



Journal of Fish Biology (2011) **78**, 227–239

doi:10.1111/j.1095-8649.2010.02854.x, available online at wileyonlinelibrary.com

Seasonal dynamics in population characteristics of European bitterling *Rhodeus amarus* in a small lowland river

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(Received 14 June 2010, Accepted 21 October 2010)

The seasonal dynamics of biological traits in a population of European bitterling *Rhodeus amarus* from a small river in central Europe (River Kyjovka, Czech Republic) were investigated from April 2007 to March 2008. The reproductive season lasted from early April to mid-June, with a peak in late April when >50% of females possessed ripe eggs in their ovaries. The sex ratio was female-biased, with a higher bias following the peak in reproduction, suggesting higher mortality of males than females over the reproductive period. The population was effectively annual, with a major decrease in adult fish abundance at the end of the reproductive period. Highest relative lipid content and condition factor were observed in February, both decreasing with an increase in investment into gonads. Seasonal dynamics in somatic condition, relative lipid content and gonad mass, and their comparison with other *R. amarus* populations, suggest that the study population allocated a disproportionately high level of resources to reproduction. © 2011 The Authors

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Key words: Acheilognathinae; annual life cycle; ecophysiology; gonado-somatic index; lipid content; somatic condition.

INTRODUCTION

Model species provide the most influential insights into biological research and this is typically accomplished during experimental manipulation. In order to provide the appropriate understanding of causes and consequences of particular experimental outputs, however, an understanding of the basic ecological characteristics of model species and populations is essential. The European bitterling *Rhodeus amarus* (Bloch) is a small cyprinid with a unique mode of reproduction, females laying their eggs into the gills of freshwater mussels, where the embryos develop for several weeks (Smith *et al.*, 2004). *Rhodeus amarus* are easy to observe both in the wild and laboratory, the quantity and quality of their spawning sites may be easily manipulated and they are highly amenable to laboratory conditions. This makes them valuable model species in behavioural and evolutionary biology (Smith *et al.*, 2004). Data on population characteristics of *R. amarus*, however, are largely incomplete and

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this is particularly true for seasonal dynamics of demographic and physiological characteristics (Holčík, 1999).

Rhodeus amarus has a wide distribution throughout Europe where it inhabits a range of standing and slow-flowing habitats (Przybylski & Zieba, 2000; Kottelat & Freyhof, 2007). During the reproductive season males defend territories around freshwater unionid mussels in which females lay one to six eggs during each oviposition event. Reproduction is triggered by an increase in water temperature, with a threshold for spawning of between 10 and 15° C (Holčík, 1999; Smith *et al.*, 2004; Kottelat & Freyhof, 2007). *Rhodeus amarus* is a batch-spawner, with each female producing several batches of eggs over a long reproductive season. Several ovipositions are completed within 1 day, divided from other such spawning bouts by a period of several days with no spawning activity. Absolute female fecundity depends on female body size and typically reaches 80–300 eggs per season (Holčík, 1999; Smith *et al.*, 2000; Kottelat & Freyhof, 2007). The eggs hatch within 24–36 h and embryos reside in the mussel for *c.* 1 month, leaving when they reach a standard length (L_S) of 10.5 mm (Aldridge, 1999). After emergence, they enter shallow, vegetated regions that serve as nursery areas until late autumn (Jurajda, 1999; Przybylski & Zieba, 2000; Reichard *et al.*, 2002; Smith *et al.*, 2004). Sexual maturity is achieved after the first winter, though gonads may already be detectable in autumn, *i.e.* before young-of-the-year *R. amarus* have survived their first winter (Holčík, 1999). *Rhodeus amarus* is reported to live up to 5 years (Holčík, 1999; Koutrakis *et al.*, 2003; Przybylski & García-Berthou, 2004; Tarkan *et al.*, 2005; Patimar *et al.*, 2010), though populations in central Europe appear to have much shorter life spans (Smith *et al.*, 2000). The name *R. amarus* was considered a junior synonym of *Rhodeus sericeus* (Pallas) until Bohlen *et al.* (2006) showed that *R. sericeus* is restricted to Far East Asia and *R. amarus* is a valid, separate species.

The aim of this study was to analyse the seasonal dynamics of important population characteristics describing somatic condition (body size, lipid content and Fulton's condition factor, K), reproductive status (gonado-somatic index, I_G , and ovarian stage) and demographic characteristics (sex ratio and size-related mortality) and their relationships in a population of *R. amarus* from the River Kyjovka (Czech Republic), a source of experimental fish for many behavioural studies.

MATERIALS AND METHODS

STUDY AREA

Sampling took place at the village of Týnec (48° 46' 46.337" N; 17° 1' 1.763" E) on the River Kyjovka, a small lowland tributary of the River Dyje in the Czech Republic. At this point, river width is 9 m and mean depth is 0.55 m. The river bottom is covered with fine sediment and aquatic vegetation comprising *Ceratophyllum* sp., *Potamogeton* sp. and amphibious bistor *Persicaria amphibia*. The long-term mean river discharge is 1.1 m³ s⁻¹ and terrestrial vegetation on the banks is regularly flooded during elevated river discharge. During this study, water temperatures reached 10° C in the last week of March, rose to 17° C by mid-March and then varied between 17 and 26° C until early October, with a peak in late August. A sudden drop in water temperature was observed from mid-October to late October, with temperatures <10° C until late March. The fish assemblage is dominated by bleak *Alburnus alburnus* (L.), white bream *Blicca bjoerkna* (L.), roach *Rutilus rutilus* (L.) and *R. amarus*. Other common species include bream *Abramis brama* (L.), Prussian carp

Carassius gibelio (Bloch), rudd *Scardinius erythrophthalmus* (L.) and perch *Perca fluviatilis* L. (Konečná, 2008).

FISH SAMPLING

Sixteen samples of *R. amarus* were collected from April 2007 to March 2008. Samples for the characteristics of adult fish were collected at 1 week intervals during the reproductive period (April 2007 to mid-June 2007), and every second week thereafter until September 2007. Five consecutive runs of removal electrofishing sampling were conducted over a 100 m stretch of the river on seven sampling dates (25 April to 13 June). The study stretch was enclosed upstream and downstream by nets (mesh-size 5 mm) and fish collected using two electrofishing backpacks (Lena; www.r-bednar.cz) applied simultaneously across the river width. In addition to the two gear operators, four people collected stunned fish with dip-nets. Individual pass abundance data were not appropriate for standard estimation of fish abundance (Zippin, 1958), and hence the total catch per five runs was used as an index of *R. amarus* abundance.

Approximately 120 adult *R. amarus* were collected on each sampling date. On those dates when removal sampling was employed, additional fish were collected immediately downstream after removal sampling was completed and the fish pooled for analysis. All fish collected were kept in an aerated container. Within 1 h after capture, fish were sexed (females identified by the presence of an ovipositor) and L_S measured to the nearest mm. The handling time was minimized and all fish were released back to the river. Analysis of reproductive traits (I_G and the presence of ripe eggs) and physiological state (lipid content and K) was undertaken on a sample of 20 males and 20 females captured from an adjacent stretch 7.5 km downstream, to avoid interference with fish abundance estimates on the original study stretch. These fish were killed with a lethal dose of anaesthetic (clove oil), stored in 4% formalin and transported to the laboratory for further analysis.

From August 2007 to March 2008, 0+ year fish were sampled at monthly intervals at Týnec. Approximately 30 individuals were randomly chosen from a sample of juvenile *R. amarus* collected by a dip-net in nursery areas, killed by an overdose of anaesthetic and stored in 4% formalin for further analysis. Larger juveniles were targeted in August and September as randomly chosen fish were too small for analysis. For this reason, 0+ year fish samples from August and September were treated separately.

Overall, 1661 adult and 148 0+ year fish were sexed and measured, and 471 juveniles sampled from August to October were measured only.

ANALYSIS

In the laboratory, each fish was measured to the nearest mm (L_S) using digital callipers, weighed to the nearest 0.01 g (total mass, M_T) and dissected to remove the gonads and gastrointestinal tract. Gonad mass (M_G) and net mass (M_N , mass without gonads and gastrointestinal tract) were then recorded. In 0+ year fish, M_G was measured from the end of August as no gonads were detectable before this date. A digital image of each dissected ovary was made and the presence of yolky spherical eggs (mature eggs) and prolonged yolky eggs (ripe eggs ready to be spawned) was recorded, as described by Solomon *et al.* (1984).

The somatic condition was expressed using K (Le Cren, 1951) as $K = (M_T L_T^{-3}) \times 10^5$, where L_T is the total length in mm. An established formula of $L_T = 1.811 + 1.176 L_S$ (Przybylski & García-Berthou, 2004) was used for conversion between L_S and L_T . To avoid the problems of the interpretation and analysis of ratio values, ANCOVA was used to statistically test the differences in M_T (\log_{10} transformed) between the sexes and among sampling dates, with $\log_{10} L_T$ as a covariate. Similarly, seasonal differences in M_G (\log_{10} transformed) were formally tested using ANCOVA with $\log_{10} M_T$ as a covariate. The relative size of gonads was also expressed by I_G as $I_G = M_G M_T^{-1} \times 10^2$ for graphical output and comparisons with earlier studies.

Methanol–chloroform lipid extraction was used to extract skeletal lipids from muscle (Folch *et al.*, 1957). Ten adult males and 10 adult females (and five males and five females from the 0+ year fish samples) were randomly chosen from the formalin-preserved sample

and dried for 2 days at 20° C. Fish dry mass was weighed to the nearest 0.1 g and the fish was then homogenized. Lipids were extracted by washing the sample in a mixture of chloroform and methanol (2:1). The sample was then centrifuged (1820g) for 5 min and filtered using a glass fibre filter. Following evaporation of the solution agents, samples were purified with ether and the ether–lipid fraction evaporated to dryness in air. After evaporation, the collected lipids were weighed. The relative lipid content (I_L) was expressed as the proportion of lipids per 1 g of M_N .

All data were checked for normal distribution and homoscedasticity of variance. Factorial ANOVA and ANCOVA using two factors (sex and sampling date) were used to test seasonal dynamics and sex differences in the variables. Sex differences in I_G were not tested statistically as female investment into gonads is inherently higher (Wootton, 1998). All analyses were conducted using Statistica 9.0 for Windows (www.statsoft.com)

RESULTS

ADULT FISH

Data from removal sampling showed a slight decline in *R. amarus* abundance during May and a sharp decrease from late May onwards [Fig. 1(a)]. The sex ratio of adult *R. amarus* was female-biased throughout the sampling, though the difference was often non-significant at the start of the reproductive season. Females represented 55–75% of all adult fish captured by electrofishing [Fig. 1(b)]. The mean sex ratio of males to females during the reproductive season (April to mid-June) was 1:2.5.

Females were larger than males (ANOVA: d.f. = 1,159, $P < 0.001$), this difference being largely due to larger female L_S from 30 May onwards (ANOVA interaction: d.f. = 1,159, $P < 0.001$; Fig. 2). Sexual dimorphism was negligible, however, with the mean difference between male and female L_S being only 0.6 mm. Both sexes showed a slow but significant increase in L_S over the sampling season (ANOVA: d.f. = 15,1628, $P < 0.001$; Fig. 2). Growth of females was more pronounced (Spearman correlation between L_S and sampling date, $r_S = 0.47$, d.f. = 1083, $P < 0.001$) than of males ($r_S = 0.17$, d.f. = 578, $P < 0.001$).

Females had consistently higher condition than males [ANCOVA on $\log_{10} M_T$ with $\log_{10} L_T$ as covariate: d.f. = 1,505, $P < 0.001$; Fig. 3(a)]. The seasonal dynamics of condition did not differ between males and females (ANCOVA interaction: d.f. = 12,505, $P > 0.05$), being high at the start of the reproductive season (mean \pm s.e., $K = 1.58 \pm 0.07$ in males and 1.63 ± 0.06 in females), decreasing significantly between the first and second sampling, and remaining stable until the end of sampling (ANCOVA: d.f. = 12,505, $P < 0.05$). Relative lipid content showed a gradual decrease over the sampling season [ANCOVA: d.f. = 12,252, $P < 0.001$; Fig. 3(b)], with no differences between sexes in I_L (ANCOVA: d.f. = 1,252, $P > 0.05$) or interaction between fish sex and sampling date (ANCOVA: d.f. = 12,260, $P > 0.05$).

Females with extended ovipositors and ripe eggs in the ovaries were observed from the beginning of sampling (4 April) until 13 June (Fig. 4). The proportion of females with extended ovipositors varied between 5 and 18% ($n = 37$ –120 females per sampling date) over the reproductive season. Spawning activity peaked on 25 April, when $>50\%$ of dissected females possessed ripe eggs in their ovaries (Fig. 4). The seasonal pattern in relative gonad mass confirmed that reproductive season ceased in mid-June, with a sharp and significant decrease in I_G between 13 and 25 June (Fig. 4) in both males (ANCOVA with M_T as covariate: d.f. = 14,258,

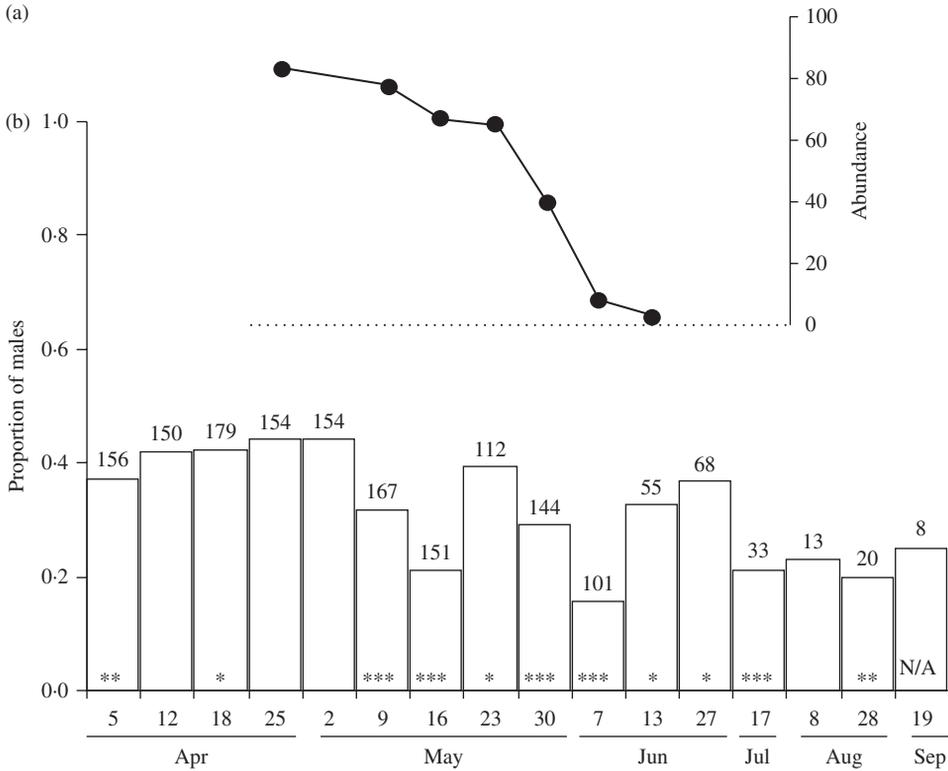


FIG. 1. Seasonal dynamics in (a) abundance of adult *Rhodeus amarus* and (b) proportion of males. Abundance was recorded in a 100 m long study stretch of the River Kyjovka (Czech Republic) by multiple-pass removal sampling by electrofishing and expressed as the total number of fish captured per 100 m of river. Sex ratio was estimated from a target sample of 150 adults collected during abundance estimation and additional sampling in the study stretch. The number of fish used for the sex ratio estimate is shown above individual bars. Significant differences (χ^2 test) are indicated (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N/A, sample size lower than test requirement) for each sampling.

$P < 0.05$; Tukey *post hoc* tests $P < 0.05$) and females (d.f. = 14,274, $P < 0.05$; Tukey *post hoc* tests $P < 0.05$).

0+ YEAR FISH

The condition of 0+ year fish was marginally higher in females than in males [ANCOVA on $\log_{10} M_T$ with $\log_{10} L_T$ as covariate: d.f. = 1,144, $P = 0.012$; Fig. 5(a)]. The 0+ year fish had lower K on the first sampling date (29 August, mean \pm S.E. 1.16 ± 0.02) than later in the season (September to March, mean \pm S.E. 1.40 ± 0.026) (ANCOVA: d.f. = 7,144, $P < 0.01$) and K values were comparable with K of adult fish (range 1.16–1.49 in 0+ year fish, 1.15–1.63 in adults).

The relative lipid content of 0+ year fish did not differ between males and females (ANCOVA on \log_{10} lipid mass with $\log_{10} M_T$ as covariate, sex: d.f. = 1,63, $P > 0.05$), but did vary among sampling dates (date: d.f. = 7,63, $P < 0.001$). There was no interaction between sex and sampling date (d.f. = 7,63, $P > 0.05$). A small

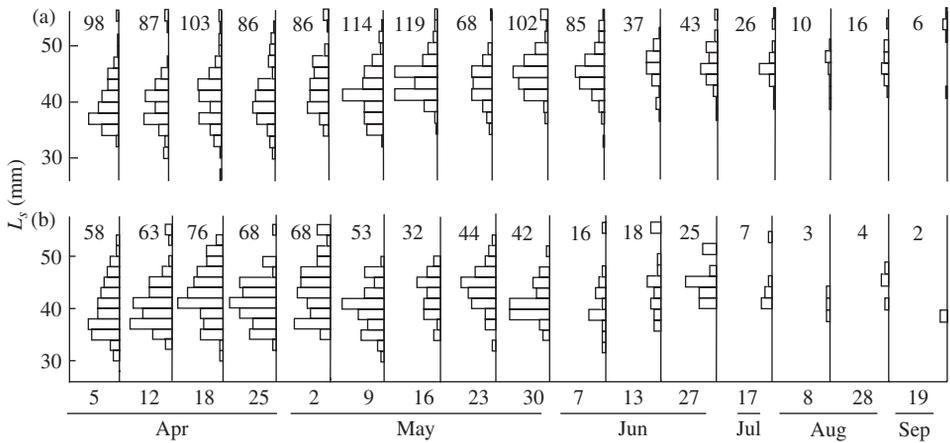


FIG. 2. Seasonal dynamics in standard length (L_S) of adult (a) female and (b) male *Rhodeus amarus* from the River Kyjovka at Tynec. Numbers are sample size.

seasonal increase was observed in relative lipid content of 0+ year fish during winter, though this decreased in March when the fish matured [Fig. 5(b)].

The M_G of 0+ year males and females increased significantly between January and February and between February and March (ANCOVA with M_T as covariate, females: d.f. = 7,70, $P < 0.05$; males: d.f. = 7,73, $P < 0.05$; Tukey *post hoc* tests, $P < 0.05$). The increase in M_G in 0+ year females coincided with the appearance of mature eggs in February. Ripe eggs were observed in March [Fig. 5(c)].

DISCUSSION

The seasonal dynamics of the main ecological and physiological traits of *R. amarus* from the River Kyjovka indicate that the population shows an annual pattern, with a sharp decrease in adult fish abundance coinciding with the end of the reproductive season in mid-June. The sex ratio was female-biased and peak reproductive activity occurred in late April. The highest relative lipid content and condition factor were observed in February and decreased with an increase in the investment into gonad growth.

ADULT DEMOGRAPHY

Abundance decreased sharply over the study site during the final part of the reproductive season. This was corroborated by a substantial increase in effort needed to capture a sufficient number of individuals for the analysis of sex ratio and reproductive condition (though unit effort was not accurately recorded for this test). Aside from an annual mode of life history, two alternative explanations could account for the observed decrease in abundance of adult fish, *i.e.* seasonal migration or sampling-induced mortality. Both these explanations are unlikely, however, for the following reasons. First, *R. amarus*, as with other bitterling species (Solomon *et al.*, 1984; Kitamura, 2007), is a philopatric fish that does not undergo a spawning migration (Holčík,

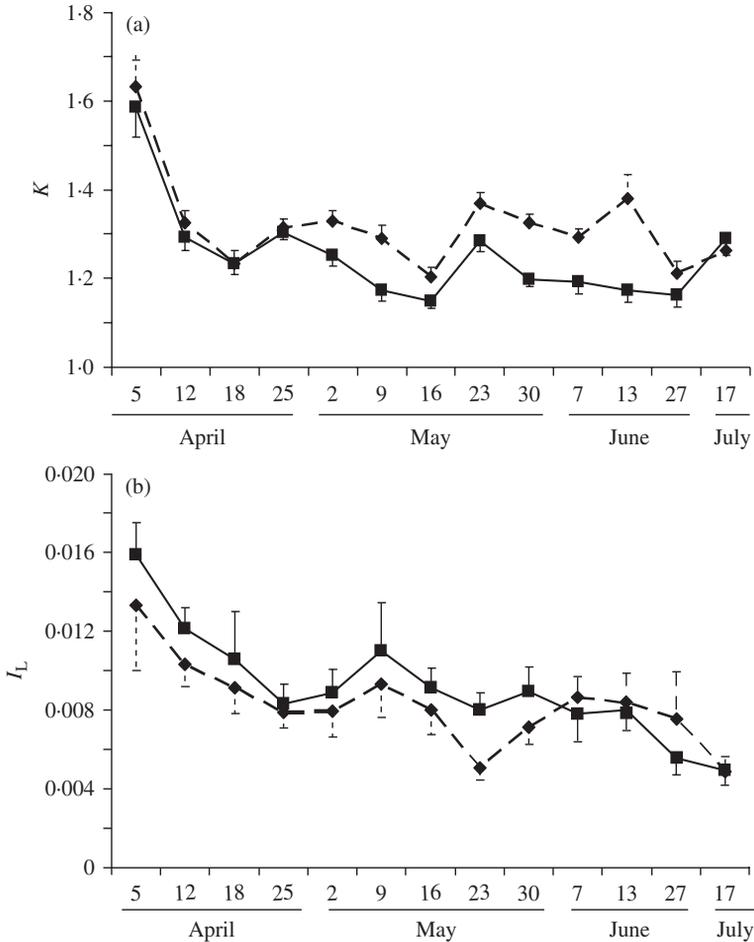


FIG. 3. Seasonal dynamics of mean \pm s.e. (a) Fulton's condition factor (K) and (b) relative lipid content (I_L) in male (■) and female (◆) adult *Rhodeus amarus* from the River Kyjovka at Tyneç.

1999; Smith *et al.*, 2004). Further, freshwater mussels, which serve as the spawning substratum for the eggs, are abundant along the entire stretch of the River Kyjovka (Reichard *et al.*, 2002; M. Reichard, unpubl. data), minimizing the need for migration from the spawning sites. Second, sampling-induced mortality can also be discounted as mortality observed during fish capture and handling was $<1\%$. Finally, it was difficult to catch adults anywhere in the river and adjacent water bodies following the end of the reproductive season, even in years when no sampling was conducted during the reproductive season (Reichard, 1998; M. Reichard, pers. obs.).

The life span of *R. amarus* varies from 1 to 5 years among populations. Smith *et al.* (2000), reading the age from scales in spring, reported that almost 95% of adult fish in a population from an oxbow lake adjacent to the River Kyjovka were 1 year old, providing further support for the annual character of the *R. amarus* populations in the area. On the other hand, Tarkan *et al.* (2005) and Koutrakis *et al.* (2003) observed that *R. amarus* up to 3 years old were abundant in populations

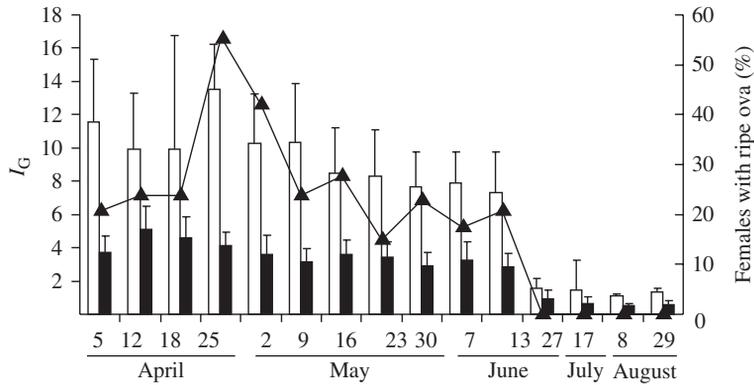


FIG. 4. Seasonal dynamics of mean + s.e. gonado-somatic index (I_G) in male (■) and female (□) adult *Rhodeus amarus* from the River Kyjovka at Tynec and the relative proportion of females with ripe ova (—▲) ($n = 20$ per sampling date).

from Western Anatolia (Turkey) and Greece and, in the southernmost populations, the population comprises mainly 1 and 2 year-old fish (Patimar *et al.*, 2010). In all three populations, fish up to 5 years old were also collected. Populations from central Europe, including a canal in central Poland (Przybylski & García-Berthou, 2004) and oxbow lakes in the Elbe floodplain in the Czech Republic (Holčík, 1961), had a comparably longer life span than that of the study population from the River Kyjovka, with 1 and 2 year-old fish dominating. This suggests that the short life span of *R. amarus* in the River Kyjovka is likely to be extrinsic. This is also supported by the age of fish kept in experimental populations (devoid of competition and predation) within the Czech Academy of Science's Institute of Vertebrate Biology in Brno, which were derived from the River Kyjovka populations. These populations contain fish up to 4 years old, with minimal postspawning mortality (M. Reichard, pers. obs.). Sexual dimorphism in L_S was low and seasonal dynamics in L_S frequency distribution were not consistent with a strong size-related mortality in either sex (Fig. 2).

The female-biased sex ratio observed throughout the season was not expected. Smith *et al.* (2000) identified equal sex ratios during electrofishing surveys conducted before the onset of the reproductive season in isolated oxbows within the floodplains of the Rivers Morava, Dyje and Kyjovka. An overall dominance of females in the population, with an increase in female bias later in the reproductive period, was also reported by Tarkan *et al.* (2005), while Koutrakis *et al.* (2003) observed a male-biased sex ratio in the River Rihios, Greece. In the present study, the sex ratio bias increased during the reproductive period, with a rapid decline in the relative proportion of males coinciding with a decrease in overall abundance (Fig. 1). This may have been caused by differences in habitat use among territorial males and females during the reproductive season, which might conceivably have affected their catchability. Territorial males defend territories and are more evenly dispersed throughout the habitat, whereas females swim in large shoals while foraging and visiting male territories (Schaumburg, 1989; Smith *et al.*, 2004). The female shoals, however, also include an abundance of non-territorial males (Reichard *et al.*, 2004) with cryptic colouration (Reichard *et al.*, 2005). In this study, both territorial and non-territorial males were recorded during electrofishing, suggesting that sampling

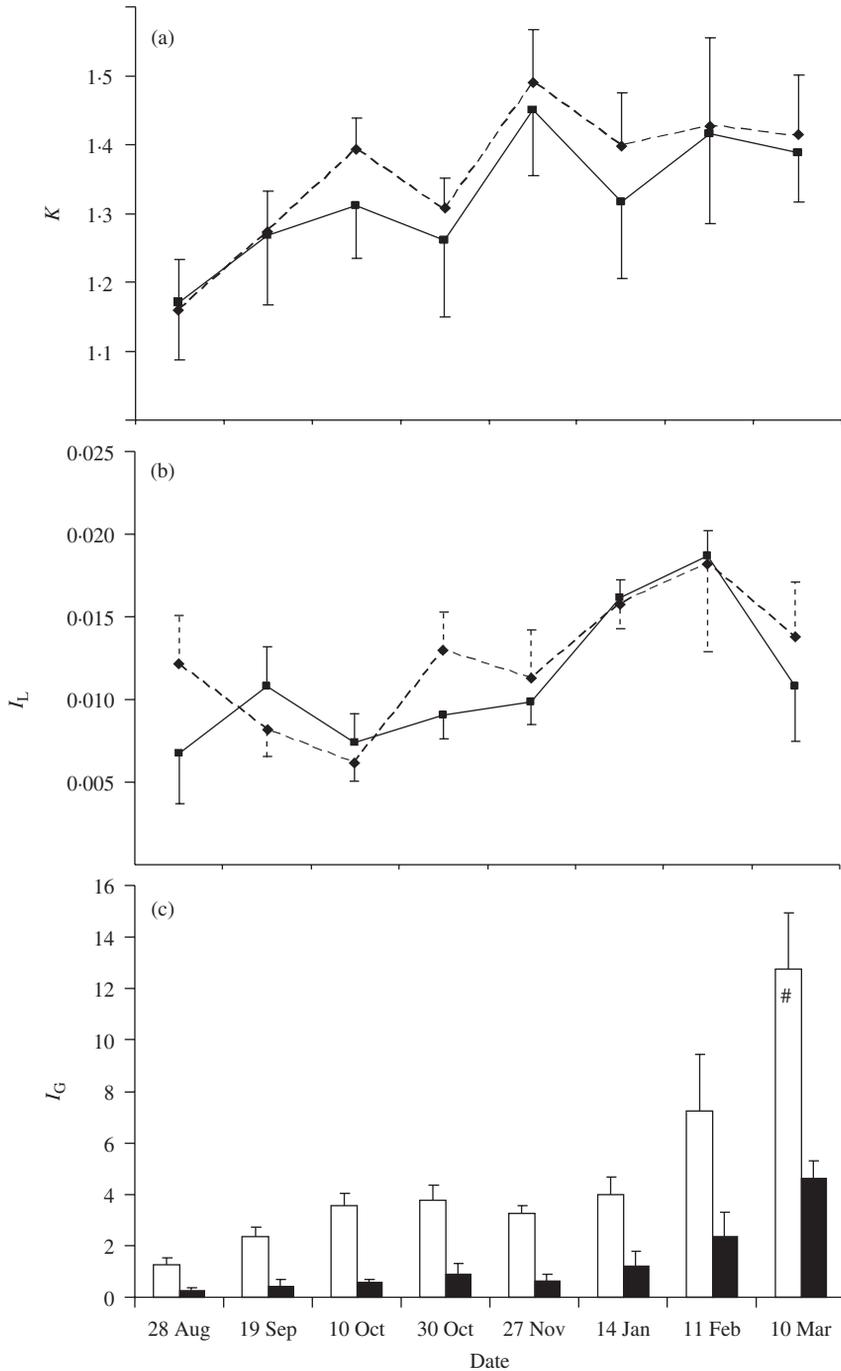


FIG. 5. Seasonal dynamics of mean + S.E. (a) Fulton's condition factor (K) (—■—, males; -◆-, females), (b) relative lipid content (I_L) (—■—, males; -◆-, females) and (c) gonado-somatic index (I_G) (■, males; □, females) for 0+ year *Rhodeus amarus* from the River Kyjovka at Tyneec. #, presence of ripe eggs in ovaries.

was effective in capturing territorial males. This is corroborated by the finding of Oshiumi & Kitamura (2009) who reported a female-biased sex ratio in the southern red tabira bitterling *Acheilognathus tabira jordani* Arai, Fujikawa & Nagata using a mark–recapture method, which is inherently robust to sampling biases.

It is suggested that the female-biased sex ratio could have been caused by higher mortality of males. Both territorial and non-territorial male *R. amarus* compete aggressively for mating opportunities (Reichard *et al.*, 2004), which is likely to be costly (Haller *et al.*, 1996; Candolin & Reynolds, 2002; Vollestad & Quinn, 2003), and higher testosterone levels in males at this time compromise immunity (Saino *et al.*, 1995; Casto *et al.*, 2001). In contrast, females spend most time feeding (Reichard *et al.*, 2004). Male somatic condition was lower than that of the females from the beginning of May until the end of the reproductive season, though the difference in male and female somatic condition disappeared when gonad mass was subtracted from fish mass. No sex-specific mortality has been observed in captivity (Reichard *et al.*, 2008, 2009a; Konečná *et al.*, 2010) and, hence, it is possible that male mortality arose from a higher predation risk to males (McKellar *et al.*, 2009; Reichard *et al.*, 2009b).

REPRODUCTIVE CYCLE

Three indicators of spawning activity (presence of females with extended ovipositor, I_G and presence of mature eggs in ovaries) were assessed, all indicating that the main reproductive season ceased sharply in mid-June. Rinchar & Kestemont (1996) state that, in multiple-spawning fishes such as *R. amarus*, I_G is a less than reliable indicator of fish ovarian maturity; only histological analysis (proportion of females with ripe eggs in their ovaries) provided precise results. In the present study, however, both I_G and histological analysis identified the same peak (24 April) and end (between 13 and 27 June) of the reproductive season (Fig. 4). The end of the reproductive season was further defined by an absence of females with extended ovipositors.

Rhodeus amarus is widely distributed throughout Europe (excluding the Scandinavian, Iberian and Apennine peninsulas), Asia Minor and the Caspian region, with a high potential for geographic variability in reproductive characteristics. Indeed, a population from the River Rihios, Greece, is characterized by a later start to the reproductive season and a later peak in I_G , occurring in May and June, coupled with consistently lower I_G in both sexes (Koutrakis *et al.*, 2003). This agrees with the findings of Rinchar & Kestemont (1996) that populations of multiple-spawning fish with an extended spawning period have lower I_G than populations with a shorter spawning period. The fact that the more southerly population has a later peak of reproductive season may be counterintuitive but it agrees with the hydrological regime experienced by the two populations. In the lowland River Kyjovka, water temperatures increase rapidly during March and may reach a spawning threshold value in April, while the River Rihios is affected by snow melt-water from the adjacent mountains, resulting in a slower increase in water temperature. A similar experience with a later onset of reproductive activity for populations in Asia Minor (Lake Sapanca and streams close to the Ömerli Reservoir in Western Anatolia, Turkey) has been reported (Ö. Gaygusuz, unpubl. data).

SOMATIC CONDITION

In fishes, skeletal muscle and the liver are major locations of lipid storage, with considerable species differences. In 'lean' fishes, such as gadoids, large amounts of lipid are stored in the liver, whereas for most other species the skeletal muscle represents the major lipid depot (Weatherley & Gill, 1987). *Rhodeus amarus* displayed a seasonal pattern in relative lipid content in muscle, with a decrease in lipid content over the reproductive season in adult fish [Fig. 3(b)] and an increase in 0+ year fish up to February [Fig. 5(a)]. There was a clear association between relative lipid content and reproduction, with a decline in lipids as the gonads of 0+ year fish matured. In adult fish, the lipid content remained low following the end of reproduction (July and August) and no differences were observed in relative lipid content between males and females. In other fish species, energetic reserves are accumulated in summer during and after the breeding season and serve mainly for survival over winter (Adams, 1999; Pangle & Sutton, 2004; Booth & Keast, 2006). Although no exact data exist on allocation of lipid stores in *R. amarus* metabolism, the fact that lipids were not depleted during winter [Fig. 5(a)] strongly suggests that they play an important role in production of the first eggs of the reproductive season and serve as an energy resource for reproductive behaviour and ovarian growth (Reznick & Braun, 1987; Meffe & Snelson, 1993; Schultz & Conover, 1997; Schultz, 1999). An increase in lipid content before spawning, followed by a sharp decrease, was also observed in the Asian rosy bitterling *Rhodeus ocellatus* (Kner) (Solomon *et al.*, 1984). The extended spawning season of *R. ocellatus* (from April until September) is the most likely reason for differences in summer lipid content between the two species, though a significant decrease in lipid content after the end of the spawning season is obvious in both species. Schultz (1999) hypothesized that this decrease could cause fish mortality following spawning, which is consistent with the data observed in this study.

In conclusion, the *R. amarus* population from the River Kyjovka has an annual character. Adult mortality was most severe at the end of the reproductive season. Seasonal dynamics in somatic condition, relative lipid content and gonad investment strongly suggest that the study population allocated a disproportionately high level of resources into reproduction. The sex ratio was female-biased and there was an indication of male-biased mortality later in the reproductive season.

This study was supported by Czech Science Foundation (206/09/1163) and the Leverhulme Trust. All experimental procedures were approved by the ethical committees of the Institute of Vertebrate Biology (Czech Academy of Sciences) and Ministry of Agriculture and are in accordance with Czech legal requirements. This study would have been impossible without the generous help of our many colleagues and friends in the field. The authors thank R. J. Wootton and two anonymous referees for valuable comments on this manuscript.

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