A study of reproductive females of the freshwater crayfish *Austropotamobius pallipes*

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Abstract

Details of the female annual reproductive cycle in the population from Northumberland are given. Mating occurs in October and is followed by egg laying in early November. Eggs are carried by females until the following July-August when hatching occurs. The smallest 'berried' female caught was 25 mm carapace length (C.L.) and this was chosen as the minimum size for adult females. Only 40–50% of adult females, hand-caught, were 'berried' in the Spring following egg laying; but this percentage was low largely because few females in the size classes below 28 mm C.L. were 'berried'. The reasons for adult females being non-reproductive in a year are discussed.

Introduction

There has been a resurgence of interest in the native species of freshwater crayfish, *Austropotamobius pallipes* (Lereboullet, 1858), stimulated in part by its increased commercial use by fish farmers. This use, unfortunately, has almost exclusively relied on the importation of exotic species, notwithstanding attendant dangers (Unestam, 1975).

However, Thomas & Ingle (1971) and Holdich, Jay & Goddard (1978) have recently provided some information on the status and distribution of the native species in the British Isles. Similarly, Bowler and co-workers have reported on growth rates (Bowler & Brown, 1977; Brewis & Bowler, 1982) in a natural population in Northumberland, and Pratten (1980) carried out a growth study on a more southern population. Brewis & Bowler (1983) have also reported on the population dynamics of the species in their study area. Nevertheless, several details of the biology of the native species remain unclear. Thus, quantitative information on the reproductive pattern and fecundity of *A. pallipes* is still insufficient. Only in the reports of Rhodes & Holdich (1982), and Thomas & Ingle (1971) is the reproductive state of females in natural populations considered. The extensive study carried out by Brewis & Bowler (1982, 1983) on a population of crayfish in Northumberland permits a more detailed report on adult female crayfish to be made and this is the purpose of this communication.

Methods

The population of this study inhabits a stretch of aqueduct feeding Hallington Reservoir East in Northumbria, part of the North Tyne catchment area. The study area is described in Brewis & Bowler (1983). The data presented were collected during a 3 year study using mark-recapture techniques. The marking system used is described in detail in Brewis & Bowler (1983). It was possible to follow the fate of an individual animal through two successive moults and, as marks could be reinforced on recapture, some individuals were followed for two or more years. Crayfish were collected by hand and the use of baited traps was not found to be

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Table 1. Numbers of reproductive females in hand fished samples 1977–79.

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

suitable for collecting 'berried' females as they are trap-shy (Brown & Brewis, 1979).

Over the three year period of the study several thousand adult females were so sampled (Table 1), and the smallest size class found to be 'berried' was 25 mm C.L. and so, for the purpose of this study, that size was assumed to be the size at which female sexual maturity was attained.

Results

The female reproductive year

Mating of crayfish in Northumbria occurs in late October. Fertilised females were first identified in samples on 22nd and 29th October 1978, 18th and 25th October, 1979. Eggs are laid within two weeks of fertilisation, and they are extruded into a mass of viscous matter ('glair'). Over winter, 'berried' females are secretive in their behaviour, probably becoming torpid in deep hides, for very few occur in hand-fished samples. Females carrying hatched young were first seen on 12th August 1977, 10th August, 1978 and 9th August 1979. The hatchlings remain attached to or near their mother for 2–3 weeks during which time they moult twice (Thomas, 1973).

Numbers of reproductive females and fecundity

The number of females, of reproductive size (25 mm C.L. and greater), captured in the years 1977–9 is shown in Table 1. The proportion of 'berried' females lay between 40 and 50% until sampling dates approached the period of egg hatching when, understandably, the percentage 'berried' fell.

Presenting these data in this way obscures a marked dependency of the likelihood of a female being 'berried' on her size. This relationship is shown in Figure 1. In females of carapace length >33 mm it is common to find 70–80% 'berried' in early Spring. Females of smaller size classes are less likely to be 'berried' and very few in the smallest size-class (25 mm C.L.) were 'berried'.

'Berried' females were collected from other sites and the number of eggs carried as a function of carapace length was determined, the results are shown in Figure 2. The number of eggs carried typically varied between 40–80. The largest number of eggs counted was 113 on a female of 37.0 mm carapace length, and larger individuals in the study population almost certainly bore more. Throughout the study females were occasionally found with far fewer eggs than would be expected for their size.

Female reproductive histories

The data shown in Figure 3 consider whether a

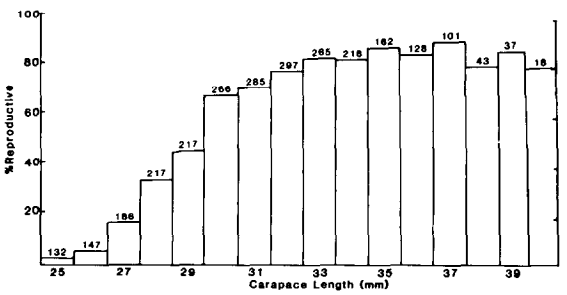

Fig. 1. Histogram showing the proportion of females in reproductive condition in hand-caught samples as a function of female size. The numbers heading each column are the sample sizes.

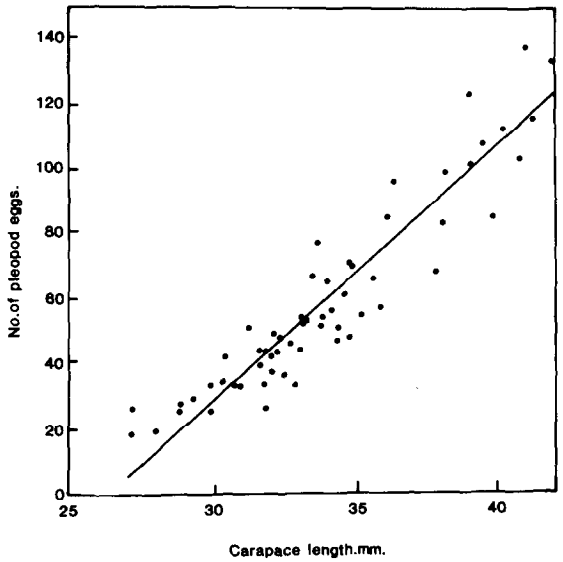

Fig. 2. Relationships between number of pleopod eggs carried as a function of carapace length for reproductive female *A. pallipes*. (y = 7.87x - 207.17, where y = No. of eggs and x = carapace length; n = 59.)
S.E. of slope = 0.41; r = 0.93; p = < 0.001.

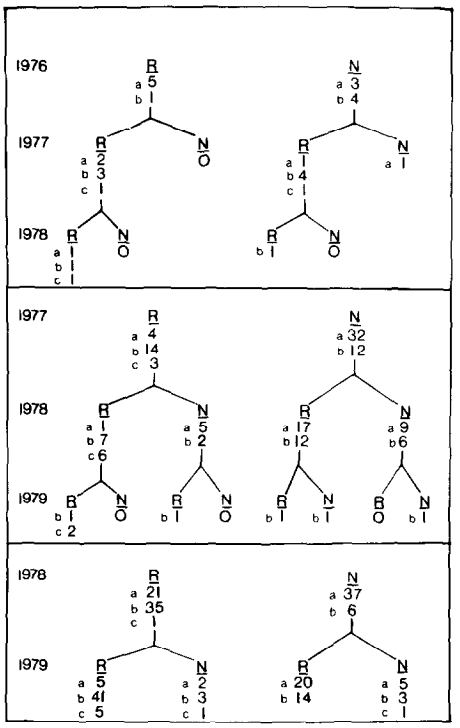

Fig. 3. The reproductive histories of individual female crayfish. (R = numbers of reproductive and N = numbers of non-reproductive females in the size-classes, a < 32 mm, b 32–37 mm and c > 37 mm carapace length).

female's reproductive history influences her reproductive future. A number of points can be raised. First, in agreement with data shown in Figure 1, females in the smaller size class (group a) are less likely to breed. Secondly, some 80% of females 'berried' in year 1 of a sequence are also 'berried' in year 2. Although the sample size is small it is clear a good proportion (about 20%) have bred in three successive years. This is likely to be an underestimate because not all 'berried' females in the total population were caught. The sample sizes in the third year will also be smaller because of female mortality at the moult and overwinter between year 2 and 3 of the sequence.

It is also unlikely that a female will be non-reproductive in two successive years, for some 70% of those non-reproductive in year one were 'berried' in year 2 of a sequence. It is not uncommon for a female to miss two breeding years. In one case only, was a female non-reproductive for three successive years. This female was in the smallest size class (group a) for 1977 and 1978, but was in group b size class in 1979, and so the non-reproductive status may reflect her small size.

Discussion

Data on the reproductive year of *A. pallipes* are sparse. In more southern populations mating and egg-laying occurred about one month earlier than in the Northumberland population, Thomas & Ingle (1971). Hatching was even more advanced in populations in Kent and the Midlands where it occurred in mid-June as compared with mid-August in Northumberland (Thomas & Ingle, 1971; Holdich, Jay & Goddard, 1978; Pratten, 1980). The earlier hatching in more southern populations is probably a cummulative result of warmer water temperatures in Spring and early Summer. The reason for the different mating dates in Autumn is less obvious; water temperature differences may be involved but a timing mechanism, by changes in day length, cannot be excluded.

Both biological and physical factors may be involved in determining whether a female will breed in any one year (Abrahamsson & Goldman, 1970).

Entry into sexual maturity in some females may occur at a smaller size than in other females. However the growth characteristics suggest in this population that sexual maturity occurs when the females are between 22 and 27 mm C.L. in size. It seems unlikely that larger sized females are not mature, but even at 29 mm C.L. less than 50% of the females caught were 'berried'. Males may have a preference to mate with larger females. As a mating strategy this would appear adaptive for as large females produce more eggs, the male will increase the chance of the survival of his genes. Very little is known of these aspects of crayfish mating behaviour and the following questions can be posed: (1) Can and do males mate with more than one female?, (2) Are females promiscuous?, (3) Is there size-selection by males for mating? and (4) Do large males prevent smaller males from mating? Crayfish mating behaviour is complex but the significance of these factors in mating success are not known.

Abrahamsson (1972, 1973) found in colder waters the percentage of smaller *A. astacus* in 'berry' was lower than in warmer waters, although this effect on the proportion of females reproductive was not evident in largest size classes. Water temperature may well be a dominant factor in female breeding success in European crayfish (Abrahamsson, 1972) and it is of interest that Lowery & Mendes (1977) found that the normal seasonal breeding pattern in *Procambarus clarkii* was lost when this species was introduced into the warm waters of Lake Naivasha in Kenya. It would be of interest to know if the same distribution of reproductive and non-reproductive females is found in more Southern, warmer waters, for the possible effect of temperature on breeding in small females might be established.

The existence of non-breeding mature females seems to be a common feature of crayfish populations (Kossakowski, 1971; 1975) and in attempting to offer explanations for it the following consequences ought to be considered. A 'berried' female can moult once a year in September after egg-hatching, and the moult increment achieved is smaller than that of a similar sized non-reproductive female. This growth differential is most marked in smaller size classes and may be not evident in large females (Brewis & Bowler 1982). This differential growth pattern between females suggests a possible stress factor is operating, but with greater severity on smaller females. Egg production may become a progressively diminishing cost to the individual with increasing age. In the terms of Gadgil & Bossert (1970), in an iteroparous species it becomes more advantageous to breed with increasing age.

If rapid growth to a large size is advantageous to a female in mate-selection and/or in withstanding nutritional demands of egg production, then a conflict of strategy to a female capable of breeding is apparent. It may be resolved, as the data in Figure 2 suggest, by smaller females being less likely to breed in successive years and by larger females 'dropping out' in occasional years.

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