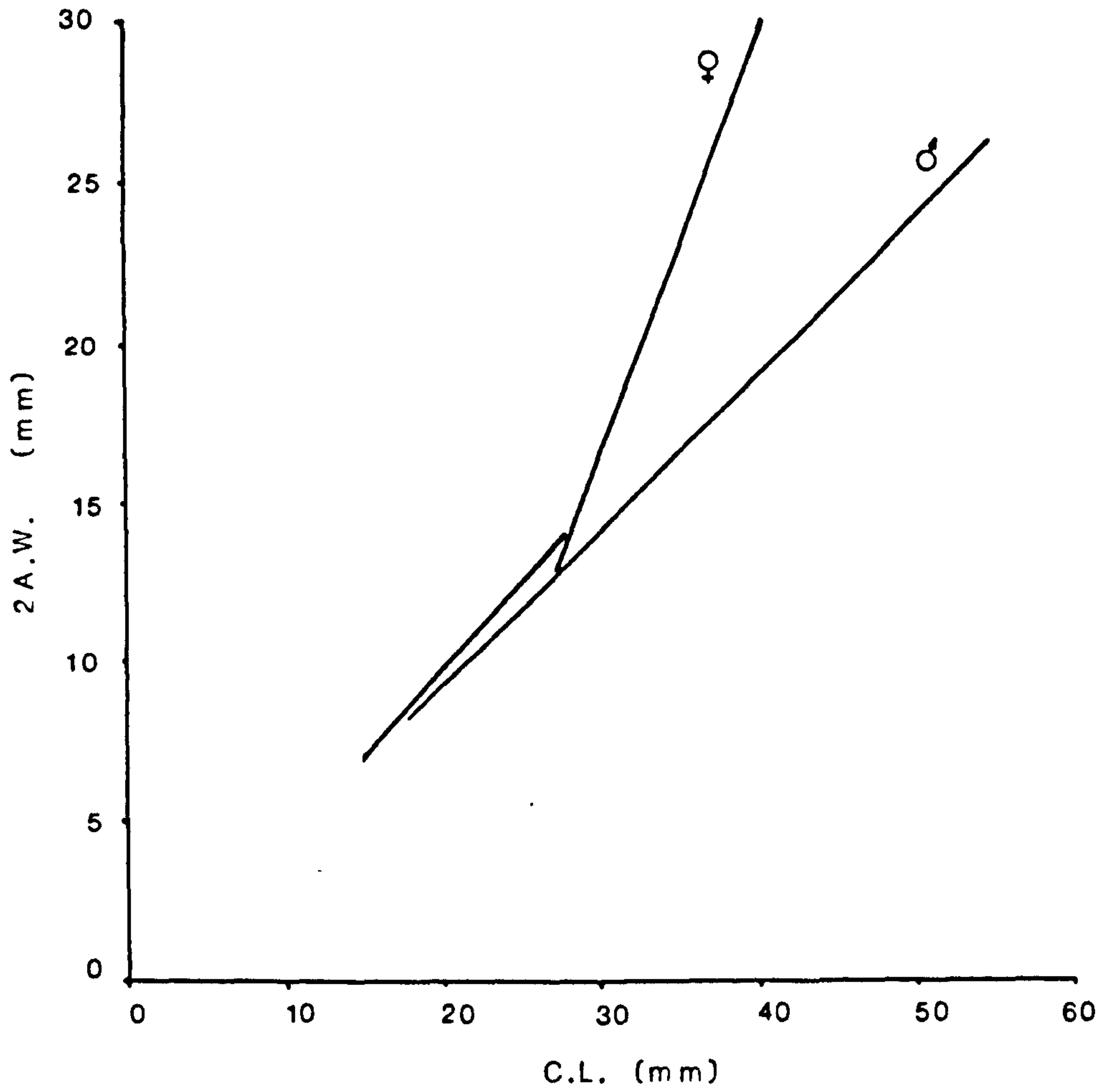


Figure 6.6 (c) Graphs showing the relationship of C.L. : Weight for A. pallipes in the Thames Catchment.

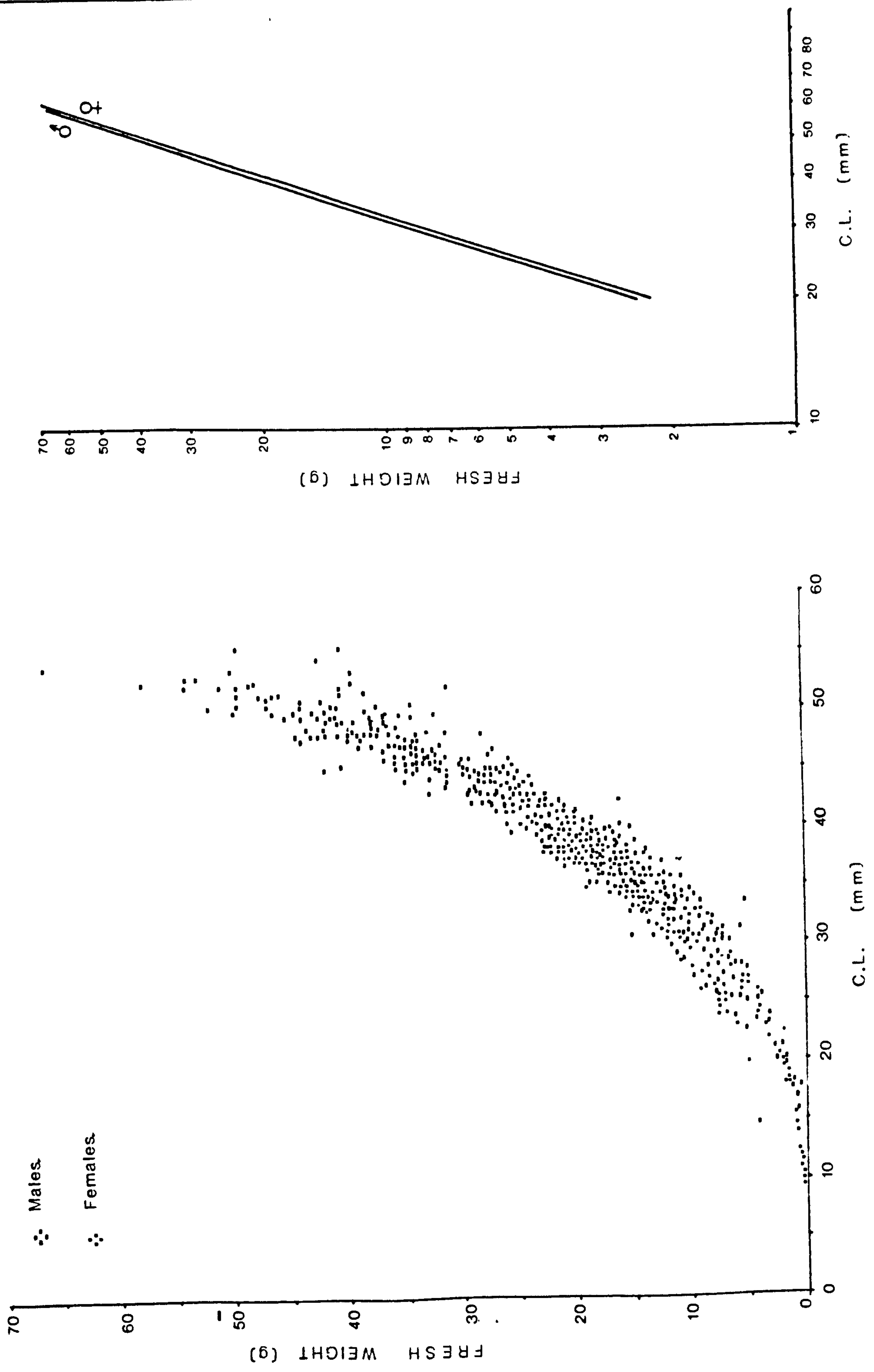


TABLE 6.4 : SIZE AT MATURITY OF A.PALLIPES IN THE U.K.
(PUBLISHED DATA.)

Sex	Size (C.L.) m.m.	Location	Reference
Males	22.0	Durham	Brown + Bowler, 1977.
	23.0	Kent	Thomas + Ingle, 1971.
	26.0	Bucks.	Pratten, 1980.
	*c32.0	Thames C.	This study.
Females	23.1	Notts.	Rhodes + Holdich, 1982.
	25.0	Durham	Brown + Bowler, 1977.
	26.0	Bucks.	Pratten, 1980.
	27.0	Kent	Thomas + Ingle, 1971.
	28.0	Ireland	Moriarty, 1973.
	*23.0	Thames C.	This study.

* Size after which sexual dimorphism is evident - see 6.2

The relationship of C.L. to T.L. for A.pallipes from Clattercote Reservoir is not significantly different ($p < 0.05$) to that of crayfish from all other sites in the Thames Catchment.

The results obtained indicate that female A.pallipes have proportionally longer abdomens (c.2%) than males at 20.0 mm C.L. but that at 50.0 mm C.L. the male abdomen is longer (c.1%). Presumably this difference facilitates maximum egg-carrying capacity in newly mature female A.pallipes. A similar feature has been recorded elsewhere for A.pallipes (Rhodes & Holdich, 1979) and P.leniusculus (Mason, 1975).

Equations describing the ratio of C.L. to C.W. (see Table 6.3(a)) are comparable with those reported elsewhere:-

$$C.W. = 0.554 C.L. - 1.716 \quad C.W. = 0.539 C.L. - 1.167$$

(Brown, 1979).

In addition to the use of C.L. and T.L. as features for measurement of crayfish size other workers have used P.O.C.L. This is measured to the mid-point of the posterior rim of the cephalothorax (see Figure 2.1) or to the most distal point of the posterior rim of the carapace (French P.O.C.L.). The calculation of the relationships between these parameters and C.L. has enabled such published data to be compared with data from the current study. The process of obtaining such measurements, in the field, highlighted the fact that the easiest, quickest and possibly most accurate method of measuring crayfish is the straightforward C.L. measured from the apex of the rostrum to the posteromedial rim of the carapace.

Together with the C.L. : C.W. relationship, Table 6.3(a), the information collected regarding the morphometry of the cephalothorax in A.pallipes in the Thames Catchment can be summarised as follows:

$$2.24 \text{ F.P.O.C.L.} : 2.07 \text{ C.L.} : 1.61 \text{ P.O.C.L.} : 1 \text{ C.W.}$$

$$2.22 \text{ F.P.O.C.L.} : 2.07 \text{ C.L.} : 1.64 \text{ P.O.C.L.} : 1 \text{ C.W.}$$

-Overall body form can be reduced to the relationship of T.L. to C.L. and C.W. For individuals from the Thames Catchment this relationship is as follows:-

4.3. T.L. : 2.1 C.L. : 1 C.W.

This is similar to the 4 : 2 : 1 relationship for a northern population of A.pallipes (Brown, 1979)

In order to assess the success of crayfish populations at different locations, often in widely differing habitats, relatively rapid and simple methods of comparison are required. The growth rate and body form are two ways by which such comparisons could be made. Growth rate itself is difficult to measure in the field but will be related to the size at which both males and females reach maturity. In female A.pallipes the abdomen of mature individuals is significantly wider, in relation to C.L., than in immature individuals and males (Rhodes & Holdich, 1982). This modification is presumed to facilitate maximum egg carrying capacity. The point at which this alteration in body form occurs has been calculated using multiple regression analysis. Unfortunately too little data was collected from juvenile crayfish (< 30 mm.C.L.) in the Clattercote population to enable the size of females at maturity to be estimated from the increase in abdomen width using this method. The data that was collected has been used to calculate this size for A.pallipes in the Thames Catchment as a whole.

The smallest ovigerous female collected: 21.0 mm.C.L. from Clattercote Reservoir (13.5.81) was very close to the calculated size for increased abdomen widening in females (23.0 mm.C.L; see Table 6.3(b)). This is smaller than the 25.0 mm.C.L. (Brown, 1979), 27.0 mm.C.L. (Thomas & Ingle, 1971) and 23.1 mm C.L. for river populations and 28.2 mm.C.L. for a reservoir population (Rhodes & Holdich, 1982) reported elsewhere but is more comparable with the 20.0 mm.C.L. recorded in Northern Ireland (Watson, unpubl). It has been observed (Thomas & Ingle, 1971) that specimens of both

sexes of 22.0 mm.C.L. mate and that females > 23.0 mm C.L. successfully receive spermatophores.

In male A.pallipes the chelae are proportionally larger in mature crayfish and it is possible to calculate the size at which this change occurs (Rhodes & Holdich, 1982). The allometric relationship of C.L. to chela length has been reported to be similar in males and females up to 30.0 mm.C.L. and to be described by the equations:-

$$\begin{array}{l} \text{Log}_{10} \text{ ChL.} = 0.025 \text{ C.L.} + 0.572 \\ \text{ChL}^{0.5} = 0.097 \text{ C.L.} + 1.445 \\ (<29 \text{ mm.C.L.}) \text{ ChL} = 0.672 \text{ C.L.} - 1.134 \\ (<30.7 \text{ mm.C.L.}) \text{ ChL} = 0.648 \text{ C.L.} - 1.037 \end{array} \left. \begin{array}{l}) \\) \\) \\) \end{array} \right\} \begin{array}{l} \text{Brown \& Bowler, 1977} \\ \text{Rhodes \& Holdich, 19} \end{array}$$

Comparable data for A.pallipes in the Thames Catchment is presented in Table 6.3(b).

These types of relationship can be interpreted to suggest that a change in growth pattern occurs just after sexual maturity (Brown, 1979). The increase in relative chela size at 32.0 mm.C.L. for both males and females from both Clattercote Reservoir and elsewhere in the Thames Catchment (see Table 6.3(b)) occurs at a larger size than the 29.0 mm.C.L. and 30.7 mm.C.L. for males and females respectively, reported elsewhere (Rhodes & Holdich, 1981). If it is assumed that this inflection point occurs at the post-maturity moult then maturity in male A.pallipes in those populations would occur at about 29.0 mm.C.L., i.e. 32.0 mm. - c.10% moult increment (Brewis & Bowler, 1982).

The minimum C.L. at maturity of A.pallipes in the Thames Catchment is compared with published data in Table 6.4. It can be seen that this value is generally larger in the Thames Catchment than figures reported in other studies. This suggests that faster initial growth of A.pallipes occurs in southern populations (c.f. P.leniusculus - Chapter 8), It has, however, also been reported that male A.pallipes of only 22.0 mm.C.L. are capable of copulation (Brown, 1979).

The calculated mean size at maturity is, therefore, apparently considerably greater than the minimum recorded size at which both male and female A.pallipes mature.

The relationship of length to live weight is often established from empirical data to enable the expected weight attainment of crayfish from natural stocks to be calculated. Equations relating length to weight are useful for assessing relative condition and growth, the comparison of data from different sites and the estimation of standing-crop and productivity. During this study the length-weight relationship of A.pallipes from Clattercote Reservoir (Chapter 4) and P.leniusculus from Stratfield Saye (Chapter 8) have been calculated.

As can be seen, Figure 6.6(c), male A.pallipes achieve a greater maximum weight than females of a similar length; a feature also reported for other populations of crayfish: e.g. A.pallipes (Rhodes, 1980), A.astacus (Kossakowski, 1966) and A.leptodactylus (Nefedov & Mazanov, 1973). In this study the slopes of the log. plots of male and female data are shown to be significantly different ($p < 0.01$). This difference can be explained by the sexually dimorphic chelae, which are larger in males than in females. Although chela size in both sexes has been shown to be dimorphic, in this study, the slope of the plot of C.L. and chela length (Figure 6.6(b)) for males is significantly greater than that for females ($p < 0.01$). Comparison of the length-weight equations for A.pallipes in the Thames Catchment, Table 6.3(c), with the following published equations suggests there is little difference between populations of A.pallipes in the U.K. when compared with similar data for P.leniusculus. The statistical significance of this apparent similarity could not be tested.

$$\left. \begin{array}{l} \log_{10} \text{wt.} = 3.325 \log_{10} \text{ C.L.} - 5.107 \\ \log_{10} \text{wt.} = 3.139 \log_{10} \text{ C.L.} - 4.823 \end{array} \right\} \text{ (Rhodes, 1980)}$$

$$\left. \begin{aligned} \log_{10} \text{ wt.} &= 3.277 \log_{10} \text{ C.L.} - 3.928 \\ \log_{10} \text{ wt.} &= 3.155 \log_{10} \text{ C.L.} - 3.749 \end{aligned} \right\} \text{ (Brown, 1979)}$$

This interspecific difference is due primarily to the possession of large chelae by adult P.leniusculus (Rhodes, 1980).

The length-weight equations derived during this study satisfactorily fit the empirical data. The 'b' values for A.pallipes in the Thames Catchment indicate allometric growth in both males and females, i.e. $b > 3$. No distinction was made between mature and immature individuals during the analysis of the length-weight data. Elsewhere juveniles have been shown to exhibit isometric growth, i.e. $b < 3$ (Rhodes, 1980).

The maximum weights attained by A.pallipes sampled during this study are tabulated overleaf, together with similar information for this and other crayfish species elsewhere in Europe. As can be seen the maximum recorded size of crayfish in Europe varies widely but A.pallipes is a relatively small species. This alone should not discount this crayfish as a candidate for commercial interest (Rhodes, 1980).

C.F. information (e.g. Table 4.7) provides a guide to the 'biological condition' of crayfish as regards food availability, population density and gonad development, etc. (Rhodes, 1980). It may be of importance when considering returns during cropping or for indicating conditions which favour high natural production. Such data may, therefore, provide a basis for implementing management operations for exploited populations.

Data from A.pallipes collected from Clattercote Reservoir revealed significant differences in C.F. between males and females and ovigerous and non-ovigerous females (see 4.4(iv)). Insufficient data was available, however,

Species	Maximum weight (gms)		Reference
	Male	Female	
A.pallipes	66.79 (Clattercote 25.9.80)	38.74 (Clattercote 17.7.82)	This study
"	60.0	-	Brown, 1979
"	58.7	-	Rhodes, 1980
"	88.0	-	Laurent & Forest, 1979
A.leptodactylus	150.0+	-	Laurent & Forest, 1979
A.leptodactylus	158.0+	43.0	Nefedov & Mazanov, 1973
A.astacus	75.0	46.0	Lindqvist & Loeckari, 1975
"	150.0	75.0	Kossakowski, 1966
O.limosus	30.0	35.5	Jestin, 1979
O.limosus	40.0+	-	Laurent & Forest, 1979
P.leniusculus	150.0+	-	Laurent & Forest, 1979
"	197.0	118.0	This study (site 2)

to enable a comparison of C.F. values from different sites to be made. Elsewhere there was no significant difference in C.F. values for A.pallipes collected from Midlands populations (Rhodes, 1980). In Sweden, however, differences in C.F. values in some populations of A.astacus, due to reduced chelar growth (Abrahamsson, 1972) and stunting (Svårdsson, 1949) have been reported.

6.4. Observations on diseases and parasites of *A.pallipes* in the Thames Catchment.

6.4.(a) The occurrence of the crayfish parasite *Thelohania contejeani*.

6.4a(i) - Introduction.

A crayfish disease that was occasionally encountered during the course of this study was 'Porcelain' or 'White-Tail' disease caused by the genus *Thelohania* (Sporozoa: Microsporidia). This parasitic organism is known from the U.S.A. (Sprague, 1950; Unestam, 1969), mainland Europe and the U.K. (e.g. Vey & Vago, 1973; Unestam, 1973; Cossins & Bowler, 1974; Lilley, 1977), Russia (Voronin, 1971), Australia (Carstairs, 1979) and New Zealand (Jones, 1980). Only one species, *Thelohania contejeani* (Henneguy, 1892) is reported to infect the European crayfish *A.astacus* (Şumari & Westman, 1969; Voronin, 1971), *A.leptodactylus* (Mazyliś, 1973) and *A.pallipes* (Pixell-Goodrich, 1956; Vey & Vago, 1973; Cossins & Bowler, 1974; O'Keefe, in press). Infection is caused by an invasion primarily of striated muscle tissue which is eventually replaced by a mass of spores (Cossins & Bowler, 1974). Crayfish parasitised by *T.contejeani* characteristically have an opaque white appearance of the abdominal muscle, if viewed through the abdominal sternites, compared with the translucent appearance of normal muscle (Cossins & Bowler, 1974) so individuals in the later stages of infection can be readily identified by visual examination of the ventral side of the abdomen. Infection is believed to be caused by the dissemination of spores from a dead host or by consumption of an infected individual by another crayfish (Cossins & Bowler, 1974; Holdich, et al, 1978) and leads to a progressive loss of muscle function, paralysis and death (Cossins, 1973). Infected crayfish may survive for several months (Vey, et al, 1971) or one to two years (Bowler & Brown, 1977).

The occurrence of T.contejeani in A.pallipes in England and Wales has been quite widely reported with infected crayfish occurring in populations in Northumberland, Derbyshire, Surrey (Cossins & Bowler, 1974) Oxfordshire, Buckinghamshire (Pixell-Goodrich, 1956) and the River Wye, Gwent (Lilley, et al, 1979). It is also known to occur in Eire (O'Keefe, in press) although previous reports stated that it had never been recorded there (Reynolds, 1979). The widespread distribution of this parasite suggests that it is a permanent feature of many, if not all, native crayfish populations in the U.K. although it may frequently be overlooked as the proportion of infected individuals in a population is generally low. In the U.K., and elsewhere, the reported incidence of infection of A.pallipes ranges from 3.4% (Lilley, et al, 1979), 9% (Holdich, et al, 1978) 9% (Brown & Bowler, 1977), 11% (Vey & Vago, 1973) to 18% (Pixell-Goodrich, 1956). Published figures for infection of A.astacus range from <2% (Nylund & Westman, 1979), 11% (Sumari & Westman, 1969) to 30% (Schäperclaus, 1954). It has, however, been concluded that T.contejeani present at such levels of incidence has little serious effect on populations of A.pallipes in the U.K.: (Cossins & Bowler, 1974) although it is reputed to have "exterminated whole populations of crayfish" elsewhere (Kossakowski, 1973).

6.4a(ii) - Methods.

During the general survey of crayfish distribution and biology in the Thames Catchment, carried out during the period 1979 to 1981, records were kept of any diseased or abnormal specimens that were collected (see Chapter 2). The presence of T.contejeani was recorded if crayfish were seen to have the opaque, white abdominal muscle characteristic of 'porcelain disease'. Presence of the parasite was confirmed in a small number of individuals (n = 34) collected from different locations. Microscopical examination of fresh and fixed samples of muscle suspected to contain T.contejeani spores was also carried out. Fresh muscle smears were

examined live under phase-contrast or stained with Toluidine Blue (Vey & Vago, 1973). Material fixed in methanol was stained with Giemsa's Solution (Cossins & Bowler, 1974) prior to examination.

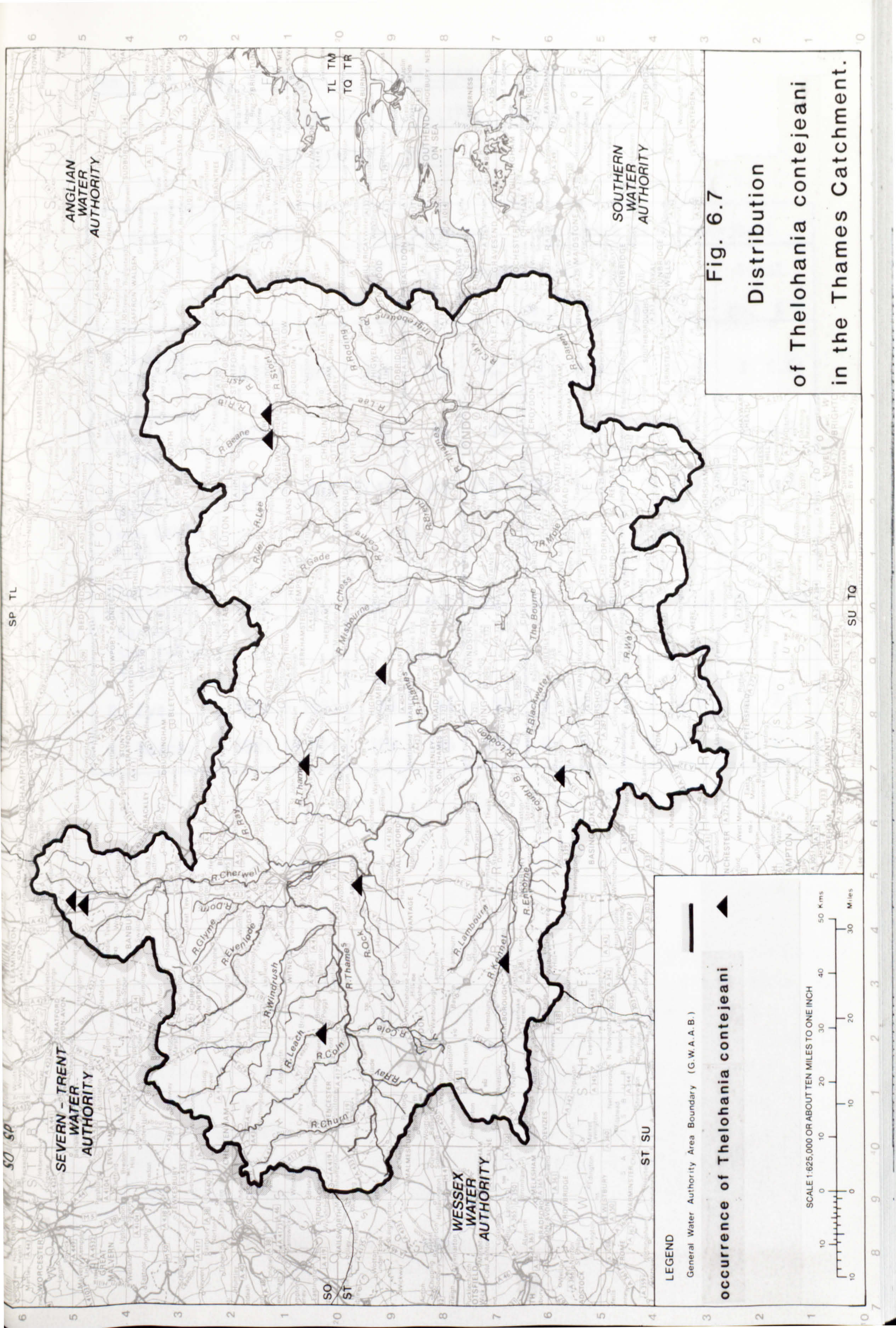
6.4a(iii) - Results.

Crayfish, A.pallipes, infected with the microsporidian T.contejeani were obtained from a total of 10 sites in the Thames Catchment. These sites, located on Figure 6.7, constitute 15% of the number of sites from which crayfish were examined.

At the six sites from which large numbers ($n > 50$) of adult A.pallipes were examined the incidence of the parasite has been calculated, see Table 6.5. The data on T.contejeani incidence obtained from Clattercote Reservoir, Banbury (see Chapter 4) and the River Lee at Ware (see Chapter 5) has also been used to assess fluctuations in the incidence of T.contejeani in crayfish populations. A comparison has also been made of the incidence of diseased crayfish occurring in hand-caught and trapped samples (see Table 4.13).

6.4a(iv) - Discussion.

The information concerning the occurrence of the crayfish parasite, T.contejeani collected during the course of this study suggests that it occurs at a relatively small number of sites in the Thames Catchment, (Figure 6.7). The figure of 15% occurrence may, however, be an underestimate as the majority of positive records of the presence of T.contejeani are at sites from which larger numbers of A.pallipes have been examined. From these positive sites an average of 700 (range 1 to 3,354) adult crayfish were examined whereas at the negative sites an average of only 68 (range 1 to 156) were examined. Consequently the small number of A.pallipes examined from some sites may have precluded the collection of parasitised individuals, although at some of the positive sites only small samples of crayfish



LEGEND

General Water Authority Area Boundary (G.W.A.A.B.)

occurrence of *Thelohania contejeani*

SCALE 1:625,000 OR ABOUT TEN MILES TO ONE INCH



Fig. 6.7

**Distribution
of *Thelohania contejeani*
in the Thames Catchment.**

TABLE 6.5 : THE INCIDENCE OF T.CONTEJEANI AT SITES KNOWN TO
CONTAIN INFECTED A.PALLIPES. (WHERE NO. OF
CRAYFISH EXAMINED >50.)

Site	Date	No. examined			Incidence of T.contejeani					
		♂	♀	Total	♂		♀		Total	
					No.	%	No.	%	No.	%
R. Loddon, Sherfield.	1979 - 1980	226	238	464	2	0.88	1	0.42	3	0.64
Scotsgrove Brook, Thame.	1979	37	59	96	2	5.4	3	5.1	5	5.2
R. Lee, Ware. (see table 5.8)	1979 + 1980	2013	976	2989	10	0.5	1	0.1	11	0.4
Clattercote Reservoir, Banbury. (see table 4.11)	1979 - 1982	2883	2905	5788	34	1.18	25	0.86	59	1.02
R. Eye.	1978 + 1981	49	46	95	5	10.2	2	4.3	7	7.4
R. Beane.	1981 (8.5)	109	146	275	0	0	0	0	0	0

were examined (n = 1 to 6) and found to include crayfish parasitised by T.contejeani. In addition, as the disease is density dependent (Brown & Bowler, 1977), infection may persist at a low, stable level for some years but could, under certain conditions, reach relatively high levels and cause a population crash (O'Keefe, in press). This may explain some reported declines in crayfish populations in the past (e.g. Duffield, 1933). Overall, then, T.contejeani occurs in at least 15% of sites examined in the Thames Catchment although the actual extent of its occurrence may be considerably higher.

The incidence of infection of A.pallipes with T.contejeani at sites from which it has been recorded during this study ranges from 0.64% to 8.8% (only sites where the crayfish samples >50). These figures are low when compared with some of the published data, e.g. 30% in Germany (Schäperclaus, 1954) and around 30% in Limoges, France (Reynolds, in O'Keefe, in press) but compare favourably with reported levels of infection from elsewhere in the U.K., e.g. 9% (Holdich, et al 1978), 0.9 to 12.9% (Brown, 1979) and 0.7 to 1.2% (O'Keefe, in press). The occurrence of T.contejeani in the Thames Catchment and the incidence of disease at the positive sites may also be underestimated due to the fact that microscopical examination of all the A.pallipes in a sample has been reported to increase the detectable incidence of T.contejeani by 1.3% when compared with a visual examination (O'Keefe, in press).

At the two sites from which crayfish have been examined for the presence of T.contejeani in consecutive years some annual and seasonal fluctuation in the incidence of the disease is evident. At Clattercote Reservoir, Banbury (see Chapter 4) the incidence of T.contejeani was found to be greatest in the month of July, for both hand caught and trapped samples, in 1980 and 1982 (see Table 4.13). In 1981 few parasitised crayfish were collected although sampling also took place in the summer months of May, June and September.

In the River Lee at Ware Lock (see Chapter 5) A.pallipes visibly parasitised by T.contejeani (see Table 6.5) were similarly found in low numbers and only occurred in June and September, 1980 and May 1981.

As very little information has been published regarding the size distribution of infected A.pallipes it is interesting to note that parasitised males of C.L. 17.0 mm. to 53.0 mm. and females of C.L. 23.0 mm. to 48.7. mm were collected during the course of this study. Elsewhere the youngest infected crayfish in an Irish population of A.pallipes was estimated to be age 3+ (C.L. 28.0 mm.) and the majority of infected animals were at least 4+ (C.L. 34.0 mm.) (O'Keefe, in press). The current data establishes that a lower minimum size of infected crayfish exists in the Thames Catchment. The influence of size on the probability of infection can be tentatively explained by the period of time from initial colonisation until visible signs of the disease are evident; in addition differences in feeding habits may be important (O'Keefe, in press) with adult crayfish being more carnivorous and cannibalistic than juveniles (Goldman, et al, 1975).

The progressively debilitating nature of the disease should render parasitised A.pallipes more susceptible to capture by hand. It has been reported that heavily infected crayfish are unable to exhibit the characteristic 'tail-flick' escape response (Cossins & Bowler, 1974) and so are less able to evade capture. Conversely it has also been suggested that the disease may influence the likelihood of infected crayfish entering traps (Bowler, in Unestam, 1973) as they are less mobile. Examination of the occurrence of diseased A.pallipes in samples collected by different methods from Clattercote Reservoir (see Chapter 4) would support this theory; only 13.6% of infected crayfish were caught by trapping (see Table 4.13). This bias would also partly explain the low incidence of T.contejeani in trapped samples of crayfish elsewhere in the Thames Catchment (e.g.

River Lee, Chapter 5 (see Table 6.5). The low incidence of infected crayfish in trapped samples reflects their reduced mobility (Cossins, 1973) which would make them less able to search for food and climb into the trap entrances (O'Keefe, in press). In addition there is also some evidence that diseased animals are forced to occupy the less favourable parts of the habitat. Indeed in an Irish study some 78% of diseased crayfish were collected from an area with no shelter and reduced food availability (O'Keefe, in press).

A small number of P.leniusculus (n =58) and A.leptodactylus (n =40) were also examined for the presence of parasites and disease during the course of this study but were not found to be infected with T.contejeani. There are no confirmed reports in the literature of the former species being parasitised by T.contejeani elsewhere, although infected P.leniusculus are reputed to occur in the U.S.A. (McGriff, unpubld, 1983) and Sweden (Fürst, in Westman & Pursainen, 1982). Other crayfish species, from New Zealand (i.e. Paranephrops planifrons - Jones, 1980), Australia (i.e. Cherax destructor - Carstairs, 1979) and the U.S.A. (i.e. Cambarus bartoni - Sprague, 1950; Cambarellus shufeldti - Sogandares-Bernal, 1962; Procambarus acutus and P.simulans - Johnson, 1977) are, however, known to be susceptible to infection by the genus Thelohania.

6.4.(b). The occurrence of the crayfish parasite
Branchiobdella astaci in the Thames Catchment.

6.4b(i) - Introduction.

Branchiobdellid worms are adapted to a life as epizoites on crustaceans. They are found on the Astacine crayfish of Europe, the Cambaroidines of eastern Asia and on both the Astacines and Cambarines of North America (Holt, 1965). They have also been recorded from other freshwater crustaceans : two families of freshwater crabs, a cave-dwelling isopod and a freshwater shrimp (Holt, 1963, 1965; Liang, 1963). There are currently more than 120 known species of Branchiobdellidae, in 17 genera, worldwide (Holt, 1977).

At present the Branchiobdellidae are included in the Oligochaeta although their systematic position is unclear and it has been proposed that a separate order, Branchiobdellida, should be formed (Holt, 1965). Morphologically these annelids are intermediate between the oligochaete worms and the leeches, Hirudinea (see Figure 6.8). The major differences between the Oligochaeta, Hirudinea and Branchiobdellida are listed in Table 6.6.

Branchiobdellids are thought to be primarily grazers, cropping the abundant supply of detritus and epizoic flora and fauna carried by their hosts. A few, such as the first formally described species Branchiobdella astaci (Odier, 1823), live in the gill chambers of their hosts apparently feeding on blood obtained by clipping the gill filaments (Holt, 1965).

The taxonomy of the European Branchiobdellidae is currently in some confusion (Holt, 1977) but has been reduced, by synonymy, to four species all in the genus Branchiobdella (Pop, 1965). A dichotomous key to these species (translated from Ude, in Dahl, 1929) is included in Appendix 7. A key to the genera of North American species has also been published (Pennak, 1978). In the U.K. there is only a single

TABLE 6.6 : COMPARISON OF MORPHOLOGY OF OLIGOCHAETES, LEECHES AND BRANCHIOBDELLIDS. (FROM HOLT, 1965)

	Oligochaeta	Branchiobdellidae	Hirudinea
No. of body segments		15	33
Setae	+/-	-	-
Prostomium	+	-	-
Suckers	-	+	+
Musculature		Hirudinean	Hirudinean
Dental placoids (Jaws)	-	2	3 (Gnathobdellids)
Nephridia		2	
Cephalisation	-	+	
Intestinal caecae		-	+/-
Reduced coelomic spaces		-	+
Ovaries posterior to testes	+	+	-

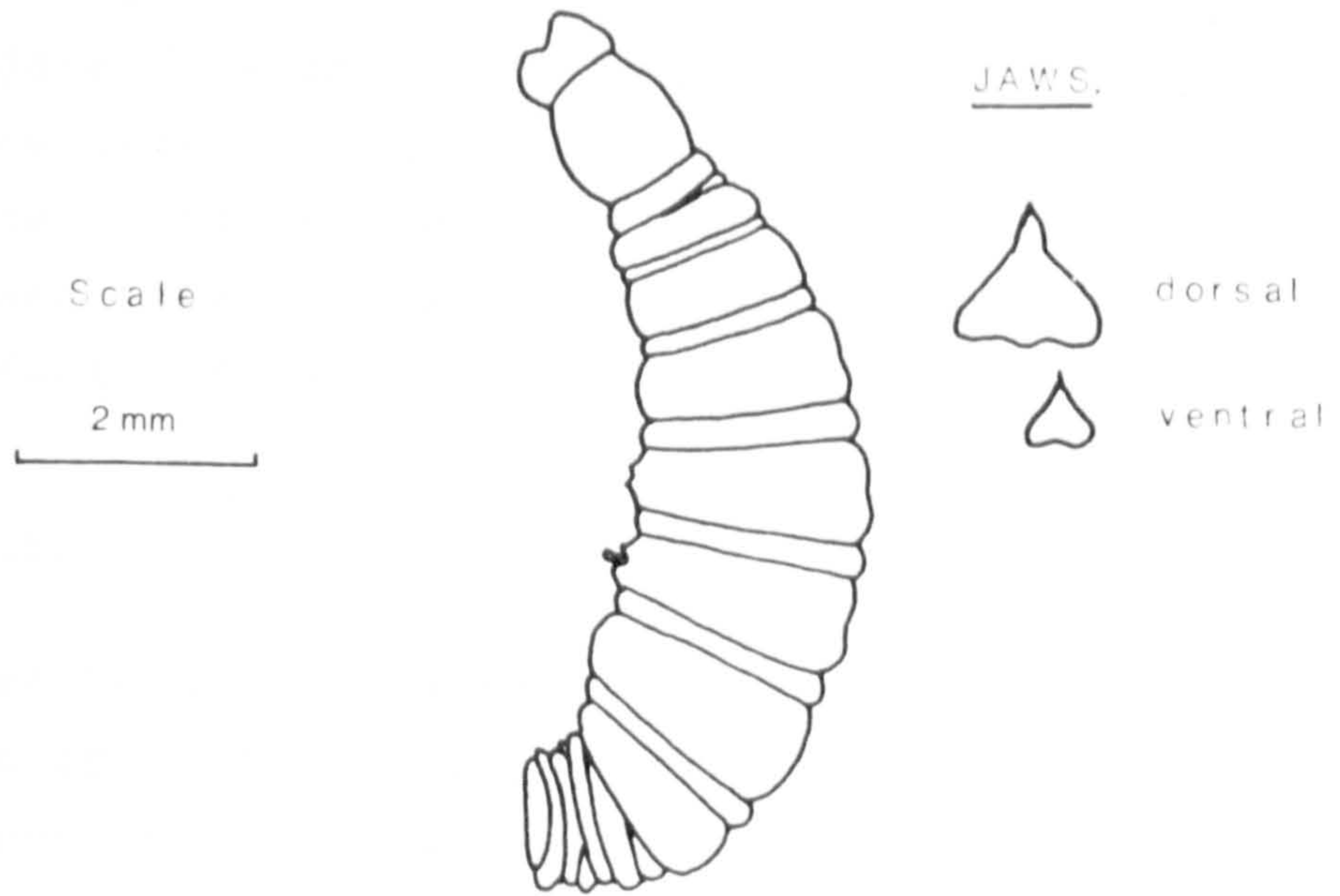
report of branchiobdellids occurring in the native crayfish, A.pallipes, (Leeke & Price, 1965). Elsewhere in Europe, however, branchiobdellids are quite widely distributed (Ude, in Dahl, 1929; Pop, 1965; Grabda & Wierzbicka, 1969; Karaman, 1970) and in some instances may cause problems in the culture and marketing of crayfish (Laurent, 1973).

6.4b(ii) - Methods.

During the current survey of crayfish distribution in the Thames Catchment crayfish have been examined, whenever possible, for the presence of branchiobdellids on the external surfaces and in the branchial chamber. For the purpose of examination crayfish were killed, usually by injection with chloroform (Mahoney, 1973), the branchiostegites removed and the gills dissected out. Removed material was examined for the presence of branchiobdellids using a Wild M8 binocular microscope. The sex, size (C.L. in mm.) and date and location of collection of the crayfish were recorded. The presence of branchiobdellids was noted if adult worms (preserved length 5.0 mm. - 12.0 mm.), juvenile worms (preserved length <1.5 mm.) or egg cocoons were found. The numbers involved in each category of infestation was determined. In some instances gill damage, typical of that observed in A.pallipes infected with branchiobdellid adults, was found and was recorded as the possible past presence of Branchiobdellidae in that individual (see Figure 6.8).

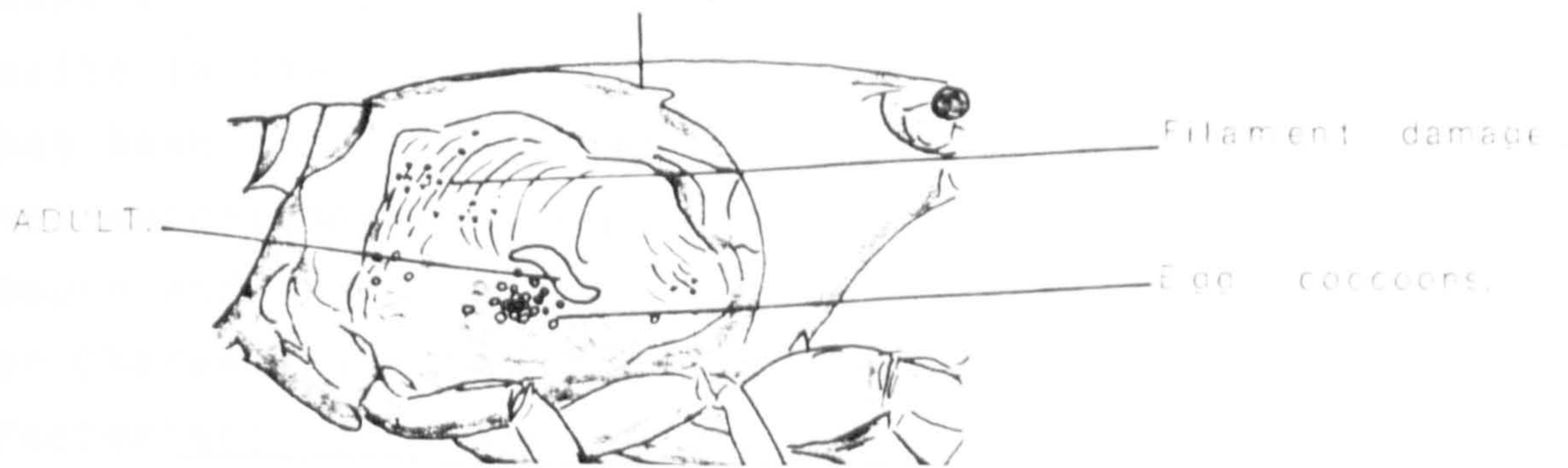
Specimens of branchiobdellid worms, if present, were removed, preserved in 70% Industrial Methylated Spirit and subsequently identified using a Wild M12 microscope and the key in Appendix 7 (transl. from Ude, in Dahl, 1929). In all cases the specimens obtained from A.pallipes in the Thames Catchment were identified as Branchiobdella astaci (Odier, 1823).

ADULT.



INFESTED A. PALLIPES.

Branchiostegite removed.



6.4b(iii) - Results:

The recorded occurrences of B.astaci, together with sites from which A.pallipes were examined but found to be free from the parasite, are illustrated in Figure 6.9. Details of site location; number, size and sex of crayfish examined; date of examination and the numbers of B.astaci found are recorded in Appendix 8. This information has been used to assess the frequency of occurrence, in terms of host size and time of year, of B.astaci at sites known to contain infected A.pallipes (see Table 6.7).

6.4b(iv) - Discussion.

As can be seen from Figure 6.9 B.astaci are not uncommon as epizoots of A.pallipes in the Thames Catchment. All specimens collected were identified as B.astaci, which is reported to infest both A.astacus and A.leptodactylus elsewhere in Europe (Pop, 1965). The distribution of this parasite in the Thames Catchment is apparently discontinuous. It has been found in all the major rivers comprising the Kennet subcatchment, i.e. the Rivers Kennet, Enborne, Lambourn and Dun; the River Eye in Gloucestershire; the River Cherwell and the Oxford Canal (South). In addition characteristic gill damage, see Figure 6.8, but no adult worms or egg cocoons, was found in specimens of A.pallipes collected from the River Whitewater in north Hampshire. The distribution of B.astaci may, however, be far more widespread than is suggested by these findings. It is interesting to note that it has not been found at sites linked to some of the positive locations, e.g. it was found in the Oxford Canal but not in the linked Clattercote Reservoir; the River Cherwell but not its tributaries the River Swere and the Sor Brook and possibly the River Whitewater but not the linked Rivers Loddon and Lyde.

There is only a single previous published record of B.astaci in the U.K. (Leeke & Price, 1965) which reported

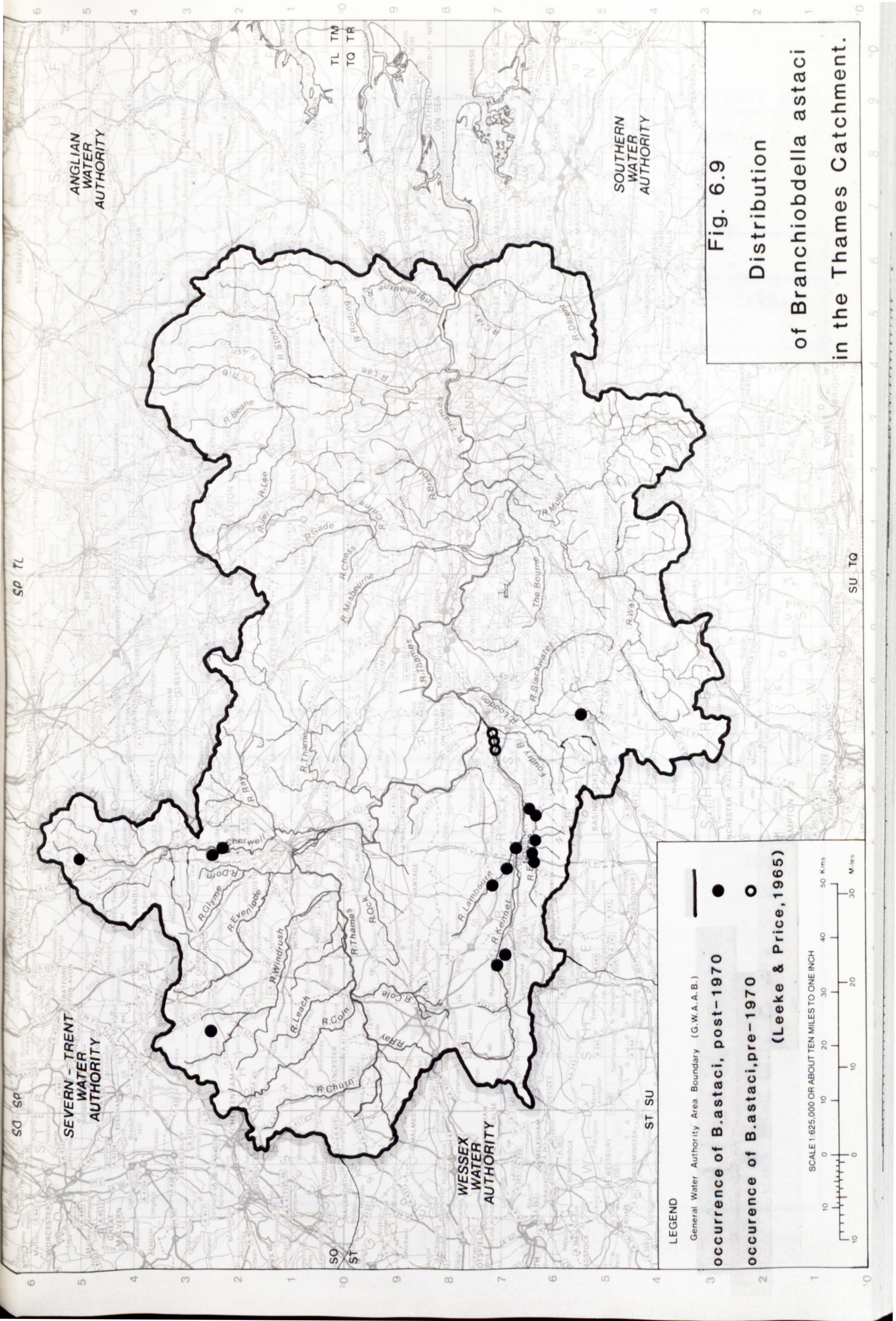


Fig. 6.9
Distribution
of Branchiobdella astaci
in the Thames Catchment.

LEGEND

- General Water Authority Area Boundary (G.W.A.A.B.)
- occurrence of *B. astaci*, post-1970
- occurrence of *B. astaci*, pre-1970

(Leeke & Price, 1965)

SCALE 1:625,000 OR ABOUT TEN MILES TO ONE INCH

0 10 20 30 40 50 Kms
 0 10 20 30 Miles

TABLE 6.7 : HOST SIZE, SEASON AND FREQUENCY OF OCCURENCE OF BRANCHIOBELLA ASTACI AT SITES KNOWN TO CONTAIN INFESTED A.PALLIPES

Size Class (C.L. mm)	♂		♀	
	No. examined	%B+	No. examined	%B+
0 - 4.9	-	-	-	-
5 - 9.9	2	0	-	-
10 - 14.9	4	0	2	0
15 - 19.9	4	25	6	33
20 - 24.9	27	22	24	17
25 - 29.9	26	42	30	40
30 - 34.9	26	65	22	82
35 - 39.9	15	67	2	50
40 - 44.9	5	60	1	100
45 - 49.9	0	0	-	-
50 - 54.9	4	100	-	-
TOTAL	99	41%	80	42.5%
Month				
J	1	100	2	100
F	2	100	3	100
M	-	-	-	-
A	4	75	-	-
M	-	-	-	-
J	5	100	6	83
J	-	-	-	-
A	10	50	15	53
S	12	50	21	52
O	7	57	5	20
N	20	18	7	100
D	-	-	-	-

infested A.pallipes from the River Kennet, and various tributary streams, in the vicinity of Reading, Berkshire. Although no crayfish could be collected from the locations reported then A.pallipes obtained from sites further upstream in the Kennet subcatchment (see Figure 6.9) were found to be infested with B.astaci. It has not been reported from elsewhere in the U.K. or Eire during studies of the distribution and biology of A.pallipes (Moriarty, 1973; Reynolds, 1979; Holdich, pers comm; Rhodes, pers comm; Pratten, pers comm; Thomas, pers comm; O'Keefe, in press).

Currently there have been no reported occurrences of B.astaci infesting the introduced 'Signal Crayfish', P.leniusculus, in the U.K. In Sweden and Finland, however, adult P.leniusculus imported from the U.S.A. were found to be infested with Xironogeton instabilis and Cambarinicola sp. (Fürst & Westman, et al, in Westman & Pursainen, 1982). It is not known if these alien branchiobdellids survived but in France introduced P.leniusculus are reported to have become heavily infested with un-named branchiobdellids (Blake & Laurent, 1982). Similarly in Spain "important colonies of branchiobdellids on some crayfish", in populations of the introduced Procambarus clarkii, have been reported (Habsburgo-Lorena, 1979).

Once mixed populations of the two crayfish species become accidentally established in the U.K. the distribution of B.astaci may increase. The transfer of crayfish stocks between river basins for aquaculture purposes may eventually increase the distribution of B.astaci and this parasite may prove to be an important economic factor where crayfish are reared in semi-intensive conditions, although to what extent parasite damage debilitates infested crayfish is not known.

The origin of B.astaci in the U.K. is unknown although it may well have been introduced from continental Europe, where it is quite widespread amongst populations of A.astacus,

A.leptodactylus and A.pallipes (Pop, 1965). It may have been present in the U.K. since at least the end of the last century, however, as it was described in a subscript to 'The Crayfish' (Huxley, 1880). Introductions of continental crayfish considerably increase the risk of further introductions of this and other species of branchiobdellid worms. A single adult specimen of A.astacus (♂, C.L. = 73.5 mm.), imported from West Germany, was examined in 1981 and found to be infested with Branchiobdella parasita (Henle, 1835) in the following numbers: adults (>5.0 mm.) - 7; juveniles (<1.5 mm.) - 18, (pers obsn). In addition some 40 adult A.leptodactylus (18♂ and 22♀; C.L. = 41.8 - 64.5 mm.), imported from France and obtained through the retail fish trade in December 1978 and December 1982, were found to be free from gill-dwelling branchiobdellids. Any external parasites, e.g. B.parasita (Grabda & Wierzbicka, 1969), that may have been infecting these crayfish in their native environment are likely to have been removed prior to sale (Young, 1965; Mazylis, 1973) or lost during handling and transportation. 58 adult P.leniusculus, obtained from sites 1, 2 and 3 (Appendix 9) were examined but no evidence of infestation by branchiobdellids was found.

Little is known about the life-history of B.astaci but from the observations reported here it has been possible to tentatively conclude that the occurrence of B.astaci in A.pallipes in this country is not seasonal (see Table 6.7) in the Thames Catchment. Adults (preserved length 8.0 mm. - 10.0 mm.) were found in A.pallipes collected from the River Eye, Gloucestershire in February, 1981.

The occurrence of B.astaci in A.pallipes is apparently restricted to crayfish of C.L. >15.0 mm, see Table 6.7, although a more extensive survey would be required to confirm this. Such a restriction of host size would lend credence to the suggestion that branchiobdellids transfer from host to host during contact between hosts, such as at mating (Young, 1965), and do not parasitise eggs or juvenile crayfish. The

incidence of infested A.pallipes increases with crayfish size at sites known to contain B.astaci (see Table 6.7), implying that once parasitised a host crayfish remains infected until it dies. There is no evidence to confirm the hypothesis that B.astaci would transfer from a dead crayfish to a new host that was consuming the former host. Whether or not B.astaci causes or increases the likelihood of crayfish death is not known although structural damage to crayfish gill filaments would certainly render that individual more susceptible to microbial infection (Unestam & Weiss, 1970; Unestam, 1973a, b).

It is clear, then, that observations made regarding the occurrence of B.astaci in the crayfish A.pallipes in the Thames Catchment are far from conclusive. Further investigation would be required to answer some of the questions raised by the information acquired incidentally during the current study of crayfish biology and distribution.

6.4.(c) Observations concerning certain crayfish diseases in the Thames Catchment.

6.4c(i) - Introduction.

A number of crayfish diseases have been reported in the literature (e.g. Vey & Vago, 1973; Vey, et al, 1975; Johnson, 1977) but there is very little information concerning their occurrence in the U.K. Crayfish collected during the course of this study were examined for external signs of disease and malformations. Detailed investigation of the causes of such diseases was not considered to be within the scope of this study but the occurrence of diseased individuals is reported here due to the absence of similar information from the Thames Catchment.

Great reliance was placed on descriptions of diseased crayfish in the literature although generally such descriptions did not refer specifically to A.pallipes. Consequently different symptoms may have been observed to those reported in the literature and subsequent recording of the disease may have been inaccurate.

6.4c(ii) - Methods.

The occurrence of diseased or damaged crayfish was recorded whenever practicable. No confirmation of the occurrence of disease organisms was attempted; identification was carried out by visual comparison with published descriptions.

6.4c(iii) - Results.

The overall incidence of diseased and damaged crayfish is listed in Table 6.8. The mean incidence and number of sites from which the observations have been recorded are tabulated.

TABLE 6.8 : OVERALL INCIDENCE OF DAMAGE, DISEASE AND PARASITES ON A.PALLIPES IN THE THAMES CATCHMENT.

Feature	Incidence		No. of sites + ve
	No.	%	
Damaged rostrum	47	1.3	7
Lost chela(e)	133	3.6	8
Regenerating chela(e)	53	1.4	8
Other exoskeleton damage	30	0.8	7
Thelohanosis	92	2.6	8
'Burn-spot'	17	0.5	6
Branchiobdella	249	15.0	14

N.B. % = incidence as % of total no. examined for that feature.

No. of sites only includes those where n>20, except Branchiobdella.

6.4c(iv) - Discussion.

The most common disease encountered was 'burn spot' disease (Unestam, 1973; Vey & Vago, 1973) in which characteristic red patches or blotches appear on the exoskeleton, not unlike the marks caused by cauterisation (see Chapter 2). The causative organism of this disease is *Fusarium solani* (Vey, in Unestam, 1973) which may invade the crayfish through damaged areas of the integument (Vey & Vago, 1973). The incidence of burn spot disease was greater in males than in females which may suggest a link with a greater level of agonistic behaviour in the males (O'Keefe, in press).

No evidence was found to suggest that *A.pallipes* in the Thames Catchment are infected with *Nosema* sp. (c.f. Pixell-Goodrich, 1956) or *Psorospermium haeckli* (Nylund & Westman, 1979; Vey, 1979). Those crayfish examined microscopically for the presence of *T.contejeani* (see 6.4) (n = 34) were also screened for the occurrence of these parasites.

Similarly no proof was found during this study that the 'crayfish plague' occurs in the Thames Catchment. This disease, caused by the fungus *Aphanomyces astaci* (Schikora, 1903) and endemic in the U.S.A. (Unestam & Söderhäll, 1977) occurs widely on the mainland of Europe (Unestam, 1972, 1973a; Arrignon & Magne, 1979; Herfort-Michieli, 1979), affecting crayfish populations from Spain (Cuellar & Coll, in press) to Scandinavia (Westman & Pursainen, 1979). In Sweden and Finland, in particular, a great deal of research has been aimed at determining the cause of the plague, diagnosis and control measures (Håstein & Gladhaug, 1975; Söderhäll, et al, 1977) with special reference to the indigenous populations of *A.astacus*. It has been reported to infect *A.pallipes* (Unestam, 1969, 1972).

There is no proof, as yet, that plague occurs in the U.K. despite unsubstantiated reports to the contrary (Richards & Fuke, 1977). During the course of this study, however,

several large scale mortalities of A.pallipes have occurred in the Thames Catchment (see Figure 3.1) and elsewhere in the U.K. (Frake, pers comm) which remain unexplained.

The investigation into the impact of engineering works (see Chapter 5) on the River Lee, in Hertfordshire, had to be concluded due to an almost total mortality of crayfish at the study site in July 1981. That these deaths were due to disease rather than pollution was quickly ascertained and subsequent investigations have shown that this mortality has extended along tributaries of the River Lee in that area. Dead and dying crayfish were to be found in some of these tributaries for the following two years, 1982 and 1983. At the same time a mass mortality of crayfish was reported from the Bristol River Avon (Frake, pers comm) again due to disease rather than pollution. Subsequently, during routine searches to ascertain crayfish distribution (see Chapter 3) large numbers of dead crayfish were found in the River Whitewater, in 1982, near Odiham, an area from which A.pallipes had not previously been reliably recorded. Extensive searches revealed no live crayfish and it must be assumed that the majority of A.pallipes in that river were killed.

The River Loddon, into which the River Whitewater flows, was formerly a site being investigated during this study and contained abundant crayfish (see 6.2). Searches made in 1983 failed to reveal live crayfish at the former study site and no crayfish were removed during weed cutting, in 1983, whereas many animals could usually be collected at this time (Penny, pers comm).

Lastly, during the summer of 1983 mortalities of A.pallipes in the River Wey (N) were reported. Investigations showed that a mortality of a similar pattern and scale to that which had occurred in the Rivers Lee and Whitewater was taking place. A.pallipes were found to be dying in parts of the River Wey over at least 25 km. Again there is no evidence of pollution; fish and invertebrate life are abundant and apparently unaffected.

The three known large scale mortalities of A.pallipes, together with their apparent disappearance from the River Loddon, are thought to have been caused by disease. Until 1983 (Sept) no evidence has been available to show that crayfish plague is the cause of these mortalities despite intensive investigations (Alderman, pers comm) although the scale and pattern of the mortalities is identical to losses of A.astacus reported from Scandinavia (Westman & Nylund, 1979). Recently, however, fungi isolated from crayfish collected from the River Wey (August, 1983) have been identified as Aphanomyces sp. (Alderman, pers comm) at the M.A.F.F. Fish Diseases Laboratory in Weymouth. It appears highly probable, therefore, that crayfish plague is the cause of these mortalities. *

If this is the case then either A.astaci has been introduced from the continent in recent years or the plague has been present in the U.K. for a number of years. In the former case A.astaci could have been imported with P.leniusculus juveniles from Sweden, which are reputed to carry the disease (Söderhäll, pers comm), or on unrecorded introductions of P.leniusculus from Europe or the U.S.A. or through the importation of A.leptodactylus or A.astacus from France to Billingsgate Fish Market. If the disease has been present in the U.K. for a number of years then it could explain crayfish mortalities reported earlier this century in the River Thames (Cornish, 1902) and the River Ock (Duffield, 1933, 1936). It is strange, however, if this is the case, that no mortalities were reported during the early part of this study (1979 - 1981) whereas at least four have occurred in the later period (1981 - 1983).

The eradication of A.pallipes from certain river systems could have far-reaching effects on the aquatic ecosystems involved. Their omnivorous nature has earned crayfish a reputation as scavengers and it is likely that where they are eradicated excessive weed growth may occur, as has been reported from Sweden (Abrahamsson, 1966) following the

* See Addendum page 210

devastation of a population of A.astacus by the 'plague'. Studies are currently being commenced into the competitive effects of A.pallipes and P.leniusculus (Holdich, pers comm) and the cause and effects of crayfish mortalities in the River Lee system (Lowery, pers comm). Together with work carried out by M.A.F.F. Fish Diseases Laboratory, in conjunction with Stirling University Institute of Aquaculture (Alderman, 1982; Alderman & Polglase, pers comm) these studies should go a long way towards elucidating the status and effects of A.astaci in crayfish populations in the U.K.

* Addendum.

It has now been confirmed (Alderman, pers comm - Oct. 1983) that the crayfish mortalities on the R. Wey (Thames Water) and R. Avon (Wessex W.A.) were caused by the crayfish plague. The causative organism, Aphanomyces astaci (Schikora, 1903), has been isolated from moribund crayfish found in these rivers, used to infect healthy crayfish and then re-isolated. Positive identification of this fungus in crayfish from the R. Lee catchment and R. Whitewater has not yet been reported.

These findings constitute the first conclusive evidence concerning the presence of the crayfish 'plague' in the U.K.

SECTION B. THE BIOLOGY AND DISTRIBUTION OF P. LENIUSCULUS IN THE THAMES CATCHMENT.

SECTION INTRODUCTION.

B.1 General Considerations.

Although large numbers of the 'Signal Crayfish' Pacifastacus leniusculus have been imported to the U.K. in recent years (Richards, pers comm) it appears that no detailed study of its biology has been undertaken in this country. Information that is available relates to this species either in Sweden or in its native U.S.A. In the former country P. leniusculus is now considered suitable as a replacement for their native A. astacus which has been devastated by the crayfish plague (Abrahamsson, 1973a; see Chapter 6). In neither country could introductions of P. leniusculus have as great a potential for affecting populations of the native or other crayfish species, or aquatic ecosystems as a whole, as in the U.K. As yet, however, research has been concentrated on the native A. pallipes and has generally ignored the fact that large numbers of P. leniusculus have been imported and are breeding successfully in this country (see Chapters 7 & 8).

B.2 Aims of Study. (Section B).

This investigation aims to provide basic biological data regarding P. leniusculus in the Thames Catchment, suitable for use as a baseline for assessing the ecological importance of introducing an alien crayfish species into the U.K. The information obtained concerns the extent and success of introductions, the level of survival of implants, measurement of growth rates and fecundity, the acquisition of life-history and ecological data and the general morphometric characterisation of this species in the U.K. The information thus obtained is intended to complement and provide a comparison with similar data

available from Scandinavia, France and North America. Such information has primarily been obtained through the study of an established population of P.leniusculus in an enclosed situation. In order to assess the degree to which the results from that site are typical of P.leniusculus populations throughout the Thames Catchment a number of other sites have also been sampled on a less regular or intensive basis.

B.3 Species Description.

PACIFASTACUS LENIUSCULUS (Dana, 1852)

Order: Decapoda
Family: Astacidae
Sub family: Astacinae
Genus: Pacifastacus

Common names: 'Signal Crayfish' (Westman & Pursainen, 1982)
'American Crayfish' (Westman, 1973)
'Californian Crayfish' (Laurent, 1979)

This species is characteristically of a large size, with chelae that are large in relation to body size. The rostrum is concave to the apex, with parallel margins, and has a faint groove rather than a median ridge. Colour is generally brown or steely blue with a white patch dorsally on the claws, at the junction of the dactylopodite and propodite, which are red ventrally. P.leniusculus may attain a large size, compared with other astacid crayfish, often exceeding 14 cm. T.L. and 150g. (Laurent & Forest, 1979; see Chapter 8).

Growth is rapid when water temperatures of 15° C. are exceeded for at least three months in the summer (Westman, 1973b). The maximum lethal temperature is in the range 25° C. - 30° C. (Goldman, 1973). No studies of growth in the U.K. have yet been published. In Sweden individuals of age 0+ (1 summer old) are 3.0 - 5.0 cm. T.L.: age 1+ are 6.0 - 9.0 cm. T.L. and age 2+ are 9.0 - 10. cm.T.L. (Abrahamsson, 1973b). The minimum size for ovigerous females

is reported to be 6.0 cm.T.L. (Mason, 1975). Sexual maturity can be attained at the age of 1+ by faster growing individuals in the U.K. (see Chapter 8) although Swedish workers report sexual maturity at age 2+ for females and age 1+ for males (Abrahamsson, 1971). Average brood size has been reported to be in the range 50 - 250 eggs (Abrahamsson, 1973a).

B.4 Life - Cycle.

The life-history of P.leniusculus is typical of that of other members of the Astacinae (see Chapter 1). Again, however, differences in timing do occur due both to average water temperatures and the more rapid growth rate of P.leniusculus compared to other members of the family. In Sweden and the U.S.A. hatching takes place in June (Abrahamsson, 1973a; Goldman, et al, 1975) and in Canada has been reported to occur in April/May (Mason, 1975). In the Thames Catchment it has been observed to occur as early as 12th. May (see Chapter 7).

B.5 Taxonomy.

Although generally referred to as a single species: Pacifastacus leniusculus (Dana, 1852) three subspecies have been proposed, as follows: P.leniusculus trowbridgii (Bott, 1950); P.leniusculus leniusculus (Dana, 1852) and P.leniusculus klamathiensis (Riegel, 1959) (Goldman, 1973). These subspecies readily hybridise and all the intermediate forms are to be found. It is of interest, however, that they do not share similar environmental requirements; some being able to inhabit warm, muddy habitats and others requiring cooler and rocky conditions (Laurent & Forest, 1979)

An alternative taxonomic system (Bouchard, 1977) lists three species in the sub-genus Pacifastacus, namely P.(Pacifastacus) leniusculus klamathiensis (Stimpson, 1857), P.(Pacifastacus) leniusculus leniusculus (Dana, 1852)

and P.(Pacifastacus) leniusculus trowbridgii (Stimpson, 1857). The sub-genus Hobbsastacus also contains three species: P.(Hobbsastacus) connectens (Faxon, 1914), P.(Hobbsastacus) gambeli (Girard, 1852) and P.(Hobbsastacus) nigrescens (Stimpson, 1857) together with a fossil species P.(Hobbsastacus) chenoderma (Cope, 1871).

Using the criteria on which the subspecies system is based all of the specimens examined during the course of this study were identified as P.leniusculus leniusculus (Dana, 1852) and will be referred to as P.leniusculus in this report.

B.6 Distribution.

P.leniusculus now occurs widely along the west coast of North America, being distributed from British Columbia to California. It is however, native to the states of Oregon and Washington (Abrahamsson, 1973b) extending in the east as far as Idaho and Nevada (Hobbs, 1972). In Europe it has been imported from the U.S.A. principally to Sweden (Abrahamsson, 1973a, b; Brinck, 1977) but also to Finland (Westman, 1973a) and Austria (Spitzzy, 1973). The commercial production of juveniles for stocking commenced, in Sweden in 1968 (Abrahamsson, 1973b) and these have been exported throughout Europe; to Finland, Poland, Russia, Luxembourg, West Germany, Austria, Switzerland, France, U.K., and Spain (Abrahamsson, 1973a, b; Laurent & Forest, 1979). In addition stocks are now being transferred from those original recipient countries, for example juveniles produced in the U.K. were successfully exported to South Africa in 1982 (Brown, pers comm).

In the U.K. importations began in 1976 and by December 1982 at least 202 sites throughout England and Wales had been stocked (Brown, pers comm; Richards, pers comm). Of these some 75% are known to have used stock imported from Sweden (Richards, pers comm; Bowler in Westman & Pursainen,

1982); it is reported that some crayfish have been imported directly from the U.S.A. As far as is known only experimental stocking has been carried out in Scotland and none have been imported to Eire due to an unofficial ban and a general policy of discouragement of such introductions by the Irish Ministry of Agriculture (Goddard & Holdich, 1979).

B.7 Biology.

In North America P.leniusculus inhabits large rivers, e.g. the Sacramento and Columbia Rivers (Shimizu & Goldman, 1979), and lakes, e.g. Lake Tahoe and Lake Natoma (Abrahamsson & Goldman, 1970; Goldman, et al, 1975). It is able to tolerate subalpine conditions in, for example, Lake Tahoe which is 1900 m. above sea level (Flint, 1975a, b) and to which crayfish were introduced in 1895 (Goldman, 1973). In the U.K. the majority of sites to which P.leniusculus have been introduced are enclosed waters such as lakes, ponds and gravel pits although some have been introduced into rivers (Sherry, 1977; Richards, pers comm; see Chapter 9) and small 'feeder' streams.

Water quality requirements are generally the same as those listed for A.pallipes. It does appear, however, that this species is able to tolerate poor water quality conditions for at least short periods of time (see Chapter 8). In California it inhabits water with a pH range of 6.1 to 8.0 and an alkalinity range of 19.0 to 45.0 mg.l⁻¹ CaCO₃, (Goldman & Rundquist, 1977).

P.leniusculus is however, considered to be euryhaline and may be found in brackish water in deltas and river mouths in the U.S.A. (Rundquist & Goldman, 1979). It is able to exist in relatively high salinities, e.g. 13‰ in Oregon and Washington (Wheatley & McMahon, 1982); as it is an osmoregulator, unlike most other crayfish species (Rundquist & Goldman, 1979).

Food requirements and predators are thought to be similar to those described for A.pallipes (see Section A: Introduction)

B.8 Economic Importance.

In the U.S.A. P.leniusculus has increased in economic importance during the last 10 - 15 years. An established fishery for this species has developed in the west coast states, primarily California, throughout the 1970's (Rundquist & Goldman, 1979). Prior to that the 'Signal Crayfish' was only important in respect of 'sport fisheries' in Lake Tahoe (Goldman, et al, 1975).

The reported size of the commercial crop was 252 tonnes in 1981 and 118 tonnes in 1982 (McGriff, 1983). Much of this harvest is from the Sacramento River (Shimizu & Goldman, 1979) and is exported to Europe (Goldman, 1973). Currently the commercial interest in P.leniusculus in the U.S.A. involves the exploitation of natural populations. Experimental attempts at intensive culture (Emadi, 1974; Mason, 1974) and polyculture with watercress (Rundquist, et al, 1977) do not appear to have been expanded to a commercial scale.

In Europe P.leniusculus has been selected by the Swedes as a replacement for A.astacus populations devastated by the crayfish plague. The establishment of a commercial hatchery in Sweden (Abrahamsson, 1973b) has provided material for stocking throughout Europe (Brinck, 1977) and the majority of commercial interest, to date, has involved sales of crayfish for this purpose. In Sweden harvests of P.leniusculus total <100 tonnes year⁻¹ with a value of 5 m. Crowns (Westman & Pursainen, 1982).

In the U.K. cropping populations of P.leniusculus, introduced in the late 1970's, commenced during 1981. Currently demand exceeds supply, which may total 2 tonnes

in 1983. A maximum retail value of £11 kg.⁻¹ has been established (Richards, pers comm).

CHAPTER 7. THE DISTRIBUTION OF CRAYFISH INTRODUCTIONS IN THE THAMES CATCHMENT

7.1. Introduction

In order to assess the scale and importance of introductions of freshwater crayfish to the U.K., and to the Thames Catchment in particular, information has been collated regarding the locations to which crayfish introductions have been made.

There is little evidence to suggest that such introductions, prior to the mid-1970's, were successful in the long term or on a scale large enough to pose an ecological threat. Reports that imported A.astacus occur in the wild in certain areas (Duffield, 1933; Davies, 1964; Anon., 1973; Clegg, 1974) remain unsubstantiated (Jay & Holdich, 1981) although at least one breeding population, established from stock imported in 1981, is known to exist in an enclosed fish farm pond. (Brown, pers comm). Introductions of A.leptodactylus are known to have been carried out (Lowery, pers comm; Jenkins, pers comm; Jay & Holdich, 1981) but the current status of this species in the U.K. is unknown. It is likely, though, that as 3.2 tonnes and 8.2. tonnes of this crayfish were imported to the U.K. from France in 1978 and 1979 respectively (Tillien, 1981) some small scale unrecorded introductions to the wild will have been made. Experimental introductions of P.clarkii from the U.S.A. are known to have taken place (Jay & Holdich, 1981; Goddard, pers comm) but it is reported that all stock was subsequently destroyed (Goddard, pers comm). Similarly at least one introduction of the Australian 'marron', Cherax tenuimanus, is reputed to have been made but again no stock survived the experiment (Moore, pers comm). There is, incidentally, no published record of the North American species Orconectes limosus having been introduced to the U.K. despite the reported success of this species in mainland Europe (Laurent, 1973; Kossakowski, 1975). The

status of all these crayfish species in the U.K. is largely unknown but it seems unlikely that large or thriving populations currently occur in the wild.

The species of crayfish which has been most frequently introduced in recent years is the 'Signal Crayfish', Pacifastacus leniusculus. The current interest in the introduction of this species was initiated in 1976 when juveniles became available for importation from Sweden (Richards & Fuke, 1977) and it is thought that no introductions of this species occurred prior to the early 1970's. The majority, if not all, the importations of this species, to date, have been carried out by Riversdale Farm in Dorset who are the sole U.K. agents for juvenile crayfish produced by the Simontorps Akvatiska Avelslaboratorium, in Sweden, the major crayfish hatchery in Europe (Karlsson, 1977).

As populations of P. leniusculus have become established in the U.K. the movement of stocks around the country has increased. Some of these intranational introductions are inevitably on a small local scale and are unlikely to be reported. Other stocking operations have involved larger numbers of crayfish of all ages and the principal company carrying out such introductions at present is Brown & Forrest in Somerset. All stock used by this company is purchased from established populations in the U.K. (Brown pers comm).

7.2. Methods

To obtain details of locations in the Thames Valley to which P. leniusculus had been introduced the importers, Riversdale Farm, were approached in 1979. They kindly provided a list of some 20 locations which had been stocked in 1977, 1978 and 1979 (Richards, pers comm). This information was also used to formulate the trapping programme described elsewhere (see Chapter 9).

The importers were again approached in early 1983 and were able to provide a map showing all locations in the U.K. to which they had introduced P.leniusculus up to and including 1982 (Richards, pers comm). Similar information was also obtained from Brown & Forrest in late 1982 (Brown, pers comm) and information regarding a small number of local introductions was also obtained from other sources (Moore, pers comm).

7.3. Results

The map, Figure 7.1, shows the locations within the Thames Catchment to which P.leniusculus is known to have been introduced prior to December 1982. The known locations to which P.leniusculus has been introduced throughout the U.K., prior to December 1982, are illustrated in Figure 7.2. In the latter case the data is plotted on the 10 km. grid system used by the I.T.E. Biological Records Centre (Heath & Perring, 1978) (see Chapter 3) and each circle on the map may represent one or more introductions to that area.

A total of 34 introductions are known to have been made to the Thames Catchment and at least 202 introductions have been made throughout the U.K. Records relate solely to introductions and the success of such introductions should not be assumed. Indeed at some sites no crayfish may have survived (see Chapter 9).

7.4. Discussion

As can be seen from the map, Figure 7.1, some 34 sites in the Thames Valley have been stocked with P.leniusculus; this represents approximately 17% of all introductions to the U.K. The large number of implantations in this area is the result of at least four factors:

- (i) The area is predominantly one of hard water (hardness range: 50-350 mg.l.⁻¹CaCO₃) and low

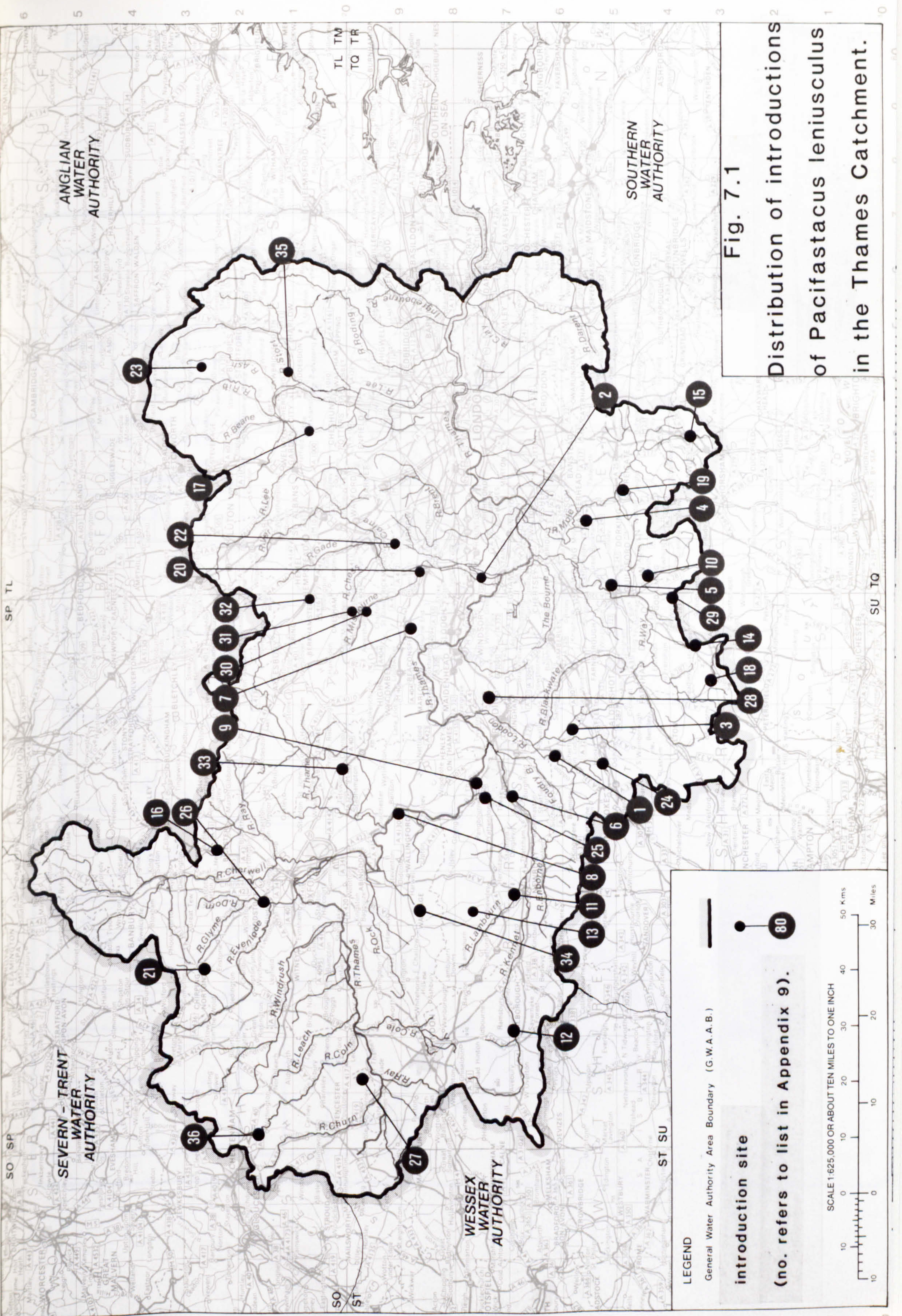


Fig. 7.1

Distribution of introductions
of *Pacifastacus leniusculus*
in the Thames Catchment.

LEGEND

General Water Authority Area Boundary (G.W.A.A.B.)

introduction site

(no. refers to list in Appendix 9).

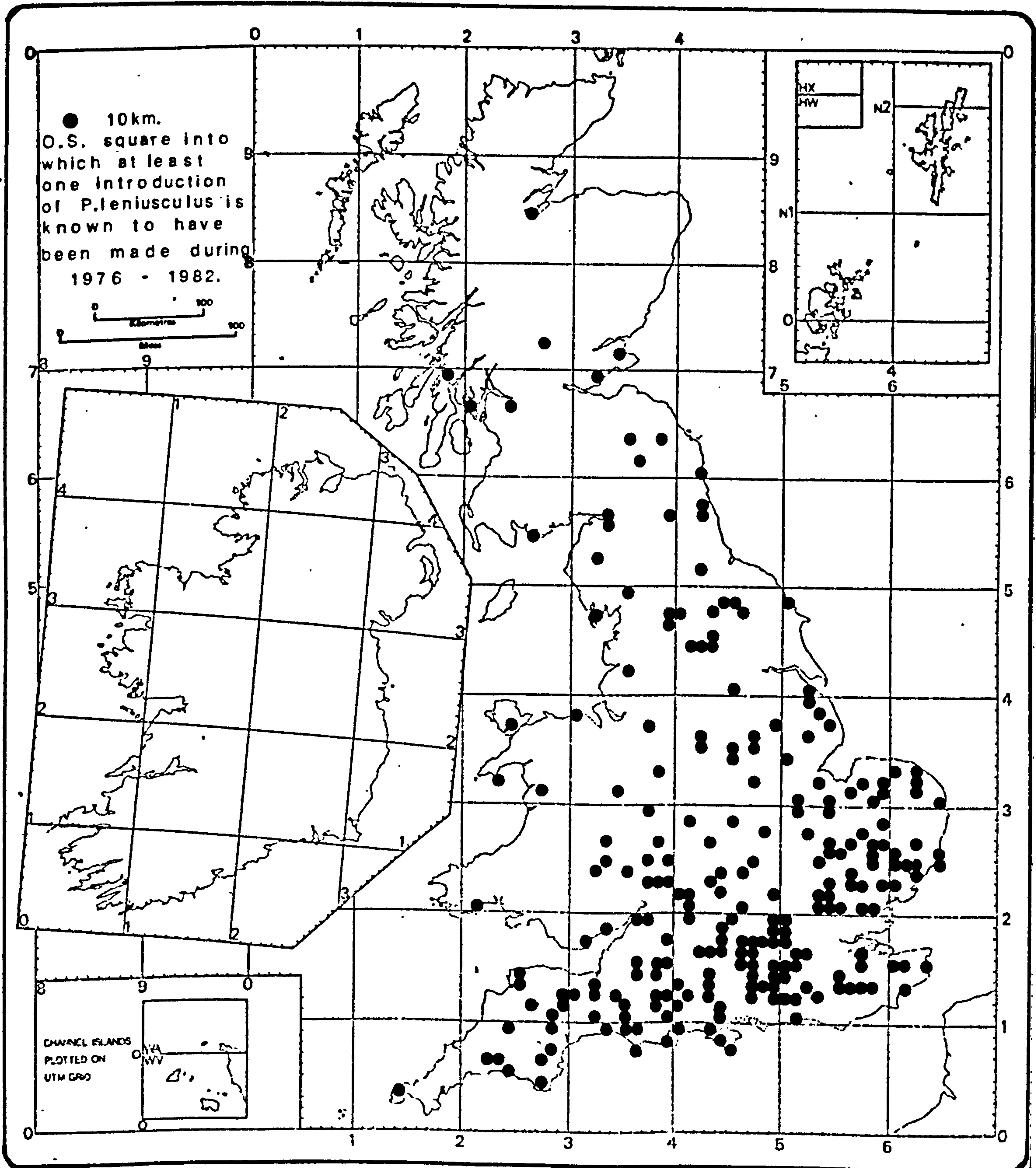
SCALE 1:625,000 OR ABOUT TEN MILES TO ONE INCH

0 10 20 30 40 50 Kms

0 10 20 30 Miles

Figure 7.2 Known locations of introductions of *P. leniusculus*

in the U.K.

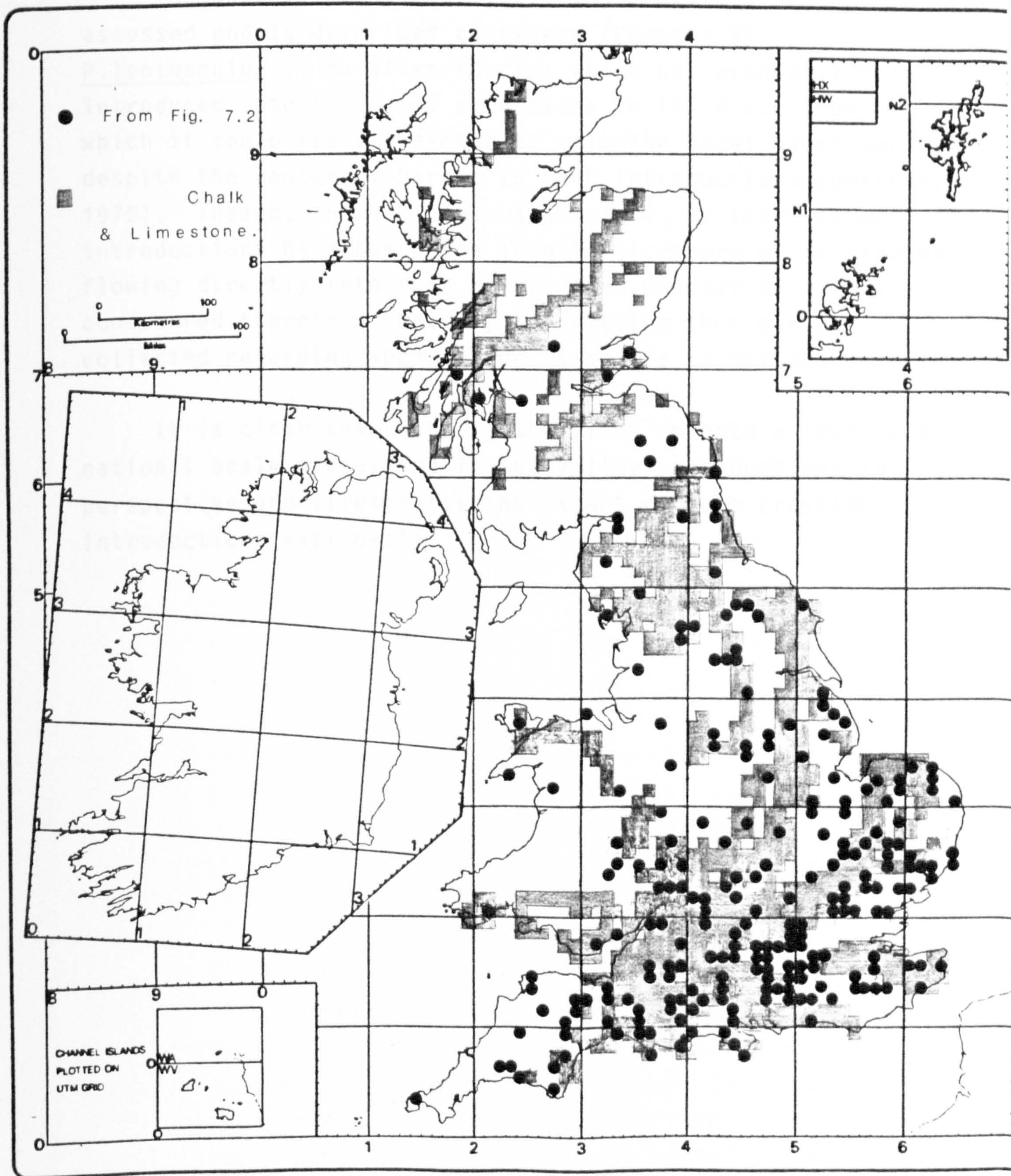


levels of industrial pollution. This results in a high incidence of water bodies suitable for stocking with crayfish. Figure 7.3 illustrates how the national distribution of introductions is related to geology. It can be seen that the majority of sites in the U.K., to which P.leniusculus has been introduced, lie on or near areas with calcium-rich substrata.

- (ii) The relatively large numbers of private estates and fish-farming operations, some 44 trout farms and 3 coarse fish farms operate within the Thames Water area (Sweeting, pers comm), has meant that both aquacultural interest and finance have been available for experimental stocking programmes.
- (iii) A large scale publicity campaign, particularly by the importers, has succeeded in stimulating the interest of (ii).
- (iy) The location of the principal crayfish stocking agencies, i.e. in Dorset and Somerset, has meant that the natural focus of their activities has been in the southern part of the U.K. (see Figure 7.2). Incidental to these factors is the fact that warmer water temperatures in southern England result in a longer growing season and the consequent faster growth to marketable size of P.leniusculus when compared, for example, with Sweden (Chapter 8). No data is, however, available from the extremities of the U.K. with which this theory could be tested.

It is not possible to determine whether or not other importations of either juvenile or adult P.leniusculus have been made as no importation regulations apply to crayfish (Holdich, et al, 1978). Those introducing 'alien animals' have not, until the introduction of the Wildlife & Countryside Act (HMSO, 1981), been obliged to notify either M.A.F.F. or the Regional Water Authority of such introductions.

Figure 7.3 The distribution of introductions of *P. leniusculus* in relation to chalk and limestone geology.



The fact that a large number of waters in the Thames Catchment area have been stocked with P.leniusculus, although with unknown success, justifies the inclusion of this species in a study of crayfish in this area.

The success of some of these introductions has been assessed and is described elsewhere (Chapter 9). P.leniusculus is an alien species which has gradually been introduced into semi-wild situations in the U.K., from which it could readily escape to colonise local watercourses, despite the dangers inherent in such introductions (Unestam, 1975). Indeed, in the Thames area alone, at least three introductions have been made into trout rivers or to streams flowing directly into such rivers (see Chapter 9). It is considered therefore that any information that can be collected regarding such introductions is of obvious benefit.

It is clear that mapping the sites on both a local and national scale places the Thames Valley introductions in perspective and illustrates the extent of such crayfish introductions nationally.

CHAPTER 8. AN INVESTIGATION INTO THE BIOLOGY OF A POPULATION OF THE 'SIGNAL CRAYFISH', PACIFASTACUS LENIUSCULUS (Dana) INTRODUCED INTO AN ISOLATED LAKE.

8.1. Introduction.

As part of the current investigation into the biology of P.leniusculus in the U.K., and in the Thames Catchment in particular, it was considered essential to obtain detailed information from an established population of this species. The time scale for the establishment of a successful breeding population of P.leniusculus is of the order of three to five years, or more, (Abrahamsson, 1973a, b; Furst, 1977) so an obvious prerequisite for this study was to locate an existing population rather than attempt to establish one.

From the known locations of introductions of P.leniusculus into the Thames Catchment (see Chapter 7) it was noted that a suitable population existed less than ten miles from the Thames Water laboratories at Reading, Berkshire. Other sites were considered to be less suitable either because they were further distant, they were used as trout fisheries, they had received too few implants or were stocked with crayfish too recently. The site selected for study was close to Reading, thereby reducing travelling time; was unfished and had been stocked with appreciable numbers of P.leniusculus in 1977, 1978 and 1979 (Ellis, pers comm). Consequently, by mid-1979, when fieldwork commenced, mature adult crayfish were already present in the lake. In addition the lake owner and his fishery manager were cooperative.

The information obtained from this investigation, together with comparable data collected from other sites (see Chapter 9) and laboratory studies provide a basis on which an ecological and economic assessment of introductions of P.leniusculus can be made. Such an assessment is of considerable importance for any species being considered as

a candidate for aquaculture (Webber & Riordan, 1976).

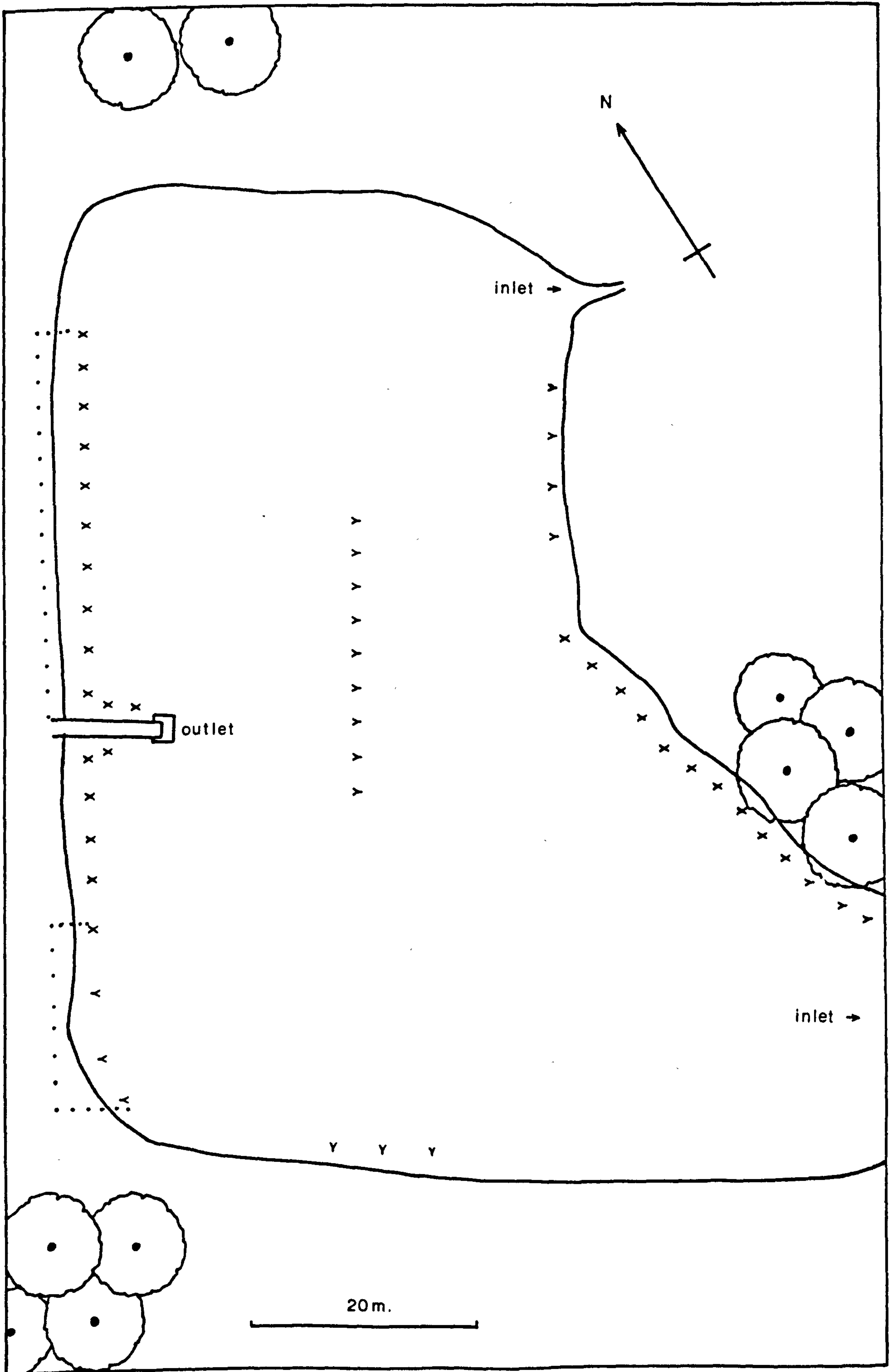
8.1(i) - Study Site.

A small enclosed lake (see Figure 8.1) on the privately owned Stratfield Saye Estate, near Basingstoke, Hampshire (NGR:SU711619) was stocked, by the owner, with 500 juvenile P.leniusculus in 1977, 1978 and 1979. The lake was artificially constructed in the early nineteenth century (Ellis, pers comm) and takes the form of a dammed valley. The main water inflow originates from a similar lake approximately 0.5 km. upstream which feeds, via a small stream, to the lower lake. Both are fed by runoff from adjacent fields and mixed woodland. The lower lake is retained by an earth dam and the outflow consists of a 'standpipe' arrangement. Overflow water flows approximately 1.0 km. through an underground pipe before discharging directly to the River Loddon (NGR:SU706623). Land use proximal to the upper lake is predominantly mixed coniferous and deciduous woodland whereas that adjacent to the study site is used for grazing cattle.

Prior to stocking with crayfish juveniles, in 1977, the lake was drained and crushed chalk rubble was spread on the bed (Ellis, pers comm). The exact location and quantity of chalk used is unknown. In addition a quantity of brick rubble was spread along one shore, in a band approximately 3.0 metres wide, to provide suitable crayfish habitat. All fish were removed during the draining and subsequently only a very small number of young tench, Tinca tinca, have been introduced (Ellis, pers comm).

The lake is approximately one hectare in area and a maximum of 4.0 m. deep, close to the outlet. Average depth is considerably less than this and is within the range 0.75 m. to 1.25 m. The bed is primarily composed of clay and silt except where the rubble and chalk have been deposited.

Figure 8.1 Sketch plan of lake at "Little Switzerland",
Stratfield Saye.



At the commencement of this investigation submerged aquatic macrophytes were sparse, limited to small strands of 'canadian pondweed', Elodea canadensis. The marginal plant species are restricted to the west bank, along which the rubble had been spread, as this was also the only area fenced to exclude cattle. These marginal plants consisted predominantly of sedges, Carex sp. and rushes, Juncus sp. with water mint, Mentha aquatica, and water forget-me-not Myosotis scorpioides, growing between. Two small willow trees, Salix sp., were also growing on this bank and a clump of mature beech trees, Fagus sylvatica, and scots pine, Pinus sylvestris, was located on the east bank.

Large flocks of wildfowl frequent the lake, consisting primarily of canada geese, Branta canadensis, with the occasional inclusion of other species of goose. Three to five breeding pairs of mallard, Anas platyrhynchos, permanently inhabit the lake as do several pairs of coot, Fulica atra. Herons, Ardea cinerea, are frequent visitors to the lake.

8.1(ii) - Chemical Water Quality.

Samples of water were collected at frequent intervals for chemical analysis, by Thames Water laboratories, the results of which are listed in Table 8.1 and illustrated in Figure 8.2. From these results it can be seen that the parameters considered to be of primary importance to crayfish (Laurent, 1980) had the following mean values:

pH	= 7.45	n = 14
Total Hardness	= 143 mg.l ⁻¹ . CaCO ₃	n = 14
Alkalinity	= 81 mg.l ⁻¹ . CaCO ₃	n = 14

The chemical water quality will be discussed in detail elsewhere (8.4(i)).

8.2. Methods.

8.2(i) - Sampling.

TABLE 8.1 : CHEMICAL WATER QUALITY. STRATFIELD SAYE. 1979 - 1980

Date	5.9.79	25.10.79	31.10.79	6.11.79	1.2.80	24.4.80	30.4.80
Time	19.30	10.00	09.50	10.00	08.30	09.00	08.30
pH	7.53	7.53	7.52	7.47	7.69	7.52	7.42
Suspended Solids (104°C)	14.0	18.2	13.3	16.0	19.0	N D	13.0
BOD (ATU)	5.2	2.2	2.8	4.6	4.7	3.5	3.6
C.O.D.	N D	N D	73.5	67.1	N D	35.0	48.1
Temperature (°C)	19.0	12.5	13.0	10.0	3.5	10.5	10.0
Dissolved Oxygen	8.0	6.15	6.30	8.35	12.20	8.8	8.05
% Saturation	86.3	57.5	59.8	74.0	91.8	78.9	71.4
Ammoniacal Nitrogen	2.0	5.7	5.8	5.1	0.92	0.36	0.49
Unionised Ammonia as N.	0.025	0.043	0.045	0.028	0.005	0.002	0.002
Total Oxidised as N.	0.3	0.3	0.4	0.4	1.30	0.7	0.7
Chloride as Cl.	32	33	32	32	30	26	27
Silica as SiO ₂	8.1	14.2	14.3	14.0	11.8	5.4	5.5
Orthophosphate as P.	0.01	0.20	0.11	0.01	0.02	0.01	0.01
Total Hardness as CaCO ₃	208	149	148	152	123	134	126
Alkalinity as CaCO ₃	97	120	115	117	60	53	54
Total Chlorophyll (µg l. ⁻¹)	18.77	14.25	25.02	29.97	N D	106	88.6

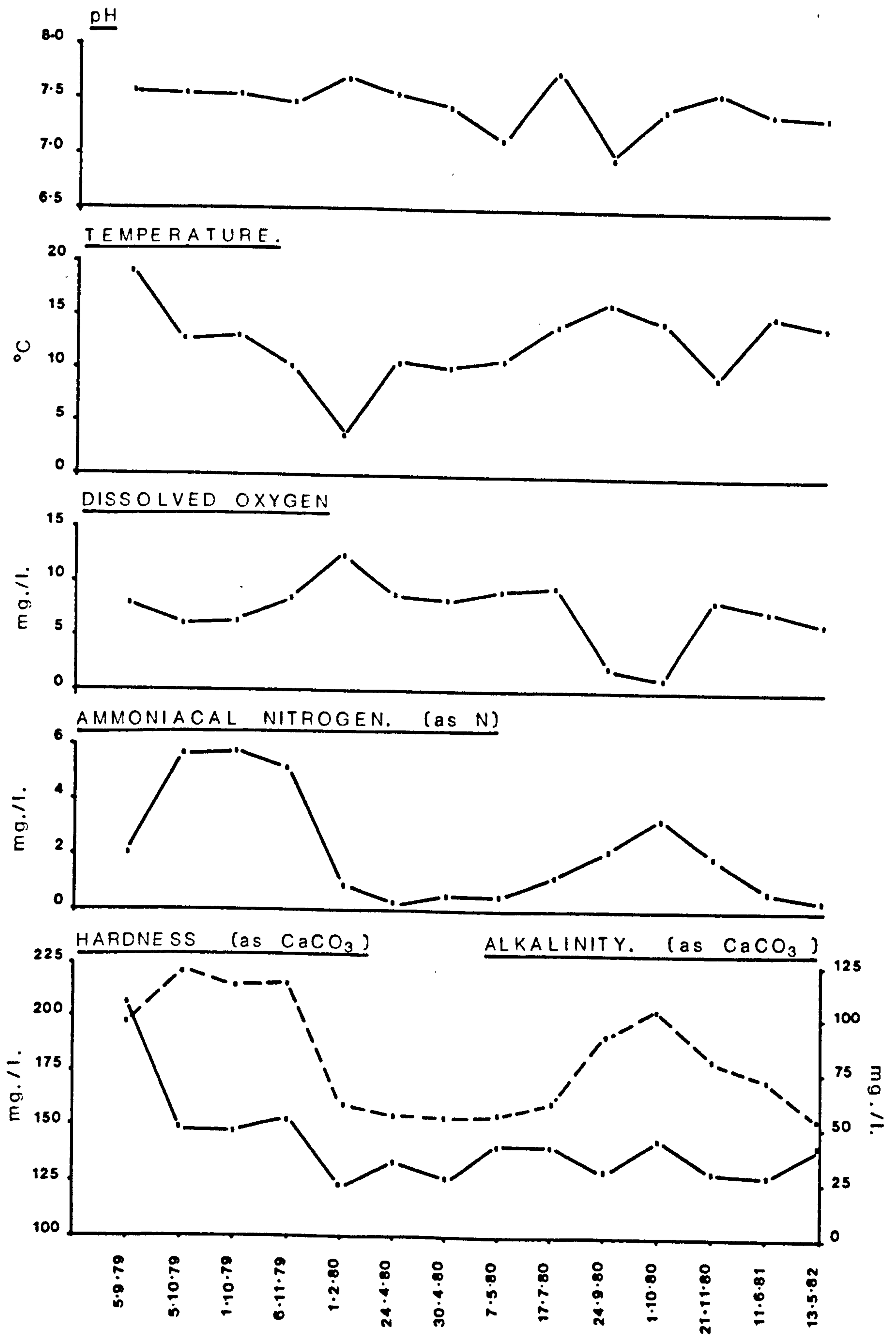
N.B. Values as mg.l.⁻¹ except pH.

TABLE 8.1 : Continued

Date	7.5.80	17.7.80	24.9.80	1.10.80	21.11.80	11.6.81	13.5.82
Time	08.30	09.00	08.30	09.00	09.00	09.00	09.30
pH	7.12	7.77	6.96	7.40	7.57	7.39	7.37
Suspended Solids (104°C)	18.0	N D	6.0	2	68	N D	40.7
BOD (ATU)	3.0	2.7	0.7	1.9	5.1	5.6	4.1
C.O.D.	N D	N D	79.4	82.1	52	N D	58.9
Temperature (°C)	10.5	14	16.0	14.5	9.0	15	14
Dissolved Oxygen	9.0	9.45	1.95	1.20	8.5	7.65	6.75
% Saturation	80.7	91.8	19.8	11.8	78.7	76	65.6
Ammoniacal Nitrogen	0.42	1.02	2.1	3.3	1.9	0.63	0.40
Unionised Ammonia as N.	0.001	0.015	0.006	0.022	0.012	0.004	0.002
Total Oxidised as N.	0.6	0.4	0.4	0.2	1.0	1.0	0.4
Chloride as Cl.	26	29	28	30	27	22	29
Silica as SiO ₂	5.6	6.8	11.1	12.1	13.8	6.2	5.0
Orthophosphate as P.	0.006	0.01	0.14	0.17	0.05	0.01	0.09
Total Hardness as CaCO ₃	142	141	130	144	130	128	142
Alkalinity as CaCO ₃	55	61	92	105	81	71	54
Total Chlorophyll (µg. l. ⁻¹)	26.1	26.2	5.21	N D	N D	57.6	32.8

N.B. Values as mg.l.⁻¹ except pH.

Figure 8.2 Graphs of chemical water quality, Stratfield Saye. 1979 - 1982.



The general methods of sampling crayfish populations have already been described (see Chapter 2). Only overnight trapping was used regularly at this site, although hand collection of juveniles was also carried out on three occasions. Traps were always set in the areas marked (x) on the diagram (Figure 8.1) and on several visits were also set elsewhere in the lake, marked (y), to try and determine the areas most favoured by the crayfish.

All crayfish were measured, as previously described (see Chapter 2) carapace length (C.L.) being the standard measurement used and with other parameters being measured on selected occasions. Mark-recapture experiments were carried out in 1979, 1980 and 1981 in order to permit estimates of abundance to be calculated. Marking was carried out, by cauterisation (see Chapter 2), for this purpose and for the collection of a small quantity of individual growth data.

8.2(ii) - Statistical Analysis.

(a) Mark-recapture data. This information was used to calculate estimates of the size of the 'trappable' population using the methods of Petersen, Schnabel, Bailey and Jolly (Ricker, 1975) which are more fully described elsewhere (see Chapter 2). Some of the assumptions made during the use of these methods are clearly not met by the conditions of the current study so the figures obtained must only be considered to be an approximation.

(b) Catchability. The results of trapping success have been expressed in terms of catch per trap per unit time in order to compare the success rate of trapping as a sampling method on different occasions and at different sites (see Chapter 9).

(c) Length-Frequency Data. The information obtained regarding the size composition of the trapped samples has

been analysed as described elsewhere (see Chapter 2). The method of analysis selected for use was the separation of the length-frequency distributions into their Gaussian components (Bhattacharya, 1967). The resulting separation of the length-frequency data into distinct size groups has been plotted against time. Then, using knowledge of the maximum possible age of the crayfish in the population (Ellis, pers comm) and the observed size of hand caught juveniles (0+), together with published data on the age - size relationship of this species of crayfish in Sweden (Abrahamsson, 1971, 1973a, b), the U.S.A. (Flint, 1975a, b ; Emadi, 1974; Abrahamsson & Goldman, 1970) and Canada (Mason, 1974, 1975) the data has been used to construct average 'growth' curves.

Due to low frequency of recaptures of individually marked crayfish only a small amount of data has been obtained concerning individual growth of P.leniusculus in this population.

(d) Morphometric Data. A considerable quantity of data has been collected concerning the morphometry of P.leniusculus. Using regression analysis (see Chapter 2) the relationships between various parameters have been established. Condition factors for individual crayfish (see Chapter 2) have been calculated for comparison with similar figures obtained from P.leniusculus at other sites within the Thames Catchment (see Chapter 9) and A.pallipes (see Chapter 6). By means of multiple regression analysis the size at which secondary sexual characteristics become apparent, e.g. chela size in the males and the width of the second abdominal segment in the females, has been determined (see Chapter 2). This information could be used to compare the assumed size at the onset of sexual maturity (Wenner, et al, 1974; Stein, et al, 1977; Rhodes & Holdich, 1979) in geographically separate populations (see Chapter 9).

8.3. Results.

8.3(i) - Population estimation by mark-recapture methods.

Estimates of the trappable population size, calculated using a number of different methods, are listed in Table 8.2. The extent of remixing of marked individuals was checked by comparing the ratio of marked to unmarked crayfish in subsequent samples using χ^2 (see Chapter 2). Satisfactory mixing was shown to have occurred ($p > 0.5$).

8.3(ii) - Catchability.

The total catch on any one occasion has been expressed in terms of catch per sampling unit per unit time, i.e. $\text{catch.trap}^{-1} \text{hour}^{-1}$ or $\text{catch.trap}^{-1} \text{night}^{-1}$. The trapping results are listed in Table 8.3 and shown in Figure 8.3a. Catchability is illustrated graphically in Figure 8.3b.

8.3(iii) - Length-Frequency data.

Growth curves have been constructed using data made available by the analysis of the length-frequency distribution of crayfish within the samples. The size range of crayfish caught by trapping throughout the period of study is shown in the histogram, Figure 8.4, and the ratio of males to females in each sample is shown in Figure 8.5. The mean C.L. of both males and females in samples collected in successive years are illustrated in Figure 8.6.

Length-frequency histograms have been constructed from the raw data. These histograms, Figure 8.7, illustrate the length-frequency distribution of crayfish in all samples and highlight the problems commonly associated with the satisfactory analysis of such data (Brown, 1979; see Chapters 2 & 4).

Following analysis of the data (see Chapter 2) generalised growth curves, with males and females shown

TABLE 8.2 : ESTIMATES OF POPULATION SIZE AT STRATFIELD SAYE.
1979 - 1981.

Date	Estimate (± 95% Confidence Limits)	Method
August 1979	193 ± 81	Adjusted Petersen
	296	Jolly
November 1979	145 ± 54	Adjusted Petersen
	200	Jolly
Autumn 1979 (combined data)	462 ± 123	Adjusted Petersen
	240 ± 81	Schnabel
July 1980	715 ± 351	Adjusted Petersen
1979 + 1980 (combined data)	390	Schnabel
	404	Schumacher
June 1981	2062 ± 1397	Adjusted Petersen
	2203 ± 1260	Bailey

N.B. Crayfish juveniles were introduced in June 1977,
1978 and 1979

TABLE 8.3 : SUMMARY OF CATCH DATA. STRATFIELD SAYE.
1979 - 1982.

Date	No. of Traps	Catch			Total	Catch. Trap ⁻¹ Night ⁻¹
		♂	♀	(♀B)		
9. 8.79	21	11	9	-	28	0.95
15. 8.79	25	14	12	-	26	1.04
21. 8.79	31	16	20	-	36	1.16
24.10.79	28	18	7	(3)	25	0.89
30.10.79	23	19	14	(14)	33	1.43
5.11.79	23	15	11	(9)	26	1.13
31. 1.80	9	4	1	(1)	5	0.55
23. 4.80	22	4	0	-	4	0.18
29. 4.80	23	1	1	-	2	0.09
6. 5.80	19	1	0	-	1	0.05
9. 7.80	37	41	37	-	78	2.11
16. 7.80	37	34	25	-	59	1.59
23. 7.80	39	16	24	-	40	1.02
23. 9.80	20	3	12	-	15	0.75
30. 9.80	20	0	1	-	1	0.05
20.11.80	16	23	15	(6)	38	2.37
28. 5.81	24	28	21	-	49	2.04
10. 6.81	25	62	50	-	112	4.48
23. 6.81	25	66	63	-	129	5.16
23. 9.81	20	96	112	-	208	10.40
12. 5.82	20	28	31	-	59	2.95
15. 9.82	40	n/d	n/d	-	163	4.07

Figure 8.3 (a)

Catch data, Stratfield Saye.

1979 - 1982.

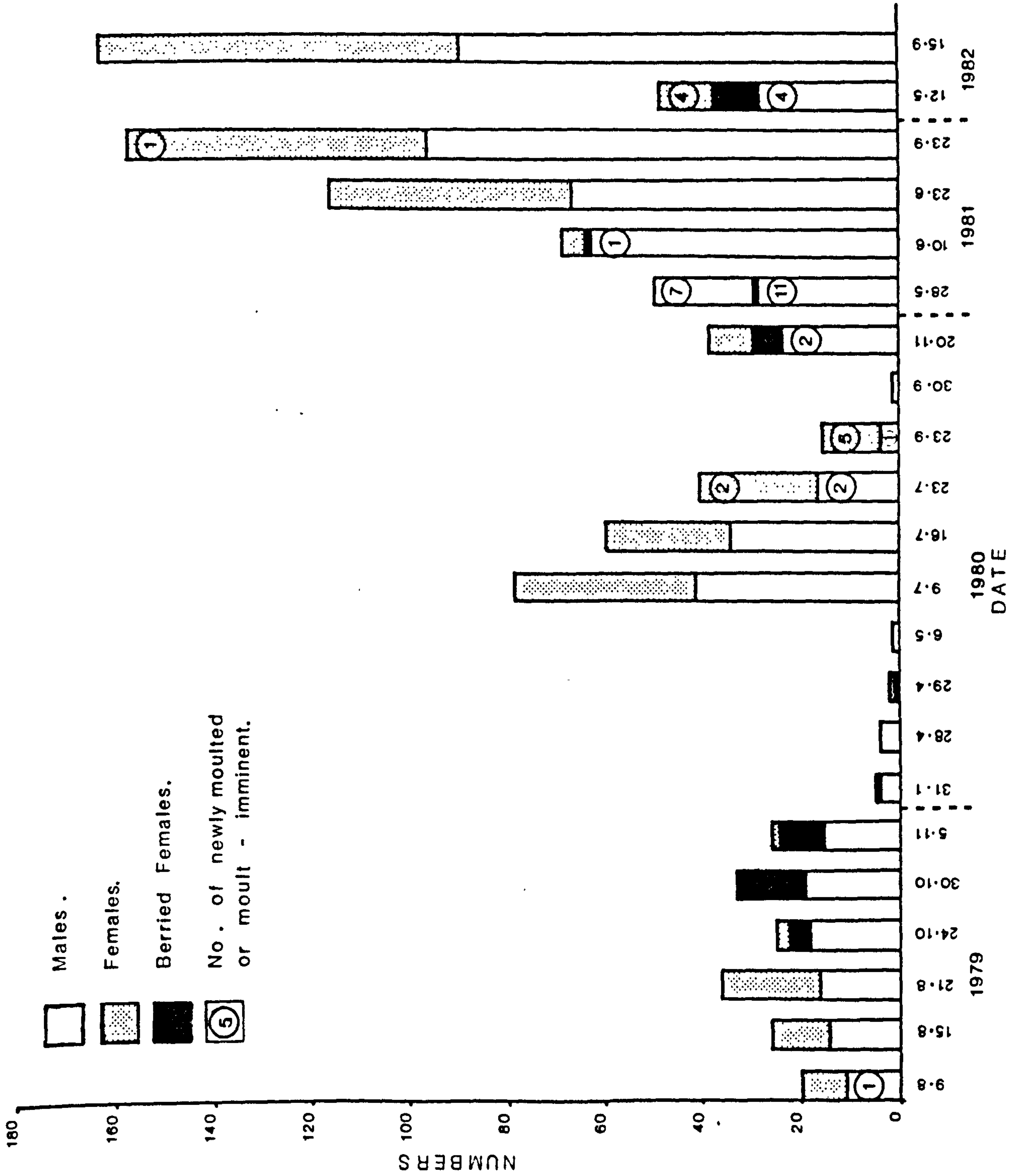


Figure 8.3(b)

Catchability of *P. leniusculus*, Stratfield Saye.

1979 - 1982.

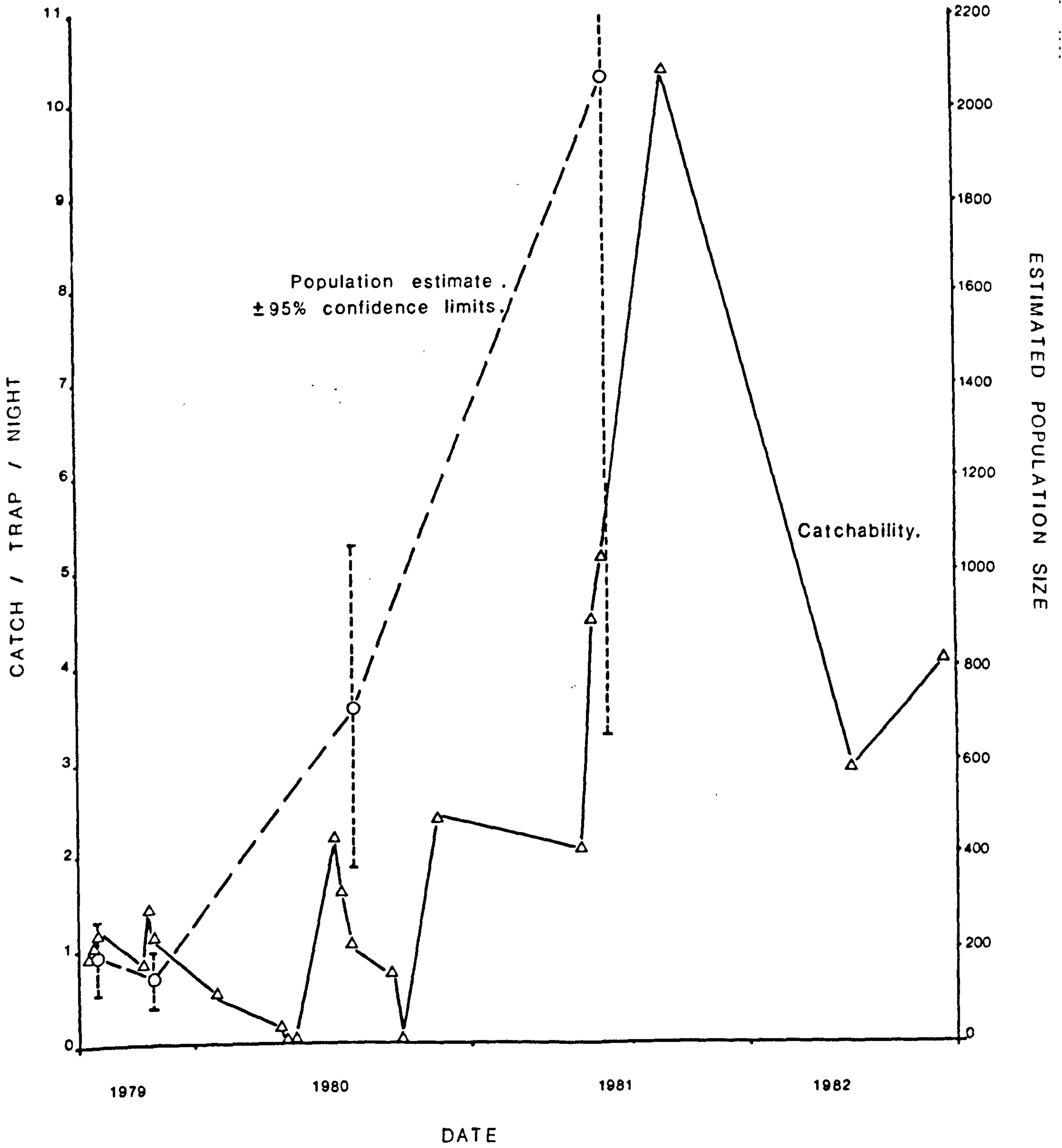


Figure 8.4 Size distribution of *P. leniusculus* in samples

collected from Stratfield Saye.

1979 - 1982.

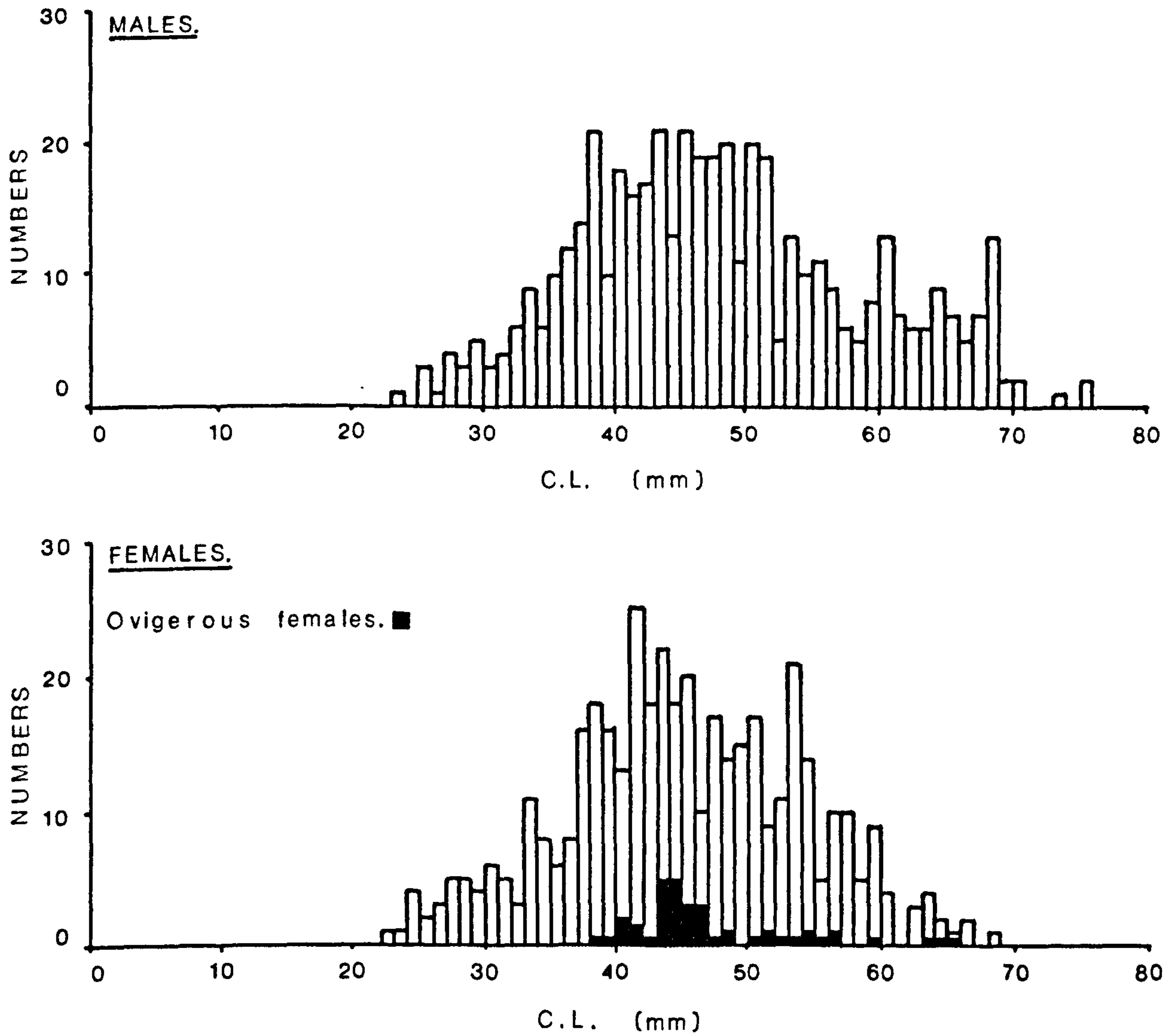
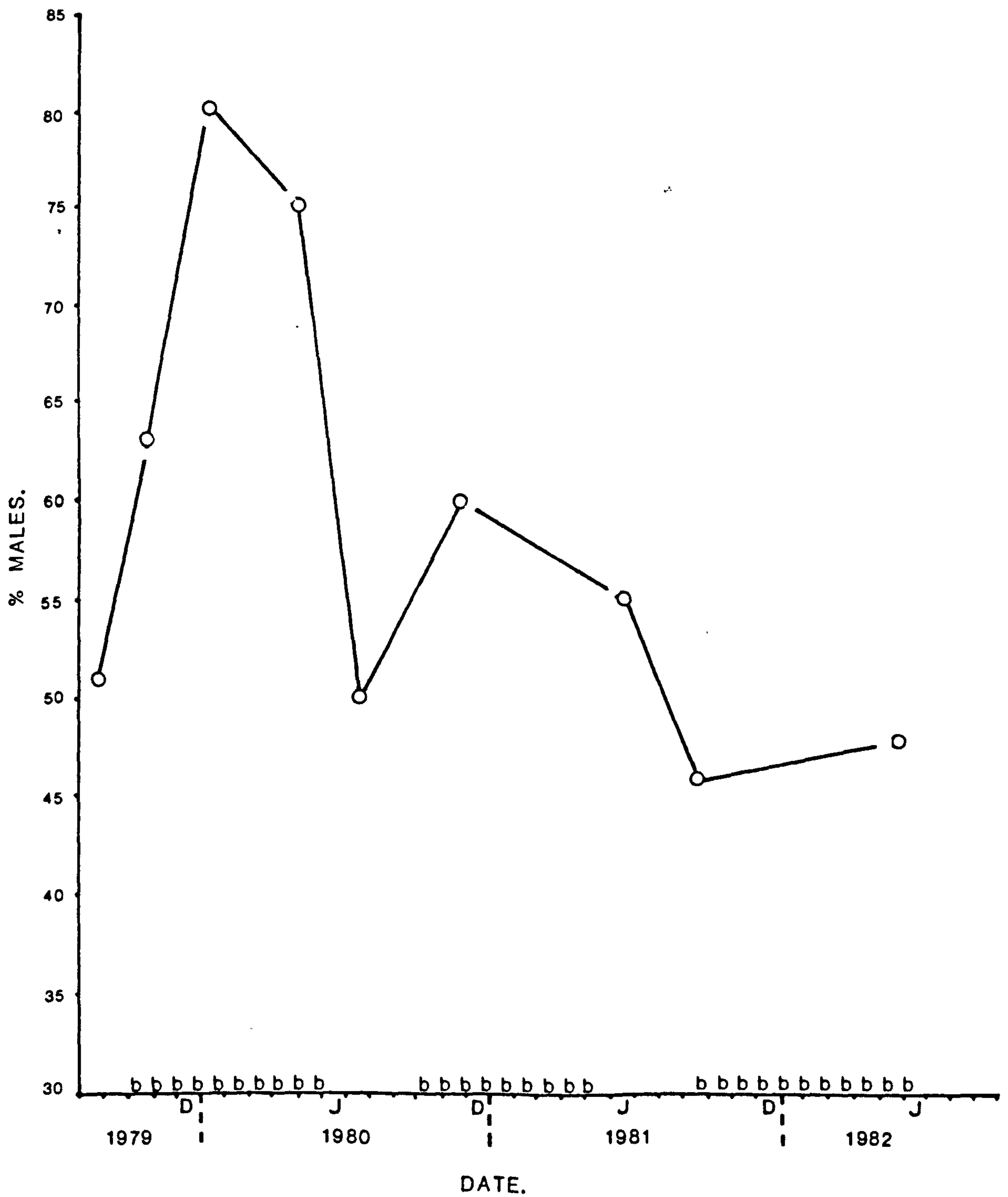


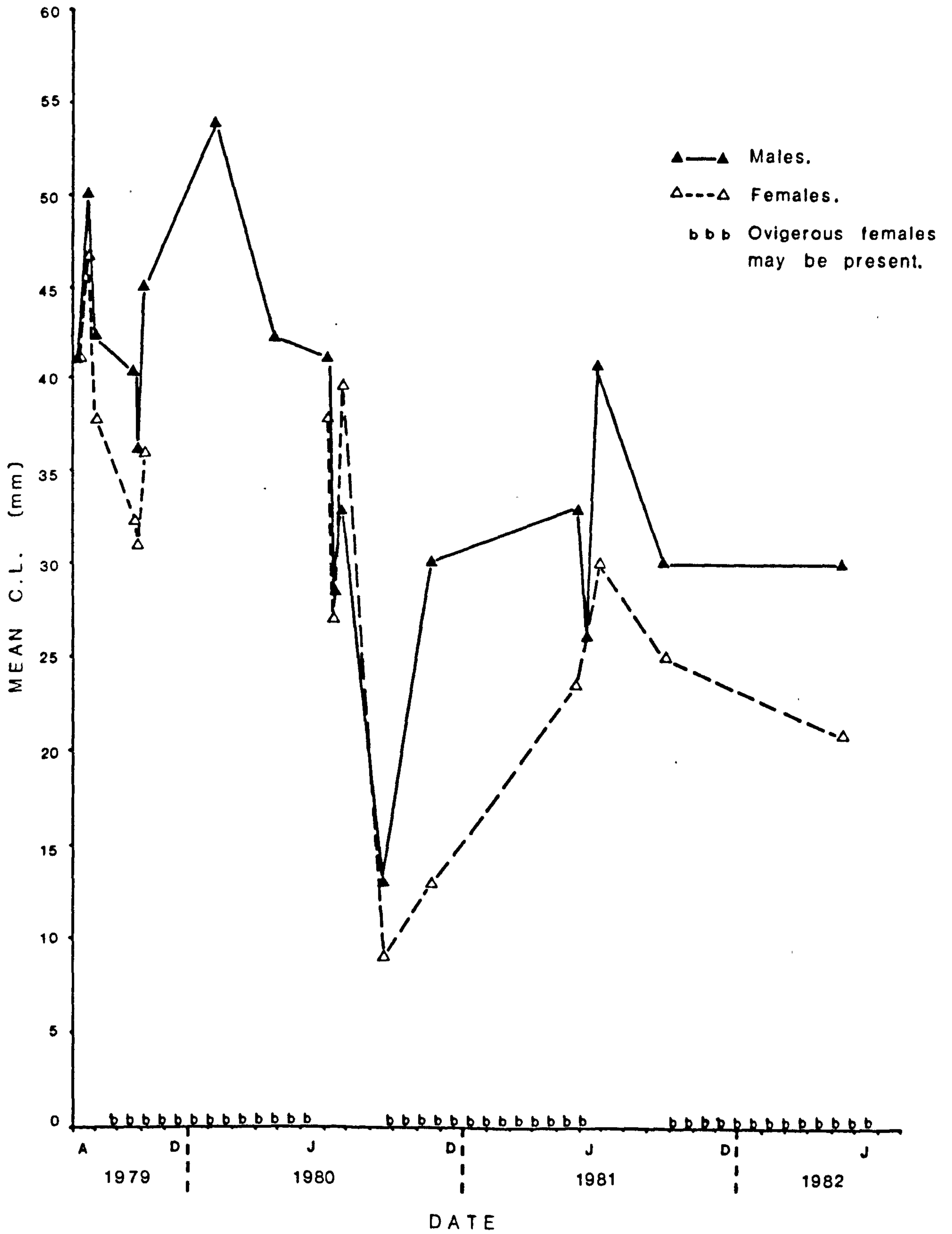
Figure 8.5 Sex ratio of *P. leniusculus* in samples
collected from Stratfield Saye.
1979 - 1982.



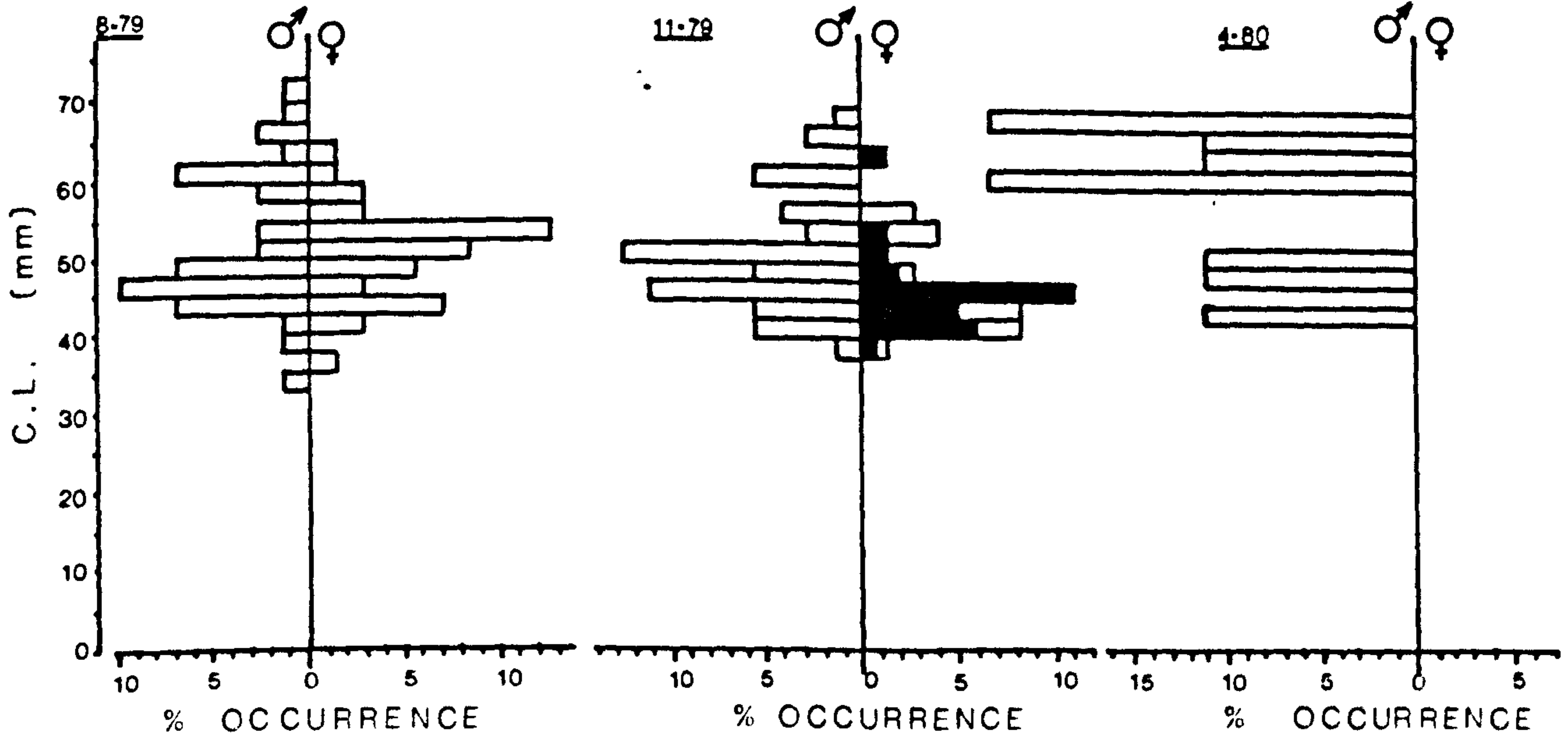
b b b b Ovigerous females may be present.

Figure 8.6 Mean C.L. of *P. leniusculus* in samples collected from Stratfield Saye.

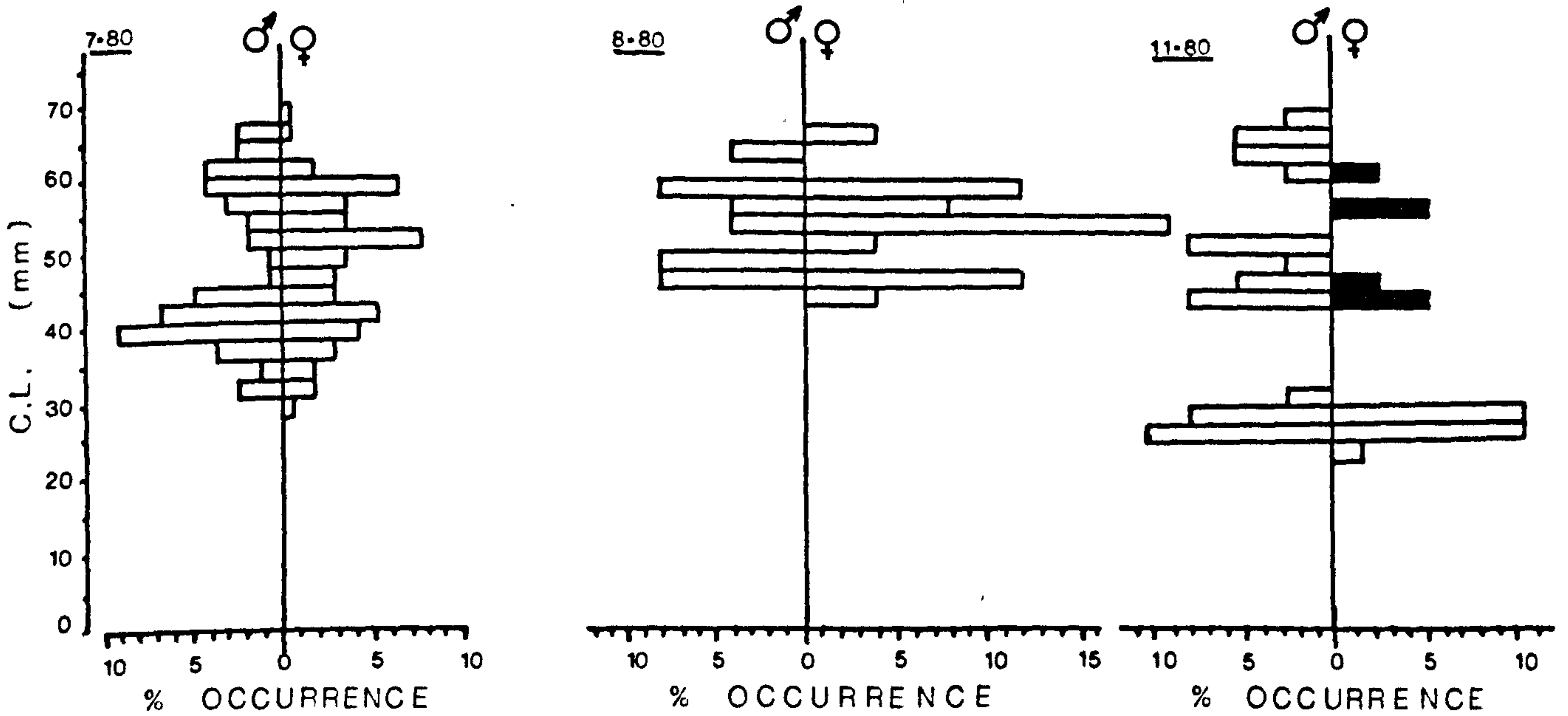
1979 - 1982.



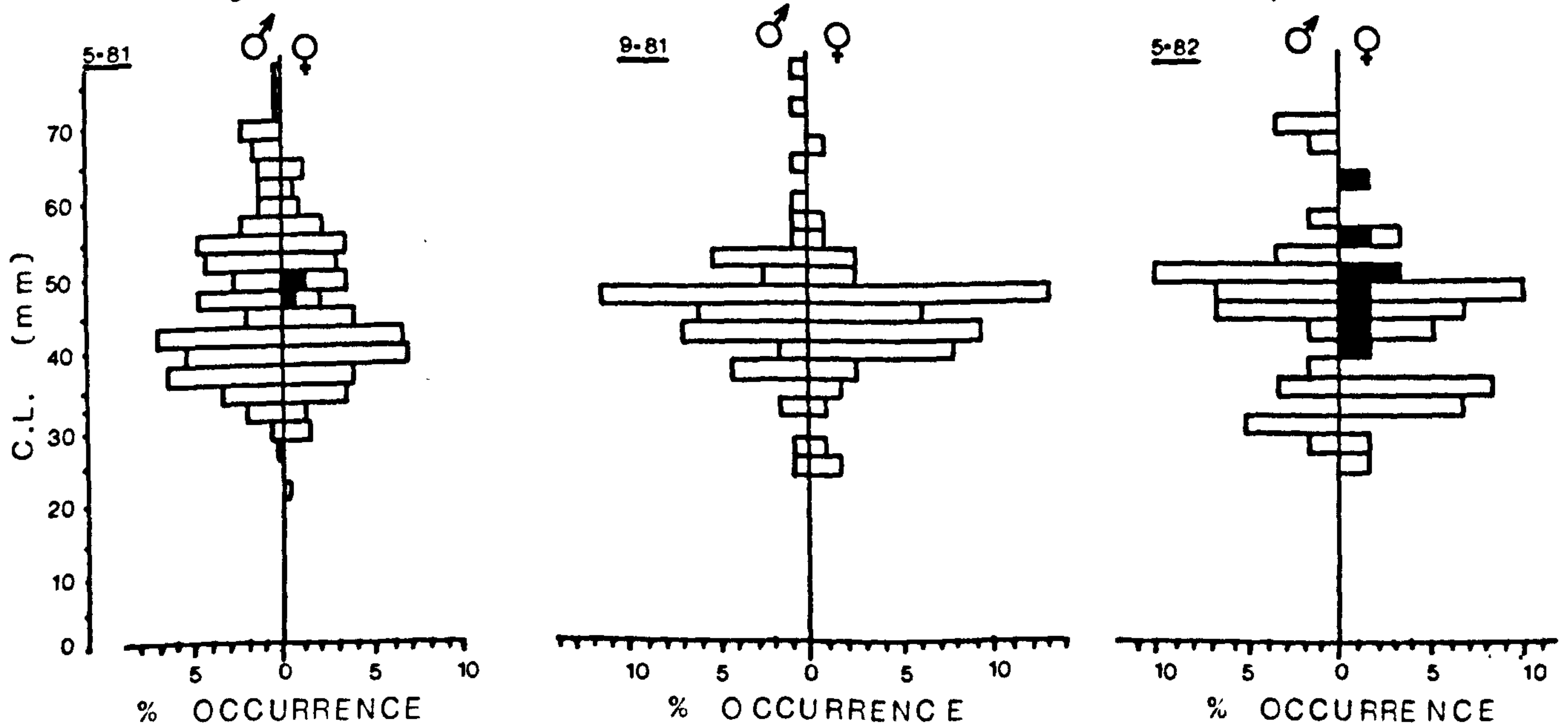
Stratfield Saye. 1979 - 1982.



NB. Histograms show the number in each size class as a % of the total sample size.



■ Ovigerous females. Data used to form monthly totals, ignoring recaptures, may originate from 1 or > 1 samples.



separately, have been drawn, see Figure 8.8, for the period 1979 to 1981. Also shown is a curve constructed using only data collected from the initial implants, i.e. during 1979. Additionally, published data are also shown, Figure 8.9, for P.leniusculus (Abrahamsson, 1973a; Emadi, 1974; Mason, 1974, 1975; Flint, 1975a, b); A.pallipes (Brown, 1979; Pratten, 1980); A.leptodactylus (Erençin & Köksal, 1977; Anon, 1980); O.limosus (Kossakowski, 1974; Jestin, 1979) and A.astacus (Westman & Pursainen, 1979; Cukerzis, 1979; Abrahamsson, 1971, 1972, 1973a).

From the mark-recapture investigation 63 individually marked crayfish were recovered. Of these 27 showed an increase of carapace length indicative of at least one moult. Measurements obtained from the individually marked adults are listed in Table 8.4. Growth increments are also shown and will be used for comparison with published data (Abrahamsson, 1973a; Emadi, 1974; Mason, 1974, 1975; Flint, 1975a, b). Moult frequency is not known, however, and can only be intuitively deduced, again using published data (Flint, 1975a, b). It is therefore not legitimate to express growth in terms of moult increment, using this data, and the relationship between pre-moult and post-moult carapace lengths cannot be calculated.

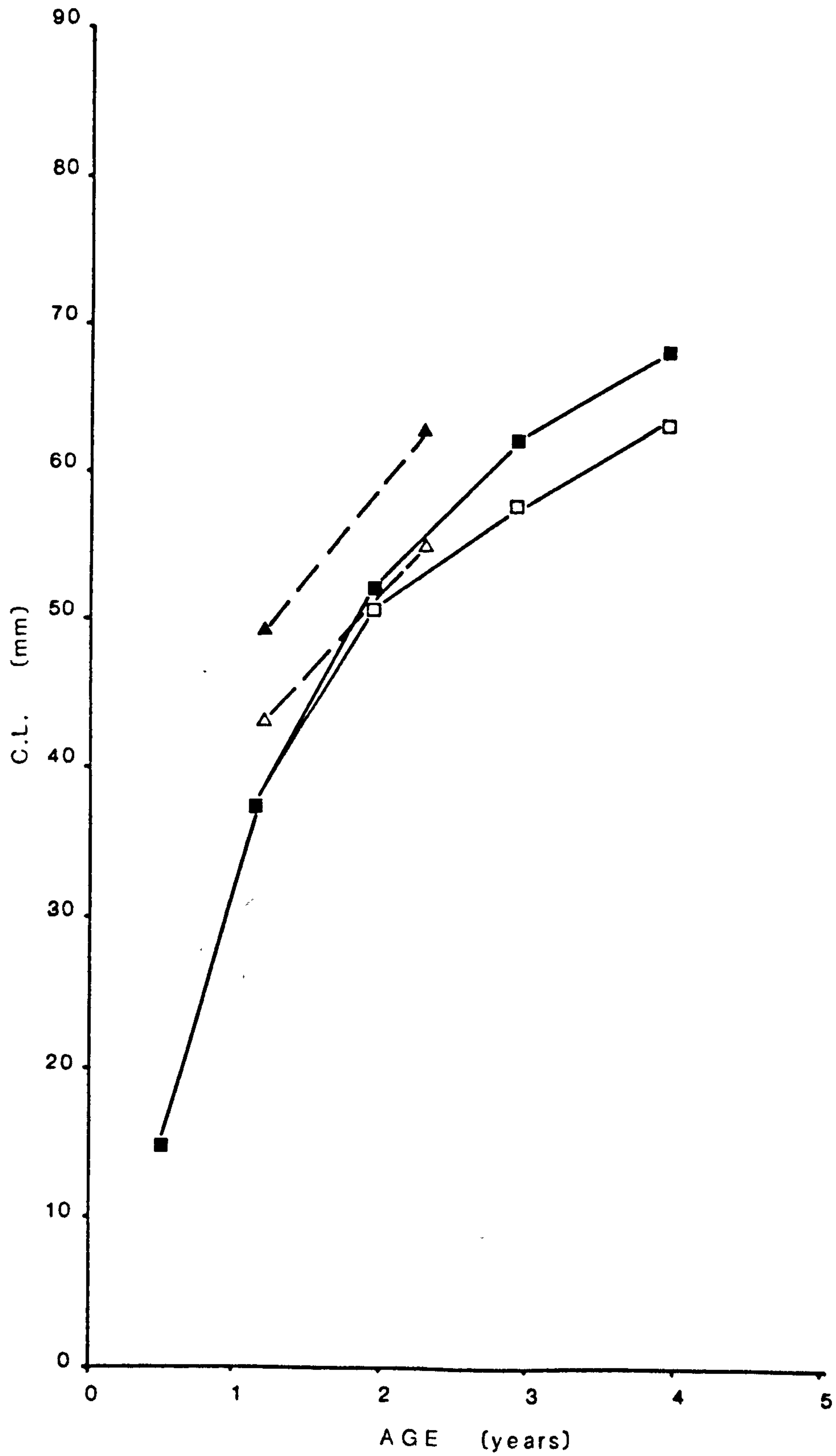
8.3(iv) - Morphometric Data.

The relationships between the various measured characteristics of individual P.leniusculus in this population have been established using regression analysis. The results of these analyses are shown in Table 8.6 and Figure 8.10. The relationship of C.L. to wet weight is clearly logarithmic so the resultant equation is exponential in form. All the other relationships have been described by simple linear regression analysis.

It is clear, however, that the relationship between C.L. and the width of the second abdominal segment, in females,

Figure 8.8 Proposed growth curves for *P. leniusculus*

at Stratfield Saye.

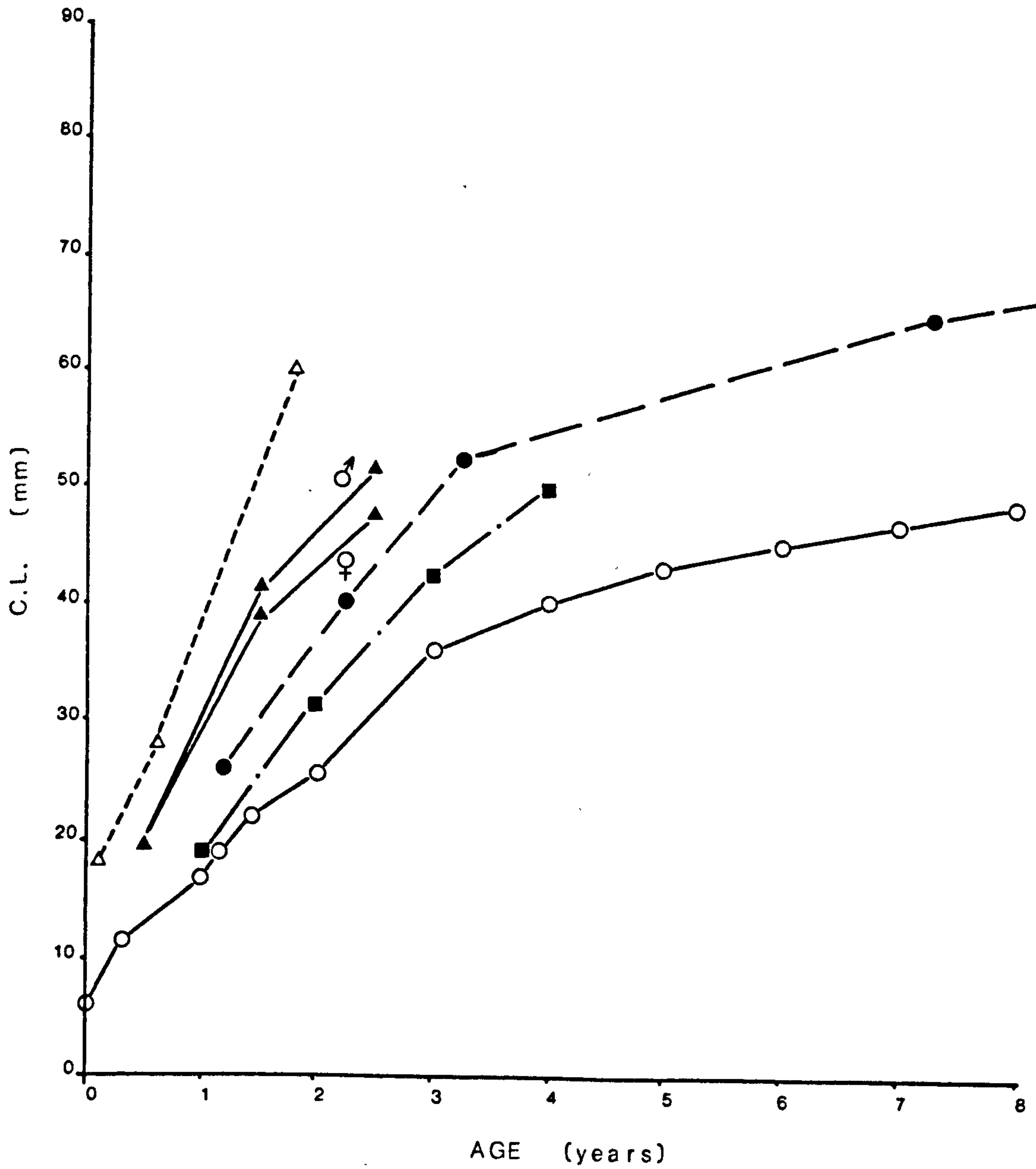


■—■ Males. 1977 - 1981
□—□ Females. 1977 - 1981
▲---▲ Males. 1977 - 1979
△---△ Females. 1977 - 1979

Figure 8.9 (a)

Growth curves for *P. leniusculus*

- published data.



- L. Tahoe, California. (Flint, 1975).
- Canada, . (Mason, 1974).
- Lithuania. (Cukerzis, 1980).
- ▲—▲ Sweden. (Abrahamsson, 1973).
- △—△ France - in culture. (Laurent, 1980).

of freshwater crayfish - published data.

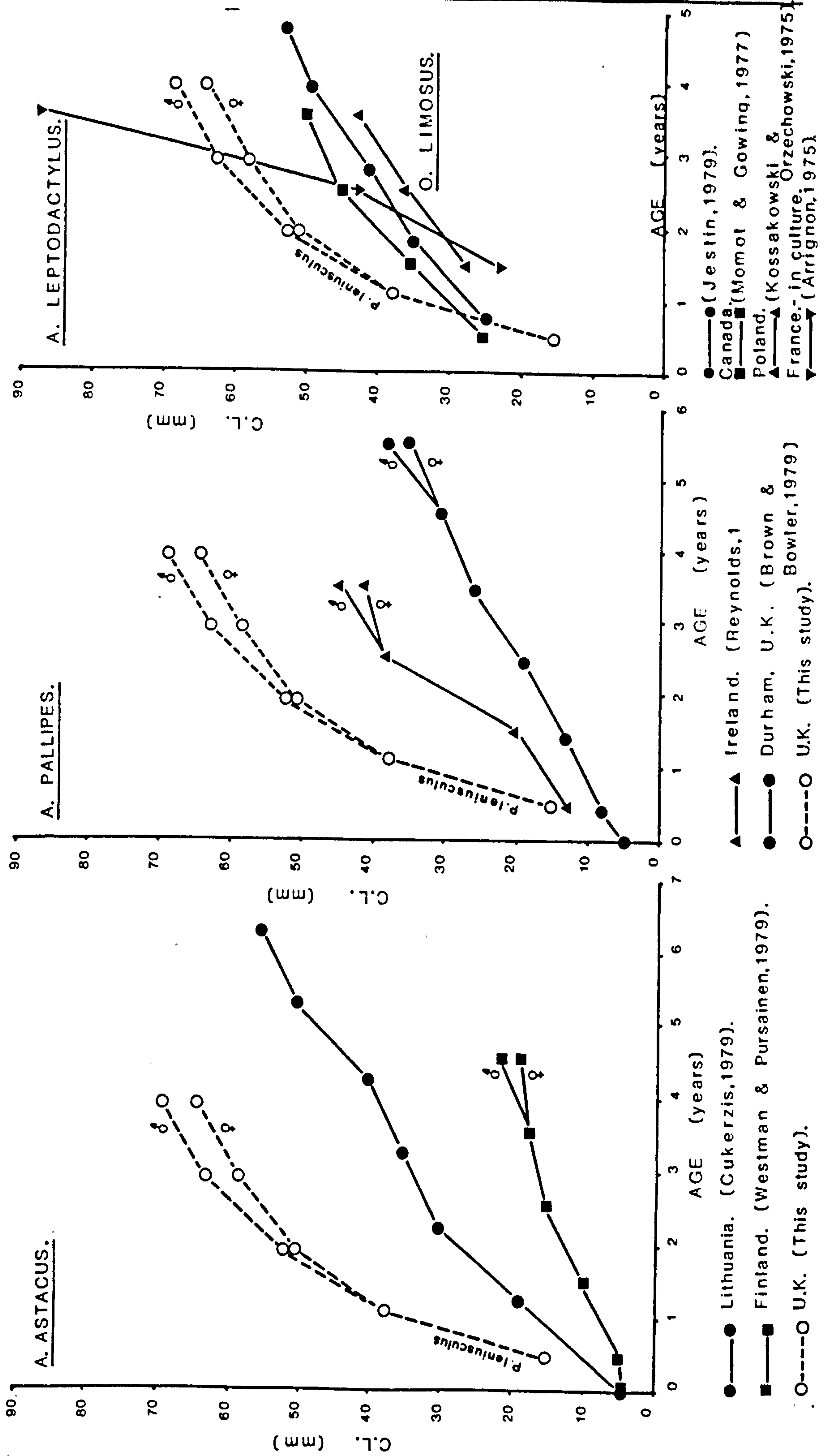


TABLE 8.4 : GROWTH INCREMENTS OF INDIVIDUALLY MARKED P.LENIUSCULUS.

STRATFIELD SAYE. 1979 - 1981.

(a) MALES. (C.L. mm)

No. -->	10	24	31	32	34	40	51	73	110	131	162	179	193	313
9. 8.79	49.9													
15. 8.79		65.8	60.1	45.6	53.2	45.1	44.0							
21. 8.79			60.1	47.7	53.1									
24.10.79			60.0					57.0						
30.10.79									53.0					
5.11.79			60.0					59.5	53.5	65.0				
31. 1.80			65.0											
23. 4.80		68.0												
9. 7.80	65.5 (R)					59.5			62.0 (R)	68.5 (R)	53.0	41.0	42.0	
16. 7.80											55.0		43.5	
23. 7.80							61.5				55.0	42.5	43.0	31.5
23. 9.80														35.0
20.11.80					64.5									
10. 6.81												47.0		
Recaptures	1	1	4	1	2	1	1	1	2	1	2	2	2	1
Growth Increment (mm)	15.6	2.2	4.95	2.1	11.35	14.4	17.5	2.5	8.75	3.5	3.0	5.25	1.25	3.5
% of Pre M.C.L.	31	3.3	8.2	4.6	21	32	40	4.4	16	5.4	3.8	12.	3.0	11

N.B. R = Individual removed.

TABLE 8.4 : Continued

(b) FEMALES. (C.L. mm)

No. -->	4	35	37	39	65	70	120	122	170	197	228	250	306
9. 8.79	43.4												
15. 8.79		53.2	47.3	53.3									
21. 8.79	43.4		47.4		58.8								
24.10.79						43.5							
30.10.79													
5.11.79				53.0 (B)			63.0 (B)	40.5 (B)					
31. 1.80													
23. 4.80													
9. 7.80		54.0 (R)	51.0	57.0 (R)	62.0			46.5	38.5				
16. 7.80	52.5		52.0				44.0			51.5	43.0		
23. 7.80	52.0					48.0	66.0		43.3		46.5	51.5	
23. 9.80													56.0
20.11.80													
28. 5.81													
10. 6.81								53.0		56.0			
Recaptures	3	1	3	2	1	1	1	1	1	1	1	1	1
Growth Increment (mm)	8.85	0.8	4.15	3.85	3.2	4.5	3.0	3.5	6.5	4.8	4.5	3.5	4.5
% of Pre M.C.L.	20	1.5	8.7	7.2	5.4	10	4.8	8.6	14	12	8.7	8.1	8.7

N.B. R = Individual removed.
B = Ovigerous female.

Only individually recognisable crayfish that had increased in size are included.
19 males + 17 females recaptured > once
(max. 3 recaptures) showed no size increase.

TABLE 8.5 : SIZE* OF P.LENIUSCULUS IN RELATION TO AGE.

(INCLUDING PUBLISHED DATA)

<u>Location</u>	<u>Age (years)</u>								<u>Reference</u>
	0+	1+	2+	3+	4+	5+	6+	7+	
Sweden	20.0	40.0	52.5	60.0	-	-	-	-	Abrahamsson, 1973 a.
Sweden	-	44.0	-	60.0	-	-	-	-	Brinck, 1975.
Sweden (hatchery)	11.0	42.5	57.5	-	-	-	-	-	Vigneux, 1979.
Finland	-	32.5	-	55.0					Westman, 1973 a. Westman + Pursainen, 1979.
Russia	-	25.0	40.0	52.5	60.0	-	-	-	Cukerzis + Terentjew, 1979.
France	12.5	22.5	35.0	-	-	-	-	-	Laurent + Forest, 1979.
France (hatchery)	30+	44.0	-	-	-	-	-	-	Vigneux, 1979.
Canada (stream)	12.5	22.5	31.5	39.5	43.6	46.8	49.5	51.8	Mason, 1975.
U.S.A. (L. Tahoe)	10.0	20.0	28.0	32.5	35.0	37.5	40.0	45.0	Goldman + Rundquist, 1977.
U.S.A. (L. Tahoe)	17.0	28.6	37.1	42.6	45.3	48.0	50.7	53.3	Flint, 1975 a.
U.S.A. (Laboratory)	10.0	25.0	40.0	48.0	-	-	-	-	Emadi, 1974.
U.K. ♂	21.0	52.5	67.5	71.0	-	-	-	-	This study
U.K. ♀	21.0	49.0	60.0	67.0	-	-	-	-	" "

* Size = C.L. in mm.

TABLE 8.6(a) : MORPHOMETRIC RELATIONSHIPS FOR P.LENIUSCULUS AT
STRATFIELD SAYE.

Regression equation	r	n	Eqn. no.
<u>C.L. x T.L.</u>			
♂ T.L. = 1.9304C.L. + 2.3108	0.983	58	[1]
♀ T.L. = 2.038 C.L. - 0.64	0.956	49	[2]
<u>C.L. x P.O.C.L.</u>			
♂ P.O.C.L. = 0.814C.L. - 1.014	0.994	51	[3]
♀ P.O.C.L. = 0.781C.L. + 0.193	0.993	50	[4]
<u>C.L. x Freshweight</u>			
♂ log ₁₀ wt. = 3.318.log ₁₀ C.L. - 4.061	0.907	102	[5]
♀ log ₁₀ wt. = 3.211.log ₁₀ C.L. - 3.885	0.895	95	[6]

TABLE 8.6(b) : MORPHOMETRIC RELATIONSHIPS OF P.LENIUSCULUS IN THE
THAMES CATCHMENT, SHOWING SEXUAL DIMORPHISM

Location	Sex	Size group	Regression equation	t-test details			Eqn. no.
				t	df	p	
<u>C.L. X 2.A.W.</u>							
All sites	♂	C.L.<42.0mm	2A.W. = 0.474C.L.-0.780	1.59	157	<0.001	[7]
	♂	C.L.>42.0mm	2A.W. = 0.528C.L.-1.497				[8]
Stratfield Saye	♂	C.L.<34.5mm	2A.W. = 0.515C.L.-1.847	0.389	102	<0.001	[9]
	♂	C.L.>34.5mm	2A.W. = 0.505C.L.-1.55				[10]
All sites	♀	C.L.<36.0mm	2A.W. = 0.497C.L.-1.132	9.16	128	<0.001	[11]
	♀	C.L.>36.0mm	2A.W. = 0.753C.L.-9.609				[12]
Stratfield Saye	♀	C.L.<33.0mm	2A.W. = 0.519C.L.-1.640	7.62	86	<0.001	[13]
	♀	C.L.>33.0mm	2A.W. = 0.745C.L.-8.683				[14]
<u>C.L. X Ch.L.</u>							
All sites	♂	C.L.<40.0mm	Ch.L. = 0.768C.L.-1.854	14.83	147	<0.001	[15]
	♂	C.L.>40.0mm	Ch.L. = 1.401C.L.-28.705				[16]
Stratfield Saye	♂	C.L.<36.5mm	Ch.L. = 0.781C.L.-2.119	8.59	63	<0.001	[17]
	♂	C.L.>36.5mm	Ch.L. = 1.348C.L.-25.844				[18]
All sites	♀	C.L.<36.0mm	Ch.L. = 0.735C.L.-1.957	7.23	114	<0.001	[19]
	♀	C.L.>36.0mm	Ch.L. = 0.969C.L.-11.201				[20]
Stratfield Saye	♀	C.L.<34.5mm	Ch.L. = 0.726C.L.-1.804	6.67	56	<0.001	[21]
	♀	C.L.>34.5mm	Ch.L. = 1.011C.L.-13.042				[22]

of C.L.: T.L. and C.L. : P.O.C.L.

in *P. leniusculus*, Stratfield Saye.

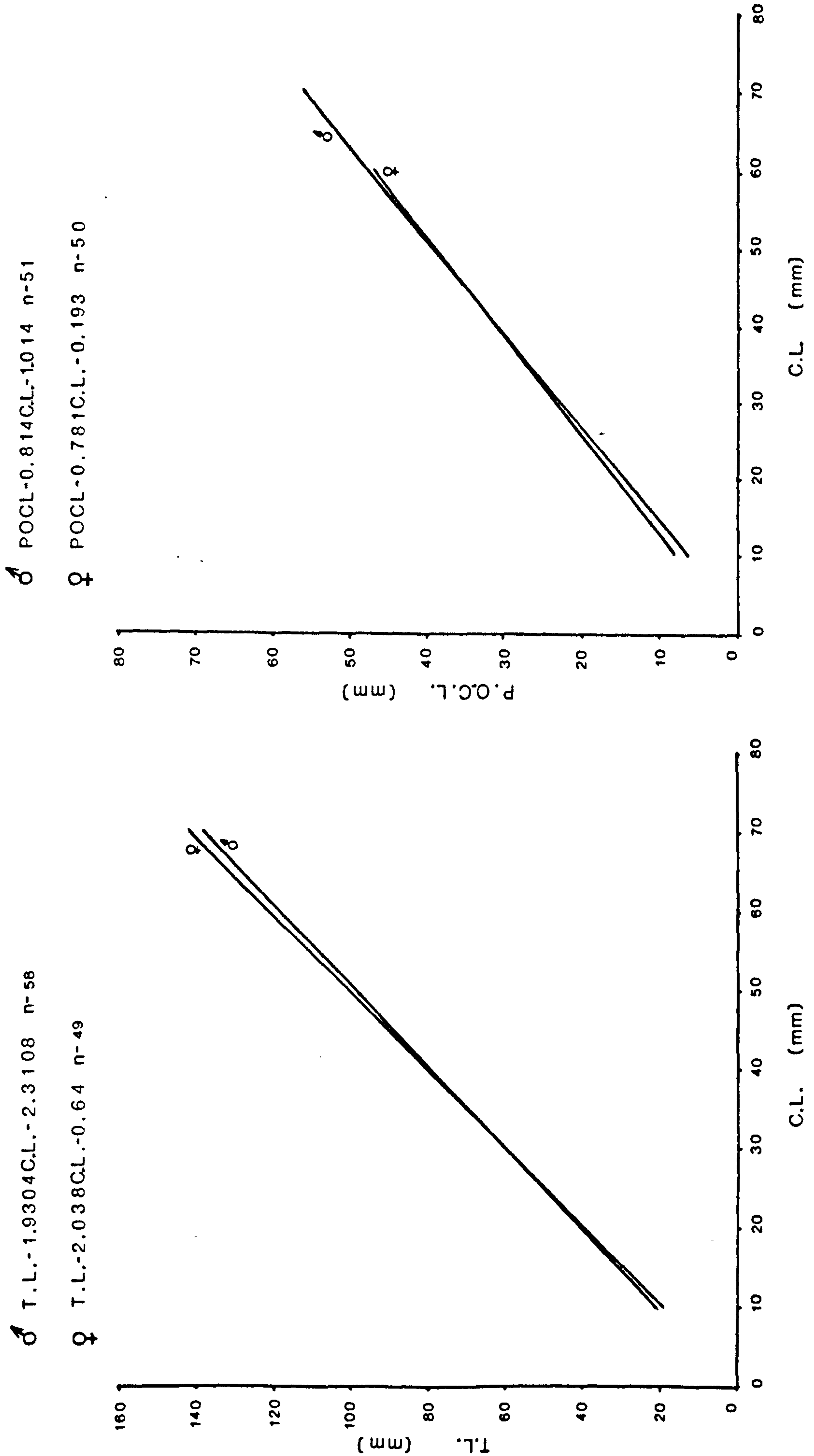


Figure 8.11 (a) Graph showing the relationship

C.L. : Ch.L. for *P. leniusculus*, Stratfield Saye.

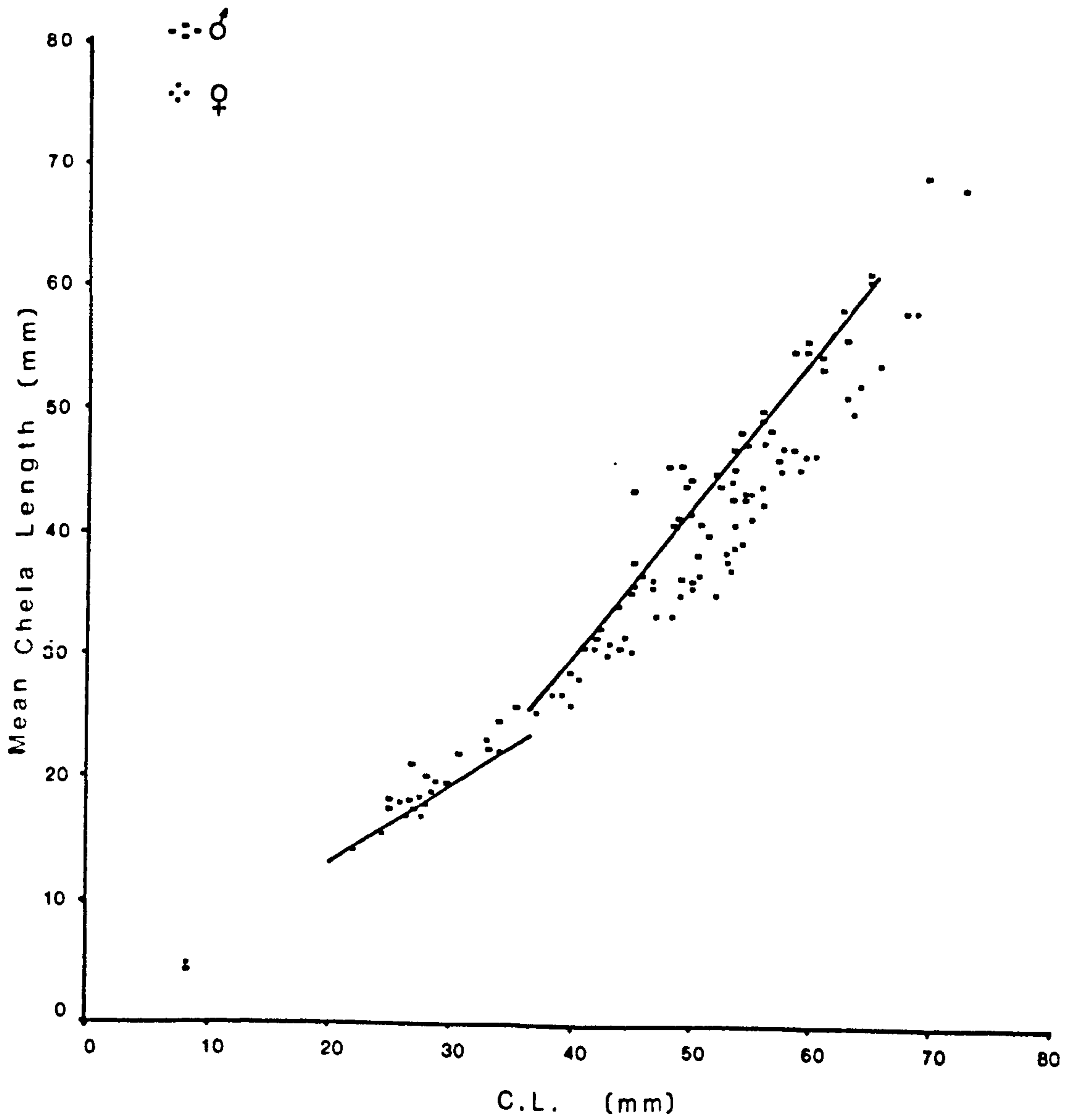


Figure 8.11 (b) Graph showing the relationship of

of C.L. : 2A.W. for *P. leniusculus*, Stratfield Saye.

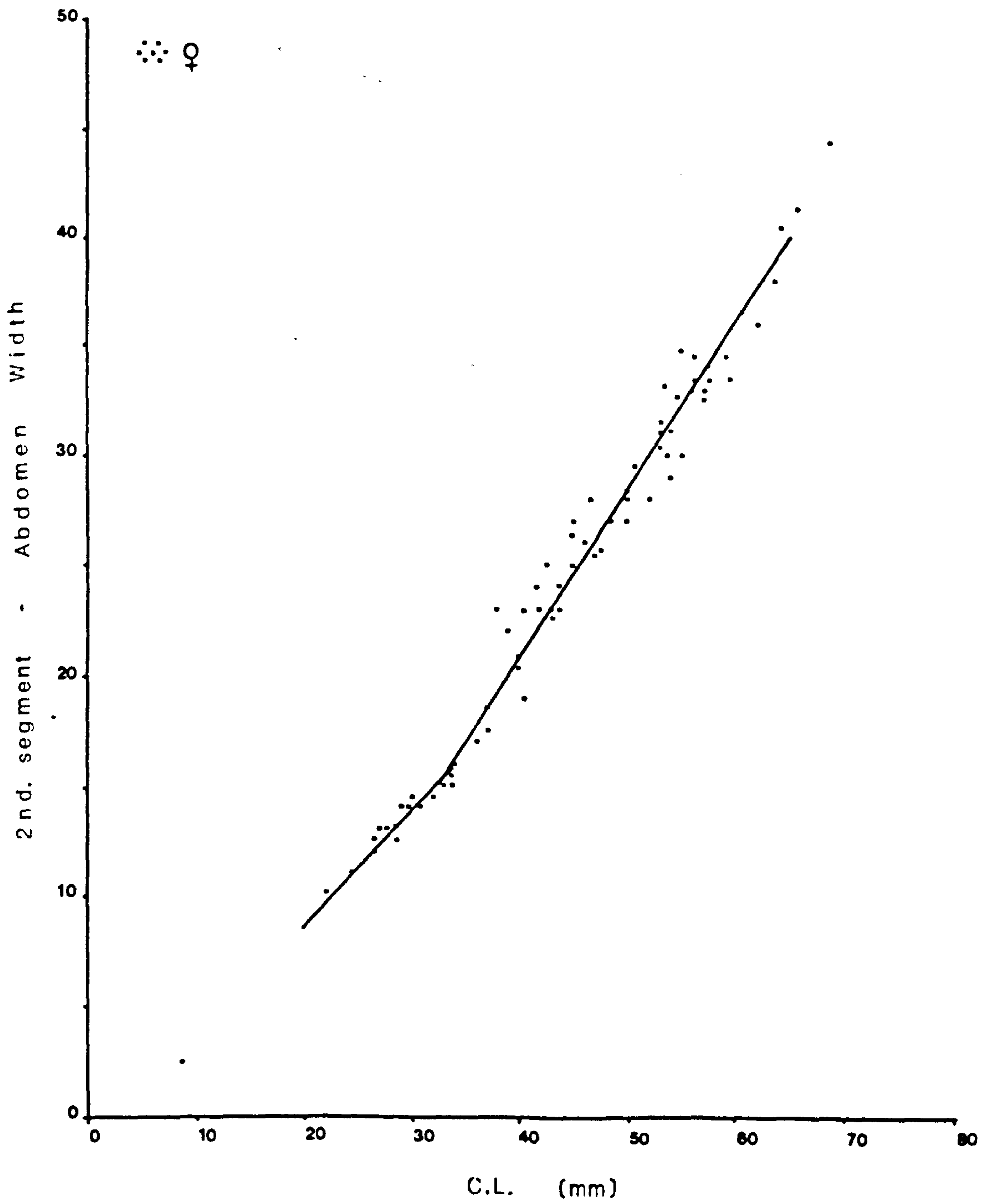


Figure 8.12 Graphs showing the relationship of

C.L. : Weight for P. leniusculus, Stratfield Saye.

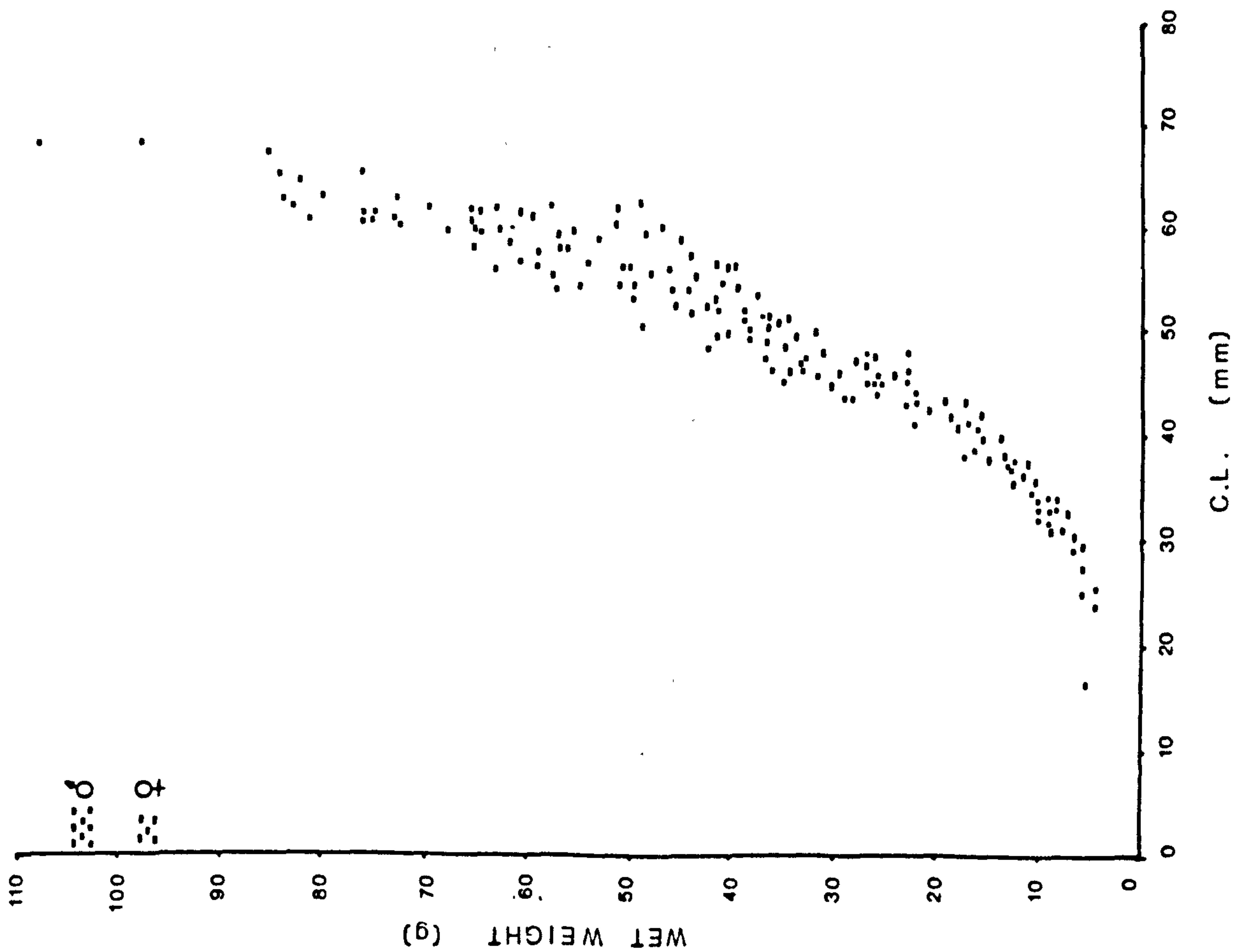
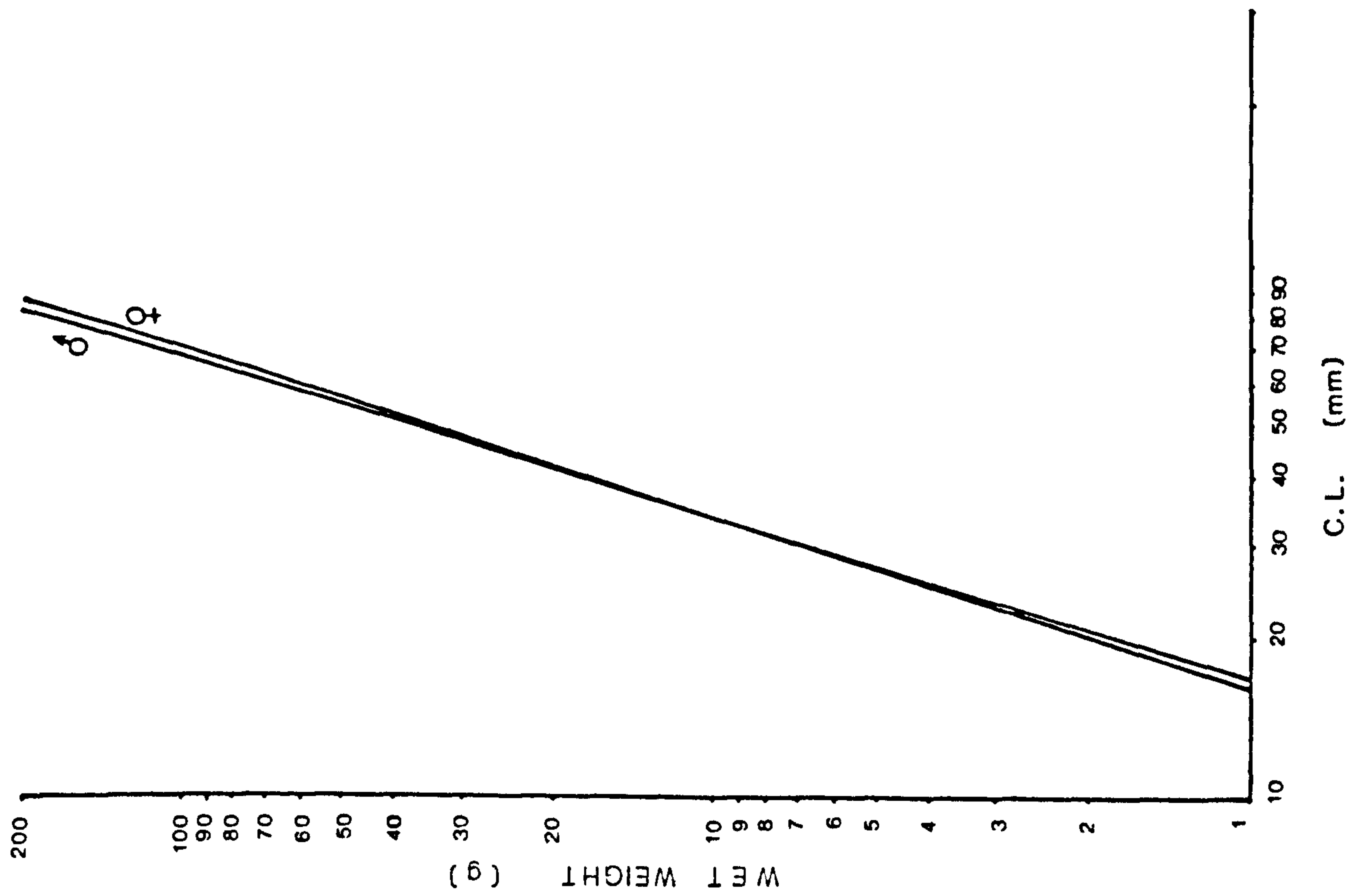


TABLE 8.7 : CONDITION FACTORS CALCULATED FOR P.LENIUSCULUS AT STRATFIELD SAYE. 1979 - 1982.

Date	Mean C.F.	n.	S.D.	
<u>MALES</u>				
August 1979	9.319×10^{-6}	30	1.16×10^{-5}	
October 1979	9.243×10^{-6}	47	9.57×10^{-6}	
Spring 1980	8.390×10^{-6}	9	4.42×10^{-6}	
Spring 1981	8.700×10^{-6}	27	1.09×10^{-5}	
Spring 1982	8.974×10^{-6}	7	4.53×10^{-6}	
	Mean 8.92×10^{-6}	120		
<u>FEMALES (ALL)</u>				
August 1979	1.320×10^{-5}	35	1.42×10^{-5}	
October 1979	1.410×10^{-5}	31	1.39×10^{-5}	
Spring 1980	1.330×10^{-5}	3	1.20×10^{-5}	
Spring 1981	1.351×10^{-5}	22	1.05×10^{-5}	
Spring 1982	1.375×10^{-5}	11	1.45×10^{-5}	
	Mean 1.357×10^{-5}	102		
<u>FEMALES (BERRIED/NON BERRIED)</u>				
October 1979	B	1.440×10^{-5}	26	1.30×10^{-5}
	⊗	1.279×10^{-5}	5	8.05×10^{-6}
January 1980	B	1.370×10^{-5}	1	-
November 1980	B	1.457×10^{-5}	6	1.17×10^{-5}
	⊗	1.401×10^{-5}	9	9.42×10^{-6}
	Mean B	1.422×10^{-5}	33	
	Mean ⊗	1.340×10^{-5}	14	

$CF = K = W/l^b$ (Ricker, 1971)

Where W = Weight

l = total length

b = constant (wt = a.TL.^b) b ♂ = 3.318. b ♀ = 3.211

(from eqn.[6]. Table 8.6(a))

and C.L. and chela length in males, Figure 8.11 are not adequately described by a single regression equation. Consequently multiple regression analysis (see Chapter 2) has been carried out in these cases and the resultant equations are listed in Table 8.6 together with the size (C.L. in mm.) at which the relationships alter. These findings have been confirmed by calculating the ratio of C.L. to abdomen width. In all females >35.0 mm.C.L. this ratio was found to be significantly greater than 2:1 ($p < 0.05$), whereas in males >37.0 mm.C.L. it was not. This finding agrees with published data available for P.leniusculus elsewhere (Mason, 1974). It is at this size that the so called 'maturity moult' occurs and this information is useful when comparing populations from different habitats (Huner & Romaine, 1979; see Chapter 9).

Using the C.L. and weight data a condition factor has been calculated for each crayfish for which such data is available. The mean values for this relationship for each season and sex are listed in Table 8.7. Comparison of the C.F. values for each sex and for berried and non-berried females has been carried out using a Students t-test. The C.F. values for males and females are not significantly different ($p > 0.05$) whereas those for berried and non-berried females are highly significantly different ($p < 0.01$).

8.4. Discussion.

The general aim of this investigation of a population of Pacifastacus leniusculus was to obtain the maximum information possible regarding the survival, growth and general biology of this species, which is an alien and only recently introduced to the U.K. Sampling has been organised to this end and, incidental to the main characteristics under consideration, a quantity of miscellaneous information regarding this species of freshwater crayfish has been collected.

8.4(i) - Water quality.

The study site is located in a predominantly agricultural setting and as a consequence of this the water is of variable quality, Table 8.1 and the graphs, Figure 8.2, illustrate this point. The chemical parameters considered to be of primary importance to astacid crayfish, i.e. pH, dissolved oxygen, calcium content and ammonia (Laurent, 1980) imply that crayfish require unpolluted, well aerated, 'hard' water and this is generally assumed to be true (Richards & Fuke, 1977).

The results of chemical analysis of water obtained from this lake show that the water is hard, total hardness 123 to 208 mg.l.⁻¹CaCO₃, and with a suitably neutral pH, 6.96 to 7.77. It has been recommended that waters to be stocked with crayfish should contain at least 14 mg.l.⁻¹ of calcium and have a pH greater than 6.5 (Laurent, 1980); although in Sweden A.astacus have successfully been introduced into lakes with a pH as low as 5.6 (Abrahamsson, 1972) and in the U.K. A.pallipes occurs naturally in waters with pH values ranging from 6.8 to 9.2 (Jay & Holdich, 1981).

In respect of pollution status the current results suggest that P.leniusculus is able to survive at low dissolved oxygen (D.O.) levels and surprisingly high levels of ammonia, at least for short periods of time. No published information is available regarding the toxicity of ammonia to crayfish. In Lake Tahoe, California, ammonia excretion by the population of P.leniusculus is considerable and provides a definite source of nutrients for primary production (Flint & Goldman, 1975). This benthic ammonia is rapidly oxidised to nitrate by heterotrophs, however, and despite the increases in benthic ammonia no significant increase in the ammonia concentration in the water column was recorded (Flint & Goldman, 1975).

As regards oxygen levels it has been shown that the

stream-dwelling crayfish, Orconectes virilis, died sooner than the related pond dweller, O. immunis, when subjected to low D.O. levels (Park, et al, 1940) implying that the latter are better adapted to survive short periods of low D.O. Lethal D.O. levels reported for coarse fish range from 0.35 to 2.50 mg.l⁻¹O₂ for tench, Tinca tinca, and carp, Cyprinus carpio and for salmonids from 0.80 to 3.70 mg.l⁻¹O₂ for brown trout, Salmo trutta, and rainbow trout, Salmo gairdneri (Anon, 1973). In crayfish it has been shown that below 2.5 mg.l⁻¹ of O₂ ventilation rate declines and extraction efficiency increases, suggesting that P. leniusculus may be more vulnerable to low D.O. levels than many other aquatic crustacea (Moshiri, et al, 1971). Lowest oxygen consumption occurs at 0°C., there is little variation between 5°C. and 12.5°C. and maximum consumption occurs at 15°C. coinciding with the maximum level of metabolic activity. Above 15°C. a decrease in respiratory activity occurs (Moshiri, et al, 1971).

The reason for such low D.O. levels in the study site in consecutive weeks in autumn, 1980, see Table 8.1, is not clear. At this time temperatures were not at a maximum and suspended solids levels were very low, as were the chlorophyll values. These factors suggest that short-term organic enrichment, for example due to the cattle returning to adjacent fields which had laid fallow during the preceding months, was not the cause. Such enrichment would characteristically be expected to result in a high suspended solids level and possibly a phytoplankton 'bloom', which would typically reduce D.O. levels during the night.

The high ammoniacal nitrogen and unionised ammonia levels in the autumn of 1979 and 1980, see Table 8.1, are perhaps more readily explained. Fields immediately adjacent to the lake are used for grazing cattle on a rotation basis, which results in the fields being left fallow in the summer months with grazing re-commencing in the autumn. It is probable, therefore, that the high ammonia levels in the lake water at

this time are largely the result of cattle returning to the vicinity of the lake. Approximately 80% of the lake margin is unfenced giving the cattle free access to the water. In addition large flocks of geese (see 8.1) overwinter on the lake and considerable quantities of faecal material must also enter the lake from this source.

That accurate and regular temperature recording was not carried out during this study is unfortunate as this would have provided, perhaps, an explanation for the apparently very rapid growth rates of crayfish in this population compared with published growth data from other locations (e.g. Abrahamsson, 1971, 1973a, b; Mason, 1974, 1977; Flint, 1975a, b). The available temperature records, see Table 8.1., are of bottom temperature and range from 3.5°C. to 19.0°C.

It is clear from the current study, therefore, that P. leniusculus are perhaps more tolerant of organic pollution than has previously been supposed. Presumably high levels of, for example, ammonia are not ideal for obtaining optimum growth and survival but it is evident that crayfish production is not totally excluded from sites with periodically poor water quality.

8.4(ii) - Methods.

All sampling at this site was carried out using baited traps (see Chapter 2) and variations in bait type and trap location were used to establish the most efficient trapping procedure. The largest catches were always achieved along the west bank, see Figure 8.1, where rubble had been provided to act as refugia and where the introductions had been made (Ellis, pers comm). Catches were also generally good along the east bank where abundant submerged tree roots provided suitable habitat. Crayfish were, on occasions caught elsewhere in the lake although very few were trapped in the centre, away from the banks.

Experimentation with bait types, although not rigorously tested, suggested that bait preference could be ordered as follows:

- (i) carp and tench;
- (ii) trout;
- (iii) kipper;
- (iv) liver;
- (v) no bait;
- (vi) pike.

Both carp and tench appeared to be the most successful baits and whenever possible these were used. Elsewhere it has been reported that liver (Laurent, 1980) and fresh meat (Abrahamsson & Goldman, 1970) are the most successful baits for trapping P. leniusculus and that bream, Abramis brama, is three times as effective as herring, Clupea harengus, (Abrahamsson, unpubl). Bait that was partially frozen prior to use was found to be particularly effective, perhaps because of additional fluids being released through cell rupture caused by freezing. This finding agrees with a similar result elsewhere (Bean & Huner, 1979). Only pike, Esox lucius, failed to attract crayfish during this study and it could be suggested that a recognition factor present in this bait deterred the crayfish but this hypothesis was not tested. Crayfish were also caught in 30% of unbaited traps when these were used.

Trapping was found to be size selective, Figure 8.4, and juveniles (C.L. < 21 mm) were never caught by this method. This figure is markedly smaller than the minimum trap sizes, for P. leniusculus, of 43.0 mm.C.L. for males and 29.0 mm.C.L. for females reported elsewhere (Laurent, 1980). The sex ratio of the population cannot be accurately determined due to the selectivity of trapping as a sampling method. In Sweden a ratio of 65% males to 45% females has been estimated (Abrahamsson, unpubl). Although it has been reported that the sex ratio in trapped samples is very seasonal, with females ranging from 0% in winter to 10% - 45% in summer (Abrahamsson, unpubl) and males comprising the larger proportion of trap catches from October to June/July with females dominating the

catches from July to the end of September (Flint, 1975a) this was not apparent in this study, see Figure 8.5. This is perhaps because sampling was largely carried out in the summer months, when the greatest trapping success could be expected, as low water temperatures in winter decrease general metabolism and slow down locomotor activity (Flint, 1977) and this agrees with the results of a similar study in Sweden (Odelström, 1977). Berried females were caught by trapping, Figure 8.4, contrary to previous reports that berried females "do not enter traps" (Brown, 1979, Abrahamsson, unpubl) and the reported decline in trapped female C.L. at this time was not observed (Flint, 1975a, b). The evident catchability of berried females bears out statements that these individuals require nourishment during the six to eight months of incubation and so food availability and foraging success at this time may influence propagative success (Mason, 1970).

The mean size of trapped crayfish declined during the course of this study and this is more evident in the males than the females, see Figure 8.6. It is suggested that this decline was largely the result of considerable numbers of adults, mostly males, being removed and the resulting increase in relative importance of the recruitment of 'subadult' crayfish to the trappable population. A similar decline in mean C.L. of trapped P.leniusculus has been reported in populations developing from juvenile introductions in France (Laurent, 1979) and from adult introductions in Sweden (Odelström, 1977). Such reports contrast with published results for A.astacus in Sweden, (Abrahamsson, 1972), where the mean size of trapped crayfish increased in the four years after the introduction of adults; perhaps in this latter case successful reproduction was not established. It has, therefore, been recommended that the exploitation of newly established populations of astacid crayfish should not commence for six to seven years after stocking (Laurent, 1979).

Marking was carried out according to a standard scheme (Abrahamsson, 1965; see Chapter 2) and this method was chosen because it resulted in relatively long-lasting marks, it persisted through the moult, it permitted large numbers of individual marks to be applied and it was both quick and cheap to carry out. The main problem encountered with this marking method was with the identification of individual marks over a long time period. The recapture frequency of individually marked crayfish was low, 10.7% see Table 8.4, but compares favourably with the 4% (n = 3,513) reported elsewhere (Flint, 1975a) although a recapture rate of ranging from 2% to 67%, according to size, has also been reported (Momot & Gowing, 1977). Consequently some useful data was lost, in this study, as marks were often unclear after a year or more. The silty nature of the substrate and the presumed infrequent moulting of large adults resulted in some individuals becoming covered in epiphytes and these, together with the silt they accumulated, acted to conceal or obscure the marks. The method of marking used was found to be ideal for short-term or 'batch' marking, for mark-recapture studies, over a period of three to four weeks but for longer term investigation of individual growth it is now clear that an internal tagging method (Weingartner, 1982) may be preferable.

8.4(iii) - Population Estimates.

Two methods for estimating the population size have been employed in this study: mark-recapture estimation and 'catchability'. Mark-recapture methods for estimating population size have been widely used for assessing the size of fish and small mammal populations (Southwood, 1966). There are, however, numerous inherent drawbacks in using such methods and their use in estimating the size of crayfish populations has been criticised (Brown & Brewis, 1979).

The mark-recapture methods used in this study,

i.e. Petersen, Jolly, Schnabel and Bailey (Ricker, 1975), have enabled estimates of population size, together with 95% confidence limits, to be calculated for this population from 1979 to 1981 (see Table 8.2). Initially of the order of 200 to 300, in August 1979, the estimate declined to 150 to 200 in November 1979, presumably due to a large proportion of females being berried at this time and consequently less readily entering traps. By July 1980, as a result of the increase in number of trappable crayfish caused by the influx of young 'subadults' to this category, the estimate increased to 715. Similarly in 1981 a large increase occurred as more young crayfish, progeny of the original introductions, exceeded the minimum trappable size. At this time the population size was estimated to be of the order of 2,000 to 2,200. The 95% confidence limits are, however, very large in relation to the estimates and for the 1981 estimate result in a figure falling within the range 665 to 3,459 (Petersen method). Other researchers have considered that estimates with confidence limits of less than $\pm 10\%$ are acceptable (Momot, 1967) and this guide is clearly exceeded in the present case where confidence limits average 44% of the estimates, (range 26% to 67%).

Despite this the figures do provide a guide to the order of magnitude of the population size, increasing from the low hundreds in 1979 to the low thousands by 1981. From a knowledge of the number of P. leniusculus introduced (Ellis, pers comm) approximate survival values can be assigned to the introductions. An approximate estimate of 20% of the 1977 and 1978 implants, totalling 1,000 juveniles, survived to late 1979; the crayfish introduced in that year would not be included in this estimate as they were not trappable at the time of sampling. This figure compares very well with the survival values reported elsewhere, see Table 8.8, and may reflect the relatively low stocking density and the absence of predators in the lake.

The mark-recapture method of estimating the size of a

TABLE 8.8 : SURVIVAL OF INTRODUCED CRAYFISH. (PUBLISHED DATA)

<u>Species</u>	<u>Location</u>	<u>Habitat</u> <u>Type</u>	<u>Stage</u>	<u>Elapsed</u> <u>Time</u>	<u>Estimated</u> <u>Survival</u>	<u>Reference</u>
<u>P. leniusculus</u>	Sweden	Lake	Juveniles (0+)	12 months	21%	Abrahamsson, 1973 b.
"	France	Pond	Juveniles	17 months	9.3%-13%	Vigneux, 1979
"	France	Pond	Juveniles	48 months	7%	Laurent, 1980
"	France	Pond	Adults	12 months	72%	Laurent, 1980
"	Canada	Creek	Adults	4 months	60%-70%	Mason, 1974
"	Canada	Creek	Adults	Overwinter	25%	Mason, 1974
"	Canada	Tanks	Juveniles	-	13%	Mason, 1974, 1979
"	Canada	Raceways	Adults	-	65%	Mason, 1974
<u>A. astacus</u>	Sweden	Lake (1)	Adults	24 months	4%	Abrahamsson, 1972
"	Sweden	Lake (2)	Juveniles?	36 months	27%	Abrahamsson, 1972
<u>C. tenuimanus</u>	Australia	Ponds	-	-	65% (16m ⁻²)	Jones, 1982

population of A.pallipes, using trapping as a sampling method, has been compared with estimates calculated from sampling by hand in a drainable aqueduct in the north of England (Brown, 1979; Brown & Brewis, 1979). This study concluded that trapping resulted in a consistent underestimation of population size by a factor of three. If this is also the case during the present study then survival has been excellent and the population of P.leniusculus has become very rapidly established in this lake. It should be noted, however, that other workers have considered that the mark-recapture method, using trapping as the sampling method, does provide reliable estimates of population size (Momot, 1967).

Due to the apparently clumped distribution of the population of P.leniusculus at this site little credibility can be attached to any estimate of density. A value of 0.22 crayfish m^{-2} can be calculated for the whole lake for 1981 and this compares poorly with most of the published information listed below:-

Species	Location	Density.(no. m^{-2})	Reference
<u>P.leniusculus</u>	Lake Tahoe	1.07	Flint & Goldman, 1975
" "	Ward Creek	0.16	" " " "
" "	Lake Tahoe	0.7 - 5.85	Flint, 1975a, b
" "	" "	0.9	Abrahamsson & Goldman, 1970

Crayfish population density is known to be related to the size of available cover and the bottom contours (Flint, 1975a) and, for example, in Lake Tahoe a bottom area equivalent to only 12% of the surface area is inhabited by P.leniusculus (Abrahamsson & Goldman, 1970).

A more useful relationship than density is, perhaps, the ratio of the estimated population size to the length of suitable bank. At Stratfield Saye an estimated 250 m. of the total bank length of c.650 m. is considered to be suitable crayfish habitat so an approximate figure of 2,000/2,500 i.e. 8 adult crayfish per metre can be calculated. This suggests that if all the bankside areas, estimated to

be 650 m., were to be rendered suitable as crayfish habitat then the holding capacity of the lake could be increased to approximately 5,200 adults.

8.4(iv) - Catchability.

In order to facilitate comparison between sites (see Chapter 9) and to relate the estimated population size to sampling success, the number of crayfish caught on each occasion has been expressed as catch per trap per night, Table 8.3, and Figure 8.3. This index of 'catchability' has increased throughout the period of the study, from almost 1.0. in 1979 to 10.4 in 1981, declining to a value between 3.0 and 4.0 in 1982. (Increasing again to 6.3 by August, 1983 - Penny, pers comm). Natural variation in the catchability of adult crayfish is due to alterations in locomotory activity (Abrahamsson, unpubl) and hence to moult and reproductive condition; the environmental temperature can be related to these conditions. Catchability is reported as showing a natural increase in June and July due to heavy pre and post-ecdysal feeding (Flint, 1975a) The low winter catchability is due to slow movement and low feeding rates, at low temperatures, and the crayfish remain in the immediate vicinity of their refuge (Flint, 1975a, b).

The decline in catchability from 1981, at this site, is thought to be principally due to the large numbers of crayfish removed for sale in 1982 and the smaller number removed during 1981. No accurate figures are available concerning the timing of removals or the numbers of adults removed and because the removals disrupted the marking system being used no population estimate has been calculated for 1982. It would be of interest to continue monitoring this population and follow the increase in catchability that it is assumed will occur if no further crayfish are removed.

Elsewhere research has shown that catchability can be directly related to population size and consequently may be used as a method of estimating numbers. A calibration must be carried out, however, on a population of known size and in a similar moult and reproductive condition to the population being investigated (Morrissey, 1975; Morrissey & Caputi, 1981). In the current study catchability is clearly related to population size as estimated by the mark-recapture experiments, see Figure 8.3, but there is insufficient reliable data available to enable the relationship to be quantified.

In northern Sweden the success of introductions of A.astacus has been monitored in terms of trapping success (Abrahamsson, 1972). A value of 0.2 adults trap⁻¹ night⁻¹ was obtained from a lake found to contain 56 adults when drained (from 1,400 adults introduced 3 years previously) and a value of 0.8 adults trap⁻¹ night⁻¹ in a lake containing 195 adults when drained (from 700 adults introduced 4 years previously). Similarly in Finland a population of 740 adult A.astacus resulted in a catchability of 0.7 trap⁻¹ night⁻¹ and 95 P.leniusculus adults gave a value of 0.1 trap⁻¹ night⁻¹ (Westman & Pursainen, 1979). In France a catchability of 5.75 P.leniusculus trap⁻¹ night⁻¹ has been reported (Laurent, 1975) and in California numbers per trap per night ranged from 5 to 30 in Lake Natoma and 4.5 to 6 in Lake Tahoe, over four nights (Abrahamsson, unpubl), to 13 and 18.5 respectively in another study (Abrahamsson & Goldman, 1970), with a mean of 12.04 trap⁻¹ night⁻¹ in Lake Tahoe.

8.4(v) - Length-Frequency Data and Growth.

In addition to providing information necessary for the estimation of population size trapping has also yielded samples of crayfish for length-frequency analysis for the assessment of growth rates on a population as well as an individual basis. The analysis of length-frequency

distributions, which segment a population into natural size groups (Van Deventer, 1937) has been used elsewhere to distinguish age groups within crayfish populations (Abrahamsson & Goldman, 1970; Abrahamsson, 1973a; Flint, 1975a; Brown, 1979; see Chapters 2 & 4). In Lake Tahoe statistical analysis of population frequency distributions is considered to "truly represent the growth pattern" (Flint, 1975a) whereas others have found it to be useful only up to the fourth year class, in A. pallipes, (Brown & Bowler, 1979). The method by which freshwater crayfish grow, i.e. periodic moulting, should theoretically result in modal peaks, appearing in length-frequency histograms, corresponding to age groups, or cohorts, within the population. In practice, however, the moult increments of individual crayfish may vary considerably both between crayfish of the same age and sex and in consecutive moults of the same individual; although not showing consistently larger or smaller moult increments in any one individual (Brown, 1979). This results in considerable overlapping of the age groups in the length-frequency histograms, Figures 8.7.

However, the data available from this investigation represents some of the simplest for analysis as the population is becoming established and of a known maximum age. Preliminary analysis of the data was attempted using three methods (Cassie, 1954; Tanaka, 1962; Bhattacharya, 1967) as described elsewhere (see Chapter 2). For the reasons outlined in Chapter 2 the former two methods, although used successfully elsewhere (Flint, 1975a; Brown, 1979), proved impractical in operation so only the analysis using the latter method (Bhattacharya, 1967) will be considered here. Data, consisting of combined results from samples collected within approximately one month of each other, has been used. Ideally such an analysis should only be carried out on data collected during the intermoult period, i.e. the winter months (Brown, 1979) but this is not practicable as catches are clearly lower at that time of year, see Figure 8.3. Consequently interpretation of the

data should be cautious.

The calculated age - size relationship, shown in Table 8.5, has been used to construct generalised growth curves for P.leniusculus at this site, Figure 8.8. Size data obtained from hand-caught juveniles has also been included as these are not present in the trapped samples. The curve illustrating growth over the initial period, 1977 to 1979, suggests a more rapid growth rate during this period than that given by the curve describing growth throughout the time since the initial stocking took place, 1977 to 1981. The main reason for this is thought to be the fact that prior to implantation large beds of canadian pondweed, Elodea canadensis, were present in the lake (Ellis, pers comm). This plant, known to be a popular food for other crayfish species (Dean, 1969) along with Chara sp., Ranunculus sp., Potamogeton sp. and Myriophyllum sp. (Abrahamsson, 1966, 1972; Dean, 1969; Flint & Goldman, 1975; Magnusson, et al, 1975; Serrol & Coler, 1975; Blake & Laurent, 1982), subsequently declined in abundance until, in 1982, only a few sparse patches remained. It is implied, therefore, that the P.leniusculus which have been shown to consume aquatic macrophytes as 20% of the juvenile diet and 65% of the adult diet (Flint, 1975a, b) were responsible for stripping the weed from the lake. The flocks of geese which also frequent the lake in winter could also have had an effect on macrophyte abundance but they were also present prior to the introduction of the crayfish (Ellis, pers comm). unfortunately no quantitative data is available regarding the decline of E.canadensis in the lake. Either way, though, the initial crayfish implants apparently had an extensive food supply which was subsequently greatly reduced and it is suggested that the rapid growth during the 1977 to 1979 period was a result of this. In addition, of course, the population size increased after 1979, due to recruitment, and as the density of adults increased a reduction in the overall growth rate must have occurred. From these observations it can be inferred that P.leniusculus could be useful as an agent of

weed control, as has been suggested elsewhere for this species (Blake & Laurent, 1982), A.astacus (Abrahamsson, 1966, 1972a, 1973a) and Orconectes causeyii (Dean, 1969).

Some published data for the growth of P.leniusculus elsewhere is illustrated in Figure 8.9 together with comparable data for other crayfish species. As can be seen the population currently being investigated, Figure 8.8, has a significantly faster growth rate than similar populations studied in Sweden (Abrahamsson, 1971, 1973a), the U.S.A. (Flint, 1975a, b), Canada (Mason, 1974, 1975) and Finland (Westman, 1973b). This difference in growth rates is attributed to the longer growing season in the south of England and the relatively low stocking density achieved (i.e. 0.05 m⁻² per year). No data is available to substantiate the former conclusion other than that published for A.pallipes in the U.K. (Brown, 1979; Pratten, 1980; see Chapter 4) and A.astacus in Sweden (Abrahamsson, 1973a) and the fact that hatching has been observed earlier at Stratfield Saye than has been reported from elsewhere in the wild. The potential for the commercial exploitation of this species in the southern U.K. is thus enhanced as crayfish of marketable size, i.e. greater than 50 mm C.L., can be produced in 2+ years rather than the 3+ years required, for example, in Sweden (Abrahamsson, 1973a,b) and Finland (Westman, 1973b). Similar rapid growth rates have been reported from Poland (Kossakowski, et al, 1979) and France (Laurent, 1979, 1980) but no comparable data is available from elsewhere in the U.K.

When compared with the published growth rates of other crayfish species, Figure 8.9, it can be seen that P.leniusculus is both faster growing and of a larger final size than all the other 'cold water' species in the northern hemisphere. It is significantly larger and much faster growing than A.pallipes; it is faster growing than A.astacus, although this species may achieve a similar final size and it is larger, particularly in terms of fresh weight, than A.leptodactylus. Only Procambarus clarkii, which is smaller,

grows more rapidly to a marketable size, i.e. in 6 months (Laurent & Forest, 1979) but this species requires a temperature of $>20^{\circ}\text{C}$. for maximum growth. The only species that produce individuals of a larger size than P.leniusculus are some of the Australasian crayfish. For example, Cherax tenuimanus may grow to 1.25 kg., Euastacus armatus grows to 2.5 kg. and Astacopsis gouldi grows to 3.5 kg. but these species, may require relatively warm water (e.g. 20°C . for C.tenuimanus) and up to ten years to achieve such weights (Francois, 1960; Frost, 1975; Carroll, 1980)

Table 8.9 lists some of the published data for the mean size increments achieved at moulting (M.I) and the moult frequency of P.leniusculus and some other crayfish species. Comparison of this data and that tabulated for the Stratfield Saye population, Table 8.4, suggests that in the latter case M.I. may range from 3.8% to 16%. The data in Table 8.10 shows that P.leniusculus owes its more rapid growth to marketable size to a significantly greater M.I. at each moult and generally to a greater moult frequency during its first two years. Even in those individuals with the smallest M.I. this was significantly greater than in A.astacus of a comparable initial size (Abrahamsson, 1972). There are conflicting reports in the literature of there being no significant difference in M.I. between males and females (Flint, 1975a) and significant differences in M.I. between the sexes (Svårdsson, 1949).

The published information permits cautious interpretation of the individual growth data listed in Table 8.4. As can be seen some of the measured growth increments exactly fit the M.I. equation published for P.leniusculus in Lake Tahoe (Flint, 1975a, b):-

$$\text{PoM.C.L.} = -0.993 \cdot \text{PreM.C.L.} + 2.452$$

For males the M.I. values of 3.8% to 16% are suggested and for females values of 4.8% to 12%. M.I. values are reported to decline as individual crayfish increase in size, for example from 11 - 12% at 30 mm.C.L. to 7% at 50 mm.C.L.,

TABLE 8.9(a) : MISCELLANEOUS GROWTH INCREMENT INFORMATION

(PUBLISHED DATA)

Species	Age Group	Growth Increment %		Reference
		Ambient 18°C		
<u>P.leniusculus</u>	Yearling	11.01	13.92	Emadi, 1974.
	Subadult	9.84	10.30	
	Adult	9.70	7.50	Emadi, 1974.
	PoMCL. = 1.067 PreMCL. + 0.744 (N.B. POCL not C.L.)			
" "	Adult (37.5-60.0mm C.L.)	7.8 - 15% (mean 10mm)		Abrahamsson, 1971.
	Adult (35.0-52.5mm C.L.)	7.8 - 12% (mean 8mm)		
<u>A.astacus</u>	Adult (47.5-62.5mm C.L.)	2.5-6.0% (mean 5mm)		Abrahamsson, 1971.
	Adult	(mean 2mm)		
	Adult	6.0-10.0%		Abrahamsson, 1972.
	Adult	4.3-6.1%		
<u>O.limosus</u>	PoMCL = -0.045 PreMCL + 18.1			Jestin, 1979

TABLE 8.9(b) : MOULT FREQUENCY OF P.LENIUSCULUS (PUBLISHED DATA)

	Year						Reference
	1	2	3	4	5	6	
No. of Moults	13-14	5-6	3	1-2	-	-	Mason, 1974.
	11	6	3	2	1	1	Mason, 1975.
	11+	4	3	2	1	1	Flint, 1975 a.
<u>A.pallipes</u> No. of Moults	5-6	4	3-4	3	-	-	Brown + Bowler, 1979.
	7-8	4-5	2-3	2	2	1	Pratten, 1980.

although the weight increment remains almost constant at 22% - 24% (Mason, 1970 , 1975). Population variation in M.I. has been shown to range from 1.5% to 15.2% but is relatively constant within an individual (Mason, 1974).

It is of interest to note that two mature females appear to have moulted twice in the periods August to July (No. 4) and July to June (No. 170). It is not known whether these individuals were berried during the intervening winter period. If they were, and there is no reason to assume otherwise, it means that female P.leniusculus are able to moult soon after the young leave them, i.e. in June or July, as well as prior to egg laying in the autumn. This finding agrees with a published account of post-hatching moults (Emadi, 1974) when females were "observed to moult two to three weeks after the young hatchlings left the mother." Elsewhere it has been shown that 90% of moulting in post-ovigerous females occurred by the end of August, with a peak in mid-August, but that some individuals moulted in mid-July (Mason, 1975).

The general findings regarding the timing of moults in the study population agree with some published information about periods of intensive moulting activity (Mason, 1974; Stevenson, 1975) but do not concur with other conclusions, that adults greater than 30 mm.C.L. do not moult more than once a year (Flint, 1975b). Juveniles are known to moult in late spring and early autumn and adults in June, July or early August and September (Emadi, 1974; Flint, 1975a). After mid-September moult occurrence declines more in the larger crayfish, for example only 8% of 40 to 45 mm.C.L. P.leniusculus moulted after this time compared with 28% of 30 to 35 mm.C.L. individuals (Mason, 1975). Both M.I. and frequency in A.astacus have been shown to increase with increased temperatures (Svårdsson, 1949).

8.4(vi) - Morphometric Analysis.

A considerable quantity of data has been collected during this study regarding the morphometry of P. leniusculus at this site and elsewhere in the Thames Catchment (see Chapter 10). This data has been used to assess the body form of this species by means of the regression analysis of various body characteristics. This has been carried out in order to (i) achieve comparability with published data (e.g. Emadi, 1974; Mason, 1974) in which measurements other than C.L. have been used; and

(ii) to provide information of use in assessing the commercial and comparative ecological importance of this species in the U.K.

The relationship between C.L. and total length, used in this instance as a conversion factor for comparing sets of data, is a positive relationship that has been shown to change at approximately 20 mm.C.L. (Flint, 1975b). This cannot be seen in the data presented here, Figure 8.10, as the smallest crayfish in the trapped samples were 22.0 mm. C.L.

The C.L. - fresh weight data has been used to calculate log. regression equations of the form $y = ax^b$ for each sex, see Table 8.6. The value for b, the growth coefficient, approximates closely to, but is greater than, 3 in each case indicating that growth is positively allometric (Flint, 1975b; Rhodes, 1980). There is no significant difference between the male and female growth coefficients ($p < 0.01$) and this agrees with findings in Lake Tahoe (Flint, 1975a, b) but not in a Californian coastal stream (Mason, 1975). This is despite differences in external anatomy as the positive allometric growth of the male chelae negates the disproportionate increase in abdomen width in the female. It has been shown, elsewhere, that there is a difference in growth rates between individuals larger than 15 mm.C.L. and those smaller than

15 mm C.L. (Flint, 1975b) but again no data is available from this study for comparison. The current results agree with those obtained from elsewhere for P.leniusculus with growth coefficients of 3.59 (♂) and 3.03 (♀) and A.pallipes 3.32 (♂) and 3.13 (♀) (Rhodes, 1980).

In order to compare the growth rate and characteristics of crayfish from different sites an allometric condition factor has been calculated for each crayfish; i.e. $C.F. = w/l^b$ (Ricker, 1975). This relationship provides a method of assessing the overall condition of the crayfish and can be used as a guide as to whether or not environmental conditions are optimal, assuming that no physiological or disease factors affect the relationship. Such condition factors are widely used in assessing the condition of freshwater fish stocks (Ricker, 1975). From the calculated values, Table 8.8, it can be seen that the C.F. value for the male P.leniusculus varies little throughout the season whereas that of the females is significantly affected by the presence of eggs during the winter ($p < 0.05$). This is assumed to be due to the uptake of water by the eggs during laying. The volume of P.leniusculus eggs increases by 40% on laying (Mason, 1979). The mean C.F. value for male P.leniusculus is significantly greater than that for unberried females ($p < 0.05$) resulting in these being more valuable in economic terms, if sold by weight rather than by number. Use could be made of the C.F. values for comparing crayfish from different locations and habitat types.

The relationship between size and certain secondary sexual characteristics has been used in an attempt to estimate the sizes at which crayfish in this population achieve sexual maturity. In the female Astacinae this is accompanied by an expansion of abdominal width through the elongation of the pleura, creating a shallow protective cavity within which the eggs are carried (Goellner, 1943). It has been shown (Rhodes & Holdich, 1979; Rhodes, 1980) that in A.pallipes the width of the second abdominal segment (the third in P.leniusculus according to Abrahamsson, 1971) increases

proportionally more with each moult, i.e. positive allometric growth, in mature females when compared with immature females, i.e. negative allometric growth. It has been stated that females undergo a maturation moult resulting in an abrupt acceleration in the rate of increase of abdomen width. This moult occurs in the summer or early autumn preceding the first gonadal maturation (Mason, 1974). Analysis of the available data by multiple regression analysis and the ratio method (see Chapter 2) suggests that individuals become sexually mature at an average size of 30.0 mm.C.L., i.e. 33.0 mm.C.L. - 10% M.I. (Flint, 1975b). This size is comparable with data published elsewhere, Table 8.10. Obviously individual variations in growth rate result in some females maturing at a size either larger or smaller than this so the value of 30.0 mm.C.L. should be regarded as an average. It is also at about this size, i.e. 20 mm.C.L. to 30 mm.C.L. that assimilation efficiency is at a maximum (Moshiri & Goldman, 1969).

The secondary sexual characteristic most evident in the male Astacine crayfish is the possession of large chelae (Rhodes & Holdich, 1979; Rhodes, 1980) which have also been shown to exhibit positive allometric growth (Mason, 1975). Again multiple regression analysis has been used to assess the size at which males achieve sexual maturity, i.e. 34.0 mm.C.L. (36.0 mm.C.L. - 6% M.I.). No such change in the proportional size of the chelae of female crayfish has been observed and these grow isometrically (Mason, 1975). The possession of large chelae is therefore presumably an adaptation to ensure maximum survival capability and success in intraspecific conflicts in male crayfish. It, incidentally, also results in the male crayfish having greater C.F. values than the females, with the marketing benefits this implies, as discussed previously.

There is apparently no accurate published data regarding the size at which male P.leniusculus mature. The values presented here suggest that males and females in this

TABLE 8.10 : AGE AT MATURITY OF SELECTED CRAYFISH SPECIES

(PUBLISHED DATA)

<u>Species</u>	<u>Location</u>	<u>♂ Maturity</u>	<u>♀</u>	<u>Reference</u>
<u>P.leniusculus</u>	Sweden	1+	2+	Abrahamsson, 1971.
"	Sweden	1+ (98%)	1+ (14%)	Abrahamsson, 1973 b.
"	Sweden	1+ to 2+		Karlsson, 1977.
"	L. Tahoe, California	2+	3+	Abrahamsson + Goldman, 1970.
"	L. Tahoe	-	3+ (50%)	Flint, 1975 a.
"	Washington	0+	1+ and 2+	Miller, 1960.
"	Canada	3+	2+ (60%) 3+ (100%)	Mason, 1974.
"	Poland	2+		Kossakowski, 1973.
<u>A.astacus</u>	Sweden	2+	3+	Abrahamsson, 1966, 1972.
"	Germany	5+ to 6+		Abrahamsson, 1966, 1972.
<u>A.pallipes</u>	U.K. (Durham)	3+		Brown + Bowler, 1979.
"	Eire	2+	2+	Reynolds, 1979.
<u>P.planifrons</u>	New Zealand	1+		Jones, 1981.

population mature from an age of 1+. Table 8.11 shows how this finding compares with published data from elsewhere for this and other crayfish species. As can be seen P.leniusculus have been observed to mature after only one summer; in Washington some individuals reached maturity in the year that they hatched although most were 18 months old, i.e. two summers, at maturity (Miller, 1960). Elsewhere in the U.K. berried females of two summers have been observed (T.W.A. unpubl; Brown, pers comm).

Sexual dimorphism, resulting in alterations in body form at maturity, has also been demonstrated in other decapods, e.g A.pallipes (Rhodes & Holdich, 1979; Rhodes, 1980), A.astacus (Kossakowski, 1966; Abrahamsson, 1971), O.virilis (Weagle & Ozburn, 1972). It is clear that the rapid growth of P.leniusculus results in a large size at sexual maturity, which also occurs earlier than in the other Astacinae. This could be of great benefit where this species competes with other, perhaps smaller, species. It could also prove to be a useful tool in comparing the growth rates of crayfish of the same species from different habitats (Huner & Romaine, 1979). In addition, although it has been shown that different year groups differ in M.I. and size at the onset of sexual maturity (Flint, 1975a), the large size of P.leniusculus at maturity indicates that, particularly in females where egg-carrying capacity is increased, this species is perhaps more suitable for aquaculture than other species of freshwater crayfish. Indeed it has been reported that P.leniusculus females, on average, carry 90% more eggs than A.astacus females of a similar size (Abrahamsson, 1971). This is partly because their eggs are 23% smaller than those of A.astacus (Abrahamsson, 1973a).

8.4(vii) - Adult Productivity.

Using the information already presented concerning the estimated population size and length-weight relationship of P.leniusculus at this site an approximate estimate of adult

standing crop and productivity can be calculated. The mean C.L. of trapped crayfish of each sex, see Figure 8.6, has been converted to fresh weight using equations (5) and (6), Table 8.6, for each year. These figures have then been averaged and multiplied by the estimated population size for that year, Table 8.2. Thus has been determined an approximate figure for the total standing crop for each year; the increase in adult standing crop from year to year has been determined by subtraction and provides an estimate of the annual production of adult crayfish. These calculations are summarised in Table 8.11.

These results, i.e. production figures of 6.32 kg. ha^{-1} for 1979 - 1980 and $30.96 \text{ kg. ha}^{-1}$ for 1980 - 1981 should be considered to be very approximate estimations. They do, however, compare quite favourably with published productivity figures for P.leniusculus in Lake Tahoe and elsewhere, see Table 8.12. The estimates that have been calculated for this population cannot be compared with the estimated 'possible' production figures for P.leniusculus of $1.0 \text{ kg.m}^{-2} \text{ year}^{-1}$ of suitable bottom area (Karlsson, 1977) or the measured values of 800 to 1059 $\text{kg. ha}^{-1} \text{ year}^{-1}$ for P.clarkii in rice fields (Chien & Avault, 1979) and 60 to 140 $\text{kg. ha}^{-1} \text{ year}^{-1}$ for O.virilis (Momot & Gowing, 1977). By means of artificial habitat improvement productivity can be greatly increased; this has been achieved in the pond culture of 'marron', Cherax tenuimanus, in Australia where production was raised from 50 to 250 $\text{kg. ha}^{-1} \text{ year}^{-1}$ to 900 to 3000 $\text{kg. ha}^{-1} \text{ year}^{-1}$ (Morrissey, 1979).

8.4(viii) - Miscellaneous Information.

In addition to the factors comprising the major part of this investigation this section of the study has provided some interesting and potentially useful facts regarding populations of P.leniusculus in the U.K. Growth, generally, has been very good with maximum sizes of 75 mm.C.L. and 68.5 mm.C.L. being achieved by the males and females

TABLE 8.11 : CALCULATION OF ESTIMATED BIOMASS OF P.LENIUSCULUS.

STRATFIELD SAYE. 1979 - 1981.

Year	Sex	Mean C.L. (mm)	Mean Weight (gms) [Equation:1 Table:8.6]	Adult Population Estimate [Table:8.2]	Adult Biomass Estimate (Kg.Ha ⁻¹)	Adult Production Estimate (Kg.H ⁻¹ Yr ⁻¹)
1979	♂	48.7	34.5	462	15.92	6.32
			34.35			
	♀	48.7	34.2			
1980	♂	48.5	34.0	715	22.24	30.96
			31.1			
	♀	45.9	28.2			
1981	♂	45.9	28.3	2062	53.20	
			25.8			
	♀	43.2	23.3			

TABLE 8.12 : BIOMASS AND PRODUCTIVITY OF P.LENIUSCULUS.
(PUBLISHED DATA).

Location	Biomass (kg.Ha ⁻¹)	Reference
Gournay, France	300	Vigneux, 1979
L. Tahoe, U.S.A. (littoral zone)	997.7	Flint, 1975 a.
L. Tahoe, U.S.A. (overall)	22	Abrahamsson + Goldman, 1970
	Productivity (kg.Ha ⁻¹ . Yr ⁻¹)	
L. Erken, Sweden	55 - 76	Fürst, 1977
L. Tahoe, U.S.A. (littoral zone)	305.6	Flint, 1975 a.
Stream, Canada	73 - 234; mean 130	Mason, 1975

respectively. Comparable published data indicates maxima of 71 mm.C.L. for males and 60 mm.C.L. for females, in France (Laurent, 1980). The minimum size of berried female caught was 38.5 mm.C.L., compared with 30.0 mm.C.L. in Canada (Mason, 1975), 35.0 mm.C.L. in Lake Tahoe, U.S.A. (Flint, 1975a). The minimum size of crayfish trapped was 22.0 mm.C.L. and this compares favourably with the 32.0 mm.C.L. reported elsewhere (Flint, 1975a).

It is clear that individual growth rates vary greatly and although the results obtained during this study suggest two main periods of moulting, i.e. in May and September, newly moulted adults were trapped as late as November. Berried females were caught in traps, contrary to reports for other crayfish species (Abrahamsson, 1971; Brown, 1979) and P.leniusculus elsewhere (Abrahamsson, 1971) the earliest being caught on 24th October and the latest being on 10th June. Elsewhere mating has been observed as early as the 20th September and the earliest berried female caught on 29th September (Abrahamsson, 1971). Other workers report egg laying as generally taking place during early October (Emadi, 1974; Flint, 1975a; Mason, 1975). An average of 68% (range 40% to 100%) of females in trap catches, at relevant times of the year, were berried, see Table 8.3, and this compares reasonably well with published data in which an estimated 88% of P.leniusculus, 81% of A.astacus and 66% of O.limosus females were berried (Abrahamsson, 1966; Kossakowski & Orzechowski, 1975).

Eggs were found to hatch in May and the earliest date on which a female with young was observed was 13th May. Again this compares well with hatching dates for P.leniusculus elsewhere, i.e. 12th to 25th May, Cowichan River, Canada (Mason, 1974); end of June to mid-August, Lake Tahoe (Abrahamsson & Goldman, 1970) and April to May (Mason, 1970) and with similar data for A.pallipes (Brown, 1979; Pratten, 1980; see also Chapter 4). A pleopod egg count from a single female gave a figure of 309 eggs; compared with published

figures of: 50 to 200 (Karlsson, 1977), 110 (Abrahamsson & Goldman, 1970), 104 (Mason, 1975, 1977) and 120 (Flint, 1975a). Unpublished studies on fecundity in the U.K. gave a mean juvenile production of 134 per female, range 46 - 352 (pers obsn).

Of primary importance in considering the marketable value of crayfish must be the possession of two complete chelae, i.e. that are undamaged and not regenerating. Damaged crayfish of this type in the samples collected from this population comprised less than 3% of the total caught, see Table 8.13, and it is thought that this figure would be considered to be within acceptable limits and compares well with published figures of 10% - 30% for five populations of A.astacus (Abrahamsson, 1966) and 10% for a population of A.pallipes (Arrignon & Magne, 1979). Presumably such damage is mainly inflicted during intraspecific encounters and is therefore density dependent. In a commercially managed population, assuming a sufficient supply of food and refugia, it would therefore be essential to maintain density at a level that would maximise production but minimise such damage.

8.4(ix) - Biological and Economic Importance of P.leniusculus.

The competitive effects of the alien P.leniusculus on populations of the native A.pallipes have not been studied although it is reported that interbreeding will result in sterile eggs (Richards & Fuke, 1977; Stempel, 1975; pers obsn). It seems likely, however, that the faster growing and larger species will be able to successfully compete with established populations of A.pallipes in this country. In Finland it has been reported that sympatric populations of A.astacus and P.leniusculus have become established (Fürst, 1977; Westman & Pursainen, 1979; Fürst, in Westman & Pursainen, 1982) but it is not stated whether or not the A.astacus are subsequently

TABLE 8.13 : INCIDENCE OF DAMAGED P.LENIUSCULUS IN TRAP CATCHES.
STRATFIELD SAYE. 1979 - 1982.

<u>Type of Damage</u>	<u>Male</u> (n = 589)		<u>Female</u> (n = 437)	
	No.	%	No.	%
No left chela	11	1.87	12	2.75
No right chela	5	0.85	7	1.60
No chela	2	0.34	1	0.23
Replacement left chela	2	0.34	8	1.83
Replacement right chela	10	1.70	5	1.14
Two replacement chelae	1	0.17	0	0
Damaged left chela	3	0.51	2	0.46
Damaged right chela	1	0.17	1	0.23
Damaged rostrum	37	6.28	36	8.24

declining in abundance. No hybridisation between these two species has been observed (Westman & Pursainen, 1979).

The other main biological impact of P.leniusculus introductions on the native crayfish is the likelihood of individuals infected with the plague fungus, A.astaci, being introduced. If juveniles produced at the hatchery in Sweden are carriers of the plague (see Chapter 6) then it is very likely that this disease has already been introduced to the U.K. (see Chapters 6 & 10). Alternatively plague could be brought into the country on the numerous adult A.leptodactylus imported through Billingsgate Fish Market. Once A.astaci is introduced to the U.K. it will certainly devastate populations of A.pallipes which will enable the plague resistant P.leniusculus (Unestam, 1969) to become more rapidly established in the wild. In the U.S.A. 50% of P.leniusculus in some populations, are reported to carry the plague (Unestam & Söderhäll, 1977) so populations of this species in the U.K. could act as reservoirs of infection.

In Sweden and France the removal of populations of A.astacus has been noted to result in problems with excessive weed growth (Abrahamsson, 1966, 1973a; Arrignon, 1975) and if populations of A.pallipes in the U.K. are devastated in the same way then similar occurrences could be observed. This has led to speculation that crayfish could be of some use as agents of weed control and studies to determine the degree to which crayfish may control aquatic macrophytes are being carried out in France (Blake & Laurent, 1982) and the U.K. (T.W.A. unpubl). It is clear that any such effect on the environment has far reaching implications for other aquatic organisms and whole freshwater communities would alter if crayfish were to be eliminated.

Economically 'Signal Crayfish' are of some importance in both the U.S.A. and Europe. In California, for example, harvests of P.leniusculus from natural populations were of

the order of 62 tonnes in 1971 (Goldman, 1973). In Europe the main centres of interest in crayfish consumption are located in France and Sweden. In France the production of A.leptodactylus is currently more important than P.leniusculus and only since 1976 has the latter species been imported for table production (Vigneux, 1979). France still has to import some 2,000 tonnes annually (1980) to satisfy demand. In Sweden the importation of P.leniusculus, to replace the falling production of A.astacus, commenced in 1960 (Abrahamsson, 1973a) and has led to the establishment of Europe's largest crayfish hatchery for the production of material for stocking into Swedish waters. Swedish demand for edible crayfish has led to imports totalling some 2,000 tonnes in 1976 (Karlsson, 1977).

It is clear, then, that a large potential market for crayfish exists in Europe. In the U.K. such a market is currently being developed and has led to the establishment of a marketing cooperative, the British Crayfish Marketing Association Ltd. (Harvey, 1980). Considerable numbers of crayfish, principally A.leptodactylus from France but latterly also P.clarkii from Kenya, (Moore, pers comm) are currently imported through Billingsgate fish market. Available figures class freshwater crayfish and crabs together and totalled 66.3 tonnes in 1982 (Pearson, pers comm) so it is difficult to ascertain the scale of crayfish imports to the U.K. Current demand (August, 1983) for P.leniusculus produced in the U.K. is increasing (Richards, pers comm) and (in August, 1983) they attract a price of £11 kg.⁻¹ (Moore, Richards, pers comm).

Apart from the table market there is currently also a considerable market for crayfish for stocking purposes. Until 1981/1982 this stocking was carried out using juveniles imported from Sweden but since that time both adults and juveniles produced in the U.K., as progeny of stock originally imported from Sweden, have been available for stocking purposes (Brown, pers comm).

Stocking waters with crayfish produced elsewhere in the U.K. should reduce the risks of importing crayfish diseases although populations of Swedish stock already established in the U.K. may act as reservoirs of infection (Holdich, et al, 1978; Brown, 1979). If this is the case then intranational crayfish movements could aid the spread of diseases, such as plague, throughout the U.K. Legislation restricting introductions (see Chapter 6) will theoretically limit the impact of P.leniusculus introductions on the environment although spores of A.astaci would easily be transported from so called closed systems to the wild situation.

CHAPTER 9. AN INVESTIGATION INTO THE SUCCESS OF INTRODUCTIONS
OF THE 'SIGNAL CRAYFISH' PACIFASTACUS LENIUSCULUS
(Dana) INTO THE THAMES CATCHMENT.

9.1. Introduction

Information has been presented in the preceding chapters regarding the extent of introductions of P. leniusculus into both the Thames Catchment and the U.K. (see Chapter 7) and has provided some basic biological information concerning a single population of this species (see Chapter 8). As has been stated previously (Section B: Introduction) current knowledge regarding this species is largely limited to the results of investigations carried out in the U.S.A. (e.g. Emadi, 1974; Flint, 1975), Canada (Mason, 1970, 1975, 1977a, b) and elsewhere in Europe (e.g. Abrahamsson, 1973a, b; Fürst, 1977).

In order to determine the degree to which the data presented previously (Chapter 8) is representative of introduced crayfish populations, in the southern U.K., and to assess the extent to which some of the known introductions into the Thames Catchment have been successful a number of other privately owned and stocked sites in this area were sampled during 1980, 1981 and 1982. These sites were selected from a list provided by the sole importers of juvenile P. leniusculus to the U.K. (see Chapter 7) and hence the dates and numbers of crayfish introduced had been recorded.

The sites were selected to provide as wide a cross-section of location and habitat types as possible, within the Thames Catchment. It was felt that this would not only provide information on survival but also act as a guide with which to assess the suitability of potential sites for stocking and indicate those parameters and site characteristics necessary to improve the chance of success of crayfish introductions.

9.2. Methods

An assessment of the success of introductions of P.leniusculus was carried out, in the first instance, by overnight trapping at twelve sites in the Thames Catchment, see Table 9.1. The sampling method is described elsewhere (see Chapter 2) but on some occasions was modified to suit individual site characteristics and, where relevant, this is indicated in the results. Trapping was standardised, as far as possible, regarding trap type, bait and time to enable comparisons to be made between sites and in consecutive years.

Wherever possible a visual search and hand collection was also carried out, by torchlight. This was found to be particularly useful in determining the presence of crayfish if trapping had proved unsuccessful. Large areas of shoreline and the adjacent shallow water could be searched in a relatively short time thus obviating the necessity of further or more extensive trapping operations. For example, when the 3.2 ha. and 4.3 ha. lakes (sites 5 & 4, Table 9.1) were being trapped only 28 and 30 traps were operated but by night-searching crayfish were located despite poor or non-existent trap catches. Some sites were trapped only once whereas others were trapped on more than one occasion and in successive years.

In addition crayfish were collected incidentally at one site during seine netting operations to remove coarse fish. This method was subsequently used successfully for catching P.leniusculus on more than one occasion at this site but was not attempted at any other site. At the same site unbaited fyke nets also successfully caught crayfish on one occasion.

Individual size data, in the form of C.L. or T.L. (see Chapter 2), was collected from nine of the sites sampled. At least one water sample was collected from nine of the sites and analysed by the Thames Water laboratories for the

chemical parameters considered to be of primary importance to crayfish (Laurent, 1980). If unsuitable water quality was suspected as the cause of poor survival of the introduced P.leniusculus, as indicated by repeated low or negative catches, further water samples were collected for analysis.

9.3. Results

The results obtained from this survey of the success of introductions of P.leniusculus into waters in the Thames Catchment are listed in Table 9.1. Site numbers refer to the list of introductions in Appendix 9 and the locations plotted in Figure 7.1.

Individual size data collected from nine sites is summarised in Table 9.2. The mean size (C.L.) of crayfish of each sex trapped during the period of the study from sites 2 and 3 has been compared using a Students t-test.

9.4. Discussion

9.4(i) Success of introductions.

Of the sites investigated during this study only those numbered 1 to 4 in Table 9.1 can really be considered as successful introductions, so far. Breeding has been shown to have taken place in all four. Sites 5 to 11 can really only be considered to have been moderately successful introductions; breeding was only shown to have occurred at site 5 and only small catches of adults were achieved at the other sites. Sites 12 and 13 are considered to have been complete failures as far as crayfish introductions are concerned; at neither site was the presence of crayfish detected.

The success rate of the introductions of P.leniusculus to sites in the Thames Catchment (>30%) compares favourably with that recorded from elsewhere in Europe. In Sweden some

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TABLE 9.1 : RESULTS OF TEST TRAPPINGS AT SITES INTO WHICH P.LENIUSCULUS HAVE BEEN INTRODUCED

Site	Introductions		Sampling			Trap Data			Males			Females			Damage %									
	pH	Hardness	No. -1 Year	Dates	Dates	Method	Bait	Temp. °C	No. -1 Trap	Range -1 Trap	Total	Mean	S.D.	N		Range	Mean	S.D.	N	Range				
1. Lake (1.4 ha.) †	7.77	141	500	1977-79	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
2. Gravel Pit (1.6 ha.)	8.34	236	1500	1978-80	12.6.80	Traps (30)	T	19.0	0.4	0 -3	12	64.4	5.2	11	56.6-72.2	61.8	-	-	1	-	17			
					19.9.80	Traps (25)	-	-	-	-	-	-	13	63.1	8.6	7	46.0-73.5	59.6	2.9	6	55 - 63	8		
					15.7.81	Traps (80)	RT	18.0	1.44	0 -7	36	57.6	16.6	14	57.6	16.6	14	34.5-80.5	48.8	11.6	22	30 - 68	8	
					7.7.82	Traps (57)	RT	19.5	5.5	-	439	-	-	228	-	-	-	-	-	-	-	211	-	4
					26.8.82	Traps (60)	RT	18.0	9.1	-	518	-	-	249	-	-	-	-	-	-	-	269	-	7
					22.9.82	Traps (20)	RT&C	21.0	8.5	-	510	-	-	n/d	-	-	-	-	-	-	-	-	-	0.5
					17.3.83	Traps (20)	RT&C	5.0	5.8	-	117	-	-	64	-	-	-	-	-	-	-	-	53	-
3. Lake (0.4 ha.)	7.59	214	500	1978&79	29.1.81	Seine	-	3.5	-	-	18	63.7	6.7	12	52 -74.6	54.3	11.8	6	33 - 64.8	10				
					7.8.81	Fyke	-	16.0	-	90	55.7	13.5	42	38 -87.0	54.5	9.9	48	33.5-72.0	-	-	-	-		
					11.8.81	Fyke	-	17.0	-	122	47.7	11.0	51	32 -83.0	50.9	10.0	71	34 -73.0	-	-	-	-		
					18.6.82	Traps (6) +Fyke	RT	15.0	-	21	60.3	13.7	14	-	52.0	6.4	7	-	-	-	-	0		
4. Lake (4.3 ha.)	7.70	251	1000	1978-80	28.9.82	Traps	-	18.0	-	36	52.4	4.2	24	-	49.9	4.3	12	-	1.9					
					6.8.80	Traps (30)	-	19.5	0	0	-	-	0	-	-	-	-	-	-	-	-	0		
5. Lake (3.2 ha.)	7.84	260	600	1978&79	3.8.81	Traps (30)	T	19.0	0.63	20	47.5	6.0	12	38.5-60.5	45.25	6.67	8	38 -60	0					
					13.8.81	Traps (28)	T&C	19.0	0	0	-	-	0	-	-	-	-	-	-	-	-	-		
6. Stream	8.46	288	200	1978&79	7.9.81	Traps (20)	T	16.0	1.7	34	62.9	5.1	13	57.0-37.0	55.8	4.47	21	47 - 65	6					
					26.8.81	Traps (28)	-	18.0	0.29	8	56.1	20.3	6	24 -76.5	48.2	12.9	7	24.5-64	0	0				
7. Lake (0.8 ha.)	7.64	198	300	1978	19.8.81	Traps (28)	T&C	18.0	0.04	2	-	-	-	-	-	-	-	-	0					
					11.8.80	Traps (20)	R&P	16.5	0.10	2	-	-	2	73.7-77.8	-	-	-	-	-	-	-	0		
8. Lake (0.8 ha.)	7.32	225	200	1978	21.8.80	Traps (30)	T.C. B.SM	18.0	0.17	5	67.3	2.6	4	63.7-69.7	59.0	-	1	-	0					
					2.7.80	Traps (20)	-	13.0	0	0	-	-	0	-	-	-	-	-	-	-	-	-		
9. Lake (3 ha.)	7.90	241	600	1978	13.8.80	Traps (42)	C	15.0	0.02	1	-	-	-	-	52.7	-	-	1	-	0				
					30.7.80	Traps (20)	T	15.0	0.10	2	50.5	-	1	-	-	-	-	53.0	-	-	1	-	0	
10. Lake (0.4 ha.)	7.16	52	1000	1978	5.8.81	Traps (20)	T	14.0	0	0	-	-	-	-	-	-	-	-	-	0				
					7.87	258	400	1978&79	7.87	258	400	1978&79	7.87	258	400	1978&79	7.87	258	400	1978&79	7.87	258	400	
11. River	8.54	254	400	1978	3.9.81	Traps (5)	T	21.5	0	0	-	-	-	-	-	-	-	-	-	0				
					7.04	156	500	1978	7.04	156	500	1978	7.04	156	500	1978	7.04	156	500	1978	7.04	156	500	

† See Chapter 8 for results.

• Baits T = Tench P = Pike B = Bacon Fat C = Carp R = Roach SM = Smoked Mackerel RT = Trout

**TABLE 9.2 : SUMMARY OF SIZE DATA FROM SOME POPULATIONS OF P.LENIUSCULUS
IN THE THAMES CATCHMENT. 1980 - 1983.**

Site*	Male			Female		
	Mean C.L. (mm)	Range	n.	Mean C.L. (mm)	Range	n.
2 1980	63.75	46.0 - 73.5	18	60.7	55.0 - 63	7
1981	57.6	34.5 - 80.5	14	48.8	30.0 - 68	22
1982	53.5	36.0 - 84.0	116	52.6	35.0 - 72	92
1983	51.2	39.0 - 71.0	91	47.3	37.0 - 68	26
3 1981	55.7	29.5 - 87.0	105	53.2	33.0 - 73	125
1982	55.3	40.0 - 86.0	38	50.7	42.0 - 59	19
4 1981	47.5	38.5 - 60.5	12	45.2	38.0 - 60	8
6 1981	62.9	57.0 - 77.0	13	55.8	52.0 - 65	21
7 1981	66.3	54.5 - 76.5	3	44.6	24.5 - 60	5
8 1981	-	-	-	48.0	-	1
9 1980	70.1	63.7 - 77.8	6	59.0	-	1
10 1980	-	-	-	52.7	-	1
11 1981	50.5	-	1	53.0	-	1

* see Appendix 9.

217 lakes had been stocked by 1976. Only 10% of those stocked with adults were successful compared with 81% of those into which juveniles had been introduced in two or more years (Brinck, 1977). Reproduction has, however, been demonstrated in only 20% of the Swedish lakes stocked (Fürst, 1977). In France only 9% of introductions are reported to have been successful (Laurent, 1979). No published data on the success of crayfish introductions into the U.K. is available.

The factors governing the success rate of introductions of P.leniusculus into the Thames Catchment can only be tentatively suggested. The most obvious factors that could determine the degree of success of introductions are:

- (a) Predation.
- (b) Poor chemical water quality.
- (c) Habitat unsuitability.

9.4(ii) - Predators

Eels, Anguilla anguilla, are known to be voracious predators of crayfish (see Section A: Introduction); both A.pallipes in the U.K. (Watson, in Brown, 1979) and A.astacus in Europe (Svärdsson, 1972). No information is available concerning the predation of P.leniusculus by A.anguilla, or other eel species, but there is no reason to suspect that it is any less liable to predation than other astacids. A.anguilla are known to be moderately common in parts of the Thames Catchment (Armstrong, pers comm) so it is possible that they inhabit some of the sites to which P.leniusculus has been introduced. At site 5, Table 9.1, it is known that A.anguilla were very abundant, in the years after stocking with crayfish, as some 95kg. of eels were removed by trapping in 1980 (C. Brown, pers comm).

Another predator of freshwater crayfish elsewhere in Europe (Arrignon, 1981) is the 'European catfish' or 'wels', Silurus glanis. The distribution of this introduced fish

in the Thames Catchment is unknown and it has not been reported to be a specific predator of P.leniusculus elsewhere. However it is known that this nocturnal, bottom-feeding fish is present at site 7 (Table 9.1). Two specimens of 6.8kg. and 13.2kg. were caught in 1980 (Burnham, pers comm) and it is, therefore, possibly a predator of crayfish at this site.

Sites 4 5 and 9, Table 9.1, are operated as commercial trout fisheries and the unnaturally high densities of stocked rainbow trout, Salmo gairdneri, may have resulted in a certain degree of predation on P.leniusculus. Lake trout, Salvelinus namaycush, in Lake Tahoe, California have been reported to consume considerable numbers of P.leniusculus. Some 30% of trout stomachs examined, from fish of 20"+, contained crayfish remains in the summer months (Frantz & Cordone, 1970).

Other fish species, such as chub, Leuciscus cephalus, tench, Tinca tinca, and carp, Cyprinus carpio, are known to consume crayfish to some extent (see Section A: Introduction) and are therefore likely to consume P.leniusculus if these are available. Such fish are known to occur at site 3 - chub (Moore, pers comm), sites 1, 7 and 8 - tench (Ellis, Theobald, Randolph, pers comm) and sites 2, 3 and 8 - carp (Graham, Moore, Randolph, pers comm). Similarly heron, Ardea cinerea, and mink, Mustela vison, are reported to be predators of A.pallipes (Section A: Introduction) and A.astacus (Dehli, 1981) respectively and will presumably also catch P.leniusculus if available. Both of these predators are common in parts of the Thames Catchment unlike the otter, Lutra lutra, also a known predator of A.pallipes (Harris, 1968) and A.astacus (Erlinge, 1972; Dehli, 1981), which is scarce or absent (Anon, 1977). The degree of predation by any of these species at the sites investigated is unknown, however, and their effect on introductions of P.leniusculus is purely speculative.

9.4(iii) - Water Quality

The suitability of some of the sites investigated, in terms of water quality, was considered to be doubtful (see also 9.4(v)). At site 10 the measured total hardness was only 52 to 57 $\text{mg.l}^{-1}\text{CaCO}_3$, Table 9.1, whereas at all the other sites from which such data was obtained it was well in excess of $100 \text{ mg.l}^{-1}\text{CaCO}_3$. From these hardness figures calcium values of approximately $22 \text{ mg.l}^{-1}\text{Ca}$ and $40 \text{ mg.l}^{-1}\text{Ca}$ can be calculated. Published figures for the requirements of crayfish regarding the calcium content of the water are variable and minimum values for A.pallipes range from $3.0 \text{ mg.l}^{-1}\text{Ca}$. (Laurent, 1980) to $7.8 \text{ mg.l}^{-1}\text{Ca}$ (Lilley, 1977). Generally, then, A.pallipes requires more than 5.0 to 8.0 $\text{mg.l}^{-1}\text{Ca}$. in the water (Greenaway, 1974; Sutcliffe & Carrick, 1975) but no similar information is available for P.leniusculus. From these figures it is clear that too little calcium may be available in the water at site 10. A lack of available calcium in the water results in crayfish being unable to form hard new exoskeletons during the moult. A source of utilisable calcium is essential as only 10% of the premoult exoskeletal calcium content is carried through the moult in the gastrolith (Greenaway, 1974; Adegboye, et al, 1975).

9.4(iv) - Stocking Rate

Low initial numbers of P.leniusculus stocked could have led to the poor apparent success of introductions at some sites. At site 8, for example, only 200 individuals were stocked, all in a single year. Experience in Sweden has shown that repeat stocking over at least a three year period increases the success rate of introductions of P.leniusculus (Abrahamsson, 1973b; Brinck, 1977; Karlsson, 1977). Also if estimated survival values of 20%, or less (Westman & Pursainen, 1979), after two years (Chapter 8) are applied to an introduction of only 200 individuals it will be seen that theoretically a maximum of only 40 adults will survive

to maturity. Consequently in a lake of 0.81 ha., (Site 8, Table 9.1) mating may not occur through a lack of contact between males and females.

9.4(v) - Habitat Suitability

At a number of sites habitat type was considered to be unsuitable and was thought to have been the cause of the two introductions that failed completely. Site 12, Table 9.1, was not sufficiently secure from escapes and crayfish were stocked upstream and downstream of a trout 'raceway' system. It is likely, therefore, that the crayfish migrated from the site of introduction into the trout pens or the adjacent River Kennet. Site 13 was a small pond (0.05 ha.) lined with butyl rubber. Adequate refugia were provided, in the form of brick rubble, corrugated sheeting and tile-drains. However, with no water flow and excessive deposition of organic material from adjacent trees, water quality was very poor and dissolved oxygen was measured as 28% saturation ($2.4 \text{ mg.l}^{-1} \text{ O}_2$) on 3.9.81. Published values for the oxygen requirements of crayfish are 4.0 to 6.0 $\text{mg.l}^{-1} \text{ O}_2$ for A.pallipes (Sutcliffe & Carrick, 1975).

Some of the other sites investigated were also inadequately secure from escapes of introduced crayfish, particularly sites 6 and 11. At site 11 P.leniusculus were implanted directly into the River Lambourn (see Figure 3.1), with no barrier to upstream or downstream migrations. At site 6 the crayfish were introduced into a 'feeder' stream and pond system directly linked to the River Kennet. At this latter site a single adult was trapped in the outlet stream, approximately 30 m. from the main river.

9.4(vi) - Other Considerations

From the information obtained from the sites investigated during the course of this study and from

published information the following general criteria for site suitability for introductions of P. leniusculus can be proposed:-

- (i) Security from escapes, e.g. by screening outlets, etc.,
- (ii) Freedom from predators such as eels and trout;
- (iii) Adequate chemical water quality in respect of calcium content ($>10 \text{ mg. l}^{-1} \text{Ca}$), dissolved oxygen ($>4 \text{ mg. l}^{-1} \text{O}_2$) and pH (> 7.0),
- (iv) Provision of adequate suitable habitat in the form of brick rubble, pipes, etc.

These general guidelines agree with those which have previously been proposed (Karlsson, 1977, 1978) but which have not always been followed for introductions into sites in the Thames Catchment.

In addition, although not highlighted by this study, there are three other factors that may control the success of crayfish introductions into the U.K. both now and in the future. Firstly it has been suggested that the maximum temperature for P. leniusculus survival is between 25°C . and 30°C . (Karlsson, 1978) although they may tolerate higher temperatures for a short period of time, particularly if gradually acclimated (Becker, et al, 1975). Additionally, though, there is a limiting temperature for successful breeding. It has been shown (Mason, 1970) that the temperature must fall below 14°C ., in conjunction with a reduction in day length, for P. leniusculus to breed successfully and this suggests that a constant warm water supply throughout the life-cycle would repress breeding. This is unlikely to be a problem at any of the sites investigated during this study or in other natural situations in the U.K. but it might be of direct relevance if attempts are to be made to enhance growth by utilising waste warm water.

Secondly, as movements of crayfish around the U.K. become more common the spread of parasites and diseases may

also take place, not only those that may be imported with crayfish juveniles but also those obtained from the native A.pallipes. The most serious known crayfish disease is undoubtedly the crayfish 'plague' (see Chapter 6; Unestam, 1969, 1973, 1975). Although this fungal disease has not yet been positively identified in the U.K. it could possibly be introduced with imported crayfish. Indeed it has been suggested that up to 60% of imported juvenile P.leniusculus may carry the disease (Söderhäll/Alderman, pers comm) but this has not yet been confirmed (Alderman, pers comm). Although P.leniusculus is reputedly more resistant than the native A.pallipes some individuals will be susceptible, particularly if damaged (Unestam & Weiss, 1970). The threat to both native stocks and commercial crayfish producers, with relatively intensive systems, is very real.

Similarly infection of introduced P.leniusculus with the parasitic microsporidian T.contejeani and the annelid B.astaci may occur once they come into contact with infected populations of A.pallipes. T.contejeani has been shown to infect at least 15% of crayfish populations in the Thames Catchment, at a mean incidence of about 5% (see Chapter 6), and B.astaci occurs at a mean incidence of >95% in adult A.pallipes at certain sites in this area. Whether or not these parasites will infect P.leniusculus is not known although parasitism of crayfish by the genus *Thelohania* is worldwide (see Chapter 6) and all Astacoidean crayfish are reputed to be potential hosts for branchiobdellids (Holt, 1975).

At two of the sites investigated (Nos 2 & 3, Table 9.1) considerable numbers of crayfish have been removed for economic purposes, less than 4 years from implantation, despite recommendations that harvesting of newly established populations should not commence for at least 6 years (Laurent, 1979). From these sites the mean size of P.leniusculus caught in traps each year has been calculated and compared (Table 9.2). At site 2 the mean C.L. of both

male and female crayfish sampled apparently declined in the years 1981 to 1983 but this decline was not statistically significant ($p < 0.01$). Similarly at site 3 the mean C.L. of crayfish in the samples did not decline significantly ($p < 0.01$). The apparent decline in mean C.L. of crayfish in samples from a population may be related to the occurrence and perhaps the extent of cropping. This is a difficult hypothesis to test using the current data, however, as cropping occurred at all sites where extensive sampling was carried out. At site 2 considerable numbers of crayfish, amounting to at least 1,000 adult individuals during 1982 (Rogers, pers comm), were removed for sale. Similar apparent reductions in mean C.L. were observed to occur in populations of P. leniusculus in Sweden (Fürst, 1977), at Stratfield Saye (see Chapter 8), after harvesting commenced, and in the population of A. pallipes in Clattercote Reservoir, Banbury (see Chapter 4) from which numbers of crayfish were removed.

The monitoring of the mean C.L. of crayfish in managed populations may therefore prove to be a useful guide to the effects of harvesting on that population. Such a conclusion is only tentative, however, and would require further investigation before being adopted as a reliable tool for use in the management of populations of both native and introduced crayfish.

CHAPTER 10 GENERAL DISCUSSION.

10.1 Aims of this study.

The primary aim of this study was to acquire information on the distribution and biology of crayfish in the Thames Catchment that would enable an assessment to be made of their ecological and economic importance. To this end data has been collected regarding distribution of both the native and introduced species; bionomics and life history of the two most commonly occurring species; the density of crayfish populations and the growth of individuals; the impact of river management on native crayfish and the survival and success of introduced populations of crayfish.

The results obtained during the present study have been discussed in each respective chapter. In addition the motivation for investigating the distribution and biology of the two species of crayfish under consideration has been explained. It is, however, thought to be pertinent to review these findings in the overall context of the study and although most aspects of the current findings have been discussed elsewhere some are reiterated here for emphasis.

It is apparent that crayfish are of value in both ecological and economic terms and there is currently a great deal of interest in the production of crayfish for the table (Richards & Fuke, 1977; Holdich, et al, 1978). So little is known, however, about the native crayfish, A.pallipes, or the effect that introductions of the Californian 'Signal Crayfish', P.leniusculus, may have on aquatic ecosystems in the U.K. that it was felt to be important to obtain data on both species in the Thames Catchment.

The results presented in this thesis form a data base relating to both A.pallipes and P.leniusculus in the Thames Catchment during the period 1979 to 1982. The findings of this study are considered to provide information relevant

to several aspects of the functions of Thames Water. Basic information concerning the distribution and biology of crayfish in the Thames Catchment is presented. In addition information on which the ecological and commercial management of both species of crayfish could be based is considered. Finally the findings provide a reference point concerning the status of freshwater crayfish in the Thames Catchment in a situation that is currently commencing a period of change. Such change concerns the extent and possible impact of crayfish introductions and the pattern, extent and effects of mortalities of A.pallipes due to disease.

10.2 Distribution of A.pallipes.

A considerable amount of data has been collected regarding the distribution of A.pallipes in the Thames Catchment and this forms the only recent extensive study of crayfish distribution in a single river catchment in the U.K. It is clear that this species occurs quite commonly in a wide variety of water bodies in this area and this finding agrees with reported distribution patterns throughout England (Jay & Holdich, 1981). The abundance of A.pallipes at sites recorded as positive for distribution mapping is generally not known. However it is probable that some positive sites are only inhabited by small numbers of crayfish or are of marginal suitability. Conversely at other sites, which may previously have been regarded as unsuitable crayfish habitat (see Chapter 5), surprisingly large numbers of crayfish have been found. The general pattern of abundance of A.pallipes in the Thames Catchment is, therefore, unknown. As it is known to be susceptible to pollution, river management and disease however, A.pallipes has been categorised as 'rare' in the I.U.C.N. 'Red Data Book' (Wells, 1983) and its status in the Thames Catchment must be regarded as threatened.

Some of the factors thought to influence A.pallipes distribution within the Thames Catchment have been discussed

(Chapter 3). Throughout this area the influence of solid geology on distribution, important on a national scale, was considered to be minimal. Waterbodies generally have an adequate pH and calcium content for crayfish survival. On a localised scale, though, geology may determine substratum suitability and this may influence the exact pattern of crayfish distribution. Currently it is considered that, in the Thames Catchment, levels of pollution and the extent of river management, although exerting a major influence on the distribution of A.pallipes, are of less importance than the increasing incidence of fatal disease.

The findings of this study broadly agree with general comments on the national distribution of A.pallipes (Jay & Holdich, 1981) in that crayfish occur not only in chalk streams but also in canals, reservoirs, gravel pits, etc. Elsewhere in Europe, except Eire, the distribution of A.pallipes is more restricted being limited to small streams, whilst larger streams, rivers and lakes tend to be inhabited by A.astacus, A.leptodactylus or O.limosus (Laurent & Forest, 1979). The wide range of habitat types occupied by A.pallipes in the U.K. is thought to be due to a lack of direct competition from other organisms capable of filling the same ecological niche.

10.3 Introductions.

Whereas the distribution of A.pallipes is largely controlled by natural influences, either directly or indirectly, the distribution of P.leniusculus introduced into the Thames Catchment is artificially determined (see Chapter 7). As there was no legislative control, until 1982, concerning the introduction of this species it has been introduced into a wide range of habitat types with varying degrees of suitability and security. Water quality, in terms of calcium content and pH, has not been restrictive within this area so there is no apparent pattern to the distribution of introductions. Elsewhere in the U.K. implantations have

been more or less restricted to hard water areas and by accessibility to the location of the importers. Most introductions have consequently been made to the south and east of England (see Figure 7.2) with few into Scotland and none into Eire. The type of site to which they have been introduced in the Thames Catchment has ranged from a small butyl lined pond to a well known chalk stream, ornamental ponds, gravel pits and a redundant farmyard pond. It is suspected that this range of habitat types is repeated on a national scale. That crayfish are known to have been introduced does not automatically mean that they have become established but the 25% + success rate of introductions in this area, if it can be extrapolated in this way, would suggest that some 50+ sites throughout England and Wales may contain breeding populations of P.leniusculus.

Other species of crayfish are reputed to have been introduced to the Thames Catchment in the past, notably A.astacus and A.leptodactylus, (see Section B: Introduction) but the success of such introductions has not been recorded. It is known, however, that A.astacus are successfully breeding in a closed pond system in Somerset (Brown, pers comm). The experimental importation of P.clarkii to a Midlands fish farm is known to have been terminated (Goddard, pers comm) but recently it has been learnt that P.clarkii are being imported from Kenya for the table market. This species will, no doubt, also eventually escape to form 'wild' populations. How successfully these would survive winter temperatures in the U.K. is unknown although this species is reported to overwinter at temperatures of 4°C to 6°C in the U.S.A. (Huner, pers comm).

The introduction of alien species of crayfish from elsewhere in Europe, Africa or the U.S.A. presents a serious danger to the native A.pallipes which is now known to occur widely in the Thames Catchment. The dangers are primarily the risk of introductions of disease and the possible competitive effects of faster growing and perhaps

more aggressive and pollution tolerant species. Only lately (1982) has licencing become obligatory for the introduction of foreign crayfish to the wild and it is possibly now too late to prevent serious damage to stocks of the native species. It is hoped that the information presented here will enable an assessment to be made of the ways by which crayfish populations in the Thames Catchment could be monitored. It might also encourage the development of a scheme of management, for both native and introduced species, directed at minimising the ecological damage which could be caused by the introduction of alien species whilst maximising economic benefits.

10.4 Aquaculture potential.

One of the factors of primary importance in considering the aquaculture potential of a species is the rate of growth and final size of the organism. A.pallipes, examined during the course of this study, achieve a relatively small final size; the largest male measured was 54.3 mm.C.L. (Linch Hill Fishery - 1.10.80 - trapped) and the largest female was 57.0 mm.C.L. (River Whitewater - 23.8.82 - hand caught). These sizes compare unfavourably with those of some other crayfish species; e.g. Cherax tenuimanus - 150 mm.C.L. (Frost, 1975), P.leniusculus - 83.0 mm.C.L. (this study - site 3), A.astacus - 65.0 mm.C.L. (Abrahamsson, 1973a). This difference, together with the rate at which it may attain maximum size, i.e. c.10 years to 50.0 mm.C.L. (see Chapter 4), would suggest that A.pallipes is not a prime candidate for aquaculture purposes. Despite this it has been proposed (Holdich, et al, 1978) that those interested in developing a crayfish market should examine the possibilities of harvesting natural populations of A.pallipes. Prior to the commencement of any such activities it is essential that adequate information on population biology is available and this study contributes to the body of such information.

Lacustrine populations of crayfish grow just as successfully as riverine populations and perhaps occur at greater densities due to the tendency for there to be a

greater uniformity of habitat in such situations. It is also apparent that such populations are more readily monitored and easier to crop than shallow water river populations as they are less liable to migrate and are catchable by less labour intensive methods. It would seem, therefore, that if populations of A.pallipes are to be harvested commercially, lacustrine populations and those inhabiting deep, slow flowing rivers would be more suitable than those inhabiting shallow, faster flowing sites.

10.5 Life-History.

During all stages of this investigation information has been collected regarding the timing of important features of the life history of both species of crayfish being studied. Such information, collected from as many sites as possible, is important in that it permits an assessment to be made of the success of crayfish populations in various habitat types. The minimum size of ovigerous female A.pallipes collected during this study was 21.5 mm.C.L. (see Chapter 6) and this is amongst the smallest recorded in the U.K. Knowledge of this size is important as it provides an indication of the degree to which a population is overstocked. In crayfish populations where the limiting factors are environmental an increase in biomass will result in a reduction in individual growth rate (Momot & Jones, 1976). Hence females maturing at a small size may be indicative of overstocking.

The timing of the reproductive cycle of A.pallipes in the Thames Catchment, has been discussed elsewhere (see Chapter 6) but generally mating took place in early October, oviposition occurred 5 to 10 days later and hatching was observed in late May or early June. These findings are comparable with those reported from Kent (Thomas & Ingle, 1971) but indicate that a longer growth season, i.e. 5 months, is enjoyed by A.pallipes in the Thames Catchment compared with 3 months for a population in the north-east of England. This latter population of A.pallipes is considered to be near the

northern limit of its range (Brown, 1979).

10.6 Growth.

The growth of P.leniusculus at sites in the Thames Catchment that have been investigated was found to be considerably faster than that of A.pallipes in this area (see Chapter 8) and partly explains the considerable current interest there is in the former species for aquaculture purposes. This growth rate is similar to that reported from France (Laurent, 1979) and Russia (Cukerzis & Terentjew, 1979) but is apparently faster than that reported from Sweden (Abrahamsson, 1973a; Brinck, 1977). This difference is presumably due to the longer growing season in the southern U.K. and it would be of great interest to compare growth data from populations of P.leniusculus in the north and the south of the U.K.. In addition P.leniusculus grows to a much greater final size than A.pallipes with maximum sizes of 83.0 mm.C.L. for males and 76.0 mm.C.L. for females (site 3 - Appendix 9) being recorded during the course of this study.

That introductions of P.leniusculus at certain sites in the Thames Catchment have been very successful has been demonstrated and this is despite the fact that these sites were not formerly inhabited by native crayfish. In Scandinavia stocking with P.leniusculus has generally taken place to replace stocks of A.astacus devastated by the crayfish plague (Abrahamsson, 1973a) so the sites stocked have been good in terms of crayfish habitat. In this light it is surprising that at least 25% of introductions into waters in the Thames Catchment have been successful compared with a reported success rate of 16% in Sweden (Fürst, 1977).

10.7 Economic considerations.

The economic benefits of harvesting crayfish from a population in a natural or semi-natural situation are clear. If a natural population of A.pallipes is cropped then there

is no cost involved apart from that for trapping time and equipment. At a retail value of about £3.30 kg.⁻¹ (Goddard & Holdich, 1979) good catches (200 + adults) in a single evening from, for example, Clattercote Reservoir (see Chapter 4) would have been valued at £20 to £25. Clearly a single population of the estimated size of that in Clattercote would be unable to sustain such cropping levels for long but regular harvesting of a number of similar sites could provide a considerable supplementary income. Such part-time crayfish harvesting is reported to be quite common in France (Arrignon, 1981) and Spain (Habsburgo-Lorena, in Westman & Pursainen, 1982). It is likely that such cropping does take place in certain areas of the Thames Catchment but to what extent is unknown. The estimated net annual production of A.pallipes of 171 kg. wet weight per hectare reported for a northern population (Brown, 1979) with a 'turnover ratio' (Waters, 1969) of 0.42, mean that the large populations of A.pallipes reported to be present in some waters (Holdich, et al, 1978) would be capable of withstanding commercial cropping.

Clearly the greater retail value, i.e. £9.90 to £11.0 kg.⁻¹ (August 1983), faster growth rate and greater final size of P.leniusculus mean that this species of crayfish is of greater interest to those wishing to utilise an under-used water body by stocking it with crayfish. In this instance the cost of initial stocking and site improvements, if required, may be high but the financial returns from a successful population could cover such costs in less than five years. At £11 kg.⁻¹ the value of marketable P.leniusculus sampled during this investigation from the two sites where large catches were obtained (see Chapter 9) was of the order of £200 + per night. It is currently also lucrative to sell P.leniusculus for stocking purposes within the U.K. and crayfish sold for this purpose currently command higher prices, e.g. £1.20 per adult age 2+ (Brown, pers comm). Clearly this market is limited in the long term and the ultimate aim of most prospective producers must

be to produce crayfish for the table. From the current study it is evident that a quantitative costed study of harvesting native crayfish on a commercial scale, the economic production of P.leniusculus and the consequences of cropping on both native and introduced populations is required.

The attraction of stocking little used waters with crayfish is that an extra income can be obtained for relatively little capital outlay, labour requirements are minimal and no feeding is considered necessary. Claims made for possible returns on initial outlay (Richards & Fuke, 1977) appear exaggerated from observations in the Thames Catchment but it is, however, clear that the potential for the culture of P.leniusculus for economic benefit is considerable and greater than that of harvesting natural populations of A.pallipes.

10.8 Ecological Considerations.

A continued interest in populations of both A.pallipes and P.leniusculus is potentially of considerable ecological as well as economic importance. The value of populations of crayfish as scavengers has been discussed elsewhere (see Chapters 1 & 6). Stocks of A.pallipes are currently under considerable threat from the introductions of alien species that are taking place. If populations of A.pallipes are eliminated and not replaced then environmental changes may occur. Such changes may result from the removal of the major heterotroph in the benthic food chain. This could result in an accumulation of material which may lead to changes in the structure of invertebrate communities or the build-up of detritus. The niche formerly occupied by A.pallipes might be filled by another organism. A build-up of decaying organic matter could result in a reduction of water quality. Removal of crayfish populations has also been implicated in an increase in macrophyte biomass. This is reported to have occurred in Sweden following the

elimination of a population of A.astacus (Abrahamsson, 1966, 1971). If significant removal of macrophytes by crayfish does occur then populations of A.pallipes or P.leniusculus may be of some value as agents of weed control. In France trials have shown that introduced P.leniusculus were able to reduce the biomass of Chara sp. in a small lake from $7 \times 10^4 \text{ kg. ha}^{-1}$ to $3.0 \times 10^4 \text{ kg. ha}^{-1}$ in successive years (Blake & Laurent, 1982). Similar investigations are currently being carried out by Thames Water.

From the information presented here (see Chapter 5) it is also clear that encouragement of populations of A.pallipes could be carried out at little or no extra cost during routine river management operations (Hogger & Lowery, 1982). Indeed, although it is currently uncertain whether or not recruitment is entirely density dependent (Momot, et al, 1978; Rhodes, 1980), the availability of both food and refugia will affect population size. The greatest potential for increasing the production of both A.pallipes and P.leniusculus may therefore be to provide additional refugia.

One of the main factors to which the decline in the distribution of A.pallipes in recent years has been attributed is the increasing extent to which natural watercourses are subject to alteration and management (see Chapters 3 & 5). If the deleterious effects of such operations could be minimised as discussed in Chapter 5, damage to existing crayfish populations could be reduced. In addition active stocking of certain sites could prove advantageous to the overall distribution and abundance of A.pallipes. It is now obligatory for Water Authorities to have "due regard to nature conservation" during engineering and maintenance programmes. The consideration of the habitat requirements of crayfish in the same way that fish populations are often considered in the design stage of new works, for example, would go some way towards fulfilling this duty.

Other means by which populations of A.pallipes could be reduced or eliminated from natural situations include

overfishing and the impact of introduced crayfish. Both of these threats could be controlled, to some extent, by legislation. Fishing for crayfish in non-tidal waters in the Thames Catchment requires permission, although it is thought probable that most crayfish catching is carried out without such permission. The effects of introducing other crayfish species are less easily controlled since introductions have been taking place since 1976 and control measures were only introduced in 1982 (see Chapter 7). It is suggested that Water Authority biologists and fishery staff could play a major role in ensuring that populations of A.pallipes are protected and correctly managed as much as possible and that introductions of P.leniusculus are carefully monitored and controlled.

10.9 Water Authority Considerations.

In the Thames Catchment it is considered that as crayfish are an important part of many aquatic communities it would be desirable for both scientists and engineers to have information available concerning crayfish biology that is relevant to the fisheries, pollution and land drainage functions of the Authority. It is hoped that the information obtained during the course of this study, together with published information from other studies in the U.K. and abroad, will provide the basis by which crayfish can be included during consideration of such aspects of the Authority's function. The use of crayfish for weed control, for example, could be of benefit in certain circumstances. The modification of dredging operations and incorporation of suitable habitat into new engineering structures would enable the Authority to more completely fulfil its legal obligations to nature conservation. The possible production of P.leniusculus in Authority waters, such as supply reservoirs, could provide additional income to benefit amenity and leisure facilities.

10.10 Future Studies.

It is clear that there is still considerable scope for the investigation of the role of crayfish in trophic relationships in aquatic environments. It is important that such studies are carried out before native crayfish are harvested in large numbers or devastated by the effects of disease or river management. Similarly there are many aspects of the aquaculture potential, biology and possible implications of the introduction of alien species of crayfish to the U.K. which require further study. As breeding populations, of P.leniusculus in particular, are already well established in the Thames Catchment such studies are of obvious importance. Similarly studies of methods by which maximum production of crayfish in intensive or semi-intensive conditions can be achieved could benefit the Water Authority financially. However, only when there is a similar level of interest in crayfish in the U.K. as there is in, for example, trout, is it likely that they will be more widely studied and managed in a way that is both ecologically and economically beneficial.

Bibliography.

N.B. Papers from symposia of the International Association of Astacology are listed under author. These proceedings, referred to as e.g. Freshwater Crayfish 1., are:-

- 1) ABRAHAMSSON. S.A.A. (Ed.) (1973). Freshwater Crayfish. Proceedings of the first symposium of the I.A.A. Lund, Sweden, 1972. Publ.: Studentlitteratur, Lund, Sweden. pp.252.
- 2) AVAULT. J.W. (Ed.) (1975). Freshwater Crayfish Proceedings of the second symposium of the I.A.A. Baton Rouge, U.S.A., 1974. Publ.: Louisiana State University, U.S.A. pp.676.
- 3) LINDQVIST. O.V. (Ed.) (1977). Freshwater Crayfish. Proceedings of the third symposium of the I.A.A. Kuopio, Finland, 1976. Publ.: University of Kuopio, Finland. pp.504.
- 4) LAURENT. P.J. (Ed.) (1979). Freshwater Crayfish. Proceedings of the fourth symposium of the I.A.A. Thonon-les-Bains, France, 1978. Publ.: IN.R.A, France. pp.473.

- ABRAHAMSSON. S.A.A. (1965). A method of marking crayfish Astacus astacus (L) in population studies. Oikos 16 : 228 - 231.
- ABRAHAMSSON. S.A.A. (1966). Dynamics of an isolated population of the crayfish Astacus astacus (L). Oikos 17 : 98-107.
- ABRAHAMSSON. S.A.A. (1971a). Density, growth and reproduction of the crayfish Astacus astacus (L) and Pacifastacus leniusculus (Dana) in an isolated pond. Oikos 22 : 373 - 388.
- ABRAHAMSSON. S.A.A. (1971b). Trappability, locomotion and diel pattern of activity of the crayfish Astacus astacus (L) and Pacifastacus leniusculus (Dana). (Unpubl. manuscript).
- ABRAHAMSSON. S.A.A. (1972). Fecundity and growth of some populations of Astacus astacus (L) in Sweden; with special regard to introductions in northern Sweden. Rep. Inst. Freshwat. Res. Drottningholm. 52 : 23-37.
- ABRAHAMSSON. S.A.A. (1973a). The crayfish Astacus astacus (L) in Sweden and the introduction of the American crayfish Pacifastacus leniusculus (Dana). Freshwater Crayfish 1 : 27-40.
- ABRAHAMSSON. S.A.A. (1973b). Methods for the restoration of crayfish waters in Europe. The development of an industry for the production of young of Pacifastacus leniusculus (Dana). Freshwater Crayfish 1 : 203-210.
- ABRAHAMSSON. S.A.A. & GOLDMAN. C.R. (1970). Distribution density and production of the crayfish Pacifastacus leniusculus (Dana) in Lake Tahoe, California - Nevada. Oikos 21 : 83-91.
- ADAMS. E., TAYLOR. M. & SIMKISS. K. (1982). Metal ion metabolism in the moulting crayfish (A. pallipes). Comp. Biochem. Physiol. 72A (1) : 73-76.
- ADEGBOYE. J.D., HAGADORN. I.R. & HIRSCH. P.F. (1975) Variations in haemolymph calcium associated with the moulting cycle in the crayfish. Freshwater Crayfish 2 : 227-234.
- AIKEN. D.E. (1968). The crayfish Orconectes virilis (Hagen). Survival in a region with severe winter conditions. Can. J. Zool. 46 207-211.
- ALBAUGH. D.W. (1973). Life-histories of the crayfish Procambarus acutus and P. hinei in Texas. PhD. Thesis (Unpubl.), Texas A & M. Univ., U.S.A.

- ALBRECHT. H. (1982). Das system der europäischen flusskrebse vorschlag und begründung. Mitt. Hamb. zool. Mus. Inst. 79 : 187-210.
- ALDERMAN. D.J. (1982). Crayfish plague. Bull Euro. Assoc. Fish. Path. 3 : 49-40.
- ALLEN. J.A. (1966). The rythms and population dynamics of decapod crustacea. Oceanogr. & Mar. Biol. Ann. Rev. 4 : 247-265.
- ALLEN. K.R. (1966). Some methods for the estimation of exploited populations. J. Fish. Res. Bd. Can. 23 : 1553-1574.
- ANDRÉ. M. (1960). Les écrevisses françaises. Publ. Lechevalier, Paris. pp.293.
- ANON. (1973). Report on dissolved oxygen and freshwater fisheries. Tech. Paper 19, E.I.F.A.C., Rome. pp.12.
- ANON. (1973). Crayfish:in A.A. Book of the British Countryside. Publ. Drive Publications, London.
- ANON. (1975). Where have all the crayfish gone? Tree (October 1975): 10-11.
- ANON. (1976). Bringing back the crayfish to Britain. Salmon and Trout Mag. 208 : 28.
- ANON. (1977). Otters 1977. First report of the joint N.C.C. - S.P.N.C. Otter group. N.C.C., Belgrave Sq., London. pp.26.
- ANON. (1978). Plan 1978. Report of survey - land drainage. Thames Water (Unpubl.). Nov. 1978.
- ANON. (1980). Essai d'élevage d'écrevisses Astacus leptodactylus (Esch.) à Masserac (L-A). Etud. C.M.A.G.R.E.F. 10 : pp51.
- ANON. (1980). Premieres observations sur une population naturelle d'écrevisses indigenes, A.pallipes (Lereb), a Pouydessaux dans les Landes. Etud. C.T.G.R.E.F., (Bordeaux, France) 22 : pp.52.
- ARRIGNON. J. (1975). Crayfish farming in France. Freshwater Crayfish 2 : 105-116.
- ARRIGNON. J. (1981). L'écrevisse et son élevage. Publ: Gauthier-Villars, Paris. pp.178.
- ARRIGNON. J. & MAGNE. P. (1979) Population d'écrevisses (A.pallipes pallipes) d'un ruisseau de Lozère, France. Freshwater Crayfish 4 : 131-140.

- AVAULT. J.W. (1973). Crayfish farming in the United States. *Freshwater Crayfish* 1 : 240-250.
- BAILEY. N.J. (1951). On estimating the size of mobile populations from recapture data. *Biometrika* 38 : 293-306.
- BAILEY. N.J. (1952). Improvements in the interpretation of recapture data. *J. Anim. Ecol.* 21 : 120-127.
- BEAN. R.A. & HUNER. J.V. (1979). An evaluation of selected crawfish traps and trapping methods. *Freshwater Crayfish* 4 : 141-153.
- BECKER. C.D., GENOWAY. R.G. & MERRILL. J.A. (1975). The resistance of a northwest crayfish, *Pacifastacus leniusculus* (Dana), to elevated temperatures. *Trans. Am. Fish. Soc.* 104 : 373-387.
- BEHRENDT. A. (1980). The great crayfish muddle. *Fish Farmer* 3 (6) : 25-27.
- BHATTACHARYA. C.G. (1967). A simple method of resolution of a distribution into Gaussian components. *Biometrics*, March 1967 : 115-129.
- BISHOP. O.N. (1966). *Statistics for biology*. Publ.: Longmans, London.
- BLACK. J.B. (1963). Observations on the home-range of stream-dwelling crawfishes. *Ecology* 44 (3) : 592-595.
- BLAKE. G. & LAURENT. P.J. (1982). Le faucardage par des écrevisses; résultats préliminaires. *Bull. Mins-Soc. Linn. Lyon.* 51 : 203-208.
- BOTT. R. (1950). *Die flusskrebse Europas*. Abh. Senckenberg Naturf. Ges. 483 pp.36.
- BOUCHARD. R.W. (1977). Distribution, systematic status and ecological notes on five poorly known species of crayfishes in western North America. *Freshwater Crayfish* 3 : 409-424.
- BOVBJERG. R.V. (1959). Density and dispersal in laboratory crayfish populations. *Ecology* 40 : 504-506.
- BOWLER. K. (1963a). A study of the factors involved in acclimatisation to temperature and death at high temperatures in *Austropotamobius pallipes* (Lereb). - 1). Experiments on intact animals. *J. Cell. & Comp. Physiol.* 62 : 119-132.

- BOWLER. K. (1963b). A study of the factors involved in acclimatisation to temperature and death at high temperatures in Austropotamobius pallipes (Lereb) - (2). Experiments at the tissue level. J. Cell & Comp. Physiol. 62 : 133-146.
- BOWLER. K. & BROWN. J.J. (1977). Some aspects of growth in the British freshwater crayfish Austropotamobius pallipes (Lereb). Freshwater Crayfish 3 : 295-308.
- BREWIS. J.M. (1979). Dynamics of a population of freshwater crayfish Austropotamobius pallipes (Lereb). Freshwater Crayfish 4 : 153-158.
- BREWIS. J.M. & BOWLER. K. (1982). The growth of the freshwater crayfish Austropotamobius pallipes (Lereb) in Northumbria. Freshwater Biology 12 : 187-200.
- BREWIS. J.M. & BOWLER. K. (1983). A study of the dynamics of a natural population of the freshwater crayfish Austropotamobius pallipes (Lereb). Freshwater Biology 13 : 443-452.
- BRINCK. P. (1975). Crayfish in Sweden. Freshwater Crayfish 2 : 77-86.
- BRINCK. P. (1977). Developing crayfish populations. Freshwater Crayfish 3 : 211-228.
- BRODSKY. S.Ya. (1975). The crayfish situation in the Ukraine. Freshwater Crayfish 2 : 27-29.
- BROWN. D.J. (1979). A study of the population biology of the British freshwater crayfish Austropotamobius pallipes (Lereb). PhD. Thesis (Unpubl.), Durham Univ., U.K. pp.262.
- BROWN. D.J. & BOWLER. K. (1977). A population study of the British freshwater crayfish Austropotamobius pallipes (Lereb). Freshwater Crayfish 3 : 33-50.
- BROWN. D.J. & BOWLER. K. (1979). The relationship between size and age throughout the life-cycle of Austropotamobius pallipes (Lereb). Freshwater Crayfish 4 : 35-42.
- BROWN. D.J. & BREWIS. M. (1979). A critical look at trapping as a method of sampling a population of A.pallipes in a mark and recapture study. Freshwater Crayfish 4 : 159-164.
- BRYCE. D., CAFFOOR. I.M., DALE. C.R. & JARRETT. A.F. (1978). Macroinvertebrates and the bioassay of water quality. A report based on a survey of the R.Lee. Publ. : NELPress, London. pp.44.

- CALDWELL. M.J. & BOVBJERG. R.V. (1969). Natural history of the two crayfish in northern Iowa, Orconectes virilis and O. immunis. Proc. Iowa Acad.Sci. 76 : 463-472.
- CAPELLI. G.M. (1975). Distribution, life-history and ecology of crayfish in northern Wisconsin, with emphasis on Orconectes propinquus. PhD. Thesis (Unpubl.), Univ. Wisconsin, U.S.A.
- CAPELLI. G.M. & MAGNUSSON. J.J. (1975). Reproduction, moulting and distribution of Orconectes propinquus, in relation to temperature, in a northern mesotrophic lake. Freshwater Crayfish 2 : 415-427.
- CAPELLI. G.M. & MAGNUSSON. J.J. (1980). Crayfish abundance in relation to environmental variables. F.A.O. Fish. Tech. Paper 198 : 32 (Abstract only).
- CARPENTER. K.E. (1928). Life in inland waters. Publ.: Sidgwick and Jackson, London.
- CARSTAIRS. I.L. (1979). Report of microsporidial infestation of the freshwater crayfish Cherax destructor. Freshwater Crayfish 4 : 343-348.
- CARROLL. P.N. (1980). The potential for aquaculture of Cherax destructor (the Yabbie). in : "Recent advances in animal nutrition". Ed.: D.J. Farrell. Univ. New England, Australia : 63-82.
- CASSIE. R.M. (1954). Some uses of probability paper in the analysis of size-frequency distributions. Aust. J. Mar & Freshwat. Res. 5 : 513-522.
- CERVIGNON. M.T. & MARQUES. P.R. (1964). El cangrejo de río en España. Doc. Tech. Ser. Pisc. Serv. Nacional de Pesca fluvial e Caza, Madrid. 3.
- CHAISEMARTIN. C. (1976). Maladie de la "rouille". Effets des facteurs de nuisances et de pollutions sur la métabolisme des Astacidae et de leur reproduction. Piscic. Fr. 48 : 60-64.
- CHIEN. Y.H. & AVAULT. J.W. (1979). Double-cropping rice Oryza sativa, and red-swamp crawfish, Procambarus clarkii. Freshwater Crayfish 4 : 263-272.
- CLAY. C.H. (1961). The design of fish-ways and other fish facilities. Publ. : Dept. Fisheries Canada, Ottawa. pp.301.
- CLEGG. J. (1974). The freshwater life of the British Isles. Publ. : Warne & Co., London.

- COOPER. R.A. (1970). Retention of marks and their effects on growth, behaviour and migrations of the American lobster, Homarus americanus. Trans. Am. Fish. Soc. 99 (2) : 409-417.
- CONRAN. C. (1975). Fish at its finest. Sunday Times. 12.11.78 : 88.
- CORNISH. C.J. (1902). The naturalist on the Thames. Publ. : Seeley & Co., London.
- COSSINS. A.R. (1973). Thelohania contejeani, microsporidian parasite of Austropotamobius pallipes - an histological and ultrastructural study. Freshwater Crayfish 1 : 151-164.
- COSSINS. A.R. & BOWLER. K. (1974). An histological and ultrastructural study of Thelohania contejeani, microsporidian parasite of the crayfish Austropotamobius pallipes. Parasitology 68 : 81-91.
- CUELLAR. L. & COLL. M. (1979). First essays in controlled breeding of Astacus pallipes. Freshwater Crayfish 4 : 273-276.
- CUELLAR L. & COLL. M. (in Press). Epizootology of the crayfish (Aphanomycosis) in Spain. Draft ms. for Freshwater Crayfish 5 (1981).
- CUKERZIS. J. (1968). Interspecific relations between Astacus astacus (L) and A. leptodactylus (Esch.). Ekologia Polska. (A) 16 : 629-636.
- CUKERZIS. J. (1973). Biologische grundlagen der methode der kunstlichen aufzucht der brut des Astacus astacus (L). Freshwater Crayfish 1 : 187-201.
- CUKERZIS. J. (1975). Die zahl, struktur und productivitat isolierten population von Astacus astacus (L). Freshwater Crayfish 2 : 513-528.
- CUKERZIS. J. & DOROSHENKO. J. (1976). Domination and subordination in crayfish. Inst. Zool. & Para. Acad. Sci. Lithuanian S.S.R. 73 (1) : 71-76.
- CUKERZIS. J. & TARENTJEW. A. (1979). Acclimation de Pacifastacus leniusculus (Dana) dans un lac isolé. (Transl. : P.J. Laurent.). Piscic. Fr. 56 : 13-16.
- CUMMINS. H. (1921). Spring migration of the crayfish Cambarus argillicola. Trans. Am. Microscop. Soc. 40 : 28-30.

- DAGUERRE DE HUREAUX. N. & ROQUEPLO. C. (1980). Définition du biotope préférentiel de l'écrevisse à pattes blanches. Bull. Fr. Pisc. 281- : 211-222.
- DAVIES. A.W. (1964). Crayfish in Suffolk rivers. Trans. Suffolk Nat. Soc. 13 : 11-12.
- DEAN. J.L. (1969). Biology of the crayfish Orconectes causeyii and its use for the control of aquatic weeds in trout lakes. Tech. Papers U.S. Bureau Sport Fish & Wildl. 24 (15pp.)
- DEHLI. E. (1981). Abor og ferskvannskreps. (Perch and freshwater crayfish). Fauna 34 : 64-67.
- de la BRETTONNE. L.W. & AVAULT. J.W. (1977). Population dynamics of a commercial crayfish pond. Freshwater Crayfish 3 : 133-140.
- DEMARS. J.J. (1979). Premières données sur les populations d'écrevisses de quelques cours d'eau du Haut Bassin Loire-Allier. Freshwater Crayfish 4 : 165-174.
- DUFFIELD. J.E. (1933). Fluctuations in numbers among freshwater crayfish Potamobius pallipes. J. Anim. Ecol. 2 : 184-196.
- DUFFIELD. J.E. (1936). Fluctuations in numbers of crayfish. J. Anim. Ecol. 5 : 396.
- DYE. L. & JONES. P. (1975). The influence of density and invertebrate predation on the survival of young of the year Orconectes virilis. Freshwater Crayfish 2 : 529-533.
- EASTMAN. R. (1969). The Kingfisher. Publ. : Collins, London.
- EBERHARDT. L.L. (1969). Population estimates from recapture frequencies. J. Wildl. Mgmt. 33 : 28-39.
- EMADI. H. (1974). Culturing conditions and their effects on survival and growth of the crayfish P. leniusculus trowbridgii (Dana). PhD. Thesis (Unpubl.) Oregon State Univ., U.S.A.
- ERENÇIN. Z. & KÖKSAL. G. (1977a). Studies on the freshwater crayfish (Astacus leptodactylus, Esch.) in Anatolia. Veteriner. Fakültesi. Dergisi. 24 (2) : 262-268.
- ERENÇIN. Z. & KÖKSAL. G. (1977b). On the crayfish Astacus leptodactylus (Esch.) in Anatolia. Freshwater Crayfish 3 : 187-192.

- ERLINGE. S. (1972). Interspecific relations between otter, Lutra lutra, and mink, Mustela vison, in Sweden. Oikos 23 : 327-335.
- FARMER. A.S. (1973). Age and growth in Nephrops norvegicus (Decapoda: Nephropidae). Marine Biology 23 : 315-325.
- FAST. A.W. & MOMOT. W.T. (1973). The effects of artificial aeration on the depth distribution of the crayfish Orconectes virilis (Hagen) in two Michigan lakes. Am.Midl. Nat. 89 : 89-102.
- FLINT. R.W. (1975a). Natural history, ecology and production of the crayfish Pacifastacus leniusculus in a subalpine lacustrine environment. Ph.D. Thesis (Unpubl.), Univ. California. Davis. U.S.A.
- FLINT. R.W. (1975b). Growth in a population of the crayfish Pacifastacus leniusculus from a subalpine lacustrine environment. J. Fish. Res. Bd. Can. 32 : 2433-2440.
- FLINT. R.W. (1977). Seasonal activity, migration and distribution of the crayfish Pacifastacus leniusculus in L. Tahoe. Amer. Midl. Nat. 97 : 280-292.
- FLINT. R.W. & GOLDMAN. C.R. (1975). The effects of a benthic grazer on the primary productivity of the littoral zone of L. Tahoe. Limnol & Oceanog. 20 : 935-944.
- FLINT. R.W. & GOLDMAN. C.R. (1977). Crayfish growth in L. Tahoe; effects of habitat variation. J. Fish Res. Bd. Can. 34 : 155-159.
- FOGG. G.E. (1975). Algal cultures and phytoplankton ecology. (2nd Edn.). Univ. Wisconsin Press. London. pp.175.
- FRANCOIS. D.D. (1960). Freshwater Crayfishes. Aust. Mus.Mag. 13 (7) : 217-221.
- FRANTZ. T.C. & CORDONE. A.J. (1970). Food of trout in L. Tahoe. Calif. Fish & Game. 56 (1) : 21-35.
- FROST. J.V. (1975). Australia crayfish. Freshwater Crayfish 2 : 87-96.
- FROST. W.E. & BROWN. M.E. (1967). The Trout. New Naturalist Series Publ.: Collins, London.
- FRYER. G. (1976). Crayfish eaten by tawny owl. Naturalist (Hull) 936 : 35.

- FUKE. P. (1978). Crayfish : a £5000 per acre investment?
Country landowner. Feb/Mar. : 20.
- FÜRST. M. (1977). Introduction of Pacifastacus leniusculus
(Dana) into Sweden : Methods, results and management.
Freshwater Crayfish 3 : 229-248.
- FÜRST. M. & BOSTROM. U. (1978). Frekvens av en skalsvamp
(Kräftpest) på Signal kräftor. Information från
Söttvattens laboratoriet, Drottningholm 1 : pp.24.
- GEELLEN. J.F.M. (1975). Orconectes limosus (Raf.) and
Astacus astacus (L) in the Netherlands. Hydrobiol.
Bull. 9 : 109-113.
- GLEDHILL. T. , SUTCLIFFE. D.W. & WILLIAMS. W.D. (1976).
Key to British Freshwater Crustacea : Malacostraca.
Freshwat. Biol. Assoc. Sci. Publ. 32 : pp.71.
- GODDARD. J.S. & HOLDICH. D.M. (1979). Explore the native
potential first. Fish Farmer 2 : 47.
- GOELLNER. K.E. (1943). The life-cycle and productivity of
the crayfish Cambarus immunis. PhD. Thesis (Unpubl.).
Univ. Michigan., U.S.A.
- GOLDMAN. C.R. (1973). Ecology and physiology of the
California crayfish, Pacifastacus leniusculus (Dana),
in relation to its suitability for introduction into
European waters. Freshwater Crayfish 1 : 105-120.
- GOLDMAN. C.R. & RUNDQUIST. J.C. (1977). A comparative
ecological study of the Californian crayfish
Pacifastacus leniusculus (Dana) from two subalpine
lakes. Freshwater Crayfish 3 : 51-80.
- GOLDMAN. C.R., RUNDQUIST. J.C. & FLINT. R.W. (1975).
Ecological studies of the Californian crayfish
Pacifastacus leniusculus (Dana) with emphasis on
their growth from recycling waste products.
Freshwater Crayfish 2 : 481-490.
- GRABDA. E. & WIERZBICKA. J. (1969). The problem of
parasitism of the species of the genus Branchiobdella.
Polskie Arch. Hydrobiol. 16 (1) : 93-104.
- GREEN. G.P. (1975). Food and production of the bullhead,
Cottus gobio, in the River Lambourn. PhD. Thesis
(Unpubl.). Univ. Reading, U.K.
- GREENAWAY. P. (1974a). Total body calcium and haemolymph
calcium concentrations in the crayfish Austropotamobius
pallipes (Lereb). J. Exp. Biol. 61 : 19-26.

- GREENAWAY. P. (1974a). Calcium balance at the premoult stage of the freshwater crayfish Austropotamobius pallipes (Lereb). J. Exp. Biol. 61 : 27-34.
- GREENAWAY. P. (1974c). Calcium balance at the postmoult stage of the freshwater crayfish Austropotamobius pallipes (Lereb). J. Exp. Biol. 61 : 33-45.
- GRÜNBERG. W. & HAVELEC. L. (1981). Morphometrische untersuchungen zur heterochelie beim Signalkrebs, Pacifastacus leniusculus (Dana). Wien tierarztl. Mschr. 68 (10) : 364-376.
- HABSBURGO-LORENA. A.S. (1979). Present situation of exotic species of crayfish introduced into Spanish continental waters. Freshwater Crayfish 4 : 175-184.
- HARDING. J.P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28 : 141-153.
- HARRIS. C.J. (1968). Otters. Publ. Weidenfield & Nicholson, London.
- HARVEY. G. (1980). Crayfish farmers may form co-op. Fish Farmer 3 (4) : 6-7.
- HÅSTEIN. T. & GLADHAUG. G.O. (1975). The present status of the crayfish plague in Norway. Freshwater Crayfish 2 : 273-275.
- HEATH. J. & PERRING. F. (1978). Biological Records Centre. Publ.: I.T.E., Cambridge, U.K. pp.19.
- HEPPER. B.T. (1972). The growth at moulting of lobsters, Homarus vulgaris, in the Menai Straits, North Wales. J. Cons. Perm.int. Explor. Mar. 34 (2) : 169-173.
- HERFORT-MICHIELI. T. (1979). L'écrevisses à pieds rouge en Slovénie depuis 1972. Freshwater Crayfish 4 : 185-190.
- HEWETT. C.J. (1974). Growth and moulting in the common lobster, Homarus vulgaris. J. Mar. Biol. Assoc. U.K. 54 : 370-391.
- HIATT. R.W. (1948). The biology of the lined shore crab Pachygrapsus crassipes. Pacif Sci. 11 (3) : 135-214.
- H.M.S.O. (1981). The Wildlife and Countryside Act : 1981.

- HOBBS. H.H. (1972). Biota of freshwater ecosystems. Identification Manual 9 : Crayfishes of north and middle America. Water Poll. contrl serv., U.S. Environmental Protection Agency.
- HOFMANN. J. (1980). Die flusskrebse (2nd Edn.). Publ.: K-M. Stempel, Hamburg & Berlin. pp.110.
- HOGGER. J.B. & LOWERY. R.S. (1982). The encouragement of freshwater crayfish populations by attention to the construction and maintenance of waterways. J. Inst. Wat. Eng. Sci. 36 (3) : 214-220.
- HOLDICH. D.M. (1968). Reproduction, growth and bionomics of Dynamene bidentata. J. Zool. 156 (2) : 137-153.
- HOLDICH. D.M. JAY. D. & GODDARD. J.S. (1978). Crayfish in the British Isles. Aquaculture 15 : 91-97.
- HOLT. P.C. (1963). The systematic position of the Branchiobdellidae. Am. Zool. 3 : 204 (Abstract only).
- HOLT. P.C. (1965). The systematic position of the Branchiobdellidae. System. Zool. 14 : 25-32.
- HOLT. P.C. (1968). The Branchiobdellida : epizootic annelids. The Biologist. 50 (3/4) : 79-94.
- HOLT. P.C. (1975). The Branchiobdellid associates Astacoidean crawfishes. Freshwater Crayfish 2 : 337-346.
- HOLT. P.C. (1977). A gill-inhabiting new genus and species of the Branchiobdellida. Proc. Biol. Soc. Wash. 90 (3) : 726-734.
- HOLTHUIS. L.D. (1967). Decapoda. In: 'Limnofauna Europea' Ed: J. Illies. Publ. Fischer, Stuttgart : 189-192.
- HOPKINS. C.L. (1967). Growth rate in a population of the freshwater crayfish Paranephrops planifrons N.Z. J. Mar. Freshwat. Res. 1 : 464-474.
- HUNER. J.V. & ROMAIRE. R.P. (1979). Size at maturity as a means of comparing populations of Procambarus clarkii from different habitats. Freshwater Crayfish 4 : 53-64.
- HUXLEY. T.H. (1880). The crayfish : an introduction to the study of zoology. Publ.: M.I.T. Press (Facsimile Edn. 1974). pp.371.
- HYNES. H.B.N. (1972). The ecology of running waters. Publ. : Liverpool Univ. Press, U.K.

- INGLE. R.W. (1979). Laboratory and SCUBA studies on the behaviour of the freshwater crayfish. In : 'Progress in Underwater Science.' Eds. K. Hiscock & A.D. Bourne. 2 : 1-15.
- INGLE. R.W. & THOMAS. W.J. (1974). Mating and spawning of the crayfish Austropotamobius pallipes (Lereb) (Custacea : Astacidae). J. Zool. Lond. 173 : 525-538.
- IWAO. S. (1963). On a method for estimating the rate of population interchange between two areas. Res. Popl Ecol. 5 : 44-50.
- JACKMAN. B. (1977). A nip in the tastebuds. Sunday Times. 27.11.77 : 19.
- JAY. D. & HOLDICH. D.M. (1977). The pH tolerance of the crayfish Austropotamobius pallipes (Lereb). Freshwater Crayfish 3 : 363-370.
- JAY. D. & HOLDICH. D.M. (1981). The distribution of Austropotamobius pallipes in British Waters. Freshwater Biology 11 : 121-129.
- JESTIN. J.M. (1979). Croissance et développement de l'écrevisse américaine, Orconectes limosus, dans le lac de Créteil (Val de Marne, France). Freshwater Crayfish 4 : 65-72.
- JOHNSON. S.K. (1977). Crawfish and freshwater shrimp diseases. Publ. : Texas A & M Univ. (TAMU SG-77-605) U.S.A. : pp.18.
- JOLLY. G.M. (1965). Explicit estimates from capture - recapture data with both death and immigration - a stochastic model. Biometrika 52 : 225-287.
- JONES. J.B. (1980). Freshwater crayfish Paranephrops planifrons infected with the microsporidian Thelohania. N.Z. J. Mar. & Freshwat. Res. 14 (1) : 45-46.
- JONES. J.B. (1981). Growth of two species of freshwater crayfish (Paranephrops sp.) in New Zealand. N.Z. J. Mar. & Freshwat. Res. 15 (1) : 15-20.
- KARAMAN. S.M. (1970). Beitrag zur Kenntnis der europäischen Branchiobdelliden. Int. Rev. Gest. Hydrobiol. 55 (3) : 325-333.

- KARLSSON. S.A. (1977). The freshwater crayfish. Fish Farming Inter. 4 : 8-12.
- KARLSSON. S.A. (1978). Experiences from ten years of stocking Signal Crayfish. Methods, results and mistakes. Proc. 11th Fish. Mngt. Course. Two Lakes, Romsey, U.K. Publ. : Janssen Service, London. : 84-93.
- KNOEPFFLER. L. (1979). Essai d'élevage de l'écrevisse Pontastacus leptodactylus (Esch). à l'échelle industrielle. Freshwater Crayfish 4 : 299-304.
- KOSSAKOWSKI. J. (1965). Crayfish Astacus astacus (L) and Astacus leptodactylus (Esch). Migrations in Lake Loby Poland. Ekol. Polska. (Ser. A) 13 (26) : 515-526.
- KOSSAKOWSKI. J. (1966 & 1971). Crayfish. Transl. from 'Raki'. Publ.: Panstwowe Wydawnictwo Rolnicze i Lesne. 1966. pp.292.
- KOSSAKOWSKI. J. (1967). Growth of chelae in the crayfish. Roczn. Naucro. in t.90. SH. 2.3 : 423-432.
- KOSSAKOWSKI. J. (1973). The freshwater crayfish in Poland. Freshwater Crayfish 1 : 17-26.
- KOSSAKOWSKI. J. & ORZECZOWSKI. B. (1975). Crayfish, Orconectes limosus, in Poland. Freshwater Crayfish 2 : 31-47.
- KOSSAKOWSKI. J. & KOSSAKOWSKI. D. (1979). The first introduction of the crayfish Pacifastacus leniusculus (Dana) into Polish waters. Freshwater Crayfish 4 : 195-196.
- KRAUS. O. (1976). Phylogenetische systematik und evolutionäre klassifikation. Verh. Dtsch. Zool. Ges. : 84-99.
- KURATA. H. (1962). Studies on the age and growth of crustacea. Bull. Hokkaido. Reg. Fish. Res. Lab. 24 : 1-115.
- LAURENT. P.J. (1960). Systématique des Astacidae de France. Ann. Stn. Centr. Hydiobiol. Applique. 8 : 264-280.
- LAURENT. P.J. (1973). Astacus and Cambarus in France. Freshwater Crayfish 1 : 70-78.
- LAURENT. P.J. (1979). Premières résultats des introductions expérimentales en eaux closes de Pacifastacus leniusculus (Dana). Piscic. Fr. 56 : 51-57.

Addendum:-

LAURENT. P.J. & FOREST. J. (1979). Données sur les
écrevisses qu'on peut rencontrer en France. La Pisc.
Franc. 55 (1) : 25-40.

- LAURENT. P.J. (1980a). Utilisation des etangs pour la production d'ecrevisses. In : 'La pisciculture en etang.' Ed. : R. Billard. Inst. Nat. Rech. Agron. Paris : 333-342.
- LAURENT. P.J. (1980b). Stocking of lakes with American Signal Crayfish. Proc. Fish. Mngt. Course. Two Lakes, Romsey, U.K. Publ.: Janssen Services, London. : 139-148.
- LAURENT. P.J. & SUSCILLON. M. (1962). Les écrevisses en France. Ann. Stn. Centr. Hydrobiol. Applique. 9 333-395.
- LAWRENCE. M.J. & BROWN. R.W. (1967). Mammals of Britain. Their tracks, trails and signs. Publ. : Blandford Press, London.
- LEEKE. C.J. & PRICE. A. (1965). Branchiobdella astaci in Reading. Reading Nat. 17: 18-19.
- LEWIN, J. (Ed) (1981). British Rivers. Publ. : George Allen & Unwin, London
- LIANG. Y. (1963). Studies on the aquatic oligochaeta of China. (1) Descriptions of new Naiads and Branchiobdellids. Acta. Zool. Sinica. 17 (4) : 602-610.
- LILLEY. A.J. (1977). 1. A review of freshwater crayfish in the U.K. 2. The distribution of the British freshwater crayfish Austropotamobius pallipes (Lereb). in tributaries of the R. Wye. MSc. Thesis (Unpubl) U.W.I.S.T., Cardiff, U.K. : pp.71.
- LILLEY. A.J., BROOKER. M.P. & EDWARDS. R.W. (1979). The distribution of the crayfish A. pallipes in the upper Wye catchment, Wales. Nature in Wales. 16 : 195-200
- LINCOLN. F.C. (1930). Calculating waterfowl abundance on the basis of banding returns. U.S. Dept. Agric. Circ. 118 : 1-4.
- LINDQVIST. D.V. (1977). On the principals of management stratgegies of crayfish and fish populations. Freshwater Crayfish 3 : 249-261.
- LINDQVIST. O.V. & LOUECKARI. K. (1975). Muscle and hepatopancreas weight in Astacus astacus (L) in the trapping season in Finland. Ann. Zool. Fennici. 12 : 237-243.
- LORMAN. J.G. & MAGNUSSON. J.J. (1978). The role of crawfishes in aquatic ecosystems. Fisheries 3 : 8-10

- LOWE. E.S. (1920). Crayfish eaten by rats. Lanc. Chesh Nat. 13 198.
- LOWERY. R.S. & MENDES. A.J. (1977). The biology of Procambarus clarkii in Lake Naivasha, Kenya; with a note on its distribution. Freshwater Crayfish 3 : 203-210.
- MACAN. T.T. & WORTHINGTON. E.B. (1951 & 1972). Life in Lakes and Rivers. Collins & Fontana, London. pp.320.
- MAGNUSSON. J.J., CAPELLI. G.M., LORMAN. J.G. & STEIN. R.A. (1975). Consideration of crayfish for macrophyte control. In : 'Proc. Symp. Water Qual. Management through biol. control.' Eds. : P.L. Brezoric & J.L. Fox. Publ. : Univ. Florida, U.S.A. : 66-74.
- MAGRATH. P.A.G. (1978). Possible effects and implications of varying water quality and quantity on the benthic macroinvertebrate fauna of the River Cherwell. P.C.L./M.P./T.W.A. (Unpubl). pp.66.
- MAHONEY. R. (1973). Laboratory techniques in zoology. (2nd Edn). Publ. : Butterworths, London. pp.518.
- MANN. R.H.K. (1976). Observations on the age, growth, reproduction and food of the pike, Esox lucius in two rivers in southern England. J. Fish. Biol. 8 : 179-197.
- MANN. R.H.K. (1978). Observations on the biology of the perch, Perca fluviatilis, in the River Stour, Dorset. Freshwater Biology 8 : 229-239.
- MASSE. J. (1981). Elevage d'écrevisse Astacus leptodactylus (Esch). en France. Bull. Fr. Piscic. 281 : 162-168.
- MASON. C. (1981). The biology of freshwater pollution. Publ. : Longman, New York.
- MASON. J.C. (1970). Egg-laying in the western North American crayfish Pacifastacus trowbridgii. Crustaceana 19 : 37-44.
- MASON. J.C. (1974). Aquaculture potential of the freshwater crayfish (Pacifastacus). 1. Studies during 1970. Fish. Res. Bd. Can. Tech Suppl. 440 pp.43.
- MASON. J.C. (1975). Crayfish production in a small woodland stream. Freshwater Crayfish 2 : 449-480.
- MASON. J.C. (1977a). Reproductive efficiency of Pacifastacus leniusculus in culture. Freshwater Crayfish 3 : 101-117.

- MASON. J.C. (1977b). Artificial incubation of crayfish eggs (Pacifastacus leniusculus). Freshwater Crayfish 3 : 119-122.
- MASON. J.C. (1979a). Effects of temperature photoperiod, substrate and shelter on survival, growth and biomass accumulation of juvenile Pacifastacus leniusculus (Dana). in culture. Freshwater Crayfish 4 : 73-82.
- MASON. J.C. (1979b). Significance of egg size in the freshwater crayfish Pacifastacus leniusculus (Dana). Freshwater Crayfish 4 : 83-92.
- MAZYLIS. A. (1973). The infection of the broad-clawed crayfish with Branchiobdellidae and control measures against them. Viet. TSR. Mosklu. Akad. Darb. (c) 3 (63) : 107-113.
- MCCARTHY. D.T. (1977). The effects of drainage on the Trimblestown River. (1) Benthic invertebrates and flora. Ir. Fish Invest. Ser. A. 16 : 3-7.
- McGRIFF. D. (1983). Communication to newsletter of IAA. 6 (1).
- MILLER. G.C. (1960). The taxonomy and certain biological aspects of the crayfish of Washington and Oregon. M.S. Thesis (Unpubl.). Oregon State Univ. U.S.A. pp.216.
- MOMOT. W.T. (1964). Population dynamics of the crayfish Orconectes virilis, in relation to predation by the brook trout Salvelinus fontinalis PhD. Thesis (Unpubl). Univ. Michigan, U.S.A.
- MOMOT. W.T. (1966). Upstream movement of crayfish in an intermittent Oklahoma stream. Am. Midl. Nat. 75 : 150-159.
- MOMOT. W.T. (1967a). Population dynamics and productivity of the crayfish O. virilis in a marl lake. Am. Midl. Nat. 78 : 55-81.
- MOMOT. W.T. (1967b). Effects of brook trout predation on a crayfish population. Trans. Am. Fish. Soc. 96 : 202-209.
- MOMOT. W.T. & GOWING. H. (1977). Response of the crayfish Orconectes virilis to exploitation. J. Fish. Res. Bd. Can. 34 (8) : 1212-1219.
- MOMOT. W.T., GOWING. H. & JONES. P.D. (1978). The dynamics of crayfish and their role in ecosystems. Am. Midl. Nat. 99 : 10-35.

- MOMOT. W.T. & JONES. P.D. (1976). The relationship between biomass, growth rate and annual production in the crayfish Orconectes virilis. Freshwater Crayfish 3 : 3-32.
- MORIARTY. C. (1973). A study of Austropotamobius pallipes (Lereb). in Finland. Freshwater Crayfish 1 : 57-68.
- MORRISSEY. N.M. (1970). Spawning of marron Cherax tenuimanus in Western Australia. Fish. Bull. West. Aust. 10 : 1-23.
- MORRISSEY. N.M. (1973). Normal (Gaussian) response of juvenile marron, Cherax tenuimanus, to capture by baited sampling units. Aust. J. Mar. Freshwat. Res. 24 : 183-195.
- MORRISSEY. N.M. (1975). The influence of sampling intensity on the catchability of marron, Cherax tenuimanus. Aust. J. Mar. Freshwat. Res. 26 : 47-73.
- MORRISSEY. N.M. (1978). The amateur marron fishery in Western Australia. Fish. Res. Bull. West. Aust. 21 : 1-44.
- MORRISSEY. N.M. (1979). Experimental pond production of marron, Cherax tenuimanus. Aquaculture 16 : 319-344.
- MORRISSEY. N.M. & CAPUTI. N. (1981). Use of catchability equations for population estimation of marron, Cherax tenuimanus. Aust. J. Mar. Freshwat. Res. 32 : 213-225.
- MOSHIRI. G.A. & GOLDMAN. C.R. (1969). Estimation of assimilation efficiency in the crayfish Pacifastacus leniusculus (Dana). Arch. Hydrobiol. 66 (3) : 208-306.
- MOSHIRI. G.A., GOLDMAN. C.R., MULL. D.R., GODSHALK. G.L. & COIL. J.A. (1971). Respiratory metabolism in Pacifastacus leniusculus (Dana) as related to its ecology. Hydrobiol. 37 (2) : 183-195.
- NEFEDOV. V.N. & MAZANOV. N.N. (1973). Determination of the weight of Astacus leptodactylus (Esch). Gidrobiol. Zh. 9 (4) : 102-105.
- NIEMI. A. (1977). Population studies on the crayfish Astacus astacus (L) in the River Pyhäjoki, Finland. Freshwater Crayfish 3 : 81-94.
- N.W.C. (1981). River quality : the 1980 survey and future outlook. Publ. : N.W.C. London. pp.39.

- NYLUND. V. & WESTMAN. K. (1979). Psorospermium haeckeli, a parasite of the European crayfish Astacus astacus (L) found in Finland. Freshwater Crayfish 4 : 385-390.
- ODELSTRÖM. T. (1977). The crayfish species Astacus astacus (L) and Pacifastacus leniusculus (Dana) in Lake Erken: then and now. Söttvattenslaboratoriet Drottningholm 14 : 25-32.
- O'KEEFFE. C. & REYNOLDS. J.D. (in press). The occurrence of crayfish diseases and their significance in Ireland. Draft ms. for Freshwater Crayfish 5 (1981) (N.B. Referred to as O'Keefe in this thesis).
- PARK. T., GREGG. R.E. & LUTHERMAN. C.Z. (1940). Toleration experiments by ecology classes. Ecology 21 (1) : 109-111.
- PEARSON. R.G. & JONES. N.V. (1975). The effects of dredging operations on the benthic community of a chalk stream. Biol. Conserv. 8 : 273-278.
- PENNAK. R.W. (1978). Invertebrates of the U.S.A. (2nd Edn). Publ.: J. Wiley & Son, New York.
- PIESIK. Z. (1974). The role of the crayfish Orconectes limosus in extinction of Dreissena polymorpha on steelon net. Polskie. Arch. Hydrobiol. 21 (3/4) : 401-410.
- PIXELL-GOODRICH. H. (1956). Crayfish epidemics. Parasitology 46 : 480-483.
- POP. V. (1965). Systematische revision der europäischen Branchiobdelliden. Zool. Jb. Syst. Bx. 92 (8) : 219-238.
- PORTER. E. (1978). Water management in England and Wales. Publ.: Cambridge Univ. Press., U.K.
- PRATTEN. D.J. (1980). Growth in the crayfish Austropotamobius pallipes (Lereb). Freshwater Biology 10 : 401-412.
- PRICE. J.O. & PAYNE. J.F. (1979). Multiple summer moults in adult Orconectes neglectus chenodactylus (Williams). Freshwater Crayfish 4 : 93-104.
- REYNOLDS. J.D. (1979a). Crayfish ecology in Ireland. Freshwater Crayfish 4 : 215-220.

- REYNOLDS. J.P. (1979b). The introduction of freshwater crayfish species for aquaculture in Ireland. In : The introduction of exotic species; advantages and problems. Ed. R.P. Kernan. Royal Irish Acad., Dublin : 57-64
- RHODES. C.P. (1980). Studies on the growth and feeding biology of the crayfish Austropotamobius pallipes (Lereb). PhD Thesis (Unpubl.) : Univ. Nottingham, U.K. pp.546.
- RHODES. C.P. (1981). Artificial incubation of the eggs of the crayfish Austropotamobius pallipes (Lereb). Aquaculture 25 : 129-140.
- RHODES. C.P. & HOLDICH. D.M. (1979). On size and sexual dimorphism in Austropotamobius pallipes. A step in assessing the commercial exploitation potential of the native British freshwater crayfish. Aquaculture 17 : 345-358.
- RHODES. C.P. & HOLDICH. D.M. (1981). Artificial incubation of the eggs of the crayfish Austropotamobius pallipes (Lereb). Aquaculture 25 : 129-140.
- RHODES. C.P. & HOLDICH. D.M. (1982). Observations on the fecundity of the freshwater crayfish Austropotamobius pallipes (Lereb), in the British Isles. Hydrobiol. 89 : 231-236.
- RICHARDS. K. & FUKU. P. (1977). Freshwater Crayfish : the first centre in Britain. Fish Farming Inter. 4 : 12-15.
- RICKER. W.E. (1971) (Ed). Methods for assessment of fish production in fresh waters. I.B.P. Handbook No. 3. (2nd Edn). Publ: Blackwell, Oxford, U.K.
- RICKER. W.E. (1975). Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191. pp.382.
- ROBSON. D.S. & REIGER. H.A. (1964). Sample size in Petersen mark-recapture experiments. Trans. Am. Fish. Soc. 93 : 215-226.
- RUNDQUIST. J.C., GALL. J. & GOLDMAN. C.R. (1977). Watercress - crayfish polyculture as an economic means of stripping nutrients from enriched waters. Freshwater Crayfish 3 : 141-160.
- RUNDQUIST. J.C. & GOLDMAN. C.R. (1979). Growth and food conversion efficiency of juvenile Pacifastacus leniusculus (Dana) along a salinity gradient. Freshwater Crayfish 4 : 105-114.

- SCHÄPERCLAUS. W. (1954). Fischkrankheiten. Publ : Akademie - Verlag. Berlin. pp.708.
- SCHWENG. E. (1973). Orconectes limosus (Hagen) in Deutschland, insbesondere im Rheingebiet. Freshwater Crayfish 1 : 79-87.
- SEBER. G.A.F. (1973). The estimation of animal abundance. Publ. : Griffin, London.
- SERROL. A. & COLER. R.A. (1975). Demonstrated food preferences of Orconectes immunis. Crustaceana 29 : 319-320.
- SHELTON. P.M.J. (1981). Naturally occurring abnormalities in the chelae of three species of Crustacea (Decapoda) and a possible explanation. J. Embryol. exp. Morph. 63 : 285-304.
- SHERRY. P.J. (1977). An investigation to assess the aquacultural potential of the freshwater crayfish Pacifastacus leniusculus. MSc.Thesis (Unpubl). Plymouth Polytechnic, U.K.
- SHIMIZU. S. & GOLDMAN. C.R. (1979). Population dynamics and production estimates of the Californian crayfish in the Sacramento River. (Summary only). Bull. Ecol. Soc. Am. 60 (2) : 136.
- SNEDECOR. G.W. & COCHRAN. W.G. (1967). Statistical Methods (6th Edn). Publ. : Iowa State Univ. Press., U.S.A.
- SÖDERHÄLL. K., SVENSSON. E. & UNESTAM. T. (1977). An inexpensive and effective method for elimination of the crayfish plague : barriers and biological control. Freshwater Crayfish 3 : 333-342.
- SOGANDARES-BERNAL. F. (1962). Presumable microsporidiosis in the dwarf crayfish Cambarellus puer and C.shufeldti in Louisiana. J. Parasitol 48 : 493.
- SOUTHERN. H.N. (1964). The handbook of British mammals. Publ.: Blackwell, Oxford, U.K.
- SOUTHWOOD. T.R.E. (1966). Ecological methods, with particular reference to the study of insect populations. Publ.: Methuen, London.
- SPITZY. R. (1973). Crayfish in Austria. History and actual situation. Freshwater Crayfish 1 : 10-14.
- SPRAGUE. V. (1950). Thelohania cambari : a microsporidian parasite of North American crayfish. J. Parasitol. 36 (6) : 46.

- STEIN. R.A. (1976). Sexual dimorphism in crayfish chelae : functional significance linked to reproductive activities. Can. J. Zool. 54 : 220-227.
- STEIN. R.A., MURPHY. M.L. & MAGNUSSON. J.J. (1977). External morphological changes associated with sexual maturity in the crayfish Orconectes propinquus. Am. Midl. Nat. 97 : 495-502.
- STEVENSON. J.R. (1975). The moulting cycle in the crayfish : recognising the moulting stages, effects of ecdysone and changes during the cycle. Freshwater Crayfish 2 : 255-269.
- STREMPEL. K. (1975). Künstliche Erbrütung von Edelkrebsen in Zugergläsern und vergleichende Beobachtungen im Verhalten und Abwachs von Edel- und Signal krebsen. Freshwater Crayfish 2 : 393-403.
- SUMARI. O. & WESTMAN. K. (1969). The crayfish parasite Thelohania contejeani found in Finland. Ann. Zool. Fennici 7 : 193-194.
- SUTCLIFFE. D.W. & CARRICK. T.R. (1975). Respiration in relation to ion uptake in the crayfish Austropotamobius pallipes (Lereb). J. Exp. Biol. 63 : 689-699.
- SVÄRDSSON. G. (1949). Stunted crayfish populations in Sweden. Rep. Inst. Freshwat. Res. Drottningholm 29 : 135-145.
- SVÄRDSSON. G. (1965). The American crayfish Pacifastacus leniusculus (Dana) introduced into Sweden. Rep. Inst. Freshwat. Res. Drottningholm 46 : 90-94.
- SVÄRDSSON. G. (1972). The predatory impact of the eel, Anguilla anguilla on populations of the crayfish Astacus astacus (L). Rep. Inst. Freshwat. Res. Drottningholm 52 : 149-191.
- SWALES. S. (1981). Land drainage and river ecology - past, present and future. Salmon & Trout Mag. 222 : 40-43.
- SWALES. S. & O'HARA. K. (1980). Instream habitat improvement devices and their use in freshwater fisheries management. J. Env. Manag. 10 : 167-179.
- TANAKA. S. (1962). A method of analysing polymodal frequency distributions and its application to the length distributions of the porgy, Taius tumifrons J. Fish. Res. Bd. Can. 19 : 1143-1159.

- TANNER. M.F. (1979). W.S.A.C. Research Report 5 : Wildfowl, Reservoirs and Recreation. W.S.A.C. London. pp.40.
- TAVERNER. E. (1957). Anglers fishes and their natural history. pp.213.
- TESCH. F.W. (1971). Age and growth. In : 'Methods for the assessment of fish production in freshwaters'. I.B.P. Handbook No. 3. Ed. W.E. Ricker. Publ.: Blackwell, Oxford, U.K. : 98-130.
- THAMES WATER (1974 & 1983). The environment and the river. Publ.: Thames Water, London.
- THOMAS. W.J. (1977). Crayfish reproductive structures. Freshwater Crayfish 3 : 453-461.
- THOMAS. W.J. (1979). Aspects of crayfish biology. Freshwater Crayfish 4 : 115-122.
- THOMAS W.J. & CRAWLEY. E. (1975a). The glair glands and oosetae of Austropotamobius pallipes (Lereb). Experientia 31 (2) : 183-185.
- THOMAS. W.J. & CRAWLEY. E. (1975b). The glair glands and oosetae of Austropotamobius pallipes (Lereb). Experientia 31 (5) : 534-537.
- THOMAS. W.J. & INGLE. R.W. (1971). The nomenclature bionomics and distribution of the crayfish Austropotamobius pallipes (Lereb). in the British Isles. Essex Nat. 32 : 349-360.
- TILLIEN. G. (1981). La commercialisation de l'écrevisse en France : approche économique, hygiénique et sanitaire. Bull. Fr. Piscic. 281 : 149-161.
- TOMS. R.G. (1975). The environmental impact of land-drainage work. Proc. Cons & Land Drainage Conf. (W.S.A.C.). : 10-21.
- TOWNER-COSTON. H.E. (1936). River management. Publ. : Seeley Service & Co., London.
- UDE. H. (1929). Oligochaeta. In : 'Die Tierwelt Deutschlands'. Ed. : F. Dahl. 15 : 106-108.
- UNESTAM. T. (1969). Resistance to the crayfish plague in some American, Japanese and European crayfishes. Rep. Inst. Freshwat. Res. Drottningholm. 49 : 202-209.

- UNESTAM. T. (1972). On the host range and origin of the crayfish plague fungus. Rep. Inst. Freshwat. Res. Drottningholm. 52 : 192-198.
- UNESTAM. T. (1973a). Significance of diseases in freshwater crayfish. Freshwater Crayfish 1 : 135-150.
- UNESTAM. T. (1973b). Fungal diseases of crustacea. Rev. Med. Vet. Mycol. 8 (1) : 1-20.
- UNESTAM. T. (1975a). The dangers of introducing new crayfish species. Freshwater Crayfish 1 : 135-150.
- UNESTAM. T. (1975b). Defence reactions in crayfish towards microbial parasites; a review. Freshwater Crayfish 2 : 327-336.
- UNESTAM. T. & WEISS. D.W. (1970). The host-parasite relationship between the freshwater crayfish and the crayfish disease fungus Aphanomyces astaci. Responses to infection by a susceptible and a resistant species. J. Gen. Microbiol. 60 : 77-90.
- UNESTAM. T., SÖDERHÄLL. K., NYHLÉN. L., SVENSSON. E. & AJAXON. R. (1977). Specialisation in crayfish defence and fungal aggressiveness upon crayfish plague infection. Freshwater Crayfish 3 : 321-331.
- Van DEVENTER. W.C. (1937). Studies on the biology of the crayfish Cambarus propinquus. Illinois Biol. Monogr. 15 (3) : 1-67.
- VEY. A. (1977). Studies on the pathology of crayfish under rearing conditions. Freshwater Crayfish 3 : 311-319.
- VEY. A. (1979a). Infections fongiques chez l'écrevisse Astacus leptodactylus (Esch). Freshwater Crayfish 4 : 403-410.
- VEY. A. (1979b). Recherches sur une maladie des écrevisses due au parasite Psorospermium haeckeli. Freshwater Crayfish 4 : 411-418.
- VEY. A. (1979c). Aspects fondamentaux et pratiques des recherches actuelles sur les maladies des écrevisses. Piscic. Fr. 56 : 41-45.
- VEY. A., VAGO. C. & CHARPY. R. (1971). Une microsporidiose à Thelohania de l'écrevisse Austropotamobius pallipes (Lereb). en France. C.R. Acad. Agric. Fr. 57 : 1540-1543.

- VEY. A. & VAGO. C. (1973). Protozoan and fungal diseases of Austropotamobius pallipes (Lereb). in France. Freshwater Crayfish 1 : 165-179.
- VEY. A., BOEMARE. N. & VAGO. C. (1975). Recherches sur les maladies bactériennes de l'écrevisse Austropotamobius pallipes (Lereb). Freshwater Crayfish 2 : 287-298.
- VIGNEUX. E. (1979). Pacifastacus leniusculus (Dana) et Astacus leptodactylus (Esch). premiere bilan d'exploitation en étangs. Freshwater Crayfish 4 : 227-234.
- VIGNEUX. E. (1981). Détermination rapide des écrevisses. Bull. Fr. Pisc. 281 : 185-210.
- VORONIN. V.N. (1971). New data on microsporidiosis of the crayfish Astacus astacus (L). Parazitologiya 5 : 186-191.
- WATERS. T.F. (1969). The turnover ratio in the production ecology of freshwater invertebrates. Am. Nat. 103 (930) : 173-185.
- WATSON. P.S. (Unpubl.). Studies on the distribution of the crayfish Astacus pallipes in County Fermanagh, N. Ireland; and in particular within Lough Lea. Unpubl. ms., Dept. Agric., Coleraine, Co. Londonderry.
- WEAGLE. K.V. & OZBURN. G.W. (1972). Observations on aspects of the life-history of the crayfish Orconectes virilis in N.W. Ontario. Can. J. Zool. 50 (3) : 366-370.
- WEBBER. H.H. & RIORDAN. P.F. (1976). Criteria for candidate species for aquaculture. Aquaculture 7: 107-123.
- WEBSTER. D.A. (1962). Artificial spawning facilities for brook trout (Salvelinus fontinalis). Trans. Am. Fish. Soc. 91 (2) : 168-174.
- WEEKS. K.G. (1982). Conservation aspects of two river improvement schemes in the River Thames catchment. J. Inst. Wat. Eng. Sci. 36 (6) : 447-458.
- WEINGARTNER. D.L. (1982). A field-tested internal tag for crayfish. Crustaceana 43 (2) : 181-188.
- WELCH. H.E. (1960). Two applications of a method of determining the error of population estimates of mosquito larvae by the mark-recapture technique. Ecology 41 : 228-229.

- WELLS. S.M., PYLE. R.M. & COLLINS. N.M. (1983). The I.U.C.N. Invertebrate Red. Data Book. Publ. : I.U.C.N., Gland., Switzerland. pp.632. (N.B. Referred to as Wells, 1983 in this thesis.)
- WENNER. A.M., FUSARO. C. & OATEN. A. (1974). Size at onset of sexual maturity and growth rate in crustacean populations. Can. J. Zool. 52 (9) : 1095-1106.
- WESSEX WATER AUTHORITY. (1974). Environmental and conservation aspects relating to river works. Publ. : Wessex W.A., Bristol.
- WESTMAN. K. (1973a). The population of the crayfish Astacus astacus (L) in Finland and the introduction of the American crayfish Pacifastacus leniusculus (Dana). Freshwater Crayfish 1 : 41-50.
- WESTMAN. K. (1973b). Cultivation of the American crayfish Pacifastacus leniusculus (Dana). Freshwater Crayfish 1 : 211-220.
- WESTMAN. K. (1975). On crayfish research in Finland. Freshwater Crayfish 2 : 65-76.
- WESTMAN. K. & NYLUND. V. (1979). Crayfish plague Aphanomyces astaci (Schick.) observed in the European crayfish Astacus astacus (L) in Pihlajavesi waterway in Finland. A case study on the spread of the plague fungus. Freshwater Crayfish 4 : 419-426.
- WESTMAN. K. & PURSAINEN. M. (1979). Development of the European crayfish Astacus astacus (L) and the American crayfish Pacifastacus leniusculus (Dana) populations in a small Finnish lake. Freshwater Crayfish 4 : 243-250.
- WESTMAN. K., PURSAINEN. M. & VILKMAN. R. (1979). A new folding trap model which prevents crayfish from escaping. Freshwater Crayfish 4 : 235-242.
- WESTMAN. K. & PURSAINEN. M. (1982a). Size and structure of crayfish populations in different habitats in Finland. Hydrobiol. 86 : 67-72.
- WESTMAN. K. & PURSAINEN. M. (1982b). (Eds.). Status of crayfish stocks in Europe. E.I.F.A.C. XII 82 Inf. 4. pp.97.
- WHEATLEY. M.G. & McMAHON. B.R. (1982). Responses to hypersaline exposure in the euryhaline crayfish Pacifastacus leniusculus (Dana). I. The interaction between ionic and acid-base regulation. J. Exp. Biol. 99 : 425-445.

- WOODLAND. D.J. (1967). Population study of a freshwater crayfish, Cherax albidus. PhD. Thesis (Unpubl.) Univ. New England, Australia.
- W.S.A.C. (1978). Conservation and Land Drainage guidelines: Drainage, flood protection and sea defence works, England and Wales (Unpubl. Draft). Water Space Amenity Commission, London. pp.74.
- YOUNG. W. (1965). Ecological studies of the Branchiobdellidae. Ecology 47 (4) : 571-578.

APPENDICES

<u>Appendix</u>	<u>Title.</u>	<u>Page</u>
1.	Statistical methods.	(a)
2.	Distribution records of <u>A.pallipes</u> . (Microfiche).	(e)
3.	Water Quality classification.	(f)
4.	B.M.W.P. Score system.	(g)
5.	T.W.A.B.I. System.	(h)
6.	Paper entitled: 'The encouragement of freshwater crayfish populations by attention to the construction and maintenance of waterways'. Hogger. J.B & Lowery. R.S. J.I.W.E.S. <u>36</u> (3) : 214-220.	(i)
7.	A key to the identification of European species of the genus Branchiobdella.(Transl. from Ude, 1929).	(j)
8.	Distribution records of <u>Branchiobdella astaci</u> .	(k)
9.	Distribution records of introductions of <u>Pacifastacus leniusculus</u> in the Thames Catchment.	(l)

APPENDIX 1 Statistical Methods.

The more common methods of data analysis and tests of significance i.e. regression; log. regression; t-tests; χ^2 tests, etc. have been taken from standard texts (e.g. Snedecor & Cochran, 1967).

Outlined below are methods of calculating population estimates from mark-recapture data and the programme used for the multiple regression analysis of data concerning sexually dimorphic characteristics.

A) Methods used for calculating population estimates.

(i) Lincoln Index/Petersen Method. (Lincoln, 1930; Ricker, 1971, 1975).

$$\frac{\text{Total population size (N)}}{\text{Number marked (m)}} = \frac{\text{Total in sample 2 (c)}}{\text{Total number recaptured (r)}}$$

$$\text{Hence: } N = \frac{mc}{r}$$

$$\text{If } m = c \text{ then the variance} = \frac{m^2 \cdot c(c - r)}{r} \quad (\text{Bailey, 1952})$$

If sample 2 consists of a series of subsamples and a large proportion of the population is marked, the 'recovery ratio' $\left(\frac{r}{n}\right)$ can be used to calculate the standard error of the population estimate (Welch, 1960):

$$P = \frac{m}{R_t} \quad \text{where: } R_t = \text{total recovery ratio} = \sum \left(\frac{r}{N}\right)$$

$r = \text{number of recaptures; } N = \text{catch per sample.}$

$$P \text{ variance} = \left(\frac{m}{(R_t)^2}\right)^2 \times \frac{R_t (1 - R_t)}{y} \quad \text{where } y = \text{total catch.}$$

This relationship is only valid, however, if individuals are randomly distributed in the subsamples.

Where only small samples of crayfish have been obtained the following estimate has been calculated: (Ricker, 1975)

$$N = \frac{m(c + 1)}{r + 1} \quad \text{Variance of } N = \frac{m^2 (c + 1) (c - r)}{(r + 1)^2 (r + 2)}$$

(ii) Schnabel Method (Ricker, 1975).

This method approximates the maximum likelihood estimate from multiple census according to the formula :

$$N = \frac{\sum (C_t \cdot M_t)}{R} \quad \text{Where: } C_t = \text{total sample on day } t$$

$$M_t = \text{total number of marked animals at the start of day } t$$

$$R = \text{total number of recaptures}$$

When the number of recaptures (R) is relatively large then $\left(\frac{1}{N}\right)$ is distributed almost normally and has a variance of :

$$V \left(\frac{1}{N}\right) = \frac{R}{\left(\sum C_t \cdot M_t\right)^2}$$

from which confidence limits can be calculated (using \sqrt{V} and t values for the normal curve) which can be inverted to give a confidence range for N.

(iii) Bailey Triple Catch method (Bailey, 1951, 1952: Ricker, 1975).

This method also utilises the maximum likelihood techniques and enables accurate variances of the estimates to be calculated. Being based on a deterministic model of survival the method is most reliable when large numbers are marked and recaptured (Ricker, 1975). The intervals between sampling may be of any length and must be long enough for mixing to occur but not too long to allow significant mortalities to occur.

Population on Day 2:

$$P_2 = \frac{a_2 n_2 r_3}{r_{21} r_{32}}$$

where: a_2 = number of marked animals released on day 2

n_2 = catch, day 2

r_{21} = number caught day 2, marked day 1

$$\text{Variance } P_2 = (P_2)^2 \left(\frac{1}{r_{21}} + \frac{1}{r_{32}} + \frac{1}{r_{31}} - \frac{1}{n_2} \right)$$

Where a small sample size is unavoidable the following 'corrected' formula may be used (Ricker, 1975):

$$P_2 = \frac{a_2 (n_2 + 1) (r_{31})}{(r_{21} + 1) (r_{32} + 1)}$$

$$\text{Variance } P_2 = (P_2)^2 - \frac{(a_2)^2 (n_2 + 1) (n_2 + 2) (r_{31}) (r_{31} - 1)}{(r_{21} + 1) (r_{21} + 2) (r_{32} + 1) (r_{32} + 2)}$$

(iv) Jollys Stochastic model (Jolly, 1965; Ricker, 1975).

Survival rate, which can be calculated from Baileys model, is not an exact value but a probability and is well expressed in a stochastic model. This method uses three or more successive samples and allows for immigration and emigration, mortality and animals killed or removed after capture :

$$\hat{P}_i = \frac{\hat{M}_i \cdot n_i}{r_i}$$

Where: \hat{P}_i = estimate of population on day i.

\hat{M}_i = total number of marked animals in the population on day i.

r_i = total number of marked animals caught on day i.

n_i = total catch on day i.

(c)

B) Programme for carrying out multiple regression analysis.

```

100 DIM X(1000),Y(1000)
110 DIM B1(1000),B2(1000)
200 PRINT "*****PREG2.BAS*****"
205 PRINT "PROGRAM FOR CALCULATING SUCCESSIVE INTERSECTING"
220 PRINT "PAIRS OF LINEAR REGRESSION LINES"
225 PRINT "WRITTEN BY B.GILES. MARCH 1983"
230 PRINT "*****"
240 PRINT "*****"
244 PRINT "*****"
248 PRINT "HOW MANY POINTS IN TOTAL?"
250 INPUT N5
260 PRINT\PRINT "IS THE DATA FROM A DATA FILE? Y OR N"
270 INPUT F6
280 IF F6="Y" GOTO 400
290 IF F6<>"N" GOTO 260
300 PRINT "TYPE IN DATA AS X,Y"
310 PRINT "ONE LINE AT A TIME"
320 FOR J=1 TO N5
330 INPUT X$,Y$
340 PRINT "DO YOU WANT TO CHANGE THIS? Y OR N"
350 INPUT F8
360 IF F6="Y" GOTO 330
370 B1(J)=VAL(X$)\B2(J)=VAL(Y$)
380 NEXT J
390 GOTO 460
400 PRINT\PRINT "WHAT IS THE DATA FILE NAME?"
410 INPUT N6
420 FILE #1,N6
430 FOR J=1 TO N5
440 INPUT #1,B1(J),B2(J)
450 NEXT J
460 PRINT\PRINT "DO YOU WANT TO USE ALL THE DATA POINTS? Y OR N"
464 INPUT F5$
468 IF F5$="Y" GOTO 550
470 PRINT\PRINT "WHAT IS THE 1ST DATA POINT TO BE USED?"
472 INPUT M1$
474 PRINT\PRINT "WHAT IS THE LAST DATA POINT TO BE USED?"
478 INPUT M2$
480 M1=VAL(M1$)
484 M2=VAL(M2$)
488 N=(M2-M1)+1
490 FOR J2=1 TO N
494 J=J2+M1-1
498 X(J)=B1(J)
500 Y(J)=B2(J)
504 NEXT J2
510 GOTO 600
550 FOR J=1 TO N5
560 X(J)=B1(J)
570 Y(J)=B2(J)
580 NEXT J
590 N=N5
600 PRINT\PRINT "LIMITS FOR THE SEPARATION OF THE 2 LINES"
610 PRINT "ARE IN TERMS OF VALUES OF X"
620 PRINT\PRINT "WHAT IS THE LOWER LIMIT IN X?"
630 INPUT X1$
640 PRINT\PRINT "WHAT IS THE UPPER LIMIT IN X?"
650 INPUT X2$

652 PRINT\PRINT "WHAT IS THE INCREMENT"
654 PRINT "FOR SUCCESSIVE CALCULATIONS?"
656 INPUT C$
680 PRINT\PRINT "DO YOU WANT TO CHANGE THIS? Y OR N"
670 INPUT F6
680 IF F6="Y" GOTO 620
682 PRINT
683 PRINT "DIVISION":TAB(15):"LOW X LINE":TAB(44):"HIGH X LINE"
685 PRINT "POINT SLOPE INCPNT MS RESID DF SLOPE INCPNT MS RESID
DF"
690 X1=VAL(X1$)\X2=VAL(X2$)\C=VAL(C$)
700 X7=X1
702 S1=0\S2=0\S3=0\S4=0\S5=0\S6=0
704 T1=0\T2=0\T3=0\T4=0\T5=0\T6=0
706 B1=0\B2=0\A1=0\A2=0\M1=0\M2=0
710 FOR J=1 TO N
720 IF X(J)<X7 GOTO 800
750 T1=T1+X(J)
752 T6=T6+1
754 T2=T2+X(J)**2
756 T3=T3+Y(J)
758 T4=T4+Y(J)**2
760 T5=T5+Y(J)*X(J)
770 GOTO 812
800 B1=S1+X(J)
802 S6=S6+1
804 S2=S2+X(J)**2
806 S3=S3+Y(J)
808 S4=S4+Y(J)**2
810 S5=S5+Y(J)*X(J)
812 NEXT J
816 IF S6<3 GOTO 829
821 B7=S2-(S1**2)/S6
824 S8=S1/S6
826 S9=S3/S6
828 A1=S9-(B1*S8)
829 IF T6<3 GOTO 852
830 T7=T2-(T1**2)/T6
831 B2=(T5-(T1*T3)/T6)/T7
832 T8=T1/T6
834 T9=T3/T6
836 A2=T9-(B2*T8)
850 M2=(1/(T6-1))*((T4-(T3**2)/T6)-((B2**2)*T7))
851 IF S6<3 GOTO 860
852 M1=(1/(S6-1))*((S4-(S3**2)/S6)-((B1**2)*S7))
860 D1=S6-2
870 D2=T6-2\C3=D1+D2
872 C7=M1+M2
874 IF S6<3 THEN V=M2/T7\GOTO 883
876 IF T6<3 THEN V=M1/S7\GOTO 883
882 V=M1/S7+M2/T7
883 E=SQRT(V)
884 IF B1=B2 THEN T=0\GOTO 900
885 IF B1<B2 THEN D3=B2-B1 ELSE D3=B1-B2
886 T=D3/E
900 PRINT
910 PRINT X7:TAB(5):B1:TAB(13):A1:TAB(21):M1:TAB(29):D1:TAB(34):B2:TAB(4
2):A2:TAB(50):M2:TAB(58):D2
920 PRINT TAB(10):"T = ";T:TAB(22):"D.F. = ";C3:TAB(35):"JOINT MS RESID
UAL = ";C7
940 X7=X7+C
950 IF X7<X2 GOTO 702
9999 END

```


**THESIS
CONTAINS
MICROFICHE**

APPENDIX 2.

Distribution records of A.pallipes
in the Thames Catchment (pre - 1983).



N.B. Records are listed according to watercourse.
Index on top right of 'fiche.

APPENDIX 3

NWC river classification

River Class	Quality criteria	Remarks	Current potential uses
	<p>Class limiting criteria (95 percentile)</p> <p>1A (i) Dissolved oxygen saturation greater than 80%. (ii) Biochemical oxygen demand not greater than 3mg/l. (iii) Ammonia not greater than 0.4 mg/l. (iv) Where the water is abstracted for drinking water, it complies with requirements for A2^{oo} water. (v) Non-toxic to fish in EIFAC terms (or best estimates if EIFAC figures not available).</p>	<p>(i) Average BOD probably not greater than 1.5 mg/l. (ii) Visible evidence of pollution should be absent.</p>	<p>(i) Water of high quality suitable for potable supply abstractions and for all other abstractions (ii) Game or other high class fisheries. (iii) High amenity value.</p>
	<p>1B (i) DO greater than 60% saturation. (ii) BOD not greater than 5 mg/l. (iii) Ammonia not greater than 0.9 mg/l. (iv) Where water is abstracted for drinking water, it complies with the requirements for A2^{oo} water. (v) Non-toxic to fish in EIFAC terms (or best estimates if EIFAC figures not available).</p>	<p>(i) Average BOD probably not greater than 2 mg/l. (ii) Average ammonia probably not greater than 0.5 mg/l. (iii) Visible evidence of pollution should be absent. (iv) Waters of high quality which cannot be placed in Class 1A because of high proportion of high quality effluent present or because of the effect of physical factors such as canalisation, low gradient or eutrophication. (v) Class 1A and Class 1B together are essentially the Class 1 of the River Pollution Survey.</p>	<p>Water of less high quality than Class 1A but usable for substantially the same purposes.</p>
	<p>2 (i) DO greater than 40% saturation. (ii) BOD not greater than 9 mg/l. (iii) Where water is abstracted for drinking water, it complies with the requirements for A3^{oo} water. (iv) Non-toxic to fish in EIFAC terms (or best estimates if EIFAC figures not available).</p>	<p>(i) Average BOD probably not greater than 5mg/l. (ii) Similar to Class 2 of RPS (iii) Water not showing physical signs of pollution other than humic colouration and a little foaming below weirs.</p>	<p>(i) Waters suitable for potable supply after advanced treatment. (ii) Supporting reasonably good coarse fisheries. (iii) Moderate amenity value.</p>
	<p>3 (i) DO greater than 10% saturation. (ii) Not likely to be anaerobic. (iii) BOD not greater than 17 mg/l^{oo}.</p>	<p>Similar to Class 3 of RPS.</p>	<p>Waters which are polluted to an extent that fish are absent or only sporadically present. May be used for low grade industrial abstraction purposes. Considerable potential for further use if cleaned up.</p>
	<p>4 Waters which are inferior to Class 3 in terms of dissolved oxygen and likely to be anaerobic at times.</p>	<p>Similar to Class 4 of RPS.</p>	<p>Waters which are grossly polluted and are likely to cause nuisance.</p>
	<p>X DO greater than 10% saturation.</p>		<p>Insignificant watercourses and ditches not usable, where objective is simply to prevent nuisance developing.</p>
	<p>Note (a) Under extreme weather conditions (e.g. flood, drought, freeze-up), or when dominated by plant growth, or by aquatic plant decay, rivers usually in Classes 1, 2 and 3 may have BODs and dissolved oxygen levels, or ammonia content outside the stated levels for those Classes. When this occurs the cause should be stated along with analytical results.</p> <p>(b) The BOD determinations refer to 5 day carbonaceous BOD (ATU). Ammonia figures are expressed as NH₄.</p> <p>• This may not apply if there is a high degree of re-aeration.</p> <p>•• EEC category A2 and A3 requirements are those specified in the EEC Council Directive of 16 June 1975 concerning the Quality of Surface Water intended for Abstraction of Drinking Water in the Member States.</p>	<p>(c) In most instances the chemical classification given above will be suitable. However the basis of the classification is restricted to a finite number of chemical determinands and there may be a few cases where the presence of a chemical substance other than those used in the classification markedly reduces the quality of the water. In such cases, the quality classification of the water should be downgraded on the basis of the biota actually present, and the reasons stated.</p> <p>(d) EIFAC (European Inland Fisheries Advisory Commission) limits should be expressed as 95% percentile limits.</p>	

APPENDIX 4

'B.M.W.P.' SCORE SYSTEM.

WATERCOURSE :	SAMPLE NO :
SITE :	DATE :

List of BMWP Families Found (enter X in appropriate boxes)

<p>Block 1 Families scoring 10</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,1</p> <p>Siphonuridae <input type="checkbox"/></p> <p>Heptageniidae <input type="checkbox"/></p> <p>Leptophlebiidae <input type="checkbox"/></p> <p>Ephemereididae <input type="checkbox"/></p> <p>Potamanthidae <input type="checkbox"/></p> <p>Ephemeridae <input type="checkbox"/></p> <p>Taeniopterygidae <input type="checkbox"/></p> <p>Léuctridae <input type="checkbox"/></p> <p>Capniidae <input type="checkbox"/></p> <p>Perlodidae <input type="checkbox"/></p> <p>Perlidae <input type="checkbox"/></p> <p>Chloroperlidae <input type="checkbox"/></p> <p>Aphelocheiridae <input type="checkbox"/></p> <p>Phryganeidae <input type="checkbox"/></p> <p>Molannidae <input type="checkbox"/></p> <p>Beraeidae <input type="checkbox"/></p> <p>Odontoceridae <input type="checkbox"/></p> <p>Leptoceridae <input type="checkbox"/></p> <p>Goeridae <input type="checkbox"/></p> <p>Lepidostomatidae <input type="checkbox"/></p> <p>Brachycentridae <input type="checkbox"/></p> <p>Sericostomatidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">25 <input type="checkbox"/> N</p> <p>Block 2 Families scoring 8</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,2</p> <p>Astacidae <input type="checkbox"/></p> <p>Lestidae <input type="checkbox"/></p> <p>Agriidae <input type="checkbox"/></p> <p>Gomphidae <input type="checkbox"/></p> <p>Cordulegasteridae <input type="checkbox"/></p> <p>Aeshnidae <input type="checkbox"/></p> <p>Corduliidae <input type="checkbox"/></p> <p>Libellulidae <input type="checkbox"/></p> <p>Psychomyiidae <input type="checkbox"/></p> <p>Philopotamidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">13 <input type="checkbox"/> N</p> <p>Block 3 Families scoring 7</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,3</p> <p>Caenidae <input type="checkbox"/></p> <p>Nemouridae <input type="checkbox"/></p> <p>Rhyacophilidae <input type="checkbox"/></p> <p>Polycentropodidae <input type="checkbox"/></p> <p>Limnephilidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">6 <input type="checkbox"/> N</p>	<p>Block 4 Families scoring 6</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,4</p> <p>Neritidae <input type="checkbox"/></p> <p>Viviparidae <input type="checkbox"/></p> <p>Ancylidae <input type="checkbox"/></p> <p>Hydroptilidae <input type="checkbox"/></p> <p>Unionidae <input type="checkbox"/></p> <p>Corophiidae <input type="checkbox"/></p> <p>Gammaridae <input type="checkbox"/></p> <p>Platycnemididae <input type="checkbox"/></p> <p>Coenagriidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">12 <input type="checkbox"/> N</p> <p>Block 5 Families scoring 5</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,5</p> <p>Mesovelidae <input type="checkbox"/></p> <p>Hydrometridae <input type="checkbox"/></p> <p>Gerridae <input type="checkbox"/></p> <p>Nepidae <input type="checkbox"/></p> <p>Naucoridae <input type="checkbox"/></p> <p>Notonectidae <input type="checkbox"/></p> <p>Pleidae <input type="checkbox"/></p> <p>Corixidae <input type="checkbox"/></p> <p>Halplidae <input type="checkbox"/></p> <p>Hygrobiidae <input type="checkbox"/></p> <p>Dytiscidae <input type="checkbox"/></p> <p>Gyrinidae <input type="checkbox"/></p> <p>Hydrophilidae <input type="checkbox"/></p> <p>Clambidae <input type="checkbox"/></p> <p>Helodidae <input type="checkbox"/></p> <p>Dryopidae <input type="checkbox"/></p> <p>Elminthidae <input type="checkbox"/></p> <p>Chrysomelidae <input type="checkbox"/></p> <p>Curculionidae <input type="checkbox"/></p> <p>Hydropsychidae <input type="checkbox"/></p> <p>Tipulidae <input type="checkbox"/></p> <p>Simuliidae <input type="checkbox"/></p> <p>Planariidae <input type="checkbox"/></p> <p>Dendrocoelidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">27 <input type="checkbox"/> N</p>	<p>Block 6 Families scoring 4</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,6</p> <p>Baetidae <input type="checkbox"/></p> <p>Sialidae <input type="checkbox"/></p> <p>Piscicolidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">6 <input type="checkbox"/> N</p> <p>Block 7 Families scoring 3</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,7</p> <p>Valvatidae <input type="checkbox"/></p> <p>Hydrobiidae <input type="checkbox"/></p> <p>Lymnaeidae <input type="checkbox"/></p> <p>Physidae <input type="checkbox"/></p> <p>Planorbidae <input type="checkbox"/></p> <p>Sphaeriidae <input type="checkbox"/></p> <p>Glossiphoniidae <input type="checkbox"/></p> <p>Hirudidae <input type="checkbox"/></p> <p>Erpobdellidae <input type="checkbox"/></p> <p>Asellidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">13 <input type="checkbox"/> N</p> <p>Block 8 Family scoring 2</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,8</p> <p>Chironomidae <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">4 <input type="checkbox"/> N</p> <p>Block 9 Class scoring 1</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> B,L,9</p> <p>Oligochaeta <input type="checkbox"/></p> <p style="text-align: right; margin-right: 10px;">4 <input type="checkbox"/> N</p> <p style="text-align: center; margin-top: 20px;">BMWP Score for the Sample</p> <p style="text-align: right; margin-right: 10px;">1 <input type="checkbox"/> S,C,R</p> <p style="text-align: right; margin-right: 10px;">6 <input type="checkbox"/> N</p>
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NON-BMWP FAMILIES FOUND :

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APPENDIX 5

'T.W.A.B.I.' SCORE SYSTEM.

GROUP	FAMILIES	NO
1	Haptogeniidae Leptophlebiidae Ephemerellidae Ephemeridae Siphonuridae Taeniopterygidae Leuctridae Capniidae Perlodidae Perlidae Chloroperlidae Aphaelochairidae Phryganeidae Polanidae Beraeidae Dantoceridae Glossocometidae Coeridae Lepidostomatidae Brachycentridae Sericostratidae	
2	Asteiidae Lestidae Agrilidae Gomphidae Cordulegasteridae Aeschnidae Corduliidae Libellulidae Psychomyiidae Philoptemidae Leptoceridae Tanoceridae	
3	Caenidae Nemouridae Rhacophyllidae Polycentropidae Limnephilidae	
4	Perlidae Viviparidae Ancyliidae Acroloxidae Unionidae Platycentridae Coenagrionidae Cambaridae Crangonyctidae Corophiidae	
5	Resovellidae Hydrometridae Gerridae Nepidae Nephidae Naucoridae Notonectidae Pleidae Corixidae Veliidae Hydropsychidae Hydroptilidae Planariidae Dehydrocolidae Dupesiidae Simuliidae Tipulidae Rhegionidae Beetidae Sialidae Plecoptera Malipidae Cyprinidae Noteridae Dytiscidae Nyctrobiidae Elmidae Hydrophilidae Hydraenidae Scirtidae Dryopidae Chrysomelidae Curculionidae	
6	Velvetidae Hydrobiidae Bithyniidae Lymnaeidae Physidae Planorbidae Sphaeriidae Glossiphoniidae Hirudinae Erpobdellidae Aellidae Ceratopogonidae Empididae	
7	Chironomidae Psychodidae Stratiomyidae Tabanidae Muscidae Lumbriculidae Enchytraeidae	
8	Tubificidae Naididae Syrphidae Ptychoptera	

Y.W.A.B.I. Rev. 5. 8/81

CLASS 1A	minimum requirements	25 families
		1 family from group 1.
1A+	35 or more families - including 5 from group 1.	
1A	36 or more families - including 3 from group 1. 30 to 34 families - including 5 from group 1.	
1A-	35 or more families - including 1 from group 1. 30 to 34 families - including 3 from group 1. 25 to 29 families - including 5 from group 1.	

CLASS 2	minimum requirements	10 families
		2 from groups 1 to 5
2+	25 or more families - including 2 from groups 1 to 5 20 to 24 families - including 6 from groups 1 to 5 15 to 19 families - including 10 from groups 1 to 5	
2	20 to 24 families - including 2 from groups 1 to 5 15 to 19 families - including 4 from groups 1 to 5 10 to 14 families - including 6 from groups 1 to 5	
2-	15 to 19 families - including 2 from groups 1 to 5 10 to 14 families - including 4 from groups 1 to 5	

CLASS 1B	minimum requirements	15 families
		2 families from groups 1,2,3.
1B+	35 or more families - including 2 from groups 1 to 3 30 to 34 families - including 4 from groups 1 to 3 25 to 29 families - including 6 from groups 1 to 3	
1B	30 to 34 families - including 2 from groups 1 to 3 25 to 29 families - including 4 from groups 1 to 3 20 to 24 families - including 6 from groups 1 to 3	
1B-	25 to 29 families - including 2 from groups 1 to 3 20 to 24 families - including 3 from groups 1 to 3 15 to 19 families - including 4 from groups 1 to 3	

CLASS 3	minimum requirements	1 family from groups 1 to 6
3+	11 or more families present	
3	6 to 10 families present	
3-	5 or less families present	

(h)

CLASS 4	Fauna restricted to families from groups 7 and 8

CLASS X	Fauna present inadequate to characterize water quality.

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**THE ENCOURAGEMENT OF FRESHWATER CRAYFISH
POPULATIONS BY ATTENTION TO THE CONSTRUCTION AND
MAINTENANCE OF WATERWAYS**

J. B. HOGGER, MIBiol and R. S. LOWERY, BSc, PhD

INTRODUCTION

FROM THE POINT of view of a biologist a natural watercourse is a place of fascination containing a range of plants and animals and frequently presenting a great diversity of habitats. The primary function of rivers is, however, land drainage so engineers have spent much effort and money reshaping our natural waterways to accommodate their maximum water burdens without overflowing or causing damage. Such reshaping confers considerable benefits on the human community but it frequently leaves deep, smooth banked waterways which can take a considerable time to re-establish their former diversity of animals and plants.

One of the animals that is likely to be particularly hard hit by the creation of smooth banks and river beds is the freshwater crayfish, a small lobster-like animal that may grow up to 9cm in length in the UK. Crayfish are bottom dwelling animals with nocturnal habits and although they are not frequently seen they occur quite abundantly in many British waterways, particularly where the water is hard and clean¹. Figure 1 shows a crayfish sitting in a hole with its claws facing out, the way these animals prefer to spend their days. For this reason they are found most abundantly in watercourses with plenty of hard refuges in the form of stones, rocks, eroded masonry, tree roots, sunken boats, and such like.

In the past river engineers have often lined waterways with wooden piles and jointed masonry or brickwork and as the joints gradually eroded crayfish came to occupy the holes; no doubt they contributed to the erosion! A particularly good example of such a situation is a nineteenth century waterworks channel, in the north of England, which is lined with eroded masonry in the form of limestone blocks. When the channel is drained crayfish appear from all the crevices only to return when the water is replaced².

An investigation of the distribution of crayfish in the area covered by the Thames Water Authority was undertaken to discover, among other things, whether crayfish are at present more or less abundant than previously. The consensus of opinion seems to be that they are currently less abundant and that they have disappeared from some waters but unfortunately reliable and precise information concerning past abundance is not readily available. Some people have even suggested that the native British crayfish, *Austropotamobius pallipes*, is almost extinct³ but this is clearly not the case. If a reduction in numbers has occurred then several factors, or a combination of these, might be responsible.

In the first place all crayfish native in Europe are susceptible to a lethal disease known as 'crayfish plague' and caused by the fungus *Aphanomyces astaci*. The occurrence of this disease has not been confirmed in the UK but is known to have been responsible for the widespread devastation of crayfish stocks in mainland Europe; probably being introduced on infected North American crayfish late in the last century⁴.

This paper was received on 10th December 1981 and accepted for publication on 9th February 1982. Mr Hogger is with Thames Water Authority and Dr Lowery is with the City of London Polytechnic.



Fig. 1. Freshwater crayfish *Austropotamobius pallipes*

Secondly water pollution may have taken its toll. Crayfish are normally thought to require clean, well aerated water of the sort that is found in chalk and limestone streams. They may also be found, however, in slow flowing canals and rivers, lakes and reservoirs if suitable habitat is available¹.

Thirdly crayfish may have been subjected to excessive fishing as they are good to eat and can command high prices in the restaurant and fish trades^{5,6}. The native British crayfish, *A. pallipes*, grows slowly and takes three years, or more, to reach reproductive maturity and even longer to reach marketable size, so that over-exploited stocks recover very slowly. This problem may be exacerbated because many people cannot differentiate between males and females, except when the latter are carrying eggs, so potentially reproductive animals are removed.

Lastly a reduction in numbers and distribution of crayfish may have been caused by the destruction of suitable habitat in the course of river engineering works. Crayfish like their waterways to have rough sides and bottoms and do well where there are creviced impediments and a swift flow that removes silt but these features are not usually those desired by river engineers.

There are many reasons why crayfish thrive in environments providing holes for refuge. They are primarily nocturnal animals and like to occupy dark niches during the day. They must also have refuge from predators such as fish, birds, and man; particularly in the case of juveniles which provide excellent food for fish. In addition crayfish need a refuge in order to grow, which they do by moulting. In common with other crustaceans crayfish can only grow by shedding their hard external skeleton, swelling to increase in size while out of this natural corset and then reforming a hard shell as soon as possible for protection. During moulting the animal changes dramatically from a well armoured individual to a soft flabby animal that is highly vulnerable to both predators and cannibalism. Particularly during the moulting period, therefore, it is essential that there should be sufficient hides available to avoid confrontation between individuals otherwise those animals not in the moult will eat their less fortunate fellows.

For these reasons it is not possible to maintain a dense population of crayfish unless there are abundant crevices of all shapes and sizes to accommodate both large and small individuals.

During 1978 the new flood relief works on the river Lee at Ware in Hertfordshire were identified as a site where the impact of river engineering works on crayfish populations could be examined. This part of the river is well known for its substantial populations of crayfish but no precise data were available on the actual numbers present nor on the way in which numbers might have fluctuated in past years. To try and assess the effect of more routine engineering operations on crayfish a site on the river Beane near Hertford where large numbers of crayfish were being disturbed during a routine maintenance dredging operation was investigated during May 1981.

WARE FLOOD RELIEF SCHEME

During the period 1974-1976 the river Lee at Ware was subject to extensive flood relief works. The main channel of the river was dredged and many new works were carried out including the sheet piling of sections of river bank. One of these engineering projects consisted of a flood relief overflow weir, syphon, and weir basin at Ware Lock, an area notable for crayfish. Figure 2 shows the layout of the new weir and basin in relation to the existing structures. Although there were extensive alterations and additions to the new site neither the lock nor the old lock bypass channel upstream of the site were interfered with; thus old crayfish habitats remained relatively undisturbed.

When the investigations started the new weir and the artificially protected basin below it had been in operation for about 18 months. Before this, trapping upstream of the weir had yielded crayfish. During July/August 1979 crayfish were found at sites all round the new basin and since that time substantial numbers have been caught regularly. Crayfish were collected, using baited 'lobster-pot' type of traps set overnight, then measured and marked using a standard branding technique⁷ before being returned to the water.

Apparently colonization of the new weir basin had taken place inside the 18 months that the weir had been operating. However, it was not known if this was a stable population or one composed of individuals which were simply moving through the basin; nor was it known how many animals were present and at what density. To answer the first point individual crayfish were marked permanently for day and location (zone) and recaptured crayfish were subsequently examined some months later. It was clear from the results obtained (Table I) that the majority of animals were resident in the basin and that the population was breeding, because an average of 55% of the females captured during the winter were carrying eggs.

In order to obtain an estimate of the population size the method of capture, mark, release and recapture was used on three nights during September 1980, and again during May 1981. The ratio of marked and unmarked crayfish in subsequent trapping permits an estimate of numbers to be made. Only crayfish of 'trappable size' are thus estimated and it is not possible to determine the numbers of juveniles under two years old that are growing up to reinforce the population. These smaller animals will not enter the crayfish traps and cannot be marked. The results of this exercise are given in Table II. Due to the size and pattern of water flow in the new basin it was possible to sample from only about half of its total area (approx. 1200m²) so the results obtained should be doubled for the whole of the basin. This gives an estimate of approximately 2.5 adult crayfish per square metre of the basin.

The method of estimating crayfish numbers using trap, mark, and recapture is far from ideal and independent tests of the method have shown that the figures obtained will usually be gross underestimates⁹. However the only accurate way of estimating numbers

TABLE I SUMMARY OF CATCH DATA FOR *A. Pallipes* AT WARE LOCK

Date	Total catch	Recaptures: same zone	Moved to adjacent zone	Moved more than one zone	Number of traps	Catch/trap
1.8.79	56	0	0	0	28	2.00
12.10.79	113	2	0	0	28	9.03
24.1.80	76	2	0	0	23	3.0
3.4.80	98	7	0	0	25	4.08
18.6.80	513	18	8	3	39	13.15
On the following dates traps were only set in the weir basin						
14.9.80	362	39*	1	0	40	9.05
16.9.80	594	67	1	0	40	14.85
18.9.80	458	N/D	N/D	N/D	40	11.45
2.5.81	472	N/D	N/D	N/D	40	11.80
5.5.81	279	N/D	N/D	N/D	40	6.97
8.5.81	352	N/D	N/D	N/D	40	8.80

*Recaptured from previous visits

is to drain and collect the crayfish¹⁰ which was obviously impossible at this site. Nonetheless these data indicate that there had been considerable colonization of the new weir basin within 18-24 months; it is intended to continue monitoring this population.

EFFECTS OF DREDGING OPERATIONS

During May 1981 part of the river Beane just outside Hertford was dredged as part of the normal maintenance dredging programme carried out by Thames Water Authority. At the site which was investigated a border of marginal plants (mainly *Glyceria maxima*, 'Reed Sweet Grass') was removed from one bank of the river and soft silt was dredged from the whole width of the river bed, using a bankside excavator with 0.5m³ bucket.

TABLE II SUMMARY OF MARK-RECAPTURE DATA: WARE LOCK

Date		Male	Female	Total
14.9.80	New marks (A)	200	162	362
16.9.80	New marks (B)	215	237	452
	Recaptures (A)	84	58	142
	Total caught	299	295	594
18.9.80	Recaptures (A)	52	47	99
	Recaptures (B)	64	69	133
	Total caught	222	236	458
2.5.81	New marks (A)	358	114	472
5.5.81	New marks (B)	149	52	201
	Recaptures (A)	61	17	78
	Total	210	69	279
8.5.81	Recaptures (A)	56	26	82
	Recaptures (B)	28	8	36
	Total caught	232	110	342

The normal practice of the operator carrying out the dredging was to 'rinse' crayfish from the plant material as he removed it by dunking it in the river. On the initial visit one of the authors with the co-operation of the dredger operator, examined samples of rinsed and unrinsed material. Quite large numbers of crayfish were being affected by the dredging so a further joint visit was made and three sample dredges were examined in more detail. In this case the unwashed extracted plants were deposited on a plastic sheet and about 30min spent collecting crayfish from each sample. The numbers collected are presented in Table III. The unexpectedly large numbers of crayfish found living amongst

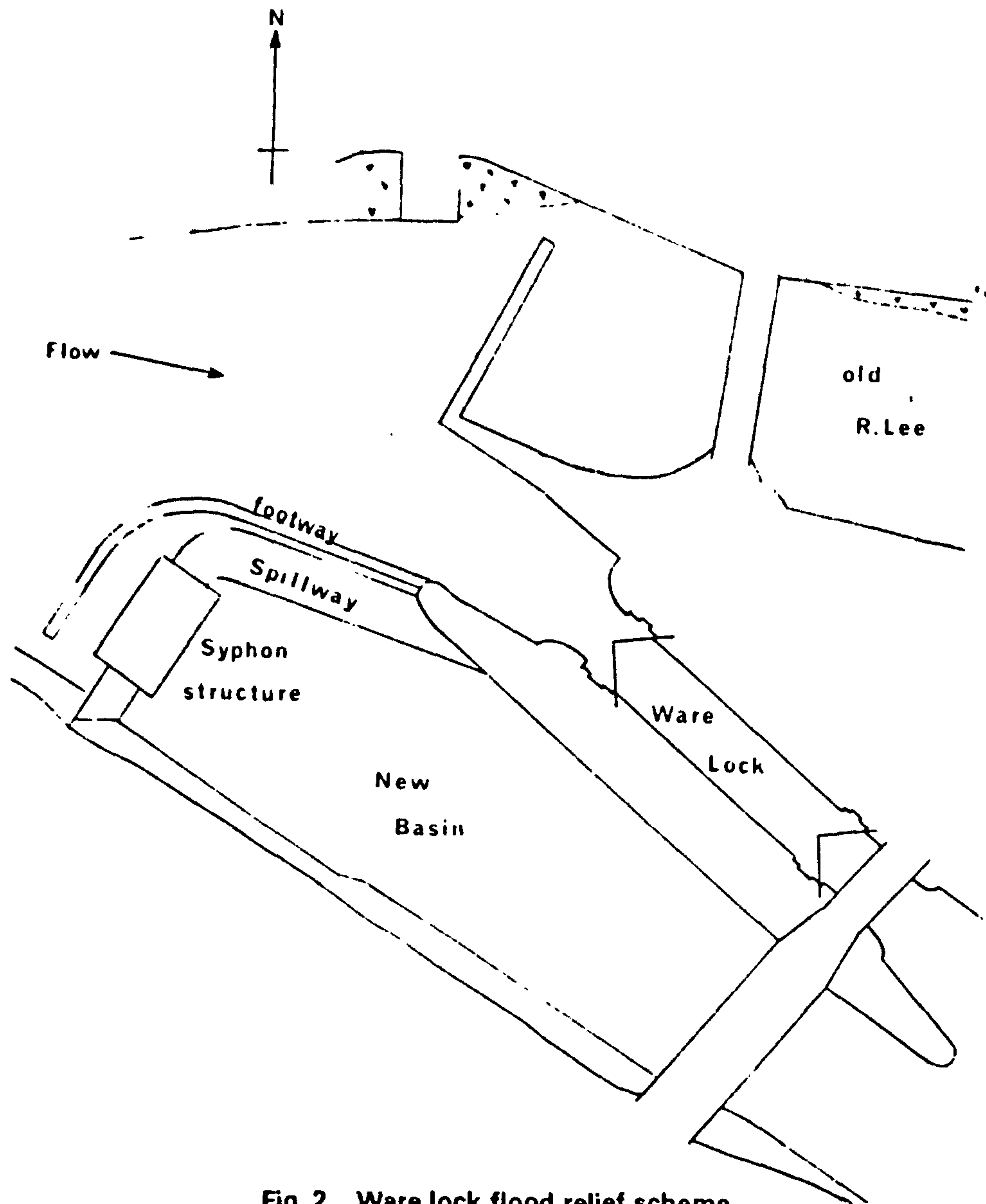


Fig. 2. Ware lock flood relief scheme

the plant roots along this stretch of river imply that crayfish could be more widespread than is commonly thought and occur in what would often be thought of as unsuitable rivers. Obviously where crayfish occur a large proportion may be removed by routine maintenance dredging. How many of these are subsequently able to return to the river remains to be investigated, but apparently the method of dredging normally used by this particular operative effectively reduces the number of crayfish removed by about 35%.

CONSTRUCTION IMPLICATIONS OF THESE RESULTS

It is suggested that the mode of construction of the new weir basin is a factor contributing to the successful colonization of the site by crayfish. The southern embankment of the basin and sections of the bed are lined with rock filled gabions and the remainder of the bed is covered with granite rubble. Such a substrate with its many and various sized holes provides an excellent habitat for these animals. In fact when crayfish are being commercially cultured they must be provided with a similar substrate¹¹.

In the case of Ware Weir this method of construction was not chosen with the object of improving the environment for crayfish or for any other aquatic organism. The authors would suggest that, where appropriate, the use of construction techniques which provide a creviced substrate should be adopted, especially in places where it is known that crayfish are present, and that after the construction of rough based water bodies native crayfish could be introduced by water authorities in an attempt to encourage the spread and recolonization of this species.

The examination of dredged plant material from the Beane showed that very large numbers of crayfish may be removed during routine maintenance dredging. The destruction of their habitat must also have a drastic effect on the crayfish population, and recolonization of such areas will be slow. If, whenever possible, washing of dredged material containing crayfish can be carried out the numbers removed can be greatly reduced. Those animals returned to the river in this way then at least have the option of migrating to find new habitat. If only one bank of the river is affected by dredging, as in this case, their journey may need only be across the river. Alternatively any new structures built during the course of a flood alleviation scheme, or for routine bank maintenance, could be designed to cater for the needs of the crayfish at no extra cost.

Such a policy of constructing and maintaining waterways to accommodate the needs of animals is not without precedent, particularly where economic factors are involved. Salmon ladders are one good example; another is the recent reconstruction by Thames Water of the channel of the river Roding at Abridge in Essex to provide fish habitats in an area where angling is important. There is considerable interest in crayfish as food so perhaps in the long term there might be some economic arguments for encouraging the growth of crayfish populations by the provision of rough surfaced channels using broken rock and similar low cost materials.

TABLE III CRAYFISH REMOVED BY DREDGING: RIVER BEANE, HERTFORD .

Date		Male	Female	Juveniles*	Total	Mean
6.5.81	Unwashed sample	—	—	—	44	—
	Washed sample	—	—	—	28	—
8.5.81	Sample 1	36	48	3	87	92
	Sample 2	54	74	9	137	
	Sample 3	19	24	8	51	

*The sex of juveniles can not easily be determined

ACKNOWLEDGEMENTS

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REFERENCES

1. Jay, D. and Holdich, D. M. 1981 *Freshwater Biol.* 11, 121, 'The distribution of the crayfish *Austropotamobius pallipes* in British waters'.
2. Brown, D. J. and Bowler, K. 1976 in 'Freshwater crayfish III' (ed. O. V. Lindqvist) 'A population study of the British freshwater crayfish *Austropotamobius pallipes*'.
3. *Salmon and Trout Mag.* 1976, 208, 28, 'Bring back the crayfish to Britain'.
4. Unestam, T. 1972 in 'Freshwater crayfish I' (ed. S. A. Abrahamsson) 'Significance of diseases in freshwater crayfish'.
5. Rhodes, C. and Holdich, D. M. 1979 *Aquaculture* 17, 345 'On the size and sexual dimorphism in *Austropotamobius pallipes*. A step in assessing the commercial exploitation of the native British freshwater crayfish'.
6. Goddard, S. and Holdich, D. M. 1979 *Fish Farmer* 2, 47 'Explore the native potential first'.
7. Abrahamsson, S. A. A. 1965 *Oikos* 16, 228 'A method of marking crayfish *Astacus astacus* (L) in population studies'.
8. Ricker, W. E. 1975 *Bull. Fish Res. Bd. Can.* no. 191, 'Computation and interpretation of biological statistics of fish populations'.
9. Brown, D. J. 1979 PhD Thesis, Durham, 'A study of the population biology of the British freshwater crayfish *Austropotamobius pallipes*'.
10. Brown, D. J. and Brewis, M. 1978 in 'Freshwater crayfish IV' (ed P. J. Laurent) 'A critical look at trapping as a method of sampling a population of *Austropotamobius pallipes* in a mark and recapture study'.
11. Karlsson, S. 1977 Proc. 9th 2 Lakes Fishery Training Course, Janssen Services, London.

APPENDIX 7. A KEY TO THE IDENTIFICATION OF EUROPEAN SPECIES
OF THE GENUS BRANCHIOBELLA (ANNELIDA : CLITELLATA).

(TRANSLATED FROM UDE, 1929)

1. JAWS TRIANGULAR - 2
 JAWS 4 OR 5 TOOTHED - 3

2(A) JAWS EQUAL IN SIZE, WITH ONE LARGE MIDDLE TOOTH
 AND THREE SMALL(ER) TEETH ON EACH SIDE. (FIG.1)

$\frac{3\ 1\ 3}{3\ 1\ 3}$

- BRANCHIOBELLA PARASITA.

(B) DORSAL JAW LARGER THAN VENTRAL. ONE LARGE MIDDLE TOOTH
 AND RUDIMENTARY OR ABSENT SIDE TEETH. (FIG.2)

$\frac{0\ 1\ 0}{0\ 1\ 0}$

- BRANCHIOBELLA ASTACI.

3(A) JAWS EQUAL IN SIZE. FIVE TOOTHED, WITH ONE LARGE
 MIDDLE TOOTH AND TWO SMALLER TEETH ON EACH SIDE. (FIG.3)

$\frac{2\ 1\ 2}{2\ 1\ 2}$

- BRANCHIOBELLA PENTODONTA.

(B) JAWS EQUAL IN SIZE. FOUR TOOTHED, WITH ONE LARGE
 TOOTH ON EACH SIDE AND FOUR AND THREE MIDDLE TEETH
 ON THE DORSAL AND VENTRAL JAWS RESPECTIVELY. (FIG.4)

$\frac{1\ 4\ 1}{1\ 3\ 1}$

- BRANCHIOBELLA HEXONDONTA.

Fig.1

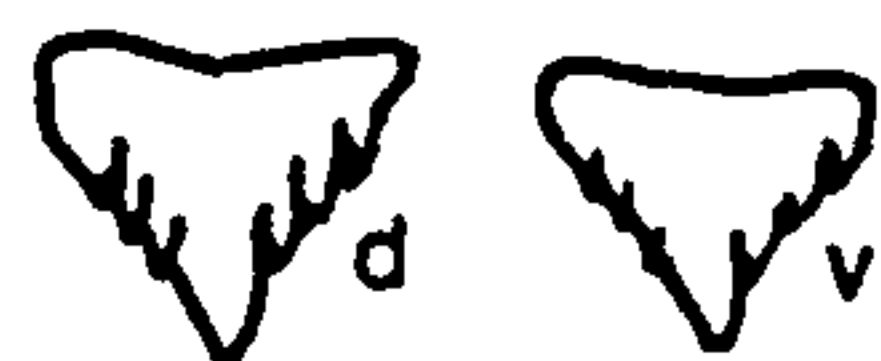


Fig.2

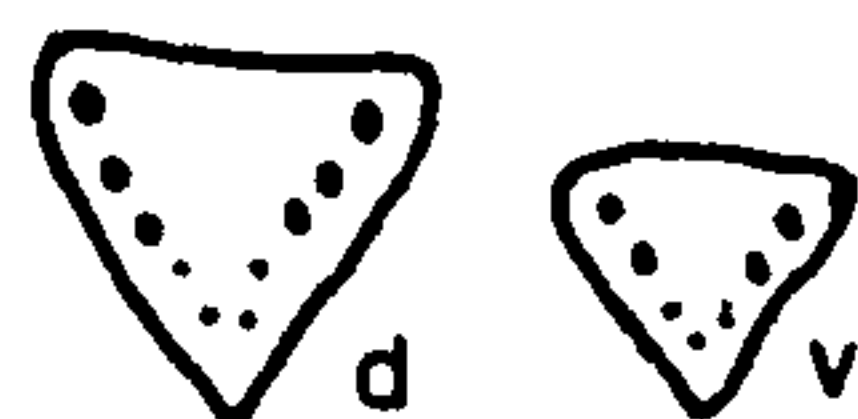


Fig.3



Fig.4



After Ude, 1929.

APPENDIX 8.

Locations in the Thames Catchment from which *A.pallipes* infested with *Branchiobdella astaci* have been collected. 1980 - 1983.

<u>Watercourse</u>	<u>Grid Ref.</u>	<u>Date</u>
R. Cherwell	SP478249	13.7.82
R. Dun	SU291682	9.9.80
R. Enborne	SU557633	4.9.80
" "	SU570649	"
" "	SU476640	27.8.80
" "	SU470637	"
" "	SU507634	"
R. Eye	SU152242	30.10.80; 9.9.81
R. Lambourn	SU453692	8.1.70 †
" "	SU415726	26.2.80
R. Kennet *	SU490671	16.10.69 †
" "	SU277716	11.2.81
Oxford Canal(s)	SP465503	3.11.81
" "	SP487227	7.7.83
R. Whitewater	SU738548	17.8.82

*see also Leeke & Price, 1965

† Preserved specimens - I.M.

N.B. In addition *A.pallipes* from 23 other sites (n = 2 - >100) were examined and found to be free from infestation.

APPENDIX 9.

Known sites of introductions of *P. leniusculus* in the Thames Catchment. (pre 1983)

1. Stratfield Saye, Hants	SU711619	19. Nr. Dorking, Surrey	TQ180480
2. Colnbrook, Middx.	TQ011758	20. Denham, Bucks	TQ030860
3. Hartley Wintney, Hants	SU748573	21. Chipping Norton, Oxon	SP320260
4. Effingham, Surrey	TQ115553	22. Northwood, Middx.	TQ080900
5. Clandon Park, Surrey	SU040522	23. Furneaux Pelham, Herts	TL420270
6. Theale, Berks	SU624693	24. Nr. Basingstoke, Hants	SU680520
7. Beaconsfield, Bucks	SU943890	25. Nr. Pangbourne, Berks	SU640740
8. Wallingford, Oxon	SU602918	26. Woodstock, Oxon	SP420140
9. Nr. Pangbourne, Berks	SU654770	27. Nr. Swindon, Wilts	SP120960
10. Shamley Green, Surrey	TQ040452	28. Nr. Reading, Berks	SU800780
11. Nr. Newbury, Berks	SU445693	29. Nr. Godalming, Surrey	SU990390
12. Nr. Marlborough, Wilts	SU213695	30. Amersham, Bucks	SU960960
13. Chaddleworth, Berks	SU412779	31. Chesham, Bucks	SP970010
14. Haslemere, Surrey	SU900340	32. Berkhamstead, Bucks	TL020060
15. Nr. Crawley, Sussex	TQ290350	33. Nr. Wheatley, Oxon	SU680990
16. Nr. Bicester, Oxon	SP550240	34. Nr. Wantage, Oxon	SU420860
17. Nr. Hertford, Herts	TL290063	35. Stansted Abbots, Herts	TL400100
18. Liphook, Hants	SU830320	36. Nr. Cheltenham, Glos	SP020150