Northern areas as refugia for temperate species under current climate warming: Atlantic salmon (*Salmo salar* L.) as a model in Northern Europe

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ABSTRACT

In this work, patterns of geographical genetic diversity in Atlantic salmon *Salmo salar* were studied across the whole Atlantic arc, as well as whether patterns (and thus genetic population structure) were affected by water temperatures. *Salmo salar* populations were here characterized using microsatellite loci and then analysed in the light of ocean surface

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temperature data from across the region. Analysis showed the presence of a latitudinal cline of genetic variability (higher in northern areas) and water temperatures (sea surface temperatures) determining genetic population structure (the latter in combination with genetic drift in southern populations). Under the current global change scenario, northern areas of Europe would constitute refuges for diversity in the future. This is effectively the inverse of what appears to have happened in glacial refugia during the last glacial maximum. From this perspective, the still abundant and large northern populations should be considered as precious as the small almost relict southern ones and perhaps protected. Careful management of the species, coordinated across countries and latitudes, is needed in order to avoid its extinction in Europe.

KEYWORDS

evolution, global change, phylogeography, population structure, *Salmo* salar, SST stimulus

1 | INTRODUCTION

Ecological change affects long-term population dynamics and can be a crucial driver of genetic diversity (Horreo *et al.*, 2016), which provides species and populations with the capacity of adaptation and resistance to adverse conditions (Frankel & Soulé, 1981). In this sense, landscape (or seascape) genetics provides a way of linking geographical and environmental factors affecting the structure and genetic variation of organisms at both population and individual levels (Manel *et al.*, 2003). Thus, the findings of landscape genetic studies have implications for ecology, evolution and conservation biology, which, in turn, help to determine the broader distributions of species. One of the key environmental factors affecting species distributions is temperature (Barbet-Massin & Jetz, 2014), which has also

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been shown to have a significant role in influencing genetic diversity (Rius *et al.*, 2014). This represents a classic case within biological science, whereby changes in thermal regime and associated environmental changes appear to drive latitudinal gradients of genetic diversity, with reduced diversity in high-latitude populations (at least within vertebrates (Adams & Hadly, 2013).

In the past, geological cycles of temperature change have shaped global biodiversity by influencing the distribution of species (Bennet, 1990). Similarly, such temperature cycles have also played an important role in influencing the distribution of genetic diversity within species. Arguably, this is most notable through the formation of glacial refugia that formed during glacial maxima when species distributions shrank and moved towards the equator; where populations persisted, they may have become hotspots of genetic diversity (Petit *et al.*, 2003; Shafer *et al.*, 2011). Subsequently, when more benign climate conditions returned, populations would have been able to expand out of their refugia and create zones of secondary contact (Hewitt, 1999). These climate-linked cycles of population retreat and expansion, especially those related to the last glacial maximum (LGM), still influence on present-day patterns of genetic diversity, or genetic landscapes. These patterns have been especially well documented in the northern hemisphere, especially in Europe and North America, with putative refugia and patterns of recolonization described for many organisms (Nesbø *et al.*, 1999; Deffontaine *et al.*, 2005; Bidegaray-Batista *et al.*, 2016; Horreo *et al.,* 2018). However, under current global climate warming, this pattern may be reversed and in the future species may be pushed poleward, to find refuge in areas of their northern distribution. This may have significant effects on the distribution of genetic diversity within species and we can anticipate that northern refugia may eventually become hotspots of genetic diversity. It can be hypothesized, therefore, that although for many species the greatest genetic diversity is currently concentrated in southern areas (Adams & Hadly, 2013),

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this trend may be changing as global temperature rises make areas at the southern limits of a species' ranges increasingly inhospitable (Pauls *et al.*, 2013).

Atlantic salmon (*Salmo salar* L. 1758) is an anadromous species distributed in North America, Iceland, Atlantic Europe and north-western Russia. Its temperature tolerance range is 0–33°C (Elliot & Elliott, 2010) and, thus, this large temperature range together with its also large natural distribution is a useful model for testing the effects of temperature on genetic landscapes in temperate areas. Both *Salmo salar* and Pacific salmon *Oncorhynchus* Suckley 1861 populations are highly structured due to their propensity to return to their natal river to breed (Hansen & Jonsson, 1994); in turn, this homing leads to reduced gene flow between populations and the development of genetically distinct river-specific populations. The homing instinct is greatly affected by an ecological stimulus, seawater temperature and salmon behaviour responses to it is less pronounced in warmer areas, or in warmer years (Valiente *et al.*, 2010); this acts to increase rates of straying away from natal rivers as returns are delayed (Valiente *et al.*, 2011). Response to rising temperatures may therefore modify the population structure of the native species (Horreo *et al.*, 2011a), and, as a consequence, the species could lose its evolutionary adaptation to local environments, reducing the viability of some populations (Frankel and Soulé, 1981).

The anadromous life history and strong natal homing of *S. salar* are thought to be major factors influencing population structure in this species, but there is also some evidence that sea surface temperature may also play a role in structuring *S. salar* populations at a regional scale (Dionne *et al.,* 2008). Sea surface temperatures (SST) have important effects on *S. salar* behavior and performance during the adult life phase at sea. For example, ocean SST directly affect growth or modify post-smolt behaviour (Friedland, 1998) such that *S. salar* migration may be altered in response to changes in temperature from as little as 2–3^{o}C, (Jensen, 1990). Indeed, water temperature has been shown to have a strong effect on

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migration behaviour in post smolts (Moriarty *et al.,* 2016) and can influence the rates of straying in returning adults (Valiente *et al.,* 2011). Despite these indirect, but strong signals of the importance of SST stimulus in *S. salar* phylogeography, few investigations have attempted to link these two factors.

This study employs an extensive data set of *S. salar* microsatellite genotypes originating from Spain, France, UK (England, Wales, Scotland) and Ireland (Griffiths *et al.*, 2010) to address two key questions: does genetic diversity in *S. salar* conform to the pattern of decreasing genetic diversity towards the pole; do SSTs influence the genetic structure of *S. salar* in the Atlantic Arc? The null hypothesis is that response to SST stimulus defines migration limits, thus, successful gene flow among populations would be restricted to populations in areas with similar SSTs. This would result in large-scale population structuring of the species and implies major consequences if global warming continues at current rates.

2 | MATERIALS AND METHODS

Average annual sea SSTs in the region of the Atlantic between northern UK and northern Spain (Figure 1), were compiled using data from the complete years 2004 and 2005 [when the majority of samples analysed by Griffiths *et al*. (2010) were collected: 3730 individuals, 57 rivers, 117 sample sites] with the Giovanni ocean radiometry online data system (http://modis.gsfc.nasa.gov). Temperatures for each river were assessed at the river mouth. Giovanni is a web-based application developed by the Goddard Earth Sciences Data and Information Services Centre (GES DISC). It was employed to analyse SSTs and to create a map showing the Modis-Aqua 4 km sea surface temperature data in the studied area (data range: 0–22°C; blue-yellow-red palette colour), with the ocean colour radiometry online

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visualization and analysis portal included in the online application. To determine regions from SST, we did take into account the criterion of ≥ 2°C. A difference of at least 2°C has been proposed for producing changes in biogeographic (Horreo *et al.*, 2014) and migration patterns (Jensen, 1990) in *S. salar*. Data were organized in regions from differences of at least 2°C in SST.

A total of 3730 *S. salar* from 57 different rivers across the Atlantic Arc (Spain, France, UK and Ireland; Figure 1), were sampled in the years 2004 and 2005. These microsatellite data have been previously published, so details of sampling, DNA extraction, PCR amplification and several genetic diversity estimations can be found in the original publication (Griffiths *et al.*, 2010). Fin clips from 1+ *S. salar* parr were obtained during in-river juvenile surveys, except in northern France, where scales from returning adult *S. salar* were obtained from rod-caught fish. DNA was extracted from both fin clips and scales and 12 microsatellite loci (Ssa1-57a, SsaD-144b, Ssa--171, SSsp2201, Ssa-289, Ssos-l85; Ssa-197, Ssa-202, SSsp-2210, SSsp-1605, SSsp-G7 and Ssos-l417) were employed for the study of their genetic diversity (see Griffiths *et al*., 2010 for details). After strict validation of microsatellite genotypes, their genetic diversity was measured as the mean number of alleles per locus (N_a), the effective number of alleles (N_e ; the number of alleles in a population, weighted for their frequencies) and the expected and observed heterozygosity (H_E and H_O, respectively). N_e was estimated in this study with Genodive.2.0.27 (Merimans & Van Tienderen, 2004). Isolation by Distance (IBD) analysis, as well as gene flow (N_m) values were estimated through the private alleles frequency with GENEPOP online (http://genepop.curtin.edu.au). Arlequin 3.5 (Excoffier & Lischer, 2010) was used for the analysis of molecular variance (AMOVA) employing the SST areas as groups and rivers as populations. Normality of the data was tested and transformed ($\log_{10}$) when needed; Spearman's *D*-tests were carried out searching correlations in these cases. We employed the

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non-parametric Kruskal-Wallis test for equal medians and the Mann-Whitney pairwise test was employed to test for genetic diversity differences between pairs of SST areas.

To test whether SST areas conform barriers in our genetic and landscape dataset within the Atlantic Arc, discontinuities–major phylogeographic breaks occurs were searched with the software BARRIER 2.2 (Manni *et al*., 2004). This software implements Monmonier's (1973) maximum difference algorithm to obtain a representation of barriers (if any) within a genetic landscape.

3 | RESULTS

The SST map (Figure 1) showed the existence of four major areas from northern (colder) to southern (warmer) regions along the Atlantic Arc (Figure 1), with water temperatures ranging between 8.8°C and 15.4°C, with 2.1–2.3°C difference among closer regions. Such SST structure separated northern Spain, northern France, south-west England and Wales + southern England and the northern regions. AMOVA results showed significant genetic differences among rivers within and among these SST areas (Table 1), representing, respectively, 1.75% and 2.07% of the total variation. IBD analysis showed that the level of genetic differentiation among samples–populations was highly correlated with distance (Figure 2) for *S. salar* populations in the Atlantic Arc. When testing for IBD within the SST detected areas, its presence was statistically significant in all cases. In contrast to it, IBD was not present within south-western England and Wales and within southern England per separate, (they are two different genetic units conforming a SST area; see below). Gene flow (number of migrants per generation, N_m) analyses showed higher connectivity within SST areas (N_m = 14.16, SD = 3.56) than between areas (Nm = 9.33, SD = 3.24), as expected from the distribution of genetic variance found in the AMOVA. Gene flow between south-western

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England and Wales and southern England (the only case of different genetic units within the same SST area; see below) was very low (N_m = 0.92). BARRIER (Manni *et al*., 2004) identified several barriers according to SST areas (Figure 1). Such barriers separated northern Spain, northern France, southern England and south-western England and Wales + northern regions. In addition to these SST areas, it also identified barriers that isolated the Rivers Eo (northern Spain), Lomond (northern regions) and Torridge (south-western England and Wales).

Genetic variability data (N_a, N_e, H_E and H_O) did not follow a normal distribution, even after log transformation. For this reason, Spearman's *D* were done for searching correlations between genetic variability and latitude. All comparisons were highly significant with increasing levels of diversity in the north (Spearman's D = 16595, 12474, 11079 and 13623 for N_a, N_e, H_E and H_O respectively; $P < 0.01$ in all cases). Genetic variability data was then estimated for four separate groups (Table 2), created depending on ocean water temperatures in the mouth of each river, following the four major SST areas. With this classification, none of the genetic data followed a normal distribution again, even after data log transformation, being temperature and latitude highly correlated (lower temperatures in higher latitudes; Spearman's D = 48301, $P < 0.01$). The N_a did not vary depending on SST region (Kruskal-Wallis H_C = 6.462; $P > 0.05$), but the effective number of alleles (N_e) did (Kruskal-Wallis H_C = 13.96; $P < 0.01$), being higher in northern (and colder) areas. Mann-Whitney pairwise tests showed statistically significant differences in N_e among all the SST area pairs, except between northern Spain and northern France, as well as between the northern regions and, south-west England and Wales + southern England. Regarding heterozygosities, both expected and observed heterozygosity showed significant differences for sample medians (Kruskal-Wallis H_C = 20.80 and 25.99 for H_E and H_O, respectively; $P < 0.01$ in both cases). Mann-Whitney pairwise tests showed more marked statistically significant differences in H_E

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among the same SST regions than did the analysis of N_e among SST area pairs. Statistically significant differences in H_O were found among all SST regions, except between Northern regions and south-west England and Wales + southern England. N_e, H_E and H_O followed a latitudinal cline of genetic variation, from higher values in northern areas to lower values in the south, with statistical differences among SST areas (Table 2).

4 | DISCUSSION

The differences in temperatures experienced by *S. salar* among the four main SST areas identified in this study (up to 6°C; Figure 1), are major, since a variation of just 2°C can produce changes in biogeographic (Horreo *et al.*, 2014) and migration patterns (Jensen, 1990). IBD (Figure 2) occurred across the whole Atlantic Arc, but also within each of the SST areas, so it is was unlikely that IBD is the main factor determining large discontinuity of gene flow among the considered SST areas. SST structure generally coincided with both the BARRIER results and the genetic population structure of the *S. salar* across this area, with some nuances. SST areas separate south-western England and Wales + southern England and northern regions, while a barrier was found between south-western England and Wales + southern England. This result indicates quite clearly that the genetic landscape inferred from microsatellite data is not determined by IBD. The genetic structure of the species in the area is divided into the following genetic units (Griffiths *et al.*, 2010): northern Spain, northern France, southern England, south-west England and Wales and the northern regions. The main difference between the genetic structure found by (Griffiths *et al.*, 2010) and the SST structure found in this work was the occurrence of two genetically different genetic units, south-western England and Wales and southern England, within the same SST area.

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IBD within south-western England and Wales as well as within southern England did not occur despite being in the south-western England and Wales + southern England SST area and a major phylogeographic break (barrier) was identified between them. The gene flow between the two areas was very low, smaller than one migrant per generation (N_m = 0.92), which is considered the maximum interchange allowed for consider two populations as independent (Mills & Allendorf, 1996). Genetic differences here cannot therefore be attributed to current SSTs. Instead they could be due to ancestral genetic differences between them. Southern England populations (sampled Rivers Avon, Itchen and Test) are placed in front of the Solent (Isle of Wight) and belong to the boreal *S. salar* race of the British Isles (Payne *et al.,* 1971). The River Avon, the river most to the west of the southern England genetic unit found by Griffiths *et al.,* (2010), has been proposed as the west limit and remnant population of the boreal race (Child *et al*. 1976). All the other rivers in this study, thus the Atlantic Arc, belong to the Celtic *S.salar* race (Payne *et al*. 1971). This may explain the genetic differences between them despite being in the same SST area. The origin of both races was produced by glacial changes during the Pleistocene (Child *et al*. 1976; Payne *et al*. 1971), genetic differences between them being therefore stronger than those produced by SSTs within the Celtic race and being maintained in the long-term.

The genetic population structure of this species across the whole Atlantic Arc is therefore related to ocean water temperatures, although occurring at a smaller scale (Horreo *et al.*, 2011a; Horreo *et al.*, 2014). Spearman correlations showed that genetic variability was significantly higher in high latitudes, which had lower temperatures, and AMOVA results (Table 1) unravel significant genetic differences among rivers within SST regions, as expected in this species, each river being generally considered as an independent population due to homing instinct (Hansen and Jonsson, 1994). Perhaps more interestingly, marked genetic differences were also apparent between *S. salar* populations from different SST areas

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(Table 1), suggesting broad-scale genetic differences related to SST areas and similar to the differences between the broader genetic units (reporting regions) identified by (Griffiths *et al.*, 2010). At the same time, gene flow (N_m) analyses showed higher gene-flow values within SST areas than between them. All together, these findings reinforce the hypothesis of SST areas corresponding to genetic units; thus, we suggest not only homing instinct, and the associated isolation of populations (Hansen and Jonsson, 1994), as a factor for shaping the population structure of *S. salar*, but also ocean water temperatures, with these having a particularly large influence at a continental scale.

The latitudinal pattern of higher genetic diversity in populations inhabiting warmer areas reported by Adams and Hadly (2013) in vertebrates is not observed in *S. salar* in this part of their range. Moreover, the contrary is observed here, with a latitudinal cline of genetic variation in northern areas and lower values in southern areas. This pattern, which has been reported in some cold-adapted species (Hirao *et al.,* 2017), as well as in other salmonids (Ninua *et al*., 2018) and other anadromous species (Hasselman *et al.*, 2013), has also been expected in *S. salar* (Valiente *et al.,* 2005), but it had been found only for major histocompatibility complex class II genes (Dionne *et al.,* 2007); to our knowledge, our study is the first report of the pattern for microsatellite markers in this species. Thus, anadromous species appear to exhibit the opposite of the pattern that usually occurs in vertebrates (Adams & Hadly, 2013). Northern refugia during geological glaciations have been proposed to determine current genetic variation of salmonids inhabiting the Black and Caspian Seas (Ninua *et al*., 2018) and could also be at play here for explaining the genetic discontinuity between northern and southern regions. Northern Spain is the current southern limit of the natural distribution of *S. salar* and, following the central–marginal genetic diversity hypothesis, higher genetic diversity would be expected in the core populations rather than at the edges of the species' range (Eckert *et al.*, 2008). The above mentioned cline of genetic

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variation could also reflect population sizes, which are typically greater in northern (colder) populations of *S. salar* across the Atlantic Arc than in southern (warmer) populations (Nikolic *et al.*, 2009; Horreo *et al.*, 2011b). However, significant statistical differences in the genetic variability of populations between SST areas suggests that seawater temperatures might have a major influence on the genetic variability of *S. salar* independent of population size.

Besides the central–marginal genetic diversity hypothesis (Adams & Hadly, 2013), another (not necessarily alternative) explanation may be associated with the current climate trend of rising temperatures. Given our hypothesis of northern refugia, we may envisage that species adapted to temperate zones may start migrating to northern areas, where genetic variation from different populations would then accumulate. This process would be effectively the opposite of that known to have happened in glacial periods (Hewitt, 1999). Similar to glacial refugia (Shafer *et al.*, 2011), northern areas may represent global warming refugia, acting as new hotspots of genetic diversity for species from temperate areas. Indeed, in *S. salar*, northern populations (not the intermediate ones) were the most variable across the Atlantic Arc.

Genetic diversity varies depending on species population structure, with two major factors influencing it: genetic drift and gene flow (Slatkin, 1987). Genetic drift decreases genetic variation within populations, but increases it between populations, while gene flow produces the opposite effect. Since genetic diversity is smaller in southern populations (Table 1), but more marked genetic differences occur between rivers in those areas (Horreo *et al.*, 2011a; Perrier *et al.*, 2013), the latitudinal cline in *S. salar* genetic variability reported here along the Atlantic Arc could therefore be explained by genetic drift acting on southern populations. Again, temperature would be critical in explaining the smaller population sizes

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in our dataset, since the populations analysed were (as far as is known) stable and were not differentially affected by recent habitat losses (*e.g.*, dam construction and their use).

Genetic drift and gene flow are not the only factors that influence population genetic diversity; natural selection may also act on it (Templeton *et al.*, 2001). Natural selection acts to reduce the spread of non-favourable alleles, while genetic drift acts to randomly reduce genetic variation. Our results are based on microsatellite loci that are located in non-coding regions and selective pressure is not generally expected to act on them. Thus, it appears that genetic drift is the key driver in the reduction of N_e, H_O and H_E in southern *S. salar* populations *via* random allele losses.

In summary, this work studying the landscape genetics of *S. salar* in the Atlantic Arc describes how its population structure, with a latitudinal cline of genetic variability (higher in northern areas), is a behavioural response that can be explained by the combined effects of ecological issues as ocean SST stimulus as well as genetic drift in southern *S. salar* populations. Genetic drift has several consequences for populations, such as the disruption of local adaptations or even extinctions (Frankel & Soulé, 1981) and the southern populations of this species appear critically endangered both because of reduced genetic variability and inhabiting some of the warmest waters this species is known to tolerate. Protection of populations inhabiting southern areas is urgently needed to avoid their extinction, especially if climate change continues at current rates. Moreover, if the species does end up being displaced to northern areas, recipient zones should be recognized as refugia and given appropriate status and protection. Careful management of this species, coordinated across countries and latitudes, is strongly recommended if the species is to maintain its numbers and diversity in Europe.

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CONTRIBUTIONS

J.L.H. and E.G.-V. conceived the hypotheses, all authors analysed the data, J.L.H. and E.G.-V. wrote the manuscript and all authors reviewed its final version.

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FIGURES

Figure 1 Map showing the sea surface temperatures on the Atlantic Arc in the years 2004 and 2005 and the separation of *Salmo salar* into temperature-related populations. ●, Rivers included in the study [see Griffiths *et al.*, (2010) for details]. ▬, Phylogeographic barriers identified from BARRIER software (barrier isolation of individual Rivers Eo, Lomond, and Torridge are not shown).

Figure 2 Isolation by Distance (IBD) plot based on pair-wise F_{ST} comparisons between *Salmo salar* populations.

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TABLES

Table 1 Analyses of molecular variance (AMOVA) of the sea surface temperature (SST) regions of the Atlantic Arc

Source of variation	df	Sum of squares	Variance of components	Percentage of variation
Among SST areas	4	408.24	0.0728*	2.07
Among rivers within SST areas	50	642.90	0.0617*	1.75
Among individuals within rivers	4126	14110.35	0.0345*	0.99
Within individuals	8361	29167.49	3.3499*	95.18

* $P < 0.05$.

Table 2 Mean (SD) genetic variability data (mean Na, Eff_Na, He and Ho) estimated for four separate groups of *Salmo salar* created depending on ocean water temperatures in the mouth of each river following the four major SST areas

	Population grouping temperature			
	8.8°C	**10.9°C**	**13.2°C**	**15.4°C**
N_a	12.57 (1.46)	12.87 (1.71)	14.02 (0.35)	12.21 (2.34)
N_e	8.78 (0.76)	8.47 (1.47)	7.33 (0.40)	6.40 (1.37)
H_O	0.84 (0.02)	0.84 (0.03)	0.78 (0.02)	0.77 (0.03)
H_E	0.82 (0.02)	0.83 (0.03)	0.80 (0.02)	0.77 (0.04)

N_a, Mean number of alleles per locus; N_e, the effective number of alleles (the number of alleles in a population, weighted for their frequencies); H_O, observed heterozygosity; H_E, expected heterozygosity.

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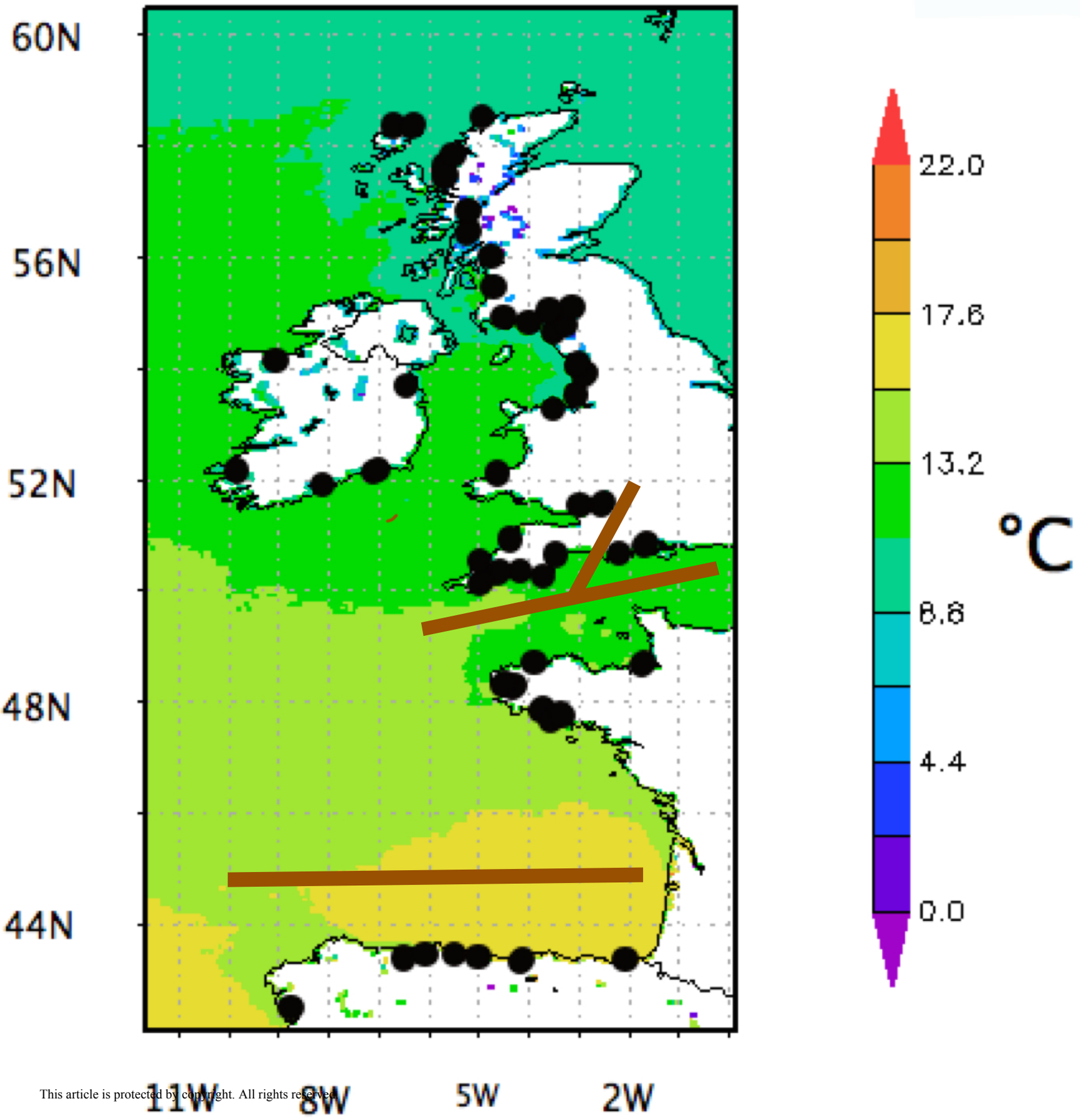

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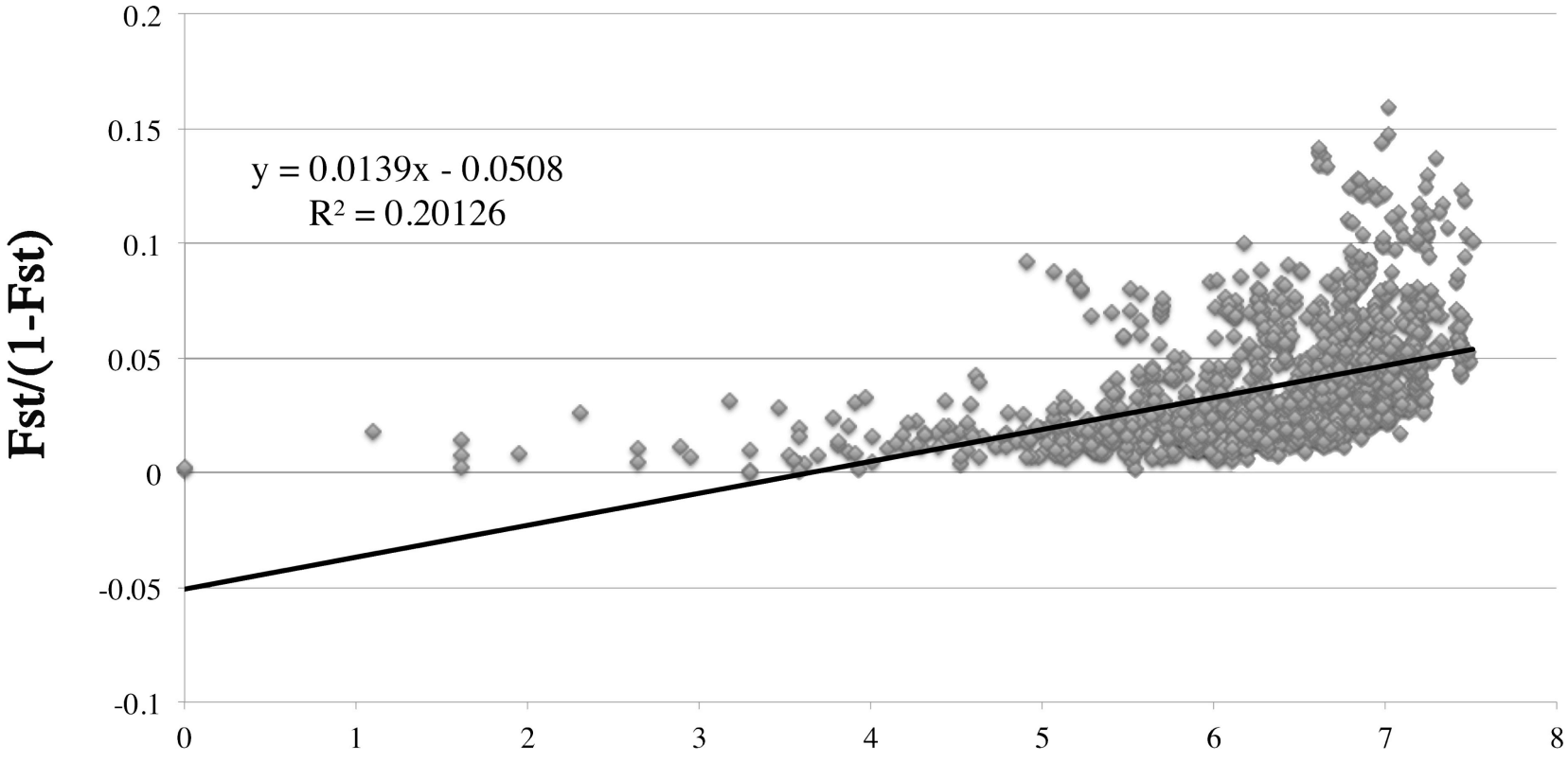

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