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The White Sea threespine stickleback population: spawning habitats, mortality, and abundance

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ABSTRACT

Hypothesis: Stickleback abundance in the White Sea is limited by availability of spawning habitats.

Organisms: Threespine stickleback, *Gasterosteus aculeatus*; eelgrass, *Zostera marina*.

Times and places: June (spawning period of stickleback) 2009–2011 and 2014; 60 locations along the White Sea coast.

Methods: We sampled with a beach seine (length 7.5 m, height 1.5 m, mesh size 5 mm in wings and 1 mm in purse) in coastal zones within 30 m of the shore.

Results: Around 60% of the entire stickleback population occurs in the northwestern part of the White Sea (Kandalaksha Bay). This region has favourable spawning habitats, i.e. protected inlets with a high density of eelgrass and other macrophytes. Other parts of the White Sea are more exposed to waves and have less vegetation. We estimated that the White Sea currently supports about 740 million stickleback at the beginning of the spawning season, with a total biomass of about 1600 metric tonnes.

Keywords: abundance, distribution, *Gasterosteus aculeatus*, habitats, mortality, threespine stickleback, White Sea.

INTRODUCTION

The threespine stickleback (*Gasterosteus aculeatus*) is one of the most widely studied fishes, being a popular model in evolutionary and behavioural research (Wootton, 1976, 1984, 2009; Bell and Foster, 1994; Östlund-Nilsson *et al.*, 2007; Huntingford and Ruiz-Gomez, 2009; Barber and Nettleship 2010; Hendry *et al.*, 2013). However, some aspects of stickleback biology have attracted little attention. This is especially true for marine populations, even though stickleback often link different trophic levels (Lemmetyinen and Mankki, 1975), thus potentially shaping entire ecosystems (Harmon *et al.*, 2009; Matthews *et al.*, 2016). Because they feed on plankton, stickleback compete with important commercial fish such as herring (Jurvelius *et al.*, 1996; Peltonen *et al.*, 2004). Stickleback have been shown to cause a decline in coastal predatory fish such as perch and pike (Ljunggren *et al.*, 2010; Bergström *et al.*, 2015; Byström *et al.*, 2015) and promote recruitment of macroalgae by feeding on invertebrate grazers (Sieben *et al.*, 2011). This species represents an important prey item for

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predatory fish such as Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) (Linko *et al.*, 1979), and for birds such as the spoonbill (*Platalea leucorodia*) (Kemper, 1995). In the White Sea, stickleback make a substantial contribution to the diets of cod (*Gadus morhua*), saffron cod (*Eleginus nawaga*), and European sculpin (*Myoxocephalus scorpius*) (Bakhvalova *et al.*, 2016), prey on plankton and benthos (Abdel-Malek, 1963a, 1963b, 1968; Demchuk *et al.*, 2015), and host a notable number of parasites (Rybkina *et al.*, 2016).

To study the role of stickleback in ecosystems, it is crucial to have quantitative data on their abundance. However, little attention has been paid to this aspect of stickleback biology (Gislason *et al.*, 1998; Wootton, 2009). Salminen *et al.* (2001) consider the available quantitative data on the stickleback population (and also on sprat *Sprattus sprattus* and sand eel *Ammodytes tobianus*) in the Gulf of Bothnia in the Baltic Sea to be insufficient for understanding their ecological role. And Bergström *et al.* (2015) consider stickleback to represent an under-studied component of the Baltic Sea offshore pelagic fish community.

Marine fish that are abundant often have high commercial value and are monitored by fisheries research institutes. Such monitoring facilitates assessment of the status of marine ecosystems. However, stickleback, one of the most prolific species in the White Sea, is not monitored because it has no direct commercial significance. A lack of statistical data on the stickleback population limits our understanding of mechanisms of change in the White Sea ecosystem. In addition, stickleback abundance varies markedly over time scales of decades: its abundance was very high in the 1930s to 1950s, declined in the 1960s to 1990s, and has bounced back since the late 1990s (Lajus *et al.*, 2013). These changes are associated with changes in the entire ecosystem. Thus, quantifying stickleback abundance is important for understanding system dynamics.

The goals of this study are to describe patterns of spatial distribution of threespine stickleback in the White Sea during their spawning period, estimate population mortality and, based on these findings, infer absolute numbers of this species in the sea.

METHODS AND MATERIALS

Stickleback density

Stickleback density was studied at 60 locations around the White Sea (Fig. 1). Sampling was mostly done in 2010–2011, although nine sites were sampled in 2009 in the Chupa Inlet, Kandalaksha Bay, and five sites in 2014 on the Onega Peninsula coast. Samples were collected from 15 to 30 June, the period of maximum spawner abundance on spawning grounds (Bakhvalova *et al.*, 2016). Our estimates are based on the abundance of the entire spawning population during this period.

Samples were collected with a 7.5-m long beach seine with wings 1.5 m high, and a mesh-size of 5 mm on the wings and 1 mm in the cod-end. The density of stickleback was estimated in two ways:

1. individuals per square metre: $D_1 = N \times S^{-1} \times CE^{-1}$
2. individuals per kilometre of shoreline: $D_2 = N \times L^{-1} \times CE^{-1} \times 1000\ \mathrm{m}$

where N is the number of fish in one haul, S is the size of the catch area (m^2), L is the length of the beach seine (m), and CE is the catch efficiency (the ratio of fish caught related to the total number of fish in the catch area).

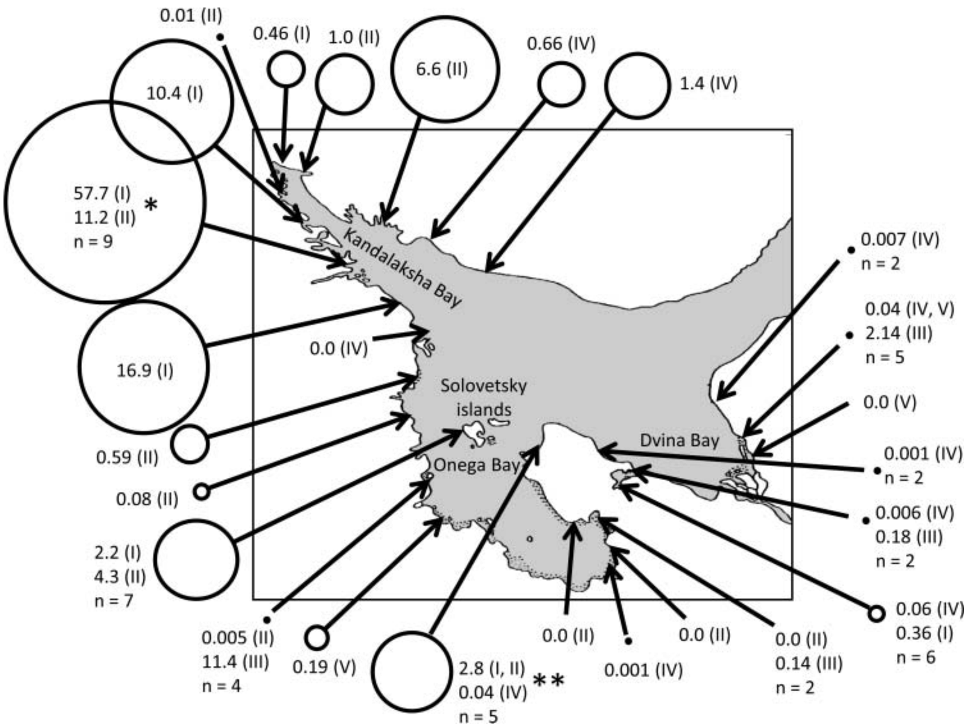


Fig. 1. Densities of spawning threespine stickleback (individuals per m^2) along the White Sea shoreline. For display purposes, we pooled results from sites situated within 10 km of each other (n = number of sites in pooled locations). Roman numerals in parentheses refer to habitats described in Table 3: I = eelgrass beds, II = fucoid seaweeds, III = littoral pools, IV = shallows, V = reeds. *Eight samples were collected in 2009 and 1 in 2010; **five samples were collected in 2014; all other samples were collected in 2010–2011.

The catch area was 120 m^2, haul length was 30 m, and catch efficiency was 0.6. Catch efficiency was measured using mark–recapture techniques (Lockwood and Schneider, 2000) in a small lagoon (T. Ivanova, M. Ivanov and D. Lajus, unpublished). The standard error of replicate beach seine hauls performed under similar conditions (2–3 hauls at 10 sites) was about 10%. Using these methods, we estimated stickleback density within the 30-m wide inshore zone. Sex ratio was estimated in the Seldyanaya Inlet by calculating number of males and females in a half-litre volume (85–110 fish).

Biotic and abiotic characteristics of sampling sites

Depth was measured at a distance of 30 m from the shoreline, and slope was calculated as the ratio of depth to distance from shore. The densities of eelgrass (*Zostera marina*) and fucoid seaweeds were assessed visually using a subjective ranking system based on eelgrass (Maksimovich *et al.*, 2005) and fucoid densities observed at 12 sites in the Chupa Inlet in 2008 (M. Ivanov, unpublished data). Correspondence between rank and biomass is based on the measurements of eelgrass and fucoid samples provided in Table 1. Types of bottom were visually subdivided into rocks, boulders, gravel, sand, mud, and their combinations.

Table 1. Ranking of variables used for description of habitats

Eelgrass		Fucoid seaweeds		Potential wave exposure	
Rank	Density (kg · m^{-2})	Rank	Density (kg · m^{-2})	Rank	PWE
0	0	0	0	0	<0.5
1	<0.1 (solitary plants)	1	<0.5 (solitary plants)	1	0.5–2
2	0.1–0.5	2	0.5–3.0	2	2–10
3	0.5–1.5	3	>3.0	3	10–25
4	1.5–3.0			4	>25
5	>3.0				

Note: PWE = potential wave exposure (see text for explanation).

Potential wave exposure (PWE) was determined according to the formula:

$$\mathrm{PWE} = GA \times AO/360°,$$

where GA = generating area and AO = angle of openness. The angle of openness was estimated using Google Earth 6.1 software as the angle of open space from the sea, and the generating area as the distance from the sampling site to the closest obstacle for an incoming wave (an opposite shore, island, etc.) within the angle of openness.

Based on the type of vegetation, type of bottom, and wave exposure, we subdivided the entire shoreline of the White Sea into six typical habitats. This was done based on our own field observations, and maps and images from Google Earth 6.1. The length of each habitat was estimated using Google Earth 6.1 at a scale of 200 m per centimetre.

Mortality

It is not possible to estimate the density of non-mature stickleback after their first winter using direct sampling with beach seines on spawning grounds. Therefore, we calculated values based on mortality models. Stickleback mortality was calculated for the Seldyanaya Inlet in Kandalaksha Bay (66°20′15″N, 33°37′26″E) based on samplings performed in 2007–2014. To determine the parameters of the mortality equations, we used field data on stickleback densities on spawning grounds during the period of maximum spawner abundance (second half of June). The proportions of different age classes were determined in 2012 using ages established via otolith analysis (Golovin *et al.*, 2015). From these data and the average multi-year density of stickleback on spawning grounds, we calculated densities of mature fish at different ages.

To estimate mortality at early life stages, we used field data on the densities of juveniles at 2 weeks (early August) and 4 weeks (middle August). Quantitative assessment of younger juveniles was impractical because of their small size. Older juveniles caught during and after the second half of August were not used because they had already begun their offshore migration (Bakhvalova *et al.*, 2016). Egg density (eggs · m^{-2}) was estimated as the average density of females multiplied by average absolute fecundity [i.e. 272 ± 6 eggs (Yershov, 2011)].

Statistical analyses

All statistical analyses were performed using Statistica v.7.0 and PAST v.3.11. We used principal component analysis (PCA) to identify the main factors determining variability of the studied habitats. Density of stickleback in different habitats was compared with ANOVA using log-transformed data. *Post-hoc* analysis was performed using Fisher's LSD test. Regression analysis was used to model the mortality of the stickleback population.

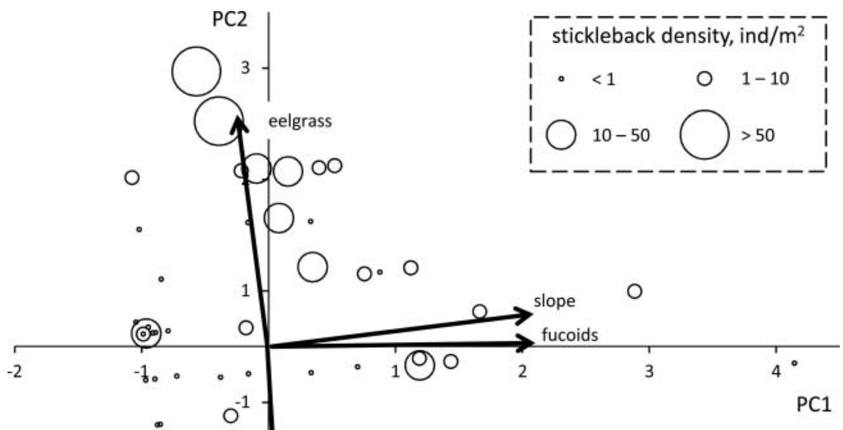
RESULTS

Spatial distribution of stickleback in the White Sea

Results of our analyses of stickleback density in the White Sea are shown in Fig. 1. In general, the spatial distribution of stickleback is heterogeneous, with a maximum density of 176 individuals per m^2 (Yakovleva Inlet in Kandalaksha Bay, 16 June 2013).

Habitats of the White Sea coastal zone and factors influencing stickleback density

To identify the main factors influencing the distribution of stickleback, we performed a principal component analysis based on 60 samples and four variables. PC1 and PC2 explain 74.9% of the total variance (Fig. 2). PC1 is determined in the main by the density of fucoid seaweeds and slope. Two variables show the highest loadings on PC2, with eelgrass being positive and wave exposure negative. Stickleback abundance is highly correlated with PC2



variable	PC 1	PC 2
eelgrass	-0.08	0.70
fucoids	0.71	0.01
slope	0.70	0.10
wave exposure	0.03	-0.71
eigenvalue	1.54	1.46
% of variance	38.4	36.5

Fig. 2. Biplot of sites and variables in the coordinates of the PC1 (abscissa) and PC2 (ordinate) axes. Circle size corresponds to stickleback density (individuals per m^2). The table shows loadings of studied variables on PC1 and PC2 (unrotated).

($r = 0.61$, $P < 0.001$) but not so with PC1 ($r = 0.13$, $P = 0.34$) (Fig. 2). Therefore, both eelgrass and stickleback are negatively associated with wave exposure and have maximum values at intermediate shore slopes. High stickleback densities (>10 individuals per m^2) are rare at PC1 greater than 0.5, which corresponds to a shore slope of 3–5%.

Based on vegetation distribution and abiotic factors, we identified six typical habitats for the coastal zone of the White Sea (Table 2). In Kandalaksha Bay and on the Solovetsky Archipelago at the entrance of Onega Bay, *eelgrass bed* and *fucoid seaweed* habitats are dominated by the very dense vegetation that give them their name. These habitats are associated with relatively steep slopes, and high densities of stickleback are usually observed there. They differ most in wave exposure: eelgrass beds are typical of protected inlets, whereas fucoid seaweeds are more often associated with open stony shores. *Littoral pools*, as a rule, do not contain vegetation. They are shallow, warm during low tide, and occur in different parts of the White Sea. *Shallows* with a sandy or stony bottom spread out 1 km from the shoreline and vegetation is usually scarce. Where vegetation in shallows is limited to the reed *Phragmites australis*, the habitat is identified as *reeds*. Shallows with and without reeds are typical of inner parts of Onega and Dvina Bays. *Rocks* are a common habitat for Kandalaksha Bay, and associated with a relatively steep slope and high wave exposure. Because it is impossible to sample such habitat with a beach seine, we have no quantitative data on stickleback densities for this type of habitat. However, visual observations detected no stickleback spawning there. Based on observations, we assume stickleback density there to be zero.

The five sampled habitats differed significantly in the density of stickleback (ANOVA: $F = 6.7$, df1 = 4, df2 = 55, $P = 0.0002$, $R^2 = 0.33$). The highest densities of fish are observed in eelgrass beds, and are significantly higher than in fucoid habitat (Fisher's LSD test, df = 55, $P = 0.0067$). Fish densities in the littoral pool and fucoid seaweed habitats do not differ significantly from one another (Fisher's LSD test, df = 55, $P = 0.96$). Densities in the shallows and reeds habitats do not differ from one another (Fisher's LSD test, df = 55, $P = 0.93$), but fish densities in both are significantly lower than in eelgrass beds (Fisher's LSD test, df = 55, both $P < 0.01$).

The absolute number of stickleback in the White Sea

To estimate the absolute number of stickleback in the White Sea, we determined the length of each habitat along the shoreline. As our samples cover 80% of the White Sea shoreline, our estimates refer only to the inner part of the White Sea, which includes three bays: Kandalaksha, Onega, and Dvina. We did not take into account a small stickleback population that may live in Mezen Bay and the Gorlo in calculating the total number of White Sea stickleback. Moreover, we excluded fish from littoral pool habitat because of the complexity of its measurement and negligible part of the shoreline it covered. Table 3 provides the lengths of different habitats along the White Sea shoreline.

The above calculations are based on adult fish sampled on spawning grounds. To estimate the total number of stickleback in the White Sea, we need also to take into account immature fish that cannot be estimated by direct beach seine sampling.

Table 2. Characteristics of main habitats of the White Sea coastal zone (values are mean ± standard error)

Habitat	No. sites	Average stickleback density, individuals per m^2	Min–max stickleback density, individuals per m^2	Eelgrass density, rank	Fucoid density, rank	Depth, m	Slope, %	Wave exposure, rank	Bottom
Eelgrass beds	11	19.1 ± 9.0	0.3–82.5	2.9 ± 0.3	1.3 ± 0.2	2.0 ± 0.2	6.5 ± 0.8	0.0	Sand
Fucoid seaweeds	24	4.20 ± 1.7	0–32	0.3 ± 0.1	2.3 ± 0.2	2.9 ± 0.7	9.7 ± 2.2	1.6 ± 0.3	Stones, sand
Littoral pools	4	3.50 ± 2.7	0.14–11	0.0	0.0	0.3 ± 0.1	—	0.0	Stones or mud
Shallows	17	0.15 ± 0.09	0–1.4	0.3 ± 0.1	0.2 ± 0.1	0.8 ± 0.1	2.7 ± 0.4	2.1 ± 0.4	Stones or sand
Reeds	4	0.06 ± 0.04	0–0.2	0.0	0.3 ± 0.3	0.6 ± 0.3	2.0 ± 1.0	0.8 ± 0.3	Sand, mud
Rocks *	—	0.0	—	0.0	1.0–2.0	>15	>50	—	Stones

*No sampling was done in this habitat. Stickleback density was estimated from visual observations.

Table 3. Length of shoreline attributed to particular habitats, and calculations of absolute adult stickleback numbers in the White Sea

Habitat	Stickleback density, individuals per km	Length of shoreline (km)				Absolute stickleback number (ind. × 10^6)			
		KB	OB	DB	%	KB	OB	DB	%
Eelgrass beds	305344	318	171	21	8.3	97.1	52.2	6.4	42.2
Fucoids	66488	1765	1314	91	51.8	117.4	87.4	6.1	57.1
Shallows	2378	322	342	342	16.4	0.77	0.81	0.81	0.6
Reeds	980	0	319	131	7.4	0	0.31	0.13	0.1
Rocks	0	756	212	12	16.0	0	0	0	0.0
Percentage		51.7	38.5	9.8		58.3	38.1	3.6	
Total			6116				369		

Note: 'Littoral pools' are excluded because of their negligible contribution. KB = Kandalaksha Bay, OB = Onega Bay, DB = Dvina Bay.

Stickleback mortality and immature fish

Mortality equations are provided for two different periods of ontogenesis (Fig. 3): period 1 = age 0 to 1 month, and period 2 = age 1 month to 4 years. Mortality curves are radically different for these two periods probably because of the different factors causing mortality.

Demographic analysis of the stickleback population based on sampling in the inshore zones shows 11-month-old fish to be less abundant than older fish (Table 4). At this age fish begin to mature: this age class is underestimated because the immature portion does not appear on the spawning grounds. Thus, we did not include it in the mortality equations, but calculated its abundance based on the densities of other age classes using an equation assuming linearity of log-transformed regression. Calculations show that the observed number of 11-month-old fish is about 18% of their expected number. Hence the population in the inshore zone at the beginning of the spawning season (i.e. early June) comprises about 51% of the actual number of stickleback in the White Sea.

Based on rough estimates, White Sea stickleback release about 54×10^9 eggs. These calculations are based on our estimates of the total number of mature stickleback

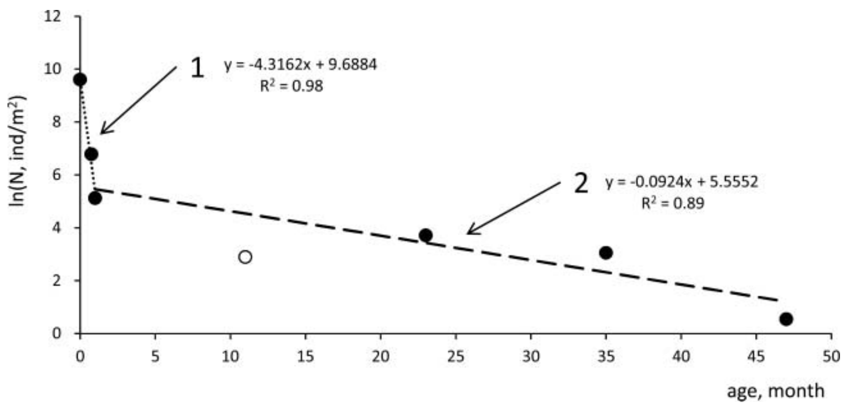


Fig. 3. Stickleback density (individuals per m^2, log-transformed) at different stages in the life cycle in Seldyanaya Inlet. Eleven-month-old fish (open circle) were not included in the equation (see text).

Table 4. Observed and expected values based on modelling the density of stickleback (Seldyanaya Inlet, 2007–2014)

		Density, individuals per m^2	
Ontogenetic stage	Age, months	Observed	Expected from the model#
Eggs	0	14850 ± 560 (n = 10)	16130 (1)
Juveniles	0.5	880 ± 717 (n = 4)	633 (1)
	1	167 ± 108 (n = 6)	215 (1), 236 (2)
Mature	11	17 ± 2 (n = 10)	64 (2)*
	23	40 ± 4 (n = 10)	31 (2)
	35	20 ± 2 (n = 10)	10 (2)
	47	1 ± 0.1 (n = 10)	3 (2)

Numbers in parentheses refer to the corresponding mortality equation (Fig. 3).
*Expected density of yearlings includes both mature and immature fish.

(369 million), the mean ratio of females to males (7:3) in Seldyanaya Inlet, average fecundity of 272 ± 6 eggs (Yershov, 2011), and production of only one clutch during spawning by stickleback in the White Sea (Mukhomediarov, 1966; Yershov, 2011). Mortality from birth to maturation (2+) is about 99.8%. During the first month of life, mortality approaches 98%. Between age 1 month and 11 months, mortality drops to 72%. In older fish, annual mortality is about 67%.

We estimate the absolute number of stickleback on the spawning grounds to be 369 million individuals, and the total number of stickleback in the White Sea during that period at roughly 740 million individuals. Of that number, more than half (58%) inhabit Kandalaksha Bay, 38% are found in Onega Bay, and only about 3.6% in Dvina Bay. The Kandalaksha Bay stickleback population is distributed evenly. In Onega Bay, the highest stickleback density is observed around the Solovetsky Islands, which comprise about 17% of Onega Bay's shoreline, yet contain about 40% of the stickleback. This area is rich in aquatic vegetation, both in eelgrass and fucoid seaweeds. In Dvina Bay, 30% of the stickleback live in Una Inlet (19% of the shoreline of the Bay) with relatively dense eelgrass beds.

The mean density of stickleback in the White Sea (with an area of 45,000 km^2, excluding the northern part) is 0.0164 per m^2. Assuming the average weight of stickleback by the beginning of the spawning season to be 3.2 g for mature and 1.1 g for immature fish, total biomass in the White Sea from 2007 to 2014 was about 1600 metric tonnes, of which 1200 metric tonnes were mature and 400 metric tonnes immature fish.

DISCUSSION

Stickleback abundance has been assessed using a variety of techniques. In lakes with a limited number of fish and relatively small area, numbers were estimated using capture–recapture methods, which required marking substantial numbers of the total fish population (Reimchen, 1990; Gislason *et al.*, 1998; Wootton, 2009; COSEWIC, 2013). In larger bodies of water, such techniques are not practical because they require marking unrealistically large numbers of fish. In such cases, stickleback abundance in the pelagic phase of their life cycle can be estimated using hydroacoustic methods combined with trawl surveys (Jurvelius *et al.*, 1996; Peltonen *et al.*, 2004). But such techniques are expensive, and only applicable to pelagic zones. Yet, stickleback spawn in shallows and grow there during their first weeks of life.

In order to sample the shallows, our study used a specially designed small beach seine. This reliable and inexpensive technique allowed us to obtain quantitative data on stickleback density immediately after sampling, and generate estimates of stickleback abundance during their massive inshore spawning migration in the second half of June.

To obtain estimates of stickleback abundance for the entire region, quantitative sampling needs to be made of the entire shoreline and its different habitats. Samplings and calculations showed that most stickleback occurred in Kandalaksha and Onega Bays (Table 3). For three other regions traditionally included in the White Sea – Mezen Bay, Gorlo and Voronka – we did not have field data. However, sampling in the northeast of the regions, in the eastern part of Kandalaksha Bay and the northeastern part of Dvina Bay, suggests that stickleback density is very low in these parts of the White Sea due to unfavourable environmental conditions. The climate here is colder, and the shores are rocky and more exposed to waves (Babkov, 1998). For these reasons, we excluded these areas from our estimate of the total number of stickleback in the White Sea. Of 740 million White Sea stickleback, 96% live in Kandalaksha (58%) and Onega (38%) Bays. These parts of the White Sea contain many islands and protected inlets with eelgrass beds and low hydrodynamic activity favourable to the fish.

The most studied sea in terms of stickleback abundance and density is the Baltic Sea, particularly its northern part, the Gulf of Bothnia (Bergström *et al.*, 2015). The Baltic Sea is relatively similar to the White Sea in terms of environmental conditions and biota, which makes it a reasonable comparison for our data. The average density of stickleback in the White Sea (0.016 individuals per m^2) is considerably lower than reported for the Gulf of Bothnia in 1991 [0.26 per m^2 (Jurvelius *et al.*, 1996)]. When considered separately, the most favourable White Sea region for stickleback, Kandalaksha Bay, with an area of about 9000 km^2, a stickleback abundance of 215 million, and density of 0.05 individuals per m^2, supports a population five-fold less than in the Gulf of Bothnia in 1991. The same disparity is true for biomass: White Sea, 1600 metric tonnes; Gulf of Bothnia, 25,000 metric tonnes (Jurvelius *et al.*, 1996). Today, total stickleback abundance in the Gulf of Bothnia is much higher, at about 160,000 metric tonnes (Bergström *et al.*, 2015); therefore, densities exceed those in the White Sea roughly 100-fold.

To help explain why stickleback abundance is lower in the White Sea than in the Baltic Sea, we evaluate several non-exclusive explanations: (1) lower biological productivity, (2) higher competition with other species, (3) a lack of spawning grounds, and (4) underuse of potential spawning habitats because the quick-growing stickleback population is not balanced with respect to its environment.

Lower biological productivity due to more severe environmental conditions

The White Sea is often referred to as the Arctic Sea and is characterized by low biological productivity (Zenkevich, 1947). This sea is connected to the ocean from the north, whereas the more southern Gulf of Bothnia connects from the south. The White Sea's orientation, in combination with its more northern location, results in a more severe climate. This may result in lower primary production: average annual production in the White Sea is 33 g $C \cdot m^{-2}$ (based on Berger, 2005), and in the Baltic Sea 118 g $C \cdot m^{-2}$ (Cloern *et al.*, 2014). Lower primary production likely results in poorer feeding conditions for fish.

Higher competition with other species

White Sea stickleback share planktonic resources with herring (*Clupea pallasii*), whose present total biomass is about 11,000 metric tonnes (S. Frolov, personal communication). There are also other consumers of plankton such as jellyfish, comb jellies, and chaetognates, which may be less abundant in the Baltic Sea due to its lower salinity. However, quantitative data on these organisms are very limited, thus we did not take them into account.

Assuming the average mass of one herring to be about 30 g, the total number of herring in the White Sea is about 370 million individuals – that is, fewer than stickleback. However, the biomass of herring is higher due to their larger size. As herring are more abundant in Onega Bay (S. Frolov, personal communication) and stickleback in Kandalaksha Bay, the biomass of stickleback and that of herring in Kandalaksha Bay may be close. Hence we assume that the contribution of stickleback ranges from a quarter to a half of pelagic fish biomass. In the Gulf of Bothnia, stickleback comprise 10–20% of total pelagic fish biomass (Jurvelius *et al.*, 1996; Ljunggren *et al.*, 2010).

The average biomass of herring in the White Sea is 0.24 metric tonnes per km^2, and average density is 0.0082 individuals per m^2. For the Baltic Sea, the respective figures are 2.89 metric tonnes per km^2 and 0.145 individuals per m^2 (Casini *et al.*, 2008). Therefore, the density of herring in the Baltic Sea is about 17 times higher than in the White Sea, and biomass is 12-fold higher. For stickleback, these figures are 16 and 15.6, respectively. The ratio of stickleback to herring is therefore similar in the two seas, and hence it is very unlikely that lower stickleback density in the White Sea can be explained by higher competition with herring alone.

Lack of spawning grounds

Although stickleback can spawn in different habitats, in the White Sea they prefer eelgrass (Table 2). It is possible that the difference in densities of adult fish in eelgrass compared with other habitats is as pronounced as it is because some fish caught in other habitats may actually have spawned in seagrass beds. We assume that stickleback prefer eelgrass because of favourable feeding conditions for juveniles as well as protection from predators (Demchuk *et al.*, 2015; Rybkina *et al.*, submitted). Compared with fucoids, the advantage of eelgrass for juveniles is also clear, because their densities in seagrass decrease more slowly over time than in fucoids (Rybkina *et al.*, submitted). Eelgrass is a boreal species, for which the White Sea is a border of distribution. It shows considerable fluctuation in abundance similar to that of stickleback (Lajus *et al.*, 2013).

A limitation of convenient spawning grounds can also be seen from the fact that, despite much lower overall densities in the White Sea than in the Gulf of Bothnia, the densities of stickleback on White Sea spawning grounds are much higher. In Kandalaksha Bay, maximum density approaches 176 individuals per m^2, with densities of 10–50 individuals per m^2 commonly observed. In the Gulf of Bothnia, the maximum density of stickleback is considered to be 10–45 individuals per m^2 (Ljunggren *et al.*, 2010). It seems that only 8% of the area along the White Sea coast provides optimal spawning conditions for stickleback. If the entire area were optimal for stickleback reproduction, and factors limiting stickleback abundance were absent (parasites, predators, food, low temperatures, etc.), their numbers in the White Sea could be about an order of magnitude higher than they are.

Underuse of potentially favourable spawning habitats

The stickleback population in the White Sea has grown markedly during the last 15 years. It may have approached its historical maximum in favourable spawning habitats, such as Kandalaksha Bay's eelgrass beds. However, less favourable but potentially suitable spawning habitats may be underused in areas with comparatively low stickleback densities such as Onega Bay and, in particular, Dvina Bay.

Therefore, we can conclude that abundance of stickleback in the White Sea is probably limited by the relatively low biological productivity of this Arctic region. However, lack of convenient spawning grounds (i.e. seagrass beds), a factor also related to severe environmental conditions, may be an even more limiting factor for the stickleback population in the White Sea.

CONCLUSION

Since the beginning of the new millennium, the White Sea has become highly populated by threespine stickleback, a fish that was almost absent there in previous decades (Lajus *et al.*, 2013). This dramatic growth has resembled the appearance of an introduced species, and probably has had similar effects on the ecosystem, although stickleback did experience similar abundances in the first half of the twentieth century (Lajus *et al.*, 2013). Stickleback live most of their lives in the open sea. We know little about this phase of their life cycle, but they are readily available for research during the short reproduction period, which is spent in close proximity to the coast. Demographic analysis of population structure facilitated estimation of the abundance of juvenile fish, which do not appear inshore at the end of their first year.

Inshore stickleback distributions can be accurately predicted based on analysis of habitats: preferred habitats offer aquatic vegetation and protected inlets and littoral pools. Superior habitats are eelgrass beds in protected inlets, which likely create the best conditions for early life stages. Average stickleback densities in the White Sea are considerably lower than in the milder Baltic, while their densities in spawning habitats are much higher. It is probable that limited availability of such habitats along the shoreline limits the total abundance of stickleback at sea, and is a consequence of severe environmental conditions in the Arctic zone.

Recent climate change has resulted in increased biological productivity and the expansion of eelgrass beds. This was likely the reason for the recent and rapid growth in the stickleback population. It is now the second most abundant White Sea fish species in terms of biomass, after herring, and, being smaller in size, is more numerous than herring. Connecting pelagic and coastal communities of the White Sea, stickleback now play a key ecological role in both communities.

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