Oceanologia (2015) 57, 280—287

Available online at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/oceano

ORIGINAL RESEARCH ARTICLE

Changes in the parasite communities as one of the potential causes of decline in abundance of the three-spined sticklebacks in the Puck Bay

Jolanta Morozińska-Gogol *

Institute of Health Sciences, Pomeranian University in Słupsk, Słupsk, Poland

Received 24 November 2014; received in revised form 4 February 2015; accepted 24 March 2015
Available online 10 April 2015

KEYWORDS
Parasites;
Three-spined stickleback;
Puck Bay;
Baltic Sea

Summary In the past, the Puck Bay was a very important area for freshwater and marine ichthyofauna. Due to anthropogenic degradation of the environment, especially eutrophication, commercially important fish species have lost spawning grounds and their distribution and abundance fell significantly. A sharp increase in the number of *Gasterosteus aculeatus* was recorded since the mid-seventies of the twentieth century. Sticklebacks had become the dominant species and were distributed evenly in the coastal waters. But now, the numbers of sticklebacks are decreasing. In this paper, the parasite community of the three-spined sticklebacks was studied. The values of parasitological indices are counted and compared with previous data. Possible consequences of the harboured parasites for body condition, fecundity and changes in host behaviour are described. Also the other possible reasons for the current reduction in the number of sticklebacks in the Puck Bay are analyzed.

* Correspondence to: Institute of Health Sciences, Pomeranian University in Słupsk, ul. Bohaterów Westerplatte 64, 76-200 Słupsk, Poland. Tel.: +48 59 84 05 910; fax: +48 59 84 05 916.
E-mail address: morgo@onet.eu.
Peer review under the responsibility of Institute of Oceanology of the Polish Academy of Sciences.

Production and hosting by Elsevier

http://dx.doi.org/10.1016/j.oceano.2015.03.001

1. Introduction

Fish from the family Gasterosteidae are distributed worldwide in the Northern Hemisphere and they inhabit freshwater, brackish water and inshore zones of the sea (Wootton, 1976). They are short-living fishes, about 2—4 years (DeFaveri and Merilä, 2013; Voight, 2007). Because of its worldwide distribution, occurrence in various habitats, omnivorous nature and a central position in the food web, three-spined stickleback *Gasterosteus aculeatus* (Linnaeus, 1758) is a very popular model host in ecological parasitology (Barber, 2013).

Parasites are a very important component of biocenosis and good indicators of the environmental changes and ecosystem health (Hudson et al., 2006; Marcogliese, 2002). Some species of parasites play a vital role in the regulation of the abundance of hosts by affecting their growth, fertility and behaviour (Marcogliese, 2004; Pojmańska and Niewiadomska, 2010). They may also change the host's colouration making them easier to be seen and easier to be caught by the other hosts (Pojmańska and Niewiadomska, 2010).

Among the parasites of *G. aculeatus* we found generalists as well as specialists. Some of them can contribute to the reduction of sticklebacks population, e.g., *Schistocephalus solidus* inter alia affect their fertility (Heins and Baker, 2008), *Diplostomum* spp. reduced vision and can lead to blindness (Valtonen and Gibson, 1997; Voutilainen et al., 2009) and *Thersitina gasterostei* reduced respiration (Rokicki, 1994).

Barber (2013) reported that 155 parasites, including 120 metazoans, were recorded from the three-spined sticklebacks worldwide. From Euroasia region 86 metazoan species of parasites were known (Poulin et al., 2011). In Poland, totally 51 species of parasites, including one alien species *Anguillicola crassus* Kuwahara, Niimi & Itagaki, 1974, have been noted (Morozińska-Gogol, 2006).

A significant increase in the number of the three-spined sticklebacks was recorded since the mid-seventies of the twentieth century. They became the dominant species and were distributed evenly and in large numbers in the coastal waters of the southern Baltic Sea, especially in the Puck Bay (Skóra, 1992, 1993). The next change in the composition of ichthyofauna of the Puck Bay was observed in the nineties, when the alien invasive species, the round goby *Neogobius melanostomus* (Pallas, 1811), appeared and spread rapidly (Sapota, 2004). Over the last few years, changes in the occurrence of *G. aculeatus* in the coastal waters are observed. Formerly sticklebacks occurred in large number in the Gdynia Marina and the fishing port in the Puck for the whole year. Presently, their abundance in these locations has significantly decreased. Reduction in the number of sticklebacks in these areas could be a result of changes in the abiotic and biotic elements of the environment, including relationships with other species, like competition, predation and parasitism.

The first information about parasites of stickleback from the Polish Coast was printed in 1883 by Girdwoyń, who described the plerocercoids *S. solidus*. Afterwards parasitofauna of *G. aculeatus* from the Polish coastal waters was studied in detail by Fidelus (1975), Morozińska-Gogol (1999, 2002) and also by Sulgostowska and Vojtkova (2005), when the sticklebacks were the dominant fish species in the habitat. More than 30 species of parasites of the sticklebacks were recorded from the entire Polish coastal waters, including lagoons, estuaries and coastal lakes (Morozińska-Gogol, 2006).

In this paper, the recent decline in the abundance of the three-spined sticklebacks in the Puck Bay is reported. Some of the parasites that infected sticklebacks caused health effects and induced changes in host behaviour. This research is carried out for a better understanding of the role of the parasite communities in the fluctuations in host abundance, their health and circulation of the parasites in the food web of the ecosystem of the Puck Bay.

2. Study area

The Puck Bay is the western part of the Gulf of Gdańsk. This reservoir is separated from the open sea by the Hel Peninsula. The border between the Puck Bay and the Gulf of Gdańsk is a line connecting the tip of the Hel Peninsula with Kamienna Góra — the hill in Gdynia. The sandbank, Rybitwia Mielizna, divides the Puck Bay into the inner and outer Puck Bay. The inner part is also called the Puck Lagoon. Both parts have different conditions. The outer eastern part connected with the Gulf of Gdańsk is deeper with higher salinity and lower summer temperature. The Puck Lagoon is a shallow semi-enclosed basin with less salinity and more susceptibility to changes in weather and strong anthropogenic pressure (Kruk-Dowgiałło and Szaniawska, 2008).

In the past this basin was inhabited by many species of freshwater, migratory and marine fish (Skóra, 1993). From the 1970s, adverse changes in the ecosystem structure because of increasing eutrophication and pollution were observed. Structure of ichthyofauna has changed, including the disappearance of many fish species and expansion of Gasterosteidae and also Gobiidae (Kruk-Dowgiałło and Szaniawska, 2008; Skóra, 1993). The biomass of the three-spined stickleback was 99% of all fish biomass in this basin in the 1990s (Skóra, 1993).

3. Material and methods

The three-spined sticklebacks were caught with a manual fishing lift net in two ports of the Puck Bay, in the Gdynia Marina (54°31′0″N, 18°33′12″E) situated in the outer Puck Bay and in the fishing port in Puck (54°43′22″N, 18°24′40″E) located in the Puck Lagoon. Fish were caught from the Gdynia in November 2012 and April 2013 and from the Puck in April and June 2013. In the remaining months fishing of the samples was unsuccessful.

Lateral plate morphs were determined, where *trachurus* is a fully plated form, *semiarmatus* is partially plated on the pectoral and caudal parts of the body, and *leiurus* is a low plated form (Bańbura and Bakker, 1995). Fish were weighed and measured. Sex of the sticklebacks was also determined. Fulton's condition factor (CF) was calculated with the formula: $CF = 10^5 \times W/L^3$ (Coop and Kovač, 2003), where W is fish weight in grams and L is total fish length in millimetres. If stickleback was infected with *S. solidus*, because of significant weight of the parasites, plerocercoids were removed before fish weighing. Statistical significance of the differences in CF between males and females as well as between infected and uninfected sticklebacks was tested with t-test.

Sticklebacks were examined for ectoparasites and endoparasites using the standard procedures of parasitological examination. The body surface, gills, eyes (lens and vitreous humour), body cavity and visceral organs have been viewed. Parasitic identification was based on taxonomic keys (e.g., Dzika, 2008; Kabata, 1992; Niewiadomska, 2003; Pojmańska, 1991). Parasitological indices (prevalence, mean and range intensity) were calculated according to Bush et al. (1997). Prevalence is the percentage of hosts infected with parasites, mean intensity is the average number of parasites found on one infected host and range intensity is the range from the lowest to the highest number of parasites found in one infected fish.

4. Results

A total of 145 three-spined sticklebacks were examined. Two morphotypes, *trachurus* and *semiarmatus*, were identified with preponderance of *trachurus*. Average body weight was 1.8 g (range 1.2—3.2 g) and length was 6.3 cm (range 5.1—6.9 cm). Plerocercoids of *S. solidus* were removed from the body cavity of infected fish and were also weighed (0.3—0.6 g).

The overall mean Fulton's condition factor was 0.67 (SD = 0.17); when considering sex of fish, CF was higher for females than for males, respectively 0.73 (SD = 0.18) and 0.66 (SD = 0.07) ($p < 0.05$). Fulton's factors were also counted for fish infected with *S. solidus* as 0.68 (SD = 0.10) and for uninfected as 0.70 (SD = 0.06) ($p > 0.05$).

Eight species of parasites and digeneans of the genera *Diplostomum* were collected in the samples. Of these two were ciliates *Trichodina domerguei* Wallengren, 1897 and *Trichodina tenuidens* Faure-Fremiet, 1944 and one each were of microsporidia *Glugea anomala* (Moniez, 1887), monogenean *Gyrodactylus arcuatus* Bychowsky, 1933, digenean *Apatemon gracilis* (Rudolphi, 1819), cestode *S. solidus* (Müller, 1776), leech *Piscicola geometra* (Linnaeus, 1758), and also the copepod *T. gasterostei* (Pagenstecher, 1861).

A single specimen of the leech was found on the skin of the stickleback from the Puck. The remaining parasites were collected at both locations. Parasitological indices are given in Table 1. The most prevalent parasites were *T. gasterostei* and *T. domerguei*.

The allogenic community comprised three taxa, all present as larval stages: *Diplostomum* spp., *A. gracilis* and *S. solidus*, and the remaining parasites belong to the autogenic community. Five species of the ectoparasites were noted: *T. domerguei*, *T. tenuidens*, *G. arcuatus*, *P. geometra* and *T. gasterostei*. Sticklebacks were infected by the species of specialist, like *G. anomala*, *G. arcuatus*, *S. solidus* and *T. gasterostei*.

4.1. Microparasites of the three-spined stickleback

4.1.1. *Trichodina domerguei*

These ciliates were located on the body surface of the sticklebacks — skin and fins, mostly on the caudal fin. Intensity of infection with ciliates was defined as low, medium or high. The highest intensity of infection was observed in the case of sticklebacks from Puck. Also prevalence was highest in samples from Puck (Table 1).

4.1.2. *Trichodina tenuidens*

Parasites were recorded in the gill cavity, mostly on the gill operculum. *T. tenuidens* was found only in Puck with highest prevalence in April (Table 1). Intensity was lower than that observed for *T. domerguei*.

4.1.3. *Glugea anomala*

Xenomas with microsporidian *G. anomala* were located in the subcutaneous tissue and visible on the body surface or on the viscera as white round cysts up to 5—8 mm of diameter. The highest values of parasitological indices were recorded in June in Puck (Table 1).

4.2. Macroparasites of the three-spined stickleback

4.2.1. *Gyrodactylus arcuatus*

This monogenean parasite was recorded on the gills and fins, rarely on the skin. Parasites were found only in June in Puck (Table 1).

4.2.2. *Apatemon gracilis*

Encysted metacercariae of *A. gracilis* were collected from the vitreous humour of eye. *A. gracilis* occurred in all samples

Table 1 Mean intensity (range) and prevalence of infection of the three-spined stickleback from the Puck Bay. *I* — mean intensity (range) [individuals], *P* — prevalence [%].

Species of parasite	Gdynia				Puck			
	November 2012 *n* = 32		April 2013 *n* = 45		April 2013 *n* = 37		June 2013 *n* = 31	
	I	*P*	*I*	*P*	*I*	*P*	*I*	*P*
Trichodina domerguei	None	0	Low	44.4	High	81.1	Medium	87.1
Trichodina tenuidens	None	0	None	0	Medium	37.8	Low	9.7
Glugea anomala	0	0	1.1 (1)	2.2	4.0 (1—7)	5.4	16.3 (1—45)	9.7
Gyrodactylus arcuatus	0	0	0	0	0	0	6.9 (1—26)	45.2
Apatemon gracilis	1.8 (1—5)	18.8	1.4 (1—3)	11.1	1.5 (1—2)	5.4	4.2 (1—11)	16.1
Diplostomum spp.	1.3 (1—2)	9.4	1.3 (1—2)	6.7	0	0	14.4 (1—35)	25.8
Schistocephalus solidus	1.0 (1)	12.5	1.0 (1)	6.7	1.0 (1)	2.7	1.6 (1—5)	74.2
Thersitina gasterostei	2.9 (1—12)	50	1.8 (1—5)	66.7	2.4 (1—6)	56.8	113.0 (8—253)	100

with highest values of mean intensity in June in Puck and its prevalence in November in Gdynia (Table 1).

4.2.3. *Diplostomum* spp.

Metacercariae of digeneans from this genus were found in the lenses of the eye. Both parameters of infection have reached high values in June in Puck (Table 1).

4.2.4. *Schistocephalus solidus*

Plerocercoids of *S. solidus* occurred in the body cavity of sticklebacks. Parasites are very large relative to the size of the host. Plerocercoids were removed from the body cavity of infected fish and were also weighed (0.3—0.6 g). The highest parasitological indices were recorded in June in Puck (Table 1). Males and females were infected with plerocercoids in different levels. The highest prevalence was observed in the case of males, in Puck 66.7% and in Gdynia 10.3%, while in females, it was respectively 14.6% and 7.9%. Some of the sticklebacks harboured more than one plerocercoid, maximum 5 parasites.

4.2.5. *Thersitina gasterostei*

Copepods aggregations were found first of all on the ventral inner side of the operculum, and in the case of high infection also on the gill lamellae and under pectoral fins and spines. Copepods were found in all samples with prevalence higher than 50% (Table 1). In June all of the fish from Puck were infected and infection intensities were of up to 253 parasites.

5. Discussion

In our own studies carried out in the mid-1990s of the 20th century, 20 species of parasites were found in the Gulf of Gdańsk (Morozińska-Gogol, 1999). In contrast, today, a significant decrease in the diversity of the parasites is observed, with only eight species being present. Some of the formerly frequent species, e.g. *Proteocephalus filicollis* (Rudolphi 1810), restricted to sticklebacks in also other parts of the Baltic Sea (Zander et al., 1999), have not been reported. Now, parasitofauna has a low diversity and is limited to a few species; first of all specialists, like *S. solidus* or *T. gasterostei*, and generalist infected most of the fish species in this region, like *Diplostomum* spp. According to many views in the literature, the majority of the currently found parasites affect the body condition and fertility and modify the behaviour of the host.

As shown in Figs. 1 and 2, some changes in the values of prevalence and intensity of the most frequent parasites were found. Increase in the prevalence of both ciliates and *S. solidus* was observed. The greatest prevalence decrease was noted for *Diplostomum* spp. and marine copepod *T. gasterostei* (Fig. 1). The values of mean intensity are very similar, with the exception of *Diplstomum* spp. and *T. gasterostei* for which intensity has increased (Fig. 2).

Species such as *G. anomala*, *G. arcuatus*, *S. solidus* and *T. gasterostei* are specialist parasites of gasterosteid fish (Dzika, 2009; Kabata, 1992; Stentiford et al., 2013; Zander, 2007). According to many authors physiological condition and/or behaviour of sticklebacks are affected by *S. solidus* (e.g. Barber and Huntingford, 1995; Barber et al., 2004; Schultz et al., 2006), *T. gasterostei* (Rokicki, 1994), *G. anomala* (Ward et al., 2005) and also flukes located in the eyes (e.g. Voutilainen et al., 2009). Kalbe et al. (2002) reported that sometimes combination of different parasite species may cause parasite-induced host mortality. According to these authors parasites also act as selective agents of the host's divergence. Many authors reported that the host—parasite interaction is not simple and has various regulating mechanisms. The relationship between both, parasite and host, and abundances could be regulated by parasite-induced host mortality and also by host-induced mortality of parasites (e.g. Stanko et al., 2006). Abundant hosts usually tend to harbour richer parasitofauna (e.g. Hechinger and Lafferty, 2005; Vazquez et al., 2005). If the species of the host becomes less numerous, its parasitofauna may become less rich. In this study correlation between infection and fish mortality was not found.

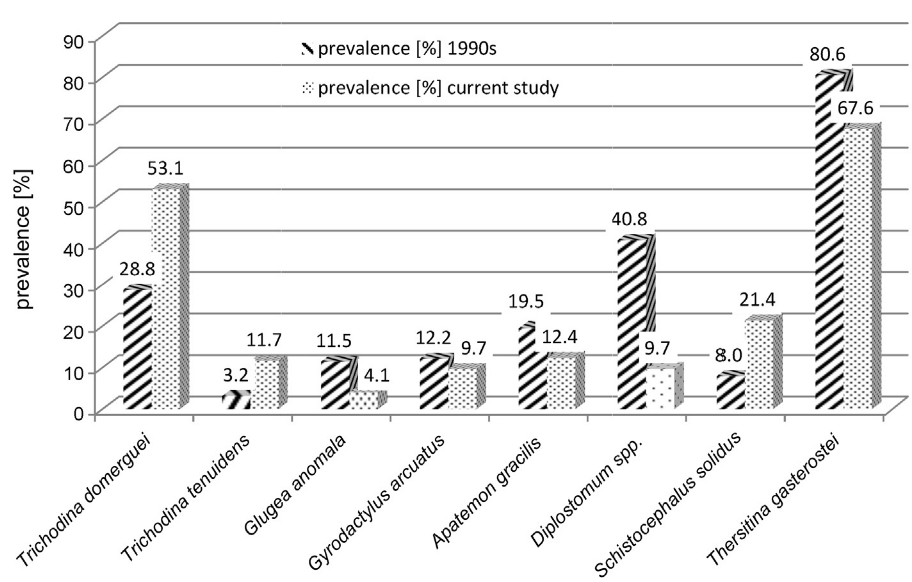

Figure 1 Prevalence of selected parasites of sticklebacks from the present study compared with data from the 1990s.

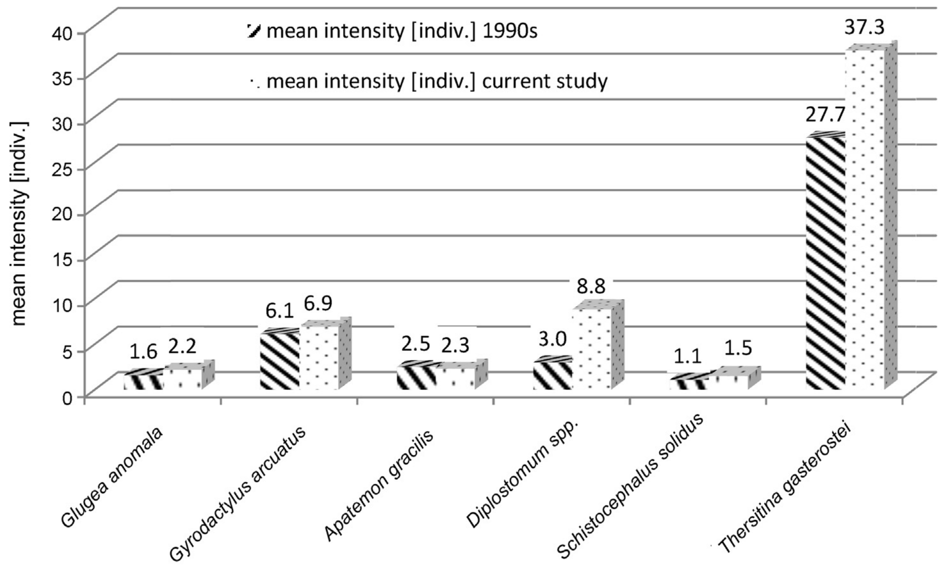

Figure 2 Mean intensity of selected parasites of sticklebacks from the present study compared with data from the 1990s.

Rohde (1993) and Yeomans et al. (1997) reported that the ciliates infected generally fish from the eutrophic and polluted environments. Changes in occurrence of the ciliates depend on the environmental factors. Ward et al. (2005) observed reduction of the fish growth, nutritional drain and increasing energetic costs of locomotion through disfigurements by tumours caused by *G. anomala*. Mortality, especially among young fishes, is also observed (Arnold et al., 2003). Cysts of *G. anomala* can indirectly affected survival — infected fish are less agile and more visible to predators.

Some effects caused by macroparasites were also noted by many authors. Barber et al. (2000) indicate that the metacercariae *Diplostomum* spp. causes severe effects on vision and several other damages, also causing cataract and leading to blindness, when parasites migrate and aggregate in the part of lens with minor illumination. Infected fish spend more time near the water surface, where they are more visible for the avian predators and more susceptible to attack (Barber et al., 2000; Valtonen and Gibson, 1997). Infection, because of reduction of visual acuity, also reduces their success in nutrition and consequently reduces the body condition (Owen et al., 1993). Höglund (1999) reported in heavily infected fish loss of body condition, even death, especially in young fish. The increase of mean intensity observed in the Puck Bay do not affect the body condition, but it is possible that heavily infected sticklebacks notice the predators later and therefore do not have sufficient time to escape and so are eaten by predators. Also Pennycuick (1971) concluded that the heavily infected host may not die but may be eaten by a predator. She refers this phenomenon to the generalist *Diplostomum* and the specialist *S. solidus*.

S. solidus changes the host appearance; infected fish have a distended abdomen (Arme and Owen, 1967) and often have a pale body colour. Nuptial colouration of males affected by parasites is less intense than the uninfected, which reduced their chance of mating (Bakker and Mundwiler, 1994; Barber et al., 2000; Rowland, 1982). Because the intensity of male nuptial colouration positively correlates with physical condition, females preferred brightly coloured males (Milinski and Bakker, 1990). Heins et al. (2010) documented also the mass mortality of stickleback infected with *S. solidus* and reduction in the reproductive capacity in the Walby Lake in Alaska in the years 1996—1998.

Dietary stress and increased oxygen demand in the case of infected stickleback were described in many papers (cf. LoBue and Bell, 1993). Arme and Owen (1967) explain in detail the effects of parasitisation, which among others is the reduction of liver weight, delay in oocyte maturation or inhibition of spawning in the case of heavily infected sticklebacks. Also changes in behaviour facilitate the transmission of the parasites (Ness and Foster, 1999) and reduce the body condition (Tierney et al., 1996) were observed. Infected fish are usually slower than the uninfected, prefer swimming in shallow water or close to the water surface and become more susceptible to avian predators (Barber et al., 2000; LoBue and Bell, 1993; Ness and Foster, 1999). According to LoBue and Bell (1993) the reason is higher oxygen demand, and the higher concentration of oxygen is in the upper part of the water column.

In Gdynia in the winter of 2008, prevalence was very high and reached 94% with intensity even to 6 individuals (Morozińska-Gogol, 2011), and indeed, some fish were pale. These high parameters of infection indirectly could be one of the reasons for the decrease in the abundance of sticklebacks, because infected fish can more often be caught by cormorants. This is probably because infected fish spend more time near the water surface and because of their distended belly they were more visible for the predators and were less agile. The final hosts of *S. solidus* are about 40 species of piscivorous birds (LoBue and Bell, 1993) in these cormorants (Milinski, 2006). In Poland, *S. solidus* was noted in several species of fish eating birds (cf. Morozińska-Gogol, 2011), and also cormorants (Kanarek and Rokicki, 2005; Kanarek and Zaleśny, 2014). The Gulf of Gdańsk is an important breeding and wintering area for water birds (Bzoma and Meissner, 2005; Kanarek and Zaleśny, 2014). In the recent years, in the Puck Bay and the Gulf of Gdańsk population of the great cormorants *Phalacrocorax carbo sinensis* (Blumenbach, 1798) has been regularly and significantly increasing. Thus, the role of cormorants as predators and potential hosts has increased in this region. Many cormorants spend winter in this region (Bzoma and Meissner, 2005). In the Baltic region sticklebacks as well as round gobies are an important food component of the cormorants (Bzoma and Meissner, 2005; Winkler et al., 2012).

Copepod *T. gasterostei* is the most abundant parasite in the Puck Bay. Zander et al. (1999) found the highest prevalence for this species. Poulin and Fitzgerald (1987) did not find significant differences in the body condition factors of fish infected and uninfected and they did not find a situation where the copepods aggregated on the gills. Kabata (1981) as well as Rokicki (1994) found that intense infection of *T. gasterostei* with aggregation on the gills affect growth and survival of hosts. Rokicki (1994) observed high mortality of heavy infected sticklebacks in the summer months, when temperature increases and dissolved oxygen decreases in the shallow waters of the Puck Bay. One fish often harboured more than 100 copepods. Sticklebacks were also infected with *G. anomala*, *S. solidus*, *Diplostomum* spp. and *A. gracilis*. Unfortunately, he did not give the value of the body condition factor. Similarly Threlfall (1968) observed mass mortality of stickleback in Newfoundland as an effect of stress induced by the combination of heavy infection with three species of parasites, *S. solidus*, *T. gasterostei* and *Argulus canadensis* Wilson, 1916. The increase of mucus secretion in the gills of sticklebacks infected with *T. gasterostei* was observed. It is a defence against parasites, but from another aspect, this heightened secretion impeded respiration.

The Fulton's condition factor of examined fishes was lower than CF found by Voight (2007), but in its study CF was higher for female than for males, and was statistically significant ($p \leq 0.05$). Voight (2007) for sticklebacks from the coastal waters of western Gulf of Finland recorded overall CF as 0.87 ($\pm$0.11), and CF for females and males were respectively 0.92 ($\pm$0.11) and 0.88 ($\pm$0.08). This author calculated also that the average weight of the large parasites (*S. solidus*) constituted 25% of the weight of the infected fish and it was confirmed in the present study, where weights of plerocercoids were 0.3—0.6 g. He has not counted CF for infected and uninfected fish. In the present study, uninfected fish have a little higher CF, but the difference was statistically insignificant ($p > 0.05$).

A variety of abiotic and biotic factors, like salinity, pollution, eutrophication, and relationships with other species, determine distribution of organisms, including also the parasites. In the Baltic Sea two abiotic stressors are important. There is decreasing salinity dependent on the influx of saline waters from the North Sea and eutrophication with oxygen deficiency in the deep and shallow water (Zander, 1998).

Adverse changes caused by high pollution and eutrophication of estuarine and coastal marine ecosystems lead to changes in the littoral zone and in the structure of food webs (Heuschele et al., 2009; Smith, 2003; Smith et al., 2006; Zander et al., 1999). Changes in fish communities were observed in all regions of the Baltic Sea and in the Puck Bay they were significant (Kruk-Dowgiałło and Szaniawska, 2008; Rajasilta et al., 1999; Skóra, 1993). Primarily changes in the abundance of commercially exploited fish species were described, but some authors, like Rajasilta et al. (1999), observed also reducing the abundance of *G. aculeatus*, probably as a consequence of eutrophication in the Archipelago Sea (part of the Baltic Sea between the Gulf of Finland and the Gulf of Bothnia). Changes in parasite community e.g. decline in species richness of parasites of gobies fish exposed to environmental stress — eutrophication — was also observed in the Baltic Sea (Zander, 1998).

The possible reasons for reduction in the number of sticklebacks in the Puck Bay could be also the increasing abundance of competitors such as round gobies and predators such as cormorants or the introduced rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792). The Hel Marine Station at the University of Gdańsk managed project "Rainbow trout" which aims at introducing to the food web of the Puck Bay predatory fish like rainbow trout for reduction of undesirable fish species, including sticklebacks (Skóra, 2010).

Summing up, the fall in the abundance of the three-spined sticklebacks in the recent years is a result of the combination of diverse factors. In this study we did not find direct significant correlation between structure of parasite community, parasitological indices and mortality of host. However, parasites may contribute to the selective eating of the infected individuals by predators or in special conditions in combination with other parasites and/or abiotic factors e.g. temperature, oxygenation affects the survival of the host. Moreover changes in the species diversity, e.g. increase of the number of cormorants, emergence of expansive species like round goby or introduction of predators as rainbow trout, and also environmental changes such as pollution and eutrophication of the Puck Bay play an important and multidirectional role.

References

Arme, C., Owen, R.W., 1967. Infections of the three-spined stickleback, *Gasterosteus aculeatus* L., with the plerocercoid larvae of *Schistocephalus solidus* (Müller, 1776), with special reference to pathological effects. Parasitology 57, 301—314.

Arnold, K.E., Adam, A., Orr, K.J., Griffiths, R., Barber, I., 2003. Sex-specific survival and parasitism in three-spined sticklebacks: seasonal patterns revealed by molecular analysis. J. Fish Biol. 63, 1046—1050.

Bakker, T.C.M., Mundwiler, B., 1994. Female mate choice and male red coloration in a natural three-spined stickleback (*Gasterosteus aculeatus*) population. Behav. Ecol. 5, 74—80.

Bańbura, J., Bakker, T.C.M., 1995. Lateral plate morph genetics revisited: evidence for a fourth morph in three-spined sticklebacks. Behaviour 132, 1153—1171.

Barber, I., 2013. Sticklebacks as model hosts in ecological and evolutionary parasitology. Trends Parasitol. 29, 556—566.

Barber, I., Hoare, D., Krause, J., 2000. Effects of parasites on fish behaviour: a review and evolutionary perspective. Rev. Fish Biol. Fish. 10, 131—165.

Barber, I., Huntingford, F.A., 1995. The effect of *Schistocephalus solidus* (Cestoda: Pseudophyllidea) on the foraging and shoaling behavior of three-spined sticklebacks, *Gasterosteus aculeatus*. Behaviour 132, 1223—1240.

Barber, I., Walker, P., Svensson, P.A., 2004. Behavioural responses to simulated avian predation in female three-spined sticklebacks: the effect of experimental *Schistocephalus solidus* infections. Behaviour 141, 1425—1440.

Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83, 575—583.

Bzoma, S., Meissner, W., 2005. Some results of long-term counts of waterbirds wintering in the western part of the Gulf of Gdańsk

(Poland), with special emphasis on the increase in the number of cormorants (*Phalacrocorax carbo*). Acta Zool. Lit. 15, 105—108.

Coop, G.H., Kovač, V., 2003. Sympatry between threespine *Gasterosteus aculeatus* and ninespine *Pungitius pungitius* sticklebacks in English lowland streams. Ann. Zool. Fenn. 40, 341—355.

DeFaveri, J., Merilä, J., 2013. Variation in age and size in fennoscandian three-spined sticklebacks (*Gasterosteus aculeatus*). PLOS ONE 8 (11), e80866, http://dx.doi.org/10.1371/journal.pone.0080866.

Dzika, E., 2008. Parasites of Polish Fish (Identification Key). Monogenean — Monogenea. Polskie Towarzystwo Parazytologiczne, Warszawa, (in Polish).

Dzika, E., 2009. A checklist of fish monogeneans from Poland. Wiad. Parazytol. 55, 315—324.

Fidelus, H., 1975. Parasites of the three-spined stickleback (*Gasterosteus aculeatus*) in the Baltic Coastal Waters. Zesz. Nauk. Akad. Rol. Szczec. 51, 21—26,(in Polish).

Girdwoyń, M., 1883. Parasites of Our Fish. Warszawa (in Polish).

Hechinger, R.F., Lafferty, K.D., 2005. Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. Proc. R. Soc. B 272, 1059—1066, http://dx.doi.org/10.1098/rspb.2005.3070.

Heins, D.C., Baker, J.A., 2008. The stickleback — *Schistocephalus* host—parasite system as a model for understanding the effects of a macroparasite on host reproduction. Behaviour 145, 625—645.

Heins, D.C., Birden, E.L., Baker, J.A., 2010. Host mortality and variability in epizootics of *Schistocephalus solidus* infecting the threespine stickleback, *Gasterosteus aculeatus*. Parasitology 137, 1681—1686.

Heuschele, J., Mannerla, M., Gienapp, P., Candolin, U., 2009. Environment-dependent use of mate choice cues in sticklebacks. Behav. Ecol. 20, 1223—1227.

Höglund, J., 1999. *Diylostomum spathaceum* larvae (Diplostornosis) (Digenea) in fish. ICES Identification Leaflets for Diseases and Parasites of Fish and Shellfish. Leaflet No. 53. 4.

Hudson, P.J., Dobson, A.P., Lafferty, K.D., 2006. Is a healthy ecosystem one that is rich in parasites? Trends Ecol. Evol. 21, 381—385.

Kabata, Z., 1981. Copepoda (Crustacea) parasitic on fishes: problems and perspectives. Adv. Parasitol. 19, 1—71.

Kabata, Z., 1992. Copepods parasitic on fishes: keys and notes for identification of the species. Synopses of the British Fauna No. 47. London.

Kalbe, M., Wegner, K.M., Reusch, T.B.H., 2002. Dispersion patterns of parasites in 0+ year threespined sticklebacks: a cross population comparison. J. Fish Biol. 60, 1529—1542.

Kanarek, G., Rokicki, J., 2005. The status of studies on the helminth fauna of the Great Cormorant (*Phalacrocorax carbo sinensis*) in northern Poland. Wiad. Parazytol. 51, 165.

Kanarek, G., Zaleśny, G., 2014. Extrinsic- and intrinsic-dependent variation in component communities and patterns of aggregations in helminth parasites of great cormorant (*Phalacrocorax carbo*) from N. E. Poland. Parasitol. Res. 113, 837—850.

Kruk-Dowgiałło, L., Szaniawska, A., 2008. Gulf of Gdańsk and Puck Bay. In: Schiewer, U. (Ed.), Ecology of Baltic Coastal Waters. Ecological Studies, vol. 197. Springer-Verlag, Berlin/Heidelberg, 139—165.

LoBue, C.P., Bell, M.A., 1993. Phenotypic manipulation by the cestode parasite *Schistocephalus solidus* of its intermediate host, *Gasterosteus aculeatus*, the threespine stickleback. Am. Nat. 142, 725—735.

Marcogliese, D., 2002. Food webs and the transmission of parasites to marine fish. Parasitology 124, S83—S99.

Marcogliese, D., 2004. Parasites: small players with crucial roles in the ecological theater. EcoHealth 1, 151—164.

Milinski, M., 2006. Fitness consequences of selfing and outcrossing in the cestode *Schistocephalus solidus*. Integr. Comp. Biol. 46, 373—380.

Milinski, M., Bakker, T.C.M., 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. Nature 344, 330—333.

Morozińska-Gogol, J., 1999. Dynamic of the select parasites infestation of the three-spined stickleback in dependence to the place of catching in the southern Baltic. Balt. Coast. Zone 3, 77—88.

Morozińska-Gogol, J., 2002. Seasonal variation of parasite infestation of the three-spined stickleback (*Gasterosteus aculeatus* L.) in the southern Baltic. Wiad. Parazytol. 48, 359—373.

Morozińska-Gogol, J., 2006. A checklist of parasites recorded on sticklebacks (Actinopterygii: Gasterosteidae) from Poland. Parasitol. Int. 55, 69—73.

Morozińska-Gogol, J., 2011. Changes in levels of infection with *Schistocephalus solidus* (Müller 1776) of the three-spined stickleback *Gasterosteus aculeatus* (Actinopterygii: Gasterosteidae) from the Gdynia Marina. Oceanologia 53, 181—187.

Ness, J.H., Foster, S.A., 1999. Parasite-associated phenotype modifications in threespine stickleback. Oikos 85, 127—134.

Niewiadomska, K., 2003. Parasites of Polish Fish (Identification Key). Trematoda — Digenea. Polskie Towarzystwo Parazytologiczne, Warszawa, (in Polish).

Owen, S.F., Barber, I., Hart, P.J.B., 1993. Low level infection by eye fluke, *Diplostomum* spp., affects the vision of three-spined sticklebacks, *Gasterosteus aculeatus*. J. Fish Biol. 42, 803—806.

Pennycuick, L., 1971. Frequency distributions of parasites in a population of three-spined sticklebacks, *Gasterosteus aculeatus* L., with particular reference to the negative binominal distribution. Parasitology 63, 389—406.

Pojmańska, T., 1991. Parasites of Polish Fish (Identification Key). Tapeworms — Cestoda. Instytut Parazytologii PAN, Warszawa, (in Polish).

Pojmańska, T., Niewiadomska, K., 2010. Parasites — inconvenient element in the structure of ecosystem food web. Kosmos 59, 99—110, (in Polish).

Poulin, R., Blanar, C.A., Thieltges, D.W., Marcogliese, D.J., 2011. The biogeography of parasitism in sticklebacks: distance, habitat differences and the similarity in parasite occurrence and abundance. Ecography 34, 540—551.

Poulin, R., Fitzgerald, G.J., 1987. The potential of parasitism in the structuring of a salt marsh stickleback community. Can. J. Zool. 65, 2793—2798.

Rajasilta, M., Mankki, J., Rantaaho, K., Vuorinen, I., 1999. Littoral fish communities in the Archipelago Sea, SW Finland: a preliminary study of changes over 20 years. Hydrobiologia 393, 253—260.

Rohde, K., 1993. Ecology of Marine Parasites: An Introduction to Marine Parasitology. CAB International, Wallingford, United Kingdom.

Rokicki, J., 1994. *Thersitina gasterostei* (Copepoda) the cause of selection of the sticklebacks in the Puck Bay. XVII Congress of the Polish Parasitological Society. Gdynia, 15—17 September 1994, Biul. Met.-Org. Inst. Med. Mor. Trop. 27, 50, (in Polish).

Rowland, W.J., 1982. The effects of male nuptial coloration on stickleback aggression: a reexamination. Behaviour 80, 118—126.

Sapota, M.R., 2004. Round goby (*Neogobius melanostomus*) fish invader in the Gulf of Gdańsk — case of species introduction into the Baltic. Hydrobiologia 514, 219—224.

Schultz, E.T., Topper, M., Heins, D.C., 2006. Decreased reproductive investment of female threespine stickleback *Gasterosteus aculeatus* infected with the cestode *Schistocephalus solidus*: parasite adaptation, host adaptation, or side effect? Oikos 114, 303—310.

Skóra, K.E., 1992. Fishery. Stud. Mater. Oceanol. 61, 205—220.

Skóra, K.E., 1993. The causes of changes in the composition and quantities of ichthyofauna stocks in Puck Bay. In: Pliński, M. (Ed.), Proceeding of Conference, Part 1. Marine Environment. The Ecology of Baltic Terrestrial, Coastal and Offshore Areas — Protection and Management, Sopot, 11—12 December 1992. University of Gdańsk, 115—127.

Skóra, M., 2010. Rainbow Trout in the Food Web of the Puck. Hel Marine Station Web, http://www.hel.ug.edu.pl/ryby/pstragi_teczowe_w_lancuchu_troficznym.htm, (accessed 08.08.14).

Smith, V.H., 2003. Eutrophication of freshwater and coastal marine ecosystems. A global problem. Environ. Sci. Pollut. Res. 10, 1—14.

Smith, V.H., Joye, S.B., Howarth, R.W., 2006. Eutrophication of freshwater and marine ecosystems. Limnol. Oceanogr. 51, 351—355.

Stanko, M., Krasnov, B.R., Morand, S., 2006. Relationship between host abundance and parasite distribution: inferring regulating mechanisms from census data. J. Anim. Ecol. 75, 575—583.

Stentiford, G.D., Feist, S.W., Stone, D.M., Bateman, K.S., Dunn, A.M., 2013. Microsporidia: diverse, dynamic, and emergent pathogens in aquatic systems. Trends Parasitol. 29, 567—578.

Sulgostowska, T., Vojtkova, L., 2005. Parasites of sticklebacks (Actinopterygii: Gasterosteidae) from South-Eastern Baltic Sea (Poland). Wiad. Parazytol. 51, 151—155.

Threlfall, W., 1968. A mass die-off three-spined sticklebacks (*Gasterosteus aculeatus* L.) caused by parasites. Can. J. Zool. 46, 105—106.

Tierney, J.F., Huntingford, F.A., Crompton, D.W.T., 1996. Body condition and reproductive status in sticklebacks exposed to a single wave of *Schistocephalus solidus* infection. J. Fish Biol. 49, 483—493.

Valtonen, E.T., Gibson, D.I., 1997. Aspects of the biology of diplostomid metacercarial (Digenea) populations occurring in fishes in different localities of northern Finland. Ann. Zool. Fenn. 34, 47—59.

Vazquez, D.P., Poulin, R., Krasnov, B.R., Shenbrot, G.I., 2005. Species abundance and the distribution of specialization in host—parasite interaction networks. J. Anim. Ecol. 74, 946—955.

Voight, H-R., 2007. Concentrations of mercury and cadmium in perch (*Perca fluviatilis* L.), ruffe (*Gymnocephalus cernuus* L.), three-spined stickleback (*Gasterosteus aculaeatus* L.), and nine-spined stickleback (*Pungitius pungitius* L.), from SW Finnish Coastal Waters. Acta Univ. Carol. Environ. 21, 151—159.

Voutilainen, A., Valdez, H., Karvonen, A., Kortet, R., Kuukka, H., Peuhkuri, N., Piironen, J., Taskinen, J., 2009. Infectivity of trematode eye flukes in farmed salmonid fish — effects of parasite and host origins. Aquaculture 293, 108—112.

Ward, A.J.W., Duff, A.J., Krause, J., Barber, I., 2005. Shoaling behaviour of sticklebacks infected with the microsporidian parasite, *Glugea anomala*. Environ. Biol. Fish. 72, 155—160.

Winkler, H.M., Starck, C., Myts, D., 2012. The feeding of cormorants and possible influences on native fish stocks in the Pomeranian Bay on the German Baltic Sea coast. In: Cormorant in the Context of Sustainable Use of Fishery Resources. Conference Materials. Gdynia, 15 November 2012. National Marine Fisheries Research Institute, 2—8, (in Polish), http://www.konferencjakormorany.pl/KonferencjaKormorany.pl-podsumowanie.pdf (accessed 06.08.14).

Wootton, R.J., 1976. The Biology of the Sticklebacks. Academic Press, London.

Yeomans, W.E., Chubb, J.C., Sweeting, R.A., 1997. Use of protozoan communities for pollution monitoring. Parassitologia 39, 201—212.

Zander, C.D., 1998. Ecology of host parasite relationships in the Baltic Sea. Naturwissenschaften 85, 426—436.

Zander, C.D., 2007. Parasite diversity of sticklebacks from the Baltic Sea. Parasitol. Res. 100, 287—297.

Zander, C.D., Reimer, L.W., Barz, K., 1999. Parasite communities of the Salzhaff (Northwest Mecklenburg, Baltic Sea). 1. Structure and dynamics of communities of littoral fish, especially small-sized fish. Parasitol. Res. 85, 356—372.