Evolutionary Ecology Research, 2019, **20**: 297–315

Homing ability and site fidelity of marine threespine stickleback on spawning grounds

T.S. Ivanova[1], M.V. Ivanov[1], A.E. Bakhvalova[1], N.V. Polyakova[1], P.V. Golovin[1], A.V. Kucheryavyy[2], A.O. Yurtseva[3], K.A. Smirnova[1] and D.L. Lajus[1]

[1]*Saint-Petersburg State University, St. Petersburg, Russia,*
[2]*A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia and* [3]*Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia*

ABSTRACT

Hypothesis: Marine threespine stickleback manifest homing ability and site fidelity during their spawning period.

Organism: The threespine stickleback, *Gasterosteus aculeatus*.

Time and places: June 2015 and June 2016 (during the stickleback spawning period), Koliushkovaya Lagoon, Kandalaksha Bay, the White Sea.

Methods: Stickleback were tagged on their inshore spawning grounds about 2 weeks after their inshore migration. We attached plastic tags to their dorsal spines, displaced them 100–300 m away from shore, and recaptured them inshore after periods of one hour to four days.

Results: Stickleback caught on their spawning grounds in the lagoon, tagged and displaced a few hundred metres, were able to return to their home site within a day. Males and females exhibited no differences in homing ability. Most fish left their home site within four days of returning, however, indicating that site fidelity is weak. Stickleback caught outside the lagoon in the sea, and tagged and released in the lagoon, spread along the shore in accordance with the density of local fish.

Keywords: fish tagging, *Gasterosteus aculeatus*, homing, site fidelity, threespine stickleback, White Sea.

INTRODUCTION

Many animals displaced from a familiar site to an unfamiliar one are able to return to their home site, thereby demonstrating homing ability (Gerking, 1959; White and Brown, 2013). In fish, two types of homing have been identified (Thyssen *et al.*, 2014): (1) long seasonal spawning or feeding migrations of up to thousands of kilometres common in salmon, herring, cod, and sturgeon (Hansen *et al.*, 1993; Dittman and Quinn, 1996), and (2) comparatively shorter movements of up to

Correspondence: D.L. Lajus, Saint-Petersburg State University, 7–9 Universitetskaya nab., St. Petersburg 199034, Russia. email: dlajus@gmail.com

hundreds of metres typical, for instance, of small intertidal fish (Monteiro *et al.*, 2005; Lindholm *et al.*, 2006; White and Brown, 2013; Thyssen *et al.*, 2014). The marked difference in scale between these two types of homing ability suggests different underlying mechanisms, the first using true navigation, such as orientation by magnetic fields, and the second using mostly topographic characteristics of home sites (Dodson, 1988; Reese, 1989; Braithwaite and De Perera, 2006; Mitamura *et al.*, 2012), but occasionally involving true navigation (Jorge *et al.*, 2012).

Another aspect of homing behaviour, home site fidelity, refers to an animal's ability to remain at its home site without being displaced. Homing behaviour is considered to have fitness advantages in almost every case. Small-scale homing, for example, reinforces knowledge of the location of food sources, of shelters from predators, and of the local ecological community (Piper, 2011). Higher mortality among animals displaced from their home sites demonstrates the importance of familiar locations (Reinert and Rupert, 1999; Letty *et al.*, 2003, 2007). Therefore, enhancing our knowledge of the patterns and mechanisms of homing behaviour may increase our understanding of local adaptation processes, one of the key concepts in population ecology.

Males and females often demonstrate different patterns of homing behaviour that reflect their different reproductive roles. Males and females may have different home ranges, which seems to be connected with morphological differences in brain areas related to spatial orientation (Parker and Bell, 2010; Costa *et al.*, 2011). Technically, obtaining information on homing behaviour in fish is approached by tagging individuals and tracing their migrations under natural conditions, with or without displacement (Griffiths, 2003; White and Brown, 2013), or under entirely artificial conditions (Jorge *et al.*, 2012). However, such studies are labour-intensive and require convenient model organisms. One such organism, the threespine stickleback (*Gasterosteus aculeatus*), is commonly used in population and behaviour studies. To date, however, stickleback have only been used to study spatial orientation using visual signals within small areas (Odling-Smee and Braithwaite, 2003; Parker and Bell, 2010).

A number of characteristics make stickleback an attractive model species for homing behaviour studies: (1) a vast amount of information on their population biology and behaviour (Bell and Foster, 1994; Östlund-Nilsson *et al.*, 2007; Hendry *et al.*, 2013); (2) sexual dimorphism of external characters associated with parental care performed by males (Kitano *et al.*, 2007; Aguirre *et al.*, 2008); (3) adaptation to both open water and coastal habitats, which suggests the use of alternative mechanisms of spatial orientation (Ziuganov, 1991; Ivanova *et al.*, 2016; McCleave *et al.*, 2018); and (4) resilience to manipulation and characteristic spines that optimize tagging potential (Barber and Ruxton, 2000; Ward *et al.*, 2002, 2013; Webster and Laland, 2009).

Homing behaviour in threespine stickleback is not well studied. Although return to home sites has been reported for lake and stream stickleback (Bolnick *et al.*, 2009), and Ward *et al.* (2013) observed short-distance homing in stickleback inhabiting small creeks, there are no such data regarding marine stickleback. Studies on local stickleback migrations have focused on fish activity and shoal fidelity (Ward *et al.*, 2002), shoaling in laboratory conditions (Barber and Ruxton, 2000; Frommen and Bakker, 2004), density-dependent behaviour (Candolin and Selin, 2012), and differences in spatial orientation ability between populations (Girvan and Braithwaite, 1998; Odling-Smee and Braithwaite, 2003). For marine stickleback in the Baltic Sea, it has been shown that genetic differentiation in males is lower than in females on the scale of tens of kilometres. Therefore, males are more migratory, and populations exhibit male-biased dispersal patterns (Cano *et al.*, 2008).

Using White Sea stickleback for such studies has the benefit of a vast amount of information about the different aspects of their population ecology:

1. *Spatial heterogeneity*: in the White Sea, the most favourable spawning grounds are seagrass (*Zostera marina*) beds in protected inlets, where the density of stickleback reaches tens of individuals per square metre (Ivanova *et al.*, 2016; Rybkina *et al.*, 2017).
2. *Population structure and dynamics*: threespine stickleback in the White Sea show very strong, long-term fluctuations in abundance, and are currently close to their historical maximum (Lajus *et al.*, 2013; Yershov and Sukhotin, 2015; Bakhvalova *et al.*, 2016).
3. *Important role in the White Sea ecosystem*: adult stickleback on inshore spawning grounds prey mainly on benthos, with up to half of their diet consisting of stickleback eggs; by the end of summer, juvenile stickleback feeding in coastal habitats shift from smaller to larger prey and from benthic to planktonic food, depending on availability. Stickleback are also an important food source for many fish and seabirds in the White Sea (Yershov, 2010; Demchuk *et al.*, 2015, 2018; Bakhvalova *et al.*, 2016; Rybkina *et al.*, 2016).
4. *Predation-related and non-predation-related mortality on spawning grounds* (Golovin *et al.*, 2019): it is important to note that, throughout their spawning migrations – moving inshore, spawning, and returning to sea again – White Sea stickleback spend only one to three weeks in the inshore zone, perhaps even less, because post-migration fish change their spawning location as they constantly compete for higher quality spawning grounds (Dorgham *et al.*, 2018).

Our aim here was to analyse spatial and temporal aspects of the homing ability and site fidelity of threespine stickleback during their spawning period.

METHODS AND MATERIALS

Sampling sites

The study was conducted in Koliushkovaya Lagoon, situated near the Marine Biological Station of St. Petersburg State University on Kandalaksha Bay in the White Sea (66.314063°N, 33.641516°E; Fig. 1). This semi-isolated marine lagoon covers an area of 58,000 m^2, has a perimeter of about 1000 m (measurements were conducted using Google Earth Pro 7.3.2.), and a depth of up to 4 m. It connects to the sea via one strait suitable for stickleback migrations at high tide. Lagoon fish include Pacific herring *Clupea pallasii*, Arctic flounder *Liopsetta glacialis*, and ninespine stickleback *Pungitius pungitius* (T. Ivanova, M. Ivanov and D. Lajus, unpublished data). Threespine stickleback are very abundant in the lagoon in June and early July when spawning takes place there. Stickleback spawning dynamics in the lagoon resembles that in adjacent marine biotopes, with higher numbers of spawning fish observed in the second half of June (Bakhvalova *et al.*, 2016; Golovin *et al.*, 2019). The current study was conducted from 20 to 25 June in both 2015 and 2016.

Sampling design

Fish were tagged with polyvinyl chloride tubes (internal diameter ~0.8 mm, length 1.5–2.0 mm) applied manually to the first or second dorsal spine (Fig. 2 and evolutionary-ecology.com/data/3164Appendix.pdf). To assess the risk of injury and reliability of this method, we conducted preliminary studies in 2012 when we tagged the first and second dorsal spines of 123 fish and placed them in a tank (0.5 × 0.7 × 4.0 m) equipped with running sea water. Using two tags per individual allowed us to distinguish between

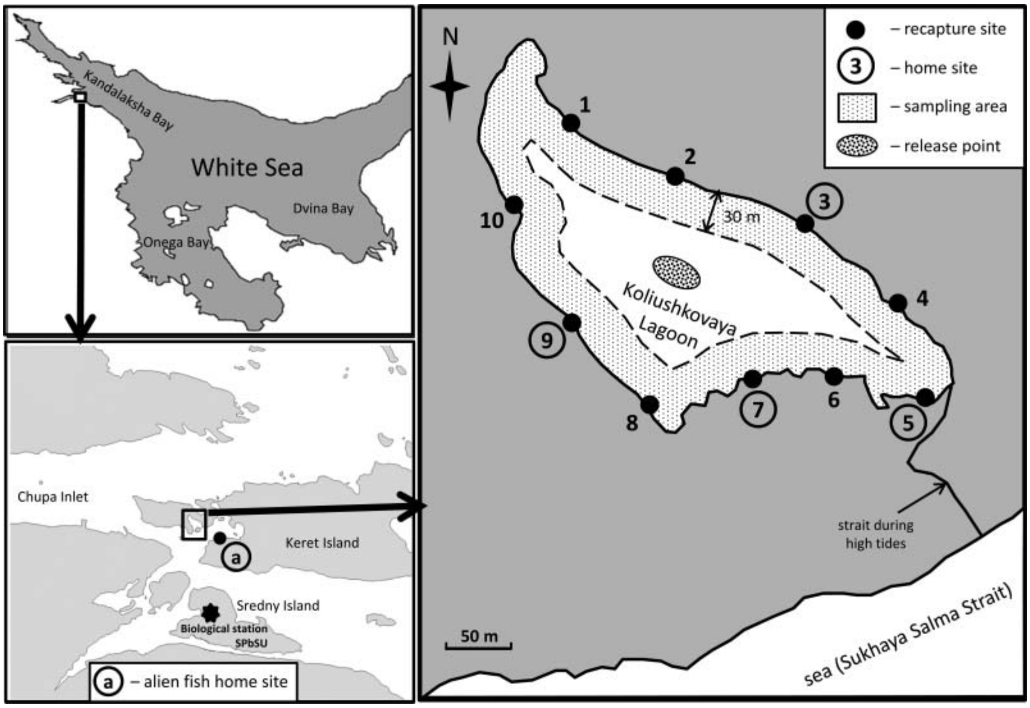

Fig. 1. Study site. The sampling area in the lagoon (within 30 m of the shoreline) was 23,200 m^2.

experimental and reference fish (110 individuals), even if one tag had been lost, so experimental and reference fish were kept in the same tank. The experiment was run for six days. Injury risk was assessed using mortality rates (the proportion of tagged fish that died). Tagging reliability was assessed as the proportion of all tags that were lost.

Fish were caught using a beach seine with a wing length of 30 m, height of 1.5 m, and mesh-size of 5 mm on the wings and 1 mm in the cod-end. Hauling ropes were 30 m long and the catch area was approximately 510 m^2. The speed of the beach seine watercourse was about 0.25 m/s. At each point in time, we made one haul without repetition to avoid disturbances from previous hauls. Sampling was conducted in the inshore zone of the lagoon within 30 m of the shore, thus the area affected by the seine was 23,200 m^2 (Fig. 1). More than 90% of sticklebacks congregate in this area (T. Ivanova. M. Ivanov and D. Lajus, unpublished data based on gillnet sampling). Two groups of fishes were tagged: 'local' fish caught in the lagoon, and 'alien' fish caught at sea about 400 m from the entrance to the lagoon (66.30988°N, 33.65168°E; Fig. 1). In addition, local fish were caught at several locations labelled 'home sites' (Fig. 1) and tagged with tubes of different colours. Three home sites were sampled in 2015 and four in 2016 (Table 1).

Tagged fish were kept in sea cages in the lagoon for no longer than three days between capture and release. All tagged fish were simultaneously released in the centre of the lagoon (100–300 m from their home sites). Recapture was performed over periods ranging from one hour to four days after release.

At recapture, we counted the number of tags of each colour (representing different home sites) separately for females and males, and the total number of fish caught to measure

Fig. 2. The dorsal spine of threespine stickleback is able to retain a tag due to its many thorny notches. (A) Dorsal spine; (B) a tag made of polyvinylchloride shrink tubing (internal diameter ~0.8 mm, length 1.5–2.0 mm).

density. All fish, including tagged fish, were released back into the lagoon. Fish density (N, individuals/m^2) at each site was estimated using the formula:

$$N = \frac{N_{catch}}{S_{seine} \times GE}, \tag{1}$$

where N_{catch} = the number of caught fish, S_{seine} = catch area of the beach seine (m^2), and GE = gear efficiency of the beach seine.

Gear efficiency estimations were calculated using three different techniques:

1. Recapture of tagged fish released in the catch area. Tagged fish were released in front of the seine just before hauling. In total, we performed six experiments (five with 30 fish and one with 50 fish) in Koliushkovaya Lagoon in 2012. GE was estimated as the proportion of all tagged fish that were recaptured.

Table 1. Number of tagged threespine stickleback released

Origin	Year	Home site	Number of tagged fish		
			Female	Male	Total
Local (lagoon)	2015	3	370	130	500
		5	325	275	600
		7	765	615	1380
		Total	1459	1021	2480
	2016	3	166	291	457
		5	197	211	408
		7	149	237	386
		9	210	205	415
		Total	722	944	1666
Alien (outside lagoon)	2015*	a	—	—	1170
	2016	a	491	628	1119

Note: Numbers and letters of home sites are in accordance with Fig. 1. *In 2015, about 90% of tagged alien fish were females.

2. Comparison of fish abundance based on seine surveys with an independent estimate based on the mark-and-recapture method. Tagged fish caught at sea (1170 and 1119 individuals in 2015 and 2016, respectively) were released in Koliushkovaya Lagoon ('alien' in Table 1). Several control beach seine hauls (10 in 2015 and 11 in 2016) assessed the number of tagged and non-tagged fish. The total number of recaptured tagged fish was 95 and 78 in 2015 and 2016, respectively. The absolute number of stickleback in the lagoon was calculated based on the total number of tagged fish released, the number of tagged fish recaptured, and the number of non-tagged fish in the catches (Ricker, 1975; Lockwood and Schneider, 2000). This figure was divided by the sampling area of the lagoon (23,200 m^2, Fig. 1) to obtain the density of fish (N1). The second density estimate (N2) was based on 17 and 19 beach seine surveys (in 2015 and 2016, respectively), where the number of fish in each catch was divided by the area affected by the seine [as in formula (1), without GE] and then samples for each year were averaged. We thus have two estimations of stickleback density: N1 is independent of gear, and N2 is based on seine surveys where gear efficiency is not taken into account. The ratio of these two estimations (N2/N1) is gear efficiency. Data for the two years were averaged.
3. Comparison of the number of fish in the first catch with fish abundance in the catch area based on removal sampling. A series of sequential hauls were carried out in June 2003 in the freshwater lake Nikolskaya Lambina (66.195274°N, 33.875915°E), which is similar in morphology to Koliushkovaya Lagoon. The experiments were performed with roach *Rutilus rutilus*, an abundant species in the lake. Four sequential beach seine hauls were performed and the total number of juvenile roach recorded (age 1+, total length 80–90 mm). Subsequently, Zippin's (1958) method was used to determine the total number of fish in the area affected by the seine. GE was the ratio of the fish in the first catch to the estimated total number of fish in the affected area. We tried to use this technique on stickleback, but without success because beach seine operations attract new stickleback to the affected area, thus resulting in an increase in fish numbers instead of the decrease necessary to apply this method.

Spatial distribution of tagged fish

The entire shoreline of the lagoon was subdivided into ten equal segments, each approximately 100 m long. One sampling site was situated in the middle of each segment. To analyse the distribution of local fish, we measured the distance from the sampling site to the home site. The home site was assigned a position of 0 m; the other sampling sites located clockwise from it along the shore were designated 100, 200, 300, 400, and 500 m, while those counter-clockwise were designated −100, −200 m, etc. Thus sites '500 m' and '−500 m' were in fact the same site. Different sets of sites were considered as replicates in further calculations.

Due to differences in the numbers of released tags of different colours, to measure the fish returning to a particular site, we used the ratio of the number of recaptured tags at that site to the number of released tags of the same colour. This ratio was used as a dependent variable in the analysis of variance (ANOVA) below.

To assess the influence of different factors on fish distribution, ANOVA was applied using the factors 'site' [for local fish, the distance from the home site (0 m, 100 m, 200 m, etc.); for alien fish, the site number], 'time after release', and 'sex'. Each ANOVA included several groups of fish (from three different home sites in 2015, and four in 2016; Table 1). There were no replicates for alien fish, thus we used main effect ANOVA for this group. Recapture in 2015 took place one to four days after release. Different sites were sampled each day (10 stations in total), and all data were pooled in the analyses. In 2016, recapture was carried out after one of three intervals: one hour (4 stations), one day (7 stations), and four days (5 stations) after release. For this reason, the factor 'time after release' was analysed for the 2016 data only.

To describe the distribution of tagged stickleback for each sampling site (i.e. 100, 200 m, etc. from home site) along the lagoon shoreline, we calculated the ratio (%) of tagged fish in a sample to the total number of recaptured tagged fish. For analysis of alien fish, we evaluated the correlation between the number of recaptured tagged fish and the density of all stickleback across all sites.

All statistical procedures were performed using the Statistica v.7.0 program.

Estimates of the number of tagged fish in the lagoon

In addition to analysing the spatial distribution of tagged stickleback, we estimated the total number of tagged fish remaining in the lagoon for each sampling period. This information was necessary for two reasons. First, we used it to assess the validity of our sampling technique. Just after release, the number of released fish (N_{REL}) should approximate the number of tagged fish estimated directly from the beach seine surveys (N_{EST}). If the numbers coincide, this means that we did not strongly over- or underestimate fish numbers due to methodological errors and most tagged fish are available for sampling. Secondly, these estimates are used to trace the dynamics of tagged fish.

We calculated the density of tagged fish (separately for each sex) at each station using formula (1). In order to determine the number of tagged fish in the lagoon, we multiplied average tagged fish density by the total area of the sampling zone (23,200 m^2). While estimating the number of fish in the lagoon using an incomplete dataset, we need to determine if there are there some 'special' sites, where the number of fish systematically differs from other sites (i.e. distribution of fish is non-random), or sites do not differ from each other, meaning that the density of fish varies randomly (i.e. distribution is random). A non-random distribution is only possible when fish tend to prefer or avoid some sites more than others. If the distribution is random, one can average any number of sites by using the simple average without risk of bias, because the density of fish is statistically the same in all sites. If the distribution of fish is non-random, one cannot use the simple average and it is necessary to apply the weighted average instead.

We used ANOVA to formally distinguish between random and non-random distributions (see above for details), where a significant effect of the factor 'site' indicates a non-random distribution, and a non-significant effect means the distribution is random. Nevertheless, even for random distributions, actual differences between the fish densities of sites can be rather high, but not consistent across sites.

RESULTS

Preliminary methodological studies

Tagging methodology

In the six-day experiment, three out of 123 tagged fish died (mortality = 2.4%), whereas four out of 110 fish died in the control group (mortality = 3.6%). Of the 123 fish tagged with two tags, only three tags were lost, so the percentage of lost tags was ~1%. Thus, our preliminary experiments showed that tags do not increase fish mortality when compared with a control group, and the number of lost tags was negligible.

Gear efficiency

The three different techniques yielded similar results, giving an average beach seine GE of 0.6 (Table 2). This GE can be used to estimate the density of small fish with a total body length of 50–90 mm, including stickleback, for beach seine surveys with parameters similar to ours. We used this GE in formula (1).

Homing ability

To discern which factors influence the distribution of local tagged fish, we performed ANOVA and *post hoc* analyses. Significance was observed for the factors 'site' (2015: $F_{8,36} = 13.9$; 2016: $F_{8,70} = 8.57$, both $P < 0.0001$), 'time after release' (2016: $F_{2,70} = 3.78$, $P = 0.027$), and their interaction (2016: $F_{16,70} = 4.17$, $P < 0.0001$). *Post hoc* analyses for 2016 showed that the number of tagged fish was higher at home sites (all $P < 0.0001$), but only

Table 2. Gear efficiency (GE) of beach seine calculated using different methods

Method	Species (total body length)	GE
Capture of tagged fish released in the area affected by seine	Stickleback (50–80 mm)	0.59 ± 0.13
Mark and recapture	Stickleback (50–80 mm)	0.50 ± 0.05
Removal sampling	Roach (80–90 mm)	0.72
Average		0.60 ± 0.06

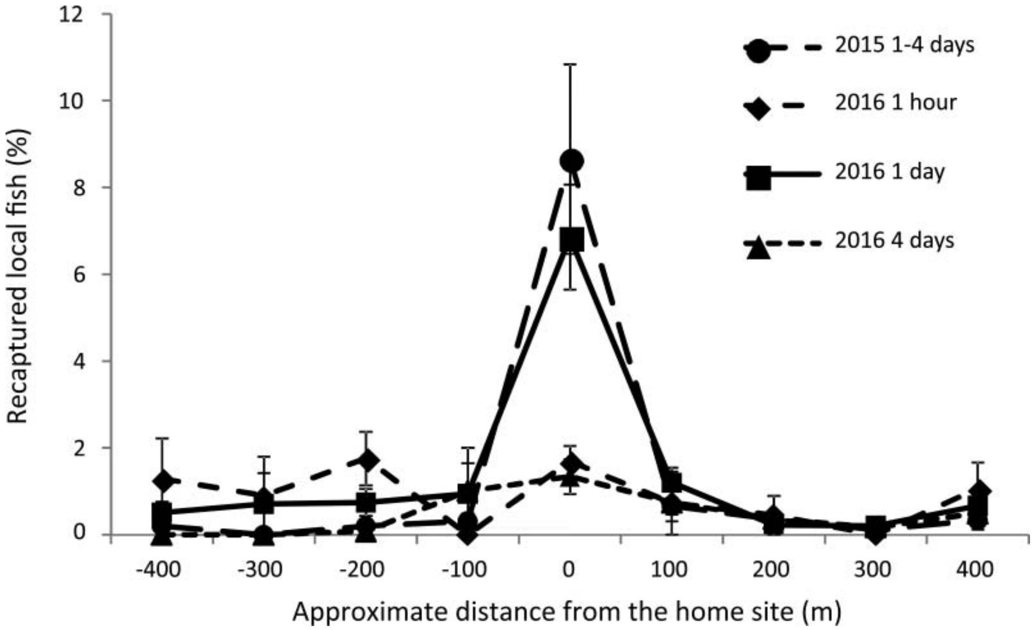

Fig. 3. Recaptured local tagged stickleback as a proportion of the total number of tagged fish released at different intervals after release in 2015 and 2016 (mean ± S.E.).

one day after release: no differences between the home site and other sites were observed one hour or four days after release. In all other cases, sites did not differ from one another ($P > 0.05$ in all cases), i.e. the distribution of tagged fish outside home sites did not differ from the random distribution (Fig. 3). In 2015, the distribution of tagged fish was similar to that one day after release in 2016, and no difference was observed between males and females in either year (2015: $F_{1,36} = 0.31$, $P = 0.57$; 2016: $F_{1,70} = 2.17$, $P = 0.15$). These experiments clearly substantiate stickleback homing one day after release.

Distribution of local fish

In 2015 when fish were recaptured one to four days after release, the average proportion of tagged fish in their home sites was 74.2 ± 11.4% (range 52–89%) of the total number of tags recaptured at the ten sites; at non-home sites, it averaged 2.9 ± 0.8% (range 0–18%) (Fig. 4A). In 2016, we performed several surveys at different times after release to provide a more detailed picture of the temporal dynamics of homing. One hour after release, the distribution of tagged fish along the shoreline was random, as shown by ANOVA (see above), with 10.0 ± 1.8% of tagged fish recorded in home sites on average (range 0–27%) (Fig. 4B). One day after release, a homing effect was observed, with an average of 56.7 ± 8.6% (range 43–81%) of tagged fish in home sites but only 5.0 ± 1.0% (range 0–18%) of tagged fish in non-home sites (Fig. 4C). Four days after release, many stickleback had left their home sites – the average percentage there decreased to 26.0 ± 5.4% (range 11–35%) – with the percentage of tags at non-home sites being 7.4 ± 2.3% (range 0–33%) (Fig. 4D).

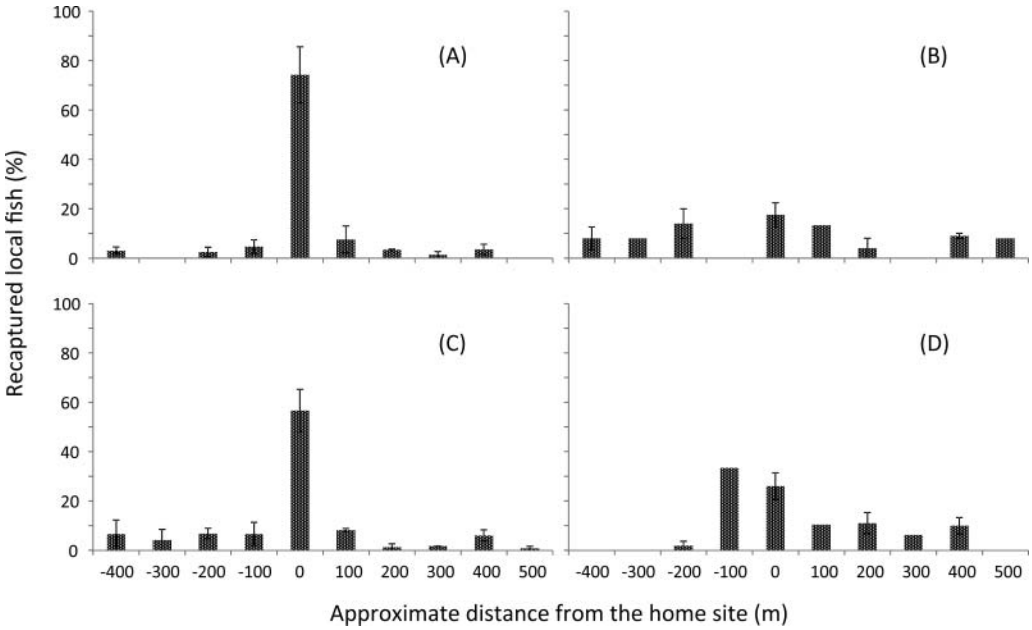

Fig. 4. Recaptured local tagged stickleback as a proportion of the total number of recaptured fish at different distances from the home site (mean ± S.E.): (A) 2015 (1–4 days), (B) 2016 (1 hour), (C) 2016 (1 day), (D) 2016 (4 days).

Distribution of alien fish

We tagged alien fish to compare their behaviour with that of local fish for reference purposes. Three-way main effect ANOVA (factors: 'time after release', 'site', 'sex') based on the 2016 data only found the effect of 'time after release' to be significant ($F_{2,22} = 11.34$, $P = 0.0004$). *Post hoc* tests indicated that the number of recaptured tagged fish decreased over time. Thus, tagged alien fish did not concentrate in or avoid specific sites.

In 2015, a correlation between the number of recaptured alien tagged fish and the density of stickleback across all sites was significant and positive (Fig. 5A). In 2016, no such correlation was observed in samples taken one hour and one day after release (Fig. 5B, C), but there was a significant positive correlation for samples taken four days after release (Fig. 5D).

On the whole, during four days of sampling, alien stickleback altered their distribution in the lagoon from random to patterns that correlated with resident fish densities.

Abundance and dynamics of fish released in the lagoon

To correctly interpret the results of our tagging experiments, it is important to demonstrate that our recapture surveys do not under- or overestimate fish abundance due to methodological issues. Different models were used to estimate the total number of tagged local and alien fish in the lagoon.

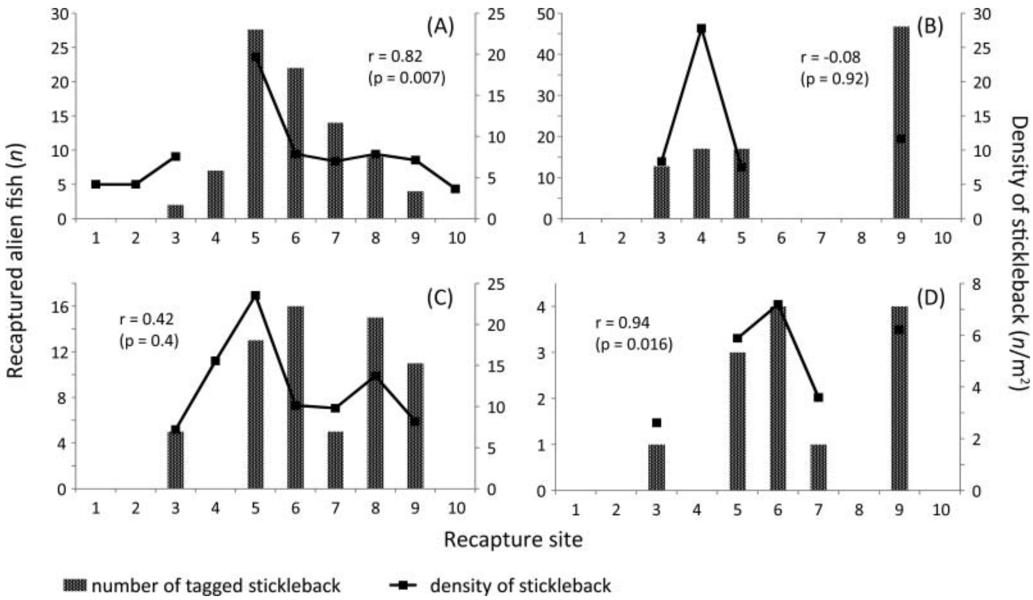

Fig. 5. Number of recaptured alien stickleback and the density of resident stickleback at sampled sites: (A) 2015 (1–4 days), (B) 2016 (1 hour), (C) 2016 (1 day), (D) 2016 (4 days). Pearson correlation coefficients (*r*) between the number of tagged fish and densities are provided. Numbers of recapture sites are equivalent to those in Fig. 1.

1. The distribution of local stickleback assumes two types of site (home and non-home) that differ in the density of tagged fish. Our previous analyses showed that these two types of site differ significantly in the numbers of tagged fish, whereas no differences were observed among non-home sites. We used a weighted average of tagged fish density.
2. Alien fish are distributed randomly along the lagoon shoreline and do not systematically aggregate in a single location. Thus, we used average density of tagged fish.

One day after release, no notable difference between N_{REL} and N_{EST} was observed (Table 3), thus we did not systematically underestimate fish numbers, and most tagged stickleback remained in the lagoon at that time. Occasionally, N_{EST} exceeded N_{REL} (Table 3, cases marked with an asterisk). We believe that these differences are due to sampling error. In the case of alien fish (one hour, 2016), sampling error was high because of the small number of samples (four sites) taken due to time constraints, combined with uneven fish distribution, likely due to the short time post-release.

Over time, the decrease in the number of tagged fish in all cases likely indicated out-migration of stickleback from the lagoon. Another reason for the decrease in the number of tagged fish could be natural mortality, but we have shown that natural mortality accounts for only a fraction of a percent of dead fish in total stickleback abundance, and thus cannot notably change the number of fish over short periods of time (Golovin *et al.*, 2019). The dynamics of tagged stickleback in the lagoon is different for local and alien fish, as well as for males and females (Table 3, Fig. 6).

Table 3. The number of released tagged stickleback (N_{REL}), and abundance estimates based on beach seine surveys of tagged fish (N_{EST})

Origin	Year	Time after release	Females		Males		Total	
			N_{REL}	N_{EST}	N_{REL}	N_{EST}	N_{REL}	N_{EST}
Local (lagoon)	2015	1–4 days	1459	1017	1021	952	2480	1969
	2016	1 hour	722	725	944	644	1666	1369
		1 day		887*		778		1665
		4 days		269		197		466
Alien (outside lagoon)	2015	1–4 days	—	—	—	—	1170	986
	2016	1 hour	491	967*	628	806*	1119	1772*
		1 day		433		271		704
		4 day		91		106		197

*Estimated abundance of tagged fish is greater than the number of released tagged fish.

The number of local fish did not decrease by much the day after they were released. In fact, it was at least 70% and averaged about 90% of all tagged fish. We don't know the pattern of decrease on the second and third days after release, however, surveys on the fourth day found that tag ratios had fallen to 30% of the number released, i.e. most tagged females and males had left the lagoon (Fig. 6A).

Alien fish, especially males, left the lagoon sooner post-release. One day after release, only 43% of alien males remained in the lagoon, compared with 88% of the females (for the pooled sample, the figure is 63%). Four days after release, the ratio of tagged alien fish decreased to 18% of the total number released, including both males and females (Fig. 6B).

In 2016, for both local and alien fish, the proportion of males compared with the number of fish released (N_{EST}/N_{REL}) was less than that of females in all cases (sign test, $P = 0.031$), confirming that males left the lagoon sooner than females.

It is worth noting that the dynamics of local and alien females was similar: a day after release most females remained in the lagoon, whereas a decrease in their numbers was observed four days after their release. Local and alien males exhibited different dynamics, however. Local males remained in the lagoon for at least a day and out-migrated later, like the females; alien males, in contrast, left the lagoon immediately (more than half of them had out-migrated one day after release).

Data from 2015 cannot be grouped by time of recapture, but they resemble those for one day after release in 2016. In 2015, the number of tagged fish in the lagoon did not fall below 70% of the number released even four days post-release. These differences in stickleback behaviour may be due to differences in tidal dynamics during the study periods in 2015 and 2016. The 2016 study was conducted during spring tides, with maximum water levels of 1.9–2.1 m, which would facilitate the out-migration of fish from the lagoon. The 2015 study was carried out during neap tides with maximum water levels of 1.8–1.9 m, which is less suitable for migrating fish. This difference might cause both alien and local fish to leave the lagoon more slowly in 2015.

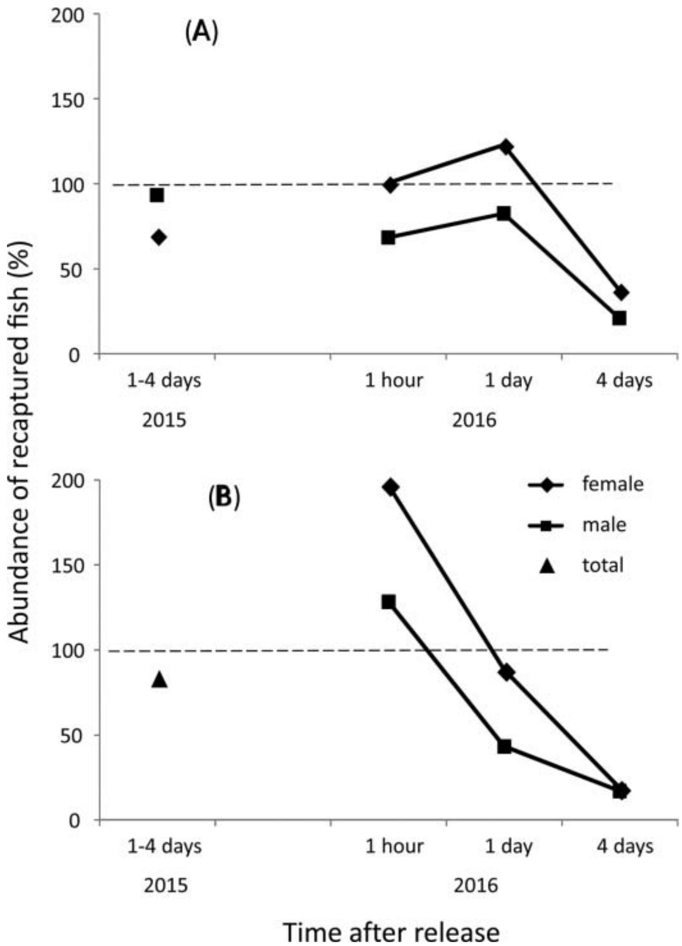

Fig. 6. Estimated abundance of recaptured fish (N_{EST}) as a proportion of the number of released fish (N_{REL}): (A) local fish, (B) alien fish.

DISCUSSION

Stickleback tagging methods

Studying homing behaviour and site fidelity in nature would be almost impossible without tagging. For relatively large fish (tens of centimetres), acoustic transmitters (9–13 mm in diameter, 30–35 mm long) can be utilized (Lindholm *et al.*, 2006; Lowe *et al.*, 2009). However, stickleback are too small for such devices, which are also labour-intensive and expensive. Instead, fluorescent elastomer tags are widely used (Griffiths, 2003; White and Brown, 2013; Thyssen *et al.*, 2014). Studies have confirmed the low risk of injury to fish, easy visualization and long-term performance of these tags (Willis and Babcock, 1998; Malone *et al.*, 1999; Griffiths, 2002), although a single tagging operation is time-consuming, taking about two minutes per fish (White and Brown, 2013). Fluorescent elastomer tags were successfully used in threespine stickleback research some years ago (Bolnick *et al.*, 2009).

The external morphology of threespine stickleback offers another possibility for tagging using their dorsal or pelvic spines. The first option employs a small piece of soft plastic tubing (internal diameter 0.8–1.0 mm, length 0.5–2 mm). Barber and Ruxton (2000) attached coloured plastic tubes to the left pelvic spines. Ward *et al.* (2002) attached numbered tags to the dorsal spines to identify individual fish. Another option is to place small plastic circular tags (4–5 mm in diameter) with holes in their centre on the dorsal spines. This method is especially convenient for laboratory studies, as tag inscriptions can be read from above with cameras (Webster and Laland, 2009); it was also successfully used in the field (Ward *et al.*, 2013).

In the present study, we used tubes of different colours to identify different groups of fish. A single tagging operation took 20–30 seconds, which is comparable to using plastic circular tags (Webster and Laland, 2009), making it possible to tag several hundred or thousand fish for a single experiment. Studies using tubes and circular discs have demonstrated their effectiveness (Ward *et al.*, 2002; Webster and Laland, 2009; present study), thus we recommend this method for studying stickleback in the field. Using tagging with stickleback in our study allowed us to address the following research questions.

Do stickleback demonstrate short-range homing during their spawning period?

Yes, fish returned to their home site after they were displaced 100–300 m away from it, clearly proving the existence of a homing effect. Homing has been repeatedly demonstrated in fish living in intertidal rock pools. In a study by Griffiths (2003), at least 50% of displaced fish of eleven resident species returned to their original rock pools. White and Brown (2013) showed that 60–75% of tagged individuals of three species that permanently inhabit rock pools returned to their home site upon the day of their release, and two species of secondary residents, which inhabit rock pools only as juveniles, returned at a rate of 50%. Thyssen *et al.* (2014) found that 67% of rock pool blenny (*Parablennius parvicornis*) returned home within a few days of being displaced. Rock pool sculpins also exhibit homing behaviour (Yoshiyama *et al.*, 1992). For threespine stickleback, homing was demonstrated in research on their migrations in small canals where they live permanently (Ward *et al.*, 2013). It has also been shown that 90% of displaced lake and stream stickleback were able to return to their home habitats (Bolnick *et al.*, 2009).

Our study yielded two specific findings not reported previously. First, after migrating inshore from offshore wintering locations, the spawning fish had spent no more than two to three weeks in their home sites prior to our experiments. Likely, most stickleback spend even less time familiarizing themselves with their home sites due to active migrations possibly associated with competition for spawning grounds (Dorgham *et al.*, 2018). Yet, even this short amount of time was sufficient to stimulate homing behaviour. Second, our fish were released some distance from the shoreline in open water without visual landmarks, which would have hindered homing over large distances to relatively precise targets if the fish only use visual landmarks for orientation and not true navigation (Gould and Gould, 2012).

How quickly do fish return?

Adult stickleback were able to cover the distance from their place of release to their home site (100–300 m) in less than one hour. In our experiments, all stickleback approached the inshore area within an hour, but their spatial distribution was random. Homing became apparent the next day. Ward *et al.* (2013) reported that stickleback could find their home site within two days after displacements of 80–160 m. However, it is not easy to compare our results with those of Ward *et al.* because of differences in experimental design. Ward *et al.* studied freshwater stickleback, which might have spent a year or more near their home sites prior to the experiment. In our study, fish familiarized themselves with their home sites over a few weeks. In addition, Ward and co-workers' study involved stickleback fishes in canals, where the fish primarily orient themselves along the length of the canal, whereas our lagoon fish had more degrees of freedom. Finally, in our study it was difficult to estimate the distance a fish covered to find their home site.

In similar research, White and Brown (2013) showed that, after displacement of 10–40 m, the majority of tagged individuals of several other fish species returned to their home sites within one day, regardless of distance. Thyssen *et al.* (2014) found that rock pool blenny (*P. parvicornis*) returned to their home site within 48 hours when released 200 m away, but return time was extended to 134 hours if the fish were displaced 400 m. Greasy grouper (*Epinephelus tauvina*) returned home from a distance of 2.6 km, taking four to 19 days to do so (Kaunda-Arara and Rose, 2004).

According to research described in the literature, freshwater stickleback are able to retain spatial landmarks in memory for about one week on average, while it is slightly longer for pond fish and slightly shorter for river fish (Brydges *et al.*, 2008). In our study, the fish were released one to three days after capture and demonstrated homing a day later. Thus, their ability to remember spatial landmarks persisted for at least four days. It has also been shown that predator presence reduces stickleback fishes' ability to memorize landmarks (Brydges *et al.*, 2008). In this respect, our study area, Koliushkovaya Lagoon, is a favourable location because isolation from the sea eliminates predatory fish such as sculpins, Atlantic cod (*Gadus morhua*), and navaga (*Eleginus nawaga*) (Golovin *et al.*, 2019). Commonly found on more open stickleback spawning grounds in the White Sea, 50–100% of the diet of these predators can be made up of sticklebacks and their eggs (Bakhvalova *et al.*, 2016; Golovin *et al.*, 2019).

How precise were fish at homing?

As the fish were collected and recaptured with a 30 m beach seine, with distances between recapturing sites of about 100 m, and the numbers of recaptured fish did not differ significantly between sites adjacent to the home site and those located farther away, we estimate homing precision in our experiment to be ±50 m. Ward *et al.* (2013) reported similar results (±40–60 m) in their stream study.

How do stickleback orient themselves?

We suggest that, in our study, released stickleback first approached the inshore zone, swimming in random directions from the release point near the centre of the lagoon, then moved along the shoreline in search of familiar landmarks. The fish did not use true navigation because they would have arrived at their home site within an hour if they did so. The stickleback's ability to use spatial landmarks has been shown previously (Girvan and Braithwaite, 1998; Odling-Smee and Braithwaite, 2003). It has also been shown that pond fish are more likely to use spatial landmarks than riverine stickleback (Brydges *et al.*, 2008). Judging from the hydrodynamic patterns of our study site, the lagoon resembles a pond more than a river, which increases the probability that marine stickleback use spatial landmarks for orientation. At the same time, White Sea stickleback spend most of their lives in the open sea, probably far from the bottom and without spatial landmarks. Interpreting the results of our study did not require mechanisms of true navigation, such as magnetic fields (Gould, 2014), which are unknown for stickleback but are apparent in rock pool fish like shanny (*Lipophrys pholis*), which, in experimental conditions, returned to their home sites from unfamiliar places, apparently using magnetic fields (Jorge *et al.*, 2012).

What do fish do after returning to their home site?

Although stickleback returned to their home site within a day, about two-thirds of the fish abandoned their sites within three days, thus demonstrating weak site fidelity. Site fidelity is described in many bottom fish species, and rock pool fishes are well studied in this respect. Griffiths (2003) found that 60% of non-displaced tagged fish were re-caught in the same location 120 days later. Thyssen *et al.* (2014) reported that more than 57% of tagged fish remained in their rock pool after four months of observation. In coral reefs, site fidelity was observed in parrotfishes (*Scarus coeruleus* and *S. taeniopterus*) using acoustic transmitters embedded in the fish (Lindholm *et al.*, 2006). It has also been demonstrated for 19 months in littoral pipefish (*Nerophis lumbriciformis*) (Monteiro *et al.*, 2005) and for 2 years in some demersal species living near offshore oil platforms (Lowe *et al.*, 2009).

Why was stickleback site fidelity so weak in our experiments? We suggest the following explanations: (1) Only a few fish recaptured at their home sites were actively nesting or spawning. For other fish, the site was likely a transit area where they were caught as they searched for suitable spawning grounds. They returned to that site only for orientation purposes and continued their migration. (2) The location of our study is probably an attractive area for spawning stickleback due to its shallow waters and seagrass beds, which provide good habitat for spawning and maturing stickleback in the White Sea (Demchuk *et al.*, 2015; Ivanova *et al.*, 2016; Rybkina *et al.*, 2016). Stickleback actively compete for such ideal spawning locations (Dorgham *et al.*, 2018): after a few days' absence, the returning tagged fish may have been displaced by other males and had to look for new, less convenient locations. This may also have been a problem for returning females, who found most males already to have enough eggs in their nests. They, too, needed new grounds in order to spawn.

CONCLUSION

For the first time, we were able to demonstrate homing behaviours of marine threespine stickleback in a small lagoon in the White Sea. After being displaced 100–300 m from shore, tagged fish were able to return to their home site by the next day. Alien fish caught outside the lagoon distributed themselves according to local fish density, and left the lagoon sooner than local fish, probably striving to return to their home sites elsewhere. After returning to their home sites, the majority of fish left again within 3 days, probably because the sites had become occupied by competitors during their absence. We found no significant differences between the homing abilities of male and female stickleback.

ACKNOWLEDGEMENTS

This work was supported by RFBR grant No. 18–04–01052A 'Threespine stickleback *Gasterosteus aculeatus* as a link between the inshore and offshore communities of the White Sea'. A.Y. was supported by the Ministry of Science and Higher Education of the Russian Federation, project

AAAA-A19-119020790033-9. Karen Alexander helped to improve the English. The authors also thank the administration of the White Sea Biological Station of the St. Petersburg State University for the opportunity to conduct year-round research in the White Sea.

REFERENCES

Aguirre, W.E., Ellis, K.E., Kusenda, M. and Bell, M.A. 2008. Phenotypic variation and sexual dimorphism in anadromous threespine stickleback: implications for postglacial adaptive radiation. *Biol. J. Linn. Soc.*, **95**: 465–478.

Bakhvalova, A.E., Ivanova, T.S., Ivanov, M.V., Demchuk, A.S., Movchan, E.A. and Lajus, D.L. 2016. Long-term changes in the role of threespine stickleback *Gasterosteus aculeatus* in the White Sea: predatory fish consumption reflects fluctuating stickleback abundance during the last century. *Evol. Ecol. Res.*, **17**: 317–334.

Barber, I. and Ruxton, G.D. 2000. The importance of stable schooling: do familiar sticklebacks stick together? *Proc. R. Soc. Lond. B: Biol. Sci.*, **267**: 151–155.

Bell, M.A. and Foster, S.A. 1994. *The Evolutionary Biology of the Threespine Stickleback*. Oxford: Oxford University Press.

Bolnick, D.I., Snowberg, L.K., Patenia, C., Stutz, W.E., Ingram, T. and Lau, O.L. 2009. Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution*, **63**: 2004–2016.

Braithwaite, V.A. and De Perera, T.B. 2006. Short-range orientation in fish: how fish map space. *Mar. Freshw. Behav. Physiol.*, **39**: 37–47.

Brydges, N.M., Heathcote, R.J.P. and Braithwaite, V.A. 2008. Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks. *J. Anim. Ecol.*, **77**: 229–235.

Candolin, U. and Selin, M. 2012. Density-dependent habitat selection in a growing threespine stickleback population. *Int. J. Zool.*, **2012**: 378913. Available at: https://doi.org/10.1155/2012/378913.

Cano, J.M., Mäkinen, H.S. and Merilä, J. 2008. Genetic evidence for male-biased dispersal in the three-spined stickleback (*Gasterosteus aculeatus*). *Mol. Ecol.*, **17**: 3234–3242.

Costa, S.S., Andrade, R.P., Carneiro, L.A., Gonçalves, E.J., Kotrschal, K. and Oliveira, R.F. 2011. Sex differences in the dorsolateral telencephalon correlate with home range. *Brain Behav. Evol.*, **77**: 55–64.

Demchuk, A., Ivanov, M., Ivanova, T., Polyakova, N., Mas-Marti, E. and Lajus, D. 2015. Feeding patterns in seagrass beds of three-spined stickleback *Gasterosteus aculeatus* juveniles at different growth stages. *J. Mar. Biol. Assoc. UK*, **95**: 1635–1643.

Demchuk, A.S., Ivanov, M.V., Ivanova, T.S., Polyakova, N.V., Golovin, P.V. and Lajus, D.L. 2018. Pitanie belomorskoy trekhigloy kolyushki *Gasterosteus aculeatus* (Linnaeus, 1758) na nerestilishakh [Feeding of the threespine stickleback *Gasterosteus aculeatus* (Linnaeus, 1758) in spawning grounds]. *Trudy Karel'skogo Nauchnogo Tsentra RAN*, **4**: 42–58 [in Russian].

Dittman, A.H. and Quinn, T.P. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *J. Exp. Biol.*, **199**: 83–91.

Dodson, J.J. 1988. The nature and role of learning in the orientation and migratory behavior of fishes. *Environ. Biol. Fish.*, **23**: 161–182.

Dorgham, A.S., Golovin, P.V., Ivanova, T.S., Ivanov, M.V., Saveliev, P.D. and Lajus, D.L. 2018. Geterogennost' morfologitsheskikh priznakov trekhigloy kolyushki *Gasterosteus aculeatus* na razhykh etapakh neresta [Heterogeneity of morphological traits of the threespine stickleback *Gasterosteus aculeatus* at different stages of spawning]. *Trudy Karel'skogo Nauchnogo Tsentra RAN*, **4**: 59–73 [in Russian].

Frommen, J.G. and Bakker, T.C.M. 2004. Adult three-spined sticklebacks prefer to shoal with familiar kin. *Behaviour*, **141**: 1401–1409.

Gerking, S.D. 1959. The restricted movement of fish populations. *Biol. Rev.*, **34**: 221–242.

Girvan, J.R. and Braithwaite, V.A. 1998. Population differences in spatial learning in three-spined sticklebacks. *Proc. R. Soc. Lond. B: Biol. Sci.*, **265**: 913–919.

Golovin, P.V., Bakhvalova, A.E., Ivanov, M.V., Ivanova, T.S., Smirnova, K.A. and Lajus, D.L. 2019. Sex-biased mortality of marine threespine stickleback (*Gasterosteus aculeatus* L.) during their spawning period in the White Sea. *Evol. Ecol. Res.*, **20**: 279–295.

Gould, J.L. 2014. Animal navigation: a map for all seasons. *Curr. Biol.*, **24**: 153–155.

Gould, J.L. and Gould, C.G. 2012. *Nature's Compass: The Mystery of Animal Navigation*. Princeton, NJ: Princeton University Press.

Griffiths, S.P. 2002. Retention of visible implant tags in small rockpool fishes. *Mar. Ecol. Prog. Ser.*, **236**: 307–309.

Griffiths, S.P. 2003. Homing behaviour of intertidal rockpool fishes in south-eastern New South Wales, Australia. *Aust. J. Zool.*, **51**: 387–398.

Hansen, L.P., Jonsson, N. and Jonsson, B. 1993. Oceanic migration in homing Atlantic salmon. *Anim. Behav.*, **45**: 927–941.

Hendry, A.P., Peichel, C.L., Matthews, B., Boughman, J.W. and Nosil, P. 2013. Stickleback research: the now and the next. *Evol. Ecol. Res.*, **15**: 111–141.

Ivanova, T.S., Ivanov, M.V., Golovin, P.V., Polyakova, N.V. and Lajus, D.L. 2016. The White Sea threespine stickleback population: spawning habitats, mortality, and abundance. *Evol. Ecol. Res.*, **17**: 301–315.

Jorge, P.E., Almada, F., Gonçalves, A.R., Duarte-Coelho, P. and Almada, V.C. 2012. Homing in rocky intertidal fish: are *Lipophrys pholis* L. able to perform true navigation. *Anim. Cogn.*, **15**: 1173–1181.

Kaunda-Arara, B. and Rose, G.A. 2004. Homing and site fidelity in the greasy grouper *Epinephelus tauvina* (Serranidae) within a marine protected area in coastal Kenya. *Mar. Ecol. Prog. Ser.*, **277**: 245–251.

Kitano, J., Mori, S. and Peichel, C.L. 2007. Sexual dimorphism in the external morphology of the threespine stickleback (*Gasterosteus aculeatus*). *Copeia*, **2007**: 336–349.

Lajus, D.L., Ivanova, T.S., Shatskikh, E.V. and Ivanov, M.V. 2013. 'Volny zhizni' belomorskoy kolyushki ['Waves of life' of the White Sea stickleback]. *Priroda*, **4**: 43–52 [in Russian].

Letty, J., Aubineau, J., Marchandeau, S. and Clobert, J. 2003. Effect of translocation on survival in wild rabbit (*Oryctolagus cuniculus*). *Mammal. Biol.*, **68**: 250–255.

Letty, J., Marchandeau, S. and Aubineau, J. 2007. Problems encountered by individuals in animal translocations: lessons from field studies. *Ecoscience*, **14**: 420–431.

Lindholm, J., Knight, A., Kaufman, L. and Miller, S. 2006. Site fidelity and movement of the parrotfishes *Scarus coeruleus* and *Scarus taeniopterus* at Conch Reef (northern Florida Keys). *Caribb. J. Sci.*, **42**: 138–144.

Lockwood, R.N. and Schneider, J.C. 2000. Stream fish population estimates by mark-and-recapture and depletion methods. In *Manual of Fisheries Survey Methods II: With Periodic Updates* (J.C. Schneider, ed.). Fisheries Special Report #25. Ann Arbor, MI: Michigan Department of Natural Resources.

Lowe, C.G., Anthony, K.M., Jarvis, E.T. and Bellquist, L.F. 2009. Site fidelity and movement patterns of groundfish associated with offshore petroleum platforms in the Santa Barbara Channel. *Mar. Coast. Fish. Dynam. Manage. Ecosyst. Sci.*, **1**: 71–89.

Malone, J.C., Forrester, G.E. and Steele, M.A. 1999. Effects of subcutaneous microtags on the growth, survival, and vulnerability to predation of small reef fishes. *J. Exp. Mar. Biol. Ecol.*, **237**: 243–253.

McCleave, J.D., Zydlewski, G.B. and Vieser, J.D. 2018. Biology of four sympatric sticklebacks in Cobscook Bay, Maine, a boreal, macrotidal bay. *Environ. Biol. Fish.*, **101**: 1443–1465.

Mitamura, H., Uchida, K., Miyamoto, Y., Kakihara, T., Miyagi, A., Kawabata, Y. *et al.* 2012. Short-range homing in a site-specific fish: search and directed movements. *J. Exp. Biol.*, **215**: 2751–2759.

Monteiro, N.M., Vieira, M.N. and Almada, V. 2005. Homing behaviour and individual identification of the pipefish *Nerophis lumbriciformis* (Pisces; Syngnathidae): a true intertidal resident? *Estuar. Coast. Shelf. Sci.*, **63**: 93–99.

Odling-Smee, L. and Braithwaite, V.A. 2003. The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. *Anim. Behav.*, **65**: 701–707.

Östlund-Nilsson, S., Mayer, I. and Huntingford, F.A., eds. 2007. *Biology of the Three-Spined Stickleback*. Boca Raton, FL: CRC Press.

Parker, P.J. and Bell, M.A. 2010. Variation of telencephalon morphology of the threespine stickleback (*Gasterosteus aculeatus*) in relation to inferred ecology. *J. Evol. Biol.*, **23**: 1261–1277.

Piper, W.H. 2011. Making habitat selection more 'familiar': a review. *Behav. Ecol. Sociobiol.*, **65**: 1329–1351.

Reese, E.S. 1989. Orientation behavior of butterflyfishes (family Chaetodontidae) on coral reefs: spatial learning of route specific landmarks and cognitive maps. *Environ. Biol. Fish.*, **25**: 79–86.

Reinert, H.K. and Rupert, R.R. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridu*. *J. Herpetol.*, **33**: 45–61.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, **191**: 1–382.

Rybkina, E.V., Demchuk, A.S., Lajus, D.L., Ivanova, T.S., Ivanov, M.V. and Galaktionov, K.V. 2016. Dynamics of parasite community during early ontogenesis of marine threespine stickleback, *Gasterosteus aculeatus*. *Evol. Ecol. Res.*, **17**: 335–354.

Rybkina, E.V., Ivanova, T.S., Ivanov, M.V., Kucheryavyy, A.V. and Lajus, D.L. 2017. The habitat preference of the three-spined stickleback juveniles in experimental conditions and in the wild eelgrass. *J. Mar. Biol. Assoc. UK*, **97**: 1437–1445.

Thyssen, L., Triay-Portell, R., del Pino, A.S. and Castro, J.J. 2014. Homing behaviour of rock pool blenny *Parablennius parvicornis* (Pisces: Blenniidae). *J. Nat. Hist.*, **48**: 1169–1179.

Ward, A.J.W., Botham, M.S., Hoare, D.J., James, R., Broom, M., Godin, J.-G.J. *et al.* 2002. Association patterns and shoal fidelity in the three-spined stickleback. *Proc. R. Soc. Lond. B: Biol. Sci.*, **269**: 2451–2455.

Ward, A.J.W., James, R., Wilson, A.D.M. and Webster, M.M. 2013. Site fidelity and localised homing behaviour in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behaviour*, **150**: 1689–1708.

Webster, M.M. and Laland, K.N. 2009. Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus*. *J. Fish Biol.*, **75**: 1868–1873.

White, G.E. and Brown, C. 2013. Site fidelity and homing behaviour in intertidal fishes. *Mar. Biol.*, **160**: 1365–1372.

Willis, T.J. and Babcock, R.C. 1998. Retention and in situ detectability of visible implant fluorescent elastomer (VIFE) tags in *Pagrus auratus* (Sparidae). *N.Z. J. Mar. Freshw. Res.*, **32**: 247–254.

Yershov, P.N. 2010. Changes in the diet of the coastal cod *Gadus morhua marisalbi* in the Kandalaksha Gulf of the White Sea under conditions of increased abundance of three-spined stickleback *Gasterosteus aculeatus*. *J. Ichthyol.*, **50**: 84–88.

Yershov, P.N. and Sukhotin, A.A. 2015. Age and growth of marine three-spined stickleback in the White Sea 50 years after a population collapse. *Polar Biol.*, **38**: 1813–1823.

Yoshiyama, R.M., Gaylord, K.B., Philippart, M.T., Moore, T.R., Jordan, J.R., Coon, C.C. *et al.* 1992. Homing behavior and site fidelity in intertidal sculpins (Pisces: Cottidae). *J. Exp. Mar. Biol. Ecol.*, **160**: 115–130.

Zippin, C. 1958. The removal method of population estimation. *J. Wildl. Manage.*, **22**: 82–90.

Ziuganov, V.V. 1991. *Semeistvo koliushkovykh (Gasterosteidae) mirovoi fauny* [*Family Gasterosteidae of World Fauna*]. Leningrad: Nauka [in Russian].