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Fish biology

FECUNDITY OF NINESPINE STICKLEBACK (*PUNGITIUS PUNGITIUS* L., 1758) IN THE PUCK BAY

PLÓDNOŚĆ CIERNICZKA (*PUNGITIUS PUNGITIUS* L., 1758) Z ZATOKI PUCKIEJ

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The material was collected in the spring-summer period of 1993 and 1995–96. Ninespine stickleback is abundant in the brackish waters of the Puck Bay and its catchment area. The species is common in the overgrown littoral zone. Spawning in the bay is extended, lasting from March to August, the eggs are laid in batches. The fecundity of these fish is relatively low, as with others which show parental care. Sticklebacks lay up to 199 eggs, this being higher than the fecundity of sticklebacks from North America and Eastern Europe and lower than in one of the Japanese forms. The relation between absolute fecundity and body length, and body weight is described by the equations: $F = 1.8052 \cdot 10^{-3} \cdot L^{2.71}$ and $F = 103.77551 \cdot W^{0.99}$, respectively. The fecundity of a fish depends primarily on its weight. The body size and fecundity had no effect on egg size.

INTRODUCTION

The ninespine stickleback is a representative of the family Gasterosteidae widely distributed in the northern hemisphere, occurring in the temperate zones (Nelson 1976; Wootton 1976). Being cosmopolitan with considerable ability to adapt to different environmental conditions (Rawlinson and Bell 1982), it inhabits sea waters of low salinity and fresh water (Wheeler 1978). It constitutes a component of the Baltic, mainly inshore, brackish water ichthyofauna (Wolski 1927; Nellbring 1988; Zander and Westphal 1991). The ninespine stickleback is the smallest predator of the Puck Bay. It has no economic importance and competes for food with commercially valuable fishes. Furthermore it feeds on their spawn and fry (Bubinas 1979; Delbeek and Williams 1987; Kotwicki 1992), while itself protects eggs laid in the nest, as well as the hatching. The sticklebacks dominate in the littoral zone of the bay during spring and summer under optimal reproductive condi-

tions. Sticklebacks constitute 93% of all fishes in their numbers as well as in the biomass (Skóra 1993). Because of the abundance of sticklebacks in the Puck Bay, interest has increased in its biology and the role it plays in the ecology of the basin.

A number of descriptions of the biology and ecology of the stickleback reproduction were published (Wootton 1976; Zjuganov 1991), many dealing with the spawning-associated behaviour (McKenzie and Keenleyside 1969; Jevgenejevič 1978; Russell and Russell 1985; FitzGerald 1993). The spawning behaviour was also studied under laboratory conditions by Kulamowicz (1959). Jones and Hynes (1950) determined the rate of maturity and age at first spawning. Poulin and FitzGerald (1989) assessed the influence of environmental conditions on the survival rate of eggs and development of fry. Coad and Power (1973), Griswold and Smith (1973), Tanaka and Hoshino (1979), FitzGerald (1993), Zjuganov (1991), and Chae and Yang (1993) were also engaged in the problem of maturation and fecundity in *Pungitius*. The only information available on the sticklebacks of the Puck Bay, is that by Wolski (1927) on several specific morphological features, and unpublished data of Gubernator (1981). No papers are available on reproduction and fecundity of this fish in the southern Baltic. Information on the fecundity constitutes an essential element of the biology of the species and may contribute to the growth and biomass forecast of the population.

The aim of this paper was determination of the fecundity of sticklebacks from the Puck Bay region and relation between the quantity and size of spawn and the body measurements of the fish.

MATERIAL AND METHODS

Study area

The Puck Bay (Fig. 1) is situated in the western part of the Gulf of Gdańsk. The bay is separated from the open sea by the Hel Peninsula. An underwater shelf called the Gulls Reef constitutes the boundary between the external and internal (Puck Lagoon) part. The various depths of the two parts affect the environmental relations (Table 1). The eastern region, contacting directly with the Gulf of Gdańsk is deeper, of high salinity and a lower summer temperature. The Puck Lagoon, on the other hand, has a differentiated bed and is shallow, which affects its thermal character, becoming colder or warmer much faster. The lagoon is much less saline, mainly due to the influx of river waters and spring thaws. Here the wave movement is less pronounced, but the water freezes much faster (Nowacki 1993). Thanks to its configuration and limits, the area is ecologically unique and has the features of an estuary. The surface sediments are mainly sandy. The principal algae in the region are: *Pilayella littoralis* (Pheophyta), *Cladophora*, *Enteromorpha* (Chlorophyta) seasonally, and also vascular plants which occur only in the lagoon: *Zostera marina* and *Potamogeton*

sp. (in the Reda River estuary). Several typically freshwater species were noted amongst the vascular plants.

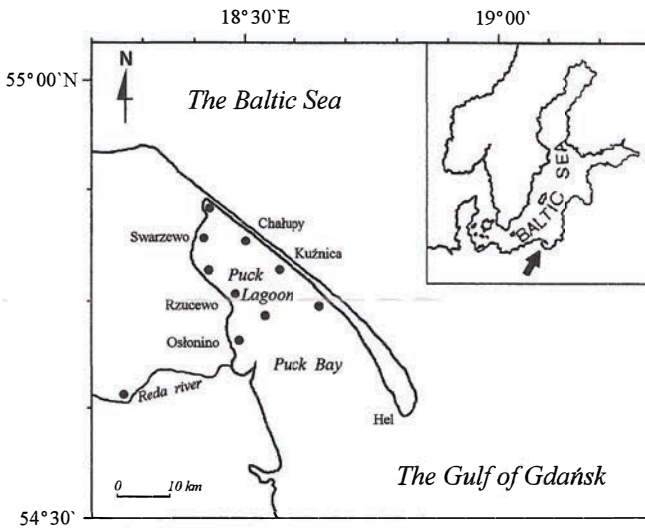


Fig. 1. Sampling stations on the Puck Bay

Table 1

Natural conditions in the Puck Bay

Water region	Depth [*] (m)	Salinity (‰)	Temperature [*] (°C)
Puck Lagoon (inner part)	3.5	5.08–7.97	17.0
outer part	20.5	7.25–7.97	12.5

* Average value.

The Reda River belongs to the Puck Bay catchment area and is supplied by influxes from neighbouring rivers, lakes, and waterlogged terrain. Its sandy channel 6–9 m wide and 0.5 m deep, overgrown with vegetation, is of a natural character in a considerable stretch. The Reda is one of the cold rivers with an average annual temperature of 7.5°C, becoming warmer at the turn of April and May, to reach about 14.5°C in July and August.

Material and methods

The fish were collected from March to July 1993, as well as in July 1995 and 1996, at 10 sampling sites (Fig. 1) by means of landing net, dragnet or traps. Immediately on capture, the fish were preserved in 4% formaline, only females being taken for further analysis.

The following measurements were taken: total body length (up to 1 mm), total body weight (up to 1 mg), weight of gutted fish (up to 1 mg) (viscera were removed to avoid any

error arising from fluctuation of body weight due to differences in the degree to which the stomachs were full; hereafter the "weight" of fish means that of gutted fish).

The stage of gonad development was determined using a dissecting microscope based on a 6-degree scale of development (Griswold and Smith 1973). To determine the absolute (total numbers of eggs) and relative fecundity (number of eggs per gram of body weight), the total number of oocytes in the ovaries of the sexually mature females was counted.

The relation of absolute (individual) fecundity to the length and weight was studied on the basis of the simple formula $y = a + bx$ and the curve described by the formula $y = ax^b$, where: y —dependent variable (absolute fecundity— F); x —independent variable (total body length— L (mm) or body weight— W (g)); a , b —permanent coefficients calculated by the least square method.

In fish of identical length and weight, the absolute fecundity frequently has a wide range and fluctuates considerably (Szypuła 1979). In view of this, the average fecundity values in the particular size classes have been designated: lengths (every 1.0 mm) and weight (every 0.05 g).

Oocytes representing various degrees of maturity were taken from ovaries and using a dissecting microscope fitted with a measuring eye-piece, the diameter of the oocytes was recorded to the nearest 1 μm . The relation between the size of eggs and the body length and weight, as well as fecundity of the sticklebacks was thus measured.

RESULTS

A total of 628 female sticklebacks were examined. Of that number, 95 fish with total length of 41–54 mm and weight of 0.291–0.828 g were sexually immature with gonads in the resting, spent stage. Another 68 females with length of 38–57 mm and weight of 0.244–0.953 g had gonads containing from several to a dozen or so single, mature eggs. This was probably the last of several batches of eggs which would shortly be finally spawned or the ova remnants of the last spawning which would be reabsorbed into the ovaries. The resorption of eggs had already been noted in the gonads of two of the females analysed. The remaining 465 females were fully mature with gonads in the pre-spawning, ripe stage. Their total length was 38–55 mm and weight 0.270–1.139 g.

Frequency in length classes and weight classes

Frequency distribution of lengths and weights was calculated for sexually mature females. That in length classes was of a single-peak character, fish of from 44 to 47 mm predominating. Both highest and lowest classes were represented by single individuals (Fig. 2a). The longest fish measured 55 mm and the smallest 38 mm, the average length of the Puck Bay stickleback was 45.2 mm. Predominant in the overall weight groups were

fish of 0.70–0.85 g (Fig. 2b). The average weight of sticklebacks was 0.781 g. After gutting, the majority weighed between 0.45 and 0.50 g (Fig. 2c). The average weight was 0.486 g.

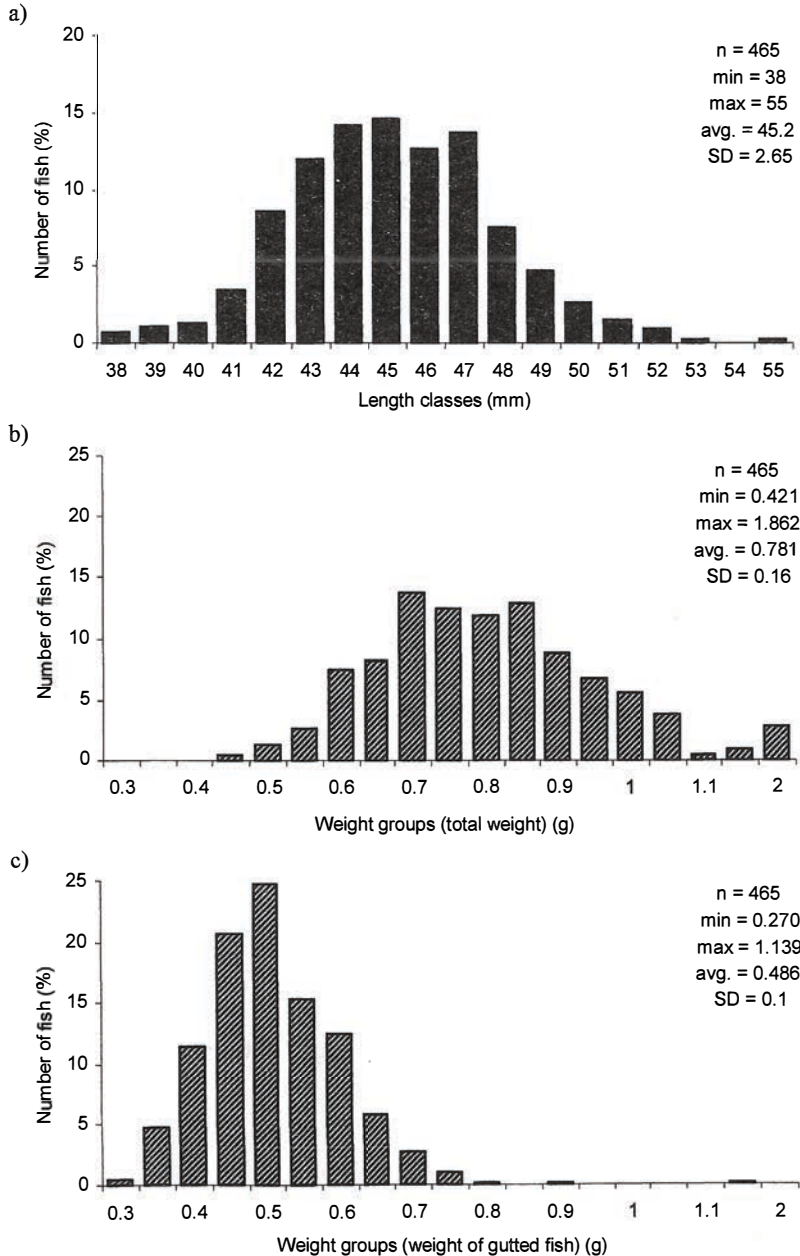


Fig. 2. Frequency distribution of ninespine stickleback for length (a), total weight (b) and weight of gutted fish (c). Absolute and relative fecundity

The individual fecundity of mature fish was between 25 and 199 eggs for individuals with lengths of 42–46 mm and weights of 0.305–0.524 g with an average of 53. The highest number of eggs (199) was in a female of 44 mm and 0.507 g. The smallest—38 mm individuals with a weight of 0.270–0.320 g produced 35–37 eggs. The longest female—57 mm and weight of 0.835 g with only 12 eggs, was omitted when describing fecundity. The heaviest one was from the Reda River measuring 55 mm and weighing 1.139 g. Its individual fecundity was 140.

The relative fecundity of 465 females was calculated. This ranged from 47 to 393 eggs per gram of body weight and the average was 109. Depending upon the length of the fish, the relative fecundity differed, there was no relationship with length. In the 0.45–0.65 g class, the fecundity was relatively constant at 108 eggs per gram.

Relation between fecundity and body length and weight

The relations between absolute fecundity and body length and weight of the fish were studied on the basis of the following formulas: $y = a + bx$ and $y = ax^b$. The relation of fecundity to both body features was statistically significant (Table 2).

Table 2

Regression analysis ($p < 0.01$; $n = 465$)

Relation	Function	Coefficients	Correlation coefficient
Fecundity–length	$F = aL + b$	$a = 3.91487$ $b = -120.902$	$r = 0.83$
	$F = aL^b$	$a = 1.8052 \cdot 10^{-3}$ $b = 2.7047$	$r = 0.91$
Fecundity–weight	$F = aW + b$	$a = 114.064$ $b = -5.68586$	$r = 0.98$
	$F = aW^b$	$a = 103.77551$ $b = 0.989364$	$r = 0.98$

Based on the average fecundity in length classes the relation between length of the fish and its absolute fecundity was also determined. For the length the relation was a power function: $F = 1.8052 \cdot 10^{-3} \cdot L^{2.7047}$ ($r = 0.91$; $p < 0.01$; $n = 465$) (Fig. 3a). The fecundity increases with the length unequally and rises faster than length. Based on the average number of spawn in weight groups, the relation between weight and the fecundity was assessed. The relation with weight was described better by: $F = 103.77551 \cdot W^{0.989364}$ ($r = 0.98$; $p < 0.01$; $n = 465$). The fecundity increases faster than weight (Fig. 3b).

The weight of individuals of the same species and lengths may differ. In order to present an accurate definition between the fertility and body length and weight the average fecundity values in the increasing length classes and weight groups have been compared (Table 3). Despite the fact that sticklebacks of equal lengths sometimes contain different quantities of spawn, it was observed that fecundity increases noticeably with weight in in-

dividuals of the same length class. On the other hand, given the same weight, the quantity of spawn is highly differentiated and does not indicate growth with length of an individual. This means that fecundity of sticklebacks of the same length class depends primarily on their weight.

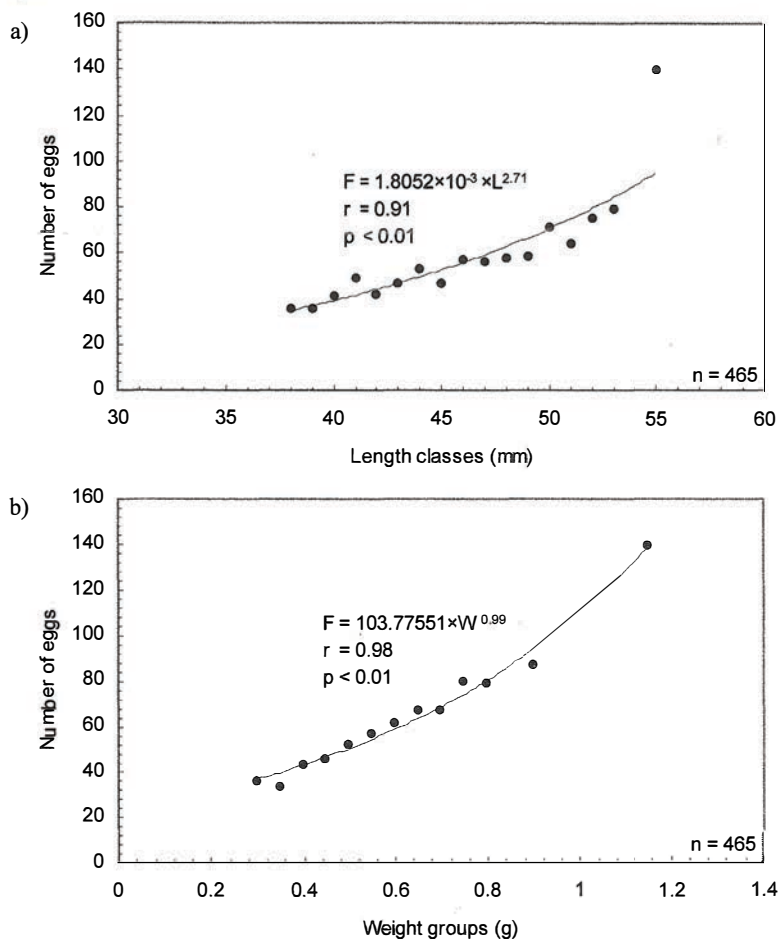


Fig. 3. Regression curves showing the relations between number of eggs and total length (a) and weight of body (b) of ninespine stickleback

Size of eggs

The size of the spawn was measured in 419 individuals. The diameters of the eggs studied were in the range of 528–1872 μm . In smaller and maturing eggs the diameter was 942 μm on average, whereas in the generation of mature eggs ready to spawn, the average was 1366 μm . In fish of similar body sizes and the same fecundity, the sizes of eggs within corresponding generations were often fairly differentiated. Consequently, constitute the av-

erage size of eggs for consecutive length classes and groups of the weight as well as suitable fertility. The size of the eggs of two generations did not change however, remaining at the same level depending upon the growth rate of the body (Figs. 4a, b) and fecundity of the fish (Fig. 4c).

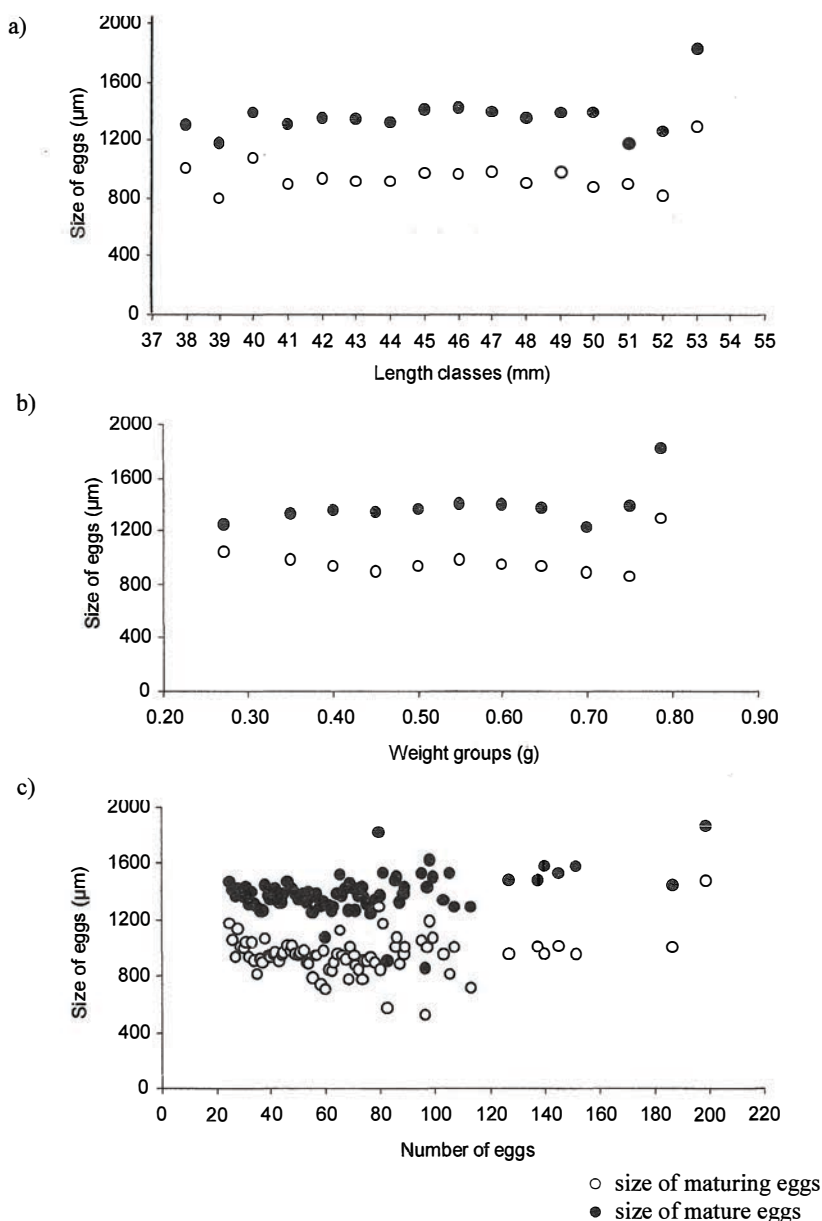


Fig. 4. The relation between size of eggs (max = 1872 μm , min = 572 μm) and total length (a), weight (b) and fecundity (c) of ninespine stickleback (n = 419)

Table 3

The relation between fecundity and body measurements

Length classes (mm)	Number of fishes	Weight groups (g)												
		0.3	0.35	0.4	0.45	0.5	0.55	0.6	0.65	0.7	0.75	0.8	0.9	1.15
38	3	36 (1)*	36 (2)											
39	5	36 (1)	37 (3)	33 (1)										
40	6		30 (2)	45 (3)	49 (1)									
41	16		39 (4)	53 (8)	50 (4)									
42	40		31 (8)	40 (16)	51 (14)	49 (1)	40 (1)							
43	56		34 (4)	44 (17)	45 (22)	60 (13)								
44	66			39 (5)	48 (26)	53 (26)	79 (8)	47 (1)						
45	68			36 (2)	42 (19)	47 (36)	57 (8)	53 (2)		97 (1)				
46	59			38 (1)	32 (4)	57 (22)	59 (20)	66 (10)	60 (2)					
47	64				42 (4)	48 (16)	50 (20)	68 (19)	82 (4)	33 (1)				
48	35					51 (1)	49 (5)	55 (14)	64 (13)	62 (2)				
49	22				40 (1)		55 (8)	66 (6)	56 (3)	55 (3)	86 (1)			
50	12						72 (1)	55 (6)	98 (3)	78 (2)				
51	7								30 (2)	74 (3)	84 (2)			
52	4									68 (1)	73 (2)		87 (1)	
53	1											79 (1)		
55	1													140 (1)
Total:	465													

() * number of fish.

DISCUSSION

Sticklebacks (Gasterosteidae) are common in inland waters and sea water of the northern hemisphere. In temperate regions, their spawning is in spring and summer (Nelson 1968; Griswold and Smith 1973), whereas at lower latitudes it commences in February and lasts until July (Chae and Yang 1993) or September (Tanaka and Hoshino 1979). The fry appears at the end of April and remains until November. In the Puck Bay region the spawning takes place from March (the Reda River) until August, with the height of the season in May, June, and July. According to the Leiner's (1934) laboratory observations sticklebacks are considered to be able to spawn in autumn. Although reproduction in this season not confirmed with respect to fish in their natural environment, he found that the juveniles appearing in spring are the product of the autumn spawning. Neither the present studies, nor results obtained from other authors (Jones and Hynes 1950; Coad and Power 1973) have confirmed this theory.

Stickleback individual fecundity is relatively low, compared with species spawning in the pelagic zone. In the Puck Bay, sexually mature *P. pungitius* females with a body length of 38–55 mm have from 25 to 199 eggs. Their fecundity is thus higher than in other representatives of the genus found in Europe. The fecundity of females from the Schodnia river near Moscow is 140–160 eggs on average, whereas for *Pungitius platygaster* from the Black Sea drainage-basin in the region of Odessa it is from 80 to 90 (Zjuganov 1984). The Baltic stickleback also has a higher fecundity than the North-American freshwater forms with similar body sizes. *P. pungitius* specimens of 30–54 mm from the Matamek River System in Canada produce 10–71 eggs (Coad and Power 1973), and from the St. Lawrence River estuary from 37 to 176 (FitzGerald 1983). In Lake Superior in the USA in sticklebacks 58–81 mm long, 61–112 eggs were found (Griswold and Smith 1973). A characteristic feature of the populations on the east coasts of Asia is their low fecundity. *Pungitius sinensis kaibarae* (Tanaka) from the Kumho River (Chayang stream) in Korea, 26–53 mm in size, produce 21–110 eggs (Chae and Yang 1993), whereas the Japanese *P. sinensis kaibarae*—from 58 to 186 eggs, most frequently 70–150 (Kobayashi 1933). *P. pungitius* found on the island of Hokkaido, having body length of 37–61 mm, contains 44–82 eggs in its ovaries (Goto et al. 1979). The only exception is *P. sinensis* Guichenot originating from the Kamokawa stream in Japan, attaining lengths of 40–60 mm, which has the most eggs, a maximum of 232 having been found in April. The greatest number of maturing fish can be found there towards the end of May, the first fully mature fish appearing in June (Tanaka and Hoshino 1979). It is most probably the warmer insular climate which favours the extended, lasting almost 8 months spawning. Sticklebacks spawn in June and July under laboratory breeding conditions of 18.5°C. Based on the number of living larvae, Ku-

lamowicz (1959) states that in artificial conditions, only about 20 eggs are hatched from one female.

The quantity of eggs produced by sticklebacks from the Puck Bay increases faster than the length of fish. The other authors indicate straightforward character of this relation (Table 4). Although the relation between increased fecundity and weight is generally presented as proportional and uniform growth, in the case of the present data, it is of a curvilinear character ($r = 0.98$; $p < 0.01$; $n = 465$), suggesting that the fish weight is a better index with which to define reproductive possibilities than length. In view of the maturation of gonads, during the reproductive season, the female's weight increased by over 10% in relation to the winter months. Thus, most of the annual increment of weight is due to the production of eggs, faster body growth taking place only on completion of spawning. The somatic growth of mature females is thus much less than in the males (Griswold and Smith 1973).

Table 4

Character of relationship between fecundity and length reported by different authors

Function	Correlation coefficient	Source
$F = 0.22 \cdot L + 29.12$	$r = 0.74$	Coad and Power (1973)
$F = 2.37 \cdot L - 79.75$	$r = 0.71$	Griswold and Smith (1973)
$F = 2.857 \cdot L - 55.134$	$r = 0.89$	Chae and Yang (1993)

Favourable conditions for the growth and reproduction of sticklebacks exist probably in the Puck Bay. The Baltic specimens greater than 55 mm (the largest caught was 57 mm in size) can theoretically produce a similar quantity of eggs as *P. sinensis* Guichenot. Lack of information on *P. pungitius* in other brackish water basins precludes comparison with representatives of the species inhabiting similar environments. However, reproduction of sticklebacks found on three different continents is similar, irrespective of the living conditions or phenotype of fish.

Lack of data on the subject of the age of females studied precludes the determination of the influence of age on fecundity. In freshwater roach (*Rutilus rutilus*), age does not play a role in fecundity (Załachowski 1961) and the increase in the number of eggs produced with that of age is the result of growth in body size. Prior to maturity most of the available energy (obtained from food) is spent on growth and only after maturity on the production of gonads and spawning (Nikolsky 1963). Somatic growth is most intensive during the first years of life, when the majority of *P. pungitius* first attain sexual maturity. After the first year, the growth rate slows down considerably, then ceases almost totally (Jones and Hynes 1950). Thus the ability to reproduce does not depend on longevity, but the attaining of an adequate body size.

The size of the eggs is similar for the various species of sticklebacks. Nelson (1968) analysed the eggs of the deep-water population of *P. pungitius* from Crooked Lake, their diameters varied from 1400 to 1800 μm . A similar size (1800 μm) is attained by the eggs of *P. sinensis kaibarae* (Tanaka), but only after being laid in the nest. The eggs swelled due to the absorption of water (Chae and Yang 1993). In Lake Superior Griswold and Smith (1973) found the fish with the largest eggs, with a diameter of almost 2000 μm . Sticklebacks caught in the same time on the eastern coast of Canada (Coad and Power 1973) had fairly small eggs. With a body size similar to the Baltic individuals, these fish had also low fecundity. This may be due to the severe climate of the region, as the energy resources required in the production of eggs are mainly utilized during the short season of growth (Coad and Power 1973). According to Staff (1950) and Kulamowicz (1959) the size of eggs most frequently noted in the stickleback are those with a diameter of barely 1000 μm . The size of eggs in all the ninespine stickleback's populations studied was not related to the size of the fish.

Some of the oocytes present in the ovaries may become atrophied, this phenomenon being noted in some females studied during spawning. It has also been noted frequently in female sticklebacks immediately prior to spawning. The reduction of the number of eggs is from 24 to 39%, irrespective of the size of the fish. This is considered to be a physical reaction to the pressure resulted by the maturing of ovaries increasing their volume (Vladykov 1956).

P. pungitius is a plastic species with a wide spectrum of occurrence and numerous possibilities of adaptation. One of these is the high species fecundity, which denotes the ability to protect its reproductiveness and in effect its high efficacy as well as the maintaining of the size of its population in the face of the unfavourable external conditions. The relatively low fecundity in Gasterosteidae is compensated by the highly organised reproduction strategy.

CONCLUSIONS

1. Maximum absolute fecundity of the ninespine stickleback in the Puck Bay is 199 eggs.
2. The absolute fecundity is related to the size of fish. Fecundity increases faster than length and weight according to the logarithmic functions: $F = 1.8052 \cdot 10^{-3} \cdot L^{2.71}$ and $F = 103.77551 \cdot W^{0.99}$, respectively.
3. The fecundity of individuals of the same length is primarily dependent upon their weight.
4. The relative fecundity is 109 eggs (on average) per 1 gram of body weight and has no relationship with body length.
5. The size of mature oocytes is 1366 μm on average and has no relationship with body sizes and fecundity.

6. The absolute fecundity and size of eggs of the ninespine stickleback from Puck Bay (southern Baltic Sea) corresponds with data of other populations from other regions in the world.

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PŁODNOŚĆ CIERNICZKA (*PUNGITIUS PUNGITIUS* L., 1758) Z ZATOKI PUCKIEJ

STRESZCZENIE

Materiał zbierano w okresie wiosenno-letnim w latach 1993 oraz 1995–96. Cierniczek licznie występuje w słonawych wodach Zatoki Puckiej oraz na terenie jej zlewiska. Gatunek ten jest popularny szczególnie w zarośniętej strefie litoralnej. Jego tarło w zatoce jest wydłużone w ciągu roku, trwa od marca do sierpnia, a składanie ikry ma charakter porcyjny. Płodność tych ryb jest stosunkowo niska, podobnie jak innych gatunków, które uprawiają strategię ochrony potomstwa. Cierniczki składają do 199 jaj, co oznacza, że ich płodność jest wyższa niż płodność cierniczek z Ameryki Północnej i Europy Wschodniej oraz nieco niższa niż u jednej z odmian japońskich. Ilość produkowanej ikry rośnie ze wzrostem ryby wg funkcji logarytmicznej. Zależność między płodnością absolutną a długością oraz masą ciała opisują odpowiednio równania: $F = 1.8052 \cdot 10^{-3} \cdot L^{2.71}$ oraz $F = 103.77551 \cdot W^{0.99}$. Płodność ryby zależy przede wszystkim od jej masy. Rozmiary ciała i ilość produkowanych jaj nie mają wpływu na ich wielkość.

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