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VARIED SOMATIC GROWTH AND SEX CELL DEVELOPMENT IN RECIPROCAL HYBRIDS OF ROACH *RUTILUS RUTILUS* (L.) AND IDE *LEUCISCUS IDUS* (L.)

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ABSTRACT. Body length and weight and the developmental stage of sex cells were determined in 1.5- and 3-year-old specimens of the F₁ generation of reciprocal hybrids of roach *Rutilus rutilus* and ide *Leuciscus idus*. Body length and weight and the developmental stage of sex cell varied in reciprocal hybrids of roach and ide. The hybrids obtained from crossing *R. rutilus* females with *L. idus* males (*R. rutilus* × *L. idus*) were larger than those obtained from crossing *L. idus* females with *R. rutilus* males (*L. idus* × *R. rutilus*) ($P < 0.001$). At the ages of 1.5 and 3 years the hybrids had a similar body length and weight to *L. idus* ($P > 0.05$) and a greater body length and weight than *R. rutilus* ($P < 0.001$). The hybrids of *L. idus* × *R. rutilus* were smaller than *L. idus* and larger than *R. rutilus* ($P < 0.001$). Two-thirds of the studied *L. idus* × *R. rutilus* hybrid females were sexually mature at age 3, and only one *R. rutilus* × *L. idus* hybrid female exhibited signs of cytological maturation. In the control samples, roach females reached sexual maturity, while ide females were immature. The testes of 3-year-old *R. rutilus* × *L. idus* hybrid males contained spermatogonia and spermatocytes, while those of *L. idus* × *R. rutilus* hybrid males most often contained spermatocytes. The ovaries of female reciprocal hybrids of *R. rutilus* and *L. idus* contained not only developing oocytes, but also sex cells which stopped developing at an early stage of gametogenesis. These constituted approximately 50-60% of the area of ovary sections in 13% of the studied females, while in other females they were observed singly. The results obtained indicate that rapid somatic growth exhibited by *L. idus* is inherited by hybrids to a greater extent through *L. idus* males than through females. The differences in achieving sexual maturity exhibited by the females of reciprocal hybrids of *R. rutilus* and *L. idus* suggest that male genomes may have an important impact on this process.

Key words: ROACH (*RUTILUS RUTILUS*), IDE (*LEUCISCUS IDUS*), HYBRIDS, SOMATIC GROWTH, SEX CELL

INTRODUCTION

The principle aim of fish hybridization studies is to find increasingly better quality characters useful in commercial production (Makeeva and Sukhanova 1966, Makeeva 1972, Andryasheva 1973, Duthu and Kilgen 1975, Beck et al. 1980, Cherfas et al. 1981, 1994, Issa et al. 1986). One of the aims of hybridization is to decelerate or even stop sexual maturity. When hybrids with interesting quality characters are fertile, it is possible to obtain several types of hybrids, such as F₂, reciprocal hybrids and triple

hybrids and also to transfer a specific character from one species to another through successive back crossing. Hybridization is used to halt sexual maturation in intensive aquaculture where the most important factors are the coefficient of meatiness and meat quality, both of which depend largely on the fish not maturing (Chevassus 1983).

A relatively high number of natural hybridization combinations were confirmed in Cyprinidae (Hubbs 1955), although the development of sex cells was studied only in a small number of them (Stoumboudi et al. 1992, Fishelson et al. 1996, Stoumboudi and Abraham 1996). With the exception of being a potential source for commercial hybrids, natural fish hybridization can pose a danger to the maintenance of genetic purity in natural fish populations (Legendre et al. 1992). Of the Cyprinidae hybrids, that of roach and common bream was fertile (Wood and Jordan 1987, Yakovlev et al. 2000).

One of the natural Cyprinidae hybrids is that of roach, *Rutilus rutilus* (L.), and ide, *Leuciscus idus* (L.) (Holčík and Bastl 1973, Naiksatam 1976), both of which differ in body size and age at sexual maturity (Tadajewska 2000, Załachowski 2000). This paper analyses the somatic growth and sex cell development of roach and ide hybrids obtained through artificial hybridization.

MATERIAL AND METHODS

Artificial spawning of roach and ide was conducted at the Dgał Experimental Hatchery of the Inland Fisheries Institute in Olsztyn in May 1997. Reciprocal hybridization of the species and fertilization within species were conducted. The resulting hybrids were as follows: roach spawn fertilized with ide sperm (roach × ide); ide spawn fertilized with roach sperm (ide × roach). In hybrid onomastics, the first name refers to the female parental species and the second to the male. Control specimens were obtained by fertilizing roach spawn with roach sperm and ide spawn with ide sperm. The parental species (roach and ide) originated from natural populations inhabiting the lakes of northeastern Poland.

The larvae and then juvenile specimens obtained were reared from May to September at the Dgał Experimental Hatchery. Further cultivation was conducted in a closed recirculation system at the University of Warmia and Mazury in Olsztyn. The water temperature was regulated during the studies, and from November to April it was $10.9 \pm 2.85^\circ\text{C}$ and from May to September it was $17.2 \pm 1.27^\circ\text{C}$ (average \pm SD). The fish were fed trout feed (protein/fat – 54/18, 19.5 MJ kg^{-1}).

The body length (l.c.) of the studied fish was measured to the nearest 0.1 cm, and the body weight was determined to the nearest 0.1 g. The Mann-Whitney test was used to analyze the lengths and weights of roach, ide and the hybrids. The zero hypothesis, which states that the compared factors are the same, was verified using STATISTICA 6 PL software (license number AXXP1127977706AR).

The gonads of all the specimens collected for the study were subjected to histological examination (Table 1).

TABLE 1

Body length (l.c.) and body weight of roach, ide and their hybrids

Species, Hybrids	Sex	n	Body length range in cm	Body weight range in g
Age: 1.5 years old				
Roach	♀	7	5.9-7.1	2.7-4.8
	♂	3	6.3-6.5	3.6-3.7
	Total	10	5.9-7.1	2.7-4.8
Ide	♀	11	9.1-10.5	12.0-18.4
	♂	3	9.3-10.8	13.0-20.4
	Total	14	9.1-10.8	12.0-20.4
Roach × ide	♀	10	9.5-10.5	12.5-18.0
	♂	5	8.2-11.4	7.1-20.4
	Total	15	8.2-11.4	7.1-20.4
Ide × roach	♀	4	7.7-8.8	6.7-9.5
	♂	12	7.3-9.7	5.6-14.8
	Total	16	7.3-9.7	5.6-14.8
Age: 2.5 years old				
Roach	♀	12	8.0-10.8	6.5-20.0
Ide	♀	14	10.0-13.8	14.5-43.7
Age: 3 years old				
Roach × ide	♀	10	11.1-14.3	21.0-53.7
	♂	4	10.4-13.4	9.2-38.6
	Total	14	10.4-14.3	9.2-53.7
Ide × roach	♀	15	9.2-12.2	10.6-26.8
	♂	14	8.5-12.2	7.6-25.9
	Total	29	8.5-12.2	7.6-26.8

The gonads of roach, ide and the hybrids were collected in October 1998, those of roach and ide females were collected in October 1999 and those of the hybrids were collected again in April-May 2000. After the samples were collected in 2000, the cultivation of the hybrids was concluded. The gonads were preserved in Bouin's solution or buffered formaldehyde, dehydrated in increasing concentrations of alcohol, exposed to chloroform and submerged in paraffin. Sections of 5 or 10 µm thick were cut from the middle parts of both the right and left gonads. They were later dyed with

Delafield's hematoxylin and eosine (Zawistowski 1986). Photographs of the gonad cross sections were taken using an Olympus digital camera. Oocyte diameter was measured to the nearest 0.005 mm with an MMI – 2 microscope. Gonad maturity degree was determined using the gonad maturity scale proposed by Sakun and Butskaya (1968).

RESULTS

DIVERSITY OF BODY SIZES

The differences in the body length and weight of the studied roach and ide specimens were statistically significant ($P < 0.001$). Roach specimens were, on average, shorter and lighter than ide specimens in both age groups (Fig. 1, Table 1). Similar differences were also confirmed with the hybrids ($P < 0.001$); roach \times ide hybrids were longer and heavier than ide \times roach hybrids. Roach \times ide hybrids were statistically the

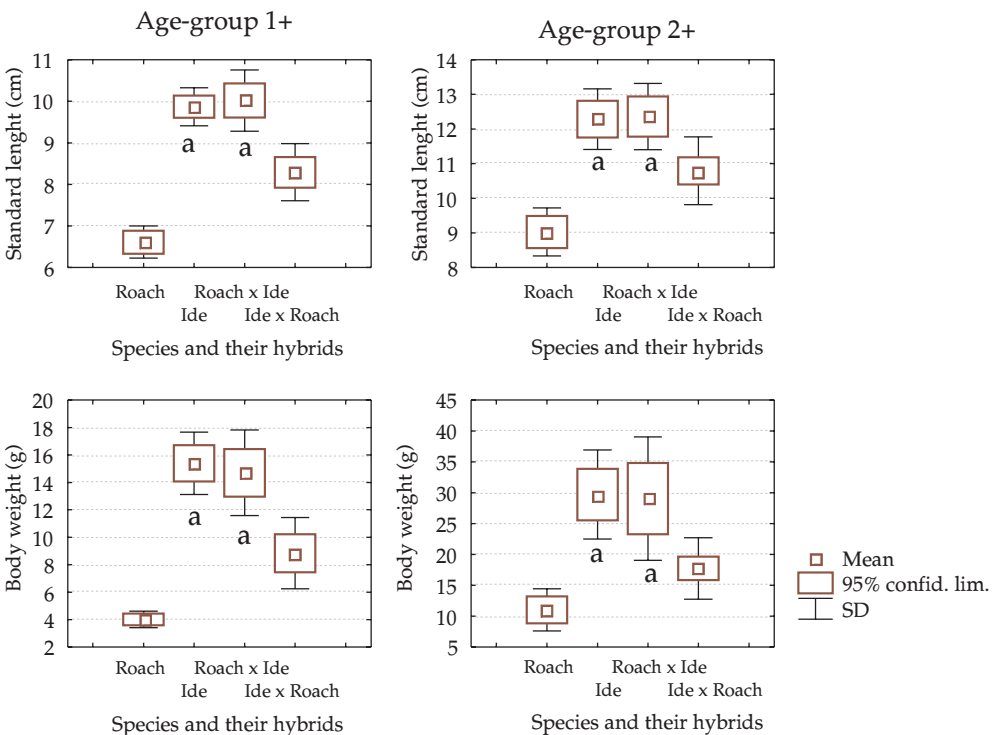


Fig. 1. Body length and weight of roach, ide and their hybrids; index a indicates that the average values were the same statistically ($P > 0.05$)

same as ide, both in terms of body length and weight ($P > 0.05$), which made them larger than roach specimens. The average body lengths and weights of ide \times roach hybrids were statistically smaller than those of ide and the roach \times ide hybrids and greater than for roach ($P < 0.001$).

SEX CELL DEVELOPMENT

Two gonad types were observed in the reciprocal hybrids of roach and ide; either there were typically built testicles or ovaries, in which there were properly developing female sex cells and sex cells whose development had stopped in early gametogenesis (Photo 1A, B). Sex cells with halted development were observed among 87% of females in either single or several small aggregations. In other females, they occupied approximately 50 – 60% of the area of the gonad cross section.

At an age of 1.5, the oocytes of reciprocal hybrids were in the previtellogenesis stage (II stage of ovary maturity, Photo 1A, B). The oldest previtellogenesis oocyte generations in reciprocal hybrids had, similarly to roach and ide, a homogeneous cytoplasm and a nucleoli near the nuclei membrane. The diameters of these oocytes varied from 125 to 195 μm for female roach \times ide hybrids, from 110 to 160 μm for female ide \times roach hybrids, from 150 to 195 μm for roach females and from 95 to 135 μm for ide females. The testes of roach and ide reciprocal hybrids of the same age were more diverse. The majority of hybrids from both groups contained spermatogonia and spermatocytes (II stage of maturity), and in the others – only spermatogonia (I stage of maturity, Photo 1C, D). The testicles of ide males contained aggregations of spermatogonia (I stage), while those of roach contained spermatogonia and spermatocytes (II stage).

In terms of oocyte development, the ovaries of 3-year-old fish were similarly diverse between hybrids, roach and ide specimens. The ovaries of a majority of female roach \times ide hybrids (with body lengths of 11.1 to 13.0 cm and weights from 21.0 to 35.7 g) and one-third of the studied ide \times roach hybrid females (with body lengths from 9.2 to 11.0 cm and weights from 10.6 to 19.5 g) were in maturity stage II. The ovaries of the rest of the ide \times roach hybrids (with body lengths from 10.3 to 12.2 cm and weights of 16.4 to 26.8 g) were in maturity stages III and IV. However, the ovaries of roach \times ide female hybrids (with a body length of 14.3 cm and weight of 53.7 g) were in maturity stage III. In the control samples in October, the ovaries of ide females were in maturity stage II when the specimens had body lengths from 10.0 to 13.8 cm

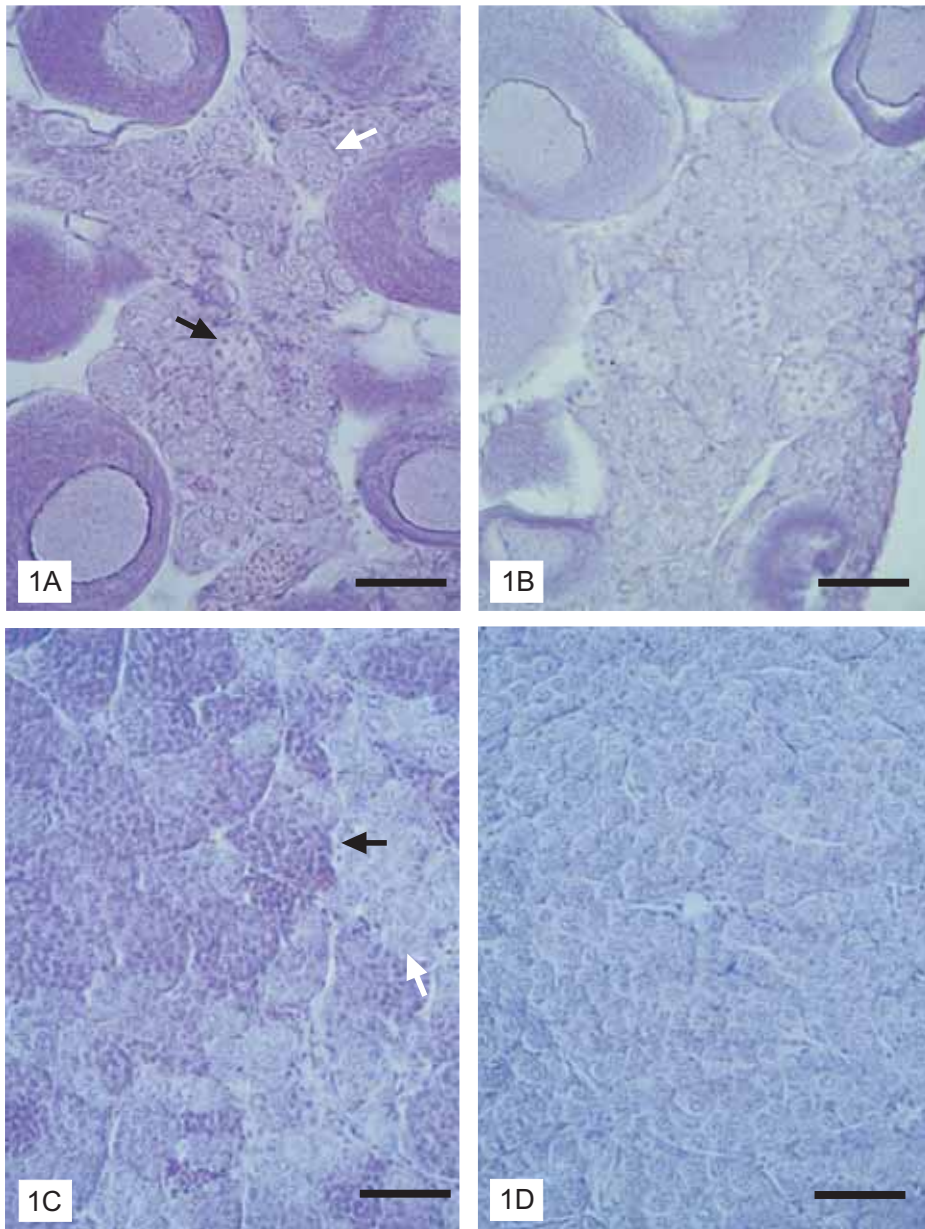


Photo 1. Cross sections of gonads of 1.5-year-old roach and ide reciprocal hybrids. (A) ovaries of a *R. rutilus* × *L. idus* hybrid in maturity stage II with halted sex cells development (white arrow - gonia, black arrow - degenerating cells), (B) ovaries of a *L. idus* × *R. rutilus* hybrid in maturity stage II with halted sex cell development, (C) testes of an *L. idus* × *R. rutilus* hybrid in maturity stage II with spermatozoa (white arrow) and spermatocytes (black arrow), (D) testes of an *R. rutilus* × *L. idus* hybrid in maturity stage I with spermatozoa. Scale = 50 μ m.

and weighed from 14.5 to 43.7 g, with the exception of one female (12.5 cm and 30.9 g) whose ovaries were in maturity stage III. Roach ovaries were in maturity stage III in specimens with body lengths from 8.0 to 10.8 cm and weights from 6.5 to 20.0 g.

In both groups of hybrids some females whose ovaries were in maturity stage II were observed to have single oocytes in which vacuolization had begun. In both groups, roach \times ide and ide \times roach, vacuolization started from the oocyte cell membrane. In the control roach, vacuolization started from the oocyte cell membrane, while in the control ide the first vacuole appeared in the central strip of cytoplasm. The diameters of oocytes with a single vacuole ring were 210 – 320 μm for roach \times ide hybrids, 215 – 330 μm for ide \times roach hybrids, 220 – 280 μm for ide and 255 μm for roach.

Of the females with ovaries in maturity stage III, three specimens of the ide \times roach hybrid, in addition to the previtellogenic oocytes, also had several oocytes in the final stage of vitellogenesis. The ovaries of one female from the roach \times ide group contained innumerable oocytes in the previtellogenic and vacuolization stages. In this female 60% of the area of the ovary cross section was occupied by sex cells whose development had stopped (Photo 2A).

In ovaries of ide \times roach hybrids in maturity stage IV, there were oocytes in the migrating nucleus stage (Photo 2B) and oocytes which lacked the morphological nucleus structure. The diameters of ide \times roach female hybrid oocytes ranged from 745 to 1325 μm .

At the age of three, the testes of reciprocal hybrid males were in maturity stage II (Photo 2C, D). The testes of roach \times ide hybrid males contained spermatogonia and spermatocytes, while the majority of those of ide \times roach hybrid males contained spermatocytes.

DISCUSSION

Chevassus (1983) reported that the growth of hybrids is usually the average growth for the parental species. The results obtained in the current study indicate that the reciprocal hybrids of roach and ide varied in growth. The growth of *R. rutilus* \times *L. idus* hybrids was similar to that of ide, while *L. idus* \times *R. rutilus* hybrids exhibited the average growth of roach and ide. The growth of ide was faster than that of roach, and this difference was statistically significant. The conclusion can be drawn that *R. rutilus*

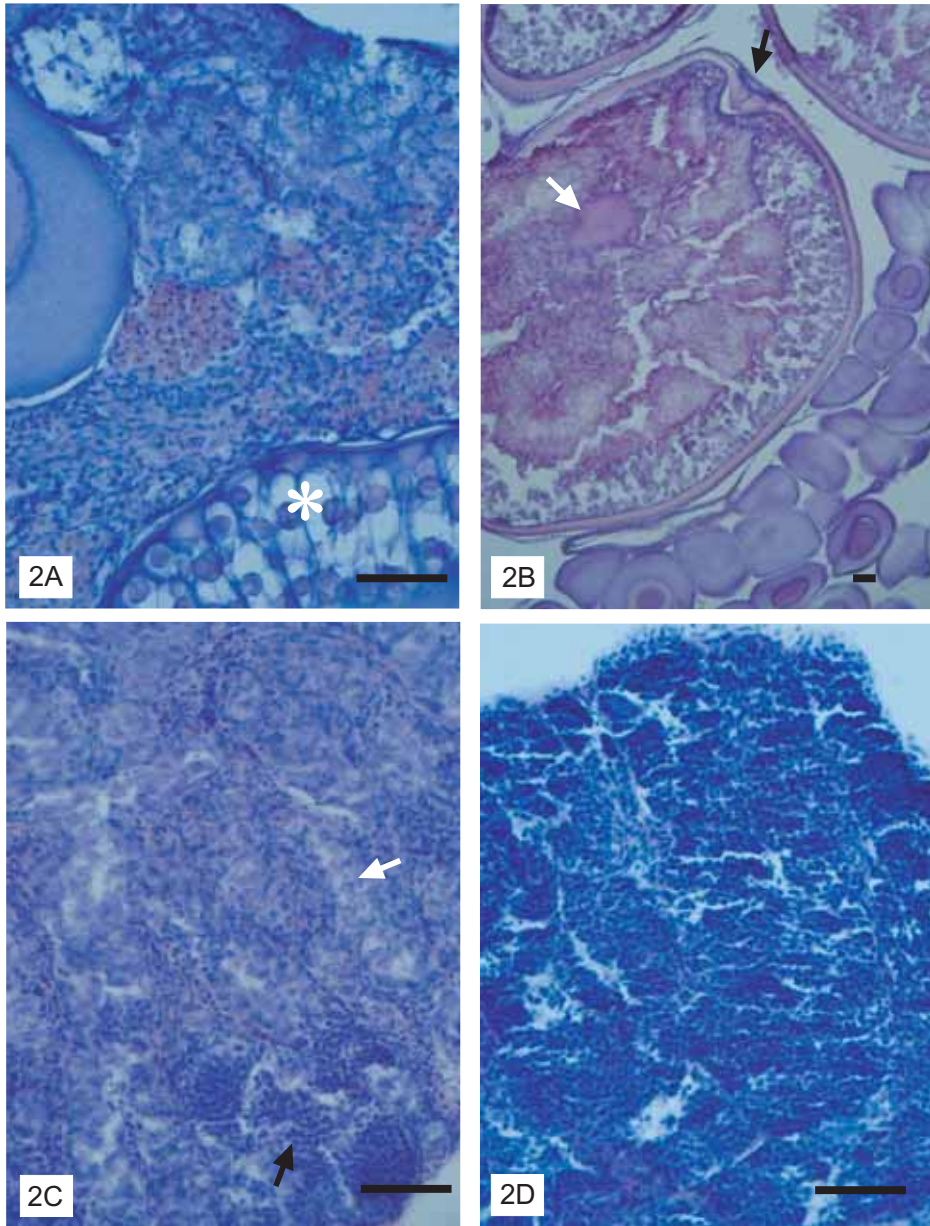


Photo 2. Cross sections of gonads from 3-year-old roach and ide reciprocal hybrids. (A) ovaries of a *Rutilus rutilus* × *Labeo idus* hybrid in maturity stage III with halted sex cells development (star – vitellogenic oocyte), (B) ovaries of a *Labeo idus* × *Rutilus rutilus* hybrid in maturity stage IV (black arrow - micropyle, white arrow – nucleus), (C) testes of a *Rutilus rutilus* × *Labeo idus* hybrid in maturity stage II with spermatogonia (white arrow) and spermatocytes (black arrow), (D) testes of a *Labeo idus* × *Rutilus rutilus* hybrid in maturity stage II with spermatocytes. Scale = 50 μm.

× *L. idus* hybrids inherited the growth characteristic for ide from the ide male to a greater extent than *L. idus* × *R. rutilus* hybrids from the ide female. One specimen in the *R. rutilus* × *L. idus* group had a body length which exceeded the upper size limit of ide; this may indicate the phenomenon of heterosis. This phenomenon was observed in an experiment with hybrids of *Clarias gariepinus* and *Heterobranchus longifilis*, in which the growth rate was similar to the faster growing *H. longifilis*. Hybrids of *H. longifilis* females and *C. gariepinus* males exhibited faster growth than *H. longifilis* (Legendre et al. 1992).

The degree of sex cells development in the roach and ide reciprocal hybrids in this study also varied. Sex cells of *R. rutilus* × *L. idus* hybrids were less developed than those of *L. idus* × *R. rutilus* hybrids, and the sex cells of ide were less developed than those of roach. Among the 3-year-old *R. rutilus* × *L. idus* hybrids, cytological symptoms of sexual maturity (oocyte vacuolization) were observed only in one female, which had by far the largest body size of the hybrids in this group, while among the *L. idus* × *R. rutilus* hybrids, sexual maturity was achieved by two-thirds of the studied females. In the control samples, the roach females were mature but the ide females were still immature. Under natural conditions roach usually matures at the age of 3, while ide does so at the age of 3 - 5 years (Tadajewska 2000, Załachowski 2000). The body size and sexual maturity of the hybrid females and the female parental species indicate that, with regard to the achievement of sexual maturity, the hybrids are similar to the parent species in the male line. It can also be assumed that the achievement of sexual maturity by hybrid females (as well as the parental species) may be influenced by male genomes. In reciprocal hybrids of *C. gariepinus* and *H. longifilis*, the parental species of which matured at different ages, the first female sexual maturity occurred at a later age (Legendre et al. 1992). A relation between sex and growth rate was confirmed for *C. gariepinus*, one of the parental species of these hybrids (Henken et al. 1987). This relation was not observed in *C. gariepinus* and *H. longifilis* hybrids (Legendre et al. 1992).

The halted development of a portion of the sex cells and the further development of other sex cells in the gonads, which was observed in the hybrids in the current study, has also been reported in other fish hybrids (Legendre et al. 1992, Fishelson et al. 1996). Among these sex cells, those of the opposite sex from the one that was developing (Fishelson et al. 1996) or of the same sex were observed (Legendre et al. 1992). The testes of the studied roach and ide hybrids did not contain oocytes. Sex cells

whose development had stopped were observed only in the ovaries of females of roach and ide hybrids. The results of the studies do not allow for the sex of the sex cells whose development had been halted to be determined because this process occurred at an early stage of gametogenesis.

In summary, the results of the studies indicate that the reciprocal roach and ide hybrids varied in size and in the stage of sex cell maturity. Sex cells of the faster growing hybrids of *R. rutilus* females and of *L. idus* males developed more slowly, and the females were not sexually mature at the age of 3 years. The majority of the females of the slower growing hybrids of *L. idus* females and *R. rutilus* males reached sexual maturity at the age of 3 years. The differences in achieving sexual maturity among female hybrids indicate that male genomes may influence female sexual maturity. The presence of sex cells whose development had stopped in early gametogenesis varied in the ovaries of females of roach and ide hybrids.

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STRESZCZENIE

ZRÓŻNICOWANIE WZROSTU SOMATYCZNEGO ORAZ ROZWÓJ KOMÓREK PŁCIOWYCH U OBUSTRONNYCH MIESZAŃCÓW MIĘDZYRODZAJOWYCH PŁOCI *RUTILUS RUTILUS* (L.) I JAZIA *LEUCISCUS IDUS* (L.)

Określono długość (l.c.) i masę ciała oraz stadia rozwoju komórek płciowych u 1,5- i 3- letnich osobników pokolenia F₁ obustronnych mieszańców płoci *Rutilus rutilus* (L.) i jazia *Leuciscus idus* (L.) (tab. 1). Mieszańce uzyskane ze skrzyżowania samic *R. rutilus* i samców *L. idus* (*R. rutilus* × *L. idus*) były istotnie statystycznie większe, niż mieszańce uzyskane ze skrzyżowania samic *L. idus* i samców *R. rutilus* (*L. idus* × *R. rutilus*), (P < 0,001, rys.1). W wieku 1,5 i 3 lat miały zbliżoną długość i masę ciała do *L. idus* (P > 0,05) i większą długość i masę ciała od *R. rutilus* (P < 0,001). Mieszańce *L. idus* × *R. rutilus* okazały się mniejsze od *L. idus*, a większe od *R. rutilus* (P < 0,001).

W jajnikach samic mieszańców płoci i jazia, oprócz rozwijających się oocytów, występowały komórki płciowe, których rozwój zatrzymał się we wczesnej gametogenezie (fot. 1A, B). U 13% badanych samic zajmowały one około 50 - 60% powierzchni przekroju jajników, u pozostałych samic występowały w pojedynczych skupieniach. W wieku 1,5 roku - jajniki samic mieszańców były w II stadium dojrzałości, a jądra samców w I - II stadium dojrzałości (fot. 1A-D). Dojrzałość płciową w wieku trzech lat osiągnęło dwie trzecie badanych samic mieszańców *L. idus* × *R. rutilus*, a cechy cytologicznego dojrzewania wykazywała tylko

jedna samica mieszańców *R. rutilus* × *L. idus* (fot. 2A, B). Jądra trzyletnich samców były w II stadium dojrzałości (fot. 2C, D).

Otrzymane wyniki wskazują, że wzrost somatyczny charakterystyczny dla jазia jest w większym stopniu dziedziczony przez hybrydy poprzez samce jазia, aniżeli samice tego gatunku. Różnice w osiągnięciu dojrzałości płciowej przez samice obustronnych mieszańców płoci i jазia sugerują, że w osiągnięciu dojrzałości płciowej samic mogą mieć znaczenie genomy samców.

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