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Personalities influence spatial responses to environmental fluctuations in wild fish

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Abstract

1. Although growing evidence supports the idea that animal personality can explain plasticity in response to changes in the social environment, it remains to be tested whether it can explain spatial responses of individuals in the face of natural environmental fluctuations. This is a major challenge in ecology and evolution as spatial dynamics link individual- and population-level processes.
2. In this study, we investigated the potential of individual personalities to predict differences in fish behaviour in the wild. Specifically, our goal was to answer if individual differences in plasticity of space use to sea surface temperature could be explained by differences in personality along the reactive–proactive axis.
3. To address this question, we first conducted repeated standard laboratory assays (i.e., open-field test, novel object test and mirror stimulation test) to assess the personality type of 76 wild-caught Atlantic cod (*Gadus morhua*). Next, we released the fish back into the sea and monitored their spatial behaviour over large temporal (16 months) and spatial (a whole fjord) scales, using high-resolution acoustic tracking.
4. We demonstrate that (a) cod personality traits are structured into a proactive–reactive syndrome (proactive fish being more bold, exploratory and aggressive), (b) mean depth use of individuals is mainly driven by sea temperature and (c) personality is a significant predictor of home range changes in the wild, where reactive, but not proactive, individuals reduced their home range as sea temperature increased.
5. These findings expand our understanding of the ecological consequences of animal personality and the mechanisms shaping spatial dynamics of animals in nature.

KEYWORDS
animal personality, Atlantic cod, behavioural plasticity, home range, proactivity, spatial ecology

1 | INTRODUCTION

Natural and human-induced environmental changes have notable effects on the life history, behaviour and distribution of numerous species (Charmantier et al., 2008; Sih, Ferrari, & Harris, 2011). Populations can respond to such alterations through adaptive changes across generations. However, the first and fastest way to cope with a novel situation is often an individual behavioural response that ultimately depends on the behavioural plasticity that has evolved under past conditions (Sih et al., 2011; Wong & Candolin,

2015). Plasticity in spatial behaviour is particularly important because spatial dynamics determine the interaction with conspecifics, with other species and with the surrounding abiotic environment (Clobert, Galliard, Cote, Meylan, & Massot, 2009; Spiegel, Leu, Bull, & Sih, 2017). Accordingly, interindividual differences in movement ecology, and the range of spatial plasticity, likely play an important role in determining the ecological and evolutionary dynamics of populations (e.g., Harrison et al., 2014; Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2017).

Animal personality has the potential to explain individual differences in average levels of spatial behavioural traits (Spiegel et al., 2017). For instance, bolder or more aggressive individuals tend to be more exploratory and disperse further (Cote, Clobert, Brodin, Fogarty, & Sih, 2010). Yet, empirical evidence of personality-dependent spatial behaviour for traits other than dispersal is still scarce (Spiegel, Leu, Sih, Godfrey, & Bull, 2015; Spiegel et al., 2017). Personalities may also explain the differences in plasticity observed between individuals in response to changes in their social environment (Aplin et al., 2013) and population dynamics (Cote & Clobert, 2007). However, there have been few attempts to resolve whether animal personalities may explain changes in the spatial dynamics of individuals in response to natural environmental changes (e.g., temperature, food abundance), even though environmental fluctuations are a typical feature of virtually all habitats. Most notably, Spiegel et al. (2015) found that personality (especially aggressiveness) of sleepy lizards (*Tiliqua rugosa*) affected space use and their response to ecological factors such as refuge and food availability. One potential reason for this knowledge gap is the methodological challenge in obtaining, for the same individuals, independent and repeated personality assessments and large-scale, long-term movement data in the wild while accounting for other environmental factors that may contribute to movement variation (Spiegel et al., 2015, 2017). Whereas most studies that investigate individual behavioural plasticity are conducted in standardized captivity conditions, studying this phenomenon in wild populations is essential for understanding the drivers and adaptiveness of plastic responses to environmental conditions across natural temporal and spatial scales (Brommer, 2013; Dingemanse, Kazem, Réale, & Wright, 2010; Nussey, Wilson, & Brommer, 2007).

In this study, we aimed to resolve underlying relationships between animal personality and movement ecology under fluctuating environmental conditions. We hypothesized that individual differences in spatial responses to sea temperature changes of free-swimming fish may be explained by differences in personality, as described by the reactive–proactive axis common to many vertebrates. To test this hypothesis, we first conducted standardized personality assays on wild-caught individuals of Atlantic cod (*Gadus morhua*) from southern Norway to estimate their reactive–proactive tendency. In contrast to more proactive individuals, reactive individuals are shy, slow and thorough explorers, lowly aggressive, and more sensitive to changes in their environment (Coppens, de Boer, & Koolhaas, 2010). We then released the animals back to their natural environment and monitored their movements over a period of up to 16 months using acoustic telemetry. In parallel, we recorded variation in sea surface temperature. Fjord cod populations in southern Norway are well suited to investigate behavioural responses to temperature, as previous studies have shown that cod space use and movements are consistent at the individual level (Olsen, Heupel, Simpfendorfer, & Moland, 2012; Villegas-Ríos et al., 2017) and also highly temperature-dependent (Freitas, Olsen, Knutsen, Albretsen, & Moland, 2016; Freitas, Olsen, Moland, Ciannelli, & Knutsen, 2015).

2 | MATERIALS AND METHODS

2.1 | Experimental protocol and laboratory assays

Seventy-six cod were caught using unbaited fyke nets in spring (n = 47) and autumn (n = 29) 2014 in the Tvedestrand fjord, south Norway (Figure 1). Mean body size of captured individuals (range = 30–56 cm) did not differ between sampling seasons (spring = 44.3 [SD = 6] cm; autumn = 43.0 [SD = 6] cm; ANOVA: F = 0.786; df = 1; p = 0.378). Captivity duration was kept as short as possible to minimize disturbance of the individuals and allow them to recognize their home areas after release. Upon arrival in the laboratory (day 0), fish were housed at low densities (max 10 fish per tank) in cylindrical tanks (1,500 L, 130 cm diameter, 100 cm high) and fed *ad libitum* with frozen shrimps. The holding tank provided shelter (plastic plants) and running saltwater. Photoperiod followed natural day-light cycle. After one day of acclimatization (day 1) in the housing tanks, fish were scored for their behaviour in days 2–6. We chose the open-field test, novel object test and mirror-image stimulation test because they describe important aspects of the behavioural strategies of fish: their tendency to explore new habitats and resources, their boldness and their aggressive competition (Adriaenssens & Johnsson, 2012). Forty-five minutes before the start of tests, a subgroup of four randomly selected individuals were each transferred into one of the four experimental tanks (600 L, 140 × 140 cm). Fish were subject to a 30-min acclimatization period in the "home area" of the experimental tank (140 × 50 cm), an area partially covered by a roof (70 × 50 cm) that served as a shelter for the individuals. After that period, a door (60 cm) was lifted with a string via a pulley allowing the fish enter the "open arena" (140 × 90 cm) and behaviour was recorded with a webcam (D-link DCS-2136L). In the open-field test (five replicates of 5 min in days 2–6), a suite of variables were measured in order to score the tendency to explore the open arena and the undisturbed swimming pattern of cod (Table 1). The mirror-image stimulation test (two replicates of 20 min in days 3 and 5) was used to score the aggressiveness of the individuals (Table 1). Mirrors were cut to the form of one of the sides of the tanks and fitted temporarily to the tank edge opposite to the shelter. In the novel object test (two replicates of 20 min in days 4 and 6), the individual's tendency to leave the refuge and explore a plastic cylinder (diameter = 20 cm, height = 7 cm) placed in the middle of the arena was measured (Table 1). To encourage the individuals to leave the home area, the roof was removed in the novel object test. Maximum latency times were assigned to a small percentage of fish that did

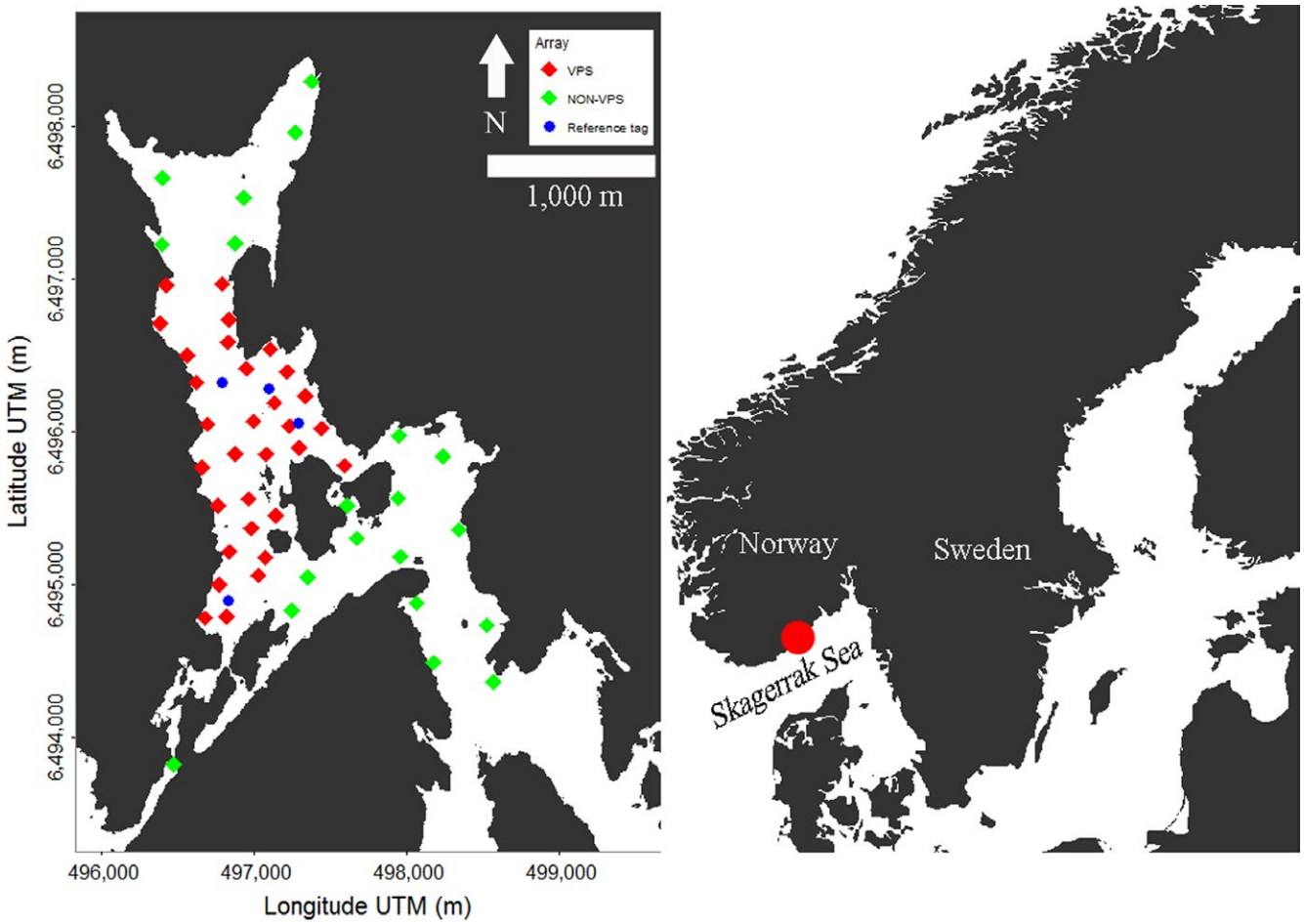

FIGURE 1 Study area showing the telemetry array deployed in Tvedestrand fjord, south Norway. The array includes 51 receivers, of which 31 form a Vemco VPS array using four reference tags. Yellow arrow: location of sea temperature loggers

not show the focal behaviour (Table 1). When the open-field test and the boldness or mirror stimulation test were conducted on the same day (days 3–6), we proceeded as follows: we first placed the fish on the home area for a habituation period of 30 min. We then lifted the door allowing the fish to explore the open arena for 20 min (open-field test). After 20 min, the fish was directed to the home area again and the door closed. In that moment, the novel object or mirror was placed in the arena and the door lifted again to allow the fish interact with the novel object (novel object test) or mirror (mirror stimulation test) for 20 min. By doing this, we were sure that the fish was not reacting to the arena (which the fish had just explored); rather the reaction and variables recorded were a response to the novel object or mirror. We used behavioural coder software (Solomon coder) to get the relevant behavioural information from the videos.

On day seven, 64 individuals were randomly selected from the bulk of 76, anesthetized with clove oil, surgically implanted with an acoustic transmitter (see details in Olsen et al., 2012) and tagged with a plastic T-bar tag below the dorsal fin. On day 8–9, tagged individuals were released at the exact same position as they were initially captured. All fish swam gently towards the bottom when released. Tagged fish were tracked from release date until 31 August 2015 (end of the experiment) or until expiry (natural or harvest mortality).

2.2 | Study area and telemetry array

Our study was carried out in the Tvedestrand fjord on the Norwegian Skagerrak coast (Figure 1). The study area was monitored with a presence/absence acoustic system comprised of 51 Vemco VR2W omnidirectional receivers (i.e., "extended array," Figure 1) deployed at a three-metre depth. Thirty-one of those receivers were deployed in the central part of the study area and formed a Vemco positioning system allowing for detailed information on fine-scale fish movement based on triangulation (i.e., "VPS array"; Figure 1). Synchronization tags (V16-4x, random delay interval: 500–700 s) were moored along with each VPS receiver, and reference tags (three V13-1x and one V13T-1x, random delay interval: 500–700 s) were placed within the VPS grid to measure system performance (Figure 1). Fish id and depth, detection time and receiver id were downloaded regularly from the receivers.

Sea temperature was recorded hourly in the study area using temperature loggers (Hobo Pendant®) deployed at 1, 5, 10, 15 and 20 m depth (Supporting Information Figure S1). We used average weekly temperature at 1 m depth (hereinafter "surface temperature") as a descriptor of the thermal environment in the fjord. Surface temperature ranged from <5°C during winter to >20°C during summer and was correlated with temperature at other depths (Pearson correlation

TABLE 1 Behaviours displayed by individual Atlantic cod during captive personality assays (time in seconds), including percentage of fish that did not show the focal behaviour

Assay	Behavioural variable	Description	Mean	Range	Unresponsive
Open-field	Latency to exit	Time since door opens until the fish leave the home area	102.6	0–300	13%
	Time active in the arena	Proportion of time active in the arena	0.53	0–0.99	
	Time in shelter	Proportion of time under the roof	0.31	0–1	
Novel object	Latency to exit	Time since door opens until the fish leave the home area	293.87	0.8–1,200	15%
	Latency to first approach	Time until first entrance into the novel object area	369.70	2.0–1,200	17%
	Time in novel area	Proportion of time in the novel object area after first visit	0.05	0.0–0.24	
	Time in home area	Proportion of time in the home area	0.61	0.03–1.0	
	Swims	Number of times the fish swims over the novel object	1.93	0–14	
Mirror image	Latency to exit	Time since door opens until the fish leave the home area	326.20	0.20–1,200	14%
	Latency to first approach	Time until first entrance into the mirror area	341.20	0.6–1,200	14%
	Time in home area	Proportion of time in the home area	0.56	0–1	
	Time in the mirror area	Proportion of time in the mirror area after first visit	0.37	0–1	

between temperature at 1 m and temperature at 5 m, $r_{1,5} = 0.93$; $r_{1,10} = 0.81$; $r_{1,15} = 0.62$; $r_{1,20} = 0.14$; all values: $p < 0.001$; $n = 19{,}737$, Supporting Information Figure S1). To reinforce our conclusion, we replicated the analyses with temperature at 5, 10 and 15 m yielding the same results (not presented).

2.3 | Estimation of movement traits in the wild

Data from the VPS array were sent to Vemco for postprocessing of fish positions. VPS positions were calculated using hyperbolic positioning, which is a technique based on measuring differences in transmission detection times at pairs of time-synchronized receivers, and converting these to distance differences using the signal propagation speed (Freitas et al., 2016; Smith, 2013). Three movement traits were estimated for each fish. Weekly home range size was estimated as the kernel utilization distribution with a probability level of 95% using all the VPS locations, provided that the fish were present in the array for at least four, not necessarily consecutive, days in a particular week. Based on previous analysis of similar data (Villegas-Ríos et al., 2017), a fixed smoothing factor was used ($h = 40$) and *extent* was set to 0.5; analyses were conducted using the *adehabitatHR* library in R (Calenge, 2006). Following Freitas et al. (2015), average short-term changes in depth recorded in the extended array were used here as a proxy for the fine-scale fish vertical activity. The standard deviation in depth for every 1-hr period was calculated and then averaged for each given week. Mean depth was estimated for each week averaging all the depth values from the extended array.

2.4 | Statistical analyses

2.4.1 | Laboratory assays of personality

Based on preliminary analyses (Supporting Information Text S1), one variable per laboratory assay was selected as an indicator of the focal behaviour described by each assay. The indicator variables selected were *latency to exit the shelter* for the open-field test (denoted as Ind_{exp}) and the novel object test (Ind_{bol}), and *latency to first approach to the mirror* (Ind_{agg}) in the mirror stimulation test (Supporting Information Table S1). Repeatability of Ind_{exp}, Ind_{bol} and Ind_{agg} (log transformed) was estimated using mixed-effects models (with normal error distributions) using the *lmer* function in the *lme4* library in R (Bates, Mächler, Bolker, & Walker, 2015). The following fixed effects were included in the model regardless their significance, as we were mainly interested in the variance components: trial order (factor of two levels in the mirror and novel object test; continuous variable with five values per fish in the open-field test), scaled body size and season. Fish identity was included as a random effect. Repeatability was estimated as the ratio of the among-individual variance (V_{ind}) on the sum of the among- and the within-individual variance ($V_{\text{ind}} + V_{\text{res}}$) (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). Repeatability was considered significantly different from zero when there was support for including the random effect in the model, which was tested by AIC comparison of a model with and without random effects. To take uncertainty in laboratory personality traits forward into follow-up analysis, we performed simulations of the mentioned models to produce a distribution of 1000 estimates of each individual

random effect for each of the three laboratory behaviours, using the *sim* function of the *arm* library (Gelman & Su, 2016).

Given that preliminary results showed that boldness, exploration and aggressiveness were strongly correlated (Supporting Information Text S1), we ran 1,000 PCAs randomly picking one realization of each individual random effect for each behaviour at each run, to obtain 1,000 estimates of each individual principal component score of personality along a reactive–proactive axis; we termed that score "PC proactivity" (low scores: reactive fish; high scores: proactive fish).

2.4.2 | Behavioural plasticity of movement traits in the wild

We investigated the effect of PC proactivity on home range, vertical activity and mean depth (all log transformed) by running three separate mixed-effects models (with normal error distributions) using the *lme* function in the *nlme* library (Pinheiro, Bates, DebRoy, & Sarkar, 2011). In addition to PC proactivity, the following fixed effects (scaled) were included: body size, sea surface temperature, the interaction between body size and sea surface temperature and the interaction between PC proactivity and sea surface temperature, to test for size-dependent and personality-dependent temperature effects, respectively.

The protocol for linear mixed-effects model fit and validation followed Zuur, Ieno, and Meesters (2009). We started with a model containing the full suite of fixed effects and searched for the optimal random structure using the Akaike Information Criteria, AIC (Burnham & Anderson, 2004), with restricted maximum-likelihood (REML) estimation procedure. We hypothesized that both the intercept and the slope of the effect of surface temperature on cod spatial behaviour could differ among individuals; we therefore included individual random intercepts and individual random slopes and tested for their significance. Autocorrelation functions showed temporal autocorrelation of model residuals so an autoregressive term (corAR1) was added to the models (Dormann et al., 2007). Residuals vs. fitted values were plotted to verify homogeneity, and residuals against each explanatory variable were plotted to check independence. Then, the optimal fixed structure was selected by checking the significance of each fixed factor using likelihood ratio tests. If the effect of a fixed factor was not significant, the factor was dropped from the model and a new mixed-effects model updated. Eventually, the optimal model was refitted using restricted maximum-likelihood estimation and validated by examining residual plots.

Original data and model residuals indicated some nonlinearities in the relationship between mean depth and surface temperature that recommended the use of generalized additive mixed-effects models (GAMMs) with normal error distribution. GAMMs were fitted using package *mgcv* (Wood, 2001) using the optimal random and fixed-effect structure as selected in the linear models. Repeatability of home range, vertical activity and mean depth was calculated from the best-fitted models to corroborate that fish were behaving in a consistent way in the wild.

Each of the above models was run for 1,000 times, picking one realization from the distribution of PC proactivity scores in each run to produce a distribution of the estimated parameters and their confidence interval while taking into account the uncertainty in the laboratory measures of personality. An effect was considered significant when after 1,000 runs, the confidence interval of the effect did not include the zero in at least 95% of the cases. However, for practical reasons model selection and visualization was based on models run using the mean of PC proactivity for each fish.

3 | RESULTS

3.1 | Laboratory assays of personality

Behavioural variables measured in the laboratory showed some variation among assays (Table 1). Repeatability of $Ind_{exp,}$ Ind_{bol} and Ind_{agg} was 0.50, 0.75 and 0.49, respectively (Supporting Information Table S2). The inclusion of the random effect of fish was supported in all models (ΔAIC >16 in all cases).

Results of the PCA runs showed that $Ind_{exp,}$ Ind_{bol} and Ind_{agg} loaded strongly on the first component (i.e., PC proactivity) that explained on average 73% (range: 64%–80%) of the total variance of the original variables (loadings: Ind_{bol} = 0.85 (0.76–0.92); Ind_{agg} = 0.85 (0.72–0.92); Ind_{exp} = 0.87 (0.78–0.92); eigenvalue = 2.20 (1.92–2.41)).

3.2 | Drivers of movement traits in the wild

Average monitoring period in the field was 244 days, yielding more than 8.5 million detections. Individuals displayed great variation in their vertical and horizontal movement ranges (Supporting Information Figure S2) featuring a mean (± *SD*) depth of 14.1 m (± 8.4) and a weekly home range of 0.06 km^2 (± 0.06); vertical activity was on average 1.21 (± 0.54).

The best-fitted model explaining variation of cod home range in the wild included a random intercept for individual identity, which explained 30.3% of the variance (i.e., the repeatability of home range was 0.30), and sea temperature, PC proactivity and their interaction as fixed effects, which explained 5.6% of the variance (Table 2, Supporting Information Table S3). The main effect of PC proactivity was significant in the model that fitted mean PC proactivity values; however, when the model was run 1,000 times to take into account the uncertainty of the laboratory behaviour, 55.8% of the times the confidence interval of such effect included the zero meaning that the effect cannot be considered significant (Figure 2). A significant negative effect of temperature was found meaning that cod reduce their home range when the water is warmer. However, we also found that the effect of temperature depends on the personality of the individuals meaning that the negative effect of temperature of home range was more pronounced in reactive fish than in more proactive phenotypes. In fact, extremely proactive fish slightly increased the size of their home range with warmer waters (Figure 3). Notably, this interactive effect between personality and sea temperature

TABLE 2 Results of the best-fitted linear models (fitted with restricted maximum likelihood) explaining variation of wild behavioural traits of Atlantic cod in the Tvedestrand fjord. Mean PC proactivity scores were used in these models

Response variable	Model components	Estimate	*SE*	*df*	*p*-value
Home range	*Fixed effects*				
	Intercept	−3.06	0.050	1101	<0.0001
	PC proactivity[a]	0.10	0.049	56	0.0454
	Surface temperature	−0.10	0.027	1101	0.0004
	Interaction	0.07	0.027	1101	0.0077
	Random variance				
	Intercept (among-individual)	0.096			
	Residual variance (within-individual)	0.221			
	Correlation				
	corAR1	0.62			
	Repeatability	0.30			
	R^2 marginal[b]	0.05			
Vertical activity	*Fixed effects*				
	Intercept	0.76	0.018	2127	<0.0001
	Random variance				
	Intercept (among-individual)	0.12			
	Residual variance (within-individual)	0.20			
	Correlation				
	corAR1	0.62			
	Repeatability	0.35			
	R^2 marginal[b]	0.00			
Mean depth	*Fixed effects*				
	Intercept	2.49	0.042	2102	<0.0001
	Surface temperature	−0.26	0.021	2102	<0.0001
	Random variance				
	Intercept (among-individual)	0.057			
	Residual variance (within-individual)	0.194			
	Correlation structure				
	corAR1	0.81			
	Repeatability	0.23			
	R^2 marginal[b]	0.22			

Note. [a]This effect was nonsignificant when the whole distribution of PC proactivity scores for each fish were used. [b]R^2 were calculated using the *r.squaredGLMM* function in the *MuMIn* library in R.

was supported after accounting for the uncertainty in laboratory assays (Figure 2). Individual random slopes explained a negligible and nonsignificant proportion of the variance in home range (they increased AIC by 3 units; Supporting Information Table S3) as compared to the best-fitted model and were removed from the model after checking that the estimates of the fixed effects and their significances were not affected by their removal (Schielzeth & Forstmeier, 2009). Including an autocorrelation structure reduced the AIC of the model by 427 units.

We also found a personality-dependent temperature effect on vertical activity when mean PC proactivity scores were fitted to the model (estimate = 0.020, *SE* = 0.0088, *df* = 2125, *t*-value = 2.0, *p* = 0.020). However, such an effect did not stand when the uncertainty in laboratory measures was taken into account (Figure 2): 25.7% of the models yielded a CI for the interaction that included the zero. After removing the interaction from the models, we ended-up with a reduced model with no fixed effects influencing vertical activity. The inclusion of a random intercept for fish was supported and random variance explained 35.3% of the total variance (repeatability = 0.35). Random slopes were not supported by the model (AIC increase of 3 units; Supporting Information Table S3). The inclusion of an autocorrelation structure was strongly supported (AIC reduction of 727 units).

The best-fitted model for mean depth included individual random intercepts that explained 22.7% of the total variance (i.e., repeatability of mean depth was 0.23; Table 2, Supporting Information Table S3). The

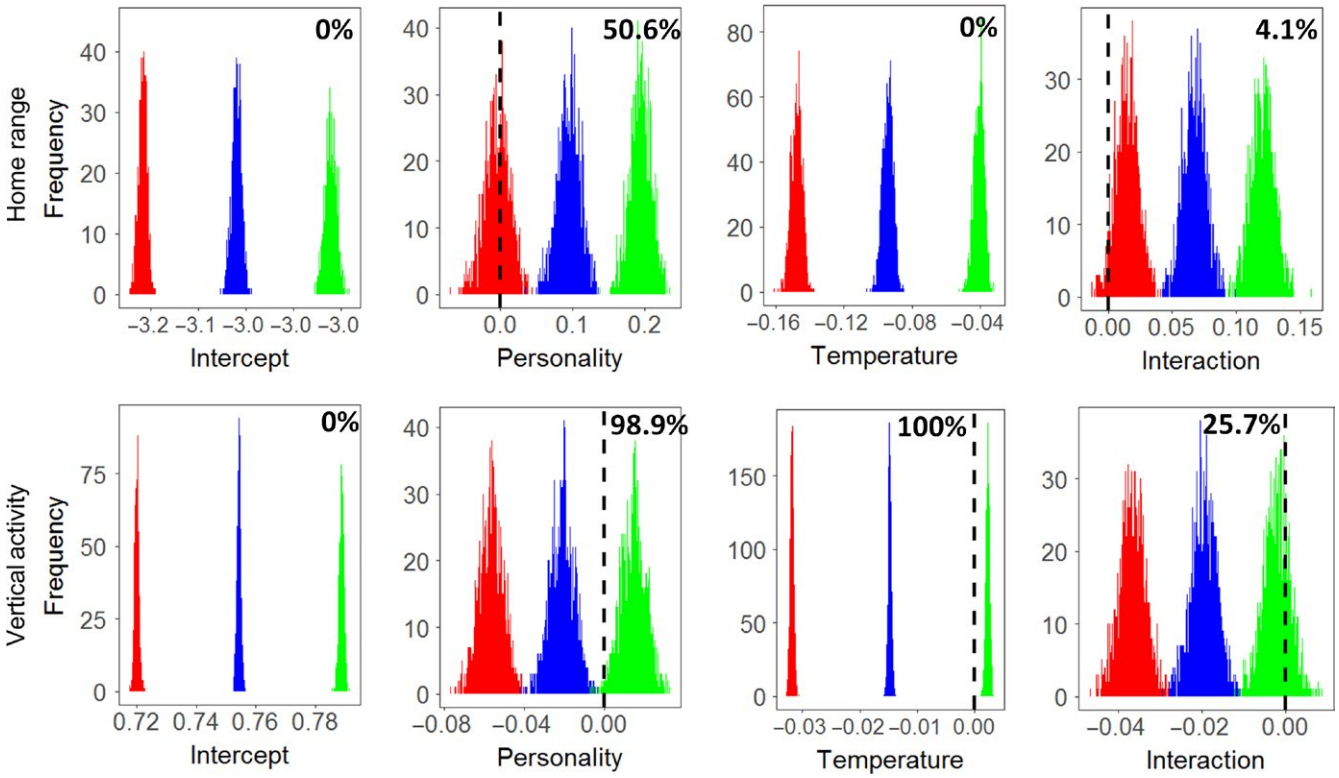

FIGURE 2 Histograms of the point estimates of the mean effect (blue), lower (red) and upper (green) confidence interval (CI) of each fixed effect and intercept as obtained from the 1,000 runs of the mixed-effect models fitted to home range (upper panels) and vertical activity (lower panels) of cod. The percentage of model runs that yielded a CI interval including the zero (dashed line) for any of the effect is shown. An effect was considered significant when <5% of the runs resulted in CI including the zero

model with individual random slopes did not converge. Including an autocorrelation structure reduced the model's AIC by 1,760 units. PC proactivity did not affect mean depth and was removed from the model. Surface temperature had a negative effect on depth, that is, warmer waters resulted in deeper positions and explained 22% of the total variance (Table 2, Supporting Information Table S3). The GAMM model revealed that the relationship was not linear, and predicted that cod occupied deep waters at warm temperatures, shallower waters at mild temperatures and deeper waters again at low temperatures (Figure 4). Interestingly, although deep waters were used at both very warm and very cold waters, the variability in depth use was much higher at cold waters.

4 | DISCUSSION

By combining standard behavioural assays in the laboratory and high-resolution tracking of wild fish in their natural environment, we resolve how personality relates to plasticity of space use in the face of varying environmental conditions. Our data show that as the sea temperature warms up, individuals with a reactive personality reduce their home range, whereas more proactive animals tend to maintain, or even increase, their home range. This represents a significant advance in our understanding of the wider ecological consequences of animal personality and the mechanisms that shape the spatial dynamics of animals in nature.

Earlier studies have found a relationship between average levels of behaviour in captivity and average levels of the analogous, or different, behaviours in the wild (Fisher, James, Rodríguez-Muñoz, & Tregenza, 2015; Herborn et al., 2010). In contrast, our results suggest that personality is not a significant predictor of average levels of behaviour in the wild but, instead, it affects how individuals adjust space use when environmental conditions fluctuate. Importantly, our results were obtained using a modelling strategy that specifically accounted for the uncertainty in laboratory assays of personality. It is possible the differences in space use at different temperatures by proactive and reactive fish may be due to the existence of physiological constraints. Indeed, evidence that behavioural, physiological and life-history traits are correlated under a pace of life syndrome (POLS) is gaining ground (Nakayama, Rapp, & Arlinghaus, 2016; Réale et al., 2010). Proactive fish, having larger levels of boldness, activity and aggressiveness, may have a bigger metabolic engine and therefore higher energetic needs (Careau, Thomas, Humphries, & Réale, 2008; Rey, Digka, & MacKenzie, 2015). To satisfy those needs, proactive fish may need a higher amount of food and therefore forage actively on larger spatial scales all year long. Reactive fish, in contrast, may have lower energetic requirements (Careau et al., 2008) and thus they might slow down and use a smaller activity space in summer, when food is more abundant (Kobler, Klefoth, Mehner, & Arlinghaus, 2009). Alternatively, it might be possible that the differences in movement behaviour by the different personality

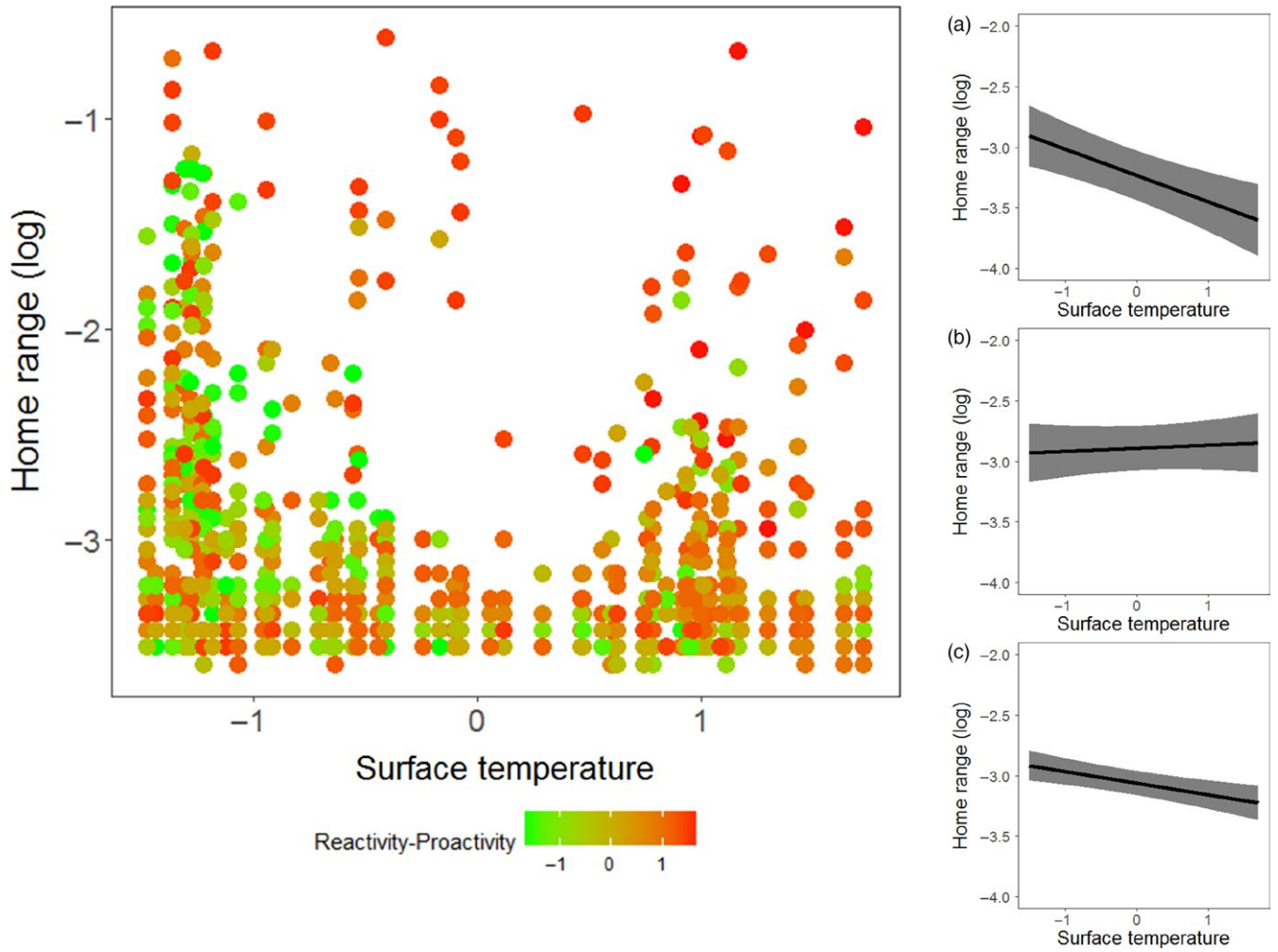

FIGURE 3 Relationship between home range of cod in the wild and surface temperature as a function of fish proactivity (colour of the dots; a). Surface temperature is on a standardized scale, which corresponds to the range 3.5–22.6 degree Celsius. The three subplots represent the mean and 95% confidence interval of the relationship between these two variables for three levels of proactivity (centred and scaled): highly reactive (PC proactivity = −1.7) (b), intermediate (PC proactivity = 0) (c) and highly proactive (PC proactivity = 1.7) (d), as predicted from a linear mixed-effects model run with the mean values of personality for each fish

types during summer might be due to correlated differences in the dietary specialization. Indeed, in burbot *Lota lota*, a freshwater gadoid fish, interindividual differences in movement behaviour were explained by the interaction between trophic niche and prey reliance (Harrison et al., 2017). Finally, reactive and proactive fish may have differences in how they manage uncertainty in their natural environment (Mathot, Wright, Kempenaers, & Dingemanse, 2012). For instance, differences in the variance sensitivity may generate differences in how individual cod respond to changing stimuli from the environment (Mathot et al., 2012). Interestingly, proactive–reactive tendency is thought to be connected with variance sensitivity, with reactive, variance-averse animals showing higher behavioural plasticity, and proactive, variance-prone individuals showing lower behavioural plasticity, as observed in our study (Mathot et al., 2012; Quinn, Cole, Bates, Payne, & Cresswell, 2011). We acknowledge that the proportion of variability in home range explained by the combined effect of sea temperature and personality is low, which will hinder the ability to predict space use based on the personality of the individuals. Indeed, multiple alternative biotic (e.g., reproductive state) and abiotic factors (e.g., habitat availability), not considered in our study, may affect space use of animals (Heupel & Simpfendorfer, 2014). Still, the fact that we found a significant relationship between personality, sea temperature and space use represents a notable contribution towards our understanding of animal movements and the ecological significance of animal personality.

We used surface temperature as a proxy of more general environmental conditions, but acknowledge that individuals might not be responding directly to temperature changes, but instead to other correlated abiotic and biotic variables that were not measured by us, such as resource availability (e.g., Kobler et al., 2009), salinity or oxygen concentration (Freitas et al., 2015; Halvorsen, 2013). Strictly speaking, therefore, our study does not describe thermal reaction norms. Note also that we did not observe any personality-dependent depth use (i.e., all fish occupied deeper water with warmer temperatures) meaning that all cod, regardless their personality, tended to avoid summer warm waters. This matches previous observations for

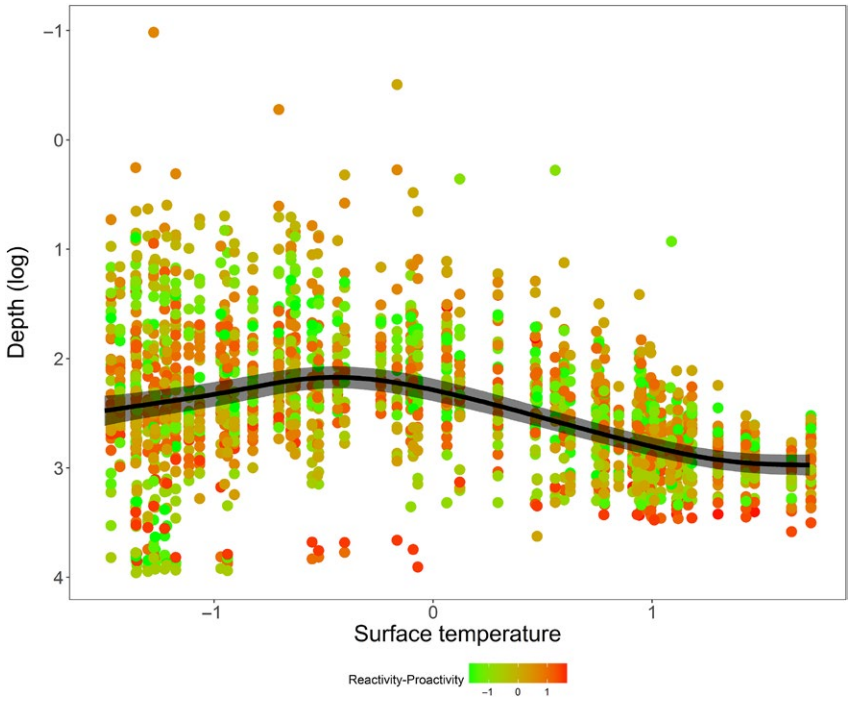

FIGURE 4 Mean and 95% confidence interval of cod weekly mean depth position as a function of surface temperature (standardized scale, which corresponds to the range 3.5–22.6 degrees) as predicted from a generalized additive mixed model (GAMM). Coloured dots represent the original data and are coloured according to the proactivity level of the fish (see legend). Note that the *y*-axis has been reversed to facilitate the interpretation of depth values

the species and suggests a major role of temperature in determining the water column use likely related to physiological constraints of this cold-water species (Freitas et al., 2015).

Although the relationship between personality and vertical activity was found to be significant when mean personality scores per fish were used, it did not stand after accounting for the uncertainty in laboratory assays, and therefore, contrary to our expectations, we conclude that both variables are not correlated. If as explained above, personality is related to the metabolic engine and physiological needs of the individuals, it is possible that our measure of activity in the wild is simply not a good indicator of the internal needs of the fish. Previous studies revealed a complex relationship between vertical activity and sea temperature (Freitas et al., 2015) which may explain why we did not find any linear relationship between these two variables.

The observation that individuals within a population differ in their spatial dynamics to environmental change depending on their personality may have important implications for population demography and dynamics (Spiegel et al., 2015, 2017). In many animals, including Atlantic cod, home range size and dispersal tendency are correlated into a behavioural syndrome (Bowman, Jaeger, & Fahrig, 2002; Villegas-Ríos et al., 2017). We can therefore predict a temperature-personality interactive effect on dispersal from our results, characterized by all personalities moving and dispersing equally at cold temperatures, but only proactive animals tending to disperse at warmer waters. Fjord populations of Atlantic cod are structured into local populations on the scale of tens of km with a strong potential for local adaptations, meaning that population connectivity and associated processes, may depend on individuals with phenotypes more likely to roam over a large area and disperse (Jorde, Knutsen, Espeland, & Stenseth, 2007). A nonrandom distribution of personalities in the pool of dispersers may have important consequences if, for instance, the dispersers do not harbour enough phenotypic plasticity (on behavioural and correlated traits) to adapt to the conditions of the new location (Cote et al., 2010). This mechanism might be especially relevant in the face of future climate scenarios characterized by warmer waters which would favour the dispersal of proactive—but not reactive—animals with implications for many ecological processes including disease spread, habitat selection, species interaction, habitat selection and disease dynamics, and therefore affecting major management-related issues (Spiegel et al., 2015).

To conclude, our study reveals how personality traits can influence movements and responses to changing environments in the wild. Given that animal movement shape ecosystems and relationships among individuals, we emphasize the importance of including personality differences in studies on spatial ecology and evolution, especially in the face of future climate change scenarios.

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AUTHORS' CONTRIBUTIONS

E.M., C.F., D.V.-R. and E.M.O. collected data; D.V.-R., D.R. and E.M.O. performed modelling work and analysed data; D.V.-R. wrote the first

draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.qt8s031 (Villegas-Ríos, Reale, Freitas, Moland, & Olsen, 2018).

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