A reserve of the oocytes of protoplasmatic growth in the ovaries of bream (Abramis brama L.) females in Lake Śniardwy

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A reserve of the oocytes of protoplasmatic growth was estimated in the ovaries of 47 bream females from Lake Śniardwy. This reserve ranged from 78.9 to 96.6% of the oocytes. It exceeded 4 to 28 times the absolute fecundity of females during the reproductive season.

INTRODUCTION

Individual fecundity of the females is established in many fish species during the period of indifferent gonad development and in course of sex differentiation (Persov 1975). Protoplasmatic growth of the oocytes takes place since the completion of sex differentiation till sexual maturity of the females. The reserve of sex cells in the ovaries is made up in course of the reproduction, after spawning, thanks to mitotic divisions of the oogonia. Sex cell resources in the ovaries and their dynamics are not fully known as yet. Proportions of sex cells were assessed in some fish species in order to define developmental stage of the ova (Menič 1953, Messtorff 1959, Gotting 1961, Yamamoto...
This paper presents the results of studies on the reserve of the oocytes in the ovaries of bream females. Studies were made on a bream population characterized by an average fecundity (Kopiejewska 1987), inhabiting a lake with natural environmental conditions.

**MATERIALS AND METHODS**

Materials were collected in 1978–1980, from commercial catches of the State Fish Farm Giżycko, Mikołajki Branch. 58 females of body length 24.9–40.8 cm and individual weight 350–1520 g were collected. Their age was from five to ten years. Scraps of ovaries were obtained with the paraffin method and stained with Delafield's haematoxylin and eosine. Stages of oocyte development were described according to Majen (1927), after Brylińska and Długosz (1970), and according to Kuznecov (1975) after Andreeva (1983). Reserve of the oocytes of protoplasmatic growth was presented in per cents, taking the whole number of the oocytes of proto- and trophoplasmatic growth in a scrap as 100%. While counting the oocytes, only those were taken into account the sectioning of which ran through the cell nucleus. Reserve of the oocytes of protoplasmatic growth was determined for 47 females for which two groups of the oocytes could have been distinguished: those for the nearest spawning and the reserve.

**RESULTS**

Annual cycle of ovary maturation.

Bream females in Lake Śniardwy commence spawning in May-June. Female ovaries after spawning contained follicles, oocytes of protoplasmatic growth and, sporadically, oocytes with a single row of vacuoles. Oocytes of protoplasmatic growth (phase B according to Mejen 1927, phase I–VII according to Kuznecova 1975 after Andreeva (1983) were characterized by dark-staining cytoplasm, a circular nucleus with peripheral nucleoli. The nucleus changed its position in the cell, from a decentric to central one. Diameter of these oocytes ranged from 0.02 mm to 0.23 mm. Oocytes with a single row of vacuoles close to the cell membrane (phase C according to Mejen 1927) were characterized by visible follicle membrane. Post-spawning ovaries of bream females in Lake Śniardwy were defined as being in stage VI–II of maturation according to the scale of Sakun and Buckaja (1968). In June, July and August, oocytes with various degree of vacuolization were present in the ovaries — phase C and D according to Mejen (1927) as well as oocytes of protoplasmatic growth (phot. 1). Vacuolization progressed from the cell membrane toward the nucleus. Phot. 1 presents the oocytes with a single ring of vacuoles close to the cell membrane (phase C) and the oocytes of bigger diameter and
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Phot. 1. Part of ovary section; ovary in stage III of sexual development. Female caught on 13 July, 1978.

Phot. 2. Part of ovary section; ovary in stage IV of sexual development. Female caught on 25 May; 1979.
broader ring of the vacuoles (phase D). Nucleus in these cells is centrally located. Oocytes filled with yolk and fat (phase E according to Mejen 1927) were present in the ovaries since September till May, together with the oocytes of protoplasmatic growth (phot. 2). Since June till May the ovaries were in the III and later IV stage of maturation according to Sakun and Buckaja (1968). Nuclei filled with yolk moved in the oocytes of trophoplasmatic growth toward the cell micropyle just prior to spawning (phot. 3). The ovaries contained also the oocytes of protoplasmatic growth. According to Sakun and Buckaja (1968) this was stage IV–V of maturation. Similarly as in other fish species, stage V of the ovaries of bream females in Lake Śniardwy was very short. At this moment, successive stages of ovum division and ovulation took place in the oocytes ready for spawning. However, it was not possible to observe this process in the collected materials.

Two periods could have been distinguished in the annual maturation cycle of an oocyte generation designated for the nearest spawning (Fig. 1): the final period of protoplasmatic growth since May-June after spawning till September, and the period of trophoplasmatic growth since June till May next year. Vacuolization of the oocyte generation of the next spawning commenced in June and lasted for a few months – till September. Gradually, this process took place in the oocytes of consecutive generations, in which the protoplasmatic growth had ended. Oocytes in phase C, in which
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Table 1 presents percentage of the oocytes of protoplasmatic (B) and trophoplasmatic (DE) growth in female ovaries together with individual features of these females. Reserve of the oocytes of protoplasmatic growth ranged from 78.9 to 96.6%.

Bream females in Lake Śniardwy attain sexual maturity at the age of six, seven years (Szostak and Gajewski 1964). One 5-years old female was found in the materials, the ovaries of which contained oocytes of trophoplasmatic growth, and one 7-years old female which was immature (phot. 4). Hence, it may be concluded that 6 and 7-years old females spawned for the first or second time in their life. Reserve of the oocytes in these

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Fig. 1. Growth, phases of the oocytes of next spawning in the annual cycle of bream ovary development.

cacuolization commenced, were observed in bream ovaries till mid-September. No oocytes in this phase were observed in the ovaries in October and in the next months, until spawning. Hence, number of cells in the ovaries was determined by the end of September, and this number may be spawned in spring if conditions for the reproduction are favourable.

Reserve of the oocytes of protoplasmatic growth in the ovaries.

The oocytes of a few females contained oocytes in the vacuolization phase after spawning. These oocytes were resorbed and the ovaries passed into II stage of development.
Percentage of the oocytes of proto- and trophoplasmatic growth in the ovaries of bream females from Lake Śniardwy

| Age | n | Body length (l.c.) (cm) | Body weight (Wo) (g) | Gonad weight (Ow) (g) | Oocytes of protoplasmatic growth (B) (%) | Oocytes of trophoplasmatic growth (DE) (%) |
|-----|---|------------------------|----------------------|-----------------------|------------------------------------------|------------------------------------------|
| 5+  | 1 | 26.9                    | 400                  | 28.2                  | 87.4                                     | 12.6                                     |
|     |   | 29.3                    | 580                  | 8.1                   | 95.9                                     | 4.1                                      |
|     |   | 30.6                    | 620                  | 0.10                  | 96.4                                     | 3.6                                      |
|     |   | 29.0                    | 490                  | 15.0                  | 95.4                                     | 4.6                                      |
|     |   | 31.9                    | 680                  | 34.9                  | 94.9                                     | 5.0                                      |
|     |   | 30.2                    | 510                  | 40.5                  | 94.8                                     | 5.1                                      |
|     |   | 29.6                    | 520                  | 54.5                  | 92.8                                     | 7.2                                      |
|     |   | 29.8                    | 520                  | 61.0                  | 89.2                                     | 10.8                                     |
|     |   | 30.5                    | 715                  | 65.2                  | 82.8                                     | 17.1                                     |
|     |   | 27.7                    | 400                  | 68.4                  | 85.6                                     | 14.4                                     |
|     |   | 31.1                    | 650                  | 11.7                  | 95.5                                     | 4.5                                      |
|     |   | 32.2                    | 740                  | 13.9                  | 95.2                                     | 4.8                                      |
|     |   | 32.9                    | 800                  | 15.6                  | 87.5                                     | 12.5                                     |
|     |   | 32.4                    | 680                  | 17.9                  | 95.1                                     | 4.9                                      |
|     |   | 33.9                    | 825                  | 20.1                  | 91.9                                     | 8.1                                      |
|     |   | 33.6                    | 790                  | 21.0                  | 96.3                                     | 3.7                                      |
|     |   | 31.9                    | 650                  | 22.5                  | 93.9                                     | 6.1                                      |
|     |   | 31.6                    | 645                  | 25.0                  | 95.7                                     | 4.3                                      |
|     |   | 36.5                    | 1030                 | 25.2                  | 96.6                                     | 3.4                                      |
| 6+  | 9 | 33.7                    | 770                  | 28.2                  | 94.9                                     | 5.0                                      |
|     |   | 28.5                    | 460                  | 31.0                  | 87.1                                     | 12.9                                     |
|     |   | 32.2                    | 720                  | 40.0                  | 95.2                                     | 4.8                                      |
|     |   | 32.5                    | 720                  | 50.0                  | 93.8                                     | 6.2                                      |
|     |   | 31.8                    | 670                  | 63.2                  | 81.4                                     | 18.6                                     |
|     |   | 32.2                    | 620                  | 64.0                  | 89.7                                     | 10.3                                     |
|     |   | 34.5                    | 850                  | 75.5                  | 92.5                                     | 7.4                                      |
|     |   | 32.7                    | 660                  | 91.0                  | 91.3                                     | 8.7                                      |
|     |   | 31.3                    | 630                  | 93.5                  | 85.1                                     | 14.9                                     |
|     |   | 32.2                    | 640                  | 111.4                 | 87.0                                     | 13.0                                     |
|     |   | 34.5                    | 880                  | 53.2                  | 93.7                                     | 6.3                                      |
|     |   | 33.0                    | 680                  | 59.2                  | 96.0                                     | 4.0                                      |
|     |   | 37.2                    | 930                  | 71.0                  | 94.0                                     | 6.0                                      |
|     |   | 34.9                    | 830                  | 73.0                  | 95.4                                     | 5.6                                      |
|     |   | 30.9                    | 550                  | 79.5                  | 90.7                                     | 9.3                                      |
| 7+  | 19| 34.1                    | 740                  | 95.2                  | 87.5                                     | 12.5                                     |
|     |   | 33.9                    | 770                  | 96.5                  | 92.5                                     | 7.5                                      |
|     |   | 33.5                    | 690                  | 97.0                  | 84.5                                     | 15.5                                     |
|     |   | 35.3                    | 870                  | 99.6                  | 86.8                                     | 13.2                                     |
|     |   | 33.7                    | 700                  | 116.7                 | 89.7                                     | 10.3                                     |
|     |   | 33.6                    | 820                  | 60.4                  | 81.2                                     | 18.8                                     |
|     |   | 35.5                    | 790                  | 104.0                 | 85.7                                     | 14.3                                     |
|     |   | 35.2                    | 820                  | 122.1                 | 92.4                                     | 7.6                                      |
|     |   | 37.7                    | 960                  | 127.0                 | 88.8                                     | 11.2                                     |
|     |   | 37.0                    | 930                  | 138.0                 | 78.9                                     | 21.1                                     |
|     |   | 38.2                    | 1060                 | 142.8                 | 92.2                                     | 7.8                                      |
|     |   | 40.2                    | 1240                 | 192.3                 | 80.4                                     | 19.6                                     |
| 8+  | 10| 33.7                    | 700                  | 116.7                 | 89.7                                     | 10.3                                     |
|     |   | 33.6                    | 820                  | 60.4                  | 81.2                                     | 18.8                                     |
|     |   | 35.5                    | 790                  | 104.0                 | 85.7                                     | 14.3                                     |
|     |   | 35.2                    | 820                  | 122.1                 | 92.4                                     | 7.6                                      |
|     |   | 37.7                    | 960                  | 127.0                 | 88.8                                     | 11.2                                     |
|     |   | 37.0                    | 930                  | 138.0                 | 78.9                                     | 21.1                                     |
|     |   | 38.2                    | 1060                 | 142.8                 | 92.2                                     | 7.8                                      |
|     |   | 40.2                    | 1240                 | 192.3                 | 80.4                                     | 19.6                                     |
| 9+  | 7 | 40.8                    | 1140                 | 144.7                 | 84.8                                     | 15.2                                     |

Table 1
A reserve of the oocytes in the ovaries of bream

Phot. 4. Part ovary section; a 7-years old immature female caught on 19 July, 1979.

Table 2

Correlation coefficients (r) for the dependence between percentage of the oocytes of trophoplasmatic growth (DE) and individual features of bream females from Lake Śniardwy

| Data | Body length (l.c.) | Body weight (Wo) | Gonad weight (Ow) | Age (A) |
|------|-------------------|------------------|-------------------|---------|
| DÈ   | 0.194             | 0.174            | 0.599**           | 0.350*  |
| 2    | 0.149             | 0.076            | 0.639**           | 0.316*  |

1 – data values
2 – logarithmic values
r_{0.01} = 0.372
r_{0.05} = 0.287
females ranged from 81.4 to 96.6% i.e. was 4 to 28 times higher than fecundity during spawning. Assuming that average fecundity of the females in consecutive reproductive seasons increased by 50% (Kopiejewska 1987), the oocytes of protoplasmatic growth would determine the fecundity in two consecutive seasons in case of the females with low

Fig. 2. Dependence between percentage of trophoplasmatic oocytes (DE) and ovary weight (Ow) for bream females from Lake Śniardwy (log DE = 0.425 lgOw + 0.194)

Fig. 3. Dependence between percentage of trophoplasmatic oocytes (DE) and female age (A) for bream from Lake Śniardwy (log DE = 1.143 lgA - 0.069)
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reserve, and in five consecutive seasons in case of the females with high reserve. Range of these data suggests that bream females are characterized by considerable differences as regards functioning of the ovaries already during sexual maturation.

Regression analysis of the percentage of trophoplasmatic oocytes – DE in the ovaries versus such individual features as body weight, body length, weight of the ovaries and age showed that percentage of DE oocytes in the ovaries correlated with ovary weight and age of the females (Tab. 2). Dependence between percentage of DE cells in the ovaries and ovary weight presented in Fig. 2 suggests that the same increments of ovary weight corresponded to decreasing increments of the percentage of oocyte generation of the nearest spawning. As regards the dependence between percentage of DE oocytes in the ovaries and age (Fig. 3), percentage value of the DE index increased evenly. Increase of the DE index together with weight of the ovaries and female age points to growing share of the oocytes of older generations on the one hand, and to decreasing percentage of the young oocytes of protoplasmatic growth on the other, i.e. to decreasing oocyte reserve in the ovaries. Thus, intensiveness of oogonial divisions decreases in relation to the amount of spawned eggs as the females grow older and weight of their ovaries increases.

DISCUSSION

Single or multi-portion spawning is observed in bream depending on the habitat and thermal conditions in the environment. Bream reproduction in lakes located in north-south direction changes from single to multi-portion as move southward (Driagin 1939, Šichšabekov 1972). Multi-portion spawning is also observed in thermally polluted reservoirs (Statova 1973). In Poland, bream spawns with a single egg portion (Pęczalska 1963, Brylińska, Długosz 1970). Sych (1955) stated that in 1952 in the Konfederacka Backwater (middle course of the Vistula River) bream was characterized by multi-portion spawning. Preliminary analysis of the ovaries of females inhabiting these waters revealed two generations of these oocytes filled with yolk. Lack of histological data, however, makes observations unreliable. Histological picture of bream ovaries in Lake Radolno (54° lat.) (Brylińska, Długosz 1970) and Lake Śniardwy (54° lat. (own studies) suggests single portion spawning. Bream females spawn in these Lakes in May-June (Pęczalska 1963, Brylińska 1963). In the Konfederacka Backwater, spawning takes place in May (Sych 1955), and in Rybiński Reservoir (USSR, 58° lat.) in April-May (Andreeva 1983). Single-portion bream spawning in the delta of the Terek River (USSR, 44° lat.) is extended in time, lasting since April till May (Šichšabekov 1972).

Length of particular growth phases of the oocytes belonging to the oldest generations was similar in bream females from Lake Radolno and Lake Śniardwy (Fig. 1). In Lake Śniardwy, vacuolization of the oocytes commenced after spawning and lasted till mid-September. In Lake Radolno, vacuolization also commenced after spawning but lasted till mid-October. Vitellogenesis in the bream ovaries commenced in August in both lakes. Vacuolization and vitellogenesis in bream ovaries in Rybiński Reservoir and
Kučurganski coastal salt lake (USSR) Statova 1973) commenced at the same time as in Polish lakes. In the Terek River delta, vacuolization of the oldest oocyte generation commenced in August, and vitellogenesis in October. These data confirm a regularity observed in water bodies located at different geographic latitudes, i.e. that the phase of trophoplasmatic oocyte growth is much shorter in southern bream stocks compared to northern ones (Košelev 1974).

From among various oocyte generations, the oldest one, which should be spawned in course of the nearest spawning season, emerges from the oocytes of protoplasmatic growth during vacuolization. Number of the oocytes to be spawned next is then determined, and these are in fact spawned if the vitellogenesis in winter and the spawning process in spring are not disturbed by some other factors, such as unfavourable environmental conditions (Volodin 1979, 1980). Younger oocyte generations will determine subsequent fecundity. In bream females from Lake Śniardwy the oocyte reserve was to 4 to 28 times higher than the absolute fecundity in the given season. Oocyte reserve in relation to the oocytes to be spawned was estimated in marine fishes as 4:1, 5:1 and 2:1 (Messtorff 1959, Gotting 1961, Dunn, Tyler 1969). Crossland (1977) calculated oocytes in the sections of Chrysophrys auratus ovaries and estimated the percentage of the oocytes of protoplasmatic growth as 47.6–97.0%. Pimpicka (1987) found the reserve of protoplasmatic oocytes in tench from Lake Drwęckie was 3–19 times higher than the share of trophoplasmatic oocytes.

In all fish species studied, the reserve of the oocytes of protoplasmatic growth was always higher than the fecundity in the given season. This suggests that fecundity in the given season was determined by the protoplasmatic oocytes present in the ovaries at least two years before spawning. Lower range of the percentage of protoplasmatic oocytes in Chrysophrys auratus suggests that female fecundity will decrease in the next spawning season. Other authors also suggested that the ovarian cells matured for a longer period than one year (Franz 1910, cit. after Messtorff 1959, Bohl 1957, cit. after Gotting 1961, Yamamoto, Yamazaki 1961, Yamamoto 1956, others). Gotting (1961) stated that the ratio between young, reserve oocytes and matured ones, as well as period of cell maturation, were species-specific. Studies by Crossland (1977), Pimpicka (1987) and myself suggest that proportions of the oocytes in the ovaries differed in the females of the same species. Data related to the females spawning for the first time (Tab. 3) suggest that these differences were established already in early stages of the ontogenesis. It is well known that gonad development is strongly related to the type and level of the organism metabolism. This, in turn, depends on the progeny quality, environmental conditions, and ability of physiological adaptation of the organism to these conditions (Košelev 1971, Bagenal 1978 and others). Notwithstanding the differences in the percentage of the oocytes in female ovaries, these values are characteristic for the stock of a given species. Average percentage of protoplasmatic oocytes in the ovaries in age classes (Tab. 3) points to higher share of younger oocytes in the ovaries of bream females in Lake Śniardwy compared to tench females in Lake Drwęckie. This value tends to decrease slightly with bream age, while it remains at the same level of 81.4–84.6% in tench. Tench ovaries (the species is characterized by a multi-portion spawning) contain
numerous oogonia clusters (Kazanskij 1949, Pimpicka 1987). Kazanskij (1949) found numerous places of oogonial divisions in tench ovaries during entire spawning season, suggesting formation of new oocyte generation. No such places were observed in species with single-portion spawning, such as bream in the northern areas of its range of occurrence.

| Age | Tench (Drwęckie Lake) (Pimpicka 1987) | Bream (Śniardwy Lake/autor's data) |
|-----|-------------------------------------|-----------------------------------|
|     | n        | x       | Range       | n | x       | Range       |
| 3+  | 7 | 83.3    | 76.3–91.7   |    |          |             |
| 4+  | 24 | 84.6    | 69.8–95.0   |    |          |             |
| 5+  | 28 | 81.7    | 68.1–90.8   | 1  | 87.4    | 82.8–96.4   |
| 6+  | 35 | 82.5    | 74.0–93.2   | 9  | 92.0    | 81.4–96.6   |
| 7+  | 9  | 84.2    | 71.4–92.6   | 19 | 91.9    | 84.5–96.0   |
| 8+  | 4  | 81.4    | 76.6–90.1   | 10 | 91.1    | 78.9–92.4   |
| 9+  | 7  | 85.7    |             |    |          |             |
| 10+ | 1  | 84.8    |             |    |          |             |

CONCLUSIONS

1. Annual cycle of ovary development in bream females from Lake Śniardwy was similar as in bream females from Lake Radolno and Rybiński Dam Reservoir:
   a) females spawned in May-June,
   b) oocyte vacuolization commenced after spawning and lasted till September,
   c) oocyte vitellogenesis lasted from August till May next year.

2. Size of the reserve of the oocytes of protoplasmatic growth in reproducing bream females from Lake Śniardwy differed, ranging from 78.9 to 96.6% of the oocytes. This reserve exceeded 4 to 28 times the absolute fecundity in the given reproductive season.

3. Percentage of protoplasmatic oocytes in the ovaries of bream females in Lake Śniardwy decreased with increasing weight of the ovaries and fish age.
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ZAPAS OOCYTÓW PROTOPLAZMATYCZNEGO WZROSTU W JAJNIKACH SAMIC LESZCZA (ABRAMIS BRAMA) W JEZIORZE ŚNIARDWY

STRESZCZENIE

Zbadano roczny cykl rozwoju jajników samic leszcza w jez. Śniardwy oraz określono zapas oocytów protoplazmatycznego wzrostu w jajnikach tych samic. Do badań pobrano 58 samic o długości ciała 24,9–40,8 cm, masie ciała 350–1520 g i wieku 5–10 lat. Zapas oocytów protoplazmatycznego wzrostu określono u 47 samic. Roczny cykl rozwoju jajników samic leszcza w jez. Śniardwy przebiega podobnie jak u samic leszcza w jez. Radolno i w zbiorniku Rybińskim:

– rozród samic odbywa się w miesiącach maj–czerwiec,
– proces wakuolizacji oocytów rozpoczyna się po rozrodzie i trwa do września,
– proces witellogenezy oocytów odbywa się w okresie od sierpnia do maja.

Wielkość zapasu oocytów protoplazmatycznego wzrostu w jajnikach samic waha się od 78,9–96,6% oocytów. Zapas ten przewyższa 4 do 28 razy płdoność absolutną w danym sezonie rozrodczym. Procentowy udział oocytów protoplazmatycznego wzrostu w jajnikach samic zależy od masy jajników i wieku samic, zmniejsza się wraz ze zwiększającą się masą jajników i wiekiem samic.

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