

Sexual dimorphism patterns of the White Sea threespine stickleback (*Gasterosteus aculeatus*)

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Abstract

Sexual dimorphism (SD) in the threespine stickleback *Gasterosteus aculeatus* reflects the different roles of the sexes in reproduction and their adaptations to different ecological niches. We quantified SD in one population of marine stickleback from the White Sea, collected during the spawning period from three spawning grounds, each at a distance of 5 km or less from the others. We used a landmark-based approach to quantify variation in 44 morphometric linear traits. In total, 749 females and 693 males were analyzed. In males, anterior body parts are larger — the base of the caudal fin and armor structures such as the first and second dorsal spines and the pelvic spine. Females have larger posterior bodies — the abdomen, pelvic girdle and the third dorsal spine. The SD of caudal body parts exhibits complex patterns. In White Sea threespine stickleback, SD patterns are generally similar to other populations of the species, but more often show male-biased patterns. Female-biased size SD may be associated with the female biased sex ratio of White Sea stickleback.

Keywords: threespine stickleback, sexual dimorphism, morphological variation, body shape, body size, White Sea

Introduction

The threespine stickleback *Gasterosteus aculeatus* is one of the most numerous fish species of the White Sea (Ivanova et al., 2016; Lajus et al., 2020a). During the summer spawning period, it comprises more than 90 % of total fish abundance in inshore areas (Ivanova, Lajus, and Ivanov, 2011). Stickleback play an important role in the ecosystem, actively consuming a variety of prey organisms (Demchuk et al., 2015), and serve as a food source for common predatory fish (Bakhvalova et al., 2016). It is also a key species in parasitic chains (Rybkina et al., 2016). Stickleback abundance has grown rapidly during the last quarter century and now is close to its historical maximum. Arctic warming is likely the main cause of the population's exceptional growth (Lajus et al., 2021). Hence, studying the population biology of threespine stickleback in the White Sea not only helps us to assess the effects of environmental changes on this species, but also to understand the mechanisms underlying climate's impact on the entire ecosystem.

In the White Sea, stickleback spend most of their lives offshore feeding on plankton, coming inshore to spawn from late May or early June until mid-July. At that time they reach very high densities on spawning grounds, often exceeding

100 ind/m² (Ivanova et al., 2016; Lajus et al., 2020a). We found differences between male and female feeding patterns (Demchuk et al., 2018) and both predator-related and predator-unrelated mortality (Golovin et al., 2019). Preliminary analyses of the spatial heterogeneity of the fish showed that males and females actively redistribute on spawning grounds during their spawning period (Dorgham et al., 2018).

White Sea threespine stickleback show ontogenetic changes in sex ratio. The results from a recent analysis of genetic markers show that in juveniles up to the age of 1.5 months, sex ratio is not biased, but that females prevail among older juveniles (Artamonova et al., in press). Female-based sex ratios are consistently observed at spawning grounds (Yershov and Sukhotin, 2015; Ivanova et al., 2016; Golovin et al., 2019; Lajus et al., 2020a) and in open waters within a few km from the shoreline among sexually mature fish during their spawning period (T. Ivanova and M. Ivanov, unpublished data). Female prevalence is also reported for a number of other populations of this species (Aneer, 1974; Kynard, 1978; Wootton, 1984; Arnold et al., 2003; Pichugin, Sidorov and Gritsenko, 2003; Saat and Turovski, 2003; Niksirat, Hatef and Abdoli, 2010; Patimar, Najafabadi and Souraki, 2010; Rollins et al., 2017). Sex ratio is an important population characteristic that directly influences population fecundity and, therefore, plays an important role in population dynamics (Wootton, Fletcher, Whoriskey and Smith, 1995). Sex ratio is closely related to sexual dimorphism (SD; i.e., differences in appearance between males and females) and is associated with different sex roles in reproduction. SD is very common in threespine stickleback (Kitano, Mori and Peichel, 2007; Aguirre, Ellis, Kusenda and Bell, 2008; Leinonen, Cano and Merilä, 2011a). Male stickleback take care of their offspring by protecting their spawning territory, embryos and larvae from other conspecifics and predators. The females' need to develop and carry eggs is facilitated by their larger body size, which also influences their swimming performance and susceptibility to predators (Rodewald and Foster, 1998). SD in structures closely associated with reproduction is typically interpreted in terms of the adaptation of females and males to their particular reproductive roles (reviewed by Greenwood and Adams, 1987; Andersson, 1994; Short and Balabban, 1994; Mealey, 2000; Fairbairn, Blanckenhorn and Székely, 2007). It has been suggested that SD in structures not directly related to reproduction result from adaptation of the sexes to different ecological niches (Slatkin, 1984; Hedrick and Temeles, 1989). Therefore, SD patterns can be interpreted in terms of local adaptation.

This study aims to quantify patterns of sexual dimorphism in White Sea stickleback on spawning grounds and discusses its possible role in local adaptation.

Material and methods

Sample collection

Stickleback were sampled from three spawning grounds in the Keret Archipelago, Kandalaksha Bay, White Sea, near the Belomorskaya Educational and Research Station of St. Petersburg State University (66°41'N; 33°45'E). Sampling took place five times during the spawning period from the end of May to the end of June 2018. In total, 1442 individuals (749 females and 693 males) were collected with a small beach seine (7.5 m in length, 1.5 m in height, with 120 m² of catchment area) at the approximate time of low tide. The specimens were stored in 10% formalin according to Reimchen and Nosil (2006). Altogether, we collected 15 samples, each comprising an approximately equal number (more often 50) of males and females.

For this study we selected three spawning grounds situated a distance of 5 km or less from each other (see Lajus et al., 2020b for more details). Seldianaya Inlet (SEL) is a triangular bay with a wide entrance and a depth of up to 8 m. Tidal amplitude here and at the second site, Sukhaya Salma Strait (SSS), is up to 2.5 m, whereas depth at SSS is up to 10 m. Predatory fish consuming stickleback (Atlantic cod *Gadus morhua*, European sculpin *Myoxocephalus scorpius* and navaga *Eleginus nawaga*) are quite abundant in these locations (Bakhvalova et al., 2016). The density of stickleback spawners on SEL is high (usually about 80 ind/m²) due to dense beds of eelgrass *Zostera marina* at the top of the inlet. Because SSS is deeper, with sparse eelgrass beds, its spawner density is notably lower. Koliushkovaya (KOL) is a small muddy lagoon (0.058 km² in area) up to 4 m deep (averaging 1.5 m) with some eelgrass beds. The lagoon is characterized by a high density of filamentous algae, which stickleback frequently use for spawning. Due to limited connection to the sea, tidal amplitude here is only 0.3 m, predatory fish are virtually absent, and the water is warmer than at the two other sites. Spawning stickleback density in the lagoon is intermediate between that of the two other sites.

The sex of collected stickleback was determined by visual examination and coloration, and, if necessary, by analysis of gonads.

Scanning setup

The “wooden pool” scanning technique (Herler et al., 2007) used in this study relies on a quick setup that is less complicated than photography, and offers high resolution digital images of small fish in the laboratory, as well as — with some restrictions — in the field. The most important advantages of this technique are that specimens can be easily manipulated and positioned, expected image quality can be quickly controlled using the scanner's preview mode and, compared to photographic techniques, image quality is high and processing is easy (Herler et al., 2007). The specimens were scanned using an Epson Perfection V600 Photo scanner at a resolution of 1200 dpi.

Specimens, fully submerged in water, were scanned in the lateral position from the right and ventral sides. The wooden pool was made of a wooden frame, glass, and plasticine to fill gaps between the glass and wood (Herler et al., 2007). The pool was placed on the scanner glass and filled with fresh water about 2 cm deep. The water was allowed to settle for several hours before use to eliminate bubbles, which can stick to the glass bottom and the specimens, and mar images. Crooked fish spines were straightened using wooden sticks.

Traits

Trait selection was based on those described in previous studies of threespine stickleback (Baumgartner, Bell and Weinberg, 1988; Hermida, Fernández, Amaro and Miguel, 2005; Zanella et al., 2015). In total, 27 landmarks were digitized using ImageJ software (Fig. 1 and Supplement 1)¹. Injured structures, in particular broken spines, were observed very rarely — about 0.1 % of their total number — and were excluded from the analyses. Only evenly tipped spines were measured. Based on the coordinates of these landmarks, we created 44 linear traits (Supplement 2). Distances between the landmarks were calculated in Microsoft Excel. All traits of an individual were divided by standard length (SL) to minimize the effect of fish size (Allendorf et al., 1987). For one bilateral structure, the pelvic spine, we measured both sides in order to analyze fluctuating asymmetry, representing deviation from perfect symmetry (Palmer, 1994).

All traits were *a priori* subdivided into several groups according to their position and function: 1) body (27 traits excluding standard length), 2) head (6 traits), 3) armor structures (6 traits) and 4) fins (4 traits) (Supplement 3).

Statistical analyses

Before analyses, all SL-standardized traits were checked for departure from normality using Shapiro-Wilk's test separately on each sample; Levene and Box's test was used to check homoscedasticity. Next, a Bonferroni correction for multiple comparisons (Rice, 1989) was applied. Principal component analysis (PCA) was used to analyze the data using IBM SPSS Statistics computer software V19.0 (Statistics Inc., version 19, 2011). We used only PCs with eigenvectors exceeding 1. Based upon differences from the standardized means for males and females of body SL, we computed an SDI index (SDI) according to Borgognini and Repetto (1986):

$$SDI = \frac{\bar{X}_{male} - \bar{X}_{female}}{\bar{X}_{female}} * 100,$$

where \bar{X}_{male} and \bar{X}_{female} are mean trait values for males and females, respectively.

This index shows differences in trait size as a percentage: male-biased traits are positive, female-biased traits are negative. Differences in SDI and PC between the sexes were tested for significance using a Student's t-test.

Fluctuating asymmetry of pelvic spines was measured according to Palmer and Strobeck (2003):

$$FA = |R - L| / 0.5 * (R + L),$$

where R and L are a trait's right and left values, respectively. As this index is distributed non-normally, we used non-parametric Mann-Whitney and Kruskal-Wallis H-tests to estimate the significance of the effect of sex on fluctuating asymmetry.

Results

Sexual dimorphism in body size

Standard length (SL) in our samples ranged from 5.28 to 7.18 cm for females with an overall average of 6.16 cm, and from 4.90 to 6.43 cm for males with an overall average of 5.63 cm; females exceeded males in SL by 8.6 % (Supplement 3, Fig. 2).

Sexual dimorphism of body shape

Among 43 SL-standardized traits, two (Pred-C and TD) showed significant departure from normality. Thus, we used non-parametric statistics for their analysis. Of the analyzed traits, 15 were significantly female-biased, 23 were significantly male-biased, and 5 did not differ significantly between sexes (Supplement 3).

Principal component analysis (PCA) was conducted on 43 traits using orthogonal (or varimax) rotation. Eleven PCs with eigenvalues exceeding 1 explained 76.4 % of the total variance (Supplement 4, Table 1). Among these PCs, four showed significant differences between sexes: PC1 (21.8 % of total variance) can be interpreted as anterior body shape; PC4 (7.2 %) — length of spines; PC6 (5.2 %) — size and shape of the caudal part, and PC8 (4.9 %) — size and shape of the dorsal posterior part. Other PCs did not show significant differences between the sexes (Table 1).

Comparing traits with higher loadings on these PCs with *a priori* groups of traits shows only partial coincidence between them. Among armor traits, all spines appear in the same PC except DS3, which is in another PC describing variation in posterior parts of the back: PGL groups with traits describing the anterior body. Unpaired fins group with other traits describing adjacent parts of the body. Head traits are divided into two groups, one associated with length, and the other — with depth of the anterior body. Body shape traits, a heterogeneous group, belong to all PCs except PC4 (Table 1, Supplement 2).

¹ Supplemental material to the article is available at <https://biocomm.spbu.ru/article/view/10125>

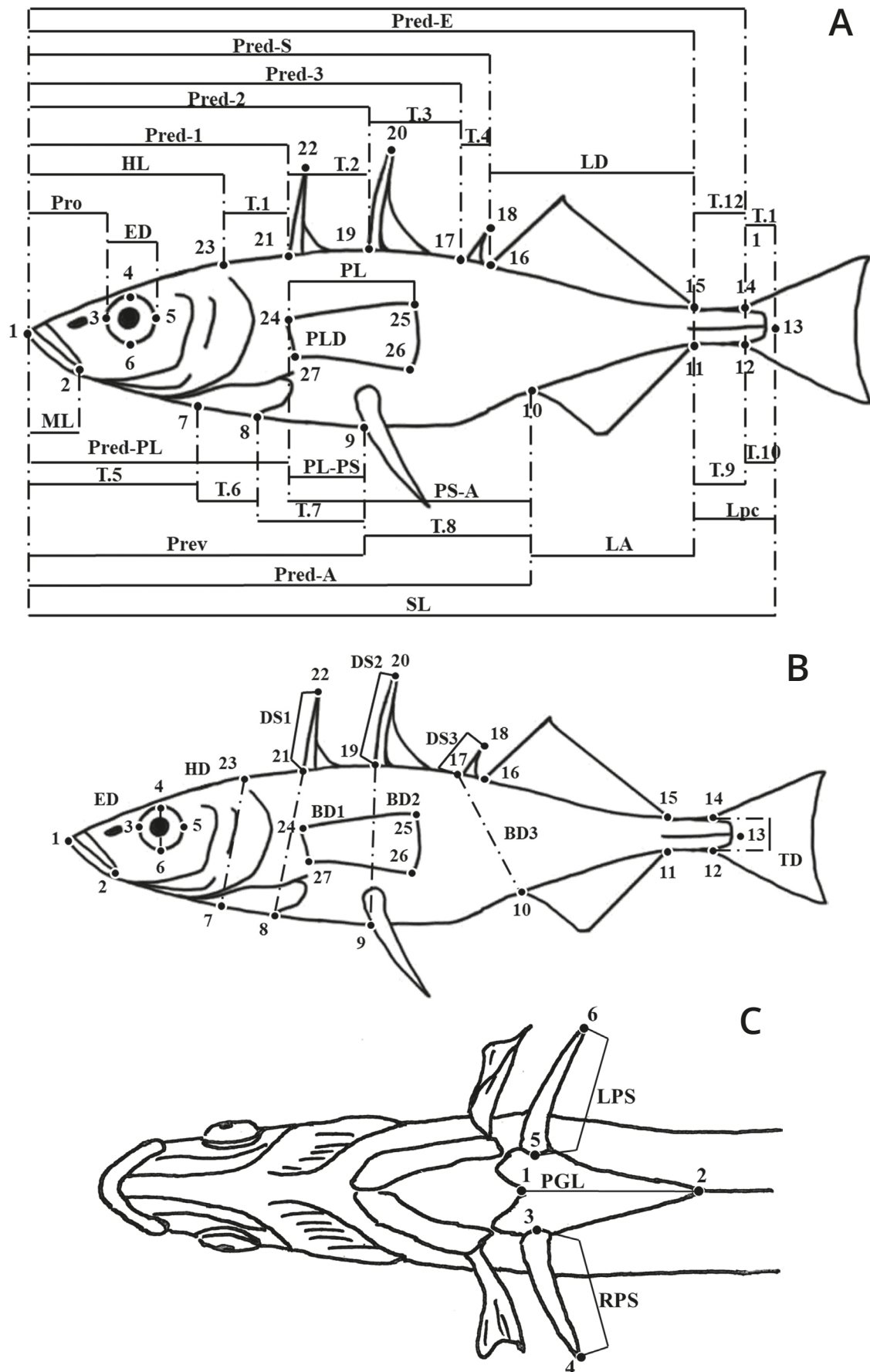


Fig. 1. Landmarks and linear measurements used for description of sexual dimorphism of threespine stickleback. A and B are lateral views and C is ventral view. See full description of landmarks and traits in Supplements 1 and 2.

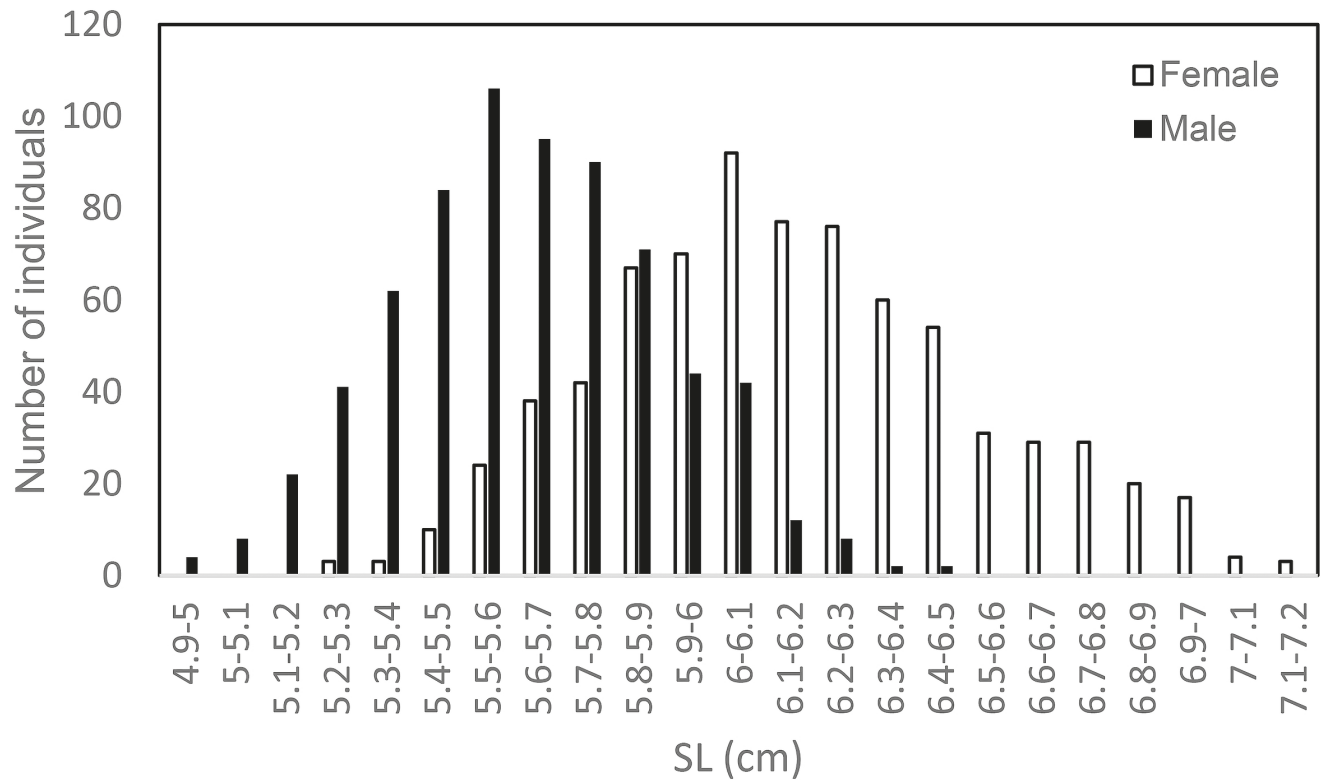


Fig. 2. Standard length distribution of stickleback males (n=693) and females (n=749) from Keret Archipelago, White Sea, May–July 2018.

Table 1. Average scores of Principal Components (PCs) for males and females, and traits showing high absolute loadings on these PCs (varimax raw rotation)

| PC and percentage of total variance explained (in brackets) | Description | Significance of sexual dimorphism, t-test | Traits with high (>0.4) positive loading | Traits with high (<-0.4) negative loading |
|---|---|---|--|---|
| PC1 (21.8) | Size of anterior body | P<0.001 | Pred-PL, HL, SnL, Pred-1, Prev, Pred-2, T. 5, ED, ML | PS-A, T. 8, BD3, T. 3, PGL |
| PC2(8.3) | Body length | NS | Pred-C | T. 10, T. 11 |
| PC3 (7.6) | Body depth | NS | BD1, BD2, EDp, HD, TD | |
| PC4 (7.2) | Length of spines | P<0.001 | DS2, DS1, LPS, RPS | |
| PC5 (6.0) | Size of postanal body part | NS | Pred-A | |
| PC6 (5.2) | Size and shape of caudal part | P<0.001 | LA | T. 9, LPC |
| PC7 (5.0) | Size and shape of lower medial part | NS | PL-PS, T. 7, T. 6 | |
| PC8 (4.9) | Size and shape of dorsal upper posterior part | P<0.001 | LD, Pred-E, T. 12 | |
| PC9 (3.9) | Size and shape of medium back part | NS | Pred-S, T2 | |
| PC10 (3.3) | Size and shape of third dorsal spine and adjacent body part | NS | T. 4, DS3 | |
| PC11 (3.2) | Size and shape of anterior back part | NS | T. 1 | |

Males have larger anterior body parts, including heads, eyes and mouths, up to approximately the level of the pectoral fins. Preorbital distance (Pro) shows the highest SDI value (SDI = 21.1), followed by another proximate trait — mouth length (SDI = 16.7). Pred-PL, head length (HL) and T.5 also exhibit SDI values higher than 10 — 10.2, 11.6 and 14.1, respectively (Supplement 3). In addition, males have larger tail fin bases and some armor structures, such as the first and second dorsal spines and the pelvic spine. SDI of these structures is lower than for the anterior part of the body; overall, it ranges between 3.2 and 5.8. Three dorsal spines show a clear decrease in the absolute value of SD from the anterior to the posterior part of the body, with SDI of 5.8, 3.9 and -2.8 for DS1, DS2 and DS3, respectively. The absolute length of the first dorsal spine (DS1) is 3–4% less than that of the second (DS2), and the third dorsal spine (DS3) is notably smaller than the others: only 37% as long as DS2.

Females have larger posterior body parts, except the caudal part. They have a larger abdomen (the distance between the base of the pelvic spine and anus (T.8) shows the highest female-biased SDI [21.5]), deeper body (distance between the base of DS3 and the anus, BD3 [SDI = -14.8]), larger pelvic griddle (SDI = -8.9), and larger DS3 (SDI = -2.8). SD of the caudal part of the body exhibits complex patterns. Males have deeper (TD, SDI = 6.2) and longer (LPC, SDI = 4.0) caudal peduncles and larger tail bases (SDI = 9.2 and 7.9 for T.10 and T.11, respectively), but the distance between the end of the dorsal fin and beginning of tail is longer on females (T.12 SDI = -8.0). This is likely because the upper parts of their caudal fins are smaller. Other fins show heterogeneous patterns: females have longer (SDI of PL = -1.5) but narrower (SDI of PLD = 4.8) pectoral fins, and smaller anal fins (SDI of LA = 10.4). Dorsal fin length does not differ between sexes.

For a bilateral trait, the length of pelvic spines, directional asymmetry tests did not reveal significant differences between the lengths of left and right pelvic spines (Mann-Whitney U-test, $p = 0.665$), and the distribution of R-L values showed no significant departure from normality, therefore, asymmetry of this trait is fluctuating. Fluctuating asymmetry was not associated with standard length (Spearman correlation coefficient, $p = 0.321$). No significant differences between males and females were found in the fluctuating asymmetry of the length of pelvic spines (t-test, $p = 0.303$).

Discussion

General patterns of sexual dimorphism

Additive genetic variances, covariances and heritability of both threespine stickleback sexes have been shown to be similar in terms of genetic architecture. This imposes

limitations on developing SD (Leinonen, Cano and Merilä, 2011a). However, empirical data showing considerable heterogeneity in SD among different populations suggest that genetic limitations are not as strong as commonly thought (Leinonen, Cano and Merilä, 2011a). SD represents a major source of interpopulation heterogeneity in threespine stickleback, showing high variation in several morphological traits describing different aspects of body size and shape (Aguirre, Ellis, Kusenda and Bell, 2008).

Our sampling locations are situated within a few km of each other. They are filled with stickleback coming from wintering locations likely situated only dozens of km apart during the spawning period (Lajus et al., 2020a). Thus, we can say with a high level of confidence that the fish we analyzed belong to a single population. As this study aims to describe generic patterns of White Sea stickleback SD, we did not study within-population spatial and temporal variation. Such variation occurs (Dorgham et al., 2018), and may result in heterogeneity of SD, but as it is caused by spatial distribution patterns of individuals in the same population, it is not addressed in this study.

Fluctuating asymmetry (FA) was examined in only one bilateral trait, pelvic spines, and showed no differences between sexes. To the best of our knowledge, in this family the only example of difference in FA between sexes was reported for brook stickleback *Culaea inconstans* from Canada: there, males showed higher FA than females in a number of rays and pectoral fin lengths (Hechter, Moodie and Moodie, 2000; see also Lajus et al., 2019 for review of FA studies in stickleback). In animals, SD in FA is very rare, although there are several examples in humans, which are probably caused by social factors (Graham and Özener, 2016). An advantage in our study is its large sample size — almost 1500 specimens — which increases confidence that there is actually no difference in FA between males and females. Our results were not caused by small sample size, which is often the case in FA studies (Palmer and Strobeck, 2003). Below, we discuss patterns and interpretation of SD in different trait groups of threespine stickleback, comparing SD in White Sea fish with species-wide patterns.

Body size

Female-biased body size is reported in the overwhelming majority of studies on SD in threespine stickleback (Ikeda, 1933; Mori, 1984, 1990; Lavin and Mcphail, 1993; Reimchen and Nosil, 2006; Kitano, Mori and Peichel, 2007, 2012; Leinonen, Cano and Merilä, 2011a). Furthermore, other stickleback species such as *Apeltes quadracus* (Blouw and Hagen, 1984), *Gasterosteus wheatlandi* (Sargent et al., 1984), *Culaea inconstans*

(Moodie, 1986), *P. sinensis*, *P. tymensis*, and *P. pungitius* (Ikeda, 1933; McKenzie and Keenleyside, 1970) have the same pattern. Unusual male-biased SD is reported for Canadian threespine stickleback lacustrine populations (Bentzen and McPhail, 1984; Schluter and McPhail, 1992; Boughman, Rundle and Schluter, 2005), and there are additional examples (Kitano, Mori and Peichel, 2007, 2012; Leinonen, Cano and Merilä, 2011a).

Female-biased size SD is commonly explained by male preferences, as larger females can usually consume larger amounts of nutrients, thus increasing fecundity (Wootton, 1973; Bagenal, 1978; Baker, 1994; Kraak and Bakker, 1998; Bonnet et al., 2001). Kitano et al. suggested that larger females have higher reproductive success because they produce larger numbers of eggs and are favored by courting males (2007). Indeed, there is a positive correlation between female body length and fecundity in many wild populations (see Baker, 1994, for review). However, a negative association may also occur, as is shown for Alaskan fish (Baker et al. 1998, 2005), suggesting a potential trade-off between offspring number and quality (Smith and Fretwell, 1974; Wootton, 1979; Parker and Begon, 1986; Stearns, 1992). Size SD may be associated with life history patterns — it is more pronounced in lake populations than those in marine and river habitats (Spoljaric and Reimchen, 2008).

The magnitude of stickleback body size SD may also be caused by size-dependent selection in males, which exhibits complicated patterns. Larger males are more likely to succeed in male-to-male competition for nesting grounds (Rowland, 1989; Dufresne, FitzGerald and Lachance, 1990; Candolin, 1999; Kraak, Bakker and Mundwiler, 1999b), less likely to be victims of sneaking than smaller males (Parker, 1992; Largiadèr, Fries and Bakker, 2001), and may have advantages in guarding nests (Parker, 1992). However, there are also advantages for smaller males, which can mature and start breeding earlier than larger ones (Andersson, 1994). Because annual mortality in the White Sea is about 2/3 (Ivanova et al. 2016), this increases the probability of smaller males participating in spawning. Smaller males may start breeding earlier in the season, occupy better breeding territories, and eventually achieve higher reproductive success than later-breeding, larger males (Mori, 1993; Candolin and Voigt, 2003).

White Sea stickleback clearly exhibit the female-biased size SD typical of the species. In addition to the factors considered above, this pattern may be associated with the almost two-fold, female-biased sex ratio observed on White Sea spawning grounds (Golovin et al., 2019; Lajus et al., 2020a). Normally, larger fish live longer than smaller fish. Therefore, if one sex is larger, its life span will likely be longer (Claisse et al., 2009; Charvet, Santana, De Lima and Lessa, 2018). Hence,

larger female stickleback size may explain their prevalence in the White Sea population.

Anterior body

Sizes of the head, mouth and eyes (HL, HD, ML, Pro, ED, EDp) are frequently used in studies of stickleback SD (McPhail, 1992; Reimchen and Nosil, 2006; Kitano, Mori and Peichel, 2007, 2012; Aguirre and Akinpelu, 2010; Kermoyan, 2013; Reimchen, Steeves and Bergstrom, 2016). Mature males have larger heads than females in different parts of the world: in Japan (Mori and June, 1984; Mori, 1987a; Mori and Takamura, 2004; Kitano et al., 2007), Canada (McPhail, 1992; Reimchen and Nosil, 2006; Spoljaric and Reimchen, 2008), Iceland (Kristjánsson et al., 2002a), the USA and Europe (Kristjánsson, Skúlason and Noakes, 2002b; Leinonen, Cano and Merilä, 2011a, 2011b). Notably, other related species *Pungitius tymensis*, *P. sinensis*, *P. pungitius* have similar SD patterns (Kobayashi, 1959; Chae and Yang, 1990).

Mouth size, dentition, head size and shape, and body depth imply adaptation by males to a benthic trophic niche (Bentzen and McPhail, 1984; Caldecutt and Adams, 1998; Caldecutt, Bell and Buckland-Nicks, 2001; Kristjánsson, Skúlason and Noakes, 2002b; Reimchen and Nosil, 2006; Kitano, Mori and Peichel, 2007; Spoljaric and Reimchen, 2008). Males build nests using their mouths to collect sand and fibers. Also, they frequently manifest biting behavior in interactions with other males and during courtship, which is rare for females (Wootton, 1984). During breeding season, males mostly occur near the bottom protecting their territory and nests, while females spend additional time in the water column. This niche divergence results in different food preferences, and also in different predation pressure. Males are more exposed to bottom predators, whereas females are vulnerable to avian predation (Reimchen, 1980; Reimchen and Nosil, 2004). In the White Sea, we also observed that males spend more time near the bottom during the spawning period (Lajus et al., 2020a), consuming more benthic organisms than females (A. Demchuk, unpublished). More often than females, males are consumed by demersal predators such as cod and sculpin (Golovin et al., 2019). Thus, the above interpretations are in accordance with the life history of stickleback in the White Sea, despite the fact that they spend a small portion of their lives near shore, and the rest of their lives is spent in the water column of the open sea (Lajus et al., 2020a).

Deeper bodies imply male adaptation to benthic trophic niches, including increased protection from predators (Bentzen and McPhail, 1984; Caldecutt and Adams, 1998; Caldecutt, Bell and Buckland-Nicks, 2001; Kristjánsson, Skúlason and Noakes, 2002b; Re-

imchen and Nosil, 2006; Kitano, Mori and Peichel, 2007; Spoljaric and Reimchen, 2008). In the White Sea, selection towards larger male size may be caused by predation. Usually, body depth SD is positively associated with SD in the pectoral fins and caudal peduncle. These results suggest an adaptation for rapid acceleration and maneuverability (Webb, 1984; Taylor and McPhail, 1986; Domenici and Blake, 1997; Walker, 1997; Spoljaric and Reimchen, 2007, 2008), possibly facilitated by divergent predation regimes among the sexes (Reimchen, 1980, 1994; Reimchen and Nosil, 2004). In most stickleback populations, a greater body depth in males could also present an advantage during male-to-male interactions, while during egg fanning, the larger pectoral fins associated with deeper bodies may promote trunk stability and also be attractive to females (Van Iersel, 1953; Wootton, 1976, 1984; Bell and Foster, 1994; Kraak, Bakker and Mundwiler, 1999a).

Armor structures

Functionally, the dorsal and pelvic stickleback spines are important for display by males (Symons, 1966; Wilz, 1970; Huntingford, 1976) and for predator defense (Hoogland, Morris and Tinbergen, 1956; Moodie, 1972). Hoogland et al. (1957) and Reimchen (1983) showed that the first dorsal spine is commonly shorter than the second one, and the latter works as a functional unit with the pelvic spines to protect the fish from predators. Reimchen suggested that highly developed armor in marine stickleback was due to more puncturing predators and post-capture adaptations than greater predation rates (1994). At the same time, niche breadth is larger in lakes than in smaller ponds, which can result in reducing SD magnitude (Spoljaric and Reimchen, 2008; Leinonen, Cano and Merilä, 2011a).

In White Sea stickleback, three dorsal spines, from the first to the third, show a decrease in SDI from a strong male bias to a female bias. This is a good example of decrease in male-biased SD towards the posterior part of the body. This may reflect a greater necessity for females to protect the posterior parts of their bodies. We note this pattern for the first time because we did not find data on the SD of the third dorsal spine. Male-biased SD of the pelvic spine in our sample differed from a species-wide pattern, as authors more often report a female-biased pattern of this trait (Jones, Brown, Pemberton and Braithwaite, 2006; Kitano, Mori and Peichel, 2007; Aguirre, Ellis, Kusenda and Bell, 2008; Leinonen, Cano and Merilä, 2011a). At the same time, the pelvic (or ventral) girdle in literature often shows a female-biased pattern, as we found in our study. Because this bony structure covers the ventral surface of the fish, the pelvic girdle may be a primary defensive mechanism to protect eggs in the abdominal cavity (Bell and Foster, 1994).

Caudal peduncle

Authors who reported male bias in caudal peduncle length SD explain this by males' need for greater maneuverability, which is important during the breeding season. At the same time, longer caudal peduncles can be additional manifestations of more fusiform female bodies, which lower friction during open water swimming, as has been described for various taxa (Aleyev, 1977; Vogel, 1981; Webb, 1984; Domenici and Blake, 1997; Walker, 1997). Our data on White Sea stickleback show male bias in caudal peduncle length, which may be due to the need for greater maneuverability in males.

Fins

SD of stickleback fins has attracted research attention to a different extent. SD of spines, originated from the fin rays of dorsal and pelvic fins, was discussed above. The most attention has been paid to the dorsal fin, which usually showed male bias (Leinonen, Cano and Merilä, 2011a, Supplementary data), but in White Sea fish we did not find SD in this structure. SD of anal fins was studied by Kristjansson et al. (2002), who found male-biased SD in two samples, which is similar to our findings. As anal and dorsal fins are responsible for maneuverability (Aleyev, 1977), which is more important for stickleback males, these results are in accord with expectations.

Pectoral fin length was reported to have female bias in one study (Aguirre, Ellis, Kusenda and Bell, 2008), and White Sea fish demonstrate the same pattern. Most probably, this is because pectoral fins in stickleback are important swimming structures, along with tails (Aleyev, 1977). At the same time, pectoral fin depth, which shows a male-biased SD in our study, may be beneficial for more effective egg fanning and maneuverability (see above).

Conclusion

Sexual dimorphism of threespine stickleback reflects the different roles of the sexes in reproduction. It also optimizes the use of available population resources. Female-biased sexual size dimorphism is very common in stickleback and probably serves to increase population fecundity. It might be an essential factor in the nearly twofold predominance of females in the White Sea. This preponderance is observed in juveniles only a few weeks old. In spawning fish, it may be caused by higher predation mortality in males, and high energy loss during the spawning period (Golovin et al., 2019).

In our study, most of the traits used in describing body shape show statistically significant SD. It is possible to distinguish several groups of structures where SD patterns are similar. The anterior body is relatively larger in

males. This is likely associated with their role in guarding the nesting area and the offspring, which requires spending more time near the bottom during breeding season. Feeding on benthic organisms leads to specialized adaptations in males, such as larger mouths. Conversely, females spend more time in the water column, where a more fusiform body is more adaptive. The larger body posterior part also allows females to carry more eggs.

Armor structures are more developed in male anterior body parts due to their importance in male-to-male competition and in protecting nests and offspring. In contrast, female armor structures are more developed in their posterior body parts to protect large gonads. The three dorsal spines clearly manifest a pattern in which male-biased SD decreases from the first to the second spine and shifts to female-biased in the third (in White Sea fish). Larger ventral plates in females may provide stronger protection for their eggs, especially from attacks from below. SD of the caudal peduncle and tail part of the body are rather heterogeneous in a species-wide context.

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