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Original article

Body size versus gonad maturation form in under-yearling precocious males of the sea trout (*Salmo trutta* m. *trutta* L.)

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Abstract – The study was aimed at analysing body size in relation to form of gonad maturation (amount of mature germ cells) in 329 under-yearling sea trout males. The fish, aged 7 months, were caught in late October–early November in 3 streams located in north-western Poland. Each stream supported fish belonging to a different sib group. Standard histological techniques and a computer image analysis programme were used to detect the class of gonad maturation and percentage of the gonad area occupied by tubules with active spermatogenesis. Gonad maturation forms were distinguished based on the latter criteria. Gonads with developing germ cells occupying less than 90% of gonad area were classified as incomplete forms of gonad maturation, others as complete maturation forms. In each sib-groups analysed, even the smallest individual were already precocious, their gonads being incompletely mature. The smallest maturing male measured 7.1 cm in length. The average size of an incompletely maturing individual was slightly smaller than that of the completely mature one but the difference lacked statistical significance ($P > 0.05$). The sib-group of smaller fish contained less precocious, and the gonads of the more precocious were incompletely mature, compared to the sib-group of larger fish ($P < 0.001$). It seems that the incomplete form of gonad maturation (defected maturation) occurs at a smaller critical fish size than the complete gonad maturation form. Incomplete maturation is more frequent smaller individuals and possibly in among slow-growing groups of fish.

***Salmo trutta* / testis / precocious / incomplete maturation / partial maturation / attempted maturation**

1. INTRODUCTION

As indicated by the results of numerous studies, fish body growth rate affects the development of the reproductive system. Sexual differentiation is faster in larger fish [1] and their gonadogenesis is faster as well [2]. According to numerous authors, precocious maturation, common in salmonid males at the parr stage (juveniles mature prior to their first descent to the sea) occurs in the largest individuals [3–15].

In the opinion of many authors, for precocious maturation to begin, salmonid males have to grow to a certain threshold length. A certain critical body size is also necessary for a fish to adapt to a changed habitat, i.e., to smoltification [16–18]. The critical length necessary to smoltification is higher than that at which maturation begins [19, 20].

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In salmonids, different parts of the germ cell were observed to have remained inactive during the reproductive cycle in the gonads of precocious males [2, 20–25]. The gonads features different forms of gonad maturation [26]. This study was aimed at analysing the body length-maturation relationship with reference to the different forms of testis maturation in underyearling precocious sea trout.

2. MATERIALS AND METHODS

The 7-month old parr of the sea trout (*Salmo trutta* morpha *trutta* L.) examined were harvested in October and November of the same year from the brooks Pniewa, Trawna, and Smerdnica, located in the vicinity of Szczecin (Western Pomerania, Poland). All the streams were monitored. They have class I water quality and comparable food availability, good for salmonids. The streams were not inhibited by salmonid fish before, due to unfavourable conditions downstream such as dams and water pollution by sewage. The streams had been stocked with sea trout swimming larvae (20.7−22.5 mm total length in each stream) grown out at the Polish Anglers' Association in Goleniów. The fertilised eggs had been obtained by artificial spawning of breeders caught in the Rega River. Each stream had been stocked with larvae bred by a single parental pair. The study involved 176 males from the Pniewa, 67 from Smerdnica, and 86 from Trawna. The fish, after they had been sacrificed and the abdomen opened, were fixed in Bouin fluid. The fish were measured (fork length, *longitudo caudalis*) to 1 mm and weighed to 0.1 g; subsequently, the gonads were removed and weighed to 0.05 mg. The Fulton condition factor ($CF = 100\ WL_F^{-3}$ where W = weight of whole fish, g; L_F= fish fork length, cm) and the gonadosomatic index ($GSI = 100\ W_G\ W^{-1}$ where W_G = gonad weight, g; W = weight of whole fish, g) were calculated. The fish were divided into length classes (8.0−8.4; 8.5−8.9; 9.0−9.4 cm, etc.).

Histological mounts were made, with the standard paraffin technique, with tissue fragments dissected from mid-length of the larger gonad. The 4 μm-thick sections were Heidenhain iron haematoxylin-stained and examined under a Jenaval (Zeiss) light microscope. Gonad maturity stage was determined using a 9-point scale developed by Dziewulska and Domagała presented in Table I [26]. Gonad maturity form was assessed from the percentage of the gonad cross-section (c-s) area occupied by the tubule-containing developing cells (cyst from SG B to SZ plus actively dividing SG A). The c-s gonad area and the area occupied by the developing cells were determined from a manually delimited area measured with a Leica QWin computer image analysis programme. The cells allowed to distinguish between attempted maturation (AM; developing cells occupying < 30% gonad c-s area, Fig. 1a), partial maturation (PM; developing cells occupying 30−90% gonad c-s area, Fig. 1b), and complete maturation (CM; developing cells occupying more than 90% gonad c-s area, Fig. 1c). The first two forms were considered incomplete gonad maturation (IM). The details are described in Dziewulska and Domagała [26].

The significance of differences between fish fork length of three sib-groups and of different maturation forms in each sib-group was tested with the non-parametric Kruskal-Wallis test. A chi-squared test was used to compare the frequencies of precocious males and incomplete maturation in the three sib-groups (table 3 × 2). When the frequencies were different ($P < 0.05$), a Fisher exact test was applied to test for significant differences between the groups (3 tests for 2 × 2 tables). The statistical analyses were performed with the STATISTICA programme.

Table I. Histological observations-based on the gonad maturity scale of precocious salmonid males (SG A, spermatogonia A; SG B, spermatogonia B; SC I, primary spermatocyte; SC II, secondary spermatocyte; SD, spermatid; SZ, spermatozoa).

Class	SG		SC I	SC II	SD	SZ	Sperma-tion
	A	B					
I	+	–	–	–	–	–	–
II							
$II_{N,A}$ [a]	+	+	–	–	–	–	–
III	+	+	+	–	–	–	–
IV	+	+	+	+	+	–	–
V	+	+	+	+	+	+	–
VI	+	+	+	+	+	+	+
VII	+	–	+	+	+	+	+
VIII[b]							
VIII-I	+	–	–[+]	–[+]	–[+]	+	+
VIII-$II_{N,A}$	+	*	–[+]	–[+]	–[+]	+	+
IX							
IX-I	+	–	–	–	–	+	–[ˆ]
IX-$II_{N,A}$	+	*	–	–	–	+	–[ˆ]
IX-III	+	*	*	–	–	+	–[ˆ]
AM	+	+s	+s	+s	+s	+s	–

[a] Sub-class separation based on the number of spermatogonia divisions.
II_N, 4-cell cyst/s of SG B and number of dividing spermatogonia < 32 mm^{-2}.
II_A, 4- cell cyst/s of SG B and number of dividing spermatogonia ≥ 32 mm^{-2} or cyst/s containing more than 4 SG B.
[b] SZ occupy more than 50% of gonad cross-section (the percentage of motile spermatozoa, with 50% as the critical level, is an additional criterion of identifying Classes VIII and IX).
* Cells of the subsequent spermatogenic cycle.
[ ], rare cases: [+], few cysts, covering < 5% gonad cross-section area [ˆ], sperm in the sperm duct.
AM, attempted maturation, i.e., a particular case of maturation resulting from a low number of cells maturing during the cycle (and one of gonad maturation forms); absence of any uniform cell pattern; spermatozoa do not enter the sperm duct; developing cells occupy up to 30% gonad cross-section.
s, Cells not always visible in sections.
[a, b] Reprinted from Aquaculture, 250, 3-4, Dziewulska K., Domagała J. Differentiation of gonad maturation in sibling precocious males of the sea trout (*Salmo trutta* m. *trutta* L.) in their first year of life, 2005, 713–725, with permission from Elsevier.

3. RESULTS

The males examined in late October–early November showed gonads at various developmental classes. The gonads of most individuals were at Class I and some showed their gonads to be at Class II. The remaining individuals were precocious: their gonads were at Classes III−VIII or showed attempted maturation (AM). The gonads of the Smerdnica fish only were advanced not further than Class V. In the 3 groups studied, early maturation was also revealed in the smallest individuals. In fish

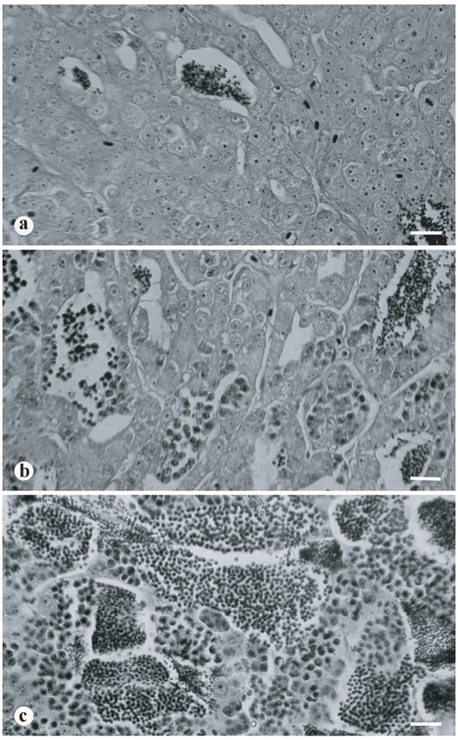

Figure 1. The form of gonad maturation assessed from the percentage of the gonad cross-section (c-s) area occupied by the tubule-containing developing cells (cyst from SG B to SZ plus actively dividing SG A). (a) Attempted maturation – developing cells occupying < 30% gonad c-s area; (b) partial maturation – developing cells occupying 30−90% gonad c-s area; (c) complete maturation – developing cells occupying more than 90% gonad c-s area. The first two forms were considered as incomplete gonad maturation.

of mean length (FL) 12.3, 11.0 and 10.0 cm precociously maturing/mature individuals accounted for about 40, 32 and 12%, of all the males in the Trawna, Pniewa, and Smerdnica, respectively (Tab. II). Some males at Classes III−VIII featured partial maturation (PM), while others underwent complete gonad maturation (CM).

In the Trawna, the smallest (9.5 cm) male showed gonads at Class II. The smallest maturing male in the group measured 10.0 cm, had gonads at Class III that revealed PM (developing cells occupied 80% of the gonad c-s area). Other two males, measuring 10.2 and 10.4 cm, showed AM (developing cells in both males were occupying about 20% of the gonad c-s area). Gonad tissue mounts of the first revealed spermatogonia B and primary spermatocytes; primary spermatocytes and spermatozoa were visible in mounts of the other male's gonad tissue. The smallest male with complete maturation measured 10.8 cm and had gonads at Class VII. The gonads of the remaining maturing males were at Classes III−VIII (except for Class VI) and AM. They exhibited the three maturation forms: AM, PM, and CM (17, 15, and 68% of the maturing males, respectively). The length-frequency distribution of gonad maturation form is shown in Figure 2a. The mean fork lengths were 12.5, 12.1 and 12.6 cm, respectively; the fork length differences were not significant (Kruskal-Wallis test, $P > 0.05$).

In the Pniewa, the fork length of the smallest maturing male (which was, at the same time, the smallest individual in that sample) was 8.8 cm; the fish had gonads at Class III and revealed PM. Developing cells in the gonads of that individual occupied about 40% of the gonad c-s area. Another maturing male was slightly larger (8.9 cm), with few cells at a similar spermatogenesis stage; the developing cells occupied about 20% of the gonad c-s area and the male was classified as AM. The gonads of a slightly larger male (9.1 cm) were at Class IV and showed PM as well (the developing cells occupied about 90% of the gonad c-s area). On the contrary, the smallest male showing CM measured 9.2 cm and had gonads at Class VI. Gonads of larger maturing males were at Classes III−VIII and AM. Among the maturing males, the AM, PM, and

Table II. Major characteristics of the males examined. The values represent mean ± SD; the values in parentheses represent ranges.

Stream	No. of fish	Body fork length (cm)	Weight of fish (g)	Fulton condition factor	Gonad weight (mg)	Gonadosomatic index	% precocious males	% IM in precocious
Trawna	86	12.35 ± 1.21 (9.5–16.3)	25.30 ± 7.52 (11.9–52.6)	1.31 ± 0.11 (1.07–1.66)	247.47 ± 462.67 (8.50–186.75)	0.906 ± 1.631 (0.038–6.928)	39.5	32.3
Pniewa	176	10.98 ± 1.1 (8.8–14.1)	16.63 ± 5.27 (8.1–32.5)	1.22 ± 0.1 (1.01–1.54)	49.46 ± 122.96 (5.90–873.15)	0.306 ± 0.764 (0.038–6.204)	32.4	70.2
Smerdnica	67	10.00 ± 1.54 (7.1–13.2)	12.44 ± 6.16 (4.4–30.1)	1.15 ± 0.15 (0.63–1.32)	11.77 ± 5.57 (3.30–26.40)	0.103 ± 0.042 (0.032–0.263)	11.9	100.0

IM: incomplete form of gonad maturation.

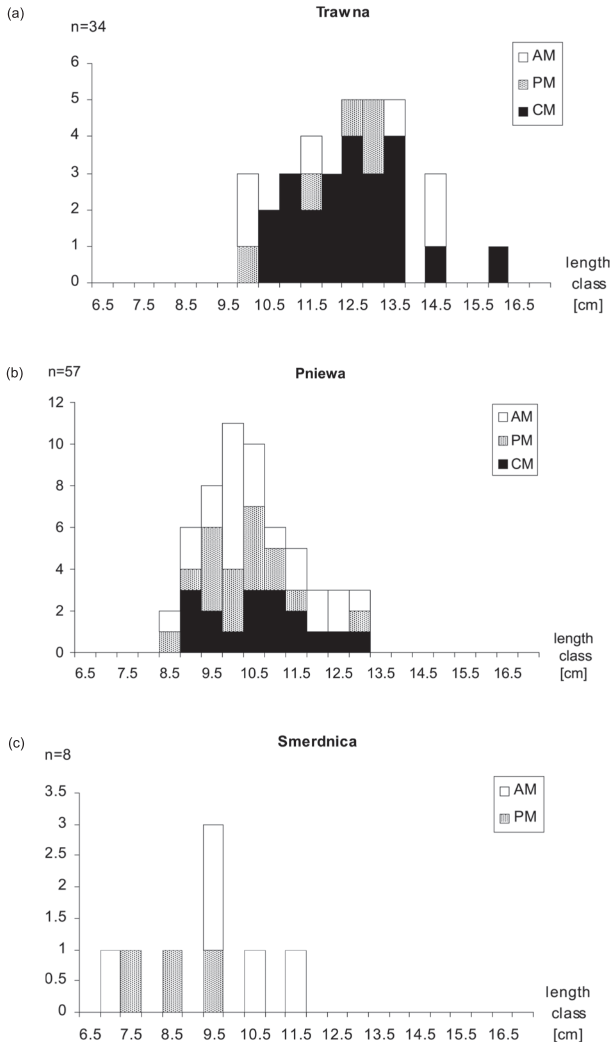

Figure 2. Length-frequency distribution of gonad maturation form in precocious under-yearling males of three sibling sea trout groups. Forms of gonad maturation: AM, attempted maturation; PM, partial maturation; CM, complete maturation, (AM and PM – incomplete maturation).

CM individuals accounted for 40, 30, and 30%, respectively. The length-frequency distribution of gonad maturation form is shown in Figure 2b. The mean fork lengths were 10.7, 10.5, 10.8 cm, respectively; the fork length differences were not significant (Kruskal-Wallis test, $P > 0.05$).

The gonads of all maturing males in the Smerdnica showed incomplete maturation only. The smallest male measured 7.1 cm in fork length and matured as AM (developing cells occupied about 20% of the gonad c-s area and occurred as spermatogonia B and spermatozoa). Another male measured 7.9 cm and had gonads at Class V; the developing cells occupied about 80% of the gonad c-s area (PM). The gonads of the remaining precocious males in the Smerdnica showed AM or PM and were at Classes III–IV. The AM and PM males accounted for 62 and 38% of all maturing males, respectively and their respective mean fork lengths were 9.7 and 8.6 cm; the differences were not significant (Kruskal-Wallis test, $P > 0.05$). The length-frequency distribution of gonad maturation form is shown in Figure 2c.

In the Pniewa and Smerdnica streams the mature males were smaller than immature (10.68 and 11.13 cm; 9.30 and 10.10 cm, respectively) and were statistically different ($P < 0.05$), while in Trawna they were larger (12.54 and 12.22 cm) with no statistical differences ($P > 0.05$). No statistical differences were found in the index of condition between the groups in each stream ($P > 0.05$).

The three sib-groups differed significantly in their length (Kruskal-Wallis test, $P < 0.001$). The frequencies of precocious males differed significantly in the examined groups (chi-squared test, table 3×2, $P < 0.001$). The differences between groups growing in Pniewa and Smerdnica, and Smerdnica and Trawna were significant (Fisher exact test, 2×2 tables, $P < 0.005$, $P < 0.001$, respectively); the differences between groups growing in Pniewa and Trawna was not significant (Fisher exact test, 2×2 tables, $P > 0.05$).

The frequencies of incomplete maturation in precocious males differed significantly in the examined groups (chi-squared test, table 3×2, $P < 0.001$ and Fisher exact test, 2×2 tables $P < 0.001$).

The sib-group of larger fish contained more precocious males, and the gonads of more precocious males underwent of complete maturation, compared to the sib-group of smaller fish.

It seems that incomplete gonad maturation occurs at a smaller critical fish size than the complete form of gonad maturation. The incomplete form of gonad maturation is more frequent among smaller individuals and possibly in slow-growing groups of fish.

4. DISCUSSION

Body size of the smallest maturing sea trout males were close to the minimum body size attained by precocious individuals in related species. The precocious under-yearling and 2-year-old Atlantic salmon measured 6.0–7.0 cm [7, 15, 20] or were slightly longer than 7.0 cm [11, 27]; the under-yearling Caspian trout measured 6.4–7.0 cm [28] and the under-yearling masu salmon were 7.0–8.0 cm long [14]. Among the sea trout examined in this study, even the smallest individuals were precocious. Consequently, no critical length necessary for precocious sexual maturation can be discerned in the sea trout studied; theoretically, all the individuals could be precocious as early as in their first year of life. Some authors reject the notion of the critical length being a prerequisite of precocious maturation [29], whereas Gall [30] stated that the critical length in faster-growing individuals is lower than that in the fish growing at a moderate rate. By Baum et al. [31] the size threshold above which parr matured depended on altitude, which could serve as a proxy for growth opportunity.

In the three sib-groups of the sea trout examined, the smallest precociously maturing individuals showed incomplete maturation. The smallest male (7.1 cm fork length) revealed attempted maturation, while another small male (7.9 cm) showed partial maturation. The smallest males completely maturing measured 9.2 cm in fork length. The mean fork length of the individuals incompletely maturing in each of the three examined sib-groups was lower than that of the males showing complete maturation, but the differences were not significant. Most probably, for a gonad to completely mature, it is necessary that the fish attain, i.e., a critically larger body size. In the White Sea trout, Murza and Khristoforov [25] found, too, a slightly smaller body size in the males that showed attempted maturation, compared to the fish showing complete maturation.

The three sib-groups of examined males, harvested from different streams, differed significantly in their length. The larger, on the average sib-group, showed a higher proportion of precocious males and a lower percentage of individuals with incomplete gonad maturation. In the smallest, on the average sib-group, the fish featured the lowest number of males matured precociously and the gonads of all the males showed incomplete gonad maturation. However the studied groups were sibling and proportion of precocious males obtained could have been affected by genetic traits, since heritability of propensity for precocious maturation is relatively high [29, 32–35], most probably gonad maturation is related to fish size and growth rate similarly as propensity for precocious maturation. It is likely that incomplete forms of gonad maturation are affected by low growth rate and small body size. On the contrary, defected (incomplete) maturation could not accelerate growth at a level as complete maturation [32, 36].

Besides heritability, the environmental factors influencing fish growth rate play a very important role in early triggering of the reproductive system as well [12, 29, 30, 37–41]. It is not only the body size that is important in the reproductive function take-off. Fat deposits, too, may play a role in determining whether or not some vertebrates are ready to mature [42, 43]. Some authors are of the opinion that only those fish that have accumulated suitable energy reserves [12, 19, 44] or visceral fat [45, 46] will start maturing. According to Silverstein et al. [47] an effect in fat content is more distinct in smaller fish. Moreover, it is important that the fat be accumulated at an appropriate stage of development. For instance, the Atlantic salmon will re-mature only when fat reserves are replenished by the spring (May). Fat depletion lasting until May results in a failure to mature in that year [46].

When estimating the proportion of precocious males maturing in their first year of life, it is necessary to study histology due to the very high variability in the dynamics of the first sexual cycle, as exemplified by the sea trout examined and forms of incomplete gonad maturation. It is not enough to examine the gonad morphology and/or to induce spermation by abdominal massage, because in some of the incompletely maturing fish, spermatozoa do not move to the vas deferens [20, 21, 24].

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