BURROWING BEHAVIOUR OF SIGNAL CRAYFISH, *PACIFASTACUS LEMJUICUUJS* (DANA), IN THE RIVER GREAT OUSE, ENGLAND

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Introduction

The burrowing behaviour of numerous species of crayfish has been widely reported for *Cambarus* (Audubon 1839; Girard 1852; Bundy 1882; Tarr 1884; Shufeldt 1896; Engle 1926; Hobbs & Hart 1959; Hobbs 1969; Williams et al. 1974; Grow & Merchant 1980; Grow 1981, 1982; Rogers & Huner 1985), *Orconectes* (Payne & Price 1981; Hasiotis 1993a,b), *Procambarus* (Lyle 1936, 1937; Payne 1972; Huner & Barr 1981) and *Astacoides* (Frost 1974). However, burrowing has not been observed for *Pacifastacus,* and the wide-ranging and apparently less ecologically restricted North American signal crayfish *Pacifastacus leniusculus* is believed to be a non-burrowing species (Shimizu & Goldman 1983; Hogger 1988).

Pacifastacus leniusculus (Dana) is native to north-western North America (see picture on front cover). It grows rapidly to a relatively large adult size and this had led to increased interest in its stocking and culture in Britain. Soon after its introduction from Sweden in 1976, thousands of imported juvenile crayfish were distributed to several hundred sites, where some established breeding populations (Hogger 1986a,b; Lowery & Holdich 1988; Holdich & Reeve 1991). One such population was established in the River Great Ouse, Buckinghamshire, England, in 1984. By 1989 large numbers of mature crayfish were commercially trapped annually and many crayfish were observed living in burrows in the mud banks of the river (Fig. 1). This was especially noted when the water was disturbed and crayfish came out and stayed at the opening of the burrows. As signal crayfish have always been considered as non-burrowing animals, their behaviour raises the questions: were these burrows excavated by other animals or by the signal crayfish, and if the crayfish

FIG. 1. Burrows of signal crayfish in the banks of the River Great Ouse. *Above*: Burrows at and below the waterline. *Below*: Collapse of the bank caused by crayfish burrows.

did excavate the burrows what is the extent and capability of their burrowing? Since 1993 I have carried out field investigations and laboratory experiments in order to determine the main aspects of burrowing behaviour of this species. Some results and conclusions of general interest are briefly summarised here.

Study sites

In Buckinghamshire, the River Great Ouse used to be dominated by the native British white-clawed crayfish *Austropotamobius pallipes* (Lereboullet), of which the verified last sighting was in 1981. The present

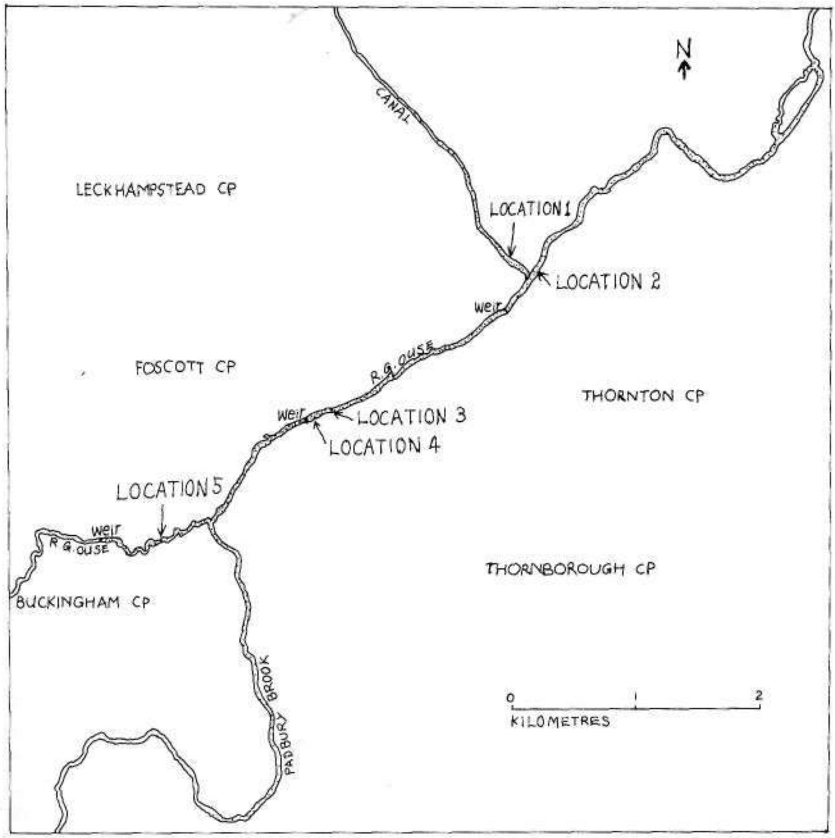

FIG. 2. Map of the River Great Ouse in Buckinghamshire, showing five locations investigated for burrows of introduced signal crayfish (*Pacifastacus leniusculus*). Dotted portions indicate the section of river occupied by crayfish in 1994. CP = Civil Parish.

population of signal crayfish was established in 1984, when ca. 100 summerling and 40 larger crayfish were released at Thornborough Mill. Since then the population has grown rapidly and spread up and down the river to occupy ca. 11 kilometres of river by June 1994 (Fig. 2).

After some general observations had been made on crayfish burrows in the occupied sections of river, five locations were chosen for further investigation (Fig. 2). Location 1 was a 360-metre stretch along a small canal which joins the River Great Ouse near Thornton Bridge (map reference: OS 752364). In summer the canal was 1.5-2 m wide and 10-25 cm deep along this stretch. The bottom was compact sand and gravel with a few pebbles and cobbles. The west bank was mainly mud and clay while the east bank was mainly sand and gravel. Locations 2 (OS 752364) and 5 (OS 719344) were very similar physically. Both comprised 100 m stretches of the main river, 13-16 m wide and 20-120 cm deep with mud banks and bottom. Location 3 (OS 735353) was also a 100 m stretch of the main river, 15 m wide and shallow on the south side (10-20 cm deep) whilst deep on the north side (80 cm). The south bank was sand and gravel whilst the north bank was silt and clay. The compact bottom consisted of sand, gravel and pebbles. Location 4 (OS 736353) had a platform-like clay bottom, 30-40 cm under water, 8 m wide and 20 m long, and connected to location 3 by a pool 2-4 m deep on the right-hand side.

Density of crayfish burrows in the river

Numerous crayfish burrows (upper Fig. 1) were observed within the 11 km river section occupied by signal crayfish. Burrows above the water-line in summer were not inhabited (n = 20) and were apparently excavated by crayfish in winter when the water level was high. Therefore, only the burrows under the water surface were taken into account when calculating the density of burrows. For this the number of crayfish burrows was counted and averaged for the submerged banks on both sides in locations 1, 2, 3 and 5 and in the clay platform of location 4. The density at each location was then calculated from the total number of burrows in both banks, divided by the total length of both banks, irrespective of whether burrows were present or not.

The burrow density declined with distance from the original site of release (Thornborough Weir) both upstream and downstream. The estimated density of crayfish burrows was 0.47 per metre of bank in location 1 (predominantly in the west bank) and 3.6 per square metre in location 4 (clay platform). The estimated densities of crayfish burrows in the banks of the main river were highest in the original release site (5.6 per metre, location 3), intermediate in location 2 (3.7 per metre) and lowest in location 5 (2.8 per metre).

The relative abundance of crayfish (catch per unit effort, CPUE) in locations 2, 3 and 5 was estimated by setting three baited traps at 45 m intervals in the afternoon and emptying them the following morning; this was repeated for three consecutive nights. Here, CPUE is the mean number of crayfish caught per trap per night. The purpose of these estimates was to document the relationship between the density of burrows and the relative abundance (CPUE) of crayfish. In fact the burrow density was not significantly correlated with the CPUE (Fig. 3) ($p > 0.05$). This may be due to several factors, such as small sample size, differences in natural shelter available, and CPUE may not well represent the crayfish density.

Thorp (1949) reported that crayfish in the Gulf Coast north to the Canadian border prefer to make burrows in the zone of red and yellow podzolic soils, and Grow (1982) claimed that *Cambarus diogenes diogenes* prefers fine-grained clays in which they can most efficiently excavate burrows, compared to coarse-grained sands. In the present study, burrows had a clumped distribution in the banks with yellow podzolic soils and none were found in the predominantly sand and gravel banks (e.g. the south bank in location 3). Serious collapse of the river bank had resulted where there was a high burrow density (lower Fig. 1).

Estimation of the total number of burrows and the crayfish population are extremely difficult to make due to the fact that some crayfish hide under rocks or modify crevices under and between rocks or tree roots to make places in which to hide. This is particularly found in shallow riffles with rocky banks and bottom. Observations by SCUBA-diving showed that many crayfish simply bury themselves in the surface mud of the river bottom, with their backs exposed. It has, therefore, not been possible to quantify the proportion of burrowing crayfish in the river. However, results from laboratory experiments (see later) where there was no natural shelter to hide in showed that the majority of smaller crayfish (carapace length less than 50 mm) made burrows whilst about two-thirds of the larger crayfish (carapace length more than 50 mm) did not, in particular the form I males with large chelae (Table 1). This is probably due to the fact that large males have bigger and more powerful chelae than females and juveniles and appear not to shelter from potential predators.

Laboratory experiments on burrowing

In order to determine whether signal crayfish can construct burrows and to study the characteristics and mechanism of burrowing, observations were made on 280 crayfish (110 males, 110 females and 60 unsexed instars) kept in containers in the laboratory. Trays (50 x 50 x 15 cm) and

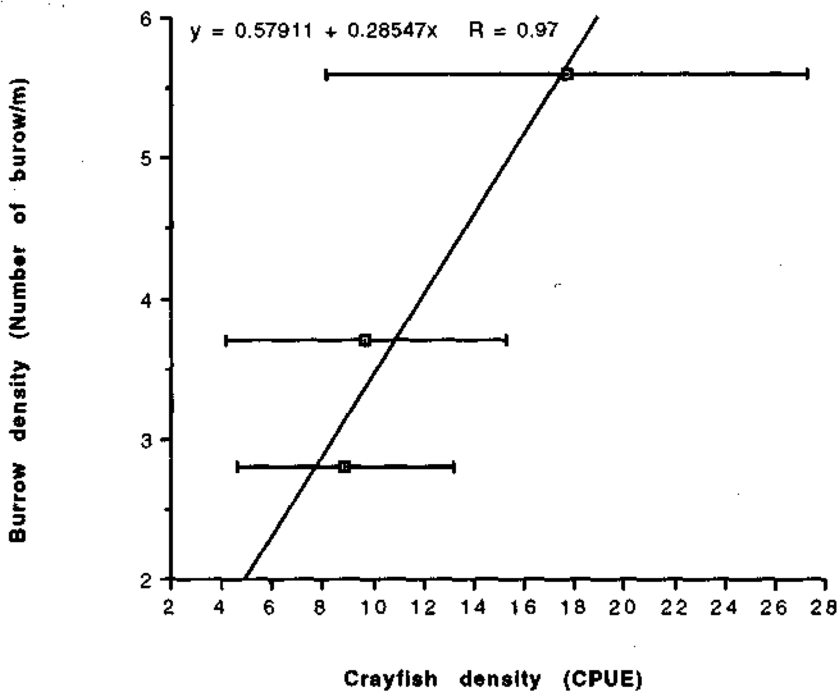

FIG. 3. The density of signal crayfish burrows (number of burrows per metre of river bank) plotted against the density of crayfish, estimated as catch per unit effort (CPUE: numbers of crayfish caught per trap per night; horizontal bars indicate standard deviations from mean CPUE) at three locations in the River Great Ouse (upper bar = location 3, middle bar = location 2, lower bar = location 5).

Table 1. Induced burrowing behaviour of crayfish, *Pacifastacus leniusculus* Dana, in containers under laboratory conditions. CL, carapace length; N, the number of crayfish tested; PB, percentage of crayfish making their own burrows.

CL	Age	Males		Females		Males + Females	
(mm)	(years)	N	PB	N	PB	N	PB
<20	0+ to 1	–	–	–	–	39	94.9
20–35	1+ to 2+	33	72.7	38	81.6	71	77.5
35.1–50	3 to 3+	26	73.1	30	73.3	56	73.2
>50	>4+	44	25.0	35	40.0	79	31.7

tanks (200 x 60 x 30 cm) were supplied with running water, 12 cm deep in the trays and 25 cm deep in the tanks. An artificial clay bank occupying one-half the volume of each container was made along the greatest dimension. Ten early instars (6 replicates) or five juveniles of 20-35 mm carapace length (16 replicates) were placed in each tray and five larger crayfish (carapace length more than 35 mm) were placed in each tank.

Burrowing was observed over a period of 5 days; the containers were then drained to examine the morphology of the burrows.

The mechanism of burrowing

Observations on the crayfish excavations which were induced in the containers revealed that no one sequence of events of burrowing by these animals was strictly adhered to at all times during an excavation process. Both the chelae and the walking legs were used to dig and move the substratum. The corner between the mud bank and the wall of the container was usually selected preferably for burrowing. This was achieved using the first pair of walking legs to make notches in the mud, followed by using the chelae, either alternately or both (together) simultaneously in a scissor-like action. The loose clay was pushed out of the burrow with the chelae and walking legs. Juveniles completed the task of creating a burrow within an hour, but adults usually required periods ranging from several hours to days in order to complete the excavations. Some burrows were continually lengthened until a certain depth was reached at which some were connected together. The crayfish are predominantly nocturnal, emerging from the burrows to forage after dark. On their return the burrows were checked for intruders before the crayfish entered, tail first.

Architecture of the burrows

The architectural morphology of burrows was very simple (Fig. 4). 100 burrows were examined in the river banks; 73 consisted of a simple chamber with one opening (Fig. 4, Type la) and nine had a branched chamber with one opening (Fig. 4, Type lb); only 18% of the burrows were relatively complex with more than one opening and various branches (Fig. 4, Type lla-d). Similarly, from the induced burrowing experiments in the laboratory, 90% of 158 burrows were Type la and lb, and only 10% were Type lla and lib. It is more likely that some of the complex burrows in the river arose from individual single burrows (Type I) becoming joined as they were extended downwards. This was also noted in the laboratory.

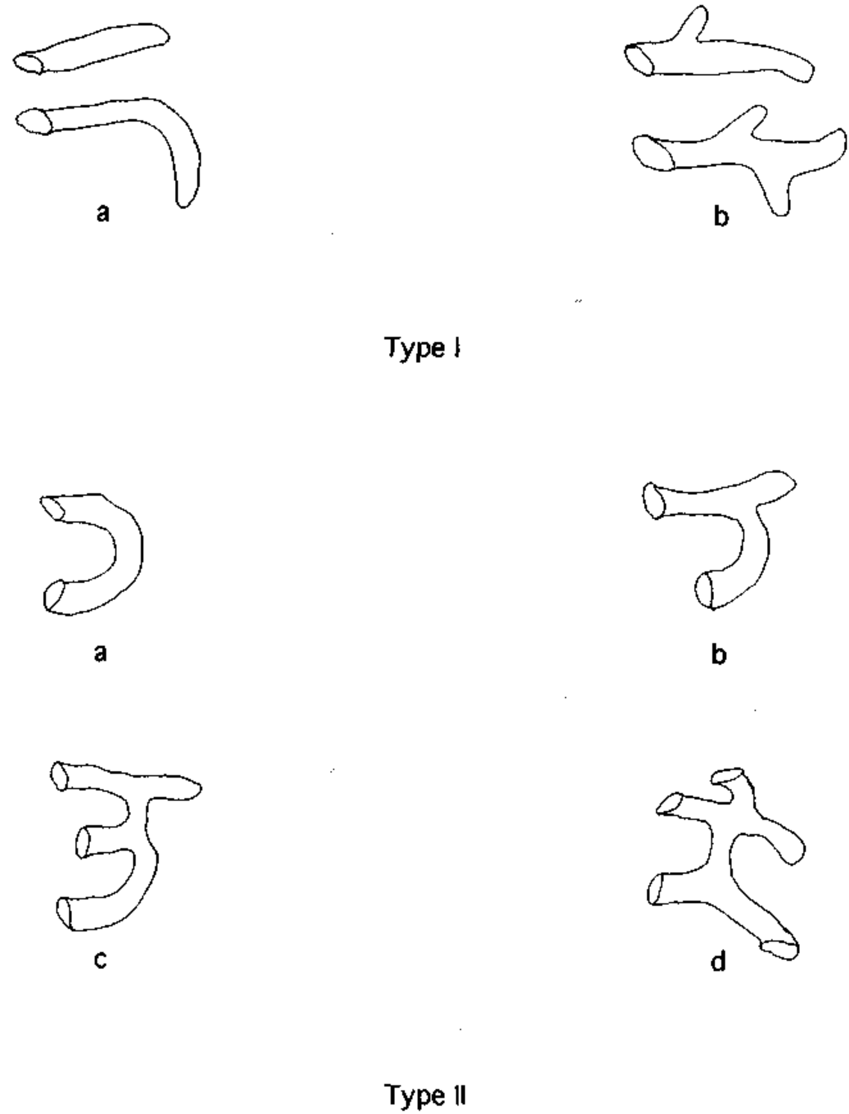

FIG. 4. Types of burrows constructed by signal crayfish in the River Great Ouse. Ia, an unbranched straight or angular chamber with a single opening; Ib, a straight or angular long chamber with one or two short branches and a single opening; IIa-IId, branching, complex burrows with more than one opening.

Three-dimensional morphology of burrows

Height, width and depth were measured on inhabited burrows, including the depth of the opening from the water surface. All measurements started from the midpoint of the opening; if a burrow had more than one opening the mean value was calculated. If a burrow had branches inside, the lengths of all branches were summed to give the total depth of the burrow. Crayfish inside the burrows were sexed and the carapace length (from the apex of the rostrum to the posterior median edge of the cephajothorax) was measured to the nearest 0.1 mm with vernier calipers. Burrows above the water surface were also checked to determine whether or not they were inhabited.

In both the field and laboratory investigations, burrow height, width and depth were all positively, significantly correlated ($p < 0.001$) to the size of burrowing crayfish (Fig. 5A-C). Jaspers & Avault (1969) and Kearney (1980) also reported that crayfish length (species of Cambaridae) was positively correlated with the burrow width and depth. From a comparison of regression lines (Lee & Lee 1982) shown in Fig. 5A-C, the correlation of width and crayfish size in the laboratory was not significantly different from the situation in the field (Fig. 5B, $p > 0.05$). However, burrow height and depth (Fig. 5A and 5C) were significantly different ($p < 0.001$); the burrows were higher but shallower in the containers than those in the river banks. One explanation for this difference in burrow height is that, in the containers, collapse of some soil from the top of the burrows may have occurred because the artificial clay "banks" were less compact than natural river banks. An explanation for the difference in burrow depth is that the experiments in the containers were for a short period (5 days), during which the excavations of some late starters might not be completed. In any case the thickness of artificial clay "banks" would have limited the burrow depth in the containers. The depth of the burrow openings beneath the water surface was positively correlated with the size of the crayfish ($p < 0.001$) (Fig. 5D).

Occupation of burrows

Two extended experimental studies (longer than 4 weeks) on the burrowing behaviour of crayfish in tanks were also undertaken, between September 1993 and July 1994, to determine (a) whether or not crayfish take over burrows that have been excavated by other crayfish, (b) do crayfish exchange burrows, (c) how often do crayfish burrow, and (d) is there any difference in burrowing behaviour between sexes and between winter and summer? Crayfish were implanted with microchips and

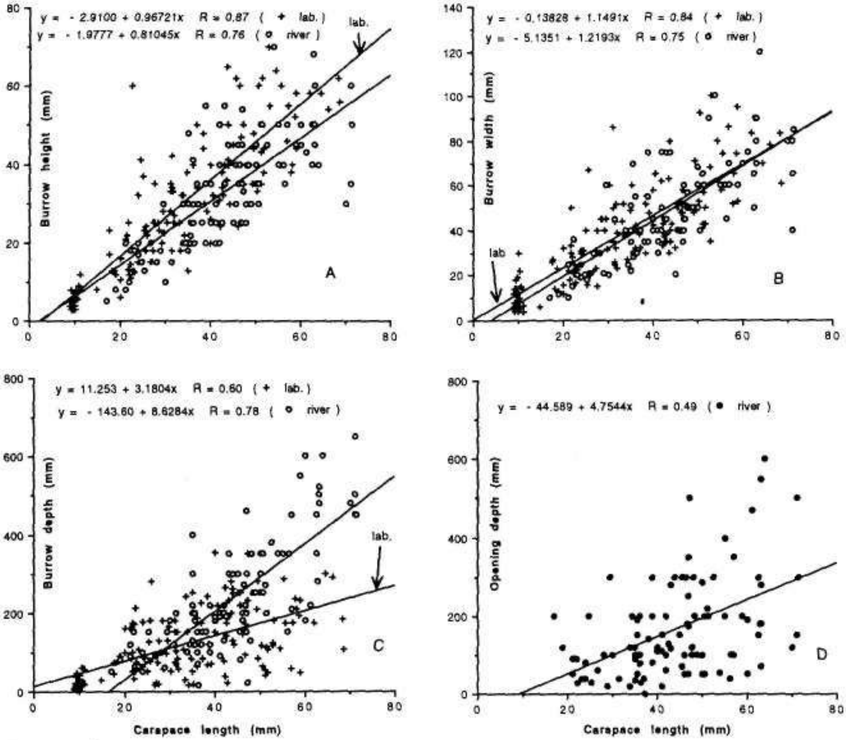

FIG. 5. Relationships between the dimensional morphology of signal crayfish burrows and crayfish body size (carapace length, mm). A, height of burrow (in mm) versus carapace length of burrowing crayfish; B, width of burrow (in mm) versus carapace length; C, depth of burrow into the bank (in mm) versus carapace length; solid lines in A–C are regression lines for burrows constructed in the laboratory (+) and in the river (o). D, depth of burrow's opening below the water surface (in mm) versus carapace length of burrowing crayfish; solid line is a regression for natural burrows in the river.

monitored twice daily (morning and afternoon). Days when crayfish hid inside their burrows during both the morning and afternoon were recorded as "burrowing days". The first occupier in a new burrow was recorded as being the excavator of that burrow if no other was observed.

There was a significant difference (one-way analysis of variance: $p < 0.01$) between the mean numbers of burrowing days in winter and summer seasons. When expressed as percentages of the total numbers of monitored days, 43.1 ± 7.1% (± standard deviation) of days in winter and 79.4 ± 8.8% of days in summer were occupied in burrowing activities. The reason for this seasonal difference is not known. There was, however, no significant difference in the percentages of burrowing days for males and females in either season, nor between gravid females and non-gravid females in the winter season (one-way analysis of variance: $p > 0.05$).

It is difficult to assess the number (percent) of crayfish that make their own burrows in the river. However, in the laboratory only 60% (10 out of 1 7 crayfish) in the winter experiment and 67% (8 out of 12 crayfish) in the summer experiment excavated their own burrows. Crayfish which did not make burrows for themselves, simply occupied burrows that had been excavated by others. Those that lost their burrows usually excavated new ones. However, most crayfish stayed at their own burrows longer than at other burrows in the winter experiment, although the difference was less clear in the summer experiment.

Conclusions

This study has clearly revealed that the signal crayfish is a burrowing species. In the River Great Ouse, signal crayfish make their own burrows at quite high densities in either the banks or the bed of the river. Most of their burrows are simple, straight or somewhat angular chambers, with a single opening below the water surface (Type I, Fig. 4). A few complex burrows (Type II, Fig. 4) occurred, probably due to a number of factors, such as the amalgamation of several Type I burrows or changes in soil type which may force a change in the burrowing direction. The burrow depth observed for this species ranged from 15 to 650 mm. Although the burrows are usually simple, a high burrow density can cause considerable damage to the river bank, ultimately resulting in its collapse.

The burrowing behaviour of *P. leniusculus* did not fall exactly into one particular category but is nearest to that of "secondary burrowers" in the classification of North American burrowing crayfish by Hobbs (1981); i.e. crayfish that spend most of their lives in burrows, but frequently move into open water during the rainy season, when the water-table rises. The behaviour is similar to "Type 1a" in Horowitz & Richardson's (1986) ecological classification of Australian burrowing crayfish; i.e. the animal lives in permanent bodies of surface water under rocks, ledges, in rock crevices, in or under logs and in short, unbranched burrows in the substratum. Its status in Hole's (1981) "Ecological Classification of Animals that Affect Soil" falls into "Endo-pedonic animals", under categories A (little dwellers in refuges), B (soil builders at the surface) and C (soil burrowers).

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