RESEARCH ARTICLE

Freshwater Crayfish 22(1):53–60, 2016
ISSN: 2076-4324 (Print), 2076-4332 (Online)
https://doi.org/10.5869/fc.2016.v22-1.53

Signal Crayfish in Lake Saimaa Could be Maladapted to the Local Conditions Due to *Aphanomyces astaci* Infection: A Seven-Year Study

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ABSTRACT

We conducted a seven-year survey (years 2009 to 2015) of the Lake Saimaa signal crayfish population. Lake Saimaa is the largest single waterbody in Finland, with a productive fishery and crayfishery. The signal crayfish were introduced to Lake Saimaa in mid-1990's and a commercial fishery was initiated in the mid-2000s. At first, there was a small proportion of noble crayfish among the catch, but after 2007, an acute crayfish plague epidemic eradicated them, and the signal crayfish stock started showing frequent gross symptoms of chronic crayfish plague infection (e.g., melanised lesions, eroded uropods and pleopods, lost appendages with melanised stumps). This stock now shows gross symptoms of the infection at a rate of 45% to 79% of the annual trap catch, in addition to showing signs of eroded swimmeret symdrome (ESS) at a rate of 2.8 to 15.4%. The CPUE has remained rather low, between one and three crayfish throughout the survey, while the proportion of the commercial grade catch has been between 35% and 68% of the total catch. The signal crayfish populations in Lake Saimaa are still rather fragmented, and production is low. It appears that the Lake Saimaa signal crayfish population has developed slowly and is producing less than expected.

ARTICLE INFO

Article History:
Submitted: 06 JUN 2016
Accepted: 24 OCT 2016
Published Online: 02 NOV 2016
Published Print: 31-DEC-2016

Keywords:
commercial trapping;
crayfish catch;
crayfish plague;
disease;
ESS;
Pacifastacus leniusculus;

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INTRODUCTION

The established populations of freshwater crayfish create the largest fraction of the bottom fauna in an aquatic ecosystem, both by their biomass and its impact on the ecosystem (Souty-Grosset et al. 2006; Ruokonen 2012; Ercoli 2014). The crayfish mainly graze on the sediments, decaying organic matter, epiphytes and bottom dwelling invertebrates, thus altering the oxygen budget of their habitats (Holdich and Lowery 1988). They also add to the circulation of aquatic nutrients and minerals by their movements, feeding, digging and searching for a suitable shelter. Crayfish in general, and signal crayfish (*Pacifastacus leniusculus* (Dana)) in particular, act as a link between the litoral and profundal zones in lakes (Ruokonen 2012), connecting these habitats and contributing to enriching native macroinvertebrate taxa, community composition and diversity, with the impacts being most pronounced at stony shores. Finally, crayfish inhabit the bottom section of the aquatic ecosystem, where water quality changes would have a great impact on them. Crayfish can be long-lived, and individuals up to 20 years old can be found (Holdich and Lowery 1988; Belchier et al. 1998; Souty-Grosset et al. 2006), making them perfect organisms for assessing long-term changes in aquatic ecosystems. These features make crayfish excellent and sensitive candidates for environmental monitoring, as changes in aquatic ecosystem quality is quickly reflected in the state of the crayfish stock (Holdich and Lowery 1988; Kuklina et al. 2013).

The crayfisheries have traditionally been an important side income in rural regions in Fennoscandian countries (Jussila and Mannonen 2004) which has encouraged the fisheries administration to introduce alien signal crayfish from North America to substitute for the declining noble crayfish (*Astacus astacus* (Linné)) stocks (Souty-Grosset et al. 2006; Jussila et al. 2014a, 2015). This has created a situation where the large lakes, previously void of crayfish for decades, have been inhabited by introduced alien signal crayfish (Westman 2000; Holdich et al. 2009). The signal

Figure 1. Eroded swimmeret syndrome (ESS) signs shown as regenerated swimmerets in a female (left) and eroded gonopods (pleopod 2) in a male signal crayfish (right) from Lake Saimaa.

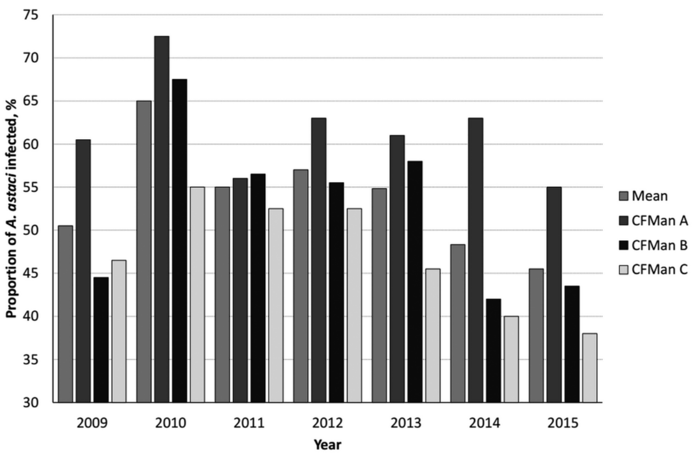

Figure 2. Percentages of *A. astaci* symptomatic signal crayfish in the catch from 2009 to 2015.

crayfish stocks have been recently reported to show maladaptation to Fennoscandian conditions, with several population crashes from both Sweden and Finland (Edgerton et al. 2004; Jussila et al. 2014a, 2015; Sandström et al. 2014) and also a recent discovery of a novel disease, eroded swimmeret syndrome (i.e., ESS), which is caused by a combined *Fusarium* SC and *Aphanomyces astaci* (Schikora) infection (Edsman et al. 2015). This partially complicates the population dynamic surveys of the signal crayfish, simultaneously making these stocks relatively more suitable for environmental monitoring with their perceived increased sensitivity to changes in the aquatic environment.

In Finland, losses among the noble crayfish stocks due to crayfish plague epidemics were supposed to be mitigated by introducing the alien signal crayfish into the waterbodies that had become unsuitable for noble crayfish (Westman 2000; Kirjavainen and Sipponen 2004). The reasons for introducing signal crayfish were based on the assumptions that the species was immune against *A. astaci* and thus would thrive under southern Fennoscandian conditions. However, recently it has been shown that the signal crayfish might not be as good a candidate as was originally expected, and it has been observed to be struggling in Fennoscandia (Aydin et al. 2014; Sandström et al. 2014, Edsman et al. 2015; Jussila et al. 2015). The signal crayfish is also a chronic carrier of *A. astaci* (Holdich et al. 2009; Jussila et al. 2015; Kozak et al. 2015) and is considered to be among the top 100 worst invasive alien species (EU 2016). Thus, the situation for signal crayfish in Fennoscandian, and in European aquatic ecosystems in general, has been re-evaluated with many recent publications casting serious doubts about the possibility of further introductions of this species (e.g., Holdich et al. 2009).

Lake Saimaa, a typically shallow, lacelike fragmented natural freshwater lake, is the largest lake in Finland and the fourth largest in Europe, with a surface area of 4,400 km^2, mean depth of 17 m and total water volume of 36 km^3 (Wikipedia 2015). Lake Saimaa has 13,710 islands and its shoreline is 14,850 km long (Wikipedia 2015). The lake was one of the original prime sites for crayfisheries around the turn of the 20th century (Lehtonen 1975). Lake Saimaa was hit by a crayfish plague epidemic in 1893, which was the first reported epidemic in Finland (Lehtonen 1975; Alderman 1996). Since then, several episodes of crayfish plague epidemics were reported and the lake was never successfully restocked with the native noble crayfish (Lehtonen 1975).

The alien signal crayfish stock was introduced into Lake Saimaa during the first half of the 1990's, which initiated a low but gradual increase in productivity, while commercial and recreational trapping of the signal crayfish started at the turn of the millennium (Jussila et al. 2013, 2014a). For a few years, there were also low numbers of noble crayfish in the catch (Tiitinen 2015, personal communication). An acute crayfish plague epidemic was observed in 2007, with symptoms such as drastic decline in the catch and a total disappearance of noble crayfish from the catch. Since then, signal crayfish production has remained at a low level for the past eight years. Furthermore, Lake Saimaa signal crayfish have shown severe gross symptoms of a chronic crayfish plague infection, with melanised lesions, eroded uropods and pleopods, and lost appendages with melanised stumps (Strand et al. 2012; Jussila et al. 2013; Edsman et al. 2015), and the infection rate, detected by both qPCR and visual observations during surveys, is above the average among the Finnish signal crayfish stocks. A discovery of ESS during the 2011 season (Edsman et al. 2015) has only complicated matters further.

We describe here the nature of the Lake Saimaa signal crayfish population. This is done largely from the point of view of a commercial crayfishermen, with emphasis on the quality and quantity of the catch and the sustainable exploitation of the alien crayfish stock in Lake Saimaa.

MATERIALS AND METHODS

During a seven-year survey (2009 – 2015) we have been monitoring the catch of three commercial crayfishermen in Lake Saimaa as part of research and development projects on the crayfisheries, crayfish handling, and storage methods (e.g., Jussila et al. 2013). Data has been collected, and catch measurements have been made, from a) three crayfishermen (from here on CFMan A, B and C), b) two test sites per crayfisherman four times per season, i.e., 3 CFMen x 2 test sites x 4 catching times during an eight week period, and c) the total annual catch as reported by the crayfishermen for each trapping day individually, both the total catch and the commercial catch (commercial grade, >10 cm total length, TL). The test trapping sites for each crayfisherman (N=2) were selected at the beginning of the survey and it was agreed that the crayfishermen would be trapping at these sites throughout the season as part of their trapping routine. This was to ensure that trapping pressure would be comparable within each site from one year to another. Otherwise, the crayfishermen were moving their traps throughout the season from one site to another, except for fishing the test trapping sites continuosly.

The crayfishermen were using popular Rapu-Rosvo® (Pirate) traps, which are of an enlongated shape with entrances on two sides. The bait was normally frozen or fresh roach (*Rutilus rutilus* (Linné)), sometimes with special artificial crayfish bait. The bait was placed inside a small perforated container inside the trap.

The commercial catch criteria are the proportion of market size signal crayfish of premium quality, meeting the following criteria, minimum 10 cm TL with equal size claws and no visible damage or gross symptoms of crayfish plague infection (Jussila et al. 2013). The crayfishermen were using roughly 70 (CFMan A), 200 (CFMan B) and 500 (CFMan C) traps daily during the crayfishing season, ranging from 1,500 to 17,874 trap nights during the whole season per crayfisherman.

In total, 12,826 signal crayfish from the test trapping sites were measured, resulting in roughly 1,833 signal crayfish measurements annually. The following measurements were taken from the catch at test sites: carapace length (CL, mm), sex (male, female), claws (intact or not), glare gland development, gross symptoms of crayfish plague infection (rated as 0 = no gross symptoms, 1 = 1 – 5 melanised lesions and all appendages intact, 2 = 5+ melanised lesions or lost appendages and melanisation), signs of ESS (rated as 0 = healthy swimmerets, 1 = melanised swimmerets, 2 = 1 – 7 lost swimmerets and 3 = all swimmerets lost) and specific additional notes on such things as carapace hardness, females carrying eggs or remains of eggs, unusual hemolymph color, etc. Notes on ESS (Edsman *et al*. 2015) have been taken since the 2013 annual survey.

The catch per unit effort (CPUE) was calculated based on the total crayfish catch of individual crayfishermen over the whole crayfish season divided by their cumulative trapping effort (see formula below). The crayfishermen reported crayfish catch and number of traps used daily. For practical resasons, we also discuss CPUE as crayfish per trap-night, with the assumption that a 10 cm TL commercial size and quality signal crayfish weighs roughly 55 g.

$$CPUE = (C_1 + C_2 + C_3 + \ldots + C_n) / (T_1 + T_2 + T_3 + \ldots + T_n),$$

where C_1 is crayfish catch on day 1 of the crayfish season (g) and T_1 is number of traps in use on day 1 of the crayfish season.

We estimated the trends in the proportion of *A. astaci* infected signal crayfish in the annual catch of the two test trapping sites for each crayfisherman. We used regression analyses and selected the fit which had highest R^2.

We used MS-Excel for data processing. The results are expressed as means with standard deviations when relevant.

RESULTS

The crayfishermen can be rated in three different categories according to their trapping effort: 1) recreational trapper (CFMan A), 2) semiprofessional trapper (CFMan B) and 3) professional trapper (CFMan C) (Table 1). These three different categories are well represented among the Finnish crayfish trappers, with the two latter normally selling most of their catch. The annual cumulative trapping effort was above 20,000 trap nights from 2010 onwards for the three test trappers.

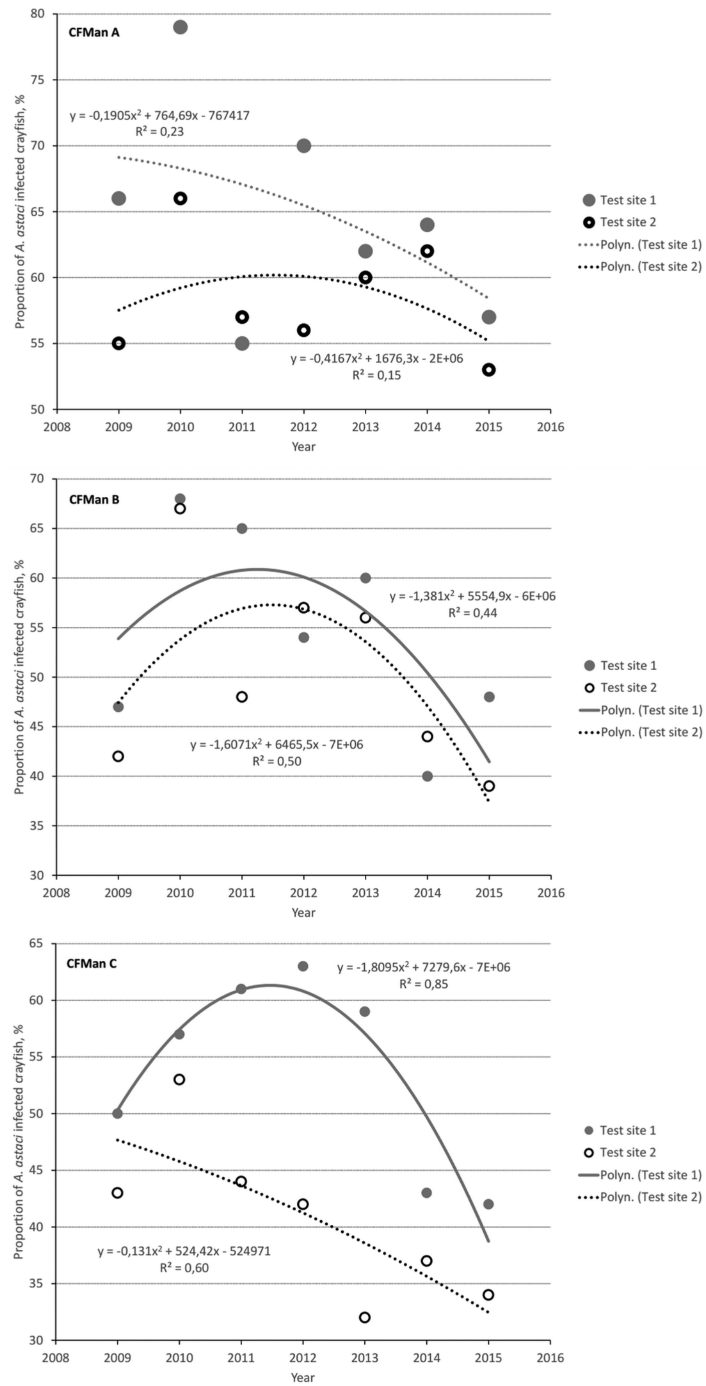

Figure 3. The proportion of the signal crayfish showing gross symptoms of the *A. astaci* infection among the test site catches annually. The annual mean is indicated by the dots for each of the crayfishermen per test trapping site per year. The trends were estimated using polynomial regression with the regression equation and R^2 value displayed.

We observed ESS among studied signal crayfish females annually and at all test trapping sites. The females have shown ESS

Table 1. Total number of trap nights per crayfisherman during 2009–2015 based on the participating crayfishermen notes. Trap nights is the cumulative number of traps used daily during the crayfish season.

	Year						
	2009	2010	2011	2012	2013	2014	2015
CFMan A	2,250	1,950	3,150	2,535	1,608	2,250	1,500
CFMan B	3,900	5,690	4,890	5,600	5,270	5,800	5,490
CFMan C	10,510	14,135	14,286	17,874	16,193	15,882	13,688
Sum	16,660	21,775	22,326	26,009	23,071	23,932	20,678

Table 2. Percentage of signal crayfish females showing eroded swimmeret syndrome (ESS) in Lake Saimaa test catches during 2013–2015 with the two test trapping sites separately displayed for each crayfisherman. Data based on test site catch measurements and observations. The ESS rating according to Edsman et al. (2015).

		Year and Test Trapping Site					
		2013		2014		2015	
	ESS rating	I	II	I	II	I	II
CFMan A	1	42.9	27.2	28.4	29.4	21.6	28.4
	2	14.3	9.1	11.3	13.0	15.0	10.5
	3	0.0	0.0	0.0	0.0	0.0	0.0
CFMan B	1	56.7	11.1	24.4	27.3	18.5	20.3
	2	6.7	2.8	15.3	15.4	10.1	15.4
	3	0.0	0.0	0.0	0.0	0.0	0.0
CFMan C	1	5.3	15.6	16.3	20.1	28.9	14.5
	2	5.2	9.4	8.9	5.8	3.5	7.7
	3	0.0	0.0	0.0	0.0	0.0	0.0

signs at a rate of 10.5 – 63.4% (Table 2) with no detection of a total loss of swimmerets among the female crayfish caught at test sites. The proportion of ESS (stage 2 and 3) in female crayfish ranged from 2.8 to 15.4% in the test catch. We have also observed that the eroded swimmerets were regenerated in some females (Figure 1). Furthermore, during the 2015 survey, a few male individuals with eroded pleopods (1 and 2) and swimmerets were observed (Figure 1). Females with eroded swimmerets in the test catches also showed indications of a longer hatching period of the eggs, as only those signal crayfish females that had ESS still had eggs or second stage juveniles under their tail in early August 2015.

The annual mean proportion of the signal crayfish showing gross symptoms of *A. astaci* infection were on average higher than 40% in the test site catches (Figure 2), except for test site catches for CFMan B in 2014 and 2015 and for CFMan C in 2013, 2014 and 2015. The highest pooled mean annual proportion of *A. astaci* infected signal crayfish was in CFMan A's catch, reaching 61.6 ± 7.1%. The lowest pooled mean annual proportion of *A. astaci* infected signal crayfish were in CFMan C's catch, averaging 47.1 ± 10.1%. CFMan B had an average of 52.5 ± 10.0% infected signal crayfish in his test site catch. The proportion of infected signal crayfish was statistically significantly higher among CFMan A's catch compared to both CFMan B's and CFMan C's catch (t-test, $p < 0.05$) while there was no difference between CFMan B's and CFMan C's catch. After an initial increase for 2 to 3 years, there was a general declining trend over time in the proportion of signal crayfish showing gross symptoms of *A. astaci* infection (Figure 3), with a polynomial fit curve showing the highest correlation (R^2) in all cases. The fit curves R^2 values were low for CFMan A data (from 0.1 to 0.2), while R^2 values showed moderate to high significance in CFMan B and C data, being from 0.4 to 0.5 and from 0.6 to 0.8, respectively. There was considerable year to year variation in the proportion of infected signal crayfish in our survey.

The average catch per unit effort (CPUE, g of crayfish per trap night), estimated from the crayfishermen's annual catch statistics, increased from 58 g (in 2009) to 135 g (in 2012) and then levelled off for the rest of the survey period at above 120 g (Figure 4). This maximum average CPUE roughly equals 1.5 commercial sized signal crayfish, and for practical reasons, we will be discussing CPUE as the number of crayfish per trap-night in the Discussion section. Overall, CFMan B had the highest CPUE, except for the year 2011, and CFMan A had the lowest CPUE, except for the year 2009. The CPUE was increasing throughout the survey for CFMan B, except in 2015, while CPUE leveled off for both CFMan A and CFMan C after 2011.

Catch data for CFMan C, collected prior to this survey, indicates that the average CPUE over the whole crayfish catching season was 59 g of crayfish per trap night in 2006, 21 g in 2007 and 33 g in 2008. During 2007, an acute crayfish plague epidemic was observed in Lake Saimaa (Jussila et al. 2013, 2014a) and the signal crayfish were rather lethargic with elevated levels of mortality during transport to processing sites (Tiitinen 2015, personal communication).

The proportion of grade I market-size signal crayfish, estimated using crayfishermen annual catch statistics, averaged roughly 40% in the commercial catch during 2010 and 2011, with a slight increasing trend throughout the monitoring period (Figure 5). The proportion of market-size signal crayfish in the catch was highest for CFMan A, except for 2014, when the differences among the test trappers were small. CFMan C always caught the smallest proportion of market size crayfish during the survey period. The variation in the proportion of market-sized signal crayfish for each crayfisherman catch was lowest during 2014 and 2015, while higher levels of variation were evident during 2010–2013. The proportion of market-sized signal crayfish in the catch was 1.5 times higher for CFMan A compared to CFMan C during 2011–2013.

DISCUSSION

We have shown that Lake Saimaa signal crayfish are suffering from chronic *Aphanomyces astaci* infection at a high rate, with up to 79% of the commercial catch showing gross symptoms of crayfish plague infection. The lowest annual mean proportion of market quality signal crayfish among the commercial trapper catch was 45%. The proportion of the market size signal crayfish (i.e., over 10 cm TL) is rather high in the commercial crayfishermen catch in Lake Saimaa, especially considering that the stock is heavily exploited. On the other hand, the CPUE has remained low so far, equaling roughly a maximum of three commercial size signal crayfish. All this information combined shows that the Lake Saimaa signal crayfish population production potential has remained rather low.

A high proportion of signal crayfish displayed gross symptoms of *A. astaci* infection, averaging between 47% and 62% among the test site catches. Previously, it has been reported that the prevalence of *A. astaci* infection in Lake Saimaa signal crayfish might be as high as 90%, based on TagMan qPCR analyses (Strand et al. 2012). This is higher than the gross symptoms proportion observed in our survey data, which could indicate that some of the infected signal crayfish might not be detected during the field surveys. Surveys in two other Finnish signal crayfish populations indicate that roughly 24% of the signal crayfish were showing gross symptoms of *A. astaci* infection (Nylund and Westman 2000), ranging from 10% to 63% in their data. In general, the signal crayfish *A. astaci* infection prevalence at the population level varies, and even healthy populations have been reported from Europe (Kozubíková et al. 2009; Filipová et al. 2013). The high infection prevalence in our survey data might affect the survival of the Lake Saimaa signal crayfish. It has been shown earlier that the signal crayfish is not indifferent to this disease and it may show increased mortality when infected (Thörnqvist and Söderhäll 1993; Aydin et al. 2014; Jussila et al. 2014a). The high prevalence of *A. astaci* infected signal crayfish could be a factor behind the low CPUE observed in our survey data.

On the other hand, we observed a declining trend in the proportion of signal crayfish showing gross symptoms of crayfish

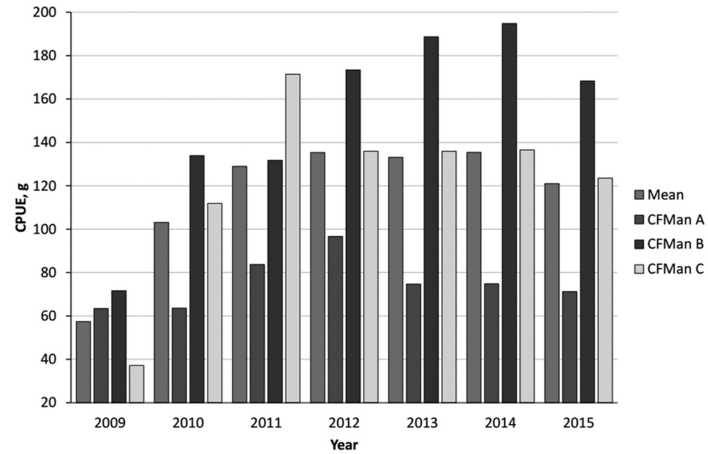

Figure 4. Estimated catch per unit effort (CPUE) based on the catch reports by the crayfishermen over seven years. CPUE expressed as g of crayfish per trap-night for the whole crayfish season. Daily crayfish catch (g) and number of traps (#) used obtained from the annual reports of the crayfishermen.

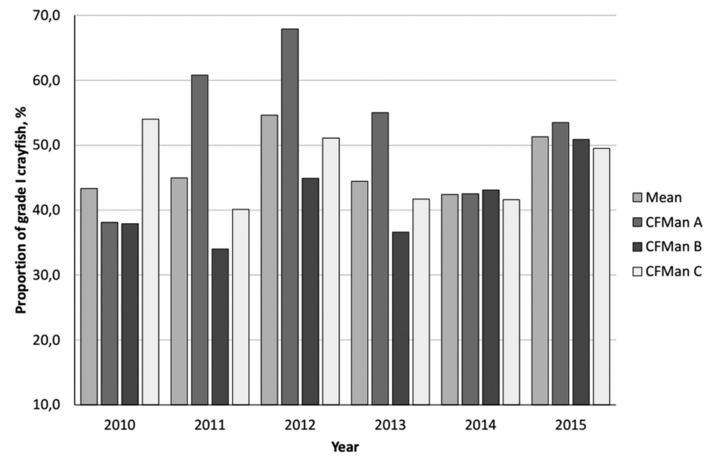

Figure 5. Proportion of market quality signal crayfish in the annual catch, i.e., signal crayfish fulfilling the criteria of minimum size 10 cm TL and no gross symptoms of *A. astaci* infection. Data for the whole crayfish season and obtained from the annual reports of the crayfishermen.

plague infection in our data over time. This finding should be treated with caution, since the trend line R^2 values were less than 0.5 in half of the cases. Furthermore, the data indicated large annual variation in the proportion of the infected crayfish, which might be the main finding here. Considering this, the effect of *A. astaci* infection prevalence and the possibility of an improved resistance among wild signal crayfish is an interesting phenomenon.

The proportion of female signal crayfish showing signs of ESS is comparable to our previous data from Finland (Edsman et al. 2015), but lower than observed in that study among collapsed signal crayfish populations in Sweden. In our data, we did not observe any females with complete swimmeret losses and also found evidence of swimmeret regeneration. Thus, there is a possibility for recovery among those female signal crayfish that do not die due to ESS and *A. astaci* infection. However, our laboratory experiment showed that even partially regenerated swimmerets are not suitable for carrying eggs during hatching and thus cause loss of the reproductive output at the population level (unpublished data).

The maximum proportion of the signal crayfish females suffering from stage 2 ESS was 15.4% in our survey. This could cause an estimated loss of 10% in the reproductive output at the population level. It has been suggested that ESS (caused by a combination of *Fusarium* SC and *A. astaci* infection), could be a biotic factor capable of controlling alien signal crayfish populations in Fennoscandian waters. This is an interesting speculative statement, as it has been reported elsewhere that several Fennoscandian signal crayfish stocks have crashed or decreased in size (Aydin et al. 2014; Jussila et al. 2014a, Sandström et al. 2014), contrary to what was earlier assumed. We have also observed that male signal crayfish can have eroded swimmerets and gonopods in Lake Saimaa. In addition, we have not observed ESS or any similar symptoms in noble crayfish (*Astacus astacus*) in Fennoscandia. The direct effects of ESS on signal crayfish viability and juvenile recruitment warrants further investigation.

For practical reasons, we are discussing CPUE in terms number of crayfish, even though the crayfishermen have reported only the total weight of their catch. The average CPUE in the commercial catch, for all size classes, fell between 1 and 3 crayfish throughout the survey period, indicating that Lake Saimaa signal crayfish population density is rather low, but still productive, and that the population might be in its growth stage, with low competition for resources. Previously, it has been reported that the development of the signal crayfish fishery might take decades, with estimates that CPUE could exceed 1 only after 20 years (Kirjavainen and Westman 1999; Westman 2000), while higher CPUEs have been observed in Europe (Guan 2000; Nyström et al. 2006; Capurro et al. 2007; Peay et al. 2009). It must be remembered that the sampling in our survey was not neutral, but rather based on effort of commercial trappers to maximize their catch. Even when the crayfish trappers are constantly reviewing their effort and aiming for cost effectiveness, the average CPUE over the season remained low, quite close to the threshold of the crayfish population being exploited (Erkamo et al. 2010; Jussila et al. 2014a). On the other hand, there were distinct differences among the test trappers and the two trappers having the highest effort (CFMan B and C) also had roughly double CPUE compared to the recreational trapper (CFMan A). Even for CFMan B and C, the best CPUE remained between 2 and 3 crayfish during the survey period.

The proportion of market size (over 10 cm TL) signal crayfish in the Lake Saimaa catch has remained high throughout the survey period, at the level of 40% to 50% on average. This is in spite of the commercial trappers using largely the same areas for trapping from one season to next. On the other hand, the individual commercial trapping sites cover large areas and Lake Saimaa itself allows plenty of habitat for the signal crayfish. It may be that crayfishermen are actively moving within each individual site while trapping, and abandoning sites of low production and moving to more productive ones. It could also be that the signal crayfish stock is still in its growth stage after 20 years and low density populations allow for faster growth. Finally, there is also the option of low juvenile recruitment and low mortality of juveniles, which results in a higher proportion of larger sized individuals but low overall CPUE in the commercial catch. The effect of long-term trapping pressure usually tends to drive towards smaller mean size (Momot 1991; Tulonen et al. 2008) but this does not show in our data and it can be partially explained by the trapping strategy of the commercial trappers aiming for the highest cost effectiveness in the crayfishery. Alternative scenarios have also been suggested as the outcome of the exploitation (Momot 1991; Huner and Lindqvist 1988). Thus, there are several possible factors that can skew the size distribution towards larger size crayfish in Lake Saimaa, but there is also room for further investigations.

The first years of the follow-up period showed an increase in CPUE among the catch of the test trappers, and after 2011, the CPUE leveled off at roughly 2 crayfish. The Lake Saimaa crayfish population, which also included noble crayfish at that time, experienced a crayfish plague epidemic in 2007 (Jussila et al. 2013, 2014b). Due to the epidemic, the CPUE declined to less than half the current rate (according to catch records from one test trapper), with those crayfish caught showing high lethargy compared to previous years. Thus, the initial increase in CPUE in our survey data during 2009 and 2010 could still be within the recovery phase from the 2007 crayfish plague epidemic. The leveling of the CPUE after 2011 might be indicating that the production capacity of Lake Saimaa signal crayfish may have been reached at a level that is quite low. Alternatively, the Lake Saimaa signal crayfish stock may still be in the low density growth phase, since Lake Saimaa is a large waterbody and, with the signal crayfish stock having been established only recently in the early to mid 1990s, it could take decades to reach carrying capacity within the lake.

In conclusion, our research indicates that the Lake Saimaa signal crayfish stock is showing indications of alien species maladaptation to environmental conditions in Fennoscandia, as it is heavily affected by *A. astaci* infection and suffering from ESS. It is also obvious that the CPUE has remained comparatively low in Lake Saimaa, but investigations of reasons for the low CPUE were beyond the scope of this study. It appears that the success of alien species introductions, when introduced into new regions, should only be evaluated after a lengthy time lag, which in this case would be several decades. Thus, similarities between habitat conditions in the native range of the species and its sites of introduction should be examined with extreme caution. These often positively biased preassumptions should not be used as a basis for decision-making per se, but should be weighed carefully against the principle of caution in introducing alien species.

ACKNOWLEDGMENTS

We are thankful to the crayfishermen in Lake Saimaa for their hospitality and the grit they exhibit under the unpredictable elements of the Finnish summer. The survey has been partially funded by the Southeastern ELY-Center using funds for fisheries compensations. LIFE+ CrayMate project (LIFE12 INF/FI/233) has partially funded this survey. Several of our colleagues have participated in the data collection and we wish to thank David Strand (Norway), Jörn Panteleit (Germany) and Hamdi Aydin (Turkey) for their professionalism during the field trips. Hobo Kukkonen (Kuopio) did some of the data processing.

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