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The Annual Reproductive Cycle of Rudd, *Scardinius erythrophthalmus* (Cyprinidae) from the Lower Oder River and Lake Dąbie, (NW Poland)

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Original article

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The rudd is a common freshwater species of the European ichthyofauna, however, this species' sexual cycle has not yet been described based on the histological analysis of its gonads. The aim of this study was to analyze the annual gonad development cycle of rudd from the watercourses of north-western Poland. Adult individuals aged 2+ to 13+, of both sexes were caught in the Oder River and Lake Dąbie. A standard paraffin technique and six-stage scales were used to assess the development of gonad maturity in both sexes. Rudd gonads developed similarly in the Oder River and Lake Dąbie. Eggs were deposited in batches from the beginning of May to the half of June. Females deposited at least two batches of eggs. In the majority of females collected from these sites, the gonads developed asynchronously throughout the year. Rudd males attained reproductive readiness in the same period as the females, but retained gametes in their gonads for a month longer than the females. Rudd avoid locations with warmer water discharged from power plants.

Key words: rudd, fish, reproductive cycle, post-cooling water, spermatogenesis, oogenesis.

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Rudd, *Scardinius erythrophthalmus* is medium-sized freshwater cyprinid fish occurring commonly in Europe (GARCÍA-BERTHOU & MORENO-AMICH 2000; FROESE & PAULY 2019). The rudd is a strictly litoral species occurring in still-water, slow-flowing rivers, and lakes with a heavily overgrown, muddy bottom (HOLCIK 1967; KENNEDY & FITZMAURICE 1974; GARCÍA-BERTHOU & MORENO-AMICH 2000). They are fairly hardy and can survive up to 15-17 years in water of poor quality (KENNEDY & FITZMAURICE 1974; NURMINEN *et al*. 2003; TARKAN *et al*. 2010).

Previous studies on rudd described their growth (ZIVKOV *et al*. 2003; TARKAN *et al*. 2010), feeding (PREJS 1984; GARCÍA-BERTHOU & MORENO-AMICH 2000; LAKE *et al*. 2002; NURMINEN *et al*. 2003), morphometrics (BOZNAK 2008), fertility (PAPAGEORGIOU & NEOPHYTOU 1982; TARKAN 2006), and population structure (BLACKWELL *et al*. 2009). The spawning period of rudd is strictly related to accessibility to sunlight and temperature (ZIVKOV *et al*. 2003). When spawning, rudd select standing waters and adhere their eggs to plants. Spawning commences in the spring when water temperatures rise above 16°-18°C (NIKOLSKY 1963; MCDOWALL 1990). The lowest water temperature at which spawning started was 10°C, recorded by PAPAGEORGIOU and NEOPHYTOU (1982), and among the highest was 23.5°C observed by TARKAN (2006). The spawning season of rudd lasts from 1 to 3 months depending on the distribution region. The onset of spawning occurs later in more northern regions than in the southern limits of their distribution area which is related to water temperature (TARKAN 2006).

Usually, the spawning period of rudd is determined by their breeding, the macroscopic appearance of ovaries, changes of the gonadosomatic index, oocyte diameter frequency distribution, and by larval occurrence (VILA-GISPERT & MORENO-AMICH 2000; TARKAN 2006; PATIMAR *et al*. 2010). The sexual cycle of the species has not yet been studied with the use of histological techniques and the microscopic analysis of the gonads except in artificially bred individuals (KOPIEJEWSKA *et al*. 2004a). The gonads of rudd hybrids with other cyprinid fish formed under controlled reproduction were studied in detail (GOODWIN *et al*. 1994; KOPIEJEWSKA *et al*. 2004b). The aim of this study was to analyze the annual gonad development cycle of rudd from the watercourses of north-western Poland.

Material and Methods

Study areas and fish sampling

Adult male and female rudd (*Scardinius erythrophthalmus* L., 1758) (Actinopterygii, Cypriniformes, Cyprinidae) from the populations inhabiting the lower section of the Oder River (1) including Międzyodrze, upstream of Gryfino (NW Poland (53°11′N,14°29′E) to 20 km above the Dolna Odra power plant, and (2) Lake Dąbie, 20 km below the Dolna Odra power plant, and the southern part of the flow-through of the lake were investigated. The characteristics of these habitats are presented in DOMAGAŁA *et al*. (2015a). Attempts to catch rudd in the canal thermally polluted by post-cooling water 200 m down from the "Dolna Odra" power plant (53°11′N, 14°29′E) were conducted as well. The habitat is warmer by 6-8°C than the neighboring Oder River. The post-cooling water canal is open and fish can freely move between the canal and the Oder River, however, the species apparently avoids this canal. In total, only 18 females and 7 males were collected during all the months of a calendar year at this site.

The fish were caught as bycatch of commercial fishing using gillnet between September 2009 and August 2010, from one to four times a month at each site. Altogether, 469 females and 148 males were caught in the natural waters (Table 1). Fish age was determined as 2+ through 13+ based on the analysis of rings on the collected scales following the method of TARKAN *et al*. (2006). The total length (TL) and standard length (SL) of each fish specimen were measured to the nearest 1 mm and each fish was weighed on an electronic scale to the nearest 0.1 g. Then, the gonads were dissected, fixed in Bouin fluid, and weighed to the nearest 0.1 mg. Two parameters were calculated: the Fulton condition factor (K) and the gonadosomatic index (GSI) using the respective formulas:

$$K = 100W_g \cdot TL^{-3} \quad \text{and} \quad GSI = 100W_g \cdot W_b^{-1}$$

where: TL is the total length of fish (cm), W_g is the gonad weight (g), and W_b is the total fish weight (g).

Histological analysis of gonads

All gonads were included in the histological analysis to determine the stage of gonadal development (Table 1). For the analysis, fragments 0.5 cm in diameter were excised from the middle part of the gonad. Standard paraffin technique and Heidenhain's iron hematoxylin or hematoxylin and eosin stains were used. Histological slides of 5 µm in thickness were made. Between 50 and 100 slides were made from each female gonad, and 25 from each male. The specimens were evaluated under a Nikon Eclipse 80i microscope with a maximum magnification of 1000×. A histological analysis of the ovaries was performed using a modified 6-stage scale proposed by SAKUN and BUCKAÂ (1963) and modified by DOMAGAŁA *et al*. (2013). Measurements of oocyte diameter in up to 20 selected preparations per substage of development per month were made following the method developed by DOMAGAŁA *et al*. (2015b).

The sexual cycle of males was described using a modified 6-stage scale proposed by SAKUN and BUCKAÂ (1963) and modified by DOMAGAŁA *et al*. (2015b). The division into early and late substages of the stages II (II_E and II_L) and III (III_E and III_L) was introduced, as well as the overlapping of the gonadal cycles designated as substage VI-II.

Statistical analysis

The nonparametric Mann-Whitney U test or Kruskal-Wallis test was used to compare the following characteristics of the fish between the investigated sites or month comparison in a calendar year: TL, SL, fish weight, K, GSI, and size of oocytes at different

Table 1

Number of individuals of rudd, *Scardinius erythrophthalmus*, used in the study

Sampling site	sex	Number of fish per month												Total
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Oder River	♀	16	22	25	50	46	37	28	11	23	20	20	12	315
	♂	6	5	6	8	18	5	8	6	5	5	7	8	87
Dąbie Lake	♀	7	12	18	17	19	16	8	13	15	18	6	5	154
	♂	2	1	5	8	14	5	5	8	6	7	1	2	61

Table 2

Characteristics of the examined rudd, *Scardinius erythrophthalmus*, from two sites in the lower Oder River section

Sex	Site	n	Total length (cm)		Standard length (cm)		Fish weight (g)		Fulton condition factor	
			Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Female	Oder	315	23.71±6.13[a]	10.9-34.5	20.65±4.48[a]	9.2-34.5	238.87±184.60[a]	12.7-691.8	1.42±0.23[a]	0.95-1.88
	Dąbie	154	23.53±4.38[a]	12.6-34.4	20.46±4.02[a]	13.5-35.7	213.03±127.21[a]	20.5-545.3	1.44±0.18[a]	1.08-1.80
Male	Oder	87	17.59±4.70[b]	10.1-30.0	14.52±3.86[b]	8.4-25.4	85.71±83.96[b]	11.6-398.4	1.25±0.18[b]	0.85-1.69
	Dąbie	61	17.89±5.44[b]	9.9-29.2	14.75±4.50[b]	7.7-23.8	105.38±91.30[b]	14.4-398.4	1.39±0.19[ab]	1.03-1.79

Oder = Oder River, Dąbie = Lake Dąbie, SD = standard deviation; Values marked with different superscript letters show significant differences between the features ($p<0.05$, ANOVA Kruskal-Wallis test).

Table 3

The GSI value changes of rudd females, *Scardinius erythrophthalmus,* in different stages of gonad maturity in April - June, mean ± SD and range

Location \ Stage	Before spawning	After first portion spawn	After last portion spawn
Oder River	10.74±3.30[a] 5.79-18.39	7.85±1.83[a] 3.93-9.88	5.35±1.03[b] 3.10-6.42
Dąbie Lake	12.29±3.14[a] 8.08-14.39	6.34±1.74[a] 4.16-8.08	2.55±0.26[a] 2.30-2.95

Values marked with different superscript letters show significant differences between the features in two sites ($p<0.05$, Mann-Whitney U test).

stages. Due to only a slight deviation of data from a normal distribution, the mean and standard deviation of the data are given in the article. The significance of differences in the number of females and males was tested using the chi-square test. All analyses were performed at a significance level of 0.05 using the Statistica v.12 software (StatSoft, Inc.).

Results

Principal somatic parameters of the fish

The fish caught were aged between 2+ to 13+. The number of sampled rudd males collected from the lower Oder River and Lake Dąbie was significantly lower than that of females ($p<0.05$). In some months, only a single male individual would be caught (Table 1). The mean standard length (SL) of females was 20.5 ± 4.4 cm, groups of 4-7 year-old females being predominant. Males were smaller, with a mean length of 14.6 ± 4.5 cm, with male individuals aged 3-4 being most numerous.

The standard length, weight, and condition factor of the females from the Oder River and Lake Dąbie did not differ significantly ($p>0.05$). These factors did not show statistically significant differences between the samples of males caught in the two sites either ($p>0.05$). However, the length, weight, and condition factor of the studied rudd from the Oder River and Lake Dąbie differed significantly between sexes ($p<0.05$). The body length and weight of the females caught at individual sites were significantly higher than those of the males collected at the same sites ($p<0.05$). The condition factor of the females caught at individual sites was significantly higher than that of the males collected in the Oder River ($p<0.05$) but similar to the males caught in Lake Dąbie ($p>0.05$) (Table 2).

Variation of GSI

F e m a l e s: During the year, the gonadosomatic index fluctuated along with the sexual cycle. The GSI of females reached maximum in May (Fig. 1A). The GSI of females in advanced vitellogenesis (stage IV), just before spawning from April to June ranges from 4.6 to 17.4 (mean 10.51). The GSI after the deposition of batches of eggs was presented in Table 3. The occurrence of gonads in various stages of development and egg depletion caused a large spread of SD

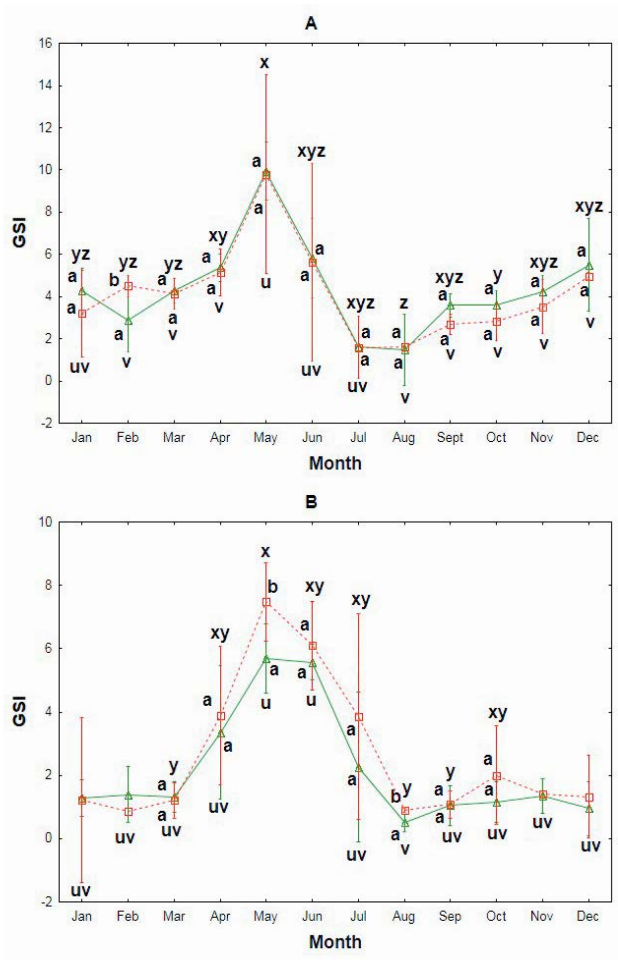

Fig. 1. Monthly distribution of the Gonadosomatic Index (GSI) of rudd, *Scardinius erythrophthalmus*; Females (A) and males (B) from the study areas: Δ Oder River; ☐ Lake Dąbie (mean ± SD). Values marked with different letters (a, b) show significant differences between sites in individual months ($p<0.05$; Mann-Whitney U test); Values marked with different letters (u,v – Oder River; x,y,z – Lake Dąbie) show significant differences in GSI between months of the calendar year ($p<0.05$; ANOVA Kruskal-Wallis test). Due to the low number of males caught in Lake Dąbie from November to February, the statistic was not performed for those months.

during the spawning period. The GSI significantly decreased after spawning ($p<0.05$) and in the winter months was 1.16 ± 0.62 and 1.59 ± 0.91 in the Oder River and Lake Dąbie, respectively (Fig. 1A).

M a l e s: The mean GSI in individuals finalizing their spermatogenesis in May (stages III_L to IV) ranged from 3.1 to 13.9 (mean 6.43) (Fig. 1B). The occurrence of gonads in various stages of development and the amount of ejaculated sperm caused a large range in SD during spawning and post spawning periods. A great reduction in the values of this parameter was reported in August. In that month mean GSI was 0.50 ± 0.24 and 0.86 ± 0.09 (stage I and II) in the Oder River and Lake Dąbie, respectively. From August to March, GSI remained at a similar level (Fig. 1B).

Reproductive cycle of females

T h e O d e r R i v e r a n d L a k e D ą b i e: The dynamic of the sexual cycle of the ovary in the Oder River and Lake Dąbie was similar. In January and February, females possessed gonads with numerous oocytes in moderately advanced vitellogenesis, with a low amount of yolk and oocytes at previtellogenesis. The development of gonads was asynchronous. In March, all females from the Oder River had gonads at stage IV in advanced vitellogenesis. Single females collected from this habitat had gonads with few oocytes in advanced vitellogenesis, occupying 50% of the surface of a gonad section, while the rest was occupied by small oocytes in previtellogenesis (stage II) (Fig. 2A).

The gonads of the females from Lake Dąbie caught in March were more variable. Their oocytes differed in size and in advancement of vitellogenesis (stage III and IV). In both sites, singular degenerating oocytes were observed in females caught in March (Fig. 2B). In April, gonad images were highly diverse. Females collected at the beginning of April had gonads with oocytes at different vitellogenesis progress stages (stage III and IV) as well as singular degenerating oocytes. A part of the individuals from Lake Dąbie had gonads developing asynchronously (oocytes prior to spawning occupied 20% of the gonad section, remaining oocytes in vitellogenesis 30%, and oocytes in previtellogenesis 50%). At the end of April, the majority of females possessed gonads filled with oocytes in advanced vitellogenesis. At the beginning of May, the majority of females from both sites began laying their first batch of eggs. Oocytes in early vitellogenesis could be also found in the section of the gonads, which perhaps would not mature in the given season as well as oocytes in previtellogenesis of the next generation. In the second half of May, all females can be divided into two groups. The first group had gonads filled with oocytes in advanced vitellogenesis at stage IV ready for spawning, the second was also filled with oocytes in advanced vitellogenesis, but with post-ovulatory follicles, left from the first batch of eggs deposited (Fig. 2C). Moreover, in mid-May, a female measuring 9.2 cm SL was collected with gonads characterized by advanced vitellogenesis (stage III) with single degenerating cells at this stage. The oocytes of that female would probably not mature in that season. In the first week of June, 20% of the females from the Oder River were still preparing for spawning while the remaining 80% had post-spawning gonads or partially emptied gonads with numerous oocytes directly prior to the deposition of their second batch of eggs as well as a low number of cases left after deposited oocytes. At the end of June, the gonads of females from Lake Dąbie, and in July, those from the Oder River started to rebuild (stage II previtellogenesis), but they still contained numerous oocytes that were degenerating and had not been laid (Fig. 2D). In August, apart

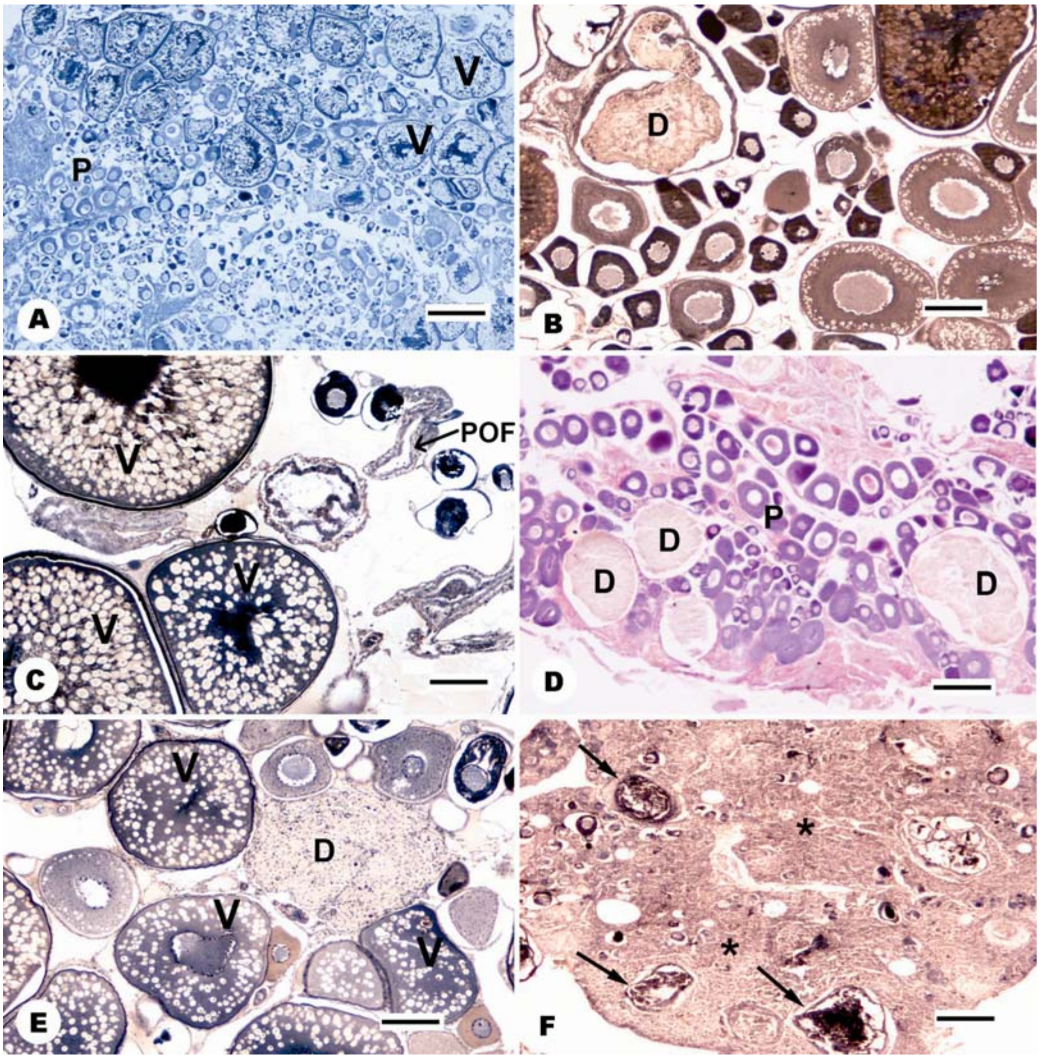

Fig. 2. Female rudd gonad, *Scardinius erythrophthalmus*; A: a gonad with oocytes in previtellogenesis (P) and vitellogenesis (V), March, bar = 500 µm; B: with numerous degenerated oocytes (D), the end of March, bar = 200 µm; C: with oocytes in advanced vitellogenesis (V), post-ovulatory follicles (POF) and the oocytes at the beginning of the next generation of previtellogenesis, May, bar = 200 µm; D: after spawning with oocytes in early previtellogenesis (P) and degenerated oocytes (D), July, bar = 100 µm; E: with oocytes in advanced vitellogenesis (V) and with numerous degenerated oocytes (D), October, bar = 200 µm; F: with few oocytes (arrows) and a large amount of connective tissue (stars), October, bar = 200 µm.

from the gonads that were at stage II, the first oocytes in the onset of vitellogenesis appeared (stage III, Fig. 3A) with degenerating oocytes occupying up to 90% of the surface of gonad section from the Oder River and 25% of those from Lake Dąbie. The majority of females from Lake Dąbie in August had gonads with oocytes commencing vitellogenesis (stage III), and in some individuals, yolks appeared in the oocytes.

The first oocytes with yolks in females from the Oder River appeared in September, and singular degenerating oocytes were observed. In all females from Lake Dąbie from September and from the Oder River from October to December, the gonads remained at stage III, they developed asynchronously with vitellogenic oocytes with varying amounts of yolk oocytes in previtellogenesis and with oocytes degenerating after spawning (Fig. 2E). In October, a female was caught in the Oder River with abnormal, degenerated gonads with a large amount of connective tissue and a low number of oocytes (Fig. 2F).

The majority of the gonads collected from rudd throughout the year had asynchronously developing gonads, typically with oocytes at various vitellogenesis stages. Analysis of both gonads in over a dozen females caught between March and April from both localities indicated that gonads develop unevenly. The differences concerned the manner in which oocytes were distributed in the gonad as well as the different stages in which each gonad was observed (one

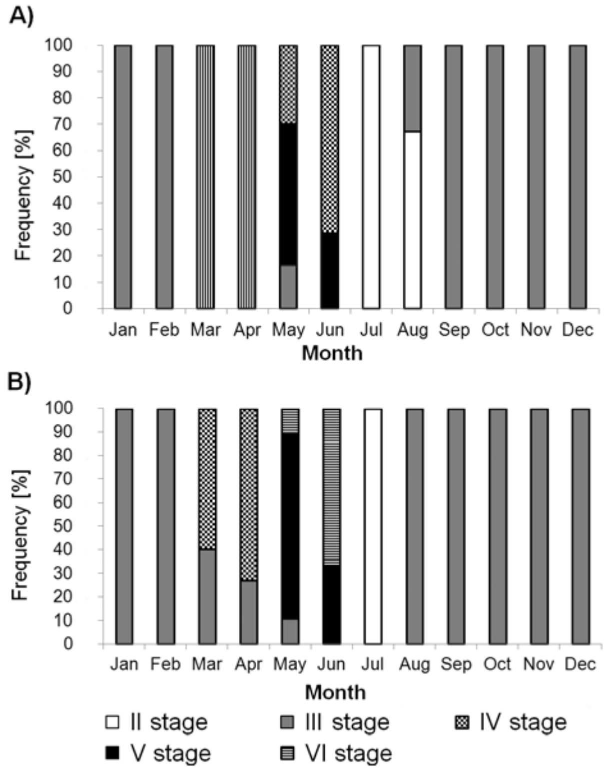

Fig. 3. Percentage contribution of the number of rudd, *Scardinius erythrophthalmus*, females with gonads in a particular stage of maturity in individual months of the calendar year from two aquatic environments: Oder River (A), Lake Dąbie (B).

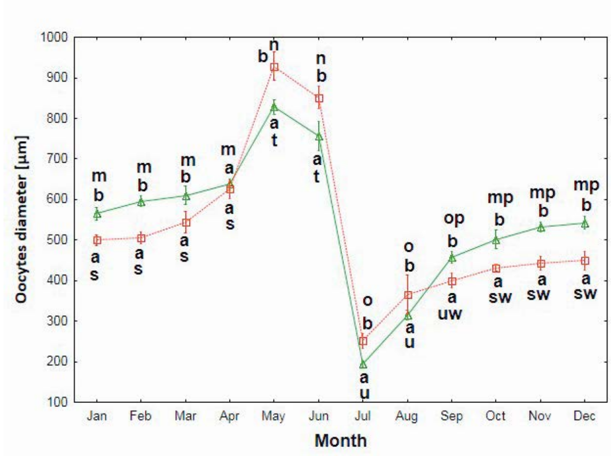

Fig. 4. Monthly distribution of the diameter of the most developed oocytes of rudd, *Scardinius erythrophthalmus*, from the study areas: Δ Oder River; ☐ Lake Dąbie (mean ± SD); values marked with different letters (a, b) show significant differences between sites in individual months ($p<0.05$; Mann-Whitney U test); Values marked with different letters (m,n,o,p – Oder River; s,t,u,w, – Lake Dąbie) show significant differences in GSI between months of the calendar year ($p<0.05$; ANOVA Kruskal-Wallis test); .

gonad in advanced vitellogenesis – stage IV, the second spawning gonad – stage V).

Based on the present study, we can determine that the rudd collected from both localities spawned from the beginning of May till the second decade of June. Detailed percentages of females with gonads at each maturity stage during the calendar year are shown in Fig. 3AB.

O o c y t e s i z e: At the completion of previtellogenesis and the finalizing point of vitellogenesis the oocytes of rudd from Lake Dąbie were larger and differed significantly from the dimensions of oocytes of rudd from the Oder River (Mann Whitney U – test, $p<0.05$) (Table 4).

Changes in oocyte size within the calendar year are presented in Fig. 4.

Reproductive cycle of males

O d e r R i v e r a n d L a k e D ą b i e. The dynamic of the sexual cycle of male testes in the Oder River and Lake Dąbie was similar to that in female ovaries. In August, the month in which the lowest GSI was recorded, male gonads were at stage I or II (substages II_E and II_L). At developmental stage I, the testicular tubules contained only spermatogonia type A (Fig. 5A). In the gonads of males at stage II, cysts with type B spermatogonia were formed with varying degrees of spermatogonia proliferation. From September to March, the gonads of all males were at late substage II_L (Fig. 5B). In the following months, from autumn to spring, the number of B type spermatogonia in the cysts gradually increased as a result of mitosis. In April, the germ cells commenced meiosis (substage III_E) and in the second half of April, the first spermatozoa were formed (substage III_L) (Fig. 5C). The majority of males attained stage IV of maturity at the beginning of May (Fig. 5D). In June, the majority of males remained at stage IV, whereas few individuals reached stage V with non-proliferating cells (Fig. 5E). Some males retained gametes in the gonads up to mid-July, whereas the remaining individuals had post-spawning gonads with a new cycle beginning: stages VI-II (Fig. 5F) or in early stage II_E.

The ratio between males with gonads in individual maturity stages caught in the Oder River and in Lake Dąbie differed to a minor degree from April to August. Detailed percentages of males with gonads at each maturity stage during the calendar year are shown in Fig. 6AB.

Table 4

Oocyte size at different stages of vitellogenesis in rudd, *Scardinius erythrophthalmus,* from two sites in the lower Oder River

Stage	Sampling site			
	Oder River		Lake Dąbie	
	Mean ± SD	Range	Mean ± SD	Range
Previtellogenesis	230.58±16.61[b]	205.11-258.07	205.73±23.95[a]	163.51-249.17
Vacuolisation	292.85±22.75[b]	255.81-329.86	270.32±20.76[a]	226.02-291.45
Yolk	601.82±57.10[a]	522.17-699.74	582.35±42.68[a]	509.87-697.04
Vitellogenesis	1008.13±40.42[a]	899.93-1160.26	1039.77±85.72[a]	897.75-1327.16

Stages: Vacuolisation = beginning of vacuolisation, Yolk = first occurrence of yolks, Vitellogenesis = vitellogenesis completed; Values marked with different superscript letters show significant differences between the features in two sities ($p<0.05$, Mann-Whitney U test).

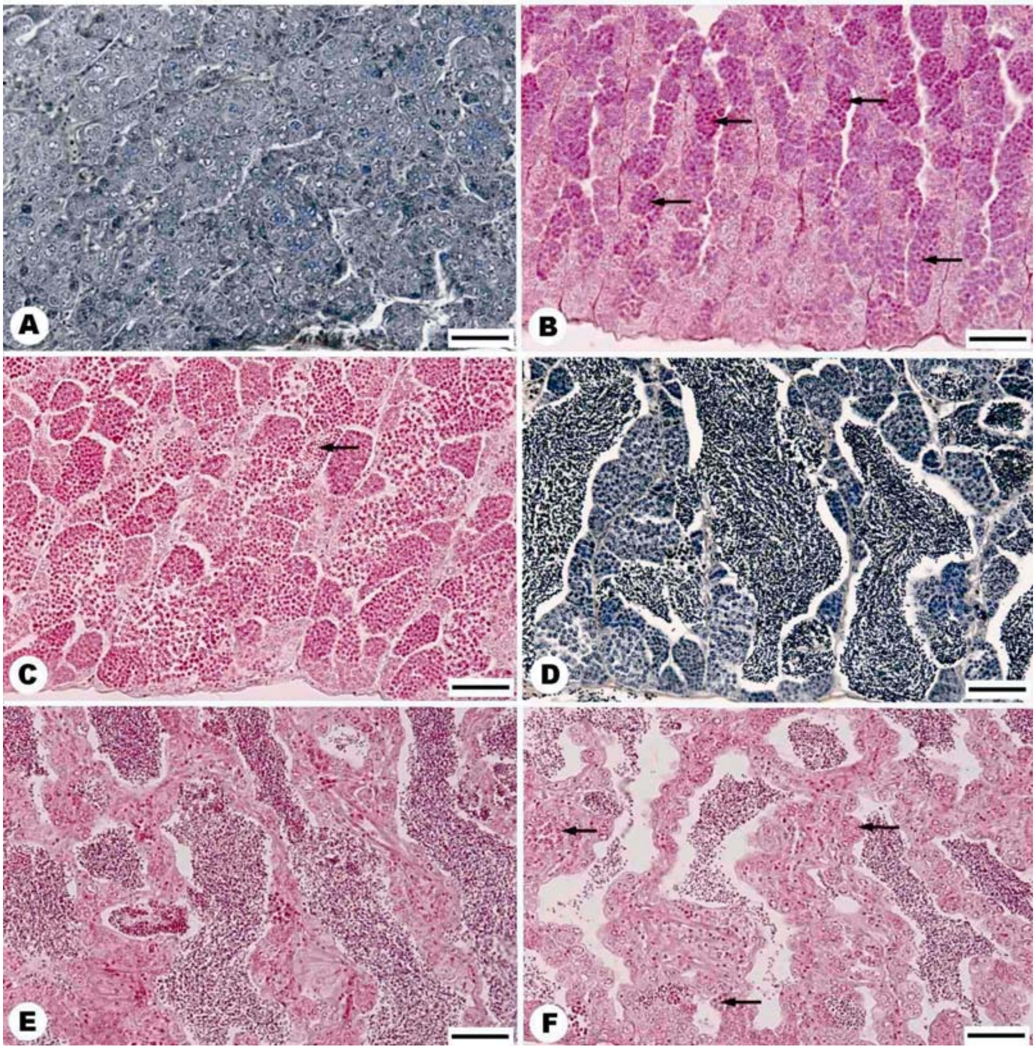

Fig. 5. Male rudd gonad, *Scardinius erythrophthalmus*; A: a rudd male gonad at stage I of maturation, by the tubule wall spermatogonia A occurred, August; B: a gonad in late stage II, the tubules contain numerous cysts with multiplying spermatogonia B (arrow), March; C: a gonad at late stage III, all types of spermatogenic cells are visible in the gonad; first spermatozoa are seen in the tubule (arrow), April; D: spawning stage IV, the tubule lumen is filled with spermatozoa, by the tubule wall there are numerous cysts with maturing cells, May; E: spawning stage V, the gonad with finalized spermatogenesis, tubules filled with spermatozoa, the tubule wall contains only the resting type of spermatogonia A, June; F: a spent gonad at stage VI-II; shrunken tubules filled with unexpelled spermatozoa; the tubule wall contains type A spermatogonia and cysts with type B spermatogonia (arrow), July. Bar = 50 µm in all images.

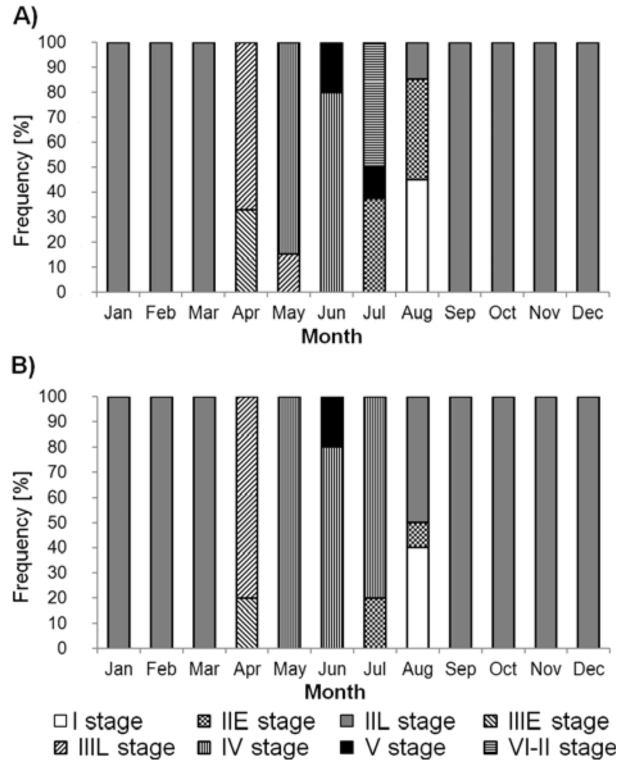

Fig. 6. Percentage contribution of the number of rudd, *Scardinius erythrophthalmus*, males with gonads in a particular stage of maturity in individual months of the calendar year from two aquatic environments: Oder River (A), Lake Dąbie (B).

Discussion

The life span of rudd collected from the Oder River and Lake Dąbie (13+) is similar to that of populations from some water bodies (14+) while shorter (19+) or longer (6-7+) compared to others (PAPAGEORGIOU & NEOPHYTOU 1982; ZIVKOV *et al*. 2003; FROESE & PAULY 2020). The length of rudd from Oder river section was larger than that of individuals of corresponding age groups from Lake Kastoria (Greece) but lower than that of the rudd inhabiting the strongly eutrophic Ovcharitsa Reservoir (cooling-reservoir, Bulgaria) (PAPAGEORGIOU & NEOPHYTOU 1982; ZIVKOV *et al*. 2003). Females were predominant in the studied population. The female-to-male ratio was 3.6:1 in the Oder River and 2.5:1 in Lake Dąbie. Similarly, female predominance has been observed in other cyprinids collected in the area (DOMAGAŁA *et al*. 2015b). In Turkish rudd populations, males were predominant in the samples and the ratio of males to females was 1.2:1 (TARKAN 2006). In Iran there was no significant difference from parity in the overall sex ratio, while females were dominant in biggest size groups and males in younger ones (PATIMAR *et al*. 2010). In other cyprinid fish, equal proportions of the sexes or domination of female or males was recorded (ALTINDAĞ 2002; KOÇ *et al*. 2007; OKGERMAN *et al*. 2012; YILMAZ *et al*. 2012; VATANDOUST *et al*. 2014).

Sexual maturity in rudd is reached at a younger age in more southern and warmer climates than in the northern area of its distribution. In Turkey, males and females reach maturity in the first year of life. This is the earliest maturation reported for any rudd population (TARKAN 2006). In other areas, rudd females typically reach maturity a year later than males. In Italy, females mature in the second year while males mature in the first year of life (ZERUNIAN *et al*. 1986). In Greece, rudd spawn for the first time at the age of 3 and 2 while in Ireland and northeastern Russia at 4 and 3, respectively (PAPAGEORGIOU & NEOPHYTOU 1982; KENNEDY & FITZMAURICE 1974). In Lake Sapanca, Turkey, males reach maturity for the first time at a mean total length (TL) of 7.1 cm while females at 8.1 cm (TARKAN 2006). In the fish we examined, the smallest male was 12.8 cm (TL) and it was aged 2+ while the female was 14.0 cm (TL) aged 3+ (in SL, 10.1 and 11.8, respectively).

The rudd spawning period varies depending on the region. The reproductive period can last from 1 to 3 months. The onset of spawning is later in more northern regions. This is due to a lower temperature regime in higher latitudes (TARKAN 2006). Spawning takes place in spring when water temperatures rise above about 16°C (NIKOLSKY 1963), 17.5-23.5°C (TARKAN 2006) or 18°C (MCDOWALL 1990). The lowest temperature, 10°C, at which spawning commenced was recorded by PAPAGEORGIOU and NEOPHYTOU (1982) in Greece and 11°C in northeastern Russia as observed by BOZNAK (2008). In Lake Kastoria, Greece, spawning occurs in the second half of April (PAPAGEORGIOU & NEOPHYTOU 1982). In the Caspian Sea (Iran), the fish spawn from mid-April to late May, with peak spawning in mid-May (PATIMAR *et al*. 2010). The spawning season in Turkey occurs from early May to late June after the spawning of roaches (TARKAN 2006). In Lake Banyoles in Spain, rudd spawns in May (VILA-GISPERT & MORENO-AMICH 2000). Irish rudd spawn mainly from late May to early July (KENNEDY & FITZMAURICE 1974). In northeastern Russia, spawning occurs from the beginning of June until mid-July (BOZNAK 2008). In the water bodies investigated in the present study, rudd spawned at 17-20ºC. First, females from the lower section of the Oder River deposited their first batch of eggs at the beginning of May and their second batch at the end of May and the beginning of June. Thus, we can say that Polish rudd lay at least two batches of eggs. Females ready to spawn were also observed in the second week of June. However, it remains unknown whether that was another batch, or if another group of females spawned at a later term and this was a second batch of eggs. The gonads of a majority of rudd females developed asynchronously, and in some individuals they developed atypically with hypertrophied connective tissue and numerous degenerating oocytes in the winter and spring gonads, which has not been observed for other cyprinids such as white bream (KOPIEJEWSKA & KOZŁOWSKI 2007; DOMAGAŁA *et al*. 2015b) and common bream (DOMAGAŁA *et al*. 2015a). Gonads with hypertrophied connective tissue were found in the whitefish of Lake Thun, where gonad anomalies are common in this species (BERNET *et al*. 2004) as well as in the hybrid of salmon and brown trout (KIRCZUK & DOMAGAŁA 2011). A similar image of asynchronously developing gonads with oocytes in previtellogenesis and at different stages of vitellogenesis was observed in rudd from artificial breeding (KOPIEJEWSKA *et al*. 2004a) and in white bream (KOPIEJEWSKA & KOZŁOWSKI 2007).

The annual development cycle of rudd from the Oder River and Lake Dąbie was similar. Spawning took place from the beginning of May to the second decade of June. Other cyprinids, such as the white bream from those locations spawn at the beginning of May to the end of June (DOMAGAŁA *et al*. 2015b), common bream from the end of April till mid-June (DOMAGAŁA *et al*. 2015a), blue bream in the Oder River spawn throughout April and in Lake Dąbie in April and May (DOMAGAŁA *et al*. 2016). In autumn and winter, the gonads of rudd females from the Oder River and from Lake Dąbie remained at stage III, similarly to those of common bream (DOMAGAŁA *et al*. 2015a). In this period, the gonads of a majority of female white and blue bream were already at stage IV (DOMAGAŁA *et al*. 2015b, 2016).

In the analyzed rudd population, the ratio of oocytes in previtellogenesis to oocytes in vitellogenesis was up to 50 to 50% of the gonad section (in the majority 30 to 70%) and in bream x rudd hybrids 23-36% (oocytes at the cortical alveoli of trophoplasmatic growth) and 64-77% (oocytes in the mature stage) (KOPIEJEWSKA *et al*. 2004b). The distribution of oocytes in different portions of the ovary depends on the gonad development stage which has also been observed for the common roach (KOPIEJEWSKA 2003).

Rudd males collected from the lower section of the Oder River were ready to spawn at the beginning of May in the same period as the females. In other cyprinid species, males became ready for reproduction earlier than females. However, similarly to other cyprinid species, rudd males maintained the ability to spawn for a longer period than females (DOMAGAŁA *et al*. 2015b,c, 2016). The stages of spermatozoa were most likely not observed in artificially bred rudd because the gonads were sectioned over large intervals of time (KOPIEJEWSKA *et al*. 2004a). During winter, the male gonads of the studied rudd population were at stage II_L similarly to bream and white bream but different from the blue bream in which gonads attain stage IV during winter (DOMAGAŁA *et al*. 2015a,b,c, 2016). KOPIEJEWSKA *et al*. (2004a) observed stage III with spermatocytes from July to April in rudd bred at a stable temperature.

The gonadosomatic index fluctuated along with the sexual cycle. In rudd from the lower Oder River section, the mean GSI of spawning gonads reached 12.3 in females and 6.4 in males. GSI decreased to 1.2 and 0.5 in females and males respectively after spawning. The fluctuations of GSI in rudd from Lake Sapanca and in other cyprinids were similar (EPLER *et al*. 2005; TARKAN 2006; DOMAGAŁA *et al*. 2015b).

Rudd avoid warm water reservoirs but this species may threaten native fish species if introduced into natural watercourse. In numerous American and New Zealandian lakes (MARSDEN & HAUSER 2009; WU *et al*. 2013), rudd is an invasive species, highly fertile, and poses a threat to the aquatic macrophytes of local lakes. As observed by NURMINEN *et al*. (2003) in the Finish Hiidenvesii Lake, large numbers of rudd contribute to the increase of nutrients in the lake and their selective feeding on selected macrophytes may contribute to the increase of pleustophytic macrophytes. Furthermore, in North America, the discussed species hybridizes with golden shiner, threatening the genetic integrity of the native species (BURKHEAD & WILLIAMS 1991; GOODWIN *et al*. 1994). Natural hybridization of cyprinid fishes is also common within their natural range. The hybrid of rudd and bream is one of the most often recorded hybrids of the family (KENNEDY & FITZMAURICE 1973; BRASSINGTON & FERGUSON 1976; ECONOMIDIS & WHEELER 1989; WYATT *et al*. 2006). Also hybrids with roach, white bream, and bleak were found (GĄSOWSKA 1968; KENNEDY & FITZMAURICE 1973). In hybrids, numerous degenerations of sex cells are observed. Degenerations in bream x rudd hybrids included a larger portion of the gonad and concern primary oocytes as well as mature oocytes at the nucleus migration stage (GOODWIN *et al*. 1994; KOPIEJEWSKA & KOZŁOWSKI 2007). In bream x rudd hybrids the diameter of those oocytes was 275-315 μm during the early stage and 400-650 μm during the advanced stage (KOPIEJEWSKA 2003). These dimensions were similar to the dimensions of oocytes of the rudd population from the Oder River analyzed in the present study.

C o n c l u s i o n. Rudd from the natural watercourse of the lower Oder River spawn in May and June. Female spawning is divided into batches, extended over the period of six weeks. Females lay at least 2 batches of eggs. In the majority of females, gonads developed asynchronously. Males attained reproductive readiness in the same period as females and maintained the ability to spawn for a month longer.

Author Contributions

Research concept and design: J.D., L.K., K.D.; Collection and/or assembly of data: J.D., L.K., K.D.; Data analysis and interpretation: L.K., K.D., M.P.-R.; Writing the article: L.K., K.D.; Critical revision of the article: J.D., L.K., K.D., M.P.-R.; Final approval of article: J.D., L.K., K.D., M.P.-R.

Conflict of Interest

The authors declare no conflict of interest.

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