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Natural history and development of the introduced signal crayfish, *Pacifastacus leniusculus*, in a small, isolated Finnish lake, from 1968 to 1993

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Abstract — Signal crayfish (*Pacifastacus leniusculus*) originating from Lake Tahoe, California, were introduced into Karisjärvi, a small (11 ha) lake in central Finland (61° 58'N, 25° 32'E), in 1968 and 1969. Since then, the population has been monitored regularly by trap catches. The stocked signals (3–5 years old) were caught until 1973, by which time they had reached ages of 7–9 years. Catches have increased slowly since the early 1980s, the peak occurring in 1991 at 2.0 individuals per trap per night. The population size was estimated as 60 trappable specimens in 1974, 95 in 1981 and 420 in 1988. The mean density of adult population in suitable biotopes was low, 0.07 specimens per m^{-2}, or 0.3 per shore metre, in 1988. The slow development of the *P. leniusculus* population has been attributed to environmental factors, mainly the limited area of good crayfish habitat. More than 90 % of all signal crayfish were caught in one-third of the shore area, i.e. in steeply sloping lake beds suitable for burrowing or rich in shelters such as rocks and submerged trees. The signals avoided flat, soft bottoms. Fifty per cent of the female *P. leniusculus* matured at 90 mm TL (smallest 64 mm), i.e. half of the females entered the breeding population in the autumn of their fourth year. The mean size of newly hatched (stage 2) juveniles was 9.7 mm TL and of one-summer olds 30.3 mm. The largest specimen trapped measured 159 mm. The signal crayfish imported into Finland and stocked were infected with crayfish plague (*Aphanomyces astaci*), but no mortality has been recorded. Two Branchiobdellidae (Annelida, oligochaeta) epibiont species new to Finland were imported from North America with *P. leniusculus*. The continuous occurrence of these commensals in the signal crayfish population indicates that they have adapted to Finnish conditions. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Freshwater crayfish / *Pacifastacus leniusculus* / signal crayfish / stocking / population development / reproduction / habitats

Résumé — L'écrevisse *Pacifastacus leniusculus*, espèce introduite dans un petit lac isolé de Finlande : suivi du développement d'une population de 1968 à 1993. L'écrevisse originaire du lac Tahoe (Californie) a été introduite dans le lac de Karisjärvi (11 ha) en Finlande (61° 58'N, 25° 32'E) en 1968 et 1969. Depuis, la population a été suivie au moyen de captures aux casiers. Les écrevisses stockées, âgées de 3 à 5 ans, ont été capturées jusqu'en 1973. Elles avaient alors atteint l'âge de 7 à 9 ans. Les captures ont augmenté lentement jusque dans les années 1980 avec un pic en 1991 à deux individus par casier et par nuit. La taille de la population a été estimée à 60 individus capturables en 1974, 95 en 1981 et 420 en 1988. La densité moyenne de la population adulte était basse dans les biotopes adaptées, 0,07 par m^2 ou 0,3 par mètre de rive en 1988. Le lent développement de la population de cette écrevisse a été attribué aux facteurs environnementaux principalement à la surface limitée de l'habitat convenant aux écrevisses. Plus de 90 % de toutes les écrevisses ont été capturés sur un tiers de la surface du lac (sur des pentes abruptes du lac, adaptées à l'enfouissement et riches en abris tels que rochers et arbres immergés). Les écrevisses évitent les fonds plats et meubles. Cinquante pour cent des femelles atteignent leur maturité sexuelle à 90 mm LT (la plus petite 64 mm) ; la moitié des femelles commencent à se reproduire à l'automne de leur quatrième année. La taille moyenne des juvéniles à l'éclosion (stade 2) était de 9,7 mm LT et après 1 an, 30,3 mm. Le plus grand individu mesurait 159 mm. Les écrevisses importées en Finlande étaient parasitées avec *Aphanomyces astaci* mais aucune mortalité n'a été enregistrée. Deux Branchiobdellidés (Annélides, oligochètes), deux espèces épibiontes nouvelles pour la Finlande ont été importées d'Amérique du Nord avec *P. leniusculus*. La présence actuelle de ces commensaux chez cette population d'écrevisses indique qu'ils se sont adaptés aux conditions environnementales de Finlande. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Écrevisses / *Pacifastacus leniusculus* / introduction d'espèces / développement d'une population / reproduction / habitat

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Table I. Water quality in Karisjärvi in 1965–1993.

	Depth 0–1 m Mean	Range	N	14 m Mean	Range	N
Colour (mg Pt·L^{-1})	19	5–45	11	22	15–35	11
Conductivity (µS·m^{-1})	35.3	27–43	10	39.4	28–43	9
pH	6.8	6.3–7.4	12	6.4	5.8–6.8	12
Alkalinity (mmol·L^{-1})	0.23	0.19–0.26	20	0.38	0.25–0.78	19
Ca (mg·L^{-1})	3.1	2.1–4.4	9	3.2	2.1–4.8	8
Fe (µg·L^{-1})	129	40–260	21	242	60–820	20
P-tot (µg·L^{-1})	10	7–13	4	30	21–39	2
N-tot (µg·L^{-1})	530	270–990	4	577	370–840	3

N: number of analyses.

1. INTRODUCTION

Crayfish plague, *Aphanomyces astaci*, which spread to Finland in 1893, has devastated the most productive populations of the native noble crayfish, *Astacus astacus*, causing great losses to fisheries [59, 60]. Attempts to contain the plague failed and, despite extensive restockings, *A. astacus* seemed incapable of re-establishing itself in chronically infected waters. It was therefore decided – encouraged by the promising results from stocking the North American signal crayfish, *Pacifastacus leniusculus* (Dana) in Sweden [53] – to introduce this plague-resistant species into Finland as well. *P. leniusculus* has now been introduced into several thousand waters in at least 21 European countries [24, 37, 62], and the extent of stocking continues to increase.

Although catch trends have been reviewed by several authors, primarily in Sweden [12, 14], the results of continuous long-term monitoring of introduced *P. leniusculus* populations are available for only a few lakes (e.g. [55, 61, 64]). Such monitoring is, however, essential when new species are introduced to ensure that even gradual reactions to altered environmental conditions are detected. The need for long-term follow-up studies is particularly important in a country such as Finland, which is on the fringe of the crayfish range and in which strong climatic fluctuations may cause highly significant changes in population dynamics.

The main aims of the present study were to determine if *P. leniusculus* had established a self-perpetuating stock and how the stock had developed over 20–30 years in a typical small Finnish forest lake. In addition, the biotope requirements of this species and aspects of reproduction, juvenile growth and population structure were investigated from 1968 to 1993.

2. STUDY SITE

Lake Karisjärvi (hereafter referred to as Lake K), one of the eight lakes into which adult *P. leniusculus* imported from California were released in 1967–1969 [59], was chosen because it was small and practically without inlets or outlets. This was to ensure that the introduced signal crayfish could not escape.

Lake K is an oligotrophic forest lake in a natural state in central Finland (61° 58’ N, 25° 32’ E). Its area is 10.8 ha, shoreline 1 450 m, mean depth 3.2 m and max. depth 15.7 m. Of the littoral area of the lake bed to a distance of about 5 m from the shore (area ca. 3.92 ha), 7 % is bedrock, 34 % boulders and stones, 10 % gravel and sand, and 49 % peat and mud. Submerged trees are widely scattered. Data gathered by SCUBA diving indicated that the lake contained 6 000 m^2 of habitats suitable for crayfish, i.e. 5.7 % of the total lake bed. The firmness of the bottom was estimated at 5-m intervals by pushing a measuring stick (bottom plate 10 × 10 cm) into the lake bed with steady force.

Trees and bushes thriving on low-nutrient soil (*Alnus glutinosa, A. incana, Betula pendula, Sorbus aucuparia, Salix* sp., *Frangula alnus, Picea abies* and *Juniperus communis*) fringe the shoreline for two-thirds of its length, with arable land elsewhere. There is no human settlement around the lake.

One small brook flows out of Lake K; another flows into it but dries up during the summer. The ice-free period usually lasts for about 200 days, from early May to late November. The lake stratifies in summer. The temperature needed for reproduction, i.e. > 15 °C [3], prevails for about 3 months (June–August).

The water is relatively clear (colour 5–45 mg Pt·L^{-1}, Secchi depth of visibility 3.7–4.6 m) and the O_2 content in the surface layer is high. pH readings have ranged from 6.3 to 7.4. The Ca concentration (mean 3.1 mg·L^{-1}) is typical of a Finnish lake but low for crayfish. No changes in water quality were recorded in the lake during the study period. The physico-chemical properties of the water are summarised in *table I*.

Aquatic vegetation was mapped on 22 August 1974 and 4 September 1988. Macrophytes occur, on average, to a depth of 3 m and a distance of 5 m from the shore. The species recorded in 1988 were, in order of abundance: yellow water lily (*Nuphar lutea*), common reed (*Phragmites australis*), parrot feather (*Myriophyllum alterniflorum*), bur-reed (*Sparganium grami-*

neum), pondweed (*Potamogeton natans*), perfoliated pondweed (*Potamogeton perfoliatus*), water-lily (*Nymphaea candida*), horsetail (*Equisetum fluviatile*), unbranched bur-reed (*Sparganium emersum*), water plantain (*Alisma plantago-aquatica*), pondweed (*Potamogeton alpinus*), branched bur-reed (*Sparganium erectum*), sedges (*Carex* sp.), tufted loosestrife (*Lysimachia thyrsiflora*) and common spike-rush (*Eleocharis mamillata*).

Aquatic vegetation seems to have become more abundant since 1974, but changes in species composition have been minor. The most significant change is the reduced coverage of *M. alterniflorum*, from 5–10 % to 1–2 %. Canadian waterweed (*Elodea canadensis*) was found in 1974, but not in 1988.

Typical Finnish fish species are found: pike (*Esox lucius*), roach (*Rutilus rutilus*), silver bream (*Blicca bjoerkna*), burbot (*Lota lota*), perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*). The lake has also been stocked with common whitefish (*Coregonus lavaretus*) and pike-perch (*Stizostedion lucioperca*). Bullheads (*Cottus gobio*) have often been caught in crayfish traps. The roach and perch populations are dense.

According to the single fisherman who trapped noble crayfish (*Astacus astacus*) prior to the introduction of signal crayfish, catches amounted to "about 500" annually in the 1960s and were "several hundred specimens" in 1967. None were caught in 1968, but dead noble crayfish were seen in the lake.

The first *P. leniusculus* (ten adult males, eight females) were introduced on 10 May 1968 and the second batch (400 females, 200 males) was released on 8 August 1969. The average total length of the latter was 80 mm, their weight 15 g (range 60–120 mm, 8–60 g) and they were estimated to be mainly age groups 3–5 years [67]. Both batches originated from Lake Tahoe, California. They were flown to Finland and taken to a fish farm, where specimens in good condition were selected for stocking. These were released from a boat at dusk at a rate of about one per 2–4 m of shoreline, such that every third was a male. Stocking was kept secret to avoid poaching. The crayfish population remained unexploited until 1981.

3. MATERIALS AND METHODS

3.1. Sampling methods

The relative abundance of the trappable crayfish subpopulation was monitored by trap catches. Trapping success is expressed as catch per unit effort (CPUE) to compare 'catchability' on different occasions and at different sites. Using CPUE requires, however, that the limitations of sampling with traps be taken into consideration. Traps are size-selective; < 50-mm crayfish seem to be only seldom caught with even fine-meshed ones [21, 22, 50]. Thus, CPUE in baited traps is only an indicator of the relative abundance of adult crayfish.

To avoid catch bias, and also trappability problems due to variations in crayfish activity and catchability caused by season, moulting and reproductive status [4, 13, 39], we used a trap model from which the crayfish cannot escape [63], standardised the trapping techniques, and took samples in late summer during an intermoult period of high activity for both sexes. Fresh or deep-frozen roach was used as bait.

Catch/trap statistics were calculated during the 23 study years (no trapping in 1980, 1982 and 1992) by a standardised sampling procedure. In seven years (1968, 1976, 1981, 1984, 1985, 1987 and 1988), trapping was carried out along the entire shore. In 1969–1975, 1977–1979, 1983, 1986, 1989–1991 and 1993, only the steep hard bottoms were sampled. The samples were taken on 33 nights (6 075 trap nights) between 20 July and 9 October. The surface water temperature varied during sampling from 9 to 19 °C. As the traps were examined three times a night until 1978, the total catch effort was 7 643 (*table II*).

In four years (24–25 June 1970, 15–16 June 1972, 1–2 July 1975 and 7–9 June 1988; 699 trap nights and 889 unit efforts) attempts were also made to catch ovigerous females.

The preferred habitats of *P. leniusculus* were studied from trap catches in 1981, 1984, 1985, 1987 and 1988, when the whole shore area was sampled (300 traps and nine trap nights). Since the traps were in much the same place on each sampling occasion, the catches per trap give a fairly good indication of the density of signals in a single limited habitat. From 1976, to ensure that the traps were always placed in the same location, they were fastened at 5-m intervals to a floating nylon line lying about 2–3 m from the shore (depth interval 0.5–3 m). CPUE correlates negatively with an increase in fishing effort, as gear competition occurs when the effective trap radius is greater than the linear trap spacing [43] resulting in a reduction in CPUE, irrespective of total stock density [40]. We therefore based the trap spacing on the effective trapping radius of 2.5 m according to studies [5], in which the capture range was about 13 m^2 for *P. leniusculus*.

In August–September 1988, juveniles in the best crayfish biotopes (depth interval 0–1 m) were sampled with a portable, hydraulic diver-operated dredge sieve [46]. Samples were taken in seven defined areas (each 1–2 m^2, total 10 m^2). As attempts to trap ovigerous females were an almost total failure, SCUBA was used to catch them during daylight hours on 8–9 June 1988 and 1 July 1988.

3.2. Population size estimates

Trapped crayfish were marked by electric cauterisation [1] and were returned to the capture areas immediately after marking and data recording. The Petersen method [48] was used in 1974, 1981 and 1988 and, in the last year, the Chapman method [11] as well, to convert mark recapture data into estimates of the trappable subpopulation size.

Table II. Trap catches (20 July–9 October) (no trapping in 1980, 1982 and 1992) and number of signal crayfish (*Pacifastacus leniusculus*) removed from Karisjärvi.

Year	Traps	Nights	Total catch	Catch/trap/night	Crayfish removed
1968*	49	1	0	0	0
1969*	81	1	0	0	0
1970	139	1	12	0.09	0
1971	200	1	11	0.06	0
1972	150	1	13	0.09	0
1973	200	1	15	0.08	0
1974	145–175	2	32	0.18	0
1975	75	1	20	0.27	0
1976*	125	2	13	0.07	0
1977	100	2	24	0.12	0
1978	200	2	24	0.07	0
1979	125	1	29	0.23	0
1981*	100–300	3	47	0.24	28
1983	185	2	129	0.43	129
1984*	286	1	90	0.45	90
1985*	300	1	120	0.60	120
1986	200	1	105	0.53	105
1987*	290	1	96	0.49	73
1988*	286–288	4	246	0.79	0
1989	200	1	108	0.54	0
1990	186	1	138	0.74	138
1991	158	1	319	2.02	148
1993	148	1	140	0.95	4

* Trapping around the lake, in other years only the best biotopes (1 250-m shoreline) were sampled.

In 1981 and 1988, the estimate covered the whole lake area, but in 1974 samples were taken only in the best biotopes. To avoid bias due to sex ratio differences, estimates were made in all three study years in late July–early October, a period of high activity for both sexes. The number of specimens marked was 32, 47 and 246 and the number recaptured 2–6 weeks later 12, 28 and 133.

To avoid behavioural dominance of large individuals in trap catches [2, 39], and thus also in the population estimate, the catch of the first trapping night was collected into a crayfish corf in 1988 using the double marking recapture method. In 1988, the mark recapture material was large enough to allow sexes and size groups to be treated separately; in 1974 and 1981, they had to be combined.

3.3. Handling the catch

Sex, carapace length (CL), female reproductive readiness, moult cycle stage (according to hardness of exoskeleton on a scale of 1–4), missing chelae, markings and melanised spots caused by the plague fungus were recorded for all 2 135 *P. leniusculus* caught; total length (TL) was also recorded on 380 specimens and wet weight on 417.

CL was measured with vernier calipers to the nearest millimetre from the tip of the rostrum to the posteriomedian margin of the cephalothorax. CL was converted to TL [67] using the following regression equation: males TL = 8.865 + 1.794 CL, females TL = 7.276 + 1.890 CL. TL is the length (cm) from the tip of the rostrum to the end of the telson of the stretched abdomen. CL is approximately half of TL (50–52 % for males and 49–51 % for females, when CL is 40–70 mm). For juveniles only TL was measured. Unless otherwise stated, the lengths given in the text are TL.

Reproductive readiness in females was determined from the visibility of cement glands on the abdomen. The age groups were visually estimated from the length–frequency distribution. Age determinations were facilitated by growth data on signals of known age from other lakes and culture facilities.

3.4. Hatching and growth of juveniles

Hatching was studied by individually placing five females with pleopod eggs caught on 7–9 June 1988 into cylindrical tubes (15 × 25 cm). A piece of netting divided each tube into two sections; the female was in the upper section and the hatched juveniles were dropped through the netting into the lower section. The experiment was completed on 1 July.

To study their growth and mortality, 25 and 50 second-stage juveniles were placed in two 1-m^2 net pens with plastic covers. Shelter was provided by lake bed material in the enclosures and by four perforated bricks. The pens were emptied for the first time on 25 August by dredge sieving. The experiment was continued later that same day by randomly placing 13 juveniles in the first net pen and 25 in the second. A sudden rise in water level after a rainstorm allowed some of the juveniles to escape from the pen before it was emptied for the second time, on 12 October.

3.5. Other studies

To make economical use of the stock and examine its ability to sustain trapping, all 'legally sized' (≥ 10 cm TL), and a number of even smaller (down to 60 mm) signals caught in August trappings were removed from 1981 onwards (except in 1988–1989 and 1993; no trapping in 1982 and 1992) (*table II*). The catch value was estimated from the mean price paid to fishermen in 1993, FIM 15 (EURO 2.5 in 1999) per crayfish.

Movement was monitored in individually marked specimens (N = 267) in 1987 and 1988; their mean size was 105 mm (range 74–144 mm) in 1987 and 106 mm (range 72–156 mm) in 1988. Movement was recorded on 120 specimens, most of which were trapped only once; a few individuals were trapped twice or more often.

Two commensal oligochaetes (Branchiobdellidae) not previously documented in Finland were found on the exoskeletons of *P. leniusculus* imported from California in 1967–1969 [44]. From 1981, all signal crayfish caught were visually inspected for the occurrence of Branchiobdellidae and parasites. Tissue samples taken from 12 randomly chosen signals were studied microscopically for the occurrence of *Psorospermium haeckeli*, white tail disease (*Thelohania contejeani*) and gill parasites.

Some of the introduced signal crayfish were infected with the plague fungus [45].

4. RESULTS

4.1. Development of *Pacifastacus leniusculus* population

A total of 6 075 trap nights (July–October) in the 24 study years produced 1 892 adult *P. leniusculus* (males 964, 51 %, females 928, 49 %) (*table II*).

Unexpectedly, none of the 618 stocked adult *P. leniusculus* were caught on the first trapping occasions (21 August 1968 and 17 September 1969, nor on 25 June 1970). In August 1970, 11 (CPUE 0.09) large signals (range 107–123 mm) probably released in 1969 (ca. 2 % of total stocked) and one smaller individual (75 mm) were caught. The latter was either a small individual stocked in 1969 or an offspring of the *P. leniusculus* introduced in 1968.

Estimated from the growth rate of *P. leniusculus* [27], the 1971 catch (11 specimens, range 111–133 mm) consisted solely of released individuals (2 % of total stocked). In 1972, the catch (14) comprised individuals of two size classes. Five larger (111–123 mm) signals were from the introduced population (1 % of stocked) and nine smaller ones (92–108 mm) were probably 2^+, i.e. had hatched in summer 1970. This was the first observation of signal crayfish reproducing in Finland. In 1973, we estimated that there were no more than three stocked specimens (121–145 mm) in the catch. About 80 % of the catch (11, range 70–118 mm) now comprised crayfish (mainly 3^+–$4^{+)}$ born in the lake. No stocked signals were caught in 1974. The Lake Tahoe *P. leniusculus* therefore lived in Lake K for no more than 4 years and became 7^+–9^+ years old.

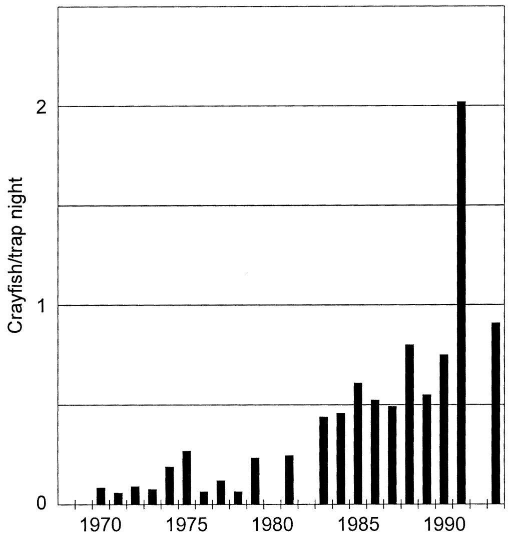

Figure 1. Mean trap catches (crayfish/trap/night) of signal crayfish (*Pacifastacus leniusculus*) in late summer in Lake Karisjärvi in 1968–1993. No sampling in 1980, 1982 or 1992. Harvesting begun in 1981, no removals in 1988, 1989 or 1993.

The mean CPUE was quite low throughout the 1970s, i.e. 0–0.27 (0–0.05 signals/trapped shore metre) (*figure 1*). Considering the great number of females stocked, we would have expected much larger 1^+–4^+ age cohorts to have been recruited for catching in 1972–1974. It was not until the mid-1980s, i.e. 16 years after stocking, that CPUE exceeded 0.5 (0.1 specimens/trapped shore metre). The largest catch during the study, i.e. 2 individuals/trap and night (0.4 specimens/trapped shore metre), was obtained in 1991 (*table II*). Despite annual variations, the mean CPUE increased after the early 1980s. No sampling has been carried out since 1993, but the owners of Lake K have sold licences for commercial catching. Unfortunately, no data on catches are available.

Water temperature was observed to have a marked effect on catch: the lower the temperature on the trapping night, the smaller the CPUE. The correlation between temperature and the unit catch of all trappings was 0.748 and the equation of the regression line: CPUE = –0.222 + 0.0481 water temperature.

In 1988 the mean weight of signal crayfish caught on the second trapping night (31.7 and 33.8 % of total catch) was significantly lower (differences in mean weight: males 4.5–19.4 g, i.e. 8.8–33.6 % and females

Table III. Numbers of signal crayfish (*Pacifastacus leniusculus*) males and females in different size groups estimated by the mark recapture methods of Chapman and Petersen in 1988.

	Male		Female	
CL (mm)	Chapman	Petersen	Chapman	Petersen
41–50	84	86	132	141
51–60	94	94	116	117
61–70	22	21	6	5
71–80	5	4	3	2
Total	205	205	257	265

Marking 11–12 August and recapture 23–24 August.
CL, carapace length (mm).

2.6–7.6 g, i.e. 6.6–18.1 %) than that of crayfish caught on the first trapping night (two-tailed *t*-test $P < 0.001$ ***).

4.2. Population size and density

The catchable *P. leniusculus* subpopulation was estimated to have comprised no more than 60 ± 29 specimens in 1974, and 95 ± 33 specimens in 1981 (an increase of only 56 % since 1974). Thereafter the population grew robustly, reaching 424 ± 62 specimens in 1988 (up 446 % since 1981). Even then, 19 years after stocking, the trappable population was smaller than the number (600) introduced in 1969. The biomass of the subpopulation based on individual mean weights was 2 284 g in 1974, 6 778 g in 1981 and 18 041 g in 1988.

When sexes and size groups were treated separately, the size of the trappable subpopulation in 1988 was estimated to be about 462 by the Chapman method and about 470 by the Petersen method. Thus, estimated by the Petersen method, the population was 10.8 % greater than when sexes and size were not separated. The size of the male population was estimated to be the same (205) by both methods, but the female population was slightly larger (8 %) by the Petersen (265) than the Chapman method (257) (*table III*).

As expected, most individuals were in the smallest size group (TL 82–100 mm). Females, which grow more slowly than males, outnumbered males in the two smallest size groups (which comprised several year classes). Females likewise outnumbered males among the crayfish of trappable size, partly no doubt because the largest males cannot fit through the narrow entrance funnels of the Evo traps.

The above estimates show that the mean density of the trappable signal crayfish population in suitable biotopes ranged from 0.01 ind·m^{-2} in 1974 to 0.07 ind·m^{-2} in 1988, or from 0.04 to 0.29 per shore metre.

Assuming that the capture range of a trap in Lake K was about 13 m^2 (cf. Methods), the total capture area of the 148 traps used in 1993 was about 1 924 m^2. Consequently, the mean density of the catch (140 specimens) in this area was 0.07 ind·m^{-2}. At its highest, in 1991, the density was about 0.2 ind·m^{-2}. The density in the best biotopes was considerably higher, as three to five crayfish were caught in each trap, giving a density of at least 0.2–0.4 ind·m^{-2}.

4.3. Habitats preferred by *P. Leniusculus*

The occurrence of signal crayfish varied greatly in different parts of the lake in the five study years (1981, 1984, 1985, 1987, 1988) (*figure 2*). The same was observed in marking and recapture trapping in 1988 (*figure 3*). Four different domains were distinguished on the basis of catches. For comparison, the proportion of signals caught in the domains on four nights in August 1988 (total catch 379 specimens) is also given.

Domain 1: mean CPUE > 1 (range 1–2, largest single catch 5 per trap). Near the shore the bed is quite steep and rocky. The shore made up only 11 % (160 m) of the total shore length but accounted for about 37 % (140 individuals) of the 1988 catch.

Domain 2: mean CPUE 0.6–1.0. Bottom covered by boulders of various sizes and by submerged trees. There was less shelter and the bed sloped more gently than in domain 1. The shore made up 29 % (415 m) of the total shore length and accounted for 40 % (150 individuals) of the catch.

Domain 3: mean CPUE 0.2–0.6. Bottom partly sand and partly gravel. Very little shelter. The shore made up 35 % (500 m) of the total shore length and accounted for 21 % (80 individuals) of the catch.

Domain 4: mean CPUE < 0.2. Bottom soft and boggy, unsuitable for burrowing and without shelter. The shore made up 26 % (375 m) of the total shore length and accounted for only 2 % (9 individuals) of the catch.

The above data suggest that *P. leniusculus* prefer steeply sloping lake beds with abundant boulders and submerged trees or a substratum, e.g. clay, suitable for burrowing. SCUBA diving revealed numerous burrows up to 1 m deep dug into clay banks by signal crayfish. Vegetation was sparse in these parts of the lake bed owing to the hardness of the bottom. There seemed to be fewer signals on the steepest slopes of the bed (> 30°) than on somewhat gentler slopes. Crayfish were only rarely trapped or seen on flat muddy and marshy bottoms. Both sexes were evenly represented in catches in all habitats.

4.4. Harvest and population structure

During the 9 years of exploitation, 835 (60–150 mm) crayfish were removed. The total number of males harvested was 437 (51 % of total male catch) and of females 398 (48 % of total female catch). The number of ‘legally sized’ (≥ 10 cm) males removed was 332 (76 %) and of females 264 (66 %). Calculated at 1993 prices, the value of the total harvested catch was FIM 12 525 (EURO = 2 106).

In the early years the catches comprised large, stocked individuals, but by 1973 signals born in the lake formed the majority (*figure 4*). Harvesting culled the number of large individuals after 1981. In most years, the mean size of crayfish trapped ranged from

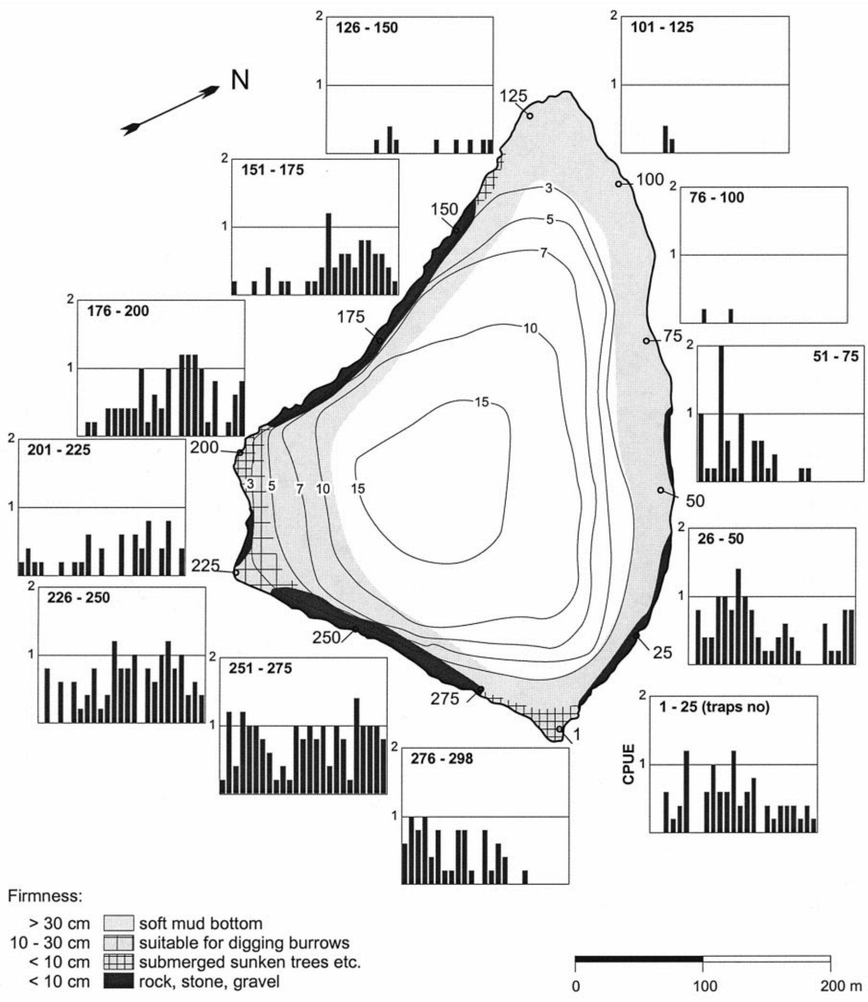

Figure 2. Mean catch per trap and night of signal crayfish (*Pacifastacus leniusculus*) in different parts of Lake Karisjärvi in 1981, 1984, 1985, 1987 and 1988 and the quality of the bottom of the littoral area. Bottom firmness was estimated with a measuring stick. Traps were fastened at 5-m intervals to a floating line (25 traps/line, lines indicated by circles, 1–25 = number of traps) located about 2–3 m from the shore (depth interval 0.5–3 m).

90 to 130 mm. The size composition of the catch varied greatly from year to year. The annual mean length of signals in trap catches in 1970–1993 (N = 1 934) diminished after 1981 owing to harvesting. No crayfish were removed in 1988 and consequently the mean length of the *P. leniusculus* in the catch in 1989 increased (*figure 4*).

The smallest male measured 54 mm and female 62 mm (*figure 5*). The largest individual was 159 mm and the heaviest 175 g (male, 150 mm); its chelipeds weighed 84 g (48 % of the weight).

Judging by CPUE, there seems to have been a slight cyclical fluctuation in population strength, with strong and weak year-classes alternating every 2–4 years (*figure 1*). In 1975, 1979, 1983, 1985, 1988 and 1991 a considerably stronger cohort was recruited for catching than in the preceding years, i.e. reproduction had succeeded well a couple of years earlier.

4.5. Reproduction

The female/male ratio was 2:1 at stocking. In the first 3 years (1970–1972), trap catches consisted of stocked individuals and the sex ratio remained nearly unchanged (proportion of females 62–67 %). Thereafter, when the bulk of the catch consisted of signals born in Lake K, the sex ratio was almost 1:1.

The size at which 50 % of the females matured (LM 50) [58] was 90 mm. Consequently, half of the females entered the breeding population in the autumn of their third year (3^+). None of the females in the 60–70-mm size class were ready to reproduce. In the 70–80-mm size class 19 %, in 80–90-mm 42 %, in 90–100-mm 89 %, in 100–110-mm 94 % and in > 110-mm 91 % of females were ready to reproduce (*figure 6*).

The smallest mature female was about 64 mm, which means that the fastest-growing females could

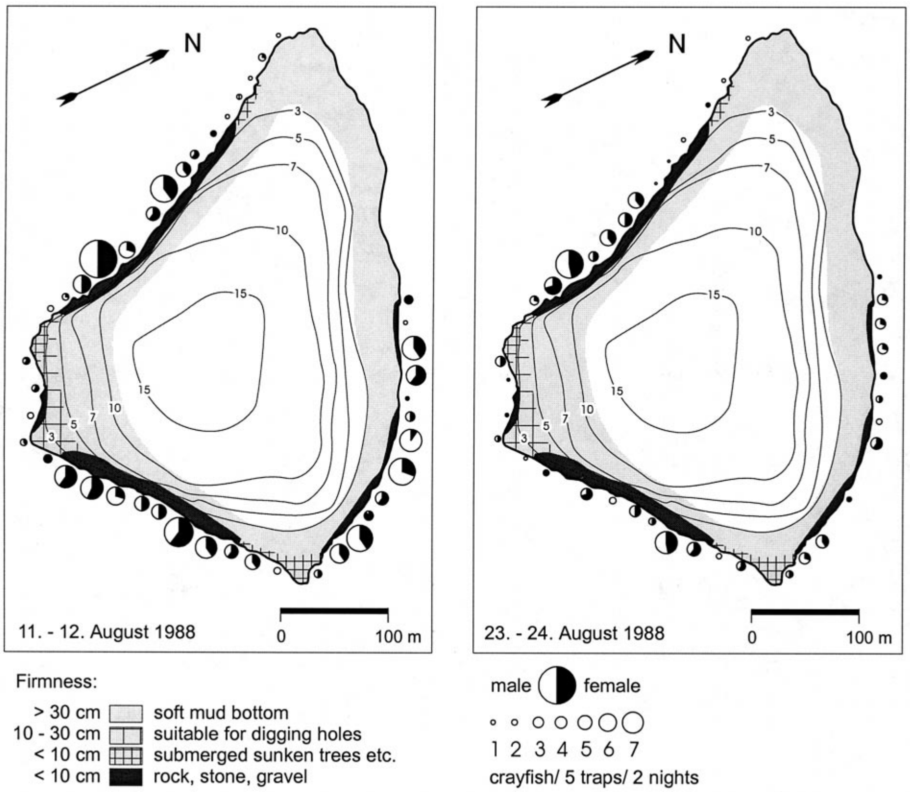

Figure 3. Distribution of signal crayfish (*Pacifastacus leniusculus*) in Lake Karisjärvi according to trap catches in marking and recapture trappings in 1988 (see caption to *figure 2* for further explanations).

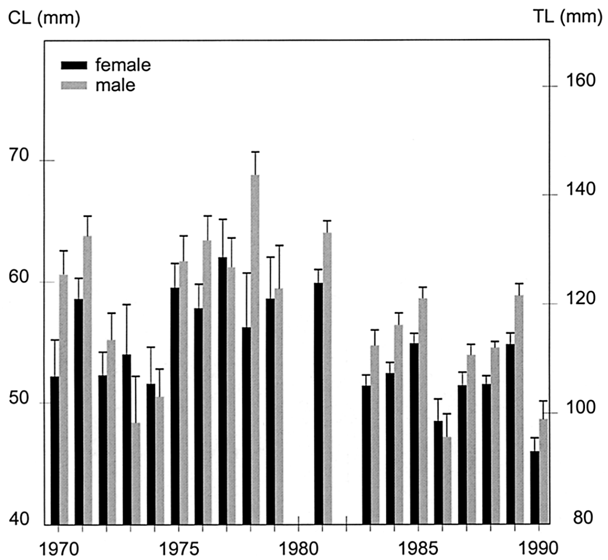

Figure 4. Length distribution of trap catches of signal crayfish (*Pacifastacus leniusculus*) in Lake Karisjärvi in 1970–1990 (no sampling in 1980 or 1982). CL, mean carapace length (mm) (vertical bars are confidence limits ± 95 %); TL, mean total length (mm).

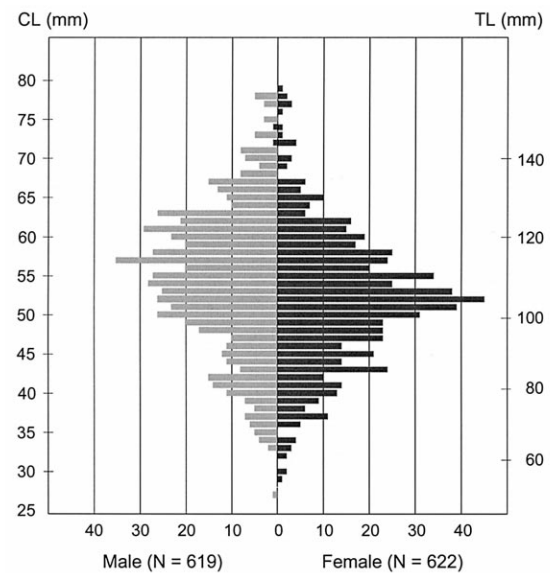

Figure 5. Length–frequency distribution of trap catches of signal crayfish (*Pacifastacus leniusculus*) in 1981–1990 (no sampling in 1980, 1982 or 1992). CL, carapace length (mm); TL, total length (mm).

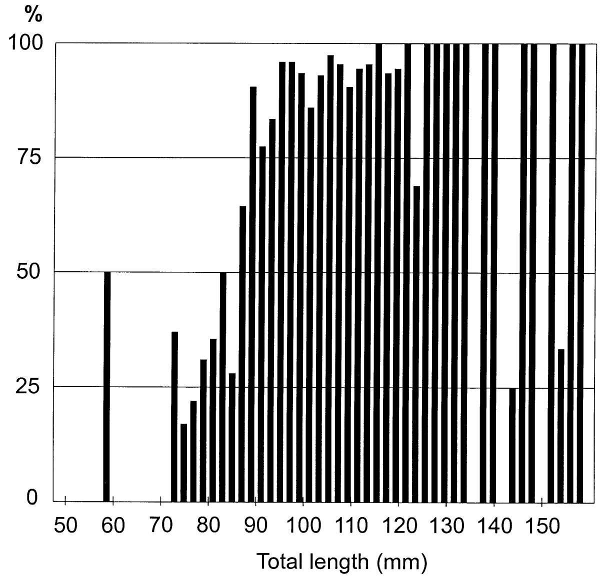

Figure 6. Percentage of reproductive signal crayfish (*Pacifastacus leniusculus*) females (= visible cement glands) in different size classes in trap catches in late summer (N = 622) in the study years 1970–1993 (no sampling in 1980, 1982 and 1992).

already breed at 2^+. The largest female ready to reproduce was 158 mm, which, according to the growth rate in this lake [27], corresponds to at least 6^+. Thus, the oldest females can apparently spawn several, possibly even four or five, times. Judging by the absence of visible cement glands, however, not all sexually mature females are ready to spawn every year. Even in the case of > 90-mm females, only about 90–95 % were ready to reproduce annually (*figure 6*).

The results of attempts to catch ovigerous females in early summer (7 June–2 July) in 1970, 1972 and 1975 were unexpectedly poor: either no females at all were caught or the only two caught had no eggs. In 1988, however, nine females were trapped and one was caught by SCUBA diving. The variation in their number of pleopod eggs was great. Visually estimated, one female had about 400, four about 100, two a few and three no eggs. One female had remnants of hatched eggs.

Altogether five females had about 800 pleopod eggs. Juveniles hatched, on average, within a day or so of 24 June 1988 and moulted for the first time about 7 days later. The females had juveniles as follows: 1) 372 (+ 4 dead eggs), 2) 76 (+ 4 dead eggs), 3) four, and 4) two. The fifth female had moulted. Consequently, 454 (60 %) second-stage juveniles hatched from the 800 pleopod eggs.

4.6. Juvenile growth

The difference in growth rates between the juveniles kept in net pens was already more than two-fold in the first summer in 1988 (*table IV*). Juveniles growing at a lower density were significantly longer than those at a higher density (two-tailed *t*-test; $P < 0.001$***). Mortality in the period 1 July–25 August 1988 was unexpectedly lower among the juveniles at high density (18 %) than among those at low density (52 %). The reason, however, is not known. The few juveniles sampled by dredge sieving at the end of August were somewhat smaller than those kept in net pens (*table IV*).

At the end of the growing season (12 October), the average length of juveniles in net pens was 30.3 mm (26–33 mm). Three of them had just moulted, although the surface temperature was only 8.6 °C. As the juveniles were about 10 mm long when hatched, they grew an average of 20.3 mm (15.7–22.8 mm) during their first summer.

4.7. Movement

Signal crayfish proved to be fairly settled in their residential pattern, as nearly 75 % (of the 120 recorded) travelled < 100 m between marking and recapture (interval 0–15 months). A few individuals nevertheless travelled very long distances, even 580 m, i.e. to the other side of the lake. There was no significant difference between the average travel distances of female (109 m) and male (75 m) crayfish (two-tailed *t*-test; $P = 0.114$).

4.8. Injuries, diseases and parasites

Cheliped losses were suffered by 11.2 % of the total catch (N = 1 719). This proportion was almost equal for both sexes (females 11.3 %, males 11.1 %).

Melanised spots indicated that some of the imported and stocked *P. leniusculus* were infected with plague, yet we did not find any signs of the disease having affected the lake's signal population and no deaths have been reported, even though the infected crayfish have been stressed by trapping and handling for research purposes [45].

Branchiobdellidae were found in just under one-third (30.6 %) of the crayfish trapped (N = 1 719), in males more often (36.2 %) than in females (24.7 %). Annual fluctuations were, however, large. In 1984, for

Table IV. Growth (total length) of juvenile signal crayfish (*Pacifastacus leniusculus*).

Date	Net pen 1 TL (mm)	Net pen 2 TL (mm)	Dredge sieving TL (mm)
1 July 1988	9.7 (9.2–10.8) (N = 25)	9.7 (9.2–10.8) (N = 50)	–
25 August	28.0 (22.0–34.8) (N = 12)	23.5 (13.8–28.3) (N = 39)	22.2 (16.5–29.3) (N = 4)
12 October	29.9 (N = 1)	30.8 (28.4–32.5) (N = 5)	29.3 (25.7–32.8) (N = 2)

example, no commensals at all were found, but in 1988 they were observed in 48.4 % of the signals investigated (N = 398). The occurrence of Branchiobdellidae correlated (0.3573**; N = 1 699) with the length (0.4505**; N = 379) and weight (0.4687**; N = 416) of *P. leniusculus*. Most commensals were observed in the chelipeds of large males.

Branchiobdellidae were distinctly more common on signals caught on the sunny and warmer north-eastern shore than on those trapped elsewhere. The number was highest on crayfish caught in trap nos 25–50 (*figure 2*) (in 53.4 % of the catch) and in trap nos 51–75 (in 45.7 % of the catch). On the south-western shore, where the *P. leniusculus* population was most dense, only 20.5 % of the catch (trap nos 176–200) were infected.

Branchiobdellidae did not apparently harm their hosts. The species was either *Xironogiton instabilius* Moore or *Cambarincola* sp., both of which were found in the signal crayfish imported from California in 1967–1969 [59] and had not previously been known in Finland [44].

Psorospermium haeckeli were not found in any of the 12 crayfish investigated, nor was white tail disease (*Thelohania contejeani*). Epibionts (*Cothurnia* sp.) were found on the gills of four specimens.

5. DISCUSSION

5.1. Methods

CPUE is a good indicator of the relative abundance of crayfish [52]. Population density estimates based on trapping have been found in many studies to be quite similar to those obtained by other methods, such as SCUBA diving [9].

Our observation that the specimens caught on the second trapping night were significantly smaller than those caught the previous night indicates that large individuals somehow prevent smaller ones from entering the traps. Other authors [4, 39] have likewise found that males, being more mobile and aggressive, and also armed with larger chelae, are able to push their way into the traps more actively than smaller specimens or even females of the same size. Partly for this reason, the proportion of smaller individuals in trap catches is lower than their actual presence in the total population would require. Owing to this size-selective vulnerability, CPUE can only be used as an indicator of the relative size of adult crayfish subpopulations. The possibility, however, that the largest specimens might not fit through the mouth of the trap does not appear to have been studied at any great length.

If the total trapping radius does not completely cover the sample area [50], the resulting population estimate will be too low. Considering the small area of Lake K, the close spacing of the traps around the lake (in 1988) and the narrowness of the littoral zone suitable for signal crayfish, we assume that the main habitats were covered relatively well. As no traps were set outwards from the shore, their capture range clearly could not cover all habitats, and we probably underestimated the size of the trappable subpopulation.

5.2. Development of *P. leniusculus* population

Productive signal crayfish populations have developed from small stockings in a number of European countries; under favourable conditions, in a matter of years (discussed in Lowery and Holdich [37]). In Finland, too, a mere 900 second-stage juveniles, corresponding to the progeny of only a few large females [49], have given rise to *P. leniusculus* populations [66]. Taking into consideration the large size and female dominance of the stocking (400 adult females) and the fecundity of *P. leniusculus* [49], the signal crayfish population ought to have increased rapidly in Lake K as well. This, however, did not happen.

Population growth was also slow in nearby Iso-Majajärvi, another small lake into which signal crayfish from the same batch had been released [67]. When Lake Tahoe signals were introduced into Sweden in 1969, only 10 % of stockings succeeded. The unexpectedly poor results were attributed to the stress of the trans-Atlantic crossing, local transportation in the heat of summer, and excessive locomotory activity within the first few days of release [14, 54].

In Finland, however, the signals were given time to recover and only individuals in good condition were stocked. Even so, despite major catch efforts, only about 2 % of the stocked *P. leniusculus* were recaptured in Lake K annually in the early 1970s. As the signals could not escape from the lake, the small and rapidly diminishing size of catches indicates high mortality after release of the crayfish. The same has been suspected in Lake Iso-Majajärvi, in which only 6 % of the Lake Tahoe signals were recaptured within a couple of years of stocking [67].

The slow development of the *P. leniusculus* populations in both Lake K and Lake Iso-Majajärvi might also be due to disturbances in reproduction, as suggested by the small number of pleopod eggs on females caught in early summer in Lake K and Iso-Majajärvi [49, 67], and the poor result of the juvenile sampling trials in the two lakes. Disturbances in reproduction may be due to differences between the Finnish lakes and Lake Tahoe, where water temperature does not fall below 5 °C, even in winter [13, 17]. The failure of some attempts to introduce *P. leniusculus* into French lakes has been attributed [30] to the coldness of the water in spring. Low water temperature has been found to have an adverse effect on crayfish reproduction (see references in [49]).

One factor affecting reproduction success is the pH of the water. Acid stress weakens egg attachment and hampers the sensitive embryonic development [7]. Some of the *P. leniusculus* stocking failures in Sweden have been attributed to low pH [14]. The pH in Lake K has periodically been quite low (6.3), at any rate clearly lower than in Lake Tahoe (7.8–8.2) [5, 17]. The small number of pleopod eggs found in Lake K females might be attributed to one or all of the following factors: disturbed fertilisation; bad attachment in pleopods; loosening due to acid stress; and the lengthy and cold hatching period.

Other water properties, too, may have contributed to the slow development of the population, especially as the Lake K signals have had little time to adapt to their new habitat. The Ca concentration in Lake K has apparently been adequate (2.1–4.4. mg·L^{-1}) for recalcification of the exoskeleton after moulting [7, 26, 56] but it is still much lower than in highly productive crayfish waters; in Lake Tahoe, for example, the calcium concentration is 8.8–9.9 mg·L^{-1} [18].

By impairing reproductive potential, heavy harvesting – even of immature signals – has certainly contributed to the slow growth of the population. As about 34 % of the removed females were < 10 cm, some of them could not have reproduced at all before being caught. This does not, however, seem to have resulted in overfishing of the reproducing females, as the population has gradually increased in size. *P. leniusculus* can, therefore, withstand trapping pressure well. The same has been observed in a number of other experimental lakes [12, 14, 22, 55, 67]. In the Sacramento Delta, California it was found [40] that the signal crayfish could sustain exploitation rates of 28–49 % in areas with abundant populations.

5.3. Habitats

The occurrence of signal crayfish in Lake K demonstrates clearly that adult signals thrive on rocky and gravel substrata, even if important vegetable food is very scarce. Similarly in Lake Tahoe and elsewhere, *P. leniusculus* appears to prefer a rocky substratum, and medium-sized boulders support the most dense populations [5, 13, 34]. The signals in Lake K were also found in other habitats providing shelter, e.g. under trees or roots. Similar observations have been made by other authors [8, 20].

Signal crayfish is a burrowing species, occupying holes dug in clay banks [19, 20]. Our observations confirm that adult *P. leniusculus* thrive on sloping bottoms suitable for burrowing. In contrast, we only occasionally found adult signals on gently sloping soft bottoms, muddy shores or sandy bottoms. The same has been observed elsewhere [8, 13, 50].

The substratum is the single most important variable related to total crayfish abundance [9]. Lakes in which < 15–20 % of the littoral zone is occupied by rocky substrata can support only very low crayfish populations [35]. In Lake K, the importance of habitat is further indicated by the great variation between catches in different parts of the lake (mean CPUE 0–2, *figure 2*) and the fact that > 90 % of all *P. leniusculus* were caught in only one-third of the shore area. This scarcity of the substrata needed by signal crayfish is probably the main reason why, even in the last years of the study, the CPUE was still considerably smaller than in many other lakes in Finland and elsewhere in Europe. For example the mean CPUE for all test fishing in Swedish waters stocked with newly hatched *P. leniusculus* juveniles in the early 1970s was already about 4, and in the best waters > 10, signals per trap per night by the mid-1980s [12]. In a small English lake, the signal catch rose to 10.4 per trap per night within 4 years of stocking newly hatched juveniles [21], and in Lake Divonne, France, the CPUE was 7.7, ten years after signals had been introduced [32].

Likewise, the estimated mean density of the trappable *P. leniusculus* population was very low in Lake K (in 1988 about 0.3 specimens per shore metre and 0.07 ind·m^{-2}) and even in the best biotopes (about 0.4 ind·m^{-2}) was low when compared with most published estimates. In some North American lakes, the average density of adult signals ranged from 0.23 to 1.13 ind·m^{-2} [5, 13, 18, 34] and in European lakes from 0.4 to 4 ind·m^{-2} [3, 8, 20, 21].

Even though the substratum often appears to be the most important single factor governing such matters as the population size and productivity of crayfish, it has been emphasised [35, 42] that many populations in marginal habitats are in fact subjected to multiple stresses. Successful introductions of *P. leniusculus* into a very wide range of habitats in Europe demonstrate the ability of the species to exploit diverse conditions discussed by Lowery and Holdich [37], and yet certain features of Lake K have inhibited population increase there. We assume that, as well as the small total area of preferred habitat, these include the periodic acidity and low Ca concentration, and that signal crayfish in Lake K are, therefore, having to contend with multiple stresses. We know nothing, however, of the interactions, if any, between the various limiting factors in the lake.

5.4. Reproduction

The sex ratio of natural crayfish populations is about 1:1 [3, 39]. In our study the sex ratio of the stocked, predominantly female, population changed from 2:1 to ca. 1:1 in the first year, when the bulk (ca. 90 %) of the catch comprised individuals born in the lake. The same was observed in Lake Iso-Majajärvi [67].

Only a few egg-bearing females were trapped in early summer (8 June–2 July) despite substantial catch efforts (total 889); the same was observed in Iso-Majajärvi [67]. The most likely reason was the trap shyness of the egg-bearing females [3, 25, 39]. Only when the juveniles have left do females enter traps as they begin an intensive search for food in preparation for the summer moult.

In crayfish, maturity is related to size rather than age, early maturity being due to higher growth rates [58]. The size at maturity of signal females varies in different populations. The minimum TL has ranged from 59 to 80 mm [3, 20, 21, 34, 39, 40, 56], but the average size is larger, ranging from 75 mm [38] to 90 mm [5]. In Lake Slickolampi, the females ranged from 76 to 95 mm at the onset of sexual maturity [64] and in Lake Iso-Majajärvi from 73 to 92 mm (LM 50

= 84 mm) [67]. In Lake K, in contrast, crayfish females matured (70–80 mm, LM 50 = 90 mm) at about the same size as in their 'home lake', Tahoe. The variations noted between populations may be environmental in origin [47].

Depending on their growth rate and size at onset of sexual maturity, signal crayfish females enter the breeding population at different ages in different waters. The fastest growing females have been found to attain maturity at age 0^+ [40] although for most females the age is 2^+ [3, 20, 32, 34, 38, 50] and in some waters, including Lake Tahoe, only 3^+–4^+ [5]. In the Finnish lakes, i.e. Slickolampi [64], Iso-Majajärvi [67] and Lake K, the smallest females entered the breeding population at 2^+.

It has long been known that not all sexually mature crayfish females spawn every year (see references in [49]). For example, in Lake Slickolampi the proportion of mature *P. leniusculus* females not ready to spawn ranged from 28 to 50 % [64], and in Lake Iso-Majajärvi the proportion was about 41 % [67]. Similarly in Lake K, in some years up to 59 % of the trappable females were not ready to spawn. According to some studies [3, 5], female *P. leniusculus* reproduce every year after reaching adult size. The complex interactions between crayfish and the factors that influence spawning frequency have been reviewed elsewhere [36, 49].

In Lake Iso-Majajärvi [67], the largest ovigerous females were 14 cm. Even larger (15 cm) reproductively active females were trapped in Lake Slickolampi [64] and Lake K (15.8 cm). Since most (10-cm individuals were effectively removed from the above lakes, even 15–16 cm is not necessarily the maximum size at which signal crayfish females may still reproduce.

5.5. Growth and life span

Juveniles in Lake K (0^+ juveniles 30 mm TL) grew at about the same rate as those (0^+ juveniles 26–33 mm) in Lake Slickolampi about 200 km further south [65] but considerably slower than juveniles in southern Sweden (Rögle ponds) (0^+ females about 38 mm and males 40 mm) [3].

Moulting and, thus, growth cease in signal crayfish, as also in many other crayfish species, when the water temperature drops to 10 °C or lower (see references in [6]). Judging by their late moult (12 October), *P. leniusculus* juveniles in Lake K were still growing at < 10 °C (8.6 °C). Growth in length may cease, but it has been observed [29] that *A. astacus* juveniles were still gaining weight at 5–7 °C. Here, too, the biomass of juveniles increased considerably in late summer. The growth and moulting of adult signals in Lake K has been discussed elsewhere [27].

P. leniusculus may grow to as long as 18 cm [41], i.e. about 2 cm more than found in Lake K. The maximum size of signals may, however, be considerably bigger than the 16 cm we recorded, as individuals much larger than that were unable to fit through the narrow entrances of our traps.

The introduced 3^+–5^+ signal crayfish only appeared in catches for 4 years, i.e. they reached an age of 7–9 years. Similarly in Sweden [54], *P. leniusculus* imported as adults from North America were trapped for 4 years after stocking and in Lake Iso-Majajärvi for 5 years [67]. Other authors [5, 14, 38] have reported that the life span of *P. leniusculus* is as long as 8–12 years. Crayfish occurring at high latitudes and in colder environments usually have a longer life cycle than those at mid and low latitudes [42].

5.6. Movement

It has been observed that signals could wander 700 m in 50 days [33] and as much as 700 m in 12 days [4], i.e. on average 58 $m \cdot d^{-1}$, even crossing a river 20 m deep. We also found a few well-travelled individuals, the longest migration here being 580 m in 1 year. Similarly some *A. leptodactylus* specimens wandered about 200 m in 1 day and about 600 m in 19 days [28]. On the contrary, *A. astacus* seemed to be much more stationary

5.7. Injuries, Branchiobdellids and crayfish plague

The frequency of non-lethal injuries, cheliped losses in particular, is a common indicator of the intensity of intraspecific competition. Cheliped loss ranging from 11 to 32 % was observed [2] in a dense, unexploited *A. astacus* population. Lower values were observed in an exploited population (loss range 1.5–16.1 %) [51]. In other studies cheliped loss in the range of 4.6 % has been reported for *A. astacus* [25], 8–34 % for *A. pallipes* [31] and 7.5–16.5 % for *P. leniusculus* [67]. The frequency of cheliped losses observed here (11 %) may be an indication of quite small degree of intraspecific competition, as may the even sex ratio (1:1), as an unnatural ratio is a sign of fierce competition [2].

Branchiobdellids are common epizoids on most freshwater decapods [23]. The introduction of two new Branchiobdellidae species [44] into Lake K with the imported signal crayfish, and probably also into the seven other lakes stocked with signals from the same shipment [59], shows that these commensals (or their eggs) had survived the long transport without water. The continuous occurrence of Branchiobdellidae in Lake K *P. leniusculus* is a further indication that these commensals have been able to adapt to a new habitat. Similarly in Sweden, the imported *P. leniusculus* were reported to carry a great many *Xironogiton instabilis* but neither this species nor other exotic Branchiobdellidae have later been recorded [15]. The spread of these harmless epibionts to Finland demonstrates the risk involved in transferring aquatic animals originating in natural waters. Due to the risk of spreading diseases and parasites, no more signals have been imported from North America to Finland since 1969.

There has been considerable debate as to whether *P. leniusculus* is plague resistant and could replace native crayfish species in plague-infected waters. Some researchers [10] have even suggested that the species might not be as plague resistant as earlier observed [57]. If that is so, the plague poses a major threat to *P. leniusculus* stockings in chronically plague-infected former *Astacus* waters.

Judging by the presence of melanised spots, some of the *P. leniusculus* imported from North America were infected with plague [45]. The disappearance of the *A. astacus* population from Lake K after the first signals (18) were stocked, in 1968, most probably resulted from plague infection, as dead noble crayfish were found 3 weeks after the signals had been introduced. The same is thought to have occurred in Lake Iso-Majajärvi [67]. Back in 1964, a mass die-off of *A. astacus* was observed in a pond at Rögle, Sweden, into which *P. leniusculus* had been introduced the previous autumn [3]. Plague has likewise exterminated *A. astacus* populations from some other Swedish lakes stocked with North American *P. leniusculus* imports [12, 16].

Plague-infected specimens represented a fairly high proportion, about 52 % of the trappable catch in Lake K in the first study year, 1979 [45], 10 years after stocking. Thereafter, the proportion declined, being about 24 % in the latest, 1993, study (Nylund and Westman, unpublished data). Crayfish plague has not appeared to affect the *P. leniusculus* population and no deaths have been reported despite the stress caused by trapping and the handling associated with research activities. The same was observed in Lake Iso-Majajärvi [67]. Thus, the introduced *P. leniusculus* stock seems to have good resistance to plague and to be suitable for management of chronic plague waters.

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