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Life history characteristics of *Argulus foliaceus* L. (Crustacea: Branchiura) populations in Central Finland

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Life history characteristics of a common fish ectoparasite *Argulus foliaceus,* poorly studied in the northern part of its range, were investigated. Field data on the seasonal occurrence, host preference, sex and size of *Argulus foliaceus* populations from interconnected lakes in Central Finland were analyzed together with experimental data on egg laying, hatching, and mating behaviour. Demographic characteristics of *A. foliaceus* from a commercial fish farm (high host density) with a water supply from the same lake system differed significantly from those of the lake population where the hosts are scarce. Extended periods of egg laying and hatching were documented in the lake population which possibly prevented the appearance of summer peaks in juveniles that were observed in the farm. The elevated activity of the males, which was most clearly observed in their high attachment/detachment rates, is suggested to result in lower survival and growth than in females. The flexibility, in both behaviour and life cycle strategy, allows *A. foliaceus* to utilize a broad spectrum of habitats of differing host abundance.

1. Introduction

The ectoparasitic crustacean *Argulus foliaceus* L. is frequently found on various species of freshwater fishes (Kollatsch 1959, Stammer 1959, Petrushevski 1970, Shulman 1970), usually in small numbers. However, epizootics may occur; Bauer (1970) reported that infestations of several hundred parasites per fish caused mortality on Russian carp farms. Even during recent years *A. foliaceus* caused epizootics and problems in Finnish fresh and brackish water fish farms. However,

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the basic characteristics of *A. foliaceus* life cycle or its population structure have not been studied in northern latitudes. All previous, mainly descriptive, studies have been done in Central Europe and the United Kingdom (Herter 1927, Bower-Shore 1940, Kollatsch 1959, Stammer 1959).

A. foliaceus is an obligatory blood sucker and can survive for only a few days without the host fish, depending on size and ambient temperature (Kollatsch 1959). Copulation in this parasite usually takes place on the fish surface, but occasionally on stones or leaves (Kollatsch 1959); gravid females leave the host in order to lay eggs and need to return to the fish periodically before the completion of laying (Shafir & van As 1986). Thus, the crucial periods of the *A. foliaceus* life cycle are strongly related to the fish host in terms of its individual and population characteristics. Limited abilities to locate and pursue a potential host, as well as the low attack efficiency of *A. foliaceus* towards fish (Mikheev *et al.* 1998), makes fish vulnerability and the population density of the fish hosts of primary importance for the parasites' survival and reproduction success. Thus, host-searching and reproduction of *A. foliaceus* should be more successful in dense fish populations. Most substantial studies on the parasite abundance, its life cycle and reproductive biology have been conducted in situations where the host density was high, for example, in small ponds or fish farms (Kollatsch 1959, Stammer 1959, Shafir & van As 1986). Three generations per year was estimated for such populations (Kollatsch 1959, Stammer 1959). Almost no information has been published on the life cycle and reproduction of *A. foliaceus* inhabiting waters with relatively sparse fish populations.

Some authors (Kollatsch 1959, Petrushevski 1970, Shulman 1970) emphasized a wide range of host species and a lack of specificity with regard to *A. foliaceus*. Such broad specificity would be an efficient strategy from the viewpoint of host searching at low fish population density. But, too wide a dispersion of parasites among potential host species makes another vitally important searching task, the search for mates, more difficult. To develop a preference for one of the potential hosts would seem to be a more rewarding strategy in the latter case. There are some indications as to fish host preference in *A. foliaceus*, both from the field (Valtonen *et al.* 1997) and experimental studies (Mikheev *et al.* 1998), but this still needs to be studied more thoroughly.

This study aimed to clarify ecology and behaviour of *A. foliaceus* in nature under the conditions of relatively sparse fish populations in the lakes of Central Finland. For comparison, data obtained at a fish farm with a high intensity of *A. foliaceus* infection were also used.

Our main objectives were:

1. to study host species preference in nature;
2. to study seasonal occurrence, sex ratio and size distribution of *A. foliaceus* in an attempt to distinguish separate generations;
3. to analyze what features of reproductive biology could account for the observed patterns of occurrence and size/sex distributions.

2. Materials and methods

2.1. Study sites

Fish host preference in *A. foliaceus* was studied in four lakes in a chain of lakes draining via lake Päijänne to the Gulf of Finland in 1986–87 (for the study site, *see* Valtonen *et al.* 1997). Seasonal occurrence, sex ratio and size structure of argulids were studied in a bay of lake Päijänne (Rutalahti) in 1997. The lakes are ice covered from late November to mid-May and their waters reach highest temperatures, 18–20 °C, in late July or the beginning of August. Size frequency distribution and sex ratio of *A. foliaceus* were also studied in 1998 on brown trout, *Salmo trutta* L. from a commercial fish farm of the same drainage area as our studied lakes.

2.2. Sampling

Fish from the lakes were collected by angling. To study host preference, 15 perch, *Perca fluviatilis* L., and 15 roach, *Rutilus rutilus* L., were sampled from the four lakes monthly (bimonthly during the period of ice cover) throughout 1986–87. Fish were taken to the laboratory alive in separate vessels with lake water immediately after being caught and were studied within a few hours.

To study seasonal occurrence, size and sex structure, both perch and roach were angled weekly from the beginning of June until the end of August 1997 from a bay of lake Päijänne. All caught fish (20–40 specimens per week) were examined. The majority of *Argulus* specimens were found on perch. Infected perch were taken to the laboratory where parasites were gently detached with forceps. The body length and sex of *A. foliaceus* were determined under the dissecting microscope. *A. foliaceus* were classified as larvae (size ≤ 0.8 mm, synonym of metanauplius in Rushton-Mellor & Boxshall 1994), immature stages (> 0.8 to ≤ 2.5 mm, second to seventh developmental stages in Rushton-Mellor & Boxshall 1994), and adults (> 2.5 mm). Immature parasites and adults were also sexed. At the fish farm, juvenile brown trout (age 1+, i.e. between 1 and 2 years old, 10–15 cm fork length) were caught individually with a hand net and immediately placed into individual plastic buckets. Fish were immobilized with MS-222, and both detached and attached parasites were collected, counted and measured. Another procedure for obtaining random samples from the same population was also used. Fish from the farm pond were collected with a net and vigorously shaken in a large plastic box. Parasites detached from fish were thoroughly stirred and random subsamples taken with a fine mesh plankton net. A comparison between the two sampling methods revealed no significant differences in the sex ratio and size frequency distributions both for females (Kolmogorov-Smirnov test: $n_1 = 331$; $n_2 = 73$; $D = 0.113$; $p > 0.05$) and males (Kolmogorov-Smirnov test: $n_1 = 328$; $n_2 = 75$; $D = 0.172$; $p > 0.05$).

2.3. Experimental procedures

Most of the laboratory observations were carried out at Tammen Mylly, a field station of the University of Jyväskylä, in June–August 1997. Collected *A. foliaceus* were kept in aquaria filled with filtered lake water under simulated natural photoperiods. Water temperature varied from 16 to 25 °C. In order to maintain an experimental stock for a long period, parasites were placed in aquaria with perch (length 10 to 20 cm), newly hatched argulid larvae being provided with 0+ perch (length 3 to 5 cm).

2.3.1. Activity of females and males

Males have been found more often free swimming than females (Stammer 1959). However, the sex ratio of *A. canadensis* attached to sticklebacks was male-biased from early July to early September (Poulin & FitzGerald 1989a). This suggests different and, perhaps, changing levels of activity between the sexes in relation to both host and mate searching. To quantify the differences, the rates of attachment to the host, the detachment from it and the proportion of time spent in active movement were studied.

2.3.1.1. Rates of attachment and detachment

Experiments were carried out between 23 June and 15 July 1997. In each of the treatments, a group of 10 adult females and 10 males of about the same body length (within the range of 2.5 to 4.0 mm), which had been pre-starved for a day, were placed separately but simultaneously in two buckets with a 10–15 cm perch in each. Treatments were replicated six times. In every replicate, a new set of parasites and hosts was used. To estimate the rate of attachment, parasites were observed every hour and the number of free-swimming animals recorded. In the same experiments, the assessment of the detachment rate started when all parasites had attached to the fish. The attachment experiments were usually completed within 24 h. The detachment experiments took much more time, as detachment occurred less frequently, so the number of the free swimming *A. foliaceus* within this part of the experiments was recorded less often (every three hours, on average). There was a break in recording during night, from 2330 to 0800 hrs. Detached animals were removed from the experimental vessels to prevent their re-attachment. Each experiment lasted for 5 to 7 days (the experiments were terminated when all parasites detached or fish died). Two replicates were run simultaneously.

For statistical treatment of the obtained data, standard time intervals were chosen: an hour for the attachment rate and a day for detachment. Otherwise, the data from the two parts of experiments were treated similarly. The number of detached (or attached) parasites for a given time interval was divided by the number of individuals attached to the host (or free-swimming) at the beginning of the interval, this serving as an index of relative detachment (attachment) rate. These indices for respective time intervals from each experiment were pooled and analyzed with the Mann-Whitney *U*-test.

2.3.1.2. Swimming activity

Five adult males and five females, removed from perch collected from the lake, were monitored individually in plastic boxes 9 × 12 × 2 cm with a grid of rectangles (2 × 3 cm) on the bottom. The number of crosses of the sides of the rectangles performed by each moving parasite during a five minute period was recorded once per day. The mean swimming speed was calculated. The monitoring lasted for 6 days. The behaviour of the same *Argulus* (swimming or attached to the walls or bottom) was then noted every 10 min for a 2-hour interval daily. The percentage of cases when *A. foliaceus* was found attached was used as another index of swimming activity. The indices obtained for males and females were compared with the Mann-Whitney *U*-test.

2.3.2. Reproduction and hatching

Ten copulation events between parasites kept in the laboratory were monitored. Males and females of various sizes collected simultaneously were kept together. Duration of the process and the body lengths of the mating partners were recorded.

Freshly caught gravid females were placed individually in plastic boxes with 300 ml of filtered lake water. They were checked twice a day, in the morning and in the evening, for egg-laying. After having laid several strings of eggs, females were transferred to the aquaria with perch and laid further eggs there. Plastic boxes with egg strings were kept in the laboratory under the simulated natural photoperiod at temperatures varying from 18.4 to 23.1 °C. Egg strings were checked once a day and hatched larvae removed. Egg laying occurred between 2 July and 18 August. The total number of eggs in the 53 strings laid was 2 092. From these, 1 350 eggs were kept constantly under simulated natural photoperiod and room temperature, and 150 eggs produced on 18 August were kept for five months at 5 °C in the dark, after which they were exposed to simulated natural photoperiod and temperature of 20–21 °C. Hatching was monitored until the end of May 1998. The water was replaced twice per week and fungi, if apparent, were removed.

3. Results

3.1. Seasonal occurrence

A. foliaceus were exceptionally rare in winter in the seasonal study carried out at the four lakes in Central Finland. Only 3 adult specimens (2 males and 1 female) were collected from perch in February plus 2 females in April 1987. Within this data set, *A. foliaceus* larvae (0.65–0.80 mm body length) were common at the end of May in 1986 (Fig. 1). Another case of the winter occurrence of *A. foliaceus* on perch was recorded from the bay of lake Päijänne during February 1997, when 5 adult specimens were found (M. Palmunen, pers. comm.).

In lake Päijänne, we did not see any peak in the presence of larvae in the spring of 1997, perhaps because the regular sampling was started only in the first week of June. In the first half of June, juvenile males and females appeared. Among these immature individuals (1.1–2.0 mm body length), a few large females (larger than 5 mm), presumably from the overwintered generation, were found (Fig. 2). The first copulation was observed on June 21 and egg laying on July 2. Females were found laying eggs at a size of > 4 mm. Such females of the new generation started to appear at the very end of June (Fig. 3A). Their numbers gradually increased towards the end of July to mid-August. Then a sharp decrease in abundance of the large, egg-carrying females was recorded. The highest production of eggs in the laboratory occurred at the same time as the highest number of large females in the lake (Fig. 3B). A mass mortality of the parasites, both males and females, occurred in the last week of August in the laboratory. At the same time, *A. foliaceus* became very rare on fish collected from the lake. Rare adults were found on the fish in September

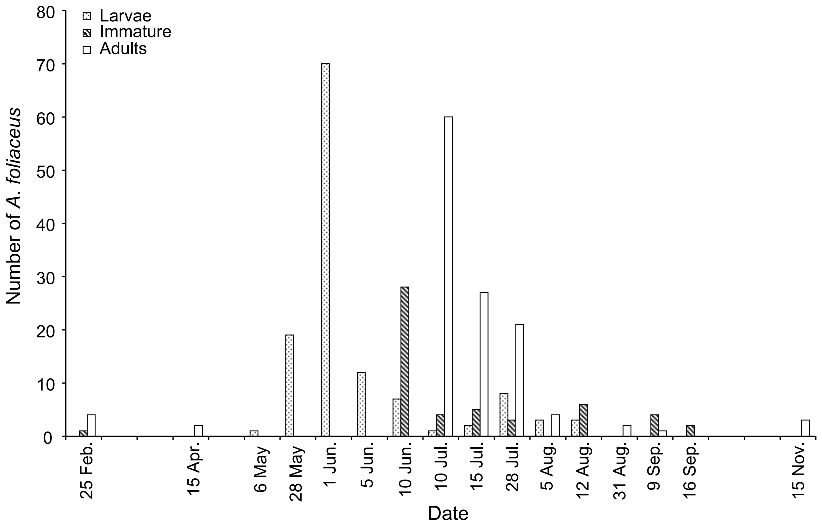

Fig. 1. Seasonal occurrence of *Argulus foliaceus* as the total number of individuals collected from the four lakes in Central Finland.

and November in the seasonally collected data from 1986–87.

3.2. Sex and size structure

The sex and size structure of the *A. foliaceus* population were analyzed in more detail in relation to the data collected weekly from the bay of lake Päijänne during the main period of reproduction, June–August. Rather narrow size frequency distributions, with a maximum of 2 to 2.5 mm in both sexes, was obtained in June. Later, in July and August, the body length range became much wider, particularly in females (Fig. 2). In the July distribution, the modal class could still be distinguished; in August both males and females were more evenly distributed over the whole size range. No peaks in juveniles, indicating the beginning of a new generation, were observed later in summer. The sex ratio was close to 1:1 during almost the whole period of observations; it changed noticeably only in August, when females predominated.

The resulting size structure describes the population of *A. foliaceus* in the lake, a habitat with a relatively low density of fish. Under such conditions, the prevalence of infection varied from 1% to 30%, and the abundance from 0.01 to 0.98 in the four lakes studied during 1986–87 (Table 1).

A much higher level of infection, with a preva-

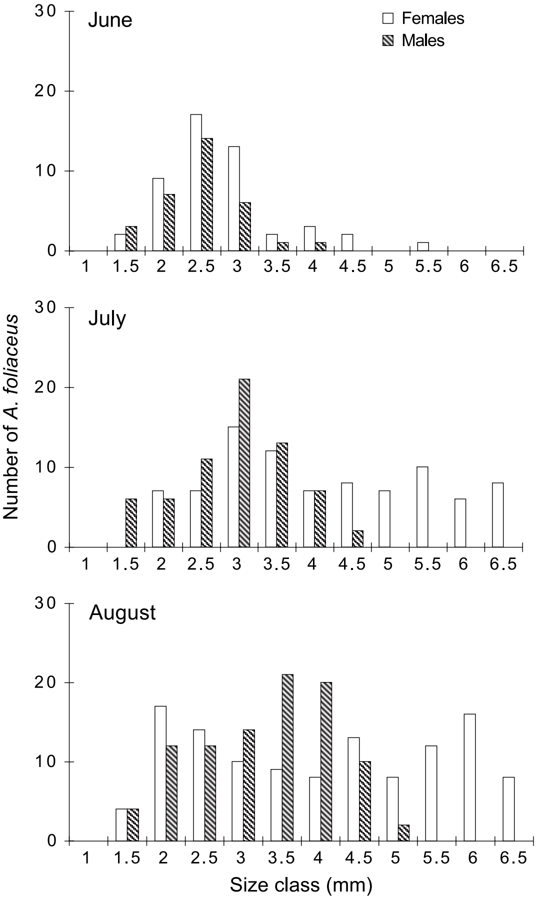

Fig. 2. Seasonal changes in size structure of the population of *Argulus foliaceus* from the bay of lake Päijänne in 1997. Empty bars: females; hatched bars: males.

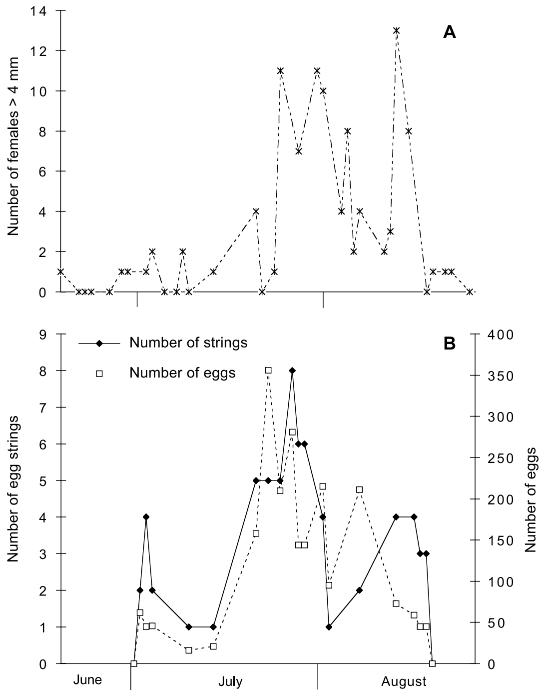

Fig. 3. Changes in abundance of large *Argulus foliaceus* females from the bay of lake Päijänne in 1997 (A: total number collected), and eggs laid in laboratory (B: number of egg strings and eggs produced by ten large females).

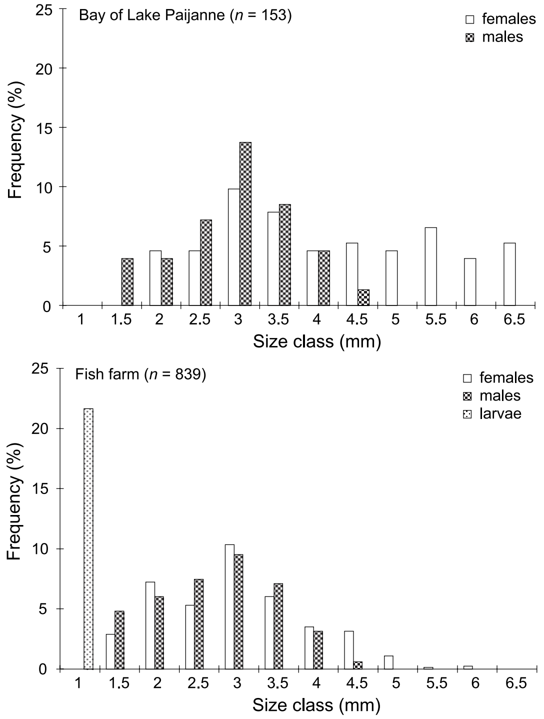

Fig. 4. Size frequency distributions of *Argulus foliaceus* from the bay of lake Päijänne (July 1997) and the commercial fish farm (Central Finland) (July 1998) for the period of most intensive reproduction.

lence of 100% and an intensity of 1–54, was recorded on juvenile (1+) brown trout at the commercial fish farm in Central Finland in July 1998. In this *A. foliaceus* population, a pronounced peak in parasite larvae was recorded in July (Fig. 4). Another difference was the absence of large females, which were numerous in the population from the bay of Päijänne during July 1997 (Fig. 4). The modal size class was the same both in males and females for the two populations.

The frequency distributions of female sizes from the two populations differed significantly, while those of the males were fairly similar. Within the population from the bay of Päijänne, distributions of male and female sizes differed, while those from the fish farm did not (Table 2).

Table 1. Prevalence (%) and mean abundance (*x* = parasites/fish studied) of *Argulus foliaceus* infection on two common fish species from the four lakes in Central Finland studied during 1986–87 on a seasonal basis (*n* = number of fish studied).

Lake	Perch			Roach		
	n	*x*	%	*n*	*x*	%
Peurunka	295	0.18	7	431	0.13	2
Vatia	123	0.98	30	253	0.01	1
Saravesi	264	0.69	21	376	0.04	4
Leppävesi	185	0.67	27	194	0.08	3

3.3. Copulation, egg laying and hatching

Copulation was observed only on a solid substrate, on the fish or in the absence of a fish, on the walls and bottoms of the aquaria. The body sizes of mating partners varied considerably, as did the duration of copulation (Table 3). At the beginning of the reproductive season, copulating individuals were smaller and more similar in size compared to those at the end of the season.

Egg-laying of females caught in the lake and monitored in the laboratory lasted from the beginning of July until the last week of August (Fig. 3). Gravid females detached from the host, usually laid 2 to 4 egg strings consisting of 2 to 6 rows of eggs and then returned to the host. They detached again to lay the next pattern of eggs after 2 to 4 days.

The first larvae hatched on 15 August from the eggs laid 21 July. The hatching time varied greatly. Even in summer time it ranged from 25 to 51 days (mean = 31.8, SD = 9.36). By the end of August when the period of reproduction was over, only 2.5% of 1350 eggs laid in July in the aquaria hatched (Fig. 5). These eggs, kept at the temperature of 19–22 °C, hatched throughout the autumn and winter. The hatching time of eggs at room temperature varied from 25 to 240 days, being asynchronous even within the same egg string. Larvae from another set of eggs (150 eggs), which had been kept at 5 °C for 5 months, first hatched 24 days after these eggs had been transferred to a room temperature of 20 °C (Fig. 5). The hatching of these eggs continued for more than 4.5 months after they had been transferred to room temperature. The overall hatching success of the first group of eggs was 76%, and of the second 66%.

3.4. Activity of females and males

Free-swimming males attached to a new fish host significantly faster than females. Rate of attachments for females was 0.186 (number of attachments per individual per hour) and for males 0.305, being 1.6 times higher in males (Mann-Whitney *U*-test: $p < 0.001$). The difference between the detachment rates was even more pronounced, being 0.021 for females (number of detachments per an individual per day) and 0.141 for males or 6.7 times higher in males than in females (Mann-Whitney *U*-test: $p = 0.0047$).

Table 2. Comparison of the size frequency distributions of *A. foliaceus* populations from the bay of lake Päijänne (low density host population) in July 1997 and the fish farm (high density host population) in July 1998 with the Kolmogorov-Smirnov two-sample test. F = females, M = males; the number of *A. foliaceus* is given in parentheses.

n_1	n_2	*D*	*p*
Lake F (87)	Farm F (73)	0.342	< 0.001
Lake M (66)	Farm M (75)	0.125	> 0.05
Lake F (87)	Lake M (66)	0.418	< 0.001
Farm F (73)	Farm M (75)	0.109	> 0.05

The swimming speed of males (1.55 cm s^{-1}) tended to be higher than that of females (1.36 cm s^{-1}), but the difference was not significant (Mann-Whitney *U*-test: $p = 0.123$). When away from the host, females spent significantly more time (54%) attached to the walls or bottom of the aquarium than males (29%), (Mann-Whitney *U*-test: $p = 0.004$).

3.5. Host species preference

Of the two common fish species, *P. fluviatilis* and *R. rutilus*, studied in the four lakes during 1986–87, perch were much more heavily infected with *A. foliaceus* in terms of both prevalence and mean abundance (Table 1). The mean abundance of the parasites was an order of magnitude higher in perch than in roach (Kruskal-Wallis ANOVA: $H_{(1,\,2121)} = 156.53$, $p < 0.001$).

4. Discussion

In the lake, we observed no distinct signs of a sequence of *A. foliaceus* generations during the main period of reproduction. Such a sequence (*see*

Table 3. Characteristics of the copulation of *A. foliaceus* in ten copulation events.

	Date	Place	Female body length (mm)	Male body length (mm)	Duration (min)
1	21 Jun.	Fish	2.7	2.7	3
2	21 Jun.	Wall	2.8	2.6	30
3	22 Jun.	Wall	2.1	2.6	60
4	22 Jun.	Wall	2.8	2.5	70
5	22 Jun.	Wall	2.8	2.6	65
6	01 Aug.	Fish	5.6	4.6	95
7	01 Aug.	Wall	5.6	3.6	130
8	02 Aug.	Wall	5.6	3.0	90
9	06 Aug.	Fish	4.2	3.9	120
10	06 Aug.	Fish	4.8	3.5	10

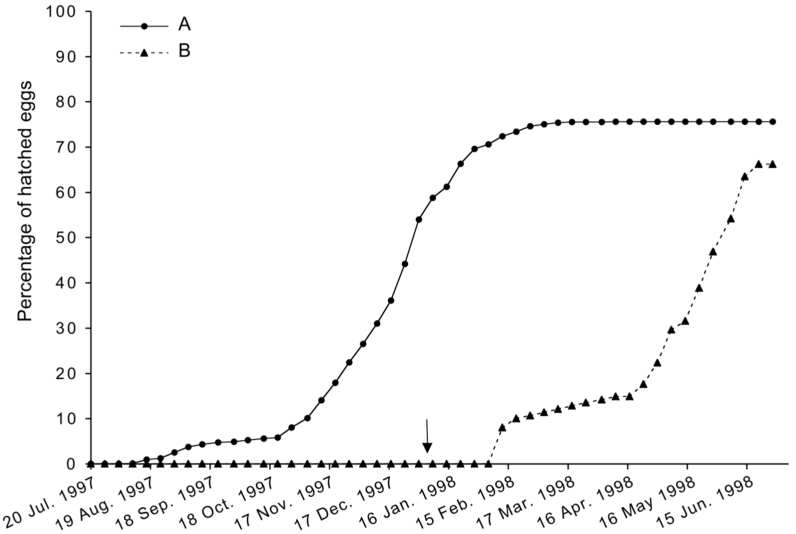

Fig. 5. Hatching of *A. foliaceus* eggs. Group of 1350 eggs was kept permanently at 19–22 °C (A), and a group of 150 eggs (B) at 5 °C for 5 months, then moved to room temperature. Arrow indicates the temperature increase from 5 to 20 °C.

Stammer 1959) should be manifested by pronounced peaks of abundance of the developmental stages starting with the larvae. This pattern is typical for aquatic crustaceans inhabiting waters with seasonally fluctuating ambient conditions (Marshall & Orr 1972, Tande & Hopkins 1981). The only peak we recorded in the occurrence of *A. foliaceus* larvae in the lake populations was at the end of May (1986–87) (*see* Fig. 1) when the water temperature increased to 8–10 °C. This temperature was shown to be critical for the hatching of *A. foliaceus* (Stammer 1959). However, such a peak was missed in 1997 although the survey of the lake was also done throughout June; this was probably because of the early summer in that year. The synchronization of hatching in the first generation of the year (shown as a peak of the size class about 3 mm in July both in the farm and in the lake) appears to be controlled abiotically, primarily by temperature. We suggest that biotic factors, primarily availability of fish hosts, may be crucial for *A. foliaceus* in the lake where fish are sparse compared with the farm.

Later on, in July the most remarkable difference in the size distributions between the lake and farm populations of *A. foliaceus* was the pronounced maximum in the numbers of larvae in the farm population which was not found in the lake (Fig. 4). This maximum points to the synchronized appearance of the second generation in the fish farm. A high abundance of immature parasites shorter than 1.5 mm observed at the fish farm at the beginning of June (P. Rintamäki-Kinnunen, pers. comm.) shows a synchronized hatching of the first generation of the year. The absence of a second maximum of immature parasites in the lake population in 1997 suggests an asynchronized recruitment. Three processes, egg laying, hatching, and the growth and development of the larvae and immature stages, influence the duration of the period of argulid recruitment. Our laboratory data showed that the hatching time of *A. foliaceus* eggs collected from the lake was extremely variable and appeared to be the main feature of extended recruitment. Non-synchronized development and hatching of eggs within the same string was observed in a closely related species, *A. japonicus* (Shafir & van As 1986) and in another branchiuran parasite, *Dolops ranarum* (Fryer 1964). However, the duration of the hatching time reported for *A. foliaceus* and *A. japonicus* was much shorter and its variability much lower than that obtained in the present study (*see* Kollatsch 1959, Stammer 1959, Shafir & van As 1986). Meehean (1940) and Hindle (1949) reported cases of *A. foliaceus* eggs which were laid in the autumn, rested throughout the winter (5–7 months) and hatched in the spring. We observed an extended period of hatching (25 to 240 days) not only at low temperature but also at about 20 °C. At similar temperatures, Tokioka (1936), Kollatsch (1959), Stammer (1959) and Shafir and van As (1986) obtained hatching times from 25 to 38 days. The main difference between these studies and ours might be found in the lower density of the fish populations from where the parasites were collected in the Finnish lakes. High variability in the hatching time and extended period of recruitment may be helpful for the parasites when hosts are scarce and their availability unpredictable. A possible mechanism underlying "stretched" hatching is not clear at present, and needs more experiments.

The other factors influencing extended recruitment in *A. foliaceus*, egg laying and the growth rate, also appear to be dependent on host availability. According to our findings, which are supported by the observations of Kollatsch (1959) and Shafir and van As (1986), females do not lay all of their mature eggs at once. After depositing one or several strings, a female has to return to the fish host. Shafir and van As (1986) found that many females laid almost all of their eggs over a period of a few hours to a few days, moving on and off the fish during the process. However, others laid one or more strings, then returned to the fish and were not observed to detach from it over a period of three weeks, although their ovaries were still 25%–75% full. This pronounced variability in egg laying occurs even under experimental conditions of high fish host availability. Thus, it seems highly probable that, under the conditions of a dispersed host population in nature, where the intervals between encounters with appropriate hosts would be longer and more unpredictable, variability in egg laying would be favourable. Similarly, the average growth rate of immature specimens would also depend on how soon they are able to find a host, which, in turn, is dependent on host availability.

Another difference in the size distributions between the lake and fish farm populations was the absence of large females at the farm, which may be associated with a mass mortality after the period of synchronized reproduction had been completed. This might have an adaptive value, as it would prevent overlap and competition between subsequent generations. Intraspecific competition in parasites may negatively impact their fitness through, for example, a "crowding effect" (Esch & Fernandez 1993).

The size distributions of males were similar in both populations. In neither case did they exceed 4.5 mm. Our experiments showed that adult males were much more active than females. This corresponds with the findings of other authors (Kollatsch 1959, Stammer 1959), who noted the larger proportion of the females on the fish hosts, whereas free-swimming males were more numerous. Male-biased sex ratio in attached parasites, was obtained in *A. canadensis* (Poulin & FitzGerald 1989a). However, the season studied by these authors was characterized by an active egg-laying by females, and the observed difference was attributed to the difference in reproductive behaviour, as females had to detach from the hosts for deposition of eggs (Poulin & FitzGerald 1989a). Outside the period of egg-laying, males, detaching from the fish hosts in search for mates and resting less often than females while free-swimming, should spend a lot more energy to sustain their more active metabolism, and, consequently, less for growth.

Resources, either in the form of hosts or mates, can be distributed in various densities and patterns, and these distributions become an important environmental determinant affecting searching success. As copulation occurs on the fish (Kollatsch 1959, our data), the observed preference for perch makes the search for a mate easier. Aggregation on a few individuals (Poulin & FitzGerald 1989b) would further facilitate the task of finding a mate. Still, this search remains a problem, and the suggestion by Stammer (1959) on size assortative mating seems dubious. Indeed, a rather variable male:female size ratio (0.65 to 1.24) in mating couples was found in our experiments. A broader size range of potential sexual partners would be favoured, in low density conditions.

The searching abilities of an individual parasite are limited (Herter 1927, Mikheev *et al.* 1998). To cope with an unpredictable availability of resources, other mechanisms resulting in changes at the population level are necessary. Other crustaceans, e.g., copepods involve dormancy or diapausing eggs to survive harsh periods (Williams-Howze 1997). Similarly, the adverse winter period with the lowest fish availability may be spent by *A. foliaceus* as overwintering eggs and/or adults. The only predictable improvement in the ambient situation in the life cycle of *A. foliaceus* occurs with the spring warming, which results in the synchronized hatching of larvae from overwintered eggs. Later on, during the season of intensive reproduction and growth, there would be no more cues enabling the tuning of recruitment to periods/areas of high fish availability. An extended and highly variable period of recruitment may serve as an insurance mechanism in parasite populations inhabiting waters where the fish host is scarce. Under the conditions of dense host populations, as in the fish farms, variability in growth, egg laying and hatching appears to be much lower which could result in several synchronized recruitment periods. Size frequency distributions with pronounced peaks of larval stages, such as obtained by Shimura (1983) for *A. coregoni*, are in accordance with our results from the fish farm in Central Finland.

High flexibility, both in the behaviour and in life cycle strategy allows *A. foliaceus* to utilize a broad spectrum of habitats with differing levels of host abundance. In conditions of low fish density, a number of individual adaptations facilitate host finding (Mikheev *et al*. 1998). Others, such as host preference, aggregation on host individuals and non-assortative mating, facilitate finding of a mate. A prolonged period of recruitment plays an adaptive role in unpredictable ambient conditions, extending a "net of infectivity" (Rea & Irwin 1995).

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