Timing of sexual reproduction in chydorid cladocerans (Anomopoda, Chydoridae) from nine lakes in southern Finland

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Abstract. Communities of chydorid cladocerans (Anomopoda, Chydoridae) were monitored weekly during the open-water season of 2005 in nine lakes from southern Finland for their sexual reproduction patterns. Most chydorid species were strictly monocyclic with an autumnal sexual reproduction period, but minor summer sexual reproduction periods of *Alona affinis* and *A. rectangula* were observed. Autumnal sexual reproduction was generally synchronous in the lakes, suggesting that deteriorating climatic conditions were the main stimulus for induction of sexual reproduction. However, considerable variation in the timing and duration of sexual reproduction among populations was observed, suggesting that other, probably ecological, stimuli may also play a role in genetically aiming for local adaptation. Sexual reproduction in chydorids is probably a response to both climatic and ecological stimuli, and adaptation by sexual reproduction may even further enhance their ecological flexibility.

Key words: Chydoridae, gamogenetic females, males, parthenogenesis, sexual reproduction, summer gamogenesis, southern Finland.

INTRODUCTION

Cladocerans (Crustacea) have two strategies of reproduction. During most of their active period, which occurs in the ice-free season in northern temperate and subarctic climates, they reproduce asexually (parthenogenetically). Sexual reproduction, or gamogenesis, usually begins towards the end of the active period and leads to hatching of males and gamogenetic females, which results in fertilized resting eggs. Resting eggs are very tolerant of extreme environmental conditions, such as freezing and drying, and ensure the survival of cladoceran populations during the winter, from which new asexually reproducing females hatch in spring.

   Much of the research on cladoceran sexual reproduction has focused on the genus *Daphnia* (e.g. Stross & Hill, 1965, 1968; Kleiven et al., 1992; Pijanowska & Stolpe, 1996; Slusarczyk, 1995, 2001), while the patterns of sexual reproduction in the family Chydoridae (chydorids) have not been widely examined. It is generally

known that sexual reproduction in chydorids also occurs in autumn in central and northern Europe (e.g. Poulsen, 1940; Mäemets, 1961; Flössner, 1964; Green, 1966; Frey, 1982; Koksvik, 1995), probably triggered by declining temperatures and shortening photoperiods (Shan, 1974; Frey, 1982). Nevertheless, the mechanisms that induce gamogenetic reproduction in chydorids have not yet been entirely clarified.

Frey (1982) generalized the life cycles of chydorids as predominantly mono-cyclic with autumnal gamogenetic periods, with some species having variable and insignificant earlier periods of gamogenesis. Berg (1929) and Flössner (1964) stated that some chydorid communities on the European mainland also have sexual individuals present during the summer months; i.e. they are dicyclic. Some chydorid species are dicyclic as far north as in Denmark (Røen, 1995) and Estonia (Mäemets, 1961). There is also one record of summer gamogenesis from southern Finland. Järnefelt (1956) recorded gamogenetic females of *Alonella excisa* (Fischer) from Lake Tuusulanjärvi in early June during a single year.

The aim of the present study was to examine the patterns of sexual reproduction in chydorids from several lakes in southern Finland. Our focus was on the timing of sexual reproduction among chydorid populations, i.e. does summer gamogenesis occur in most species and are induction and incidence of autumnal gamogenesis synchronous among populations? Nine lakes in southern Finland were monitored weekly for living chydorids and their sexual reproduction during the open-water season of 2005. Most of the lakes chosen for the study differed in their physical, chemical, and ecological conditions, but were situated in the same climate region.

SITES

The nine study lakes are located in southern Finland, near Helsinki (Fig. 1). The limnological variables of the lakes measured during three seasons are presented in Table 1. The mean annual air temperature in the area is approximately 4.5 °C, the mean July air temperature 17 °C, and the mean January air temperature −6 °C (Helminen, 1987). The open-water season lasts about 7 months, from early May to late November (Kuusisto, 1986), depending on yearly variation in spring and autumn temperatures.

Lakes Hauklampi (60°18′ N, 24°36′ E, 76.7 m above sea level, area 2.7 ha), Iso Majaslampi (60°19′ N, 24°36′ E, 92.7 m a.s.l., area 6.3 ha), and Pieni Majaslampi (60°19.3′ N, 24°35.7′ E, 97.3 m a.s.l., area about 1 ha) are located close to one another. They are acidic and oligotrophic lakes whose catchments are small and characterized by patches of mire, bedrock outcrops, and pine (*Pinus*) forests. The shores are inhabited by sedges and *Sphagnum* mosses, and the aquatic macrophyte zone consists only of European white waterlily (*Nymphaea alba*). The lakes were severely acidified during the 1980s as a result of acid deposition, but experienced a recovery process during the 1990s.
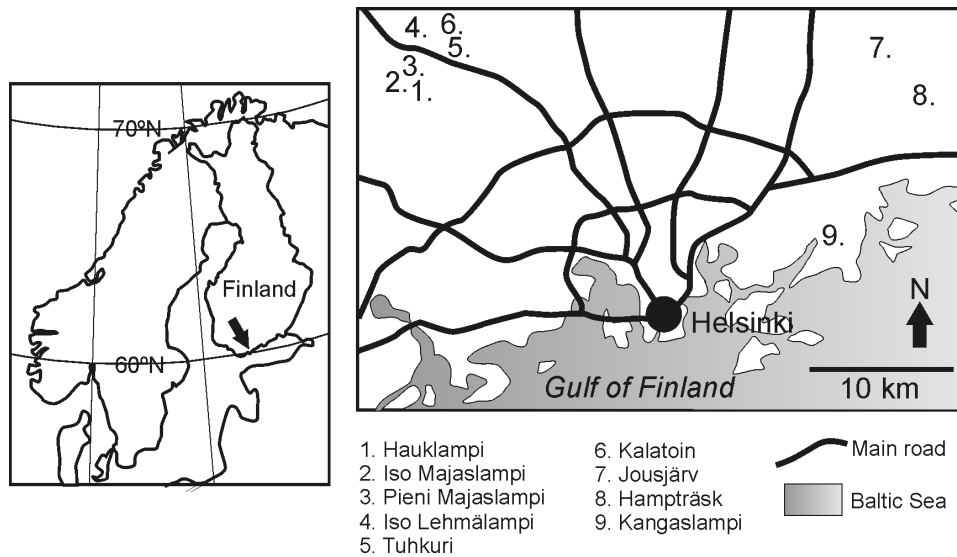
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Fig. 1. Locations of the nine study lakes in southern Finland.

Iso Lehmälampi (60°20′ N, 24°36′ E, 91.7 m a.s.l., area about 5 ha) is also an acidic and oligotrophic lake. The small catchment is characterized by bedrock outcrops and small patches of mire. The lake also experienced severe acidification in the 1980s and the succeeding recovery process in the 1990s. *Sphagnum* mosses, *Carex* spp., and submerged European yellow waterlily (*Nuphar lutea* (L.)) and *Nymphaea* spp. dominate the littoral and the shoreline.

Tuhkuri (60°20′ N, 24°37′ E, 73.7 m a.s.l.) is an oligotrophic forest lake with a slightly higher pH than the study lakes described above. It is also the largest: 13.7 ha. Several houses and summer houses are situated on its shores. The catchment of the lake is characterized by mixed forest (spruce *Picea*, *Pinus*, birch *Betula*) and some bedrock outcrops. The aquatic vegetation consists of *Phragmites australis* (Cav.) Trin. ex Steud., *Nuphar lutea,* and aquatic mosses.

Kalatoin (60°20′ N, 24°37′ E) is a very acidic and dystrophic small (about 1 ha) lake with paludified shores at an altitude of 89.5 m a.s.l. *Sphagnum* mosses and *Carex* spp. dominate the shores and the submerged vegetation consists of aquatic mosses and *Nuphar lutea*. The lake is surrounded by a small catchment with bog vegetation and several bedrock outcrops.

Jousjärv (60°20′ N, 25°11′ E, 37.3 m a.s.l.) is a very small (about 0.5 ha) dystrophic lake. *Sphagnum* mosses and *Carex* spp. cover the entire shoreline. Small hills with bedrock outcrops characterize the catchment.

Hampträsk (60°17′ N, 25°15′ E, 20.3 m a.s.l.) is a mesotrophic lake. The surface area of the lake is 3.8 ha. There are fields and houses near the lake and the paludified western shore is ditched. The aquatic vegetation consists mainly of *Phragmites australis* and *Nuphar lutea*.

Table 1. Limnological variables of the lakes from three seasons in 2005. TP – total phosphorous, TN – total nitrogen. Measurements were performed in late May (spring), mid-August (summer), and mid-December (winter)

	Season	Hauklampi	Iso Majaslampi	Pieni Majaslampi	Iso Lehmälampi	Tuhkuri	Kalatoin	Jousjärv	Hampträsk	Kangaslampi
pH	Spring	5.3	5.0	5.1	5.3	6.8	4.4	6.3	7.0	7.1
	Summer	5.0	4.8	4.9	5.1	5.6	4.5	6.2	6.6	7.2
	Winter	5.0	4.7	4.8	5.8	4.9	4.2	6.0	5.4	7.6
Conductivity, $\mu s\ cm^{-1}$	Spring	14	13	11	14	22	23	27	41	151
	Summer	19	19	16	17	25	26	34	49	157
	Winter	20	18	20	20	36	43	50	44	173
Oxygen, $mg\ L^{-1}$	Spring	10.3	10.0	9.9	8.4	9.7	7.6	7.5	9.0	6.2
	Summer	10.5	9.6	9.7	8.9	10.4	8.9	7.6	9.2	9.0
	Winter	11.1	11.4	11.0	18.1	8.0	6.6	1.7	5.4	2.1
Colour, $Pt\ mg\ L^{-1}$	Spring	7.5	10	5	20	50	125	75	75	37.5
	Summer	25	30	25	30	50	100	125	75	37.5
	Winter	15	20	15	40	150	200	150	75	25
TP $\mu g\ L^{-1}$	Spring	0	0	0	0	0	0	5.4	29.8	61.3
	Summer	<10	<10	<10	25.4	31.1	23.7	24.6	58.1	75.5
	Winter	<10	<10	<10	10.3	78.9	81.2	32.1	13.2	79.5
TN $\mu g\ L^{-1}$	Spring	221.2	295.6	226.5	343.4	364.7	423.2	476.3	981.2	960.0
	Summer	139.5	201.3	191.0	381.6	768.0	525.9	623.7	1123.4	813.4
	Winter	339.7	405.9	217.4	456.8	1735.3	1969.6	1618.1	808.3	1475.5

Kangaslampi (60°13′ N, 25°08′ E) is a very shallow, eutrophic, and disturbed park pond (about 1 ha) with a very high human impact. The pond is located in a suburb of Helsinki within a densely inhabited area. The catchment is mostly built up, except for a small park surrounding the pond. During the summer, algal blooms dominate the aquatic environment.

MATERIALS AND METHODS

Chydorids were sampled weekly during the open-water season of 2005 (from early May to mid-November) with a 100-µm plankton net. Sampling could not be performed in the first week of September. The plankton net was swept back and forth over about 1 m of lakeshore after slightly disturbing the water. In each lake the chydorid samples were taken from three locations to obtain animals from different habitats. The samples were integrated as one and stored in a coldroom in small jars with ethanol added. Sampling was stopped in Kangaslampi when fewer than 10 chydorid individuals were encountered in the samples and in other lakes when the ice cover was formed. The littoral water temperatures in the lakes were measured weekly from one of the sampling locations in each lake. The sampling and temperature measurements were mostly performed during a single day and the first lakes were sampled in the early morning and the last lakes during the afternoon, which affected the temperature measurements.

In the laboratory the samples were quickly heated in 10% KOH, sieved through a 100-µm mesh, and mounted in glycerine on preparation slides. Chydorids were examined under a light microscope at ×100–200 magnification for precise identification. Chydorid individuals were counted until a minimum of 100 individuals were encountered or four preparation slides (24 × 50 mm) were studied. Partheno-genetic females, gamogenetic females, and males were identified and marked separately. The chydorid nomenclature follows that of Røen (1995). *Chydorus sphaericus* is considered as *C. sphaericus* sensu lato, according to Frey (1986).

Detrended correspondence analysis (DCA) was used to identify major patterns in the timing of sexual reproduction during the open-water season. It was also applied to the data on the timing of sexual reproduction among populations of the most common species, *Acroperus harpae* (Baird), *Alona affinis* (Leydig), *Alonella excisa,* and *Alonella nana* (Baird), to detect differences between the populations. The DCA was run with the data on incidence (i.e. presence or absence) of sexual individuals in the samples during the open-water season. DCA is a unimodal ordination method that summarizes variation in ecological datasets and shows the relationships between samples in ordination diagrams so that the longer the distance between sample scores, the more dissimilar are the samples (i.e. sexual reproduction in the present study). The DCA was performed using the computer program CANOCO, version 4.5 (ter Braak & Smilauer, 1998).

RESULTS

The presence of parthenogenetic females and sexual reproduction (males and gamogenetic females) during the open-water season is shown in Fig. 2. Males and gamogenetic females of almost all the most common species were encountered (Fig. 2, Table 2).

Gamogenesis in Hauklampi (Fig. 2a) began in mid-September with *Alonella excisa* males and gamogenetic females, and this species had the longest period of gamogenesis. In the following week *Alona guttata* Sars and *Graptoleberis testudinaria* (Fischer) reproduced gamogenetically. Parthenogenetic females occurred at the same time and after the sexual period in *A. guttata* and *Alonella nana*. Gamogenesis began in *A. nana* and in *Acroperus harpae* in early October.

Gamogenesis in Iso Majaslampi began in late August with the appearance of *Alonella excisa* males (Fig. 2b). Other species began to reproduce sexually in late September or early October, but parthenogenesis occurred at the same time and after the sexual period. *Alonella excisa* also reproduced sexually for the longest period in this lake (11 weeks).

Gamogenesis in Pieni Majaslampi began in mid-September with *Alona guttata* and *Alonella excisa* males (Fig. 2c). *Acroperus harpae*, *A. guttata* var. *tuberculata* Kurz, and *Alonopsis elongata* (Sars) males appeared a few weeks later. The sexual period in *A. guttata* lasted longer than that of the other species. *Alonopsis elongata* had 4 weeks of intensive gamogenesis in the absence of parthenogenetic females.

In Iso Lehmälampi males of *Camptocercus rectirostris* Schoedler and *A. excisa* appeared in mid-September (Fig. 2d). *Alonopsis elongata* and *A. harpae* initiated gamogenesis a few weeks later. *Alonella nana* males and gamogenetic females did not appear until late October. *Alonopsis elongata* had the longest period of gamogenesis in this lake (7 weeks).

Males of *Alonella excisa* and *A. exigua* (Lilljeborg) were encountered in Tuhkuri in mid-September (Fig. 2e). *Pleuroxus truncatus* (Müller) became gamogenetic 1 week later and in late September *Alona affinis* males and gamogenetic females were found. Sexual reproduction in *Alonella nana* began in early October. *Chydorus sphaericus* s.l. males were encountered only at the end of the open-water season. Parthenogenesis occurred in most species contemporaneously with gamogenesis.

Two gamogenetic *Alona affinis* females were encountered in Kalatoin in early summer (Fig. 2f). Gamogenesis began in mid-September with *Alonella excisa* males. Gamogenetic females appeared 1 week later, when males of several other species were also present. The sexual period in *A. excisa* was the longest of all species (10 weeks). Gamogenesis in *A. nana* and *C. sphaericus* s.l. began in early October and parthenogenesis occurred contemporaneously during the entire sexual period.
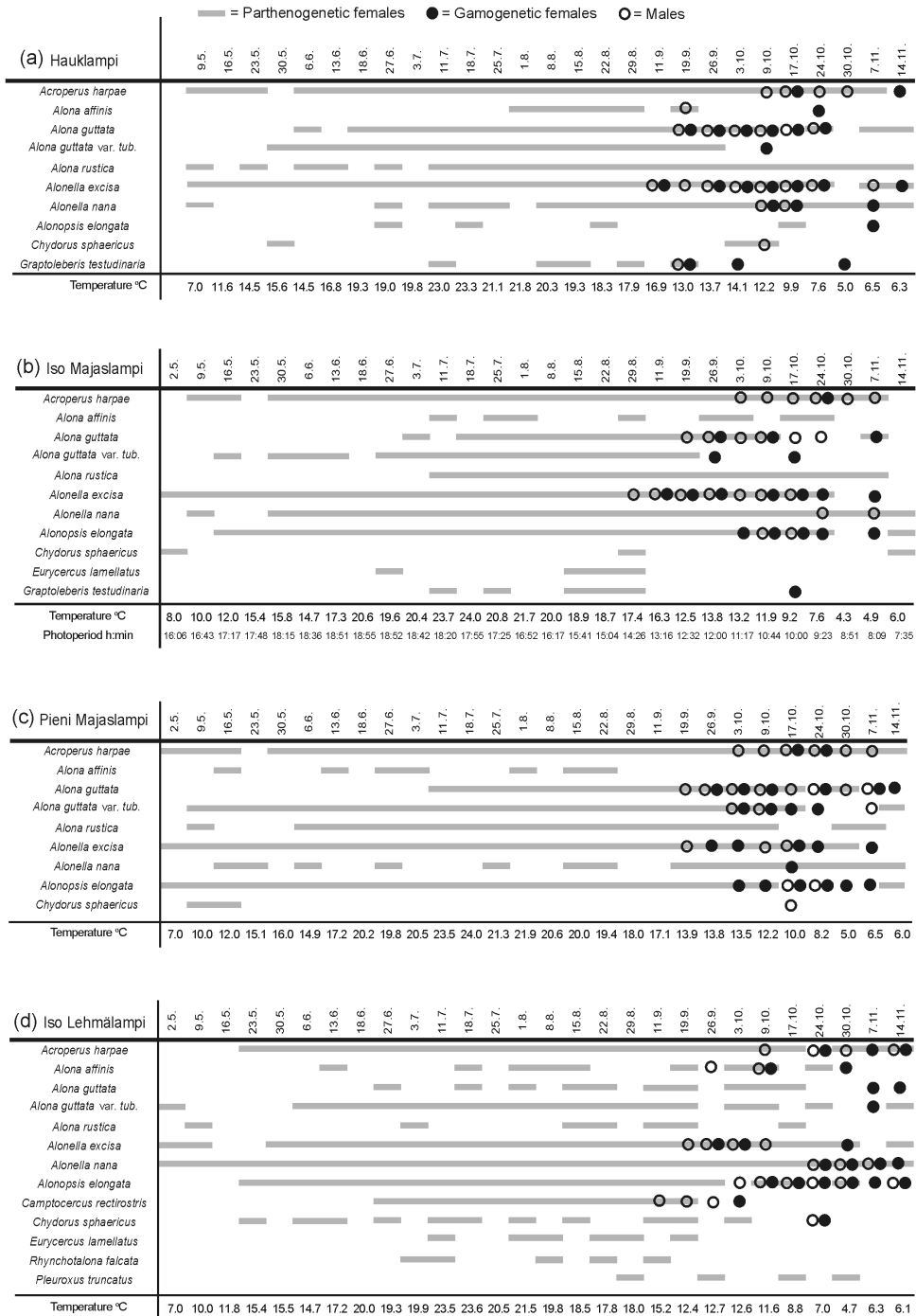
Fig. 2. Occurrence of parthenogenetic females, gamogenetic females, and males in the study lakes (a–i) during the open-water season. The weekly littoral water temperatures are shown in 2a–i and photoperiod length in the Helsinki area in 2b.
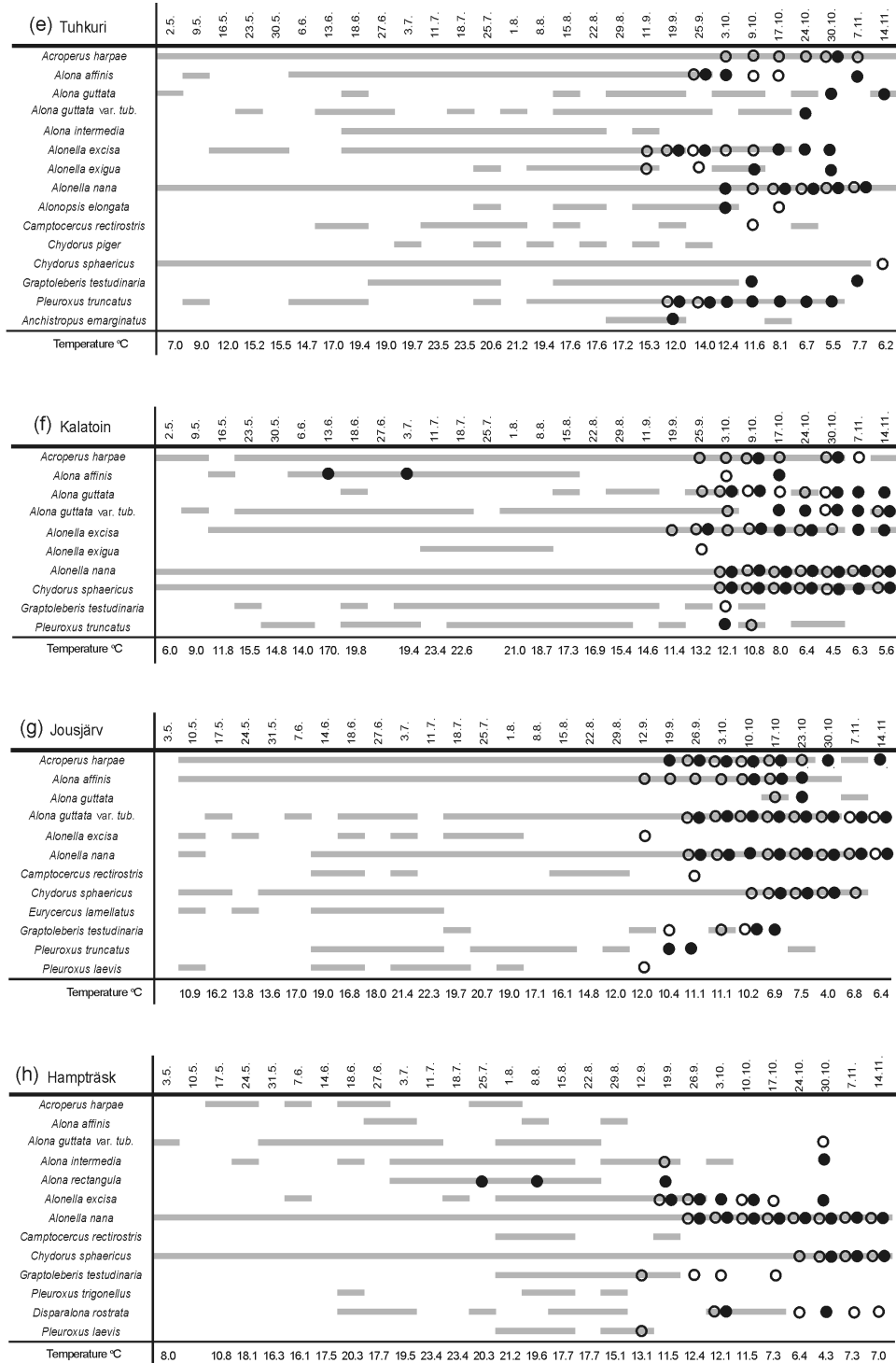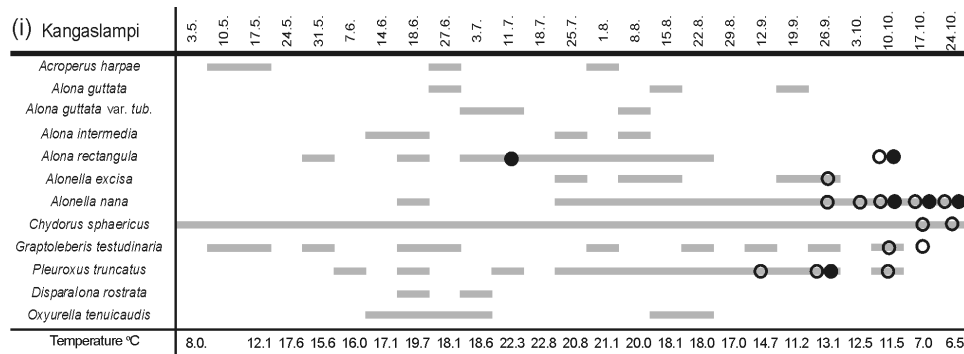
Fig. 2. *Continued.*

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Table 2. Chydorid species encountered in the lakes during the open-water season and information on their occurrences and sexual reproduction

	Number of populations	Number of sexual populations	Duration of sexual reproduction, weeks	Water temperature, °C, during induction	Photoperiod length, h, during induction
Alona affinis	8	5	1–7	7.6–14.0	9–13
Alona guadrangularis	2	0			
Alona guttata	9	7	2–9	5.5–13.9	8–12
Alona guttata var. *tub.*	9	8	1–8	4.3–13.8	8–12
Alona intermedia	4	1	7	11.5	12
Alona rectangula	3	2	1	11.5	11–12
Alona costata	1	1	1	12.4	11
Alona rustica	5	0			
Alonella excisa	9	9	1–10	11.5–17.4	12–14
Alonella exigua	2	2	1–8	13.2–15.3	12–13
Alonella nana	9	9	1–8	7.6–13.1	9–12
Chydorus piger	2	0			
Chydorus sphaericus s.l.	9	8	1–7	6.4–12.2	7–11
Chydorus latus	1	0			
Pleuroxus truncatus	6	4	2–7	12.0–14.7	11–13
Pleuroxus trigonellus	2	0			
Pleuroxus laevis	4	2	1	12.0–13.1	13
Acroperus harpae	9	7	6–9	10.4–13.5	10–13
Alonopsis elongata	5	5	1–7	6.5–13.5	8–11
Camtocercus rectirostris	4	3	1–4	11.1–15.2	11–13
Eurycercus lamellatus	5	0			
Graptoleberis testudinaria	9	5	1–6	9.2–13.1	10–13
Pseudochydorus globosus	1	0			
Anchistropus emarginatus	1	1	1	12.0	12
Rhynchotalona falcata	1	0			
Disparalona rostrata	3	2	1–7	12.1–12.6	11
Oxyurella tenuicaudis	1	0			

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In Jousjärv sexual reproduction was encountered in mid-September with *Alona affinis*, *Alonella excisa*, and *Pleuroxus laevis* Sars males (Fig. 2g). *Acroperus harpae*, *A. affinis*, *A. guttata* var. *tuberculata*, and *Alonella nana* had long periods of gamogenesis, but parthenogenetic females were present at the same time. The sexual period and open-water season ended only with the presence of gamogenetic females.

Two gamogenetic *Alona rectangula* Sars females were found in Hampträsk in late July and early August (Fig. 2h). Autumnal gamogenesis began in mid-September. Parthenogenesis and gamogenesis coexisted in *Alonella nana* and *C. sphaericus* s.l. Sexual *A. nana* individuals appeared in late September and *C. sphaericus* s.l. individuals in late October. *Alonella excisa* had an intensive 7-week-long gamogenetic period with no parthenogenetic females present at the end of its active period.

One gamogenetic *Alona rectangula* female was found in Kangaslampi in mid-July. The gamogenetic reproduction period was rather short in Kangaslampi (Fig. 2i), since the active period for chydorids was shorter, ending already in late October, when chydorids became scarce. Males of *P. truncatus* appeared first in mid-September and 2 weeks later males of *Alonella excisa* and *Alonella nana* were encountered. *Chydorus sphaericus* s.l. initiated gamogenesis in mid-October.

The DCA for incidence of gamogenetic individuals in all species and all lakes is presented as a plot diagram in Fig. 3. A compact group of samples was formed from the autumnal samples (Aug29–Nov14) from late August to mid-November. The samples that indicated summer sexual reproduction (Jun13, Jul3, Jul11, Jul25, and Aug8) were scattered.

The DCA for incidence of gamogenetic individuals among populations of the most common species is shown in Fig. 4. *Alonella excisa* had the longest sexual reproduction period, but it was most uniform among its populations (Fig. 4a) from mid-September to early November (Sep19–Nov7). Sexual reproduction in *Acroperus harpae* populations (Fig. 4b) was uniform in October–November, but some populations initiated sexual reproduction earlier (Sep19, Sep25) and some continued later (Nov14). The incidence of sexual individuals in *Alonella nana* populations (Fig. 4c)
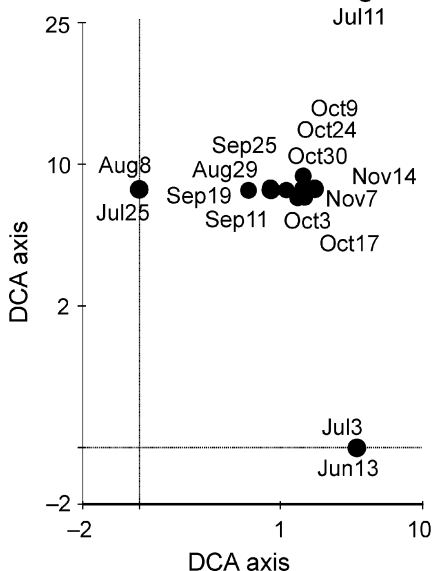

Fig. 3. DCA ordination diagram for the incidence of sexual reproduction of chydorids in the nine study lakes. The scores indicate sampling months and dates.

was rather consistent (Sep25–Nov7), and was most uniform from late September to mid-October (Sep25–Oct17). The incidence of sexual individuals among *Alona affinis* populations (Fig. 4d) was scattered, ranging from summer (Jun13, Jul3) to autumn, and no distinct period of gamogenesis occurred in the populations during the autumn.
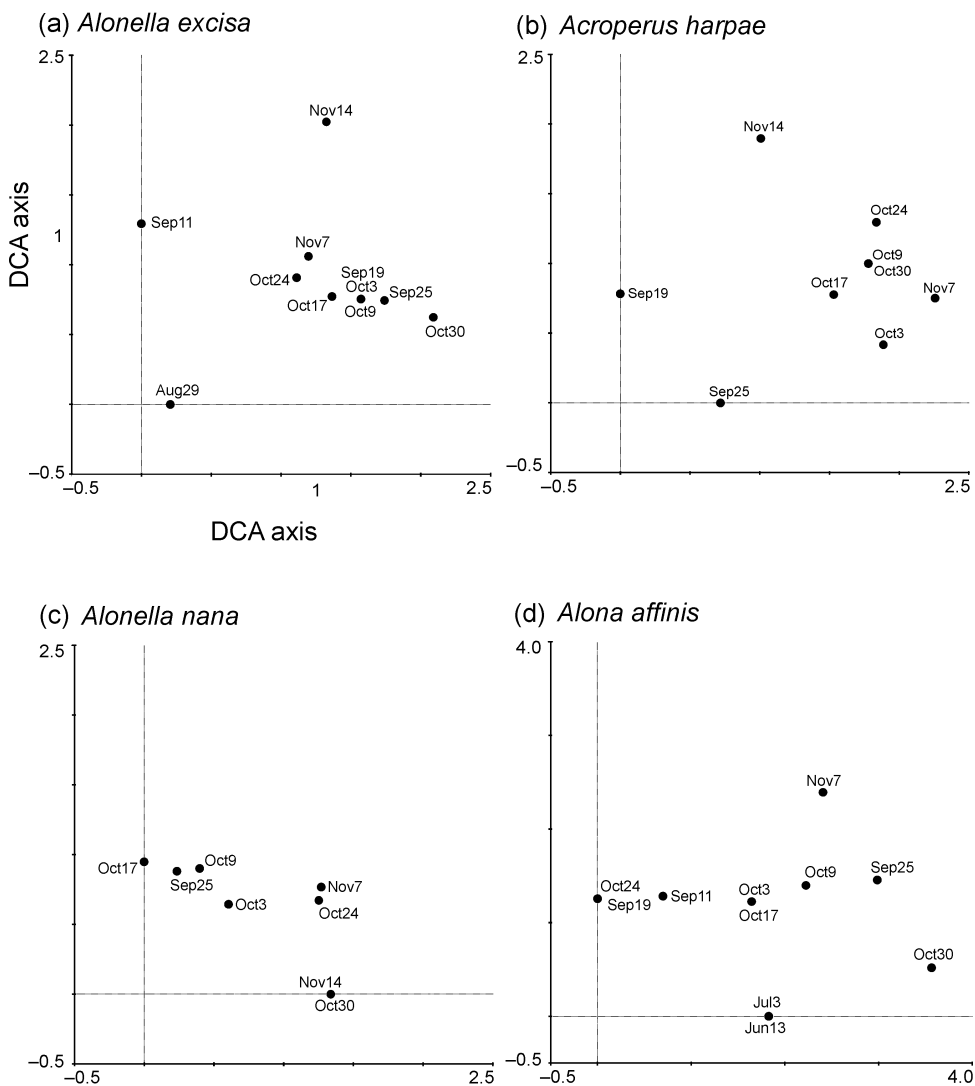

Fig. 4. DCA ordination diagram for the incidence of sexual reproduction among populations of (a) *Alonella excisa*, (b) *Acroperus harpae*, (c) *Alonella nana*, and (d) *Alona affinis*. The scores indicate sampling months and dates.

DISCUSSION

Summer gamogenesis

As mentioned earlier, Järnefelt (1956) found ephippial *Alonella excisa* females in Lake Tuusulanjärvi in southern Finland in early June. Our findings of a few gamogenetic *Alona affinis* and *A. rectangula* females in summer suggest that summer gamogenesis does occur in southern Finland and also in species other than *A. excisa*, although it is very weak and not consistent (Figs 2 and 3). However, no males were recorded during the summer.

Alona rectangula occurred only in lakes Hampträsk and Kangaslampi, and in both of them it underwent summer gamogenesis. The lakes are both rather high in nutrients and pH (Table 1) and therefore suitable habitats for *A. rectangula* (cf. Røen, 1995). According to Røen (1995), in Denmark this species is dicyclic in small and monocyclic in larger bodies of water. Mäemets (1961) recorded a similar result in Estonia in both *A. rectangula* and *Alonella excisa*. It is possible that a similar sexual reproduction pattern in *A. rectangula* exists also in Finland but it could not be observed in the present study because we had no data from large lakes.

Summer gamogenesis in *Alona affinis* occurred in mid-June and early July and in *A. rectangula* in July and early August. Together with Järnefelt's (1956) finds in early June, this indicates that summer gamogenesis does not focus on any specific period in summer. It is apparently not triggered by climatic stimuli, such as decreasing water temperature or daylight, as it is during autumn.

Therefore, some ecological or limnological stressors may be able to induce summer gamogenesis in some chydorids. The lakes in which summer gamogenesis was encountered are limnologically very different; Hampträsk is mesotrophic with a high pH, Kangaslampi eutrophic with a high pH, and Kalatoin dystrophic with a very low pH (Table 1), showing no consistent pattern. A wider monitoring would be required to find whether there are direct effects of limnology on summer gamogenesis in addition to the fact that limnological conditions largely control the structure of the food web. Crowding or predation pressure may induce summer gamogenesis in chydorids, since these stimuli are known to trigger gamogenesis in *Daphnia* (Slusarczyk, 1995, 2001; Pijanowska & Stolpe, 1996). Usually chydorid populations are largest in midsummer (e.g. Goulden, 1971; Whiteside, 1974; Whiteside et al., 1978) and invertebrate predation may considerably affect chydorid populations during that time (Goulden, 1971; Williams, 1982; Robertson, 1990).

Autumnal gamogenesis

The first sexual individual, a male of *Alonella excisa*, appeared in Lake Iso Majaslampi in late August, while in the other lakes sexual reproduction began during the following two weeks until mid-September (Figs 2 and 3). In Lake Kangaslampi sexual reproduction began mainly in late September and ended only

1 month later, as chydorids became very scarce and apparently deceased. Lake Kangaslampi is eutrophic and disturbed by a high human impact and therefore it is possible that some limnological factor, e.g. bad oxygen conditions (Table 1), caused chydorids to die earlier. In the other lakes the period of sexual reproduction continued until mid-November when the lakes froze over. It has been reported that chydorid communities become entirely gamogenetic at the end of the sexual period (Flössner, 1964; Kubersky, 1977), but in the present study they never became entirely gamogenetic, except in Jousjärv. Parthenogenesis continued along with gamogenesis throughout the autumn and even afterwards in some lakes.

Our results (Figs 2 and 3) suggest that the general timing and duration of the autumnal sexual reproduction period of chydorids was rather synchronous in all the lakes studied, beginning mainly in mid-September and lasting for approximately 2 months. The lakes are situated in the same climate and gamogenesis was probably induced by the declining temperature and/or shortening photoperiod (Fig. 2), as Shan (1974) and Frey (1982) suggested. The photoperiod length in the study area was approximately 12–14 h and water temperatures in the lakes varied approximately between 12 and 17°C when the first sexual individuals appeared (Fig. 2, Table 2). The actual water temperature range may be smaller because the sampling time during the day varied and caused a 1–2°C difference between lakes sampled in the morning and in the afternoon. A quite similar pattern in the induction and duration of sexual reproduction in chydorids was detected in central Norway by Koksvik (1995), although only males were identified separately. He stated that the first males were encountered in August and the water temperature decreased from 20 to 14°C during August.

That the induction of gamogenesis is a response to certain temperatures and day lengths is most clearly evident in *Alonella excisa*, which was the first gamogenetic species in most lakes and showed the most uniform induction time (Table 2). The photoperiod length during the induction of *A. excisa* was 12–14 h and the water temperature 11–17°C. The incidence for sexual reproduction among *A. excisa* populations was also very synchronous between mid-September and early November and it showed a long period of gamogenesis (Fig. 4a). In contrast, *Acroperus harpae* appeared to have slightly different preferences, as it initiated gamogenesis somewhat later, when the photoperiod was 10–13 h and the temperature 10–13°C (Table 2). Gamogenesis in *A. harpae* was uniform among populations mainly in October and the species had shorter periods of gamogenesis than *A. excisa* (Fig. 4a, b). These observations may suggest that some chydorid species have individual demands for photoperiod length and water temperature for the development of gamogenesis.

Although *Alonella nana* populations were gamogenetically active rather synchronously in late September and mid-October (Fig. 4c), the induction time of gamogenesis among the populations ranged between late September and late October, water temperature and photoperiod ranging from 7.6 to 13.1°C and from 9 to 12 h. The incidence of gamogenetic *Alona affinis* individuals in populations during the open-water season varied widely (Fig. 4d). The induction time of autumnal gamogenesis in *A. affinis* was also induced over a large time range –

between mid-September and late October, when the water temperature and photoperiod were 7.6–14.0 °C and 9–13 h.

As indicated by these results, some chydorid species show considerable differences in the induction and timing of sexual reproduction among their populations (Table 2) in different environmental conditions (Table 1). Such differences suggest that climate may not be the only cue for gamogenesis, and that other environmental stimuli, ecological or limnological, may also play a role. For example, *A. nana* appears to initiate its gamogenesis earlier in nutrient rich and dystrophic lakes (Fig. 2f–i, Table 1) than in oligotrophic ones (Fig. 2a–d, Table 1). It is difficult to deduce the exact nature of the stimuli on the basis of the present results because e.g. the structure of the food web and predation pressure on chydorids in these lakes are not known. More detailed information about chydorids and their reproduction from field and laboratory tests is needed before such conclusions can be made.

Shan (1974) suggested that local species populations may evolve different reproductive patterns to meet major environmental stresses in the region. The lakes in the present study differed widely in their ecological and limnological conditions, ranging form oligo- to eutrophy, from clear- to brown-water, and from nearly pristine to human-disturbed, but still the same species inhabit most of them, showing that many chydorid species can tolerate wide ranges of environmental conditions. It can be assumed that sexual reproduction in every species and population aims to produce an optimal number of resting eggs. Initiating sexual reproduction too early or too late may not lead to this optimal number (Kleiven et al., 1992). Thus, the variance in sexual behaviour of different species and populations suggests that they have probably adapted to varying environmental conditions and that their sexual reproduction is optimized for these particular environments. However, it cannot be entirely ruled out that the differences in the timing of gamogenesis between the lakes reflect yearly variation (cf. Frey, 1982).

CONCLUSIONS

Weak summer gamogenesis was found only in three lakes: in *Alona affinis* in one lake and in *A. rectangula* in two lakes. As in general only one sexual period was detected in the study lakes during the open-water season, most of the chydorid species can be characterized as monocyclic in southern Finland. Summer gamogenesis may occur only under special conditions as a response to some ecological stressors, such as predation pressure or crowding. The evidence for summer gamogenesis detected in Finland covers the time span from early June to early August and therefore climate as a stimulus may be ignored.

The general uniformity of the induction time and duration of autumnal gamogenesis among limnologically different lakes supports the theory that the main stimuli are shortening photoperiod and declining temperature. However, the considerable variation in the induction time and duration of gamogenesis among

species and populations suggests that other stimuli, perhaps ecological ones, may also play a role. Local adaptations are probably required under divergent environmental conditions, resulting in an optimal number of resting eggs in chydorid species in certain circumstances. As many chydorid species can tolerate wide ranges of environmental conditions, it is possible that this adaptation by sexual reproduction may even further enhance their flexibility in surviving under different ecological conditions.

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Vesikirbuliste sugukonna Chydoridae (Anomopoda, Chydoridae) gamogeneetilise paljunemise ajastus üheksas Lõuna-Soome järves

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2005. aasta jäävabal perioodil seirati igal nädalal Chydoridae kooslusi üheksas Lõuna-Soome järves. Enamik Chydoridae liikidest olid selgelt monotsüklilised, gamogeneetilise paljunemisega sügisel. Kahe liigi, *Alona affinis* ja *A. rectangula* puhul esines gamogeneetiline paljunemine vähesel määral ka suvel. Sügisene gamogeneetiline paljunemine oli praktiliselt sünkroonne kõigis järvedes, näidates seega, et klimaatiliste tingimuste halvenemine on peamiseks stiimuliks gamogeneetilisele paljunemisele üleminekul. Gamogeneetilise paljunemise ajastuse ja kestuse oluline varieeruvus erinevates populatsioonides näitab, et teised, tõenäoliselt ökoloogilised tegurid, on samuti tähtsad lokaalsete kohastumiste tekkes. Chydoridae gamogeneetiline paljunemine on ilmselt vastus nii klimaatilistele kui ka ökoloogilistele teguritele ja selline kohastumine suurendab antud liikide ökoloogilist paindlikkust.