BOREAL ENVIRONMENT RESEARCH 4: 387–407 ISSN 1239-6095
Helsinki 15 December 1999

Development of the introduced North American signal crayfish, *Pacifastacus leniusculus* (Dana), population in a small Finnish forest lake in 1970–1997

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Westman, K., Savolainen, R. & Pursiainen, M. 1999. Development of the introduced North American signal crayfish, *Pacifastacus leniusculus* (Dana), population in a small Finnish forest lake in 1970–1997. *Boreal Env. Res.* 4: 387–407. ISSN 1239-6095

Signal crayfish (*Pacifastacus leniusculus* Dana) originating from Lake Tahoe, California, were introduced into a small (11 ha) lake, Iso-Majajärvi, in Central Finland (61°52´N, 23°51´E) in 1969. Since then, the population has been monitored regularly by trap catching. The stocked signal crayfish (3+ to 5+ years old) were caught until 1975, by when they reached ages of 8+ to 10+ years. First juveniles were born in 1970. Catches and population sizes were low during the study period. The catch peaked in 1983 at 0.6 ind./trap/night. The population size was estimated at 670 trappable specimens. Population size then declined, and has since fluctuated between 200 and 400 individuals. Despite annual variations, mean CPUE indicate a small, but statistically significant, increase in later years. The slow development of the *P. leniusculus* population has been attributed to environmental factors, especially the combination of limited area of suitable crayfish habitat and the low Ca concentration with periodic acidity. Fifty percent of the female *P. leniusculus* matured at ca. 84 mm. Consequently, half of the females entered the breeding population in the autumn of their third year (3+). The signal crayfish imported into Finland and stocked were infected with crayfish plague (*Aphanomyces astaci)*, but no mortality has been recorded.

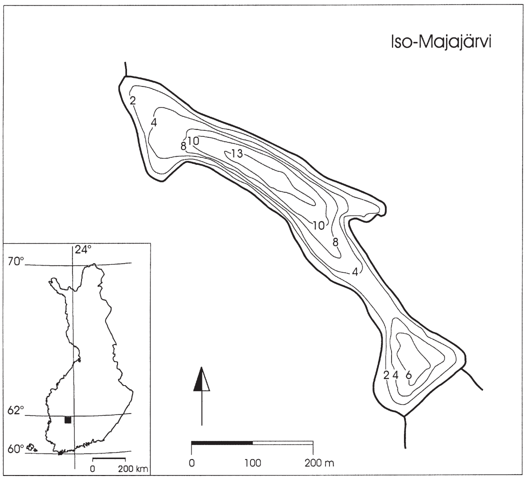

Fig. 1. Bathymetric map of Iso-Majajärvi.

Introduction

Since 1893, populations of the native noble crayfish, *Astacus astacus* (L.), in Finland have been heavily depleted by the crayfish plague (*Aphanomyces astaci* Schikora). The annual catch decreased from around 20 million individuals at the turn of the century (Järvi 1910) to 2.5–4.8 million in recent years (Leinonen 1995, 1998). This is less than domestic demand and, since 1967, Finland, once Europe's biggest exporter of crayfish, has had to resort to import (Westman 1991).

The plague fungus, which is accompanied by intense selection pressure, has been present in Europe for more than 130 years, but no resistant strains of *A. astacus* or, indeed, of any other indigenous species, have been identified (e.g. Unestam 1969, 1972, Alderman and Polglase 1988, Svärdson 1992). Efforts to combat the plague in Finland started in the early years of the century. Despite extensive restocking, *A. astacus* seem, however, incapable of re-establishing itself in chronically infected waters. The situation with no new methods of combatting the plague and the promising results from stocking the North American signal crayfish (*Pacifastacus leniusculus* Dana) in Sweden (e.g. Abrahamsson 1964, Svärdson 1965), it was decided to stock with this plague-resistant species in Finland, too (Westman 1973). Signal crayfish has now been introduced into at least 21 countries in Europe, and the stocking programmes are still expanding (e.g. Holdich 1988, Huner 1988, Lowery and Holdich 1988, Westman *et al.* 1990, Westman and Westman 1992).

Despite this extensive stocking, research results have been published for only a small number of the programmes (reviewed by Lowery and Holdich 1988), and published observations of the long-term development of the species only represents a handful of lakes (e.g. Svärdson *et al.* 1991, Westman *et al.* 1995, Kirjavainen and Westman 1995). By contrast, a fair number of general reviews of trends in signal crayfish catches have been published in Sweden (e.g. Fürst 1977a, 1977b, Fjälling and Fürst 1988).

Long-term monitoring is essential — especially 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 like 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 aim of the present study was to see if the *P. leniusculus* established a self perpetuating stock, and how the development of the stock would be over two-three decades in such a low Ca concentration and slightly acid environment. Some information on the reproduction and population structure are also presented. The research was conducted in 1970–1997. Some preliminary results have been published elsewhere (Westman and Savolainen 1995).

Study site

The lakes initially chosen for stocking studies in Finland were small and without outlets. This was to ensure that the introduced crayfish could not escape, and also to make it as easy as possible to monitor and study them (Westman 1973). Iso-Majajärvi (hereafter referred to as Lake I-M) was chosen because of both its size and familiarity from earlier studies (Sumari 1971). The small *A. astacus* population in the lake became extinct in the 1960s.

Lake I-M is an oligotrophic 11.1 ha forest lake in a natural state in Central Finland (61°52´N, 23°51´E) with a mean depth of 5 m (max. depth 14 m) (Fig. 1). Of the littoral area of the lake bed to a distance of about 5 m from the shore, 49% (1.093 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 lake hosts only a few macrophytes, all of them oligotrophic species (e.g. *Myriophyllum alterniflorum*, *Nuphar lutea*, *Phragmites australis*, *Carex* spp, *Nymphaea candida*, *Potentilla palustris*, *Calla palustris*, *Menyanthes trifoliata)*.

One small brook enters Lake I-M and another flows out of it. The lake is mainly surrounded by coniferous forest (*Picea abies, Pinus sylvestris*). There is, however, a narrow deciduous belt along the shore (*Alnus glutinosa*, *A. incana*, *Betula* sp.), and the leaves from these are supplement to the crayfish with nourishment and the juveniles with shelter.

The ice-free period usually last from May to November. The lake stratifies in summer (cf. Sumari 1971). In 1970–1994, the average temperature of the surface layer, measured during trappings, was 11 °C at the end of May, 17.5 °C in June, 19 °C in July, 18 °C in August and 13 °C in mid-September. For about 120 days, i.e. the growing season (e.g. Aiken and Waddy 1992), the temperature is above 10 °C in normal years and reaches its peak about 20 °C in July. The temperature needed for reproduction, i.e. > 15 °C (Abrahamsson 1971), prevails for about 100 days.

The water is relatively clear and low in humus. The colour of the surface water has varied from 10 to 40 mgPt l^{-1} and the Secchi depth of visibility in August from 3 to 5 m. The pH readings have been relatively low (5.7–6.7). The Ca concentration is low, on average, 1.58 mg l^{-1} (range 0.74–2.19 Ca mg l^{-1}). The physico-chemical properties of the water are presented in greater detail in Sumari (1971) and Table 1. No noteworthy changes in the water quality of the lake were observed during the study period.

In 1965, economically low-value fish were removed by treating the lake with rotenon (Sumari 1971). Then the lake was restocked with whitefish (*Coregonus muksun*) and brown trout (*Salmo trutta* m. *lacustris*). Roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*), however, invaded from the upstream lake, Pieni-Majajärvi. The roach population is quite dense, but that of perch very sparse.

The crayfish habitat was improved by culling the roach population during the 1976, 1978 and 1979 spawning seasons. The amounts of roach removed were ca. 255 kg (23 kg ha^{-1}) in 1976, ca. 20 kg (1.8 kg ha^{-1}) in 1978 and ca. 40 kg (3.6 kg ha^{-1}) in 1979.

A few *A. astacus* individuals were unexpectedly caught in the lake during test trappings in 1969, just before and one month after *P. leniusculus* was introduced (J. Laitinen pers. comm.), but none in 1970 or later.

On 31 July 1969, 840 adult *P. leniusculus* (560 females and 280 males) from Lake Tahoe were released into Lake I-M by the author (K.W.). The average length of the crayfish was 80 mm (TL) and their weight 15 g (range 60–120 mm, 8–60 g), and they were estimated to be mainly 3+ to 5+ years of age (c.f. Flint 1975, Goldman and Rundquist 1977). 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

Table 1. Water quality in Iso-Majajärvi in 1970–1994. *N* = number of analyses.

	Depth 0–1 m			Depth 10–12 m		
	Mean	Range	*N*	Mean	Range	*N*
Colour mg Pt^{-1} l^{-1}	20	10–40	23	46	20–100	20
Conductivity µS m^{-1}	27.9	25–34	19	35.5	28–59	17
pH	6.3	5.9–6.7	19	6.1	5.7–6.6	16
Alkalinity mmol l^{-1}	0.04	0.01–0.06	5	0.13	0.05–0.08	5
Ca mg l^{-1}	1.58	0.74–2.19	4	1.41	1.12–2.08	4
Fe µg l^{-1}	74	0–129	17	1 768	35–5 412	14
Al µg l^{-1} total	33	5–40	4	89	29–163	4

per 2–4 m of shoreline and every third was a male. Stocking was kept secret to avoid poaching. The crayfish population remained unexploited until 1979. In 1995, eels (*Anguilla anguilla*) were introduced to study their impact as predators on the *P. leniusculus* population.

Material and methods

The relative abundance of the trappable crayfish subpopulation was monitored by trap catching. Catch per unit effort (CPUE = the number of individuals per trapnight) was used as an indicator of crayfish relative abundance on different occasions and at different sites. 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 traps (e.g. Mason 1975, Pfister and Romaire 1983, Shimizu and Goldman 1983, Holdich and Domaniewski 1995). Thus in case of baited traps, CPUE is only an indicator of the relative abundance of adult crayfish.

Catch/trap statistics were calculated during the 25 study years (1970–88, 1990–91, 1993–94, 1996–97) with a standardised sampling procedure. In 1974, 1981 and 1988, trapping was done along the entire shore, and in 1970–73, 1975–77, 1996 and 1997, only at the steep hard bottoms. Since 1978 the same shore area, about 2 000 m long (90% of the total shore length), has been sampled excluding three shallow, muddy bays (total length 230 m). The samples were taken on 73 nights (13 344 trap nights, annual variation 140–952) from 29 July to 1 September. As the traps were examined three times a night in 1970–77, the total catch effort was 16 223 (annual variation 280–1550) (Table 2). A total of 4 468 adult *P. leniusculus* (2 144 males, 48%, 2 324 females, 52%) were caught.

In 1970–77, vertical single-mouthed dome-shaped and two-mouthed cylinder traps were used. As the signal crayfish were able to escape easily from these, the traps laid at about 17:00 hours were examined three times during the following night (beginning at about 8 p.m., 11 p.m. and 8 a.m.). To avoid catch bias, a trap model with narrowed entrances (Evo trap) that prevents the crayfish from escaping was developed (Westman *et al.* 1979).

From 1978, the traps were examined in the morning only. The mesh size was 8 mm, small enough to catch even 40-mm (TL) individuals. 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 located about 2–3 m from the shore (depth interval 0.5–3 m). CPUE correlates negatively with increased fishing effort, as gear competition occurs when the effective trap radius, i.e. the area covered by one sampling unit or capture range, is greater than the linear trap spacing (Momot 1993). Then CPUE drops irrespective of total stock density, as observed by McGriff (1983a). We, therefore, based the trap spacing on the effective trapping radius of 2.5 m according to the studies of Abrahamsson (1969) and Abrahamsson and Goldman (1970), in which the capture range of a 2-mouthed cylinder trap was about 13 m^2 for *P. leniusculus*. Fresh or deep-frozen roach was used as bait. The sampling technique is described at length elsewhere (Westman *et al.* 1985).

Trapped crayfish were marked by electric cauterisation (Abrahamsson 1965) using a portable apparatus which we developed for marking in the field (12 V accumulator, Weller TCP 12 soldering iron 35 W/12 V). A thermostat kept the temperature at the head of the iron at about 470 °C, which is high enough to burn a spot on the carapace with a quick, light push. The pattern of orange-brown dots was easily detectable through two moults (cf. Abrahamsson 1964, Flint 1975, Brewis and Bowler 1983). Immediately after marking and data recording, the crayfish were returned to the capture areas.

We used the Petersen method (Ricker 1975) to convert mark-recapture data into estimates of the trappable subpopulation size. Crayfish are in many ways ideal for mark-recapture experiments (discussed by Skurdal *et al.* 1992). When based on trap fishing, though, the mark-recapture method has been criticised for underestimating the size of the population (Brown and Brewis 1979, Shimizu and Goldman 1983, Hogger 1986). On the other hand, Momot (1967) and Momot and Gowing (1983) observed that in small lakes with rather uniform substrata, the method can be used to estimate crayfish population size as long as certain criteria (e.g. Ricker 1975) are met (cf. Skurdal *et* *al*. 1992).

The basic assumptions are that there are no mark losses or extra mortality of marked animals before recapture, that the marked crayfish are randomly mixed with unmarked ones, that marked and unmarked specimens are equally catchable and that the population studied has not been affected by immigration or emigration. Nothing indicates that catchability is affected by electric cauterisation (cf. Abrahamsson 1965, Flint 1975). As shown by Abrahamsson (1983), the widespread random movement of *P. leniusculus* in lakes mixes the marked animals effectively with the rest of the population. We, therefore, assumed that marked and unmarked crayfish had the same probability of capture. Lake I-M is without inlets or outlets and so neither emigration nor immigration affects the population.

To avoid catch bias, and also the trappability problems due to variations in the activity and catchability of crayfish caused by season, moulting and reproductive status (e.g. Abrahamsson, 1971, 1983, Mason 1975, Flint 1977, Brown and Brewis 1979, Skurdal *et al*. 1992) estimates were made in all 11 study years (1979–87, 1990 and 1993) always in August, a period of high activity for both males and females. Ovigerous females that reproduced have already moulted, and therefore, recruitment to the trappable population between marking and recapture is minimal (cf. Lappalainen and Pursiainen 1995). Because the population was sparse throughout the study, sexes were

Table 2. August trap-catches of signal crayfish (*Pasifastacus leniusculus*) in Iso-Majajärvi, size of trappable population and number of harvested specimens (≥ 10 cm) in 1970–1997.

Year	Traps	Nights	Trap-nights	Total catch	Catch /trap /night	Popul. size *N*	Confidence limits ± 95%	≥ 10 cm removed *N*	≥ 10 cm removed % of population
1970	149	1	149	48	0.34	–	–	0	–
1971	200	1	200	50	0.25	–	–	0	–
1972	200	1	200	18	0.09	–	–	0	–
1973	150	2	300	81	0.27	–	–	0	–
1974	50–175	5	750	106	0.14	–	–	0	–
1975	100	2	200	28	0.14	–	–	0	–
1976	160	2	320	32	0.10	–	–	0	–
1977	100	2	200	76	0.38	–	–	0	–
1978	200	2	400	90	0.23	–	–	0	–
1979	172–200	4	768	222	0.29	329	85	67	20.4
1980	198–200	4	798	176	0.22	203	23	41	20.2
1981	240–250	4	915	307	0.34	351	66	57	16.2
1982	238–240	4	952	415	0.43	544[1)]	137	101	–
1983	216–219	4	870	558	0.64	674	93	44[2)]	6.5
1984	210–220	4	860	365	0.43	369	54	98	26.6
1985	185–200	4	770	187	0.24	197	45	70	35.5
1986	150–218	4	793	253	0.32	407	106	34[2)]	8.4
1987	200	4	800	345	0.43	376	62	23	6.1
1988	232–250	2	482	220	0.46	–	–	106	–
1989	–	–	–	–	–	–	–	–	–
1990	174–180	4	706	141	0.20	166	47	43	25.9
1991	160	2	320	107	0.33	–	–	28	–
1992	–	–	–	–	–	–	–	–	–
1993	135–200	4	680	354	0.52	358	53	109	30.4
1994	206	2	412	137	0.33	–	–	59	–
1995	–	–	–	–	–	–	–	–	–
1996	100	4	400	119	0.30	280	148	0	–
1997	100	1	100	32	0.32	–	–	0	–

[1)] only part of the trappable population (70–100 mm)
[2)] in 1983 only $^{2}/_{3}$ and in 1986 only $^{4}/_{5}$ of >100 mm crayfish were removed

combined. Marking trappings were conducted in the first or second week of August (the number marked in a year varying from 73 to 309) and recapture trappings about two weeks later, with the annual total varying from 68 to 249 (Table 2).

Sex, carapace length (CL), reproductive readiness of females, missing chelae, markings, melanised spots caused by the plague fungus and partly also total length (TL) were recorded for the crayfish caught.

When TL is measured in the field, errors easily occur due to the articulated, flexible tail of the crayfish. CL was therefore measured with vernier calipers to the nearest mm from the tip of the rostrum to the posteriomedian margin of the cephalothorax (the "standard carapace length" (Fitzpatrick 1977) or "total carapace length" (TCL; Aiken and Waddy 1992). To facilitate comparison with earlier studies, and to take into account the fact that CL relative to TL differs slightly between the sexes, and also because the legal catch size is expressed in some countries as TL (e.g. Westman and Westman 1992), CL was converted to TL with the following regression equation; males: TL = 8.4752 + 1.802CL (N = 195, R = 0.971), females: TL = 3.873 + 1.964CL (N = 210, R = 0.970); TL is the length from the tip of the rostrum to the end of the telson of the stretched abdomen. CL is about half of TL (51% for males and 49% for females, when CL = 50 mm). Unless otherwise stated, the lengths are TL.

Reproductive readiness of females was determined from the cement glands on the abdomen; if these were visible, the female was considered ready to reproduce in the same autumn.

The age groups were visually estimated from the length-frequency distribution. Growth data collected from marked and recaptured Lake I-M specimens and signal crayfish of known age from other lakes and aquaculture facilities were used to facilitate age determinations.

To make economical use of the stock and examine its ability to sustain harvesting, all "legally-sized" (≥ 10 cm) crayfish caught during the recapture operations were removed in 1979–94 (except in 1989 and 1992 when none were removed; and in 1983 and 1986 when only part of the catch was removed) (Table 2). The catch value was estimated on the basis of the mean price paid to fishermen in nearby areas for *A. astacus* in 1994, i.e. FIM 16 (USD 3) per crayfish.

The fecundity of the *P. leniusculus* population has been discussed by Savolainen *et al.* (1997). Some of the introduced signal crayfish were infected with the plague fungus. The occurrence of the disease in the population has been examined by Nylund and Westman (1995).

Results

Size of the population

In the first sampling, in 1970, 48 large signal crayfish (mean size 110 mm, range 87–143 mm) were caught (CPUE = 0.3), i.e. 6% of the total number stocked. Roughly the same number (50) was caught in the following year, but the individuals were then larger (mean size 113 mm, range 97–138 mm) (Fig. 2). In 1972, the catch of stocked individuals fell to 17 (ca. 2%, mean size 122 mm, range 110–142 mm), but one juvenile (male, 79 mm) was also caught. From the growth rate of *P. leniusculus*, we assume that the age of the juvenile most probably was 2+, i.e. it had hatched in summer 1970. This was the second occasion on which signal crayfish were observed to have reproduced in Finland (cf. Kirjavainen and Westman 1995).

On the basis of the size distribution in 1973 and 1974, we assessed the number of stocked signal crayfish in the catches to only eight or ten specimens (ca. 10% of the catch and 1% of the total stocked). They ranged in size from 124–147 mm in 1973 to 135–154 mm in 1974 (Fig. 2). About 90% of the catches now comprised crayfish (mainly 3+ to 4+) born in the lake. No stocked crayfish were caught in 1975. The Lake Tahoe signal crayfish therefore lived in Lake I-M for no more than five years and became 8+ to 10+ years old (Fig. 2).

The mean CPUE was quite low throughout the 1970s, i.e. 0.1–0.4. Considering the great number of females stocked, we would have expected much larger 1+ to 4+ age cohorts to have been recruited for catching in 1972–74. It was not until 1977, and subsequently 1981, however, that CPUE reached the 1970 level. The largest catch to date, i.e. 0.6 individuals per trap and night, was obtained in 1983, after which CPUE declined. Despite annual variations, the mean CPUE showed a small but statistically significant increase: r_s = 0.426, P < 0.05 (Table 2, Fig. 3). The maximum number of signal crayfish was ca. 0.15/shore metre. However, catches varied greatly in different parts of the lake.

The size of the trappable *P. leniusculus* subpopulation was estimated to have been about 200–350 specimens at the end of the 1970s (Table 2, Fig. 4). Thereafter it doubled within two years, peaking at about 670 in 1983. The catchable population then decreased to about 200–400 individuals, i.e. to only about half of the number stocked in 1969. Consequently, the mean density would be ca. 0.2 crayfish/metre of bank and even in the peak year 1983 not more than 0.3 individuals/shore metre.

The total capture area of the 412 traps used in 1994 was about 5 356 m^2 (cf. Material and methods). Consequently, the mean density of the catch (137 specimens) from this area was 0.03 ind. m^{-2}. At its maximum, in 1983, the density was about 0.06 ind. m^{-2}.

Harvest

During the 14 years of exploitation, 880 crayfish larger than 10 cm (44% of the total catch) were caught (Table 2). The number per year ranged from 23 to 109 (14%–81% of the annual catch). The proportion of "legal sized" individuals varied annually from 6% to 36% of the estimated trappable subpopulation (Table 2). Length-frequency diagrams indicate that only three age groups were not harvested, i.e. the slowest-growing 3+ and younger individuals.

The total number of harvested females was 421 (37% of the total female catch, annual variation 22%–70%) and of males 459 specimens (42%, annual variation 30%–78%). On the whole, slightly more males than females were removed (52% versus 48%, i.e. 1.1 males per female).

Calculated at 1994 prices, the value of the total harvested catch was FIM 14 080 (USD 2 520). Thus the mean value of the annual catch was FIM 1 006 (roughly USD 180).

Population structure

The crayfish caught in 1970–72 were large, stocked individuals. In 1973, signal crayfish born in Lake I-M formed the majority. In most years, the trapped crayfish were from 50 to 120 mm in length, but the size distribution of the catch varied from one year to the next. The smallest individual was 40 mm and the largest 154 mm. Before the harvest started, individuals > 130-mm were caught every year. The proportion of ≥10-cm individuals in the catch has also declined since the early 1980s (Fig. 2). No length-frequency distribution histograms have been made since 1996, eel stocking having caused a shift in the focus of research.

Attempts to identify year-classes from length-frequency distribution data failed because the sizes of trappable individuals in different year-classes overlapped too much. Using growth data of individuals of known age, we were, however, able to identify visually two cohorts, i.e. 1+ and 2+, from the histograms (Fig. 2). The majority of trap catches may comprise only three or four age-groups, i.e. 1+ to 4+.

The annual fluctuation in age structure, which also affected that in mean catch size, is visible in the length-frequency histograms. In only seven (1976, 1980, 1981, 1982, 1986, 1991 and 1994) of the 25 years of study did a more numerous group of small (ca. 53–81 mm) and mainly 1+ and 2+ year individuals feature prominently in the catch.

The frequency of cheliped loss varied between 7.5% and 16.5% in the study years (1980, 1982, 1984, 1986, 1990–1994). The frequency was slightly higher among males (13.2%, range 4.8%–17.7%) than females (11.4%, range 7.1%–15.8%).

The sex ratio of the catches

The female:male ratio was 2:1 at stocking. In the first three years (1970–1972), trap catches consisted of stocked individuals and the sex ratio remained nearly unchanged (proportion of females 56%–74%). In 1973, when about 90% of the catch consisted of signal crayfish born in Lake I-M, the sex ratio was about 1:1 (females 49%, males 51%). With few exceptions, the sex ratio in August catches was close to 1:1.

Sexual Maturity

Mean size at maturity (50% of females) was ca. 84 mm, which corresponds to 3+. About 30% of

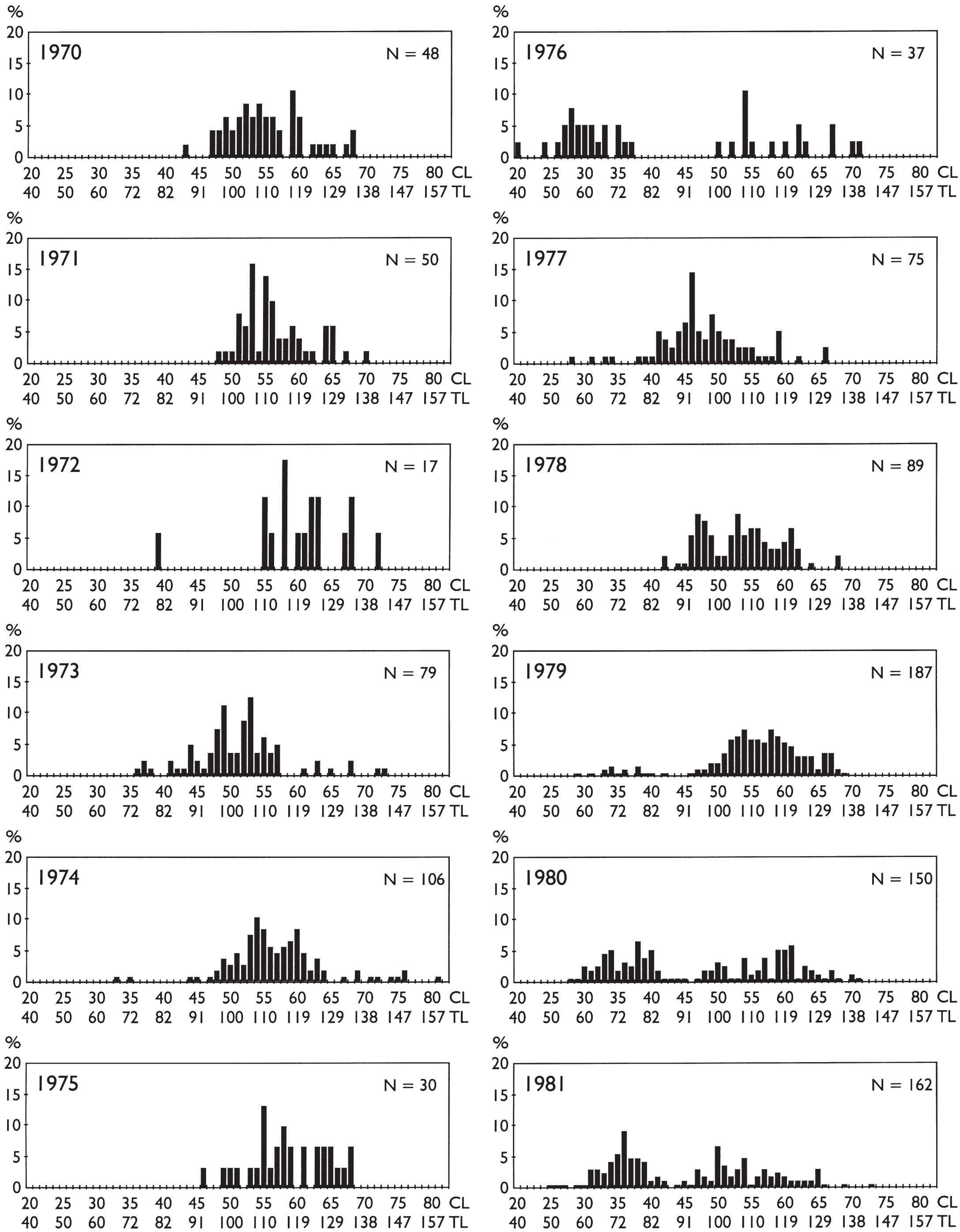

Fig. 2. Length-frequency histograms for signal crayfish (*Pacifastacus leniusculus*) trap-catches in Iso-Majajärvi in 1970–1994 (no sampling in 1989 or 1992). CL = carapace length (mm), TL = total length (mm).

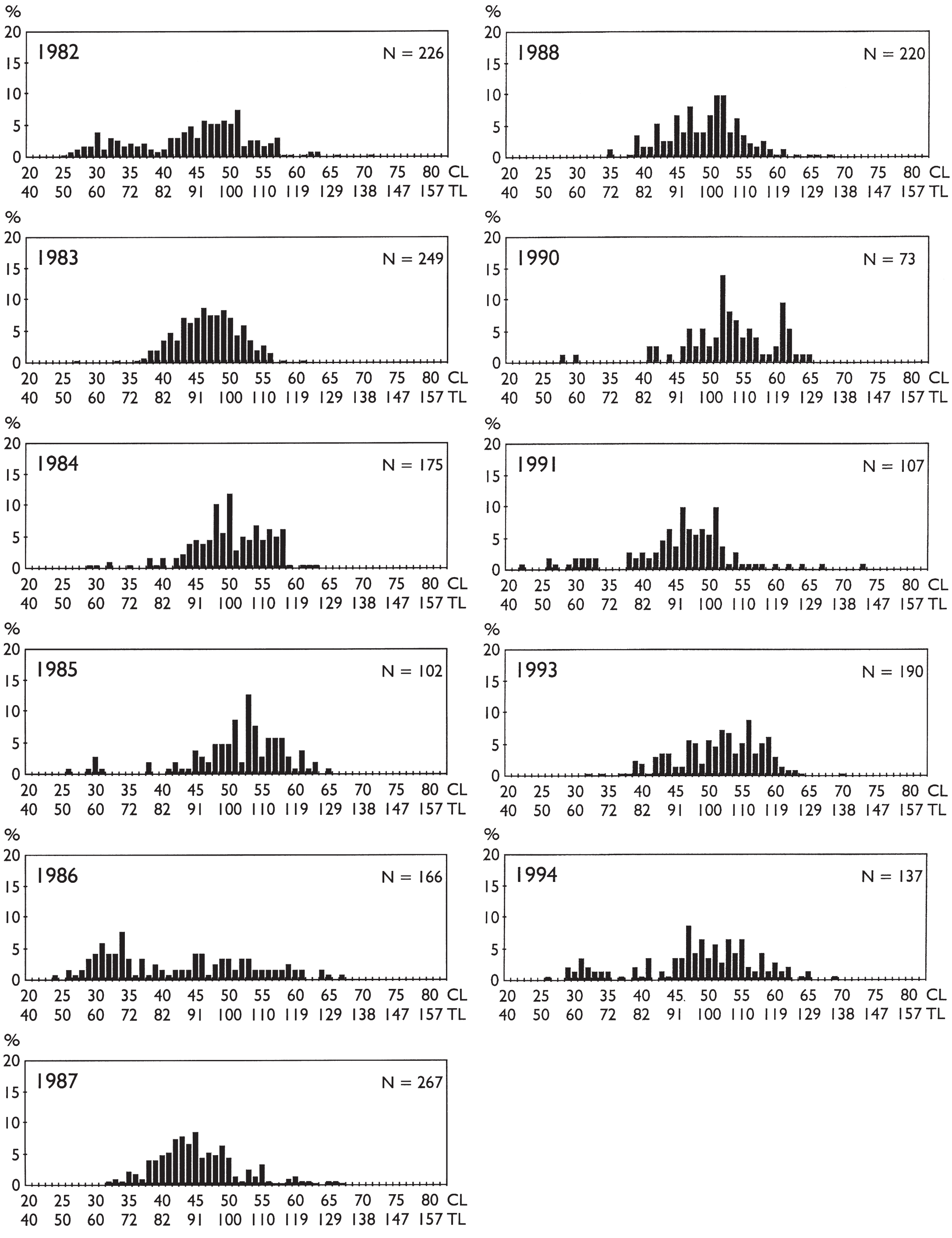

Fig. 2 (Continued). Length-frequency histograms for signal crayfish (*Pacifastacus leniusculus*) trap-catches in Iso-Majajärvi in 1970–1994 (no sampling in 1989 or 1992). CL = carapace length (mm), TL = total length (mm).

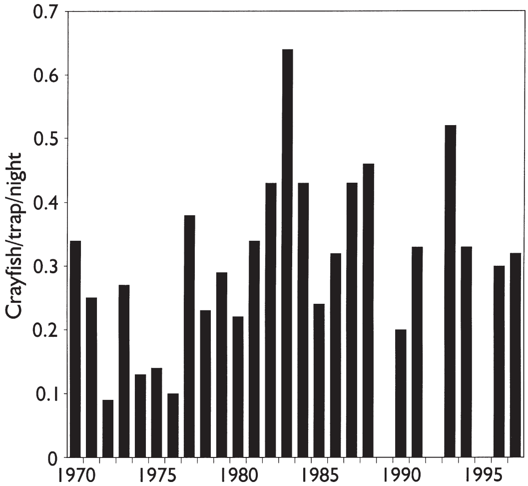

Fig. 3. Mean trap-catches (crayfish/trap/night) of signal crayfish (*Pacifastacus leniusculus*) in Iso-Majajärvi in August 1970–1997. No sampling in 1989, 1992 or 1995. Harvesting begun in 1979, no removals in 1982, 1988, 1991 or 1994.

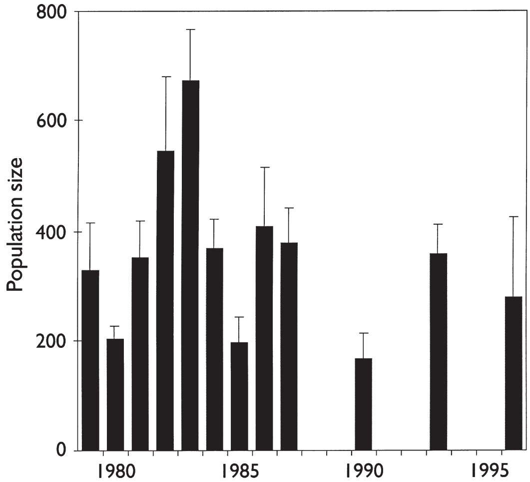

Fig. 4. Population size of trappable signal crayfish (*Pacifastacus leniusculus*) in Iso-Majajärvi estimated by Petersen's mark-recapture method. Vertical bars are confidence limits ± 95%.

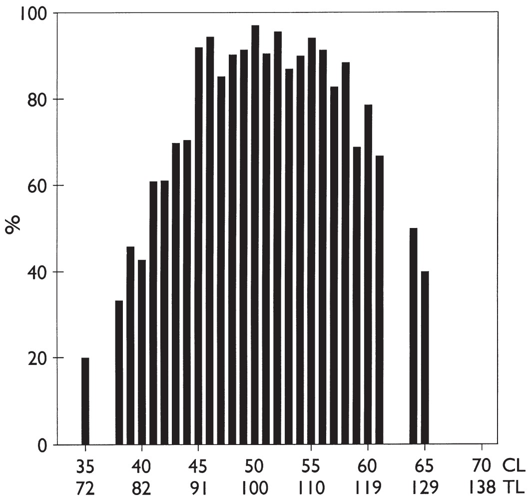

Fig. 5. Proportion (%) of reproductive signal crayfish (*Pacifastacus leniusculus*) females (= visible cement glands) in different size classes in trap catches in August 1979–1994 (*N* = 701). CL = carapace length (mm), TL = total length (mm).

80-mm and 100% of 92-mm females were mature (Fig. 5). The smallest mature female was about 73 mm. The fastest-growing females could thus breed at 2+. The largest female ready to reproduce measured 139 mm, which corresponds to 5+ or 6+. Thus, the oldest females seem able to spawn as many as four times. Judging by the absence of visible cement glands, however, not all sexually mature females appear to be ready to spawn every year (Fig. 5). Even in the case of > 92-mm females, only about 90% were ready to reproduce annually.

Of the females marked in 1987 (*N* = 139), 29 were recaptured the next year. Nine (31%) of these (71–88 mm) were immature at marking, but at recapture (85–107 mm) were breeding for the first time (cement glands –/+). Seventeen (59%) of the females (84–135 mm) were ready to reproduce both in the year of marking and at recapture (cement glands +/+). Consequently, the majority of these females spawned in two consecutive years, and an interval year, at least between the first and second spawning years, does not seem quite common. Three (10%) of the females (size at marking 80 mm, 121 mm and 126 mm) were ready to spawn only in the year of marking (cement glands +/–), i.e. the smallest individual (recapture length 98 mm) had already had an interval year after the first spawning.

Discussion

According to Skurdal *et al*. (1993, 1995), CPUE is a good indicator of the relative abundance of

A. astacus, even when the trapping effort is relatively low. This is compatible with the observation of Abrahamsson (1969) that densities of *P. leniusculus* estimated by means of trapping were similar to those obtained with SCUBA. Likewise, Capelli and Magnuson (1983) found that in Orconectide lakes direct estimates of total population biomass correlated closely with trap catches of adult males (females were not taken into account).

As pointed out by Shimizu and Goldman (1983), if the total trapping radius does not completely cover the sample area, the resulting population estimate will be too low. Considering the small size of Lake I-M, the short distance between the traps and the narrowness of the littoral zone suitable for signal crayfish, we can assume that the main habitats were covered relatively well. As no traps were set outwards from the shore, it is clear that their capture range did not cover all habitats. The size of the trappable subpopulation was, therefore, probably underestimated in all the study years. Since, however, the other criteria required for accurate use of the mark-recapture method were fulfilled, the population estimates — made annually in the same way and at the same time — give a fairly reliable picture, especially of changes in the size of the population.

It is interesting that the mean catch per trap and night was in all but one of the ten years very close to 1‰ (about 0.8‰–1.2‰) of the size of the estimated trappable subpopulation of the same year. Only in one year (1993) was the deviation greater, about 1.6‰. Thus CPUE might, with certain provisos (e.g. the sampling must effectively cover different crayfish habitats in the study area), also be used as a rough indicator of the absolute size of the trappable subpopulation (cf. Skurdal *et al*. 1993). The advantage of CPUE is that no marking is required and only one sample is needed to estimate the numbers.

The problem with the estimation of crayfish densities based on catches and the capture range of traps is the great variation in the range reported in different studies. According to Abrahamsson (1969), the capture ranges were about the same in two *P. leniusculus* lakes (13 m^2 and 12.7 m^2) and the population estimates based on these were much the same as those obtained with SCUBA. By contrast, estimates made by Lewis and Horton (1997) were much larger (92 m^2 and 116 m^2), and by Flint (1975) very much larger (1 452 m^2). The variation may be due to differences in factors such as density, habitat and trapping method. According to Lewis and Horton (1997), this is, nevertheless, still a useful method for gathering data that would otherwise not be obtained. The great differences in trap capture ranges merely indicate that more research is needed on the subject.

The signal crayfish populations of many lakes in Finland began from a few stocked individuals, some comprising as few as 500 and 900 second-stage juveniles (Westman *et al*. 1995, Tulonen *et al*. 1998), which corresponds to the progeny of only 5–10 large females (Savolainen *et al*. 1997). In many other European countries, too, productive signal crayfish populations have developed from small stockings, under favourable conditions taking only a few years to develop (discussed by Lowery and Holdich 1988). Taking into consideration the large size and female dominance of the stocking (560 adult females), the fecundity of *P. leniusculus* (op. cit.), and the fact that at least some of the females apparently produced juveniles the summer after stocking, we would have expected as many as tens of thousands of juveniles to be born, especially during the first couple of years. Even if the mortality rate among juveniles has been found to be high, exceeding 90% by the end of the second summer (Fürst 1977a, 1977b), the *P. leniusculus* population ought to have increased rapidly in Lake I-M; this did not, however, happen.

A similar slow development occurred in a nearby small lake, Karisjärvi, into which signal crayfish from the same batch had been released (Kirjavainen and Westman 1995). When Lake Tahoe signal crayfish were introduced into 67 lakes in Sweden in 1969, only 10% of the stockings succeeded. The unexpectedly poor results were attributed to the stress of the transatlantic crossing, local transportation in the heat of summer, and excessive locomotory activity within the first few days of release (Fürst 1977a, 1977b, Brinck 1975, Svärdson 1995).

In Finland, however, the crayfish were given time to recover and only individuals in good condition were used. Even so, only about 6% of the stocked *P. leniusculus* were recaptured in Lake I-M in each of the first couple of years; and in the succeeding years, despite major catch efforts (600–

1 550/yr), no more than 1%–2 % were caught. As the signal crayfish could not escape from the lake, nor, due to intensive trapping around the whole shore, could they avoid entering the capture range of traps, the small and rapidly diminishing catches indicate high mortality after release of the crayfish. The same was suspected in Karisjärvi, in which only 2% of the Lake Tahoe crayfish were recaptured within a couple of years of stocking (Kirjavainen and Westman 1995). We, therefore, suspect that the abrupt transfer to Finnish conditions of adult signal crayfish adapted to a totally different habitat in North America was the cause of the high mortality.

The slow growth of the signal crayfish population both in Lake I-M and in Karisjärvi (op. cit.) might also be due to disturbances in reproduction, as is suggested by the small number of pleopod eggs on females caught in early summer in Lake I-M (Savolainen *et al.* 1997) and in Karisjärvi (op. cit.) as well as the failure of the juvenile-sampling trials in Lake I-M and Karisjärvi.

Disturbances in reproduction may result from differences between the Finnish lakes and Lake Tahoe, e.g. the water temperature in the latter does not fall below 5°C, even in winter (Goldman 1973, Flint 1977), whereas in lakes I-M and Karisjärvi the temperature in the crayfish habitats is in the 0–4 °C range from October to May. Laurent (1980) attributed the failure of some attempts to introduce *P. leniusculus* into French lakes to the coldness of the water in spring. Low water temperature has been found to have an adverse effect on both the spawning frequency of crayfish (references in Savolainen *et al.* 1997) and the hatching of eggs (Abrahamsson 1969, Goldman 1973).

One factor affecting reproductive success is the pH of the water. Acid stress weakens egg-attachment and hampers the sensitive embryonic development (e.g. Appelberg 1986). Apparently for this reason, freshwater crayfish inhabit only waters within a narrow pH range; *A. astacus* and *A. pallipes,* for instance, are seldom found in waters with a pH below 5.7–5.5 (e.g. Jay and Holdich 1977, Tuunainen *et al.* 1991, Appelberg 1992, Fiskeriverket 1993, Foster 1995). In the light of present knowledge, *P. leniusculus* is approximately as sensitive to acidity as is *A. astacus* (Tulonen *et al.* 1998), and some of the stocking failures with *P. leniusculus* in Sweden have been attributed to the low pH (Fürst 1977a, 1977b). The pH in Lake I-M has periodically been very low (5.9 at 1 m) and even at its highest (6.7) clearly lower than in Lake Tahoe (7.8–8.2; Abrahamsson and Goldman 1970, Goldman 1973). The small number of pleopod eggs found in Lake I-M females might be attributed to one or all of the following factors: disturbances in fertilisation, bad attachment in the pleopods, and detachment due to acid stress and the lengthy and cold incubation period.

Brinck (1975) also noted that the signal crayfish population of Lake Tahoe is very dense and dominated by age groups that reproduce poorly. Unfortunately, more detailed data on the reproduction of *P. leniusculus* imported into Sweden and Finland towards the end of the 1960s are not available.

Other properties of the water may also have contributed to the slow development of the population, especially as the signal crayfish in Lake I-M have had little time to adapt to their new habitat. Calcium, for example, is essential for recalcification of the exoskeleton after moulting but the minimum Ca concentration required for population maintenance is not known exactly. Crayfish (genus *Astacus* and *Orconectes*) have been found in waters with Ca levels down to 2.0–3.0 mg l^{-1} (e.g. Capelli and Magnuson 1983, Jussila *et al.* 1995, Taugbøl *et al.* 1997), but they have been absent from waters with Ca concentrations below 5 mg l^{-1} (Greenway 1974, Jay and Holdich 1981, Foster 1995). According to Tulonen *et al.* (1998), fairly good *A. astacus* populations are still found in Finland in waters with a Ca concentration of 3.0–4.0 mg l^{-1}. However, highly-productive *A. astacus* and *P. leniusculus* populations occur in waters with Ca concentrations far in excess of those mentioned above, for example, in Lake Tahoe with 8.8–9.9 mg l^{-1} (Goldman and Rundquist 1977) and in the Norwegian Lake Steinsfjorden with as much as 12.6 mg l^{-1} (Skogheim and Rognerud 1978). By comparison, the Ca concentration in Lake I-M (mean 1.6 mg l^{-1}) is very low, indeed one of the lowest in which crayfish have been found to survive at all. The *P. leniusculus* population there is probably close to its existence minimum and hence vulnerable to any additional stress, e.g. acidification and predation (cf. Taugbøl *et al.* 1997). Foster (1995) has examined the physicochemical factors influencing the distribution and abundance of a freshwater crayfish species (*A. pallipes*) in greater detail.

The occurrence of signal crayfish in Lake I-M and in our other study lakes (Kirjavainen and Westman 1995, Westman and Savolainen 1995), as well as observations made elsewhere (e.g. Abrahamsson and Goldman 1970, Flint 1977, Shimizu and Goldman 1983, Guan and Wiles 1996, Lewis and Horton 1997), demonstrates that adult signal crayfish thrive on rocky substrata and on sloping bottoms suitable for digging but avoid gently sloping soft bottoms, muddy shores and gravel or sand bottoms.

It would appear that, owing to the scarcity of substrata providing shelter for signal crayfish in Lake I-M, the carrying capacity of this lake is quite small — more than half of the littoral zone is unsuitable, only about 32% being relatively steep hard bottom, and areas of rocky substrata being very rare. This scarcity of substrata preferred by *P. leniusculus* may be one of the main reasons why the CPUE in Lake I-M is still considerably smaller than in many other Finnish lakes (cf. Tulonen *et al.* 1998), and waters 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 just short of 10, signal crayfish/trap/night by the mid-1980s (Fjälling and Fürst 1988). In Träsksjön, the first lake to be stocked with signal crayfish in Europe (56 individuals in 1960), the CPUE had risen to about 28 by the end of the 1980s (Svärdson *et al.* 1991). In a small English lake, the catch of *P. leniusculus* rose to 10.4 crayfish/trap/night within four years of stocking with 0+ juveniles (Hogger 1986), and in the French Lake Divonne the CPUE was 7.7 ten years after signal crayfish had been introduced (Laurent and Vey 1986). It is interesting that the mean CPUE in the lakes where *Pacifastacus* originated is smaller than that in the above waters: 1.2–3.9 crayfish/trap in Lake Tahoe, 1.6–3.3 in Donner Lake (Goldman and Rundquist 1977) and 1.07 in Natoma Lake (Abrahamsson 1969).

The mean density of the trappable *P. leniusculus* population was also very low in Lake I-M (in the 1990s about 0.1–0.2 specimens/shore metre), as compared with most published density estimates. In Donner Lake, for example, the average density of adult (> 70 mm) signal crayfish varied from 0.23 to 0.44 per m^2 and in a lake in Oregon from 0.24 to 1.13 per m^2; in Lake Tahoe the mean density was 0.9 per m^2 and in Natoma Lake 1.1 per m^2 (Abrahamsson and Goldman 1970, Flint 1975, 1977, Flint and Goldman 1977, Goldman and Rundquist 1977, Lewis and Horton 1997). The mean density of the trappable population was 0.4/m^2 in one of the Rögle ponds, Sweden (Abrahamsson 1971), 0.76/m^2 in the pools of an English lowland river (Guan and Wiles 1996), 1.8/m^2 in occupied areas in a small English lake (Hogger 1986) but 4/m^2 in a gravel pit (Arrignon 1993) and 4.2–7.3/m^2 in Lake Divonne (Laurent and Vey 1986). The densities of different crayfish species are compared in a literature review by Momot *et al.* (1978).

Fish predation (e.g. Momot 1967, Stein 1977, Fürst and Andersson 1988, Lodge and Hill 1994) may also have contributed to the poor development of the signal crayfish population in Lake I-M. Because of its large populations, roach, which have been observed to reduce YOY survival (Svensson 1993), may have a marked effect on juvenile mortality. Perch, by contrast, which prey on *P. leniusculus* juveniles (Appelberg and Odelström 1988, Söderbäck 1992, Blake and Hart 1993), are relatively rare in Lake I-M. These factors, together with the role of aquatic insects (Hirvonen 1992) and other potential predators (Foster and Slater 1995), deserve further research.

The frequency of cheliped loss is a common indicator of the intensity of intraspecific competition. Abrahamsson (1966) reported a cheliped loss in the range of 11% to 32% in *A. astacus*. Similar observations were made by Skurdal *et al.* (1988) on *A. astacus* (loss range 1.5%–16.1%). In other studies cheliped loss in the range 3% has been reported for *A. astacus* (Lindqvist and Louekari 1975), 8%–34% for *A. pallipes* (Laurent 1985) and about 11% for *P. leniusculus* (Kirjavainen and Westman 1995). The frequency of cheliped losses among *P. leniusculus* in Lake I-M (7.5%–16.5%) may be an indication of quite small degree of intraspecific competition and predation. Another indication of the same is the even sex ratio (1:1); according to Abrahamsson (1966), an unnatural ratio is a sign of fierce competition.

By impairing reproductive potential, heavy harvesting (in many years 6%–30% of ≥ 10 cm subpopulation removed) has certainly contributed to the slow increase in the population. Due to the fast growth rate, some 10% of the females did apparently not manage to reproduce even once before attaining the harvesting size. The removal of numerous big females with higher fecundity (Savolainen *et al*. 1997) did not, however, seem to have resulted in overfishing of the reproducing females, as the population has gradually increased in size. Thus, exploitation based on the 10-cm minimum size did not appear to have lowered the *P. leniusculus* females' reproductive resilience too much. The same was observed in our other study lakes (Kirjavainen and Westman 1995, Westman and Savolainen 1995).

Evidence of poaching, such as traps left in the lake, has been visible since the 1980s. The effect on the crayfish population cannot be evaluated in any great detail, but footprints on the shore indicate that Lake I-M, with its remote location, may have suffered from quite heavy poaching in some years.

Food production effectively regulates both mortality and the growth of newly hatched cohorts during the first growing season (discussed by Momot 1984, Aiken and Waddy 1992). Analyses of samples of bottom fauna taken during a few years following the introduction of signal crayfish indicated that there was abundant and varied food suitable for juveniles. Since the plant food eaten by adults was also abundant, shortage of food would not appear to be a significant factor limiting the growth of the *P. leniusculus* population.

Even if the substrate may often appear to be the single, most important variable relating to total crayfish abundance, Momot (1984) and Lodge and Hill (1994) emphasised 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 1988); nevertheless there are some features of Lake I-M that limit population increase there. We assume that, as well as the small total area of preferred habitat, these include the low Ca concentration and the periodic acidity; the *P. leniusculus* in Lake I-M are therefore probably having to contend with multiple stresses. We know nothing, however, about the possible interactions between different limiting factors in the lake.

As *A. astacus* catches, too, were small before the signal crayfish were introduced, Lake I-M seems on the whole to be a poor crayfish habitat, with a low carrying capacity. Unfortunately, we did not know this 30 years ago, when the most important arguments in its favour were isolation, the impossibility of natural dispersal and small size but not suitability for crayfish. Correspondingly, some of the earliest signal crayfish introductions (Westman 1973, 1995, Lahti and Oksman 1994) seem to have failed due to the barrenness of the experimental lakes.

Even if the proportion of > 10-cm specimens removed was high in Lake I-M (about 44% of the trappable total catch in 1979–1994), annual harvesting remained quite small due to the smallness of the population as a whole. By contrast, later stockings in larger Finnish lakes better suited to crayfish have succeeded well, the total annual catch sometimes having amounted to tens of thousands of adults (Tulonen *et al*. 1998). These yields are, however, still very modest compared with those of North American *P. leniusculus* populations, e.g. in Lake Tahoe (Abrahamsson and Goldman 1970, Flint 1975) and the Sacramento River (McGriff 1983a, Shimizu and Goldman 1983). Numerous high-yielding stocks have also been developed in many European countries, e.g. in Sweden (Fürst 1977a, 1977b, Fjälling and Fürst 1988, Svärdson *et al*. 1991) and France (Laurent and Vey 1986, *see* also Lowery and Holdich 1988).

Crayfish individuals within a year-class can grow at widely varying rates due to the different number of moults and moult increments. Since differential growth rates cause overlap among various age groups, attempts to identify year-classes from size-frequency data are unlikely to succeed except with the first two or three cohorts (e.g. Miller 1960, Momot 1967, Brewis and Bowler 1982, McGriff 1983b). In our study, too, the identification of cohorts was difficult, due partly to the lack of juvenile age groups, and partly to the relatively small number of individuals. By using the lengths of individuals of known age, we could visually and subjectively extract 2–3 year-modes from the length-frequency histograms. The catches would have had to be much greater for us to be able to identify more year-classes.

Variations in year-classes observed in Lake I-M require further study. The appearance of the more numerous 1+ to 2+ age-classes in 1976, 1980, 1981, 1982, 1986, 1991 and 1994 may be attributed to favourable climatic conditions; a well-known factor affecting year-class strength in fishes (references in Lehtonen *et al.* 1997). In warm summers, crayfish juveniles can hatch weeks earlier than in cold summers and so have time to grow larger than normal before the autumn. They thus have a better chance than smaller juveniles to survive the long winter. Unfortunately, the temperature has not been monitored regularly in Lake I-M, and comparisons between years cannot therefore be made with reliability. The variations in year-class abundances between the years could also be a result of predation pressure due to cannibalism. Habitats suitable for crayfish being relatively scarce in Lake I-M, competition for them may be fierce. A vigorous new year-class will only be able to develop once the previous strong year-class has either died or been harvested in full (Fig. 2). Probably various factors, both abiotic and biotic have an affect simultaneously on the year-class strength as observed in fishes (references in Lehtonen *et al.* 1997).

In high-latitude crayfish populations, natural mortality has been found to be small after the first year (Momot and Gowing 1983, Fürst 1977b). Likewise in Lake I-M, before harvesting began, *P. leniusculus* remained abundant in annual catches until they reached a total length of 120–130 mm, i.e. at about 5+ to 6+ years, but after that they began to disappear. Similar trends were observed in our other study lakes (Kirjavainen and Westman 1995, Westman and Savolainen 1995).

The introduced 3+ to 5+ signal crayfish appeared in catches in Lake I-M for no more than five years (Fig. 2), i.e. they reached an age of 8–10 years. In Karisjärvi (Kirjavainen and Westman 1995) and in lakes in Sweden (Svärdson 1995), *P. leniusculus* imported from North America as adults were trapped four years after stocking. Other authors (e.g. Abrahamsson and Goldman 1970, Mason 1974, Flint 1975, Fürst 1977b, Cukerzis 1979) have reported that the life span of *P. leniusculus* is as long as 8–12 years. According to Momot (1984), crayfish occurring in high latitudes and colder environments tend to have a longer life cycle than those in middle and low latitudes. This ensures reproductive success, as a succession of years with climatic conditions unfavourable for reproduction and growth could seriously diminish, if not eliminate, a species with a short life cycle.

The sex ratio in natural crayfish populations is about 1:1 (e.g. Mason 1975, Abrahamsson 1971). We observed the same in the present study. The sex ratio of the stocked, predominantly female, population changed from 2:1 to about 1:1 in the first year, when the bulk of the catch (ca. 90%) comprised individuals born in the lake. The same was observed in Karisjärvi (Kirjavainen and Westman 1995).

Maturity in crayfish is related to size rather than age, earlier maturity resulting from higher growth rates in warmer waters or otherwise favourable conditions (e.g. Wenner *et al.* 1974, Brewis and Bowler 1982). The size at maturity of signal crayfish females varies between populations. The minimum size at the onset of sexual maturity in *P. leniusculus* females ranged from 59 mm to 80 mm TL (Miller 1960, Mason 1975, Abrahamsson 1971, Shimizu and Goldman 1983, McGriff 1983b, Hogger 1986, Guan and Wiles 1996, Lewis and Horton 1997). However, the average size of *P. leniusculus* females at maturity is larger, ranging from 75 mm (Mason 1974) to 90 mm (Abrahamsson and Goldman 1970), the latter observed in Lake Tahoe. In Karisjärvi, the females at the onset of sexual maturity varied from 70 to 80 mm in length (LM 50 = 90 mm) (Kirjavainen and Westman 1995), and in Slickolampi from 76 to 95 mm (Westman *et al.* 1993). *Pacifastacus* females therefore mature at a somewhat smaller size in Lake I-M (73–92 mm, LM 50 = 84 mm) than in their "home lake", Lake Tahoe.

Variations observed in size at maturity may be environmental in origin. The onset of maturity may be delayed in cold environments, but there is also evidence that stress caused by factors such as population density may promote maturation (McGriff 1983b, Shimizu and Goldman 1983, Taugbøl and Skurdal 1990). For further references, *see* Reynolds *et al.* (1992).

Depending on growth rate and size at the onset of sexual maturity, signal crayfish females enter the breeding population at different ages in different waters. Miller (1960) and McGriff (1983b) observed that the fastest growing females could already attain maturity at 0+, although most females entered the breeding population at the age of 1+ to 2+. In the Rögle ponds, Sweden (Abrahamsson 1971), two rivers in Canada (Mason 1974, 1975), the Sacramento River (Shimizu and Goldman 1983), lakes in North Poland (Kossakowski *et al*. 1979), Lake Divonne, France (Laurent and Vey 1986), a river in England (Guan and Wiles 1996) and a lake in Oregon (Lewis and Horton 1997), fast growers attain maturity at 2+ , but in some other waters, including Lake Tahoe, not until 3+ to 4 + (Abrahamsson and Goldman 1970, Flint 1975). In Slickolampi (Westman *et al*. 1993) and Karisjärvi (Kirjavainen and Westman 1995) as in Lake I-M the smallest *P. leniusculus* females entered the breeding population at 2+.

It has long been known that not all sexually mature crayfish females spawn every year (for references, *see* Savolainen *et al*. 1997). In Slickolampi, for example, the proportion of mature *P. leniusculus* females not ready to spawn varied from 28% to 50% (Westman *et al*. 1993), and in Karisjärvi it was as high as 59% in some years (Kirjavainen and Westman 1995). Similarly in the present study about 41% of the females did not seem to be ready to reproduce in two consecutive years. By contrast, according to Abrahamsson and Goldman (1970) and Abrahamsson (1971), female signal crayfish reproduce every year after reaching adult size. Brewis and Bowler (1985), Lowery (1988), Morgan and Momot (1988) and Savolainen *et al*. (1997) reviewed the factors and their complex interactions that influence the spawning frequency of freshwater crayfish.

According to Mason (1975), the largest reproducing *P. leniusculus* female in a river in Canada measured only 10.2 cm, but in culture the largest ovigerous females were 14 cm (Mason 1977), i.e. the same size as in our study. Even bigger (15.0 cm) reproductively active females were trapped in Slickolampi (Westman *et al*. 1993) and in Karisjärvi (15.8 cm) (Kirjavainen and Westman 1995). Since most > 10-cm individuals were harvested from these lakes, even 15–16 cm is not necessarily the maximum size at which signal crayfish females are still reproductive. Mason (1977) reported that the reproductive capacity of *P. leniusculus* females declines with increasing size. The same was found in Karisjärvi (Kirjavainen and Westman 1995) and in the present study (Fig. 5). Even so, large females remain the best production source of young per female because the rate of efficiency decrease does not exceed that of fecundity increase until females have reached about 65 mm CL (about 13 cm TL). In Lake I-M, as in numerous other waters, a positive correlation between female body size and fecundity was found (for references, *see* Savolainen *et al*. 1997).

Results obtained in Lake I-M and other experimental lakes (Fürst 1977a, 1977b, Fjälling and Fürst 1988, Svärdson *et al*. 1991, Holdich and Domaniewski 1995, Kirjavainen and Westman 1995, Westman and Savolainen 1995) indicate that *P. leniusculus* sustains trapping very well. The population could withstand even very high yearly exploitation rates (6%–36% of the trappable population) in Lake I-M, providing that < 10-cm individuals were not removed. Similarly, McGriff (1983b) found that the *P. leniusculus* population in the Sacramento Delta, CA, could sustain exploitation rates of 28%–49% in areas with an abundant population.

Management implications

An interesting question is what would happen if the owner of Lake I-M were to demand, in the hope of greater catches, that the harvesting size of signal crayfish be reduced from the present 100 mm to 90 mm or even less. Keeping a population productive requires that exploitation, especially that of sexually mature females, should not be too heavy. Males may copulate with more than one female and therefore be more expendable for cropping purposes. If a minimum trapping size is enforced, it should be larger than the size at maturity. According to Momot (1984), at higher latitudes the possibility of recruitment overfishing increases, especially on long-lived crayfish species of low fecundity, e.g. *P. leniusculus*. With increasing fishing pressure, older age groups are quickly harvested, resulting in a loss of reproducing individuals and a subsequent substantial reduction in brood stock size, inevitably followed by lower recruitment to the population. This could have a serious impact on population size.

The growth rate and size at maturity of *P. leniusculus* suggest that if all ≥ 90-mm specimens were trapped and removed from Lake I-M, the brood stock would rapidly be reduced to little more than a single age group. This would increase the possibility of the age of maturity falling below the mean age of the population. Each new cohort would receive at best one opportunity to spawn, and an increasingly large proportion of the females would not reproduce at all before being caught. As the size of females declines so their fecundity declines (Savolainen *et al*. 1997). A reduction in the minimum trapping size would result in overfishing of the stock and were a spawning failure also to occur, for instance, due to years with poor climatic conditions, the stock could soon collapse.

Fürst (1977b) pointed out that in Sweden expanding *P. leniusculus* populations were sometimes so heavily overfished (legal minimum catch size being 90 mm) that reproduction is impossible. In one year, intensive trapping of ≥ 90-mm signal crayfish devastated the small population in Träsksjö (Svärdson *et al*. 1991). The overfishing postulated by Momot (1984) could thus also affect the small *P. leniusculus* population in Lake I-M, and probably also other small stocks at high latitudes wherever the minimum legal size has been lowered to 90 mm and trapping pressure is high. To ensure that females in Lake I-M have a possibility of spawning at least once before being caught, the minimum size should, for safety's sake, be kept at about 10 cm.

Our observations (K. Westman and R. Savolainen, unpubl.) from Slickolampi (Westman *et al*. 1995), in which a reduction in the minimum size from 100 mm to 90 mm has not resulted in any noticeable depletion of the trappable population of signal crayfish, at least in the last four years, suggests, however, that the outcome of reducing the minimum size may not be seen for several years. Moreover, under favourable conditions and in strong stocks it may not be seen at all. In Oregon, for example, no overfishing was recorded in the 1940s and 1950s even though the minimum size of signal crayfish was 90 mm. The bulk of the commercial catch nevertheless comprised larger, 10–11-cm, individuals (Miller and Van Hyning 1970). Similarly, in the Sacramento-San Joaquin delta a minimum legal size of 92 mm has sufficed to keep the stock productive; there, the commercial catch comprised primarily 2+ and 3+ signal crayfish (McGriff 1983a). Sound management seems, thus, to depend on local conditions and, as pointed out by Lodge and Hill (1994), requires better understanding than currently exists of the factors that control natural populations and their productivity. Exploitation may cause complex population responses, such as those observed by long-term studies on *O. virilis* (for references, *see* Momot 1993).

Signal crayfish have been reported to reduce the numbers of water macrophytes (Abrahamsson 1966, Fürst 1977a, 1977b, Laurent and Vey 1986, Lowery and Holdich 1988), but no observable changes were found in Lake I-M, probably because the crayfish biomass is still small. If, however, the population increases, changes can be expected, because a dense crayfish population exerts a strong influence on the entire benthic flora, and extended foraging can modify the crayfish habitat through overfeeding on macrophytes (e.g. Flint and Goldman 1975, Momot 1995).

Ever since *P. leniusculus* was first introduced into Finland and other countries in Europe, debate has gone on as to whether the species is plague-resistant and could replace *A. astacus* and other European native crayfish species in plague-infected waters (e.g. Westman 1995). Some researchers (e.g. Smith and Söderhäll 1986, Cerenius *et al*. 1988, Söderhäll 1990) even suggested that *P. leniusculus* might not be as plague-resistant as observed by Unestam (1969, 1972) and that its resistance might even have declined (Persson and Söderhäll 1983). If that were so, the plague would pose a major threat to *P. leniusculus* stockings. Similar views were expressed in Finland (Rantamäki 1990).

Judging by the presence of melanised spots, some of the *P. leniusculus* imported into Finland from North America were indeed infected with the plague (Nylund and Westman 1995). The small *A. astacus* population in Lake I-M disappeared after signal crayfish were stocked, implying plague infection. The same is thought to have occurred in Karisjärvi (Kirjavainen and Westman 1995). According to Nylund and Westman (1995), plague-infected specimens represented a fairly high proportion, about 47%, of the trappable catch in Lake I-M in the first study year, 1979, i.e. ten years after stocking. Thereafter, the proportion declined, being about 24% in the latest, 1994, study (V. Nylund and K. Westman unpubl.). Crayfish plague has not appeared to affect the *P. leniusculus* population and no deaths were reported, even though the signal crayfish were stressed by trapping and the handling associated with research activities. This finding applies to Karisjärvi, too (Kirjavainen and Westman 1995); nor has any mortality been documented when infected specimens from Lake I-M have been used in other experiments (Järvenpää *et al*. 1986). In normal circumstances, then, the introduced *P. leniusculus* stock seems to have good resistance to plague and thus to be suitable for the management of chronic plague waters.

Acknowledgements: We are deeply grateful to the following persons who participated in the field work: Pekka Ahlfors, Esa Erkamo, Eero Kuittinen, Jarmo Louhimo, Matti Mielonen, Viljo Nylund, Klaus Sundbäck, Jukka Sutela, Jouni Tulonen, Irmeli Wallin, Pia Westman, Tapani Vänttinen and the late Aulis Keinänen. We wish to thank Olli Sumari for his contribution to the planning of stockings and also for the many other ways in which he helped with our study. The owner of Iso-Majajärvi, Metsä-Serla Oy (formerly Serlachius Oy), and especially Leo Häggman and Jorma Laitinen of that company, helped and supported the field work in many ways. Our thanks are also extended to Greg Coogan and Gillian Häkli for checking the English text and to Taina Kytöaho for drawing the figures.

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Received 11 June 1998, accepted 22 August 1999