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Batch spawning of crucian carp (*Carassius carassius* (L.)) in mono- and multispecies communities

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Open-water field studies were conducted to clarify the reproductive biology of crucian carp in mono- and multispecies fish communities in eastern Finland. Between late May and mid-July, ready-to-spawn (ripe) crucian carp entered traps mainly during periods of rising water temperature. The males tended to be smaller but remained ripe longer than the females. In all populations the gonadosomatic index of females was variable throughout the summer, but in May it was higher in fish from the multispecies community than in those from the monospecific communities. Crucian carp is a batch spawner in all the water bodies studied. After a minimum temperature of ca. 18 °C, the timing of spawning is set by any clear increase in water temperature. Normally there were two spawnings during the 65-days reproductive period. The higher the mean temperature in May, the earlier the first spawning was.

1. Introduction

For maximum fitness a fish should reproduce at the time of year which would maximize its lifetime production of offspring. Timing of seasonal reproduction is affected mainly by changes in temperature and in hours of daylight, which is clearly illustrated by species living at high latitudes (e.g. Bye 1984, Wootton 1990, Bone *et al.* 1995). Most fish species in northern inland waters are single spawners, each species using one of the three typical periods for spawning: early spring, mid-summer or late autumn (Bye 1984, Wootton 1990, McEvoy & McEvoy 1992, Bone *et al.* 1995).

When biotic and/or abiotic environmental factors are stable throughout the year, alternative patterns of spawning, continuous or multiple spawning periods, could be advantageous. A multiple or batch spawner typically produces eggs over an extended period of time (Wootton 1990) and lays them in several batches during the reproductive year (Bye 1984, Wootton 1990, McEvoy & McEvoy 1992). Although multiple spawning patterns are most common at low latitudes (Bye

1984), a few fish species such as bleak (*Alburnus alburnus* (L.)) and bream (*Blicca bjoerkna* (L.)) (Pihu 1961, Rinchard & Kestmont 1996), also display multiple spawning strategies (within a season) at higher latitudes. The advantage of exceptional spawning patterns in northern regions, like the batch spawning in bleak, is likely to be related to balancing fitness costs, e.g. allocating energy between somatic growth and reproduction (Wootton 1990).

Crucian carp (*Carassius carassius* (L.)), a common cyprinid fish in Eurasia, is well known for its wide tolerance of abiotic environmental factors, such as variable temperatures and anoxia in winter (Blažka 1958, Holopainen & Hyvärinen 1985). Crucian carp also shows great phenotypic plasticity in individual morphology and physiology, as well as strong variation in population density in different fish communities (Holopainen & Pitkänen 1985, Brönmark *et al.* 1995, Poléo *et al.* 1995, Holopainen *et al.* 1997a, Holopainen *et al.* 1997b). Small fish with shallow bodies and large heads typically form overcrowded monospecific fish communities in small forest ponds. In the multispecies fish communities in large lakes, crucian carp are large and deep-bodied with low population density (Brönmark *et al.* 1995, Poléo *et al.* 1995, Holopainen *et al.* 1997a).

Crucian carp is one of the batch-spawning cyprinids found in northern Europe. Most previous studies on the reproduction of this species have been conducted with fish from monospecific communities (e.g. Pihu 1961, Astanin & Podgorny 1968, Seymour 1981, Piironen & Holopainen 1988). In addition, previous studies have focused mainly on cell-level data (histology, gonadosomatic index) or been conducted at lower latitudes and thus under different environmental conditions.

The present paper gives data on crucian carp reproduction in three natural bodies of water in eastern Finland. In two small forest ponds, crucian carp is the only fish species present. The third study site is a small lake with many species of fish. Water temperature and crucian carp swimming activity, spawning stage, size distribution and juvenile size frequency were used to determine the type of spawning pattern used by crucian carp in these different communities.

2. Materials and methods

2.1. Study sites

Three natural bodies of water were used for data collection. The Hermanninlampi (PH) is a small forest pond (1 ha, max. depth 1.6 m) in eastern Finland (62°41´N, 29°41´E) ca. 11 km north of the town of Joensuu (for a detailed description of the pond *see* Holopainen 1991 and Holopainen & Oikari 1992). Another monospecific pond, Nimetönlampi (PN) (1.5 ha, max. depth 16 m) is located ca. 2 km south-west of PH. The water is brown and slightly acidic (pH 6.3), and the vegetation (mainly wild calla *Calla palustris* and the yellow water lily *Nuphar lutea*) is limited to small areas close to the shore. Due to anoxic conditions in winter, crucian carp is the only fish species present in these ponds. Lake Varaslampi (LV) is a small eutrophic lake (4.5 ha, max. depth 4 m) in Joensuu. It is partly covered by lush macrophytic vegetation (mainly yellow water lily) and harbours a multispecies fish community, including perch (*Perca fluviatilis* (L.)), pike (*Esox lucius* L.), roach (*Rutilus rutilus* (L.)), tench (*Tinca tinca* (L.)) and crucian carp.

2.2. Fish trapping and measurements

In PH, three Finnish-type metal fish traps (ca. 200 l) were used during one open water season from 11 May to 30 October 1998. One trap had 5 mm mesh and two had 20 mm mesh. All traps were emptied twice a week (every Tuesday and Friday) and then returned to the same spot. In PN crucian carp were trapped between 13 May and 18 October1996 with three traps similar to those used in PH. The traps were emptied 1–2 times a week. In LV fish were trapped during three different years. In 1989, from 8 May to 24 August, crucian carps were trapped continuously with four traps (200 l, 20 mm mesh). Traps were emptied two to four times a week. During the spawning season, crucian carp were also captured with one gill net (50 mm mesh) placed for 24 hours at a time. In the second year, in LV (11 May to 30 August 1997) fish were trapped with three traps (200 l, 20 mm mesh).

These traps were emptied twice a week. In the third year, (11 May to 11 September 1998) crucian carp were trapped continuously with three traps (200 l, 20 mm mesh) and also in eight 24-hour periods with two gill nets (50 mm mesh) between 9 June and 3 July.

Total length (TL), maximal depth (to nearest mm) and fresh weight (to nearest 0.1 g) of all the fish caught in PH, and in LV during 1989 and 1998 were measured. In LV in 1997 and in PN, only part of the trapped fish were measured. All trapped fish were checked for sex and gonad stage (if ripe, i.e. ready to spawn) by compressing the fish slightly for protruding eggs or sperm. Fish that were not ready to spawn (mature or immature) were classified as non-spawning individuals. Possible tubercles in the epithelium (nuptial dress) were checked and recorded for all captured fish in PN and in LV in 1998. After measurements the fish were released. To record the wet weights of the ovaria, 57 crucian carp (17 non-spawning fish, 3 males and 37 females) from PH were sacrified and dissected in 1998. In 1996, the wet weights of the ovaria of 106 females from PN were measured. Wet weights of the ovaria of 25 females from LV were measured in 1989 only.

In addition, to determine the size distribution of the 0+ juveniles, six active samplings by hand net (2 mm mesh) were made in PH between 15 August and 30 October 1998. The captured juveniles were counted and measured for total length and maximum body depth (nearest mm).

2.3. Temperature data

In PN and LV, temperatures were recorded with a manual thermometer ca. 20 cm below the water surface each time the trap was checked. In PH detailed air and water temperature data were collected by an automatic weather station (Weather Wizard III, Davies Instruments Corp., USA) placed in the study area on 11 May 1998, a day after the ice cover had melted, and removed on 30 October, four days before a new ice cover formed. This automatic station recorded both air and water (sensor placed at a depth of 25 cm) temperatures every 30 min.

2.4. Statistics

All results are given as mean ± S.D. Differences between populations were tested by one-way analysis of variance (ANOVA) and *post-hoc* Student-Newman-Keuls (S-N-K) tests. In cases where two groups were tested, only a *t*-test was used. All regression analyses were conducted using a linear regression model.

3. Results

3.1. Temperatures

In PH, the average daily water temperature (calculated from 48 daily records) followed ($r^2 = 0.85$) the average air temperature closely throughout the season in 1998. Three clearly warmer periods of water temperature were seen during the open water season: in mid-May, mid-June and throughout July (Fig. 1). In late July, the water temperature began to decrease slowly. A permanent ice cover formed on 1 November. The average air temperature during the season was 12.0 ± 5.7 °C, the minimum being –3.2 °C and the maximum 31.4 °C. In PN, two warm-water periods can be seen in 1996 (Fig. 1). The variation in temperature was not as pronounced as in PH, and the highest temperature was not reached until late August. In spring, the ice melted in the beginning of May, and a new ice cover formed in late October. In each study year, LV was free of ice from early May to the end of November. Three (1998) to four (1989 and 1997) warm-water periods were observed (Fig. 1).

3.2. Sex, size and spawning stage of the captured fish

3.2.1. Pond Hermanninlampi

A total of 1142 crucian carp were captured in metal traps. The average capture success was 23 ± 37.3 (range 0 to 217) fish per three traps and ca. three days. The number of fish caught was positively related with water temperature (regression analysis, $r^2 = 0.15$, $p = 0.005$) and especially any clear

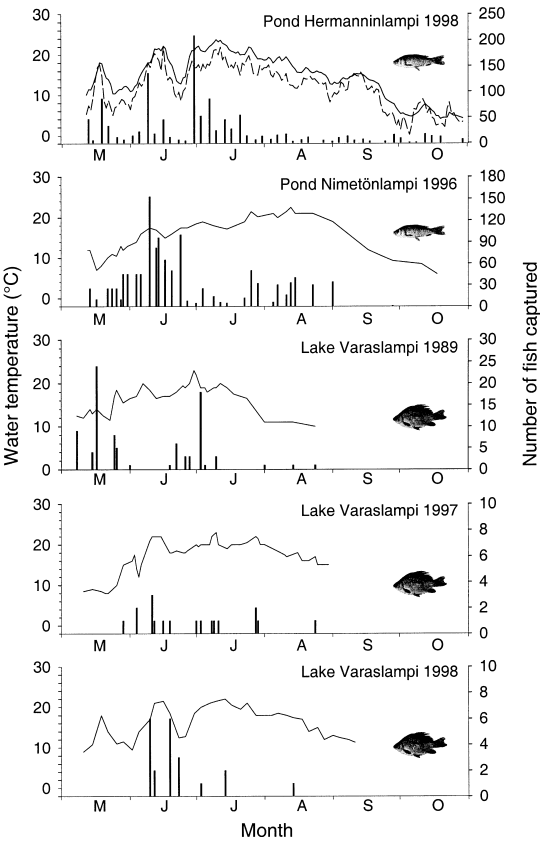

Fig. 1. Water temperatures (lines) and number of crucian carp captured (bars) from each study site. In the top figure the air temperature is shown as a dashed line. A shallow-bodied fish figure indicates a monospecific fish community, and a deep-bodied fish figure indicates a multispecies community.

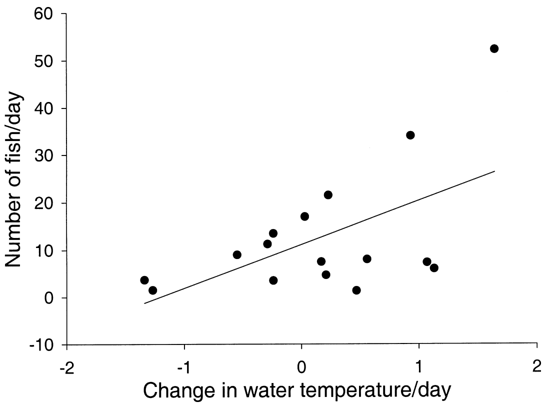

Fig. 2. Regression between the daily change in water temperature (°C) during the three or four days before trap check, and number of fish trapped in pond Hermanninlampi in June–July 1998 ($r^2 = 0.32$, $y = 9.25x + 11.17$).

increase in temperature appeared to induce activity (Fig. 2). The number of trapped fish was clearly highest in the beginning of the three warm-water periods and lowest during the colder-water periods (Fig. 1). The traps were totally empty only on 25 August, 25 September and 27 October.

The average total length of the fish in the traps varied between capture dates (One Way ANOVA $F_{46, 1095} = 6.469$, $p < 0.001$), and the variation could not be explained by changes in water temperature ($r^2 = 0.004$, $n = 1\,142$, $p = 0.02$).

The average body sizes of male, female and non-spawning fish differed (Table 1): females were longer than males and immature fish, and males were longer than non-spawning fish (TL and body depth ANOVA $F_{2, 1139} = 213.299$, $p < 0.001$, S-N-K test $p < 0.05$). In addition, the relative body depth (body height as a percentage of total length) of female crucian carp was significantly greater than that of males or non-spawning fish (ANOVA $F_{2, 1139} = 6.405$, $p = 0.002$, S-N-K test $p < 0.05$), but there was no difference between males and non-spawning fish (S-N-K test $p > 0.05$) (Table 1).

The ready-to-spawn (ripe) fish ($n = 430$) were captured between 19 May and 21 July, all within 64 days. This gives a theoretical 64-day reproductive period during the open-water season in 1998. The males remained ripe longer than the females did: the first ripe males were captured on 19 May, the first female on 5 June, and the last ripe crucian carps of both sexes were captured on 21 July (Fig. 3). Ripe males were captured almost throughout the whole 64-day reproductive period, whereas ripe females were trapped only eight times. During the short periods of colder water, only non-spawning fish were captured.

The smallest (< 6 cm in TL) crucian carp captured were immature fish. On the average, the ripe females were larger than the ripe males (Table 1). The average length of the captured ripe males varied during the summer (ANOVA $F_{12, 363} = 6.921$, $p < 0.001$), whereas the average length of the ripe females did not vary (ANOVA $F_{7, 18} = 2.582$, $p = 0.06$).

3.2.2. Pond Nimetönlampi

A total of 1 193 crucian carp were captured in traps; the average success was 30.6 ± 32 fish per capture (range 0 to 153). There was no clear relationship between number of fish trapped and water temperature ($r^2 = 0.08$, $p = 0.09$) which remained exceptionally low until late July (Fig. 1). All the ripe fish were trapped during a 26 day period between 9 June and 4 July (Fig. 3). Ripe females were caught mainly on 10 June and 24 June. Ripe males, which were more abundant than ripe females, were trapped for a short period between 9 June and 24 June (Fig. 3).

3.2.3. Lake Varaslampi

In 1989, altogether 96 crucian carp were caught (54 fish with traps and 42 fish with gill nets). The average success was 5.6 ± 6.6 fish per capture (range 0 to 24) per four traps and in ca. three days. Although the number of trapped fish was not related to water temperature ($r^2 = 0.004$, $p = 0.676$), the capture success appeared to be best when the water temperature rose quickly (Fig.1). The traps were empty during most of June and after mid-July.

The average length of the fish varied from one capture date to another (ANOVA $F_{16, 79} = 8.636$, $p < 0.001$), but the length variation showed no obvious pattern. The average body size of males was smaller than that of females or non-spawning fish (ANOVA $F_{2, 93} = 4.373$, $p = 0.015$, S-N-K $p < 0.05$). The relative body-depth index of females was lower than that of males or non-spawning fish (ANOVA $F_{2, 89} = 7.139$, $p = 0.001$, S-N-K $p < 0.05$), but there was no difference between males and non-spawning fish (S-N-K $p > 0.05$)

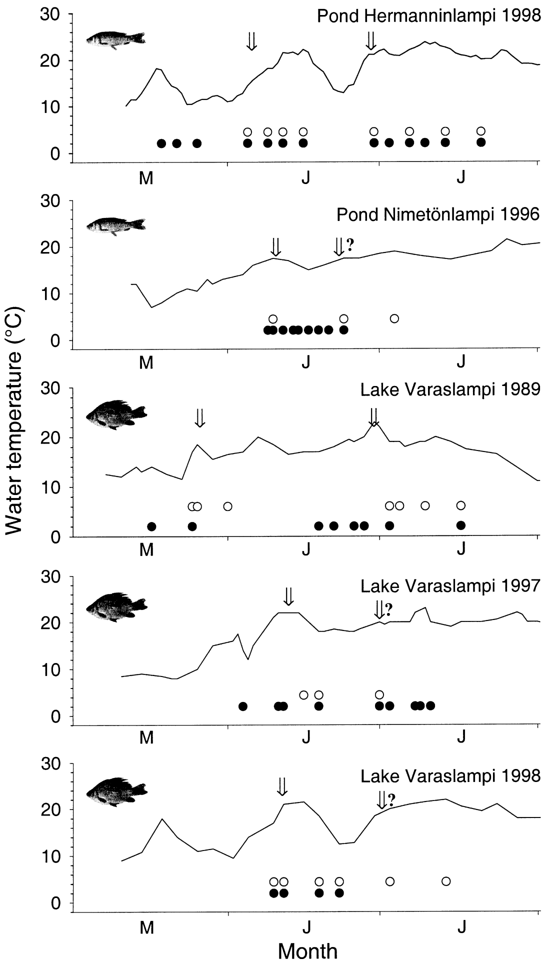

Fig. 3. Water temperatures and the presence of ripe males (dots) and females (circles) at each study site. The start of the assumed spawning period is marked with an arrow. A shallow-bodied fish figure indicates a monospecific fish community, and a deep-bodied fish figure indicates a multispecies community.

Table 1. Size distribution of the captured crucian carp in pond Hermanninlampi (PH) and lake Varaslampi (LV).

Study year	Maturation	*n*	Body length (cm)	Range (cm)	Body depth (cm)	Body depth index	Fresh weight (g)
PH 1998	nsf *	688	7.13 ± 2.2	2.5–19.9	1.96 ± 0.7	27.57 ± 2.7	12.5 ± 10.4[1)]
	males	381	8.95 ± 1.8	6.3–15.2	2.47 ± 0.6	27.44 ± 1.3	10.5 ± 6.1[2)]
	females	73	11.69 ± 2.2	7.8–19.1	3.34 ± 0.7	28.46 ± 1.3	31.2 ± 20.0[3)]
LV 1989	nsf *	33	31.33 ± 4.4	23.1–38.3	13.31 ± 1.8	42.61 ± 3.1	836.3 ± 377.3
	males	38	28.90 ± 5.5	13.9–35.7	12.36 ± 2.4	42.84 ± 2.1	640.2 ± 288.7[4)]
	females	25	32.86 ± 6.2	14.9–39.7	12.96 ± 2.4[5)]	40.43 ± 1.8[5)]	933.3 ± 339.4
LV 1998	nsf *	4	18.83 ± 7.5	11.5–25.5	8.06 ± 3.6	42.32 ± 2.8	231.4 ± 217.5
	males	8	23.28 ± 4.6	14.8–28.5	9.96 ± 2.1	42.63 ± 0.9	302.7 ± 137.2
	females	9	23.39 ± 2.3	19.3–27.5	10.09 ± 1.6	42.93 ± 2.6	311.7 ± 100.1

* = non-spawning fish, [1)] $n = 17$, [2)] $n = 4$, [3)] $n = 37$, [4)] $n = 32$, [5)] $n = 21$.

(Table 2).

The ripe crucian carps (63 fish) were captured between 17 May and 17 July, all within 60 days (Fig. 3). Male crucian carp remained ripe longer than females did: the first ripe males were captured on 17 May and the first female on 25 May. The last time that ripe crucian carp of both sexes were captured was on 17 July. Ripe females were trapped mainly in late May and early July. The average TL of both sexes clearly varied, but during the summer this variation was random (males ANOVA $F_{9, 32} = 11.881$, $p < 0.001$, females ANOVA $F_{12, 41} = 4.391$, $p < 0.001$).

In 1997, only 17 crucian carp were captured (12 fish in traps and 5 fish in gill nets). The average capture success was 0.3 ± 0.7 fish per capture, and the number of captured fish correlated positively with water temperature ($r^2 = 0.083$, $p = 0.04$). Four warm-water peaks were observed during the season (Fig. 1). Traps contained no fish 31 times, especially after early August. Three female crucian carp (18%), nine males (53%) and five non-spawning fish (30%) were captured. Ripe fish were captured within 37 days between 4 June and 11 July. Ripe males were captured during a longer period than females (Fig. 3).

In 1998, a total of 21 crucian carp were captured (9 in traps and 12 in gill nets). The average capture success was 0.6 ± 1.5 fish per capture (three traps, catch varying from 0 to 6). There was no correlation between the number of fish trapped and water temperature ($r^2 = 0.069$, $p = 0.571$) although crucian carp were caught mainly during the warm-water periods (Fig. 1). The traps were empty during May, and only one crucian carp was captured after early July. The average total length of the captured crucian carp did not vary between capture dates (ANOVA $F_{6, 14} = 1.007$, $p = 0.459$). The average body sizes (TL) of males, females and non-spawning fish were similar (ANOVA $F_{2, 18} = 1.649$, $p = 0.220$) (Table 2).

Ripe crucian carp ($n = 17$) were captured between 10 June and 14 July (within 34 days). The first ripe fish of both sexes were trapped on 10 June (Fig. 3). The last ripe male crucian carp was captured already on 23 June but the last female was not captured until 14 July. Non-spawning fish ($n = 4$) were trapped on 19 June, 14 July and 14 August. The average TL of ripe crucian carp males ($n = 8$), females ($n = 9$) and non-spawning fish did not differ (ANOVA $F_{2, 18} = 1.649$, $p = 0.220$) (Table 1). The average TL of both sexes did not vary over time during the reproductive season (males ANOVA $F_{3, 4} = 3.958$, $p = 0.109$, females ANOVA $F_{5, 3} = 6.096$, $p < 0.08$).

3.3. Gonadosomatic index

The gonadosomatic index (GSI, gonad fresh weight as a percentage of fish weight) was calculated for the female fish from PH, PN and LV in 1989. For the fish from all the sites studied, the GSI varied throughout the season (Fig. 4). The average GSI in May was higher in LV than in PH (ANOVA $F_{2, 40} = 6.577$, $p < 0.003$, S-N-K $p < 0.05$), but there was no difference between PN and PH or LV and PN (S-N-K $p > 0.05$) (Table 2). In LV, the GSI (during May) correlated positively with body weight (Fig. 5).

In the PH, GSI was calculated for fish captured on ten occasions between 19 May and 7 July 1998. It varied (Fig. 4), but the differences were not statistically significant (ANOVA $F_{9, 26} = 1.509$, $p = 0.197$) and were not affected by changes in water temperature ($r^2 = 0.086$, $p = 0.08$). In PN, the GSI was calculated for fish from the 26 samples taken between 14 May and 1 September 1996. Again, the GSI was variable (Fig. 4); furthermore, the differences were statistically significant (ANOVA $F_{25, 50} = 7.493$, $p < 0.001$). More interestingly, the GSI decreased with increasing water

Table 2. Female gonadosomatic index in May, and length of the observed reproductive period at three study sites.

Study site	*n*	GSI		Length of the reproduction period
		Average ± S.D	Range	
PH 1998	9	5.51 ± 1.36	3.92–7.91	64 days
PN 1996	12	8.59 ± 1.80	5.60–11.8	32 days
LV 1989	22	11.56 ± 5.78	3.63–20.98	60 days

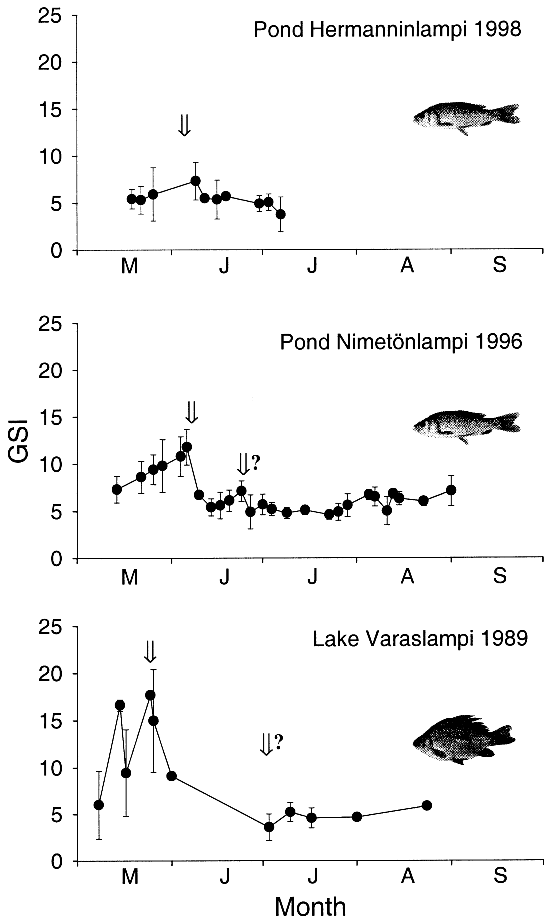

Fig. 4. Gonadossomatic index (GSI) of crucian carp females from the three study sites. The start of the assumed spawning period is marked with an arrow. A shallow-bodied fish figure indicates a monospecific fish community, and a deep-bodied fish figure indicates a multispecies community.

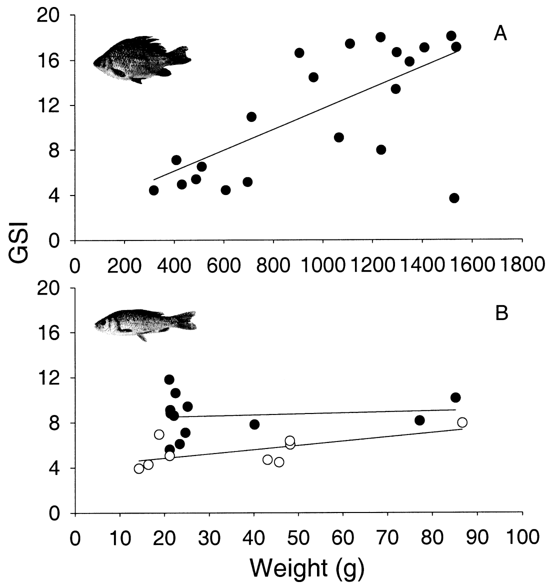

Fig. 5. Regression between GSI and body weight at three study sites in May. — A: Lake Varaslampi (r^2 = 0.42, $y = 0.0093x + 2.4$); — B: ●: Pond Nimetönlampi ($r^2 = 0.01$, $y = 0.0085x + 8.3$); ○: Pond Hermanninlampi (r^2 = 0.41, y = 0.038x + 4.1). A shallow-bodied fish figure indicates a monospecific fish community, and a deep-bodied fish figure indicates a multispecies community.

temperature (r^2 = 0.339, p = 0.002). In LV, the GSI was calculated for fish from 12 samples taken between 8 May and 24 August 1989. The GSI was variable (ANOVA $F_{11,25} = 6.418$, $p < 0.001$) but this variation could not be explained by water temperature ($r^2 = 0.02$, $p = 0.411$) (Fig. 4). Both GSI and body weight were positively correlated in fish from LV ($r^2 = 0.419$, $p < 0.001$), but not in those from PH or PN ($r^2 = 0.410$, p = 0.063 and $r^2 = 0.012$, $p = 0.738$, respectively) (Fig. 5).

3.4. Tubercles in the epithelium (nuptial dress)

Tubercles in the epithelium were recorded in fish in PN and LV in 1989. During the spawning season, both males and females developed small tubercles in the epithelium when ready to spawn. At both study sites some sexual dimorphism was observed. In males, the tubercles were more abundant, covering both head and body, but in females they were limited to the head region only. Nearly all ripe male crucian carps had tubercles. At the beginning of the reproduction period, tubercles covered only the head (forehead and *operculum*); but a few days later they were found on the body as well. In female fish the tubercles were found only on the head and *operculum*. By the end of the ripe period tubercles were absent in both sexes. At neither study site did the size of the fish correlate with the presence or number of tubercles.

3.5. Size distribution of juveniles

To observe the size distribution of crucian carp juveniles in PH, six captures were made with a hand net between 15 August and 30 October. The average size (TL) of the 833 captured fish was 4.25 ± 1.35 cm (range 2.0–13.2 cm). There were

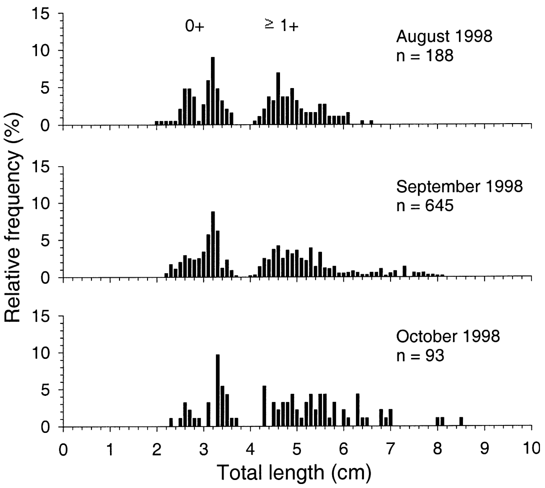

Fig. 6. Length distributions of young crucian carp captured by hand net from pond Hermanninlampi in 1998.

no crucian carp 3.8 to 4.0 cm long, and this particular size class was assumed to be the step between 0+ and one-year-old fish (Fig. 6; *see* also Tonn *et al.* 1994). The average size of the captured crucian carp less than 4 cm long was 3.01 ± 0.34 cm (n = 376, range 2.0 to 3.7 cm, skewness = –0.56).

4. Discussion

4.1. Temperature and fish catchability

In general, sexual development and spawning of cyprinid fish are modulated by temperature and photoperiod (Wootton 1990). In most species (Bye 1984, Wootton 1990), including crucian carp (Seymour 1981), temperature, rather than photoperiod, has been reported to control the timing of spawning. Moreover, spawning is not likely to occur until the water temperature reaches 17–20 °C (Kryzhanowskii 1949, Schäperclaus 1953, Seymour 1981) especially in harsh climatic conditions as those in Finland (Astanin & Podgornyy 1968).

In the present study, all the ripe female crucian carp were captured during warm-water periods (temperature above 18 °C), but the ripe (ready-to-spawn) males were not as sensitive to temperature and were trapped even at a water temperature of only 11 °C. A rapid rise in water temperature (several degrees in a few days) even when the temperature was already relatively high, seemed to be the most important abiotic factor triggering the high mobility related to spawning (Fig.1). However, probably due to inadequate gonad development and to photoperiod, temperature peaks in early spring, late summer or fall were not effective.

4.2. Size of ripe fish and length of the reproductive period

The size of the ripe crucian carp varied within and between sexes in all populations during the reproductive period, but there was no clear pattern to this variation. The more abundant (or easier to capture) male crucian carp appeared to remain ripe longer (mid-May to mid-July) than the females, which appeared to be ready to spawn only during warm-water periods.

Length of the reproductive period (the time between the first and the last captures of ripe fish) varied from 32 to over 60 days at the study sites and in the different years. Except for the short reproductive period during the cold summer of 1996, the reproductive period was about the same length at all study sites. Timing of the first batch (start of the reproductive period) varied from late May (LV 1989) to mid-June (LV 1997). The variation between years apparently was caused by different temperature conditions during May. The officially recorded mean air temperatures in May at Joensuu airport were 10.2 °C in 1989, 7.3 °C in 1996, 7.0 °C in 1997 and 8.1 °C in 1998 (Ilmatieteen laitos, Meteorological Institute). The earliest start of the reproductive period (LV in 1989) took place during the warmest May of the study years, whereas the latest start of the reproductive period (LV in 1997) occurred during the coldest May of the seasons studied (Fig. 7).

According to Piironen & Holopainen (1988), the last ripe crucian carp of both sexes were trapped toward the end of July (in the present study 21 July), even though the water temperature still remained suitable for spawning for several weeks. The late summer, however, is used to restore the large carbohydrate reserves in the liver and muscle needed for overwintering in anoxia (Holopainen & Hyvärinen 1985, Piironen & Holopainen

1988).

The average and minimum sizes of ripe males were smaller than those of ripe females. Compared with sperm, each egg represents a massive cytoplasmic investment (Wootton 1990), and this often leads to a positive correlation between absolute fecundity and body size (Bagenal 1978, Wootton 1990) also in batch spawners (Lowerre-Barbieri *et al.* 1998). A positive correlation between body size and absolute fecundity has previously been reported in crucian carp (Astain & Podgornyy 1968, Holopainen & Pitkänen 1985, Holopainen *et al.* 1997a). Here a positive correlation was shown between body size (weight) and GSI in fish from lake Varaslampi. The correlation was, however, not so clear in fish from the ponds studied, perhaps due to the small number of fish measured.

The sex ratio of the captured fish was male dominated in all the communities studied. In pond Hermanninlampi the sex ratio was 16:84 (females:males), in lake Varaslampi 40:60 in 1989, 25:75 in 1997 and 47:53 in 1998. The sex ratio for crucian carp has previously been reported to be approximately 25:75 (Astanin & Podgornyy 1968). Obviously, trapping is not an ideal method for determining the real sex ratio because any female entering a trap may attract many males to enter as well.

Mating itself is likely to take place at night or in early morning, when crucian carps are known to be most active (Holopainen *et al.* 1988). In the mating process the tubercles in the epithelium (more abundant in males) play a role which, unfortunately, is not known in detail for this species. In addition, the female reproductive hormones in crucian carp are known to function as pheromones that help synchronize reproductive activity in males and females (Bjerselius 1994).

4.3. Gonadosomatic index

Differences in the gonadosomatic index (GSI) of different fish species partly reflect differences in the temporal pattern of egg development and spawning (Wootton 1990). Among total spawners, the GSI is usually high (e.g. 30%) just before spawning; but multiple spawners have generally lower GSI values (Bye 1984, Wootton 1990).

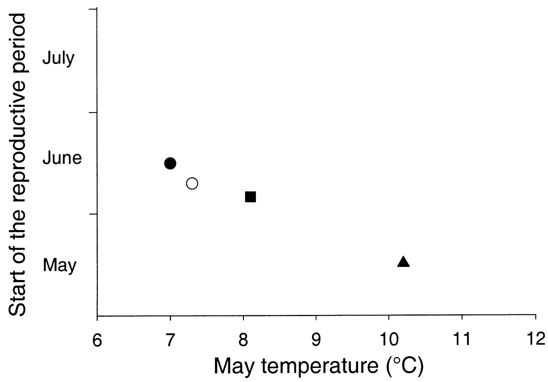

Fig. 7. Mean air temperature in May and the start of the crucian carp reproductive period during four years. ●: Lake Varaslampi 1997; ○: Pond Nimetönlampi 1996; ■: Pond Hermanninlampi 1998; ▲: Lake Varaslampi 1989.

The average GSI of the trapped ripe female crucian carp varied over time and among populations (Table 2). Similar GSI values for crucian carp from monospecific communities was previously reported by Seymour (1981) and by Holopainen & Pitkänen (1985). To our knowledge, there are no previous GSI data available for multispecific communities. The GSI comparisons in females are said to reveal only which groups are most ready to spawn (Siems & Sikes 1998). Moreover, the present GSI values for each capture time are averages for different numbers and sizes of fish, which leads to large variation.

In the present study, the GSI decreased rapidly in the beginning of the warm-water periods at about the same speed at all the three study sites. Thus, low GSI values were found from June onwards, even though ripe fish were present more than a month later. This indicates that after the first batch of eggs has been released, the numbers and/or the sizes of eggs in the next batch are clearly lower. However, female crucian carp are said to produce similar numbers of eggs during each reproductive period (Pihu 1961).

4.4. Size distribution of juveniles

The batch-spawning pattern used by crucian carp should result in separate size-classes of young-of-the-year fish (Piironen & Holopainen 1988). The 1998 size distribution of juveniles showed two peaks for fish smaller than 4 cm, indicating two separate spawnings. This is supported by Holopainen & Pitkänen (1985), who claimed that crucian carp grow 2.4 to 5.0 cm during their first summer. Laurila *et al.* (1987) and Piironen & Holopainen (1988) have reported three size classes of 0+ fish from the same pond, which indicate three separate spawnings during one reproductive season.

4.5. Number and timing of spawning periods

The present data from pond Hermanninlampi (water temperatures, trapping success, GSI, number of ripe fish and juveniles size distribution), suggest two spawnings in 1998. The first period started in early June (9 June) and the second period at the start of July (1 July). There was one relatively warm-water and high fish-activity period after mid-May, but no ripe fish were trapped during that time. The absence of ripe fish was probably due to the temperatures being too low for spawning or to inadequate development of gonads.

In the pond Nimetönlampi, due to the relatively cold summer summer of 1996, the first and the only spawning period clearly detected was in mid June (12 June). However, in the end of June there was a slight increase in water temperature, a few ripe-to-spawn female fish were trapped and the GSI also decreased slightly, indicating a second batch.

In lake Varaslampi in 1989, two spawning periods were detected: one after mid-May (20 May) and another in early July during the second warm-water period. In 1997, the first batch was released in mid-June (starting on the 15th) and an uncertain or modest second batch (small number of captured ripe females) in the beginning of July. In 1998, only one definite spawning period, starting on 10 June, was detected. A small second batch started on 1 July, but only a few ripe fish were trapped during that period.

4.6. Conclusions

In all the bodies of water studied, crucian carp is a batch spawner. The length of the reproductive period and the number of batches in a season are dependent on the water temperature in spring and early summer. The number of spawning periods varies from one to three. In warm springs (the mean air temperature in May is ca. 10 °C), the first spawning occurs during late May. Male crucian carp remain ripe throughout the reproductive period (ca. 65 days from May to July) while the females reach ripeness only during periods when the water is warm. As clearly shown by the larger trap catches, an increase in water temperature induces female spawning and male mobility.

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