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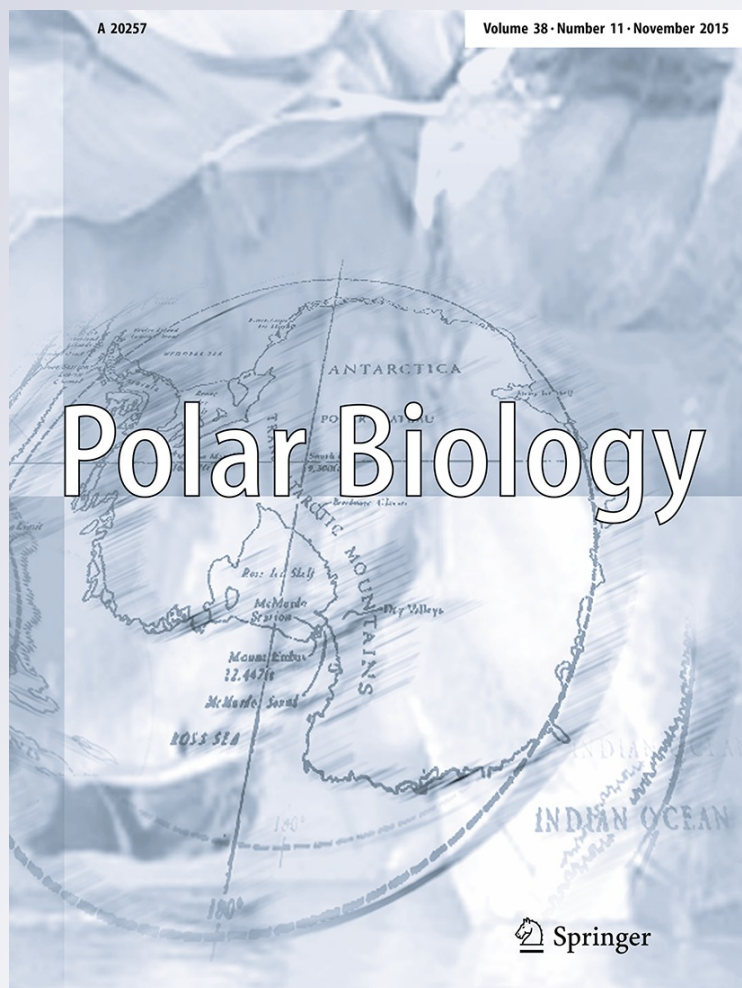
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Age and growth of marine three-spined stickleback in the White Sea 50 years after a population collapse

Peter Yershov¹ · Alexey Sukhotin^{1,2}

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Abstract In the early 1960s, the population of White Sea marine three-spined stickleback (*Gasterosteus aculeatus*), a key forage fish, declined drastically, and the species almost completely disappeared from catches. The population started to recover in the late 1990s, and its abundance has increased exponentially since then. Using contemporary and historical data, we contrast the age structure of spawning stock and fish growth before and after the population decline. Most stickleback spawners in 2009–2011 were 2 and 3 years old, with the 3-year-old fish being more abundant. The proportion of 2-year-old fish in recent catches is higher than that 50 years ago, indicating some rejuvenation of the population after the prolonged decline. Moreover, White Sea sticklebacks in the present population grow faster than those in the 1950s. The observed shifts are concurrent with the long-term changes in the temperature regime in the coastal areas of the White Sea, which determine zooplankton abundance and the duration of the feeding season of fish. The variation in life-history traits among both anadromous and marine stickleback populations within a distribution range was examined. The stickleback showed a considerable interpopulation variation in growth, longevity and age/size at maturity, which

appeared generally related to thermal conditions at the marine feeding areas.

Keywords Stickleback · Age · Growth · Sexual maturity · *Gasterosteus aculeatus* · White Sea · Population structure · Population dynamics

Introduction

Variations in the life-history traits of species reflect a complex of diverse adaptations to fluctuating local environments at the individual and population levels. Climatic shifts, commercial fishing and latitudinal environmental changes have been identified as major causes of fluctuations in growth, age at maturity, stock age composition and other characters of marine fish populations worldwide (L’Abée-Lund et al. 1989; Hutchings 2005; Ottersen et al. 2006; Thresher et al. 2007; Stige et al. 2010; von Biela et al. 2011; Gillanders et al. 2012; etc.). Most data on climate-induced and overfishing effects have been obtained for commercially important species, while those that are not targeted by fisheries have received less attention (Pörtner and Knust 2007). However, non-commercial species are of special interest. Due to low or the absence of fishing pressure, climate-induced effects on their populations could be more clearly recognized, than in exploited species. Thus, short-lived non-commercial fish showed pronounced shifts in distribution and abundance that supervened the prevailing thermal regime changes in the North Sea and inshore waters of the English Channel (Perry et al. 2005; Hiddink and ter Hofstede 2008; Genner et al. 2010).

The three-spined stickleback, *Gasterosteus aculeatus* L., inhabits coastal waters in the Northern Hemisphere,

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including subarctic regions, where it forms marine, anadromous and freshwater populations. Stickleback is a small short-lived fish, in which only one or a few age classes contribute to reproduction (Wootton 1984; Bell and Foster 1994). The marine stickleback is one of the most common and abundant fish in the Kandalaksha Bay of the White Sea. The Kandalaksha Bay area is characterized by extremely rugged sea coastline with many sheltered shallow coves and bays, where seagrass *Zostera marina* meadows serve as typical spawning grounds for the three-spined stickleback in June–July. Most part of their life cycle marine stickleback spends in open sea areas where it feeds mainly on planktonic crustaceans Copepoda and Cladocera. Spawning and juvenile sticklebacks play an important role in the food web, being one of the major food items for some common coastal fish (e.g. cod, shorthorn sculpin, navaga) as well as piscivorous birds, such as gulls, terns and fish ducks (Abdel'-Malek 1963; Mukhomedyarov 1966; Ershov 2010). In the twentieth century, the abundance of this non-commercial species in the White Sea underwent interannual variations as well as drastic fluctuations up to near extinction (Chronicle of Nature by the Kandalaksha Reserve for 1948–2006; Lajus et al. 2013). High population size of stickleback in the Kandalaksha Bay of the White Sea was recorded in the 1930–1950s. Bycatches of this species in coastal fishery could reach up to 1 ton per haul using a 40-m beach seine (Vebl 1934; Mukhomedyarov 1966). In the early 1960s, the stickleback population in the White Sea shrunk drastically and this fish almost completely disappeared from catches. One of the reasons for this sharp decline in stickleback population could be the massive loss of the seagrass *Z. marina* recorded in the White Sea in 1960–1961 (Kuznetsov and Matveeva 1963). A rise in three-spined stickleback numbers in catches of coastal fish species was recorded in 1997, and since then, their abundance has increased rapidly (Lajus et al. 2013). To date, the population size of stickleback has reached such a level that it has once again become the main food item of cod (*Gadus morhua marisalbi*) and shorthorn sculpin (*Myoxocephalus scorpius*) in the Kandalaksha Bay (Ershov 2010; Yershov 2010). Some limited demographic data are available on the White Sea stickleback breeding population prior to a collapse in the 1960s (Mukhomedyarov 1966); however, records on the stickleback population structure after a recovery are virtually absent. Importantly, during the last 50 years, shifts in temperature regimes have been detected in the coastal waters of the White Sea (Berger et al. 2003; Usov et al. 2013) and in the major freshwater lakes in this region (Georgiev 2014). We suppose that studies on short-lived non-commercial fish such as three-spined stickleback from the White Sea are potentially valuable in detecting the earlier ecological consequences of climatic changes

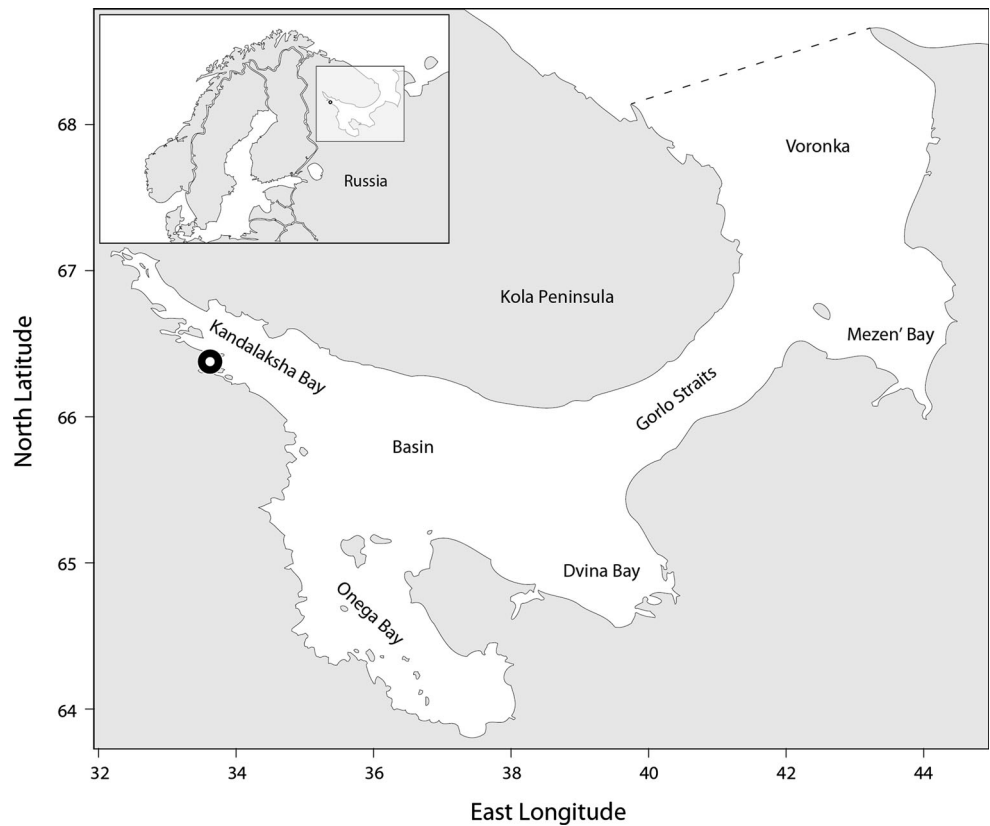
occurring in the Arctic region in recent decades (ACIA 2004). Here we present the results of a comparative investigation of the age structure of spawning stock and growth of marine stickleback before and after its population decline in the White Sea. These data are necessary to assess the possible response of this high-latitude stickleback population to environmental variability in the coastal areas of the White Sea in recent decades as well as to understand the adaptive abilities of the population located near the extremes geographical range of the species. We also evaluate the available data on the age at maturity, longevity and growth rate of marine and anadromous stickleback within a distribution range in order to examine general patterns of variation in these life-history traits and possible selective environmental factors that favour the divergence of populations across large geographical scales.

Materials and methods

Materials

A characteristic feature of the spawning migration of marine stickleback in the White Sea is a mass run to the shores. Dense shoals of migrating fish move along the coast, forming a continuous nearshore band, stretching for several kilometres and occupying sites suitable for spawning, i.e. shallow areas in small sheltered bays and coves. Observations and catches were carried out at one of the typical spawning sites in the coastal areas of the Chupa Inlet (Kandalaksha Bay, White Sea, Russia), where stickleback appears in very large numbers to reproduce each year (Fig. 1). Mature fish were collected annually from 29 June to 7 July, for 3 years (2009–2011), at the same spawning grounds using a small haul seine and a minnow trap (mesh size 5 mm). The length and height of the seine were 7.5 and 1.5 m, respectively. The bag was 1 m wide at the opening and 2 m long. The mesh size of the wing was 5 mm, and that of the bag was 1 mm. A total of 1437 adults were analysed. Immature individuals (1-year-old) were sporadically observed in the seine catches at the spawning grounds. Data on 24 yearlings were provided by Dr. Ivanova (Saint Petersburg State University). These fish were caught at the beginning of July 2009 in the same places as those in the present study. Young-of-the-year fish ($n = 100$ individuals) were caught using a dip net ($50 \times 50 \times 55$ cm; mesh size 2 mm) on 8 August 2011. The total length (L_T) and standard length (L_S) of all the fish were measured to the nearest millimetre using digital callipers. The total body mass (M_T) and gonad mass (M_G) of freshly caught adults were determined with an accuracy of 0.01 and 0.001 g, respectively. The gonadosomatic index (gonad mass as a percentage of total body mass, GSI) was

Fig. 1 Map of the White Sea. The circle denotes the study area



calculated for 337 females and 108 males. The age of all fish was determined by counting the annual rings on the operculum (Mukhomedyarov 1966; Patimar et al. 2010). The opercula were carefully dissected from both sides of the head, immersed for several seconds in hot water and scraped free of any leftover tissue. After drying, the bones were examined under normal transmitted light without the use of optics. To verify the results, the age of all the fish was determined twice by the same operator (Peter Yershov). All the adults caught were in spawning condition. The sex of the fish was determined through the analysis of the gonads after dissection. The sex of immature fish was not determined.

Calculations and statistics

For three-spined stickleback, it is known that the gonadosomatic index of females is much higher than that of males (Crivelli and Britton 1987). Therefore, the growth rates of males and females were estimated by considering the body mass without the gonads ($M = M_T - M_G$). Thus, the influence of individual variation in gonad mass on the total body mass of the fish was avoided. The relation between body mass without gonads (M , g) and length (L_T , mm) is expressed as

$$M = aL_T^b,$$

where a and b are constants. The growth rates were calculated from the length-at-age data. Body length growth is described by the von Bertalanffy equation (Brey 2001)

$$L_t = L_\infty \left(1 - e^{(-k(t-t_0))} \right),$$

where L_t is the total length (mm) at age t (years), while L_∞ , k and t_0 are constants. L_∞ is the theoretical asymptotic length that a fish would attain if it were to grow indefinitely, k is the estimated growth rate, and t_0 is the hypothetical age at which a fish has zero length. Body mass growth is approximated by the equation (Brey 2001)

$$M_t = M_\infty \left(1 - e^{(-k(t-t_0))} \right)^3,$$

where M_t is the body mass (g) without gonads at age t (years) and M_∞ is the theoretical asymptotic mass that a fish would attain if it were to grow indefinitely.

Pairwise comparison of growth curves was carried out through analysis of residual variance in separate growth regressions and a combined regression based on the pooled data. Mean sizes of fish of different ages and those from the literature were compared using Student's t test. Age composition in catches of different years and proportions of fish

of specific ages in males and females were compared by Chi-square (χ^2) test.

The possibility of separating cohorts (age groups) by means of length-frequency distributions was tested in a sample of females ($n = 797$ individuals) caught on 5 July 2009. The operculum rings were counted for each fish in this sample in order to validate the length-frequency method of age determination. Using the graphical method (Bhattacharya 1967), the size-frequency distribution of the fish was decomposed into a series of best-fit normal curves that represent separate cohorts (age groups) within the data set. The means, standard errors (SEs) and the proportion of modal groups were estimated. The separation index (I_S) between a pair of successive cohorts was calculated using NORMSEP, assuming that $I_S > 2$ indicated a difference between the distributions (Gayanilo et al. 2005). Analyses were carried out with FiSAT II software. Means \pm SEs are presented unless indicated otherwise.

Results

Age composition

The age of spawners in the catches was 2–5 years, with the vast majority (>90 %) represented by 2–3-year-old fish in each year of observations with the dominance of 3-year-old fish (Table 1). A maximum age of 5 years was recorded for only one female ($L_T = 76$ mm, $M_T = 5.2$ g). The White Sea three-spined stickleback begins to attain maturation at the age of 2 years (Mukhomedyarov 1966, our observations). Three-year-olds of both sexes die shortly after spawning, which is evident from the large difference in the proportions of 3- and 4-year-old fish (Table 1). Massive die-off of 3-year-old stickleback occurs after the fish migrate off the shores because no large numbers of dead fish were observed at the spawning grounds. Apparently, only a small fraction of the surviving fish spawn in their fourth calendar year. According to the data pooled for 3 years, the proportion of the most represented cohorts (2- and 3-year-old fish) differed among males and females ($\chi^2 = 57.4$, $p < 0.05$). The fraction of 2- and 3-year-old

males was similar (45 and 52 %, respectively), while in females, 3-year-old fish drastically dominated (70 %; Table 1) in each year of observations. This indicates that only some females reach maturity at 2 years of age, and the rest mature at the age of 3 years. In males, the fraction of 2-year-old fish was higher than in females, suggesting that on average, males mature earlier than females. Besides adults, immature 1-year-old fish were occasionally observed in catches (0.14 % of total sample) at the spawning grounds.

The length-frequency distribution of females caught by one haul of seine on the 5 July 2009 is presented in Fig. 2. The length (L_T) distribution with 2-mm intervals was clearly bimodal, composed of a lower modal group (LMG) and an upper modal group (UMG) (separation index $I_S = 2.13$). The overlap between two groups was significant. The LMG accounted for 25 % of the total sample, which was similar to the proportion of 2-year-old females (24.2 %) estimated by means of operculum readings. The UMG had a higher proportion (75 %) as compared to the number of 3-year-olds from operculum determinations (70 %). The means L_T of LMG (66.0 ± 0.26 mm) and UMG (77.2 ± 0.14 mm) were very close to the respective means L_T of the females of 2 and 3 years of age from this sample (67.2 ± 0.05 and 77.2 ± 0.1 mm, respectively). Four-year-old fish (6 % in the analysed sample) could not be detected on the basis of the length-frequency analysis and fell into the UMG. Therefore, analysis of the size-frequency distribution of female stickleback allows the identification of two groups: 2-year-olds and ‘3 and older’.

Growth

The body length L_T of adult fish in the catches varied between 52 and 89 mm (average 72.0 ± 0.2 mm), while the body mass M_T varied from 1.4 to 7.9 g (average 3.8 ± 0.03 g). The maximum individual fish length was similar in all the years of the study; females were bigger than males in all age groups (t test, $t = 11, 40$ and 9 for 2-, 3- and 4-year-olds, respectively, $p < 0.001$; Table 2). In males, the dominating size class was 64–70 mm, while in females it was 74–80 mm. All fish longer than 80 mm were

Table 1 Age composition (%) three-spined stickleback spawners in catches in the Kandalaksha Bay, White Sea, in 1957–1959 (after Mukhomedyarov 1966) and 2009–2011 (our data)

Sex	Age (years)				Number
	2+	3+	4+	5+	
Males	44.6	51.8	3.6	Not observed	444
Females	24.7	69.6	5.6	0.1	993
Both sexes	30.8	64.1	5.0	0.1	1437
Both sexes (Mukhomedyarov 1966)	18.3	74.4	7.3	+	752

(+)—5-year-old fishes were recorded by Mukhomedyarov, but their proportion in catches was not presented

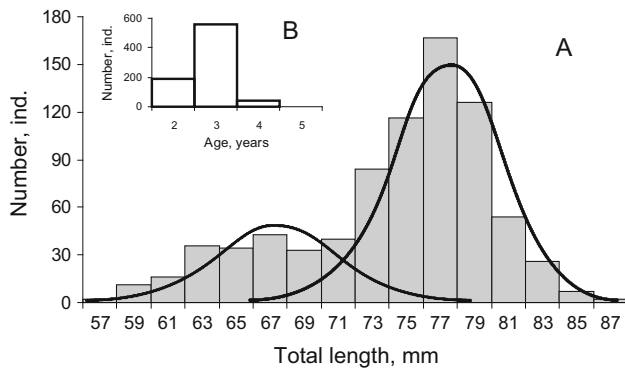


Fig. 2 Length- (A) and age-frequency (B) distributions of female three-spined stickleback caught on 5 July 2009, in the Chupa Inlet, Kandalaksha Bay. Two separate length distributions are represented by best-fit normal curves

females. Large variations were recorded in the individual growth rates in the same age group of stickleback (Table 2). The minimum size at maturity was 52 mm, regardless of sex. The relationship between absolute and standard body length in a pooled sample of the White Sea three-spined stickleback was described by the equation $L_S = 0.88 (\pm 0.003) \cdot L_T$ ($R^2 = 0.979$, $p < 0.00001$, $n = 1087$, both sexes).

The length-to-mass relationship in the studied fish is described by the equations $M = 8.5 (\pm 3.1) \times 10^{-6} \cdot L_T^{3.019 \pm 0.09}$ ($R^2 = 0.796$, $n = 336$) for males and $M = 9.6 (\pm 3.2) \times 10^{-6} \cdot L_T^{2.958 \pm 0.08}$ ($R^2 = 0.846$, $n = 337$) for females, which differs significantly ($F = 78.5$, $p < 0.001$; Fig. 3). Adult males are generally heavier than females of the same size when compared without gonads. The size of young-of-the-year fish caught at the beginning of August

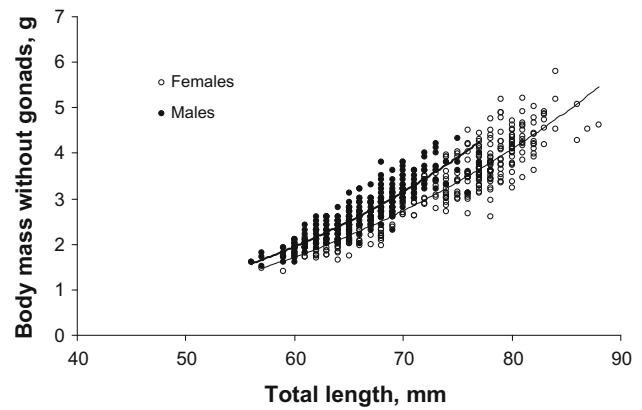


Fig. 3 Length–weight relationship in White Sea stickleback

ranged from 18 to 28 (mean 22.2 ± 0.21) mm in length L_T and from 0.042 to 0.174 (mean 0.081 ± 0.002) g in body mass.

The growth curves and the respective equations are presented in Fig. 4. In general, females grow faster than males, and the curves of both length and mass growth differ between sexes ($F = 205.0$ and $F = 80.8$, respectively, $p < 0.001$). Among the spawners, females exceeded males by length in all age classes. Regarding body mass without gonads, sex differences were recorded only in 3- and 4-year-old fish (t test, $t = 14$ and $t = 3$, respectively, $p < 0.01$). The fastest growth in length ($30\text{--}35 \text{ mm year}^{-1}$) in stickleback is observed during the first 2 years, followed by a slowdown. The growth in body mass was maximum (approximately 1.5 g year^{-1}) in the second and third years of life.

Table 2 Body size of three-spined stickleback of different ages in the Kandalaksha Bay, White Sea

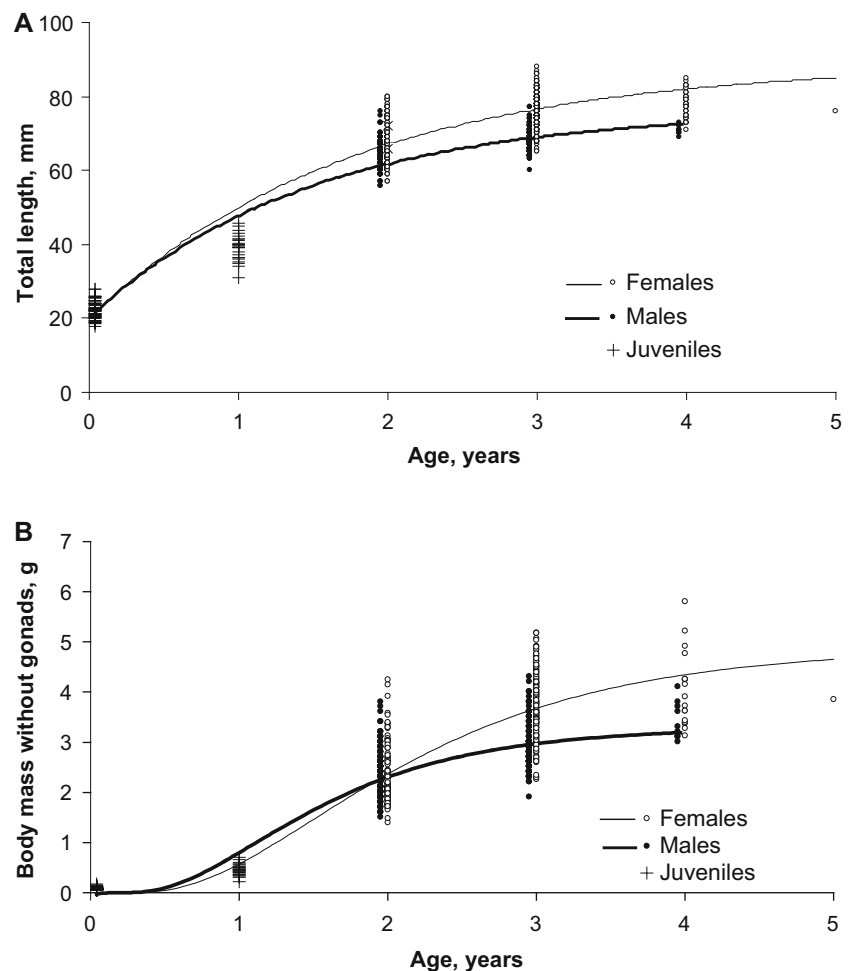
Age (years)	Number	Sex	Length (L_T , mm)			Mass (M_T , g)		
			Range of variability	Mean \pm SE	Mean length (after Mukhomedyarov 1966)	Range of variability	Mean \pm SE	Mean mass (after Mukhomedyarov 1966)
1	26	Both sexes	31–46	39.2 ± 0.7	47.7	0.22–0.70	0.46 ± 0.22	1.01
2	245	Females	52–83	$68 \pm 0.3^{***}$	63.7	1.9–7.7	$3.3 \pm 0.06^{***}$	2.02
		Males	52–76	$64 \pm 0.2^{***}$	61.4	1.4–3.9	$2.5 \pm 0.03^{***}$	1.81
3	691	Females	64–89	$77 \pm 0.1^{***}$	71.5	2.1–7.9	$4.6 \pm 0.03^{***}$	3.58
		Males	58–77	$68 \pm 0.2^*$	67.2	2.0–4.4	$3.0 \pm 0.03^{***}$	2.81
4	56	Females	71–85	$78 \pm 0.4^{***}$	80.3	3.4–7.6	$5.0 \pm 0.13^{***}$	5.55
		Males	66–79	71 ± 0.7^{ns}	71.2	2.8–4.2	3.4 ± 0.10^{ns}	3.4
5	1	Female	–	76	–	–	5.2	–

In Mukhomedyarov (1966, Table 4), sample size was 17, 136, 560 and 56 specimens for 1, 2, 3 and 4 age groups, respectively

ns not significant

* Significant differences between fish size from the late 1950s and present population

Fig. 4 Body length (**A**) and mass (**B**) growth curves of White Sea three-spined stickleback. The growth curves are described by the equations:
 $L_{\infty} = 88.9 \pm 1.0$
 $(1 - e^{(-0.57 \pm 0.02 (t + 0.44 \pm 0.02))})$
(A), $M_{\infty} = 4.88 \pm 0.18$
 $(1 - e^{(-0.87 \pm 0.06 (t - 0.22 \pm 0.08))})^3$
(B) for the females and
 $L_{\infty} = 76.5 \pm 1.0$
 $(1 - e^{(-0.67 \pm 0.03 (t + 0.46 \pm 0.02))})$
(A), $M_{\infty} = 3.29 \pm 0.07$
 $(1 - e^{(-1.21 \pm 0.06 (t - 0.19 \pm 0.05))})^3$
(B) for the males



The gonadosomatic index in females was, on average, 24.6 ± 0.3 %, which is much higher than that in males, i.e. 3.1 ± 0.1 % (t test, $t = 5.4$, $p < 0.001$). The sex ratio of the adult fish in the spawning grounds was shifted towards female predominance and ranged from 2:1 to 4:1.

Comparison with the 1950s population

We compared our data set on the present age–size structure of the White Sea three-spined stickleback with the data obtained by Mukhomedyarov (1966). He collected stickleback from June to early July in the same sites as in the present study using the same fishing gear, which ensures the comparability of these two data sets. The age composition of the stickleback spawners in the catches significantly differed between the present population and that of the 1950s ($\chi^2 = 14.4$, $p < 0.05$). In the present population, the spawners are generally younger, while in 1957–1959, the proportion of 3-year-old fish was higher (Table 1). The average size (both L_T and M_T) of 2- and 3-year-old fish of both sexes, which comprise the majority of the spawning

population, was significantly higher in the catches of 2009–2011 than in the population of 1957–1959 (t test, $t = 13.0$ and $t = 4.0$ for 2- and 3-year-old fish, respectively, $p < 0.05$; Table 2). In the catches of the 1950s and in present time, 4-year-old fish were few in number. The 4-year-old females by contrast with males were larger in the 1950s (t test, $t = 5.9$, $p < 0.01$), as compared to those from the modern fish stock.

Discussion

The White Sea stickleback population in the 1950s and 50 years later

Comparison of our data with those from previous studies shows that the adult fish of 2–5 years of age groups are observed on the spawning grounds with 2–3 year-old specimens being the most abundant both in the 1950s and after the recovery of stickleback abundance in the White Sea. Among migrants, 3-year-old fish have dominated

catches over the years. However, in the present population, the proportion of 2-year-old fish was higher and the fraction of older specimens was lower, as compared to the data from the 1950s. The minimum age of maturity for stickleback in the White Sea is 2 years (Mukhomedyarov 1966; our data), although some fish do not mature until they are 3 years old. This is evidenced by a significant predominance of 3-year-olds in the population, both in the 1950s and presently. Furthermore, males generally mature earlier than females and have an apparently shorter life cycle. Similarly, the predominance of females in older age groups has been observed in stickleback populations along the Estonian coast of the Baltic Sea (Saat and Turovski 2003). Thus, the period of maturation in male and female sticklebacks from the White Sea is prolonged; fish of both sexes become sexually mature in their second or third year.

In the White Sea, *G. aculeatus* reaches a maximum length of $L_T = 115$ mm (Vebel 1934). In our samples and in the catches of Mukhomedyarov (1966), the maximum length of the migrating spawners was around 90 mm. The largest specimens in all the catches were represented exclusively by females. According to our data, females grow faster than males, not only in length but also in weight. The fact that adult females are bigger than males has been frequently recorded in wild stickleback populations from various habitats elsewhere (van Mullem and van der Vlugt 1964; Coad and Power 1973; Crivelli and Britton 1987; Bloum and Hagen 1990; etc.). To the best of our knowledge, comparisons of body weight of anadromous stickleback of different age and sex, when the gonad mass is excluded from the body mass, have not been conducted previously. In the present study, mature males were heavier than females of similar size when compared without gonads. This may be due to sexual dimorphism in body shape and head morphology. The head of males is known to be larger than that of females (Kitano et al. 2007; Aguirre and Akinpelu 2010). Sticklebacks of the present population in the White Sea grow faster than those in the 1950s during their first 3 years of life. We can think of two possible explanations for these differences. The first potential cause of the observed differences in fish growth could be the contribution of genetic drift and (or) founder effects due to the abundance fall and subsequent recovery during the last 50 years. The genetic structure of the stickleback population before the decline and after the recovery may be somewhat different. However, we are not aware of any genetic data that would enable us to accept or reject this hypothesis. The second possible explanation may be connected with the temperature and phenological shifts in the coastal areas in the White Sea owing to climatic variations in the region in 1961–2010. Indeed, long-term change in thermal regime in the Kandalaksha Bay of the White Sea is expressed as significant extension of

hydrological summer period in the upper 10-m layer over the last 50 years (Usov et al. 2013). At present, water warming up to $+8$ °C occurs approximately half a month earlier than in the 1960s. Simultaneously, the increase in abundance and shifting in the phenology of a copepod *Calanus glacialis* were found (Usov et al. 2013). Observed changes in the seasonal dynamics of water temperature in the nearshore areas of the White Sea correspond to the positive trend of ocean surface temperature observed in the Northern Hemisphere, especially in Polar regions (e.g. Peterson et al. 2002; Comiso et al. 2008). According to Mukhomedyarov (1966), spawning stickleback appears in the coastal waters in early June, when the water temperature in the shallows reaches $+6$ – 8 °C. Migrating adult stickleback actively feeds in this period (Abdel'-Malek 1963). It is possible that in the present temperature conditions, the duration of foraging and growth period for young stickleback have increased, leading to an increase in the mean size of spawners. Apparently, the higher growth performance of immature stickleback in feeding areas has resulted in the acceleration of sexual maturation of individuals, which has led to shifts in the age structure of the spawning stock, as compared with the “old” population. Indirect evidence of the later maturation of fish in the 1950s is that 4-year-old females from those times were somewhat larger than stickleback of the same age from the present population. This may be similar to the situation recorded for stickleback from the Kamchatka river, where fish that mature late attain greater sizes (Bugayev et al. 2007).

In general, the fish populations' responses related to climate forcing in polar areas have not been intensively studied. It is assumed that the direct and indirect effects of climate change on fish populations vary among localities and depend on the life history of species (Reist et al. 2006). Thus, sea surface temperature fluctuations in the nearshore areas were found as one of the first-order mechanisms by which growth performance of some fishes (*Salvelinus malma*, *Salvelinus alpinus*) is affected by climate conditions in Arctic regions (Michaud et al. 2010; Stolarski 2013). Such temperature effects on individuals are integrated into the population-level responses which in turn have important consequences for trophic interactions, altering food-web structures and leading to eventual ecosystem-level changes.

Interpopulation variation in life-history traits

A maximum longevity of 5 years in anadromous and marine populations of *G. aculeatus* besides those in the White Sea was recorded only in stickleback migrating into the river Utkholok (Kamchatka Peninsula, Pacific coast of Russia; Pichugin et al. 2008). Sticklebacks inhabiting the

Baltic coastal waters in Sweden as well as those from the river Kamchatka (Kamchatka Peninsula) live for up to 4 years (Aneer 1973; Bugaev 1992). The longevity of three-spined stickleback from other studied populations across the area varies between 1 and 3 years. The anadromous stickleback migrating into the rivers at the Kamchatka Peninsula for spawning is generally older (3–4 years old) (Bugaev 1992; Bugaev et al. 2007; Pichugin et al. 2008) than those from the White Sea. The vast majority of spawners in other three-spined stickleback populations from Europe (e.g. Münzing 1959; van Mullem and van der Vlugt 1964; Aneer 1973; Crivelli and Britton 1987), the Middle East (Patimar et al. 2010), North America (e.g. Coad and Power 1973; Dufresne et al. 1990; Baker et al. 2008; Karve et al. 2013) and Japan (Mori 1990; Higuchi et al. 1996; Kitamura et al. 2006) consist of 1- and 2-year-old fish. In some northern populations (e.g. in the White Sea and Kamchatka regions), stickleback apparently matures later and lives longer than those from more southerly populations. Our observations support a previous suggestion by Wootton (1984) concerning such a trend in anadromous populations of *G. aculeatus*.

Notably, sticklebacks in northern Russia (White Sea and Kamchatka) differ from those from Alaska in terms of age at maturity and lifespan. Thus, according to Narver (1969), estuarine stickleback from the Chignik Lagoon (Alaska, USA) matures and attains a length of $L_T = 65\text{--}90$ mm at the age of 1 year. Baker et al. (2008) stated that the fish in many anadromous populations from the Cook Inlet region (Alaska) breed exclusively at the age of 2 years and die after reproduction. The observed differences between the northern sticklebacks in Russia and Alaska may be associated with peculiarities of reproductive strategies of fish from these populations. On the other hand, the data on the age of stickleback from the compared regions were obtained using different methods. The age estimates of fish from many Alaskan populations were based mainly on size-frequency data (Baker et al. 2008), whereas those of fish from the Russian North were based only on the otolith and operculum readings (Mukhomedyarov 1966; Bugaev 1992; Pichugin et al. 2008; our data). It is well known that age estimation based on size distributions in populations with multiple adult year classes is unreliable for the identification of older cohorts and could be misleading because of the overlap of different age groups and a small proportion of older fish (Jones and Hynes 1950; Pennycuik 1971). Our testing of the applicability of length-frequency distribution for separating age cohorts in the White Sea stickleback provides further evidence of this conclusion. Therefore, the Alaskan anadromous stickleback populations may include age groups comprising fish older than 2 years, which have not been recognized using the size-frequency histograms.

There is a little information on the gonadosomatic index of anadromous/marine *G. aculeatus* at the beginning of the spawning period. Mean GSI values in the stickleback from the White Sea fall within the range observed in the other populations of this species—from 17.1 to 28.0 % in females and about 3 % in males (Borg and van Veen 1982; Mori 1990; Patimar et al. 2010; Kume 2011).

The growth trajectory of three-spined stickleback is a characteristic that shows intra- and interpopulation variation due to environmental and genetic factors (Jones and Hynes 1950; Snyder 1991; Baker 1994). The data on body size (mean L_T or L_S) for marine and anadromous three-spined sticklebacks are numerous and based mainly on samples from catches during spawning migration. For the purposes of our comparative study, we referred to publications that provide information on the age of the fish examined. Furthermore, because L_S is presented in most cited studies, L_T if encountered was converted into L_S according to the equation $L_S = 0.88 L_T$ (Crivelli and Britton 1987; our data).

The size-at-age data on anadromous/marine stickleback within a distribution range are presented in Fig. 5 and Online Resource 1. The interpopulation variation in stickleback size at the age of 1 year is enormous—around threefold. The fastest growth has been recorded in anadromous Pacific Ocean stickleback from the Harutori Lake and Akkeshi area (Hokkaido Island, Japan; Fig. 5, Online Resource 1). They reach maturity, spawn and die at the age of 1 year, with a mean body length of around 76 mm for males and 82 mm for females (Mori 1990; Higuchi et al. 1996; Kitamura et al. 2006; Kitano et al. 2007). The most slow-growing marine sticklebacks inhabit the Askö area (Baltic Sea, Sweden), where immature yearlings have a mean L_S of 27 mm only (Aneer 1973; Fig. 5, Online Resource 1). Similar small sizes in the first year and therefore later maturation have been observed in fish from the Gulf of St. Lawrence, Canada (Coad and Power 1973), and from the White Sea (our data). The reasons for such retarded growth in these populations may be strong seasonality and low winter water temperatures in wintering areas. In the White Sea, the length of mature stickleback at 2 years is around 60 mm, which is greater than that in some more southerly populations (e.g. from the Baltic Sea, North Sea and Caspian Sea; Fig. 5, Online Resource 1). This is possibly due to the delayed maturation of the White Sea fish compared to those from lower latitudes, which start reproduction earlier and correspondingly exhibit drastically reduced somatic growth. Sticklebacks in another northern area, the Alaskan region, breed exclusively at the age of 2 years, with a mean length of 61–71 mm (Baker et al. 1998, 2008; von Hippel and Weigner 2004; Aguirre et al. 2008; Karve et al. 2008; Confer et al. 2012). The anadromous sticklebacks

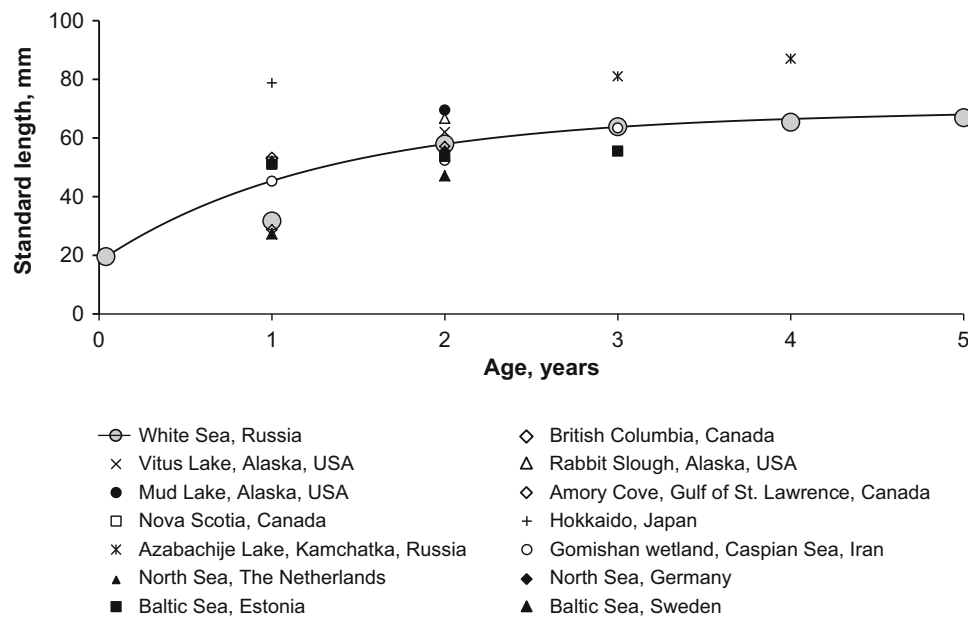


Fig. 5 Length-at-age of three-spined stickleback (both sexes) from different parts of the range. The data are taken from the following sources: White Sea—our data; Mud Lake—Karve et al. (2008); Confer et al. (2012); Hokkaido—Mori (1990); Kitano et al. (2007); North Sea, Germany—Münzing (1959); British Columbia—Saimoto (1993); Amory Cove, Gulf of St. Lawrence—Coad and Power (1973); Gomishan wetland—Patimar et al. (2010); Baltic Sea, Sweden—

Aneer (1973); Baltic Sea, Estonia—Saat and Turovski (2003); Rabbit Slough—Aguirre et al. (2008); Nova Scotia—Bloum and Hagen (1990); North Sea, The Netherlands—van Mullem and van der Vlugt (1964); Vitus Lake—von Hippel and Weigner (2004); Azabachije Lake—Bugaev et al. (2007). The curve describes fish growth from the White Sea population (our data)

inhabiting the rivers in the Kamchatka Peninsula attain maturity even later, at 3–4 years of age, and grow to a surprisingly large size over 80 mm (Bugaev et al. 2007). According to the extensive literature available, anadromous/marine three-spined stickleback that matures at the age of 1 year usually attains a length of around 45–50 mm (Aneer 1973; Coad and Power 1973; Bloum and Hagen 1990; Saimoto 1993 etc.). Such high growth rates at the first year of life are typical for most populations from southern regions. Spawning of stickleback from northernmost populations occurs at a larger size (Kamchatka, Alaska, White Sea) and older age (Kamchatka, White Sea), than their more southern conspecifics. Growth and age at maturity often exhibit latitudinal variation because of environmental gradients with a temperature being the most significant. For a widely distributed species, specimens inhabiting colder waters tend to exhibit slower individual growth than those from warmer areas. It has been shown for ectotherms that lower temperatures lead to later maturation at a larger size, while reduction in food quality causes later maturation at a smaller size (Atkinson 1994; Berrigan and Charnov 1994). It is therefore likely that immature growth rates of stickleback from the most northern populations are inhibited by reductions in temperature during the foraging period in the sea rather than by food limitations.

We suggest that interpopulation variation in the growth rates of stickleback from different parts of the distribution range is governed mainly by local environmental differences in water temperature and to a lesser extent by food availability in the marine pelagic feeding grounds. The growth rate variation in turn determines the age at maturity of fish in populations from different localities within the area. Natural selection due to environmental differences has probably contributed significantly to the variation we have observed in the life-history traits.

In conclusion, marine three-spined stickleback showed rejuvenated age composition and larger spawners in the present recovered population, as compared to those that inhabited the White Sea in the mid-twentieth century. The observed shifts are possibly caused by the long-term changes in the hydrothermal regimes of coastal areas of the White Sea, which in turn determine zooplankton abundance, the duration of the feeding period, and the peculiarities in the growth and maturation of fish. Moreover, climatic changes in the long run may lead to significant alterations in the species' life-history traits, population structure and dynamics as well as to corresponding shifts in coastal ecosystems as a whole. According to our results, three-spined stickleback showed a significant life-history variation related to long-term changes as well as to geographical differences in environmental temperature. This

makes *G. aculeatus* one of the perspective and convenient fish species in studies of multilevel ecosystem responses to climate changes and anthropogenic impacts.

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