Reproductive cycle and the related spatial and temporal distribution of the ninespine stickleback (*Pungitius pungitius* L.) in Puck Bay

OCEANOLOGIA, 44 (4), 2002.
pp. 475–490.

KEYWORDS
Ninespine stickleback
Breeding period
Spawning
Stages of maturity
Puck Bay

Ewa Sokołowska
Institute of Oceanology,
Polish Academy of Sciences,
Powstańców Warszawy 55, PL–81–712 Sopot, Poland;
e-mail: ewakub@cbmpan.gdynia.pl

Krzysztof E. Skóra
Marine Station,
Institute of Oceanography,
University of Gdańsk,
Morska 2, PL–84–150 Hel, Poland;
e-mail: oceks@univ.gda.pl

Manuscript received 3 July 2002, reviewed 23 October 2002, accepted 28 October 2002.

Abstract

The cycle of gonad development and related changes in the length structure and spatial-temporal distribution of ninespine sticklebacks (*Pungitius pungitius* L.) in Puck Bay were studied. Observations were carried out in the shallow shore zones, as well as in the deeper epipelagic zone of the Bay. Ninespine sticklebacks reproduce in the brackish environment of Puck Bay, breeding in its warmer, inshore zones. Reproduction takes place in the spring and summer months, from April to July. One female spawns several clutches of eggs during one breeding season. The average length of ninespine sticklebacks in Puck Bay was about 40 mm, and the sex ratio in the population was close to 1:1. However, both length structure and sex ratio were subject to local and periodic variations, resulting from possible breeding-related territorial divisions. Higher gonadosomatic indices in females in early spring represented the transition of fish to the advanced vitelligenous phase. The lowest GSI of males during the breeding season indicated the termination of spermatogenesis. The completion of spawning in August started a new process of gonad restoration to prepare the fish for the next breeding season.

1. Introduction

The ninespine stickleback (*Pungitius pungitius* L., family: *Gasterosteidae*) has a circumpolar distribution and is one of the most widespread species in the temperate and cool zones of the Northern Hemisphere (Wootton 1976, Zjuganov 1991). It occurs in both fresh and brackish waters, as well as inshore zones of the sea.

The ninespine stickleback is regarded as the smallest freshwater fish occurring in Polish inland waters of the northern and central part of the country. Recent studies of *P. pungitius* distribution have revealed new localities in central and south-western Poland: this could be an indication of its expansion deep inland (Kotusz et al. 1997, Kowalski et al. 1997). It is also a component of the Baltic Sea fauna, mainly in the bays and coastal lagoons. The sticklebacks are very widespread and dominate during spring and summer in Puck Bay (Skóra 1993a).

The life history and reproductive behaviour of freshwater *Pungitius* spp. from various parts of North America and Asia have been studied (Nelson 1968, McKenzie & Keenleside 1970, Coad & Power 1973, Griswold & Smith 1973, Tanaka & Hoshino 1979, Chae & Yang 1993). However, little is known about this species in Polish waters, the information concerns mainly freshwater forms (Wolski 1927, Kaj 1951 and Kulamowicz 1959, 1964). Apart from the paper by Sokołowska & Skóra (2001), no other information is available on the reproduction of this fish in the southern Baltic. Their breeding success is probably the result of their reproductive strategy. Their seasonal dominance and thus their growing importance in the study area prompted this study on their reproductive capabilities.

2. Material and methods

2.1. Study area

Puck Bay is located in the western region of the Gulf of Gdańsk (southern Baltic Sea), and is separated from the open sea by the Hel Peninsula (Fig. 1). An underwater shelf, the Ryf Mew, divides the basin into an inner part called Puck Lagoon and an outer 'marine' part. The outer part is deeper, warmer during winter, and colder in summer than Puck Lagoon. This is relatively shallow, which makes it more sensitive to changes in the weather. In winter the waters of the Lagoon cool readily, and also heat up more quickly during summer. The salinity of both parts is similar, but locally or seasonally the salinity of Puck Lagoon may fall as a result of temporary or periodic increases in freshwater inflow from rivers or melting ice (Nowacki 1993).

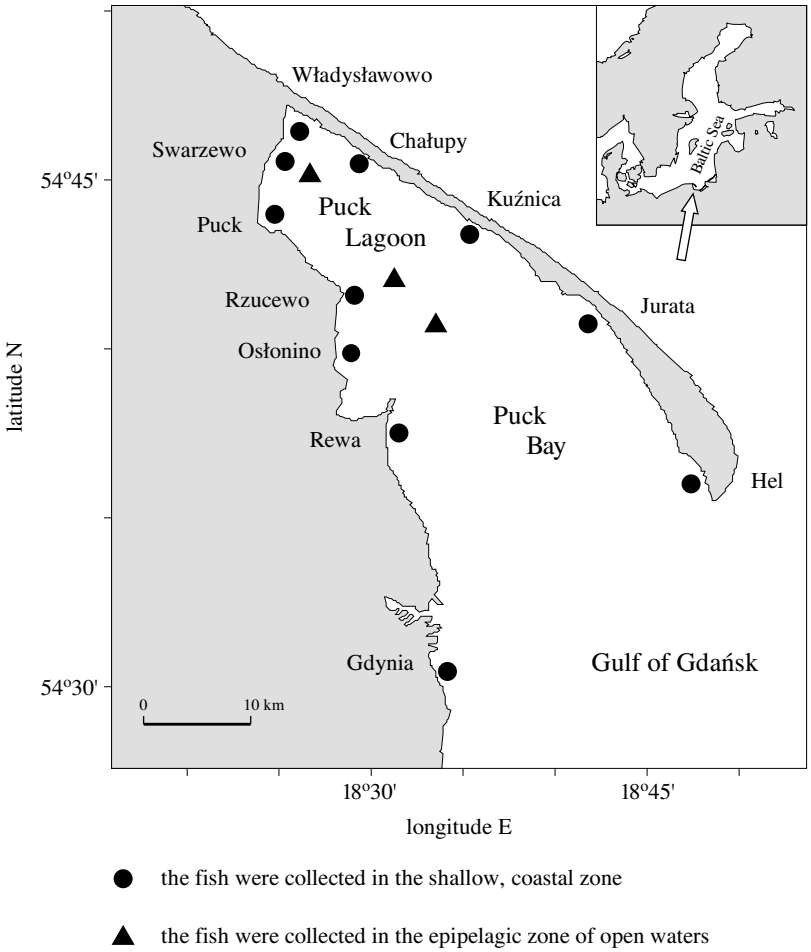

Fig. 1. Sampling stations in the Puck Bay

The hydrophysical characteristic of Puck Bay, the limited water exchange with the rest of the Gulf of Gdańsk, and the relatively homogenous ecological conditions have favoured the development of diverse flora and fauna. The basin used to be excellent for the reproduction of many species of freshwater, estuarine and marine fish (Skóra 1993b). In recent decades, however, increasing eutrophication and pollution in the Bay has resulted in marked changes in the ecosystem structure (Wiktor 1976). As a consequence, the biodiversity of ichthyofauna has altered. The basin, once rich in different fish species of commercial value, has lost its importance as an attractive fishery area. Many species have been replaced by others with a greater adaptive capacity, but which are commercially insignificant (Wiktor 1976, Skóra 1993b).

2.2. Sampling

The ninespine sticklebacks were collected once a month throughout the year (1993). 16 sampling stations were located in the inner and outer parts of Puck Bay (Fig. 1) covering:

- mainly the shallow littoral inshore zone (approaching 2 m depth) at Hel, Jurata, Kuźnica, Chałupy, Władysławowo, Swarzewo, Puck, Rzucewo, Osłonino, Rewa and Gdynia (near harbours and beaches);
- deeper epipelagic zones of the middle part of the basin (approaching 5 m depth) off Swarzewo and Rzucewo;
- the shallow of the Ryf Mew in the central part of the Bay.

The epipelagic zone was sampled only during the breeding period, in May and June. A lift net and fine-mesh trawl were used in the shallow coastal zone and a Rectangular Midwater Trawl (RMT) in the epipelagic zone. The mesh diameter of all the nets was 1 mm. Immediately after they were caught the fishes were preserved in 4% formalin.

Total body length, total body weight and gonad weight were measured to the nearest mm and mg, respectively. In order to define the spatial and temporal distribution of the fish in Puck Bay, the length frequency was divided into 5 mm length classes (25: 21–25 mm, 30: 26–30 mm, 35: 31–35 mm, 40: 36–40 mm etc.). Furthermore, the sex ratio for each season and sampling site was determined. Ovarian maturity stages in the annual cycle were determined on the basis of the 6-degree scale of ovarian maturity established for the ninespine stickleback by Griswold & Smith (1973) and modified in this study (based mainly on the appearance and external features of ovaries). For comparison of seasonal gonad changes, the gonadosomatic index was measured as GSI = (weight of both gonads/total body weight) $\times$ 100.

3. Results

3.1. Length structure

Altogether, 729 *P. pungitius* were subjected to length analysis. The greatest number was caught at Kuźnica, and the most abundant catches were taken in April. The length distribution during the year is shown in Fig. 2. The average length of the ninespine sticklebacks in Puck Bay was 40 mm. The largest specimen was 58 mm long, the smallest 24 mm. Individuals in the 40 mm and 45 mm length classes dominated. Fry appeared for the first time in July, and again in October. The most extensive length spectrum was noted in July, whereas in the winter months the population consisted mainly of individuals in the 40 and 45 mm groups.

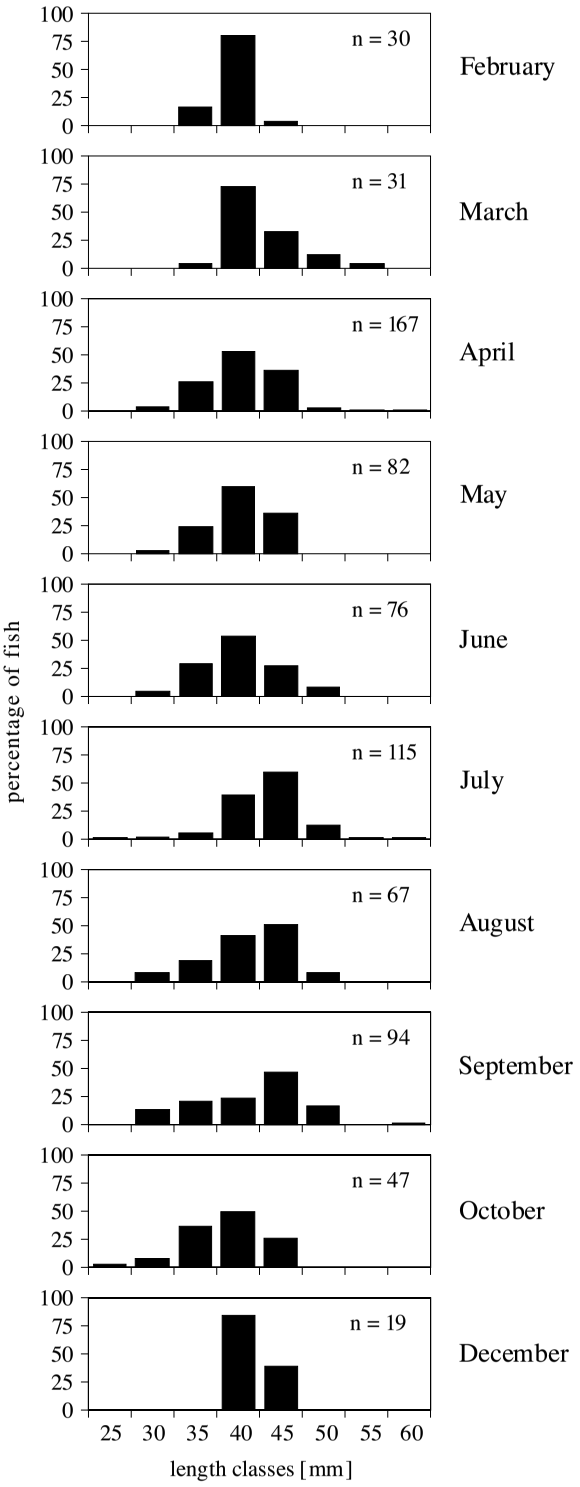

Fig. 2. Seasonal changes in the length frequency distribution of *P. pungitius* (n – number of fish, January – no fish found, November – only one individual of 34 mm length was caught)

There were no *P. pungitius* in the shore zone in January and November (except one of 34 mm taken at Kuźnica in November).

In the epipelagic zone of the Bay, specimens 40 and 45 mm long dominated at the Ryf Mew during the reproductive period. In the regions of Swarzewo and Rzucewo almost half of the sampled *P. pungitius* were shorter than 35 mm.

3.2. Sex ratio

The sex of 729 fishes was analysed. The whole group consisted of 371 females and 358 males. On an annual basis the sex ratio was close to 1:1. The number of females rose gradually from February to May, and then fell from July to October. In June the males dominated. No sticklebacks were caught in January, and only one female was caught in November (Fig. 3).

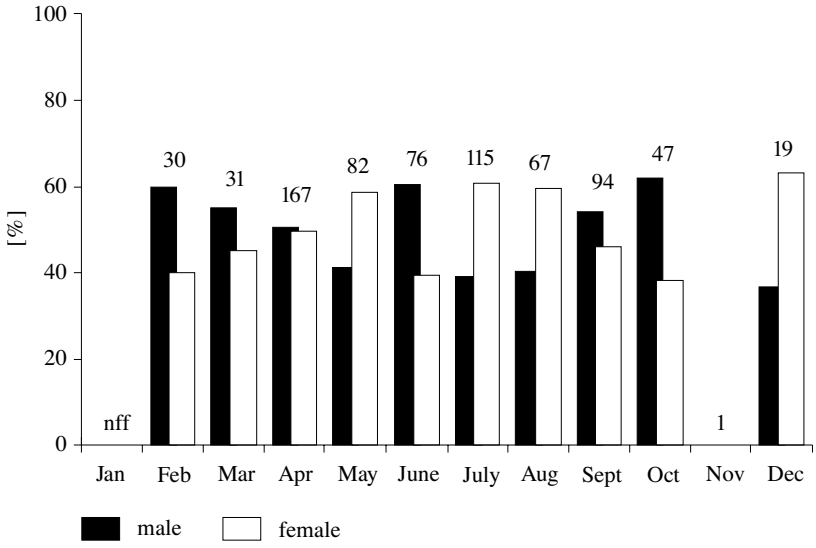

Fig. 3. Sex ratio of *P. pungitius* during the annual cycle in Puck Bay (numbers over columns-total number of fish, nff-no fish found, in November only one female was caught)

The sex ratio varied between the sampling stations (Fig. 4). Mainly females were present in the inner part of Puck Lagoon; at Władysławowo females made up above 70% of the catch. In the Rewa–Gdynia area males were more numerous. Along the Hel Peninsula the sex ratio was close to 1:1. During the reproductive period, females dominated at the Ryf Mew, but there were more males in the deeper zone at Rzucewo.

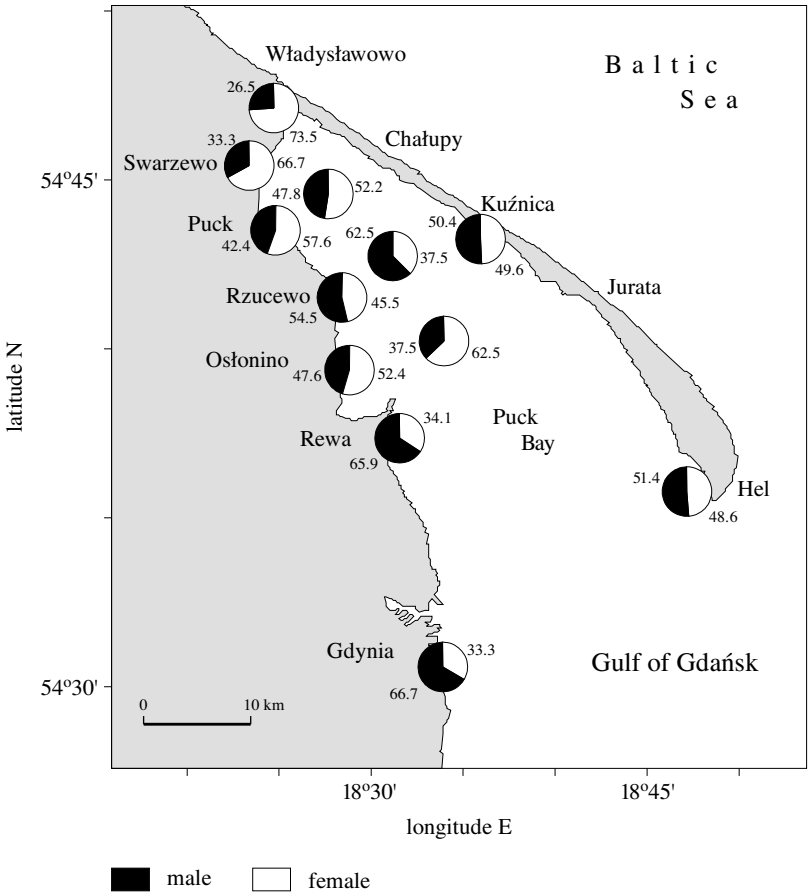

Fig. 4. Sex ratio of *P. pungitius* (%) in different regions of Puck Bay (number of fish in the coastal zone: Hel – 70, Kuźnica – 337, Władysławowo – 49, Swarzewo – 6, Puck – 59, Rzucewo – 22, Osłonino – 21, Rewa – 44, Gdynia – 6; number of fish in the epipelagic zone: Swarzewo –23, Rzucewo –48, Ryf Mew – 40). The graphs for Chałupy and Jurata are not presented due to the low number of fish – two females were caught at Chałupy and one male and one female at Jurata

3.3. Gonadosomatic indices (GSI)

The changes of GSI for females and males were studied during the year (Fig. 5). In the March–July period, the GSI image for females was distinctly related to the state of advanced vitellogenesis of oocytes. The GSI of males showed the reverse tendency: there was a gradual drop during the February–April period, the GSI were lowest in the reproductive season and an increase followed spawning.

In the coastal zone in Kuźnica, the highest values were noted in May, June and July for females in the 40, 45 and 50 mm length classes. During

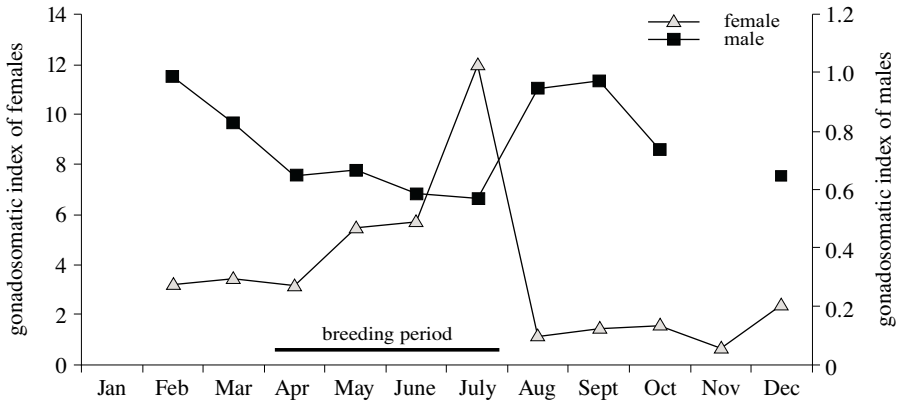

Fig. 5. Seasonal changes of gonadosomatic indices (GSI) of *P. pungitius* in Puck Bay

the breeding period in the deeper zones of the Bay, where females in the 35, 40 and 45 mm length classes occurred, the highest values were noted at Swarzewo (May). GSI recorded at the Ryf Mew were almost 50% lower, but the lowest GSI of all were noted at the deepest station at Rzucewo in June.

3.4. Stages of ovarian maturity

The stages of ovary development were determined according to the 6-degree scale established by Griswold & Smith (1973) for *P. pungitius* from The Apostle Islands area of Lake Superior. The scale was considerably modified for the brackish water population in Puck Bay:

I. Immature

The ovaries are very small, elongated, white organs. They consist only of immature, non-yolky oocytes, opaque, invisible to the naked eye. It is difficult to separate them from the body cavity (Fig. 6).

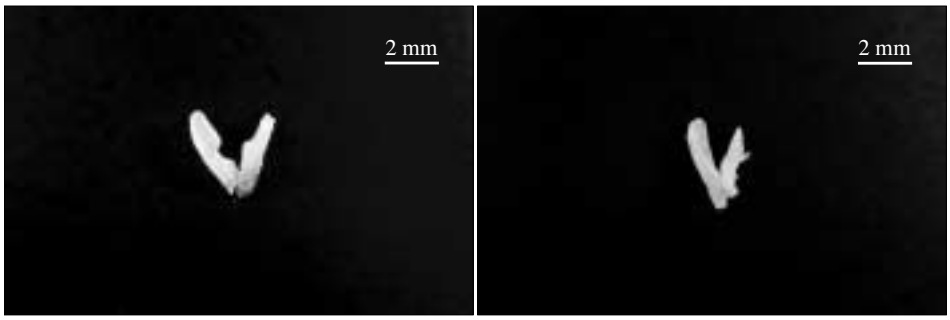

Fig. 6. Ovaries of *P. pungitius* in the immature (I) stage of maturity

II. Intermediate

The ovaries are small, slender, elongated, and frequently similar in shape and appearance to the testes, and may be yellowish, greyish or white in colour. The ova, which are difficult to differentiate, have the structure of a compact, gluey mass of cells; they gradually become transformed into whitish or yellowish grains with a compact structure. Initially opaque, they become transparent with time (Fig. 7).

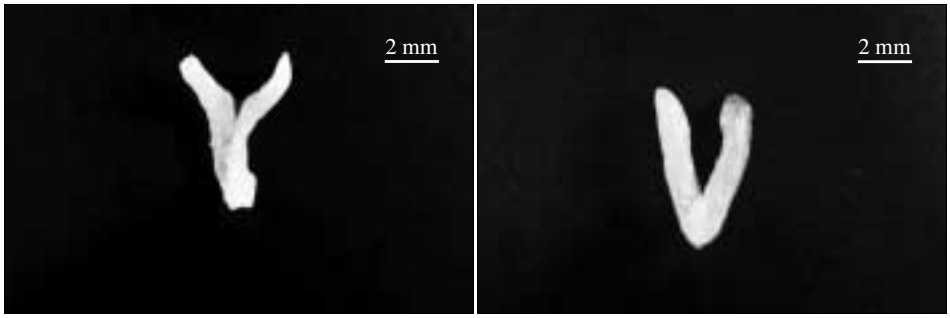

Fig. 7. Ovaries of *P. pungitius* in the intermediate (II) stage of maturity

III. Maturing

The fish is thicker. The ovaries are well formed, turgid and yellow. The eggs are spherical, transparent, most frequently yellow, and are readily separated. The ova vary widely in size. Agglomerations of white, immature oocytes in stage I (immature) and II (intermediate) occur between the maturing oocytes. Single large ova, coloured from yellow to dark yellow may occur during this phase (Fig. 8).

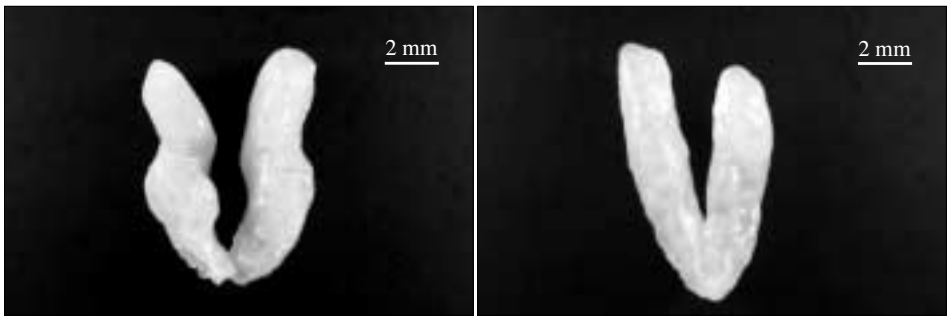

Fig. 8. Ovaries of *P. pungitius* in the maturing (III) stage of maturity

IV. Ripe

The fish is gravid, the ovaries are very large, and the ova are conspicuous through the taut skin of the ventral covers. The ovaries fill the body cavity

Fig. 9. Gravid female of *P. pungitius* in the ripe (IV) stage of maturity (made up ovaries)

to a considerable extent, displacing the internal organs upwards (Fig. 9). A single conspicuous golden-coloured oil globule appears in the yolk. The mature oocytes, the first to be expelled, are usually packed in layers in the upper part of the ovaries closest to the oviduct (Fig. 10). The ova break from the follicles and flow from the oviduct when the sides of the fish are pressed.

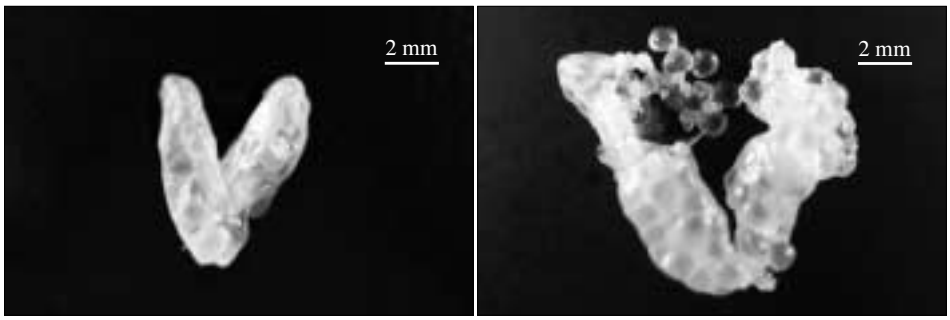

Fig. 10. Ovaries of *P. pungitius* in the ripe stage of maturity

V. Partly spent

The first portion of ripe oocytes has been spawned. Only the anterior part of the ovary contains ripe ova and the rest is flaccid. The previous stages of maturity are present in the ovaries.

VI. Spent

After spawning the ovaries are flaccid, and white or yellowish. The resorbing ova remnants are found in the ovaries. Ova maturing for the next intermediate stage are already visible to the naked eye.

The development of the ovaries of *P. pungitius* was observed during the annual cycle (Fig. 11). The females were able to spawn for almost four months of the year in Puck Bay. The appearance of fat droplets in the yolk indicated the approaching completion of gametogenesis and the onset of spawning (phase IV). The number of spawning fish was greatest in June and July although the first fully mature females had already appeared at the Hel and Kuźnica stations towards the end of April. The fish spawned until the end of July. Females with partly spent gonads (phase V) together with mature females constituted almost 100% of the population in July.

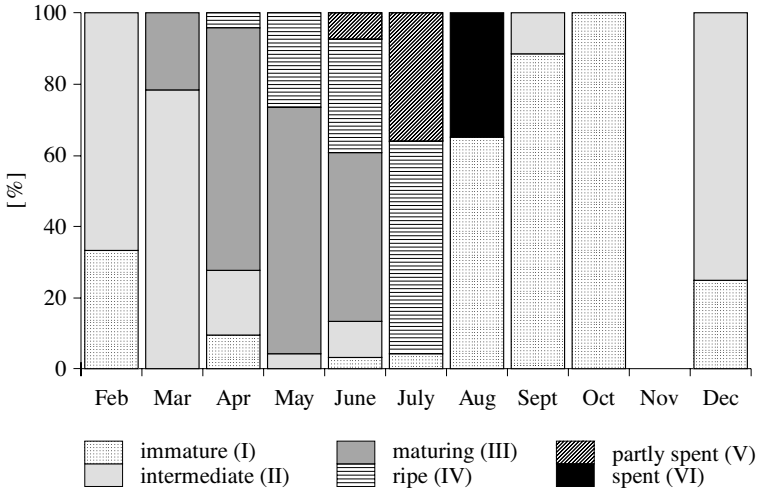

Fig. 11. Frequency of ovaries maturity stages of *P. pungitius* during the annual cycle (in November only one immature female was caught)

The presence of partly spent females shows that spawning in this species is portioned: a female can spawn several times during one breeding season. After one clutch of eggs has been laid in the nest the next batch of oocytes begins to mature in the ovaries. The first fry appeared at the end of July and completely spent females were observed in August. When spawning was complete (phase VI), the remains of the ovarian follicles and oocytes were gradually resorbed in the ovaries. The first females with immature ovaries were observed in August after which the restoration of ovaries and oocytes for the next spawning season started. Immature and intermediate stages were characteristic of ovaries in autumn and winter. Immature, non-yolky oocytes were present in the ovaries throughout the year. At the start of the intermediate stage (II), oocytes were also present at the vacuolisation stage during which the primary yolk was synthesised. The proportions of these two phases changed with time. In March, the ovaries began to mature when

the water temperature was increasing with increasing daylength. During the maturation phase (III) the oocyte pool was supplemented by eggs with secondary yolk. In this period the ovaries substantially increased in size and became intensively yellow or orange.

4. Discussion

The present observations indicate that ninespine sticklebacks (*P. pungitius*) occurred in the inshore waters of the Bay throughout most of the year, but were most numerous in the spring and summer, i.e. during the reproductive period. In winter the abundance of these fish dropped suddenly. The absence of *P. pungitius* in the shore zone in winter may have been due to their migration to deeper water layers. High numbers of the species in summer and lower numbers in winter in shallow waters had earlier been found in brackish water (Nellbring 1988, Skóra 1993a, Sokołowska & Skóra 2001) and freshwater populations (Griswold & Smith 1973).

The average length of the ninespine stickleback in Puck Bay was 40 mm. The young fish began to appear in the population of older fish towards the end of July, but there were no fry smaller than 20 mm in the shore zone during the spawning period. According to Delbeek & Williams (1987), the fry remain close to the males and do not swim far from the nest. For a certain time the offspring continue to feed in groups in the dense underwater meadows outside the shore zone, so they are only occasionally found in open areas. When young threespine sticklebacks leave the spawning area towards the end of August, the fry of ninespine sticklebacks still remain in safe quarters. According to Jones & Hynes (1950) the offspring do not move into open waters until they have a length of about 15 mm. Thus, they remain close to the guarding males and nests until the autumn (Delbeek & Williams 1987).

This study has shown that the overall annual sex ratio in the Puck Bay population of ninespine sticklebacks was close to 1:1. This result is in agreement with the theory about the relation between both sexes in fish populations reproducing under natural conditions and not commercially exploited (Starmach 1951). However, there were some fluctuations in the sex ratio, e.g. the increasing number of females in February-May or their domination in the inner part of Puck Bay. This can be explained by the territorial segregation of the sexes during spawning. Females, devoting much energy to egg formation, feed intensively mainly close to the shore. Males look after the spawn and fry and remain close to the nests, amongst dense growths of algae, outside the shore zone (Delbeek & Williams 1987). This was the case here, when the males dominated in the deeper waters of the Bay.

The June catches, which were mainly carried out in the deeper epipelagic zone, at the Rzucewo station, resulted in unexpected male domination in this month.

According to the notes of Suworow (1954) and Rutkowicz (1982), and data of Gubernator (1981), Baltic ninespine sticklebacks reproduce in June–July, April–June or April–August. The previous paper of Sokołowska & Skóra (2001) and the present studies demonstrated that the breeding season in the Bay begins at the end of April and ends in July. The first fully mature females were observed at Kuźnica. At the end of August the ovaries of all the females at Kuźnica were already in the immature stage, whereas the earlier spent stage was still dominant at Puck. At Kuźnica the sexual maturity cycle was probably completed earlier than in the other parts of the Bay. Small *P. pungitius*, 25–27 mm long, which appeared at Kuźnica at the end of July, may have originated from the April or May hatch. Gubernator (1981) and Nellbring (1988) also observed that the summer fry were a product of the May–June spawning.

Spawning of sticklebacks is related to day-length and temperature. The shortening of the night in spring and summer, together with the rising water temperature, is a signal to commence spawning. Leiner (1934) stated that ninespine sticklebacks kept in the laboratory also spawn in the autumn. He concluded that this species grew quickly (5.6–5.9 cm in 7 months) and that the small individuals appearing in the early spring were products of the autumn spawning. However, autumnal breeding of ninespine sticklebacks under natural conditions has not been confirmed by any other author. The study by Jones & Hynes (1950) showed that small ninespine sticklebacks (33 mm) were at least one year old. Gubernator (1981) also analysed small individuals (21–27 mm), most probably 2.5–3.5 years old. These data may indicate that dwarfing occurs in some fishes in a brackish-water environment. In the present study, spring observations confirmed the presence of several fish, up to 30 mm in length, but these fish did not originate from the autumn spawning. In the autumn gonads were in the immature or intermediate stage.

Both Gubernator (1981) and Nellbring (1988) agreed that the ninespine stickleback does spawn in the Baltic, despite the fact that they failed to find its nests. The occupation of territories, nest building or care of offspring are also difficult to observe, because they take place deeper than the shore zone. On the other hand, spawning (stages: ripe and partly spent) and post-spawning females (spent stage), as well as coloured, breeding males were observed in the present study. This suggests that reproduction does take place in Puck Bay. During the summer collection of ninespine

sticklebacks for fecundity determination (Sokołowska & Skóra 2001), several nest-like structures made from plaited plant fragments bound together with a mucus substance were found near the mouth of the Płutnica river.

The gonadosomatic index of females and males differ considerably as a result of different gonad weights in the two sexes. In females, the ovaries can make up as much as 20% of the total body weight during the reproductive period. On the other hand, the decrease of the GSI in males in April–July is due to the light weight of spermatozoa, which are the most abundant in the testes during breeding. The spermatozoa are the lightest and smallest cells, which finally differentiate during the spermatogenesis (Baggerman 1990). Early spermatogenetic stages, e.g. spermatogonia and spermatocytes, began to dominate after spawning in August.

The gonadosomatic indices varied in the ninespine sticklebacks from the different regions of Puck Bay. During summer, in the inshore zone at Kuźnica and in the open waters of Swarzewo and the Ryf Mew, the indices were two and even three times higher than in deeper waters (Rzucewo). There were no spawners in the deeper zones, which were occupied by maturing females. On the other hand, sexually mature individuals preferred the warmer inshore zones, where they dominated. What is more, the fish inhabiting the deeper pelagic zone were smaller than those from the inshore zone. The habitat segregation of the sexes during the breeding season is the consequence of their reproductive behaviour. The 'planned' reproductive strategy is one of several factors favouring the species, even in anthropogenically altered waters.

Acknowledgements

The authors wish to thank to Dr Ewa Kulczykowska for her critical comments on the manuscript. Thanks are also due to Dr Adam Sokołowski and Maciej Szulwach for taking the photographs of the ninespine stickleback gonads.

References

Baggerman B., 1990, *Sticklebacks*, [in:] *Reproductive seasonality in teleosts: environmental influences*, A. D. Munro, A. P. Scott & T. J. Lam (eds.), CRC Press, Boca Raton, 79–107.

Chae B. S., Yang H. J., 1993, *Spawning and growth of eightspine stickleback, Pungitius sinensis kaibarae (Tanaka) (Gasterosteidae, Pisces), in the Chayang Stream, a tributary of Kumho River, Korea*, Korean J. Zool., 36, 181–192.

Coad B. W., Power G., 1973, *Observations on the ecology and meristic variation of the ninespine stickleback, Pungitius pungitius (L., 1758) of the Matamek River System, Quebec*, Amer. Midl. Natur., 90, 498–503.

Delbeek J. C., Williams D. D., 1987, *Food resource partitioning between sympatric populations of brackishwater sticklebacks*, J. Anim. Ecol., 56, 949–967.

Griswold B. L., Smith L. L. Jr., 1973, *The life history and trophic relationship of the ninespine stickleback, Pungitius pungitius, in The Apostle Islands area of Lake Superior*, Fish. Bull., 71, 1039–1060.

Gubernator A., 1981, *The age, growth rate and food of the ninespine stickleback (Pungitius pungitius L., 1758) from Puck Bay*, M. Sc. thesis, Inst. Oceanogr. Uniw. Gd., Gdynia, 66 pp., (in Polish).

Jones J. W., Hynes H. B. N., 1950, *The age and growth of Gasterosteus aculeatus, Pygosteus pungitius and Spinachia vulgaris, as shown by their otoliths*, J. Anim. Ecol., 19, 59–73.

Kaj J., 1951, *Pygosteus pungitius L. in the Poznań area*, Pr. Kom. Biol. P. T. P. N., XII, 111–121, (in Polish).

Kotusz J., Kusznierz J., Błachuta J., 1997, *Occurence of Pungitius pungitius (L.) in Silesia (SW Poland)*, Prz. Zool., XLI (3)–(4), 247–250, (in Polish).

Kowalski M., Gwardjan M., Klauzińska M., Ostrach-Kowalska A., 1997, *Station of Pungitius pungitius in the Nida basin (Province Kielce)*, Kulon, 2 (1), 91–92, (in Polish).

Kulamowicz A., 1959, *The ninespine stickleback-Pygosteus pungitius L. from the Rydwan pond in the Bzura river basin*, Zesz. Nauk. Uniw. Łódz., 5, 115–131, (in Polish).

Kulamowicz A., 1964, *Nine-spined stickleback, Pungitius pungitius L. (Gasterosteidae), in the Basin of Pilica River*, Prz. Zool., VIII (3), 265–268, (in Polish).

Leiner M., 1934, *Die drei europäischen Stichlinge (Gasterosteus aculeatus L., Gasterosteus pungitius L. und Gasterosteus spinachia L.) und ihre Kreuzungsprodukte*, Z. Morph. Ökol. Tiere, 28, 107–154.

McKenzie J. A., Keenleside M. H., 1970, *Reproductive behavior of ninespine sticklebacks (Pungitius pungitius (L.)) in South Bay, Manitoulin Island, Ontario*, Can. J. Zool., 48, 55–61.

Nellbring S., 1988, *Abundance, biomass, and seasonal variation of fish on shallow soft bottoms in the Askö area, northern Baltic proper. Quantitative and qualitative studies of fish in shallow water, northern Baltic proper*, Sarsia, 70, 217–225.

Nelson J. S. 1968, *Deep-water ninespine sticklebacks, Pungitius pungitius, in the Mississippi drainage, Crooked Lake, Indiana*, Copeia, 2, 326–334.

Nowacki J., 1993, *Morphometry of the Bay*, [in:] *Puck Bay*, K. Korzeniewski (ed.), Fund. Rozw. Uniw. Gd., Gdańsk, 71–78, (in Polish).

Rutkowicz S., 1982, *The Encyclopaedia of marine fish*, Wyd. Mor., Gdańsk, 60, 238–239, (in Polish).

Skóra K. E., 1993a, *Ichthyofauna*, [in:] *Puck Bay*, K. Korzeniewski (ed.), Fund. Rozw. Uniw. Gd., Gdańsk, 455–467, (in Polish).

Skóra K. E., 1993b, *Reasons for the changes in the composition and quantity of ichthyofauna resources in Puck Bay*, [in:] *Ecology of the land, coastal and marine regions of the Baltic-protection and development*, M. Pliński (ed.), Mater. konf. (Sopot 11–12.12.1992), Gdańsk, 115–128, (in Polish).

Sokołowska E., Skóra K. E., 2001, *Fecundity of the ninespine stickleback (Pungitius pungitius L., 1758) in Puck Bay*, Acta Ichthyol. Piscat., 31 (1), 45–60.

Starmach K., 1951, *Life history of freshwater fish. Sketch of morphology, physiology and biology of freshwater fish*, PWRiL, Warszawa, 182–203, (in Polish).

Suworow E., 1954, *Principles of ichthyology*, PWN, Warszawa, (in Polish).

Tanaka S., Hoshino M., 1979, *Growth and maturity of ninespine stickleback, Pungitius sinensis Guichenot, in the Kamokawa, a streamlet in Toyama Prefecture*, Bull. Toyama Sci. Mus., 1, 19–29.

Wiktor K., 1976, *Changes in the biocoenosis of Baltic coastal and estuarian waters resulting from increased pollution*, Stud. i Mater. Oceanol., 15 (3), 144–168, (in Polish).

Wolski T., 1927, *Contribution to the knowledge of Pygosteus pungitius L. in Poland*, Arch. Hydrobiol. i Ryb., 119–140, (in Polish).

Wootton R. J., 1976, *The biology of sticklebacks*, Acad. Press, London, 130–230.

Zjuganov V. V., 1991, *Fauna of the USSR. Fishes. The sticklebacks family (Gasterosteidae) in the fauna of the world*, Nauka, Leningrad, (in Russian).