

Growth, density and biomass of crayfish, *Pacifastacus leniusculus*, in a British lowland river

Ruizhang Guan and P. Roy Wiles

The Clore Laboratory for Life Sciences, The University of Buckingham, Buckingham, MK 18 1EG, U.K.

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Abstract

Pacifastacus leniusculus has established hundreds of breeding populations in Britain since its introduction in 1976. One such population was established in the River Great Ouse, a major lowland river in mid-to eastern England, from 140 crayfish introduced in 1984. Estimates of growth, density and biomass of the population in 1992 are presented. Under laboratory conditions, the per moult increment (MI) and percentage per moult increment (PCMI) of crayfish were binomially correlated to their carapace length (CL), that is, the MI increased with CL and then decreased as crayfish grew old, and the PCMI decreased with increase in CL. Based on length frequency distribution data collected from the river in October and November and estimated by Bhattacharya's method, seven male cohorts while only four young female cohorts were identified because of insufficient data for old cohorts. The mean CL of each crayfish cohort was 16.6, 31.2, 41.6, 52.0, 57.8, 64.2, and 69.2 mm for 0+ to 6+ year old males respectively, and 15.4, 28.5, 39.7, and 49.8 mm for 0+ to 3+ females. There were no significant differences between growth rates of either CL or WW of males and females at age for 0+ to 3+ (no data of females > 3+ were available for comparison).

In a riffle, the densities and biomass of crayfish were significantly different between four domains with different bottom substrata and highest in the habitat with the highest density of cobbles and thus, greatest density of potential shelters. The mean densities and biomass of crayfish of all sizes in this riffle were between 10.m² and 61 g.m⁻² respectively in July and 15.m⁻² and 53 g.m⁻² in November. In a pool, mean density and biomass of crayfish > 30 mm CL, estimated by Fish-Ford multiple capture-mark-recapture methods, were 0.8 m⁻² and 37 g.m⁻² between May and August.

Keywords: *Pacifastacus leniusculus*, freshwater crustacean, growth, density, biomass, river, United Kingdom.

Croissance, densité et biomasse de l'écrevisse, Pacifastacus leniusculus dans une rivière de plaine en Grande-Bretagne.

Résumé

Depuis son introduction en Grande-Bretagne, en 1976, des centaines de populations de *Pacifastacus leniusculus* se sont établies. L'une de ces populations s'est développée dans la « Great Ouse », rivière de plaine du centre-est de l'Angleterre, provenant des 140 écrevisses introduites en 1984. Des estimations de la croissance, de la densité et de la biomasse sont ici présentées. L'accroissement par mue (MI), en pourcentage (PCMI), en conditions de laboratoire, est corrélé à la taille de la carapace (CL); ainsi MI augmente simultanément avec CL puis décroît avec l'âge, et PCMI décroît lorsque CL augmente. Au moyen de la méthode de Bhattacharya, basée sur la distribution des fréquences des tailles des écrevisses prélevées dans la rivière en octobre et novembre, 7 cohortes d'écrevisses mâles et seulement 4 cohortes de jeunes femelles sont identifiées. Les tailles moyennes CL, respectives de chaque cohorte, sont 16,6-31,2-41,6-52-58-64-69 mm pour les mâles de 0⁺ à 6 ans, et de 15,4-28,5-39,7-49,8 mm pour les femelles de 0⁺ à 3 ans. Les taux de croissance sont similaires pour les mâles et pour les femelles de 0⁺ à 3 ans (sans comparaison possible au-delà, par manque de données sur des femelles plus âgées). Dans une zone agitée de hauts-fonds, les densités et les biomasses d'écrevisses sont significativement différentes dans

les 4 domaines étudiés, plus élevées sur les graviers et dans les sites présentant des abris potentiels. Les densités moyennes sont de 10 et 15.m⁻² et les biomasses de 61 et 53 g.m⁻² en juillet et novembre respectivement. Dans une mare, la densité et la biomasse moyenne des écrevisses de taille supérieure à 30 mm CL, estimées par la méthode de capture-recapture avec marquage de Fish-Ford, sont de 0,8 m⁻² et 37 g.m⁻² entre mai et août.

Mots-clés : *Pacifastacus leniusculus*, crustacé d'eau douce, croissance, densité, biomasse, Grande-Bretagne.

INTRODUCTION

The crayfish *Pacifastacus leniusculus* (Dana) is native to north-western North America. Its fast growth and large adult size led to increased interest in its culture in Britain. It was introduced into Britain from Sweden in 1976 and soon after, thousands of imported juvenile crayfish were distributed to several hundred sites. Some of these introductions have established breeding populations (Hogger, 1986a, b; Lowery and Holdich, 1988; Holdich and Reeve, 1991). One such population has been established in the River Great Ouse, a major lowland river in mid- to eastern England.

The River Great Ouse used to be inhabited by the native white-clawed crayfish, *Austropotamobius pallipes* (Lereboullet); the verified last sighting was in 1981. The present *P. leniusculus* population has been established since its introduction in 1984 with 100 summerlings and 40 adults in 1984 at Thornborough Weir, Buckinghamshire (map reference: OS 738355). By 1989 large numbers of mature crayfish were commercially trapped from the river and by 1993 the population had spread up and down river to occupy a nine kilometre section.

Although the growth of *P. leniusculus* has been studied in various waters worldwide (Abrahamsson, 1971, 1973a, b; Brinck, 1975; Flint, 1975; Goldman and Rundquist 1977, Mason 1977, 1978a, b, Flint and Goldman, 1977; McGriff, 1983; Hogger, 1986b; Lossakowski, 1988; Lowery, 1988; Westman *et al.*, 1993a and b), there is little information about the growth of naturalized populations in British waters. In a small lake in southern England, an exceptionally high growth of *P. leniusculus* in the first four years after introduction was reported (Richards, 1983; Hogger, 1986b). However, there is still limited knowledge about the carrying capacities of various types of the British waters though the species has occupied many British waters. This paper presents the results of investigations in 1992 on the growth, density and biomass of the *P. leniusculus* population in the River Great Ouse.

MATERIALS AND METHODS

Study sites

The River Great Ouse is a lowland river with its greatest altitude less than 135 m. It has a total length of

approximately 240 km starting in Northamptonshire, running northeastwards through clay land into The Wash, where it enters the North Sea. At the study site, the annual water temperature was 10.4 ± 5.0°C with a higher temperature of 14-20°C during the crayfish growing season (April-October); the catchment area was 38.5 km²; the annual rainfall was generally 500-600 mm and mean water flow from 1980 to 1990 was 2.7 m³.s⁻¹ (range 0.1-36.4 m³.s⁻¹) with a higher flow between September and January. The main chemical components of the water in 1992 were: pH = 8.1 ± 0.2, alkalinity CaCO₃ = 232 ± 48 mg.l⁻¹, calcium = 114 ± 33 mg.l⁻¹, and dissolved oxygen = 10.1 ± 2.0 mg.l⁻¹ (NRA Anglian Region Data).

A pool and a riffle river section were selected for field investigations. The riffle was approximately 300 m downstream from the original site of crayfish introduction at Thornborough Weir, Buckinghamshire. This section was 16 m long, approximately 14 m wide and 0.2-0.8 m deep in summer. The bottom was primarily gravel, pebbles and cobbles. The water flow was fast and turbulent.

The pool was upstream of Thornborough weir. It was 360 m long, 14-16 m wide and 1.5-2.0 m deep at midstream in summer. The bottom and banks were gravel and clay. Macrophytes (mainly *Phragmites communis*) were abundant along both banks. The water flow was very slow, except after heavy rain.

Sampling methods

In the riffle, a stratified random sampling method was used as the bottom substratum was not uniform. The total area was divided into four domains with equal areas (56 m²) according to the type of bottom substratum. Approximately, in domain 1, 85% area was covered by gravel and small cobbles (Wentworth classification), the remainder being large cobbles; in domain 2, half the area was covered by pebbles and small cobbles, the other half by large cobbles; in domain 3, 85% area was large and small cobbles and 15% pebbles; in domain 4, the bottom was almost all large and small cobbles. The mean water depths were 0.27, 0.21, 0.26 and 0.23 m in July for domains 1 to 4, respectively; all were raised by about 0.15 m in November. The water flow in domains 1 and 3 was faster and more turbulent than in domains 2 and 4. Five random Surber samples (0.1 m²) in each domain were taken in July and November, respectively.

In the pool, samples were collected with cylindrical, plastic crayfish traps (50 cm long and 20 cm in diameter). Traps, including the inverted entry cones at both ends, were covered with polyethylene nets of 4 × 4 mm mesh to prevent the small crayfish entered from escaping. Eight traps, baited with fish heads, were put into the river and anchored at intervals of 45 m. Traps were set in the late afternoon and emptied early the following morning, at weekly intervals, from May 19 to August 4 (total 12 weeks). Between October 13-15 the same sampling procedure was employed but in addition the traps were rebaited in the morning and emptied in the afternoon to catch more crayfish for cohort analysis.

160 crayfish were collected by direct hand capture from other sections of the river for laboratory growth experiments. The crayfish were kept outdoors in individual containers in a recirculating water system and fed daily with pellet dog food. The water temperature ranged from 10 to 20°C during the experimental period (March-October).

Marking and measuring

Crayfish tapped weekly from the pool between May and August were marked with a unique pattern of spots branded on the uropods or telson and by clipping off part of one of the pleurons on either side of the first four abdominal segments in a unique combination. All crayfish captured and recaptured from May 19 to October 15 were weighed to the nearest 0.1 g and sexed. Carapace length (CL, from the rostral apex to the posterior median edge of the cephalothorax) were measured to the nearest 0.1 mm with Vernier calipers. The annual moult number and growth of crayfish under laboratory condition were recorded to compare with those in the river. The moulting time of crayfish in the river was examined weekly by sampling in the riffle and the pool from April to October.

Data analysis

Per moult increment (MI) and percentage per moult increment (PCMI) of carapace length were calculated from the equations:

$$MI = CL_1 - CL_0$$

$$PCMI = \frac{CL_1 - CL_0}{CL_0}$$

where CL_0 and CL_1 are the carapace length (mm) of crayfish before and after a moult respectively. The relationships between the MI, PCMI and CL were estimated by binomial, exponential and linear regression analysis.

Bhattacharya's (1967) method, incorporated in the computer programme, the Compleat ELEFAN

software package (version 1.10, October 1989) for analysis of length-frequency data in fish and aquatic invertebrates, was applied to identify the cohorts and to estimate the mean cohort carapace length of male and female crayfish based on the pooled data collected from the pool in October and the riffle in November, 1992. The asymptotic carapace length was estimated by von Bertalanffy growth function using the same computer package. The mean cohort wet weight (WW) was calculated from the equation describing the WW and CL relationship derived from the same pooled data as used for cohort analysis.

Annual instantaneous growth rates of CL (G_l) and WW (G_w) were calculated from the equations:

$$G_l = \log_e \left(\frac{CL_{i+1}}{CL_i} \right)$$

$$G_w = \log_e \left(\frac{W_{i+1}}{W_i} \right)$$

where CL_i and CL_{i+1} are the mean carapace lengths of cohort i and $i + 1$ respectively, and W_i and W_{i+1} are the mean wet weights of cohort i and $i + 1$.

Subpopulation size (N_r), variance ($v(N_r)$) and density (D_r) (Seber, 1973) in the riffle were calculated from the equations:

$$N_r = \sum N_j = \sum \frac{n_j}{p_j}$$

$$v(N_r) = \sum \frac{N_j q_j}{p_j}$$

$$D_r = \frac{N_r}{A_r}$$

where N_j is the number of animals in the j -th domain; n_j is the number of crayfish found in the sampled area in the j -th domain; p_j is the proportion of sampled area to the total area in the j -th domain and q_j is the proportion of un-sampled area to the total area in the j -th domain; and A_r is the total area of the riffle. The crayfish density in each domain was directly calculated by N_j divided by domain area (56 m²).

The weekly subpopulation size and survival rate of crayfish in the pool were estimated by Fisher-Ford method, a multiply capture-mark-recapture method (in Begon, 1979) from the weekly data collected between May and August, 1992. The weekly density (D_{pi}) and biomass (B_{pi}) of crayfish in the pool were calculated from the equations:

$$D_{pi} = \frac{N_{pi}}{A_{pi}}$$

$$B_{pi} = D_{pi} \times W_{pi}$$

where N_{pi} is the estimated subpopulation number in the pool in week i ; A_{pi} is the area occupied by the subpopulation equal to 5400 m² (360 m long and 15 m wide); W_{pi} is the mean WW of samples in week i .

RESULTS

Growth

The binomial relationship, compared to exponential and linear regression relationship, was the best to describe the correlation (t -test on the significance of the correlation coefficients, $p < 0.01$) between the per moult increase (MI), percentage per moult increment (PCMI) and carapace length (CL) of both males and females reared in the laboratory (Table 1). The MI and PCMI of both males and females increased with CL and then decreased as crayfish grew old. The data

Table 1. – Mean per moult increment (MI) and percentage per moult increment (PCMI) of *Pacifastacus leniusculus* in different carapace length (CL) classes under laboratory conditions (\pm standard deviation). No: number of crayfish; – no specimen.

CL (mm)	Male			Female		
	No	MI (mm)	PCMI (%)	No	MI (mm)	PCMI (%)
16-20	4	1.7 \pm 0.3	10 \pm 2	5	2.5 \pm 0.7	13 \pm 3
21-25	2	2.8 \pm 1.1	12 \pm 5	1	3.0	12
26-30	17	3.4 \pm 1.1	12 \pm 4	14	3.6 \pm 1.0	12 \pm 3
31-35	12	4.0 \pm 0.7	12 \pm 2	16	3.9 \pm 1.0	12 \pm 3
36-40	16	4.5 \pm 1.0	12 \pm 2	17	3.8 \pm 0.7	10 \pm 2
41-45	7	3.3 \pm 0.4	8 \pm 1	6	4.6 \pm 1.1	11 \pm 3
46-50	4	4.5 \pm 1.3	10 \pm 3	5	3.0 \pm 0.8	6 \pm 2
51-55	2	3.0 \pm 1.1	6 \pm 2	–	–	–
56-60	–	–	–	1	4.8	8
61-65	–	–	–	–	–	–
66-70	4	3.9 \pm 1.1	6 \pm 2	–	–	–

Table 2. – Mean per moult increment (MI) and percentage per moult increment (PCMI) of *Pacifastacus leniusculus* in different carapace length (CL) classes from the River Great Ouse. The MI and PCMI were calculated from the marked crayfish which had moulted when recaptured (\pm standard deviation). No: number of crayfish; – no specimen.

CL (mm)	Male			Female		
	No	MI (mm)	PCMI (%)	No	MI (mm)	PCMI (%)
31-35	–	–	–	1	4.1	12
36-40	–	–	–	–	–	–
41-45	1	4.4	10	2	4.0 \pm 0.4	9 \pm 1
46-50	5	4.2 \pm 0.9	8 \pm 2	1	3.7	7
51-55	8	5.1 \pm 1.5	10 \pm 3	4	4.7 \pm 1.4	9 \pm 3
56-60	12	5.6 \pm 0.7	10 \pm 1	2	3.9 \pm 1.7	7 \pm 3
61-65	9	5.7 \pm 0.9	9 \pm 1	–	–	–
66-70	2	4.8 \pm 0.5	7 \pm 1	–	–	–

(Table 2) of the MI and PCMI of crayfish from the river were too small and the range of crayfish CL is too narrow to determine the relationship between the MI, PCMI and crayfish CL.

The asymptotic carapace lengths estimated from the weekly data collected from the pool) were 80.6 mm for males and 76.7 mm for females. The maximum carapace lengths of trapped crayfish were 75.1 mm for males and 75.3 mm for females, and maximum wet weights were 158 g for males and 116 g for females. Under laboratory conditions, the moulting period of crayfish (21.5-59.0 mm CL, $n = 51$) was between May 13 to September 20, 1992. The first moult of the year occurred mostly between May 20-30 (35 in 51 crayfish). The annual moult number was closely related to the size of crayfish. Most crayfish of 22.5-30.0 mm CL (8 in 11) moulted three times a year while those between 31.0-46.5 mm CL (17 in 18) moulted twice excluding four females > 42.5 mm CL which moulted only once. In the river, crayfish started the first moult of the year as early as in April but mainly in early May 1992. The recorded smallest berried female 38.5 mm CL corresponded to an age of 2+ (Fig. 1) and the smallest males observed mating in the laboratory were also the similar size, this indicated that *P. leniusculus* in the River Great Ouse matured in their third growing season (2+).

Seven male and four female cohorts were identified from the length frequency distribution data collected from the pool and the riffle between October and November, 1992 (Fig. 1). The older cohorts of female could not be identified simply because of insufficient data as reproductive females were inactive and rarely trapped. The annual instantaneous growth rates of CL and WW decreased with increase in age in both males and females (Table 3). The growth rates of CL and WW of both males and females were significantly correlated (t -test on the correlation coefficient, $p < 0.01$) to their ages. When using a paired data comparison (Ryan *et al.*, 1985), no significant differences ($p > 0.05$) were found between

Table 3. – Mean carapace lengths (CL) of cohorts estimated by Bhattacharya's method and annual instantaneous growth rates of carapace length (G_l) and wet weight (G_w) of *Pacifastacus leniusculus* in the River Great Ouse (\pm standard deviation).

Sex	Age	Number	CL (mm)	Weight (g)	G_l	G_w
Male	0+	17	16.6 \pm 1.8	1.3	0.6	1.9
	1+	55	31.2 \pm 5.4	8.6	0.3	0.9
	2+	179	41.6 \pm 4.4	20.4	0.2	0.7
	3+	166	52.0 \pm 2.4	42.8	0.1	0.4
	4+	129	57.8 \pm 3.0	60.9	0.1	0.4
	5+	48	64.2 \pm 1.6	86.4	0.1	0.3
	6+	17	69.2 \pm 1.3	110.9		
Female	0+	20	15.4 \pm 2.6	1.0	0.6	1.9
	1+	52	28.5 \pm 3.9	6.6	0.3	1.0
	2+	119	39.7 \pm 3.3	17.4	0.2	0.7
	3+	34	49.8 \pm 3.7	35.4		

Table 4. – Estimated number (No), density, biomass, carapace length (CL) and wet weight (WW) of *Pacifastacus leniusculus* in each domain of a riffle in the River Great Ouse in July and November 1992. ϕ = no crayfish was sampled. SE: standard error; SD: standard deviation.

Sampling time	Domain	No \pm SE	Density (No.m ⁻²)	Biomass (g.m ⁻²)	Mean CL \pm SD (mm)	Mean WW \pm SD (g)
July	1	ϕ	ϕ	ϕ	ϕ	ϕ
	2	224 \pm 158	4	28.8	29.1 \pm 0.6	7.2 \pm 0.4
	3	672 \pm 274	12	78.0	25.6 \pm 13.1	6.5 \pm 5.3
	4	1344 \pm 388	24	136.0	23.3 \pm 11.6	5.7 \pm 6.0
	Mean	–	10	60.7	24.6 \pm 11.2	6.1 \pm 5.3
November	1	112 \pm 112	2	18.0	33.2	9.0
	2	784 \pm 296	14	39.6	18.8 \pm 7.9	2.8 \pm 4.2
	3	560 \pm 250	10	21.2	17.3 \pm 7.1	2.2 \pm 3.2
	4	1904 \pm 461	34	134.0	21.1 \pm 9.0	3.9 \pm 3.6
	Mean	–	15	53.2	20.3 \pm 8.6	3.6 \pm 3.7

the growth rates of male and female crayfish at age for 0+ to 3+ (no data of females > 3+ were available for comparison), either in CL or WW.

Density and biomass

In the riffle, the mean density and biomass were significantly different (ANOVA: $p < 0.05$) (Table 4) between four domains, both in July and November samples. They were highest in Domain 4, the habitat with the highest density of cobbles and thus, greatest density of potential shelters. There were significantly higher ($p < 0.05$) densities of crayfish in November than in July. About 30% of the July and 60% of the November population were the young-of-the-year. The mean individual CL and WW decreased significantly (ANOVA: $p < 0.05$) from July to November (Table 4). Most crayfish in the riffle were smaller than 45 mm CL (Fig. 2).

In the pool, all crayfish trapped were larger than 30 mm CL (Fig. 2), therefore, the density estimated was only for crayfish > 30 mm CL assuming that there was no significant size selection of trap on crayfish > 30 mm CL. The density increased from 0.2 to 1.2 m⁻² during the first 11 weeks (May 19–July 28), but fell to 0.8 m⁻² in the last week (August 4). The mean weekly survival rate estimated for crayfish > 30 mm CL was 0.85.

DISCUSSION

The growth of *P. leniusculus* was much faster than that of the native species, *A. pallipes*, which used to inhabit the river. The wet weights of 0+, 1+ and 2+ year old *A. pallipes* from the River Great Ouse were 0.02 g, 0.29–0.7 g and 1.74–2.31 g respectively between 1975–1978 (Pratten, 1980) while the wet weights of 0+, 1+ and 2+ year old *P. leniusculus* from the same river, in 1992, were 1.3, 8.6 and 20.4 g respectively for males and 1.0, 6.6 and 17.4 g for females. The faster growth of *P. leniusculus* together with their

larger size, greater aggression, higher reproduction (Lowery, 1988; Lowery and Holdich, 1988) and resistance to crayfish plague (*Aphanomyces astacti* Schikora) (Persson and Söderhäll, 1983; Alderman, 1993) suggest that it could replace *A. pallipes* in British freshwaters.

The growth of *P. leniusculus* in the River Great Ouse (Table 3) was faster than that in Lake Tahoe, USA (Flint, 1975; Flint and Goldman, 1977; Goldman and Rundquist, 1977) and the Sacramento River, USA (Shimizu and Goldman, 1983); was similar to that in Lake Slickolampi in southern Finland (Westman *et al.*, 1993a) but slower than in a lake at Stratfield Saye in southern England (Richards, 1983; Hogger, 1986b) and in Swedish waters (Abrahamsson, 1973a; Brinck, 1975). McGriff (1983) gave higher estimates of the growth of crayfish from the Sacramento River during the same time period than Shimizu and Goldman (1983). Many factors influence growth including temperature, food availability and density. Measurements on the growth (given above) of *P. leniusculus* have been made on introduced populations in which the age of the population may be an important factor affecting growth. Growth may be rapid when populations first invade new habitats with “unlimited” resources but slows down when density increases and resources may be limiting. For example, exceptionally high growth was reported for crayfish in the first four years after introduction to a lake in southern Britain (Richards, 1983; Hogger, 1986b).

Estimates of crayfish growth are common in the literature but comparisons are difficult because of the variety of methods employed. For example, the absolute per moult increase (MI) and percentage per moult increase (PCMI) are commonly used, but their application is limited. They are valid only when comparing the growth between different individuals, sexes or year classes of a population, or between different species but with same moult numbers in each year class. However, the annual instantaneous growth rate can be used to compare the growth under all circumstances.

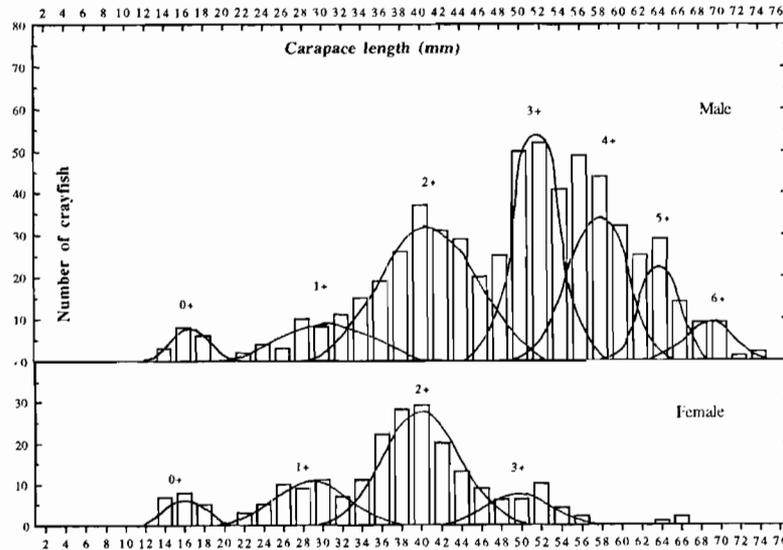


Figure 1. – Cohorts of *Pacifastacus leniusculus* from the River great Ouse estimated by Bhattacharya’s method based on the data of carapace length frequency distributions of crayfish. For both males and females, the separation index was > 2 for all cohorts, at 95% level of confidence, the expected distribution was not significantly different (χ^2 test, degrees of freedom = 10) from the observed distribution. 0+ to 6+ are the year classes of crayfish.

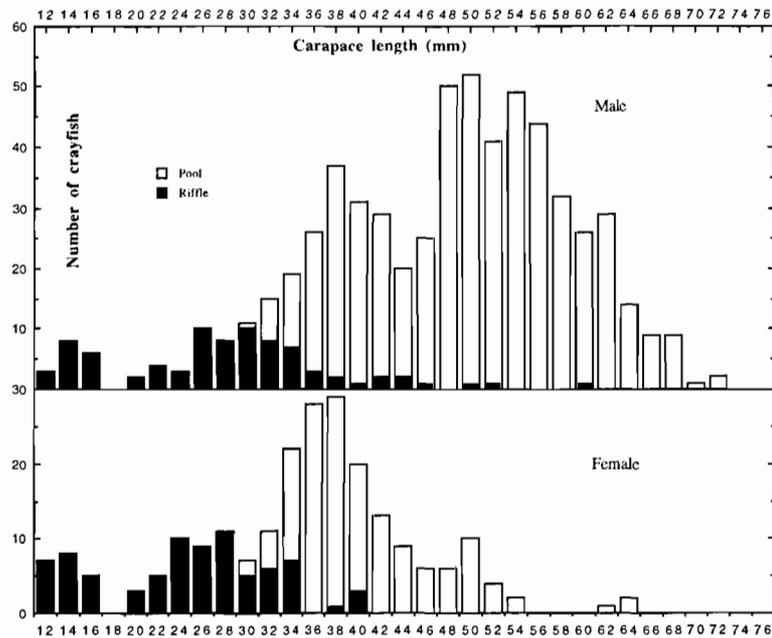


Figure 2. – The size distribution of *Pacifastacus leniusculus* collected by Surber sampler and hand capture from a riffle and trapped from a pool of the River Great Ouse (October-November, 1992).

To estimate the annual growth rate requires the mean length or weight of each cohort. Ideally, for temperate species, length or weight should be measured at the beginning (before the first moult of the year) or end of the growing season (after

the last moult). Bhattacharya’s (1967) method, which only requires data that is representative of the length frequency distribution of a population, has been used for estimating crayfish cohorts and hence their mean lengths and growth rates. Hogger (1986b) used

Bhattacharya's (1967) method to determine the size groups, which corresponded to moult classes, from the length frequency data of a 4-year old crayfish population. For such a young population, the size groups may be easily interpreted as cohorts since the length frequency distributions of young crayfish cohorts did not overlap very much. This was also the case in our data. However, for an old population which may consist of many cohorts, whether the size groups correspond to cohorts needs to be confirmed with other information, such as per moult increment and moult number of a year, and/or annual moult increment of each crayfish size class. In the present study, the per moult increment and moult number of a year estimated from laboratory experiments and river investigations was used to help in positioning the cohorts. Additionally, the cohorts of males and females should be estimated separately because their growths (per moult increment and yearly moult number) are different after maturation.

The density of *P. leniusculus*, has been estimated in a number of open waters. It was 4.2-7.3 m⁻² for an introduced population in a gravel-pit lake in France (Laurent and Vey, 1986), 0.9 m⁻² (Abrahamsson and Goldman, 1970), 1.07 m⁻² (Flint and Goldman, 1975) and 0.7-5.9 m⁻² (Flint, 1975) in Lake Tahoe, and 0.13 m⁻² (adults only) in Castle Lake (Elser *et al.*, 1994) U.S.A. In rivers a density of 0.16 m⁻² was reported by Flint and Goldman (1975). In comparison with these reported figures, the estimates of density of a naturalized population of *P. leniusculus* in the River Great Ouse were high: 10-15 m⁻² in a riffle and 0.76 m⁻² (> 30 mm CL only) in a pool, with corresponding biomass values of 53-61 g.m⁻² and 37 g.m⁻². Estimates for the pool would have been higher still if the younger crayfish (< 30 mm CL), which were hardly trapped due to trap selectivity, had been included.

In the pool, that the density of crayfish > 30 mm CL increased weekly from May to July was mainly due to the recruitment of young crayfish (< 30 mm CL) which grew to trappable size. The decrease in density in the last sampling week may be due to the sampling variation and/or large losses by predation and cannibalism.

Traps select crayfish according to size and activity. Small crayfish, newly moulted and reproductive crayfish were hardly trapped (Abrahamsson, 1983). Assuming size selection remained constant, size selectivity should not have significantly affected the estimation of density for crayfish > 30 mm

CL in the pool by the Fisher-Ford method. Also, samples were taken after the main seasonal moulting period (May) and before the reproductive period (late August). Therefore, the effect of trap selectivity on the estimation of density for the pool should be minimal.

In the same river section, the total density and biomass of fish in 1991 were 0.28 m⁻² and 43.8 g.m⁻² respectively. Crayfish biomass was similar to fish biomass and might have made an important contribution to pike production, which was the dominant species by biomass in the river, as pike prey on crayfish.

Very few crayfish, larger than 45 mm CL, were found in the riffle in the study simply because there were few suitable riverbed shelters and no mud banks to burrow into. A difference between the crayfish densities in four domains of a riffle apparently resulted from the availability of shelters under the stones, and the water depth and current. For instance, domain 1, with few shelters, had the lowest crayfish density while domains 4, with many shelters, had the highest crayfish density. The bottom substratum of domain 3 was similar to domain 4 but it was deeper and the current was faster and more turbulent than domain 4. This may account for the lower crayfish density in domain 3.

More young-of-the-year were sampled in November than in July. This may result from sampling variation due to small sample size or the continuous recruitment of new hatchlings from the adjacent deep pools. Continuous recruitment to the riffle and loss of larger crayfish moving to deep pools, resulted in the decrease of mean carapace length and weight of crayfish from July to November. The density of crayfish estimated for this riffle must be seen as a rough estimate as crayfish had an apparently clumped distribution while both our sampler and sampling area were small.

Crayfish in the pool sheltered in burrows excavated in the clay banks (Guan, 1994). About half of recaptures were caught in the same locations where they were released at least one week before (some were 10-11 weeks before) which suggests that they might have a home range. Other crayfish species have been reported to have a home range (Black, 1963).

It was clear from this study that *P. leniusculus* in the River Great Ouse had a faster growth rate and reached a greater size than *A. pallipes* which used to inhabit the river, and that they lived at a high density and biomass and became an important component of river ecosystems.

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