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Growth of the signal crayfish, *Pacifastacus leniusculus*, in a small forest lake in Finland

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The growth, growth per moult and moulting frequency of adult *Pacifastacus leniusculus* were studied in 1975–1977 and 1987–1988 in Iso-Majajärvi, an 11 ha oligotrophic lake with a very low calcium concentration (mean 1.6 mg l^{-1}) in central Finland (61°52´N, 23°51´E). Growth was determined from the relationship between premoult and postmoult carapace lengths (CL) and measured on marked specimens. The mean absolute per moult increment (MI) in CL was 5.3 mm (i.e. 10.6 mm in total length, TL) in males and 4.1 mm (i.e. 8.2 mm in TL) in females. The percentage moult increase (PCMI) in CL ranged from 4.7% to 20.0% in males and from 1.5% to 13.6% in females. The MI and PCMI of both sexes diminished with the increase in size. Males moulted more often than females. About 27% of adult males apparently moulted twice and 73% once. Among females, 30% moulted twice and about 70% once. Due to their rapid growth, more than half of *P. leniusculus* (the majority males) reached harvesting size (> 100 mm TL) at the age of 3+, by which time some were up to 115 mm (TL). Data on length/weight and carapace/total length ratios are given. The growth of adult *P. leniusculus* in Iso-Majajärvi was of the same order of magnitude as in two other Finnish lakes with a higher Ca concentration.

Introduction

To revive crayfish production in the numerous waters where native crayfish stocks have been decimated by the disastrous plague *Aphanomyces astaci*, the plague resistant North American signal crayfish (*Pacifastacus leniusculus*) has been introduced into at least 21 countries in Europe and the stocking programmes are still expanding (e.g. Lowery and Holdich 1988, Westman and Westman 1992, Henttonen and Huner 1999).

As this is a new species, there is considerable interest in its productivity in the new environments, i.e. in its growth and reproduction in comparison with native species. The growth of *P. leniusculus* has been studied increasingly since the early 1970s within its original range in North America, chiefly in response to the interest aroused by its importation into Europe (e.g. Flint 1975, Mason 1975, McGriff 1983, Shimizu and Goldman 1983, Lewis and Horton 1997). Nowadays a greater volume of data on growth of the *P. leniusculus* is also available from waters where the species has been stocked in Europe (e.g. Hogger 1986, Laurent and Vey 1986, Lowery 1988, Söderbäck 1993, Holdich and Domaniewski 1995, Guan and Wiles 1996), also from a few populations in Finland (Westman *et al*. 1993, Kirjavainen and Westman 1994, 1999), where the species was first introduced back in 1967 (Westman 2000).

From the above studies it is clear that the growth rate of crayfish varies substantially from one body of water to another, most likely due to the difference in environmental conditions. Both the number of moult cycles that crayfish can complete in a year and the growth increment per moult influence the growth rate. One factor that presumably affects the growth of crayfish is the calcium (Ca) concentration of the water. Calcium is essential for recalcification of the exoskeleton after moulting (reviewed by Aiken and Waddy 1992), and low concentrations may therefore slow down growth by delaying moulting or reducing the moult increment, or both.

Since 1970 we have monitored the development of *P. leniusculus* in Iso-Majajärvi, a Finnish lake with very slow growth of the crayfish population, possibly partly due to the lake's low Ca concentration (mean 1.6 mg l^{-1}) (Westman *et al*. 1999). The Ca concentration is indeed one of the lowest in which crayfish have been found to survive at all. The aim of the present study was to see whether, in addition to the slow development of the population, the individual growth of *P. leniusculus* was hampered by the strikingly low Ca concentration. To this end, we compared the growth, i.e. growth per moult and moulting frequency, of adult *P. leniusculus* in Iso-Majajärvi with similar growth data published from other lakes. Further aims were to see which — moult frequency or moult increment — had the greater effect on annual growth, and whether there were growth differences between sexes and size groups, and, if so, what these differences were.

Material and methods

Iso-Majajärvi (hereafter referred to as Lake I-M) is an oligotrophic 11.1 ha forest lake in a natural state in central Finland (61°52´N, 23°51´E). Its mean depth is 5 m and maximum depth 14 m. Of the littoral area of the lake bed to a distance of about 5 m from the shore, 49% (1093 shore metres) is muddy bottom, 43% (959 shore metres) is covered by submerged trees, branches, aquatic vegetation and plant detritus, and 8% (178 shore metres) consists of outcrops, stones, gravel and sand. There is no human settlement around the lake. The Ca concentration (mean 1.6 mg l^{-1}) is very low and the population is probably close to its existence limit. The lake has been described in detail elsewhere (Westman *et al*. 1999).

In 1969, 840 adult *P. leniusculus* (560 females, 280 males) from Lake Tahoe, CA, USA, were released into the lake. *P. leniusculus* has been reproducing in Lake I-M since 1970. The size of the population was very low at the two study periods, the yearly catch per trap night varying in 1975–1977 from 0.1 to 0.4 and in 1987–1988 from 0.4 to 0.5 (size of trappable population at the end of 1970s about 330 and in 1987 about 380 specimens, i.e. the mean density was ca. 0.2 crayfish/shore metre) (Westman *et al*. 1999).

Data for this study were collected from crayfish caught with baited traps. The mesh size (knot to knot) was 8 mm, small enough to catch individuals of only 40 mm total length (TL). The traps were fastened at 5 m intervals to a floating nylon line placed about 2–3 m from the shore. Fresh or deep-frozen roach (*Rutilus rutilus*) was used as bait (more details in Westman *et al*. 1999).

Growth was determined from the relationship between premoult and postmoult carapace lengths (CL) of *P. leniusculus* individually marked by electric cauterisation (Westman *et al*. 1999) and also with a water-proof pencil. The growth increment per moult was studied in 1975–1977 and 1987–1988 by examining 28 males and 24 females (length range 35–67 mm CL). These were selected from 86 recaptured specimens (329 marked during the two study periods). A large number of the recaptures had to be discounted, as their cauterised markings were indistinct owing to the fact that the crayfish had meanwhile passed through several moultings. The growth per year was studied from crayfish trapped in 1987–1988 (33 males and 30 females).

If the pencil mark was visible on the carapace at recapture the individual had not moulted. For the estimation of growth per moult only those individuals were selected which were considered to have moulted no more than once between marking and recapture. Classification of the carapace growth material and the brightness and size of the orange-brown cauterised marks, together with findings of our previous studies (Pursiainen *et al.* 1988a, Westman *et al.* 1993) and information available in the literature (references in Discussion), indicate strongly that *P. leniusculus* whose carapace had grown by more than 7 mm in males and 6 mm in females in a year had most likely moulted more than once, even though Mason (1975) found the greatest length increase at moult to be 8 mm.

CL was measured with vernier callipers to the nearest mm from the tip of the rostrum to the posteriomedian margin of the cephalothorax. TL was measured from the tip of the rostrum to the end of the telson of the stretched abdomen. CL is about half of TL. Unless otherwise stated, the lengths given in the text are CL.

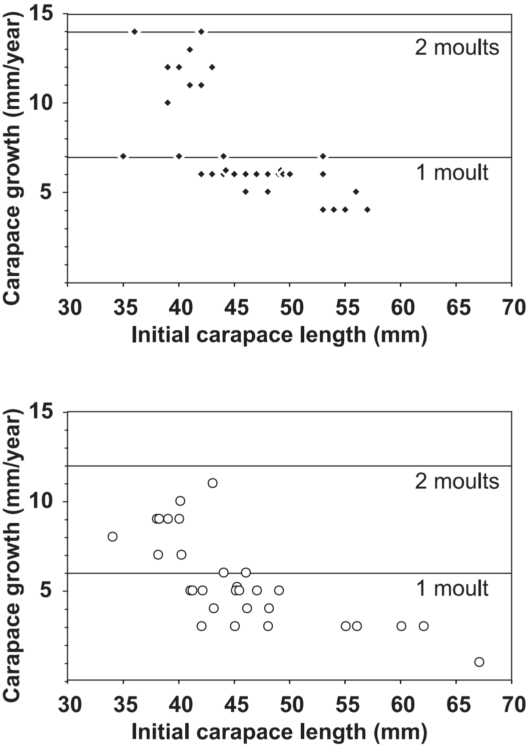

Fig. 1. Growth in carapace length of individual *Pacifastacus leniusculus* males (upper panel, $N = 33$) and females (lower panel, $N = 30$) between marking and recapture (= growth mm/year) in 1987–1988.

Results

Moulting frequency

The estimated number of moults per year in marked and recaptured *P. leniusculus* of both sexes is shown in Fig 1. Males moulted more often than females. Just over a quarter (27%) of adult *P. leniusculus* males apparently moulted twice and 73% once. Among females, 30% moulted twice and about 70% once; none of the *P. leniusculus* studied would appear to have moulted three times.

Moulting frequency, and thus also growth, was dependent on the size of *P. leniusculus;* the larger the animal the lower the moulting frequency. *P. leniusculus* males moulting twice a year were all < 44 mm whereas 83% of those moulting only once were 44 mm or over. Similarly all females moulting twice a year were < 44 mm and those moulting once ≥ 41 mm.

Among the *P. leniusculus* studied the largest male to have moulted measured 57 mm (111 mm TL), and the largest female 67 mm (135 mm TL).

Adult *P. leniusculus* seemed to have two major periods of moulting, late June–July and late August–September. Ovigerous females do not moult until they have released their young, which in Lake I-M would appear to be in mid-July or, in cold summers, at the end of July. By then it is apparently too late for females that have reproduced to moult a second time. In contrast, immature, young females nearly always achieve two moults per year.

Growth increase per moult

The mean absolute per moult increment (MI) in CL of trappable *P. leniusculus* was 5.3 mm

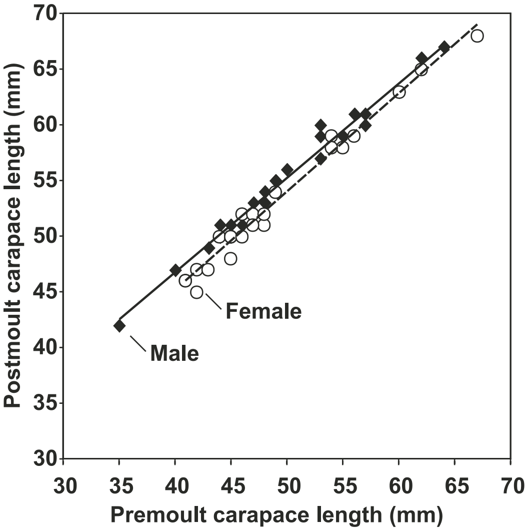

Fig. 2. Linear regression graphs for pre- and postmoult carapace lengths of *Pacifastacus leniusculus* males (N = 28) and females (N = 24).

(SD = 1.249) (ca. 10.6 mm TL) in males but markedly less, 4.1 mm (SD = 1.191) (ca. 8.2 mm TL), in females. The difference is statistically highly significant ($t = 3.518$ $p = 0.001$). The average growth of adult males in CL per moult was thus 1.2 mm mm greater than that of females. Differences in MI between *P. leniusculus* of the same size were substantial, the greatest difference among males being 3 mm and among females 2 mm. The largest MI among males and females in the present material was ca. 7 mm and 6 mm, respectively.

MI diminished with the increase in size of *P. leniusculus*, the more so in males than in females. The difference in MI between sexes was thus greatest in the smallest length classes: at premoult length (CL) 43 mm MI was ca. 6 mm in males and ca. 5 mm in females, but at premoult length 55 mm, MI was ca. 4 mm in males and ca. 3 mm in females (Fig. 2).

The linear regressions between CL before and after moult are presented in Fig. 2. The equations are as follows:

$$\text{males: } y = 12.892 + 0.849x$$
$$(R^2 = 0.98, N = 28, p < 0.001)$$
$$\text{females: } y = 9.605 + 0.888x$$
$$(R^2 = 0.98, N = 24, p < 0.001)$$

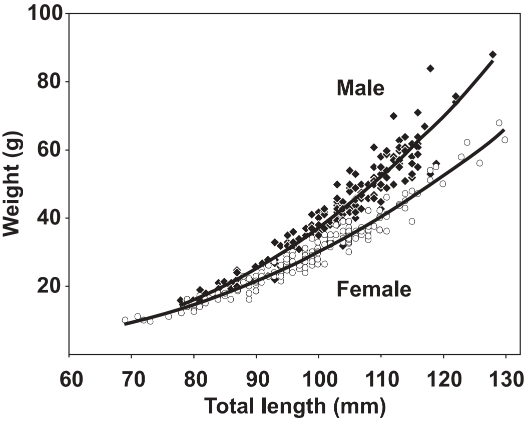

Fig. 3. Relationship between body weight and total length for *Pacifastacus leniusculus* males (N = 170) and females (N = 184).

in which y = post-moult CL length (mm) and x = pre-moult CL length (mm).

The percentage moult increment (PCMI) in CL in the present material (ca. 35–67 mm CL) ranged from 4.7% to 20.0% in males and from 1.5% to 13.6% in females. The PCMI of both males and females decreased with the increase of CL and with the age of the crayfish. There was considerable individual variation (Figs. 1 and 2).

Growth per year

The annual growth of marked and recaptured adult individuals is shown in Fig. 1. Male *P. leniusculus* measuring 37–43 mm (CL) grew through two moults by 10–14 mm (CL) in one year. Larger males seemed to have moulted only once and their annual growth to have slowed down accordingly: males measuring 44–57 mm grew by 5–7 mm.

Female *P. leniusculus* of the size group 34–43 mm (CL) grew through two moults by about 7–11 mm in one year; those measuring 41–49 mm and who had moulted only once grew by about 3–6 mm but those measuring 55–67 mm by only about 1–3 mm in one year.

P. leniusculus grow to a considerable size in Lake I-M, the largest trapped male being ca. 154 mm and female 159 mm (TL).

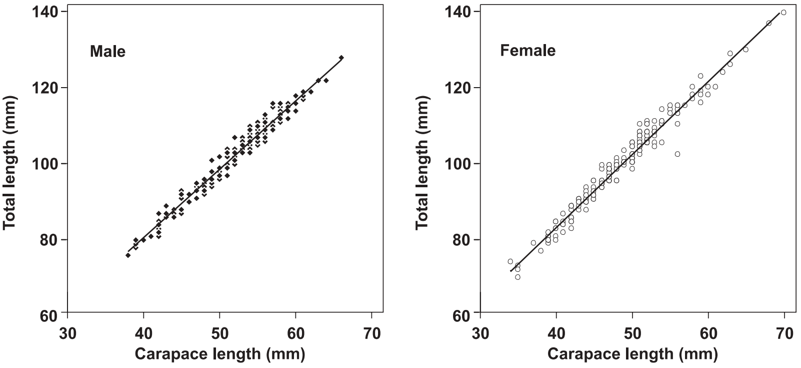

Fig. 4. Carapace length (CL) in relation to total body length (TL) in *Pacifastacus leniusculus* males (N = 195) and females (N = 210).

Length/weight and carapace/total length ratios

The correlation between TL and total wet weight calculated from trap catches in August 1988 and 1993 is shown in Fig. 3. Individuals without chelipeds or with regenerated ones have been excluded from the calculations.The TL wet weight functions are as follows:

$$\text{males: } y = 0.0143x^2 - 1.527x + 46.266$$
$$(R^2 = 0.92, N = 170, p < 0.001)$$
$$\text{females: } y = 0.0084x^2 - 0.747x + 20.224$$
$$(R^2 = 0.96, N = 184, p < 0.001)$$

in which y = total wet weight (g) and x = total length (TL, mm).

Due to allometric growth, i.e. the size of the chelipeds in relation to total length, males weighed more than females of the same size from 80 mm TL upwards (Fig. 3). The mean weight of 100 mm males was 36 g and of females 30 g, i.e. males were about 20% heavier than females. In the largest specimens studied (125 mm), males (79 g) were already 27% heavier than females (58 g).

Sexual dimorphism was also reflected in the difference in length of the abdomen in relation to total length between males and females calculated from trap catches in August 1988 and 1993 (Fig. 4). For example, in males 100 mm long, the abdomen accounted for 49% and in females for 51% of the total length. The regression lines for CL and TL were:

$$\text{males: } y = 8.475 + 1.802x$$
$$(N = 195, R^2 = 0.97)$$
$$\text{females: } y = 3.873 + 1.964x$$
$$(N = 210, R^2 = 0.97)$$

in which y = total length (TL, mm) and x = carapace length (CL, mm).

Discussion

The growth rate of an individual crayfish depends on the physiological state of the animal and on its environmental conditions, notably, temperature, food supply and population density (reviewed by Aiken and Waddy 1992, Goddard 1988, Lowery 1988, Söderbäck *et al.* 1988). Both the number of moult cycles that crayfish can complete in a year and the growth increment per moult influence the growth rate. There are considerable interspecific differences in the growth characteristics of crayfish. Growth may be progressive geometric, retrogressive geometric or arithmetic (Kurata 1962). Many studies (Mason 1975, Shimizu and Goldman 1983, Guan and Wiles 1996) have demonstrated that the absolute per moult increment (MI) and percentage moult increment (PCMI) of *P. leniusculus* males and females first increase with size and then decrease. Here, too, as in other research conducted in Finland (Westman *et al.* 1993, Kirjavainen and Westman 1994), the moult increment of > 70 mm *P. leniusculus* declined as size (and age) increased. Consequently, in *P. leniusculus* as well as in *Astacus astacus, Austropotamobius pallipes* (e.g. Abrahamsson 1973, Brewis and Bowler 1982) and *Orconectes virilis* (France 1985), growth is progressively geometric from juvenile to young adult stages, but then declines, resulting in an inverse relationship between body size and relative growth increment. Thus, with *P. leniusculus,* comparisons of length increase per moult should be made both between sexes and between size groups. By contrast, according to Jones (1981) the growth increment of New Zealand *Paranephrops* spp. is constant, irrespective of age.

The mean MI was of the same order of magnitude in Lake I-M as recorded for trappable *P. leniusculus* in two other Finnish lakes with a higher Ca concentration: mean MI of TL for males 9.4, 10.8 and 12.4 mm, females 8.5, 9.0 and 9.2 mm (Westman *et al*. 1993, Kirjavainen and Westman 1995). Elsewhere, the mean MI of TL has been found to be for trappable specimens 10 mm for males and 8 mm for females (Abrahamsson, 1971, 1973) and 4.8–9.6 mm (McGriff 1983) and 8.4–11.4 mm for males and 7.8–9.4 mm for females (calculated from CL data presented by Guan and Wiles 1996).

The PCMI in CL has varied in different studies as follows: 3.6%–12.2% (Mason 1975), 3.8%–16.0% in males and 4.8%–12.0% in females (Hogger 1986) and 6%–12% in males and 6%–13% in females (Guan and Wiles 1996). In Lake I-M, the PCMI in CL (4.7%–20.0% in males, 1.5%–13.6% in females) was somewhat greater in males than in the above studies.

The above investigations demonstrate that differences in absolute moult increment are quite small between *P. leniusculus* populations, usually being no more than a few mm in TL per moult. The implication is that differences between growth rates in various waters are mainly due to differences in moulting frequency, which seem to vary from one population to another. For example, *P. leniusculus* in the size group 60–70 mm (TL) moulted once a year in Lake Tahoe (Flint 1975) and twice in a Canadian river (Mason 1975) and in Karisjärvi (Kirjavainen and Westman 1995), i.e. as often as in Lake I-M. As the Ca concentration in these lakes is much higher than that in Lake I-M (in Lake Tahoe, for example, it is up to 8.8–9.9 mg l^{-1}; Goldman and Rundquist 1977), the extremely low Ca concentration in the present study lake would not appear to have hampered the moulting frequency, at least to any great extent. *P. leniusculus* in Lake I-M may obtain Ca needed for recalcification of the exoskeleton after moulting from food (Hessen *et al*. 1991).

Appelberg (1992) observed that growth rates of *A. astacus* were high after liming oligotrophic, low-alkaline lakes and thus the growth rate of *P. leniusculus* in Lake I-M might have been greater if the lakes Ca concentration had been higher. The slow development of the *P. leniusculus* population has been partly attributed to the low Ca concentration with periodic acidity (Westman *et al*. 1999).

Temperature, in contrast, has a major impact on growth rate through both moult frequency and the size increase at moult (Lowery 1988, Aiken and Waddy 1992). Thus, in the warm, eutrophic Sacramento River, for example, *P. leniusculus* moulted three times (McGriff 1983, Shimizu and Goldman 1983) as did a large proportion of males in Slickolampi, about 200 km to the south of Lake I-M (Westman *et al*. 1993). According to Söderbäck (1995), in a Swedish lake non-reproductive *P. leniusculus* (< 35–40 mm CL, 70–80 mm TL) moulted two, three and, occasionally, even four times per year.

Growth ceases in *P. leniusculus*, as also in many other species, when the water temperature drops to about 10 °C or lower (Kirjavainen and Westman 1999). Consequently, *P. leniusculus* can only grow for ca. 4–5 months a year in Lake I-M, resulting in slower growth than in climatically more favourable lakes (e.g. Abrahamsson 1971, Hogger 1986, Laurent and Vey 1986). On the other hand, the growth rate of *P. leniusculus* in Lake I-M was very similar to that in some other lakes in Finland (Kirjavainen and Westman 1994), in a river in the English Midlands (Guan and Wiles 1996) and in a lake in Lithuania (Cukerzis, 1979) and even higher than that in a river in Canada (Mason 1975) and in Lake Tahoe (Flint 1975), both cool waters.

Due to lengthening of the intermoult period, the larger and older the crayfish the lower is the moult frequency (e.g. Aiken and Waddy 1992). The same was seen in the present study. In Lake I-M, the largest moulting males and females were slightly smaller than in Lake Slickolampi (largest male 131 mm and female 132 TL) (Westman *et al*. 1993).

Sex also influences moult frequency, which is similar in both sexes until maturity is reached, whereafter moult frequency in the female depends on whether she reproduces or not (Lowery 1988, Aiken and Waddy 1992). In Lake I-M, most reproducing females seem to moult only once, but non-ovigerous ≤ 44 mm CL (ca. 84 mm TL) females usually seem to achieve two moults per year. This is less than we observed in Lake Slickolampi (Westman *et al.* 1993) and Söderbäck (1995) in a Swedish lake.

Consequently, in Lake I-M, the males grew faster than the females largely due to their higher average number of moults, but also to the greater length increment per moult. The lower moulting frequency of ovigerous females than of males is a consequence of moulting being delayed until the young have detached themselves from the mother. The smaller growth increment per moult may be due to the fact that the buried females remain in hiding to a greater extent than males, thereby reducing their opportunities to look for food. Ovarian growth and egg production also call for an immense energy input, which again serves to curb the growth of females (Aiken and Waddy 1992). Similarly, earlier studies have shown that *P. leniusculus* males grow more rapidly than females (e.g. Abrahamsson 1971, Lowery 1988, Westman *et al.* 1993, Kirjavainen and Westman 1994).

Sexual dimorphism in crayfish is also expressed as the difference in the ratio of abdomen length to total length in males and females. According to Pursiainen *et al.* (1988b), this ratio was 47.3% in *A. astacus* males and 48.4% in females. In *P. leniusculus* the ratio of abdomen to TL is, however, greater: in Lake Karisjärvi in 100 mm males, 49.3%, and in females, 50.9%, and in 120 mm males, 48.5%, and in females, 50.3% (Kirjavainen and Westman 1999). The same was observed in the present study (Fig. 4).

Mason (1975) observed that *P. l. trowbridgii* males > 40 mm TL weighed more than females due to allometric growth (allometry discussed by Aiken and Waddy 1992). However, in Lake Karisjärvi males weighed more than females only from 98 mm upwards (Kirjavainen and Westman 1999). We found here (Fig. 3) that males > 75 mm weighed more than females and the bigger the males the bigger the difference in weight (due to the larger chelipeds of males), even though mature females have a larger abdomen width.

According to McGriff (1983), *P. leniusculus* may grow to as long as 180 mm. The largest females found in our other experimental lakes have measured 146 mm and males 159 mm (Kirjavainen and Westman 1994). Somewhat larger individuals were caught in Lake I-M. The maximum sizes of *P. leniusculus* may, however, be considerably in excess of those mentioned, as much larger individuals are unable to fit through the narrow entrances of the trap model that we used. The length of the largest specimen found in Sweden was as much as 210 mm (Forskingsrådsnämnden 1982).

Crayfish catchers and water area owners are keenly interested in the growth of *P. leniusculus* in comparison with the native *Astacus astacus*. According to studies conducted in waters inhabited by either *P. leniusculus* or *A. astacus* alone (Abrahamsson 1971, Kirjavainen and Westman 1994), the growth of *P. leniusculus* has been more rapid than that of *A. astacus*. Growth data, particularly those on *P. leniusculus* (referred to earlier in the present paper), have also been criticised (Gydemo and Westin 1988) due to the difficulty of comparing allopatric populations exposed to diverse temperatures and circumstances (Lowery 1988). Comparison of intra- and interspecific growth rates tends to be further complicated by the fact that many studies have focused on introduced populations. Growth is often exceptionally rapid when populations first invade new habitats with abundant food resources, but it slows down when density increases and resources become more limited. For example, Richards (1983) and Hogger (1986) observed an exceptionally high growth rate within the first four years of *P. leniusculus* being introduced into lakes in England. Similarly *A. astacus* living in the favourable conditions provided by artificial ponds in a limestone quarry in Gotland, Sweden (Gydemo and Westin 1988) grew at an appreciably higher rate than did those in natural environments with less abundant food resources and inferior water quality. McGriff (1983), Momot (1984) and Lowery (1988) have reviewed the growth of freshwater crayfish, including *P. leniusculus,* living at different latitudes as well as factors that influence this growth.

Comparative growth research under identical conditions on coexisting populations (Westman *et al*. 1993) shows that *P. leniusculus* grow considerably more rapidly than *A. astacus* right from their first summer. In different years, *P. leniusculus* ranged at 0+ (late August) from 23 to 30 mm (TL) (mean 26 mm) and at 1+ from 61 to 62 mm (mean 62 mm); the figures for *A. astacus* were 17 to 21 mm (mean 19 mm) and 37 to 42 mm (mean 39 mm), respectively. The higher growth rate of *P. leniusculus* than of *A. astacus* was due to both the higher moulting frequency and greater moult increment.

According to Hogger (1986) and Lowery (1988), *P. leniusculus* stands out as the fastest growing of the northern temperate zone crayfish species on which data are available. For example, in England (op. cit.) and also in Finland (Westman *et al*. 1993, Kirjavainen and Westman 1994) the common harvesting size, 100 mm in TL, is reached within three years (3+) and among the fastest growing individuals at 2+, particularly under favourable conditions, as has also been observed in Sweden (Abrahamsson 1971). The present study, too, revealed a rather high growth rate in *P. leniusculus*, more than half of those specimens studied reaching a size of 100 mm, and some even 114 mm at 3+ even though the Ca concentration was exceptionally low in the lake.

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