Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change

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ABSTRACT: Marine ecosystems are exposed to a range of environmental and anthropogenic stressors, including climate change and overexploitation. A promising way towards understanding the impacts of such stressors on community composition is by considering species traits rather than species identity. Here, we describe the spatio-temporal dynamics in fish community traits using >30 yr of species abundance data from the North Sea combined with trait information on body size, life history, growth rate, reproduction and trophic level for demersal fish species in the area. We assessed whether the derived patterns and trends in community-weighted mean traits could be explained by a range of environmental stressors and fishing. Our results revealed strong spatial structuring and long-term changes in the trait composition of North Sea fish, with temporal changes not being uniformly distributed in space. Among the environmental drivers investigated, depth was one of the best predictors, primarily explaining the spatial variation in lifespan, growth rate, trophic level and fecundity. This can be explained by variables that co-vary with depth, e.g. temperature, seasonality, salinity and productivity. Finally, we found only weak relationships between fishing and the spatial variation of traits, suggesting that the spatial trait composition of the community is mostly determined by the environment. Yet, long-term changes in trait composition, primarily in body size, have previously been shown to be affected by size-selective fishing. Our study exemplifies how traits can be used to summarize complex community dynamics and responses to environmental and anthropogenic stressors as well as their usefulness for ecosystem-based management.

KEY WORDS: Marine fish · Traits · Spatio-temporal · Community-weighted mean · North Sea · Community composition · Climate change · Fishing

1. INTRODUCTION

Marine ecosystems are exposed to a range of environmental and anthropogenic stressors, including climate change, habitat alterations and overfishing (Millennium Ecosystem Assessment 2005). Our knowledge on how marine organisms respond to these stressors is advancing (e.g. Link et al. 2010, van Denderen et al. 2014, Poloczanska et al. 2016, Ruppert et al. 2018), yet our ability to predict future changes in marine ecosystems and the services they provide is hindered by the variety of species responses and the

complexity of species interactions (Pörtner et al. 2014). The responses of marine fish communities to stressors, such as climate change and fishing, are typically examined by studying the impacts of stressors targeting individual species, functional groups or other kinds of species aggregates (Halpern & Floeter 2008, Engelhard et al. 2011, Simpson et al. 2011). Other studies have examined changes in community structure using biodiversity metrics, size spectra or mean trophic level (Pauly et al. 1998, Daan et al. 2005, Coll et al. 2010, Wiedmann et al. 2014). Such trait-based approaches are commonly regarded as a way

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forward to understand and predict changes in community structure and function (McGill et al. 2006, Violle et al. 2014). A trait is defined as any characteristic of an organism's phenotype that can be measured at the individual level and can be related to its life history, morphology, physiology, behaviour or phenology (Violle et al. 2007). Together, traits govern an organism's fitness by determining its feeding, growth, survival and reproduction (Litchman et al. 2013). Traits can also shed light on species–environment relationships, since traits largely determine which environments a species is capable of inhabiting and additionally, with which species it interacts and coexists (Verberk et al. 2013). Moreover, traits can be used to understand how species and communities respond to environmental and anthropogenic pressures or to management measures, as having certain traits will make a species more or less vulnerable to change or disturbance (Perry et al. 2005, Mouillot et al. 2013, Coleman et al. 2015). A particular focus in marine trait-based studies has been on the response of fish life history traits to size-selective fishing and climate change. Fish species with a large size, late maturity and long lifespan are the most vulnerable to fishing (Jennings et al. 1998), whereas smaller-sized species that mature early are the first ones to shift their distribution in response to increasing sea temperatures (Perry et al. 2005). Also at the community level, trait-based metrics, such as the community mean size, weight, lifespan or growth rate, have been demonstrated to change over time, thereby revealing structural changes in fish communities in response to fishing (Jennings et al. 1999a, Greenstreet & Rogers 2006, Greenstreet et al. 2012, Coll et al. 2016) and climate change (ter Hofstede & Rijnsdorp 2011, Frainer et al. 2017).

The North Sea fish community is one of the most heavily fished systems worldwide. The overexploitation of large predatory species, such as Atlantic cod *Gadus morhua*, in the 1980s and 1990s is one of the main causes of the observed decrease in the mean size of demersal fish (Greenstreet & Hall 1996, Rice & Gislason 1996, Bianchi et al. 2000, Daan et al. 2005) and of the reduction in the proportional biomass of large fish (known as the large fish indicator, LFI) (Greenstreet et al. 2011, Engelhard et al. 2015). At the same time, large-scale climatic changes in the late 1980s led to increasing water temperatures, enhanced phytoplankton biomass and a shift in zooplankton community composition favouring small, lower trophic level fish species (Reid et al. 2001, Heath 2005, Beaugrand 2009, Kenny et al. 2009), while hampering recruitment of large, higher trophic

level species such as cod (Beaugrand et al. 2003). Besides size and trophic level, changes in other community traits have been reported for the North Sea fish community, such as an increase in the community mean growth rate and a decrease in age and length at maturity, for which trends date back to the 1920s (Jennings et al. 1999a, Greenstreet & Rogers 2006, Greenstreet et al. 2012). In the late 1990s, the European Commission initiated a fishing fleet reduction scheme and lowered the fishing quotas. A recent recovery in the LFI suggests that these management measures are successful (Engelhard et al. 2015), but as climate change continues, increasing water temperatures may counteract this recovery (ter Hofstede & Rijnsdorp 2011, Baudron et al. 2014, Engelhard et al. 2015).

In addition to the temporal changes in fish community composition, the North Sea displays pronounced spatial variation in fish species composition (Daan et al. 1990, Callaway et al. 2002). In general, the shallow southern area (Fig. 1) is dominated by flatfish, and with increasing depth towards the north, roundfish become more abundant (Daan et al. 1990, Callaway et al. 2002). The deep waters of the Norwegian trench harbour yet another community, which is characterized by benthic-pelagic and even boreal-arctic species (Bergstad 1990, Daan et al. 1990). Studies that combined the spatial and temporal dynamics of the community have revealed that temporal changes are heterogeneous in space (Daan et al. 2005, Greenstreet & Rogers 2006, Engelhard et al. 2015, Marshall et al. 2016, Frelat et al. 2017), which is often disregarded by management that treats the community as spatially homogeneous (Marshall et al. 2016).

In this study, we used long-term, spatially resolved survey data on fish species abundances and an extensive trait dataset to expand the current knowledge on fish community changes in the North Sea. The primary objectives of our study were (1) to describe how multiple fish community traits are distributed in both time and space, and (2) to identify the underlying responses of these traits to a range of environmental and anthropogenic stressors. We accomplished this by examining and comparing the temporal trends, spatial patterns and spatio-temporal dynamics across multiple fish community traits, including body size, life history, growth rate, reproduction and trophic level. We then assessed if any changes in the trait composition of the community have occurred in response to fishing, temperature or other environmental variables not thoroughly studied before.

Fig. 1. Bathymetry and topography of the North Sea. Large dashes form the 50 m depth contour, small dashes the 100 m depth contour and mixed dashes the 200 m depth contour. Bathymetry data from Amante & Eakins (2009)

2. MATERIALS AND METHODS

2.1. Data collection and treatment

2.1.1. Survey data

Fish community data were collected from the North Sea International Bottom Trawl Survey (NS-IBTS) that has been running during the first quarter of the year (January–March) with standardized gear since 1983 (ICES 2015). Data for the years 1983 to 2014 were extracted from the publically accessible database hosted by ICES (<https://datras.ices.dk>). Sampling is based on a stratification of 1° longitude by 0.5° latitude. The data consisted of catch per unit of effort, representing an indirect measure of species abundance in number of individuals caught per hour of fishing. The fishing gear used in the survey is the GOV trawl ('chalut à grande ouverture verticale'). Only hauls between 25 and 35 min and deeper than 20 m were kept to ensure similar sampling efforts and to remove strictly coastal species. In addition, we included only survey grid cells that were sampled in at least 80 % of years to account for any kind of temporal

variation between years, e.g. weather conditions (Hiddink & ter Hofstede 2008). This resulted in 9552 unique hauls and 147 survey grid cells. Subsequently, pelagic fish were excluded, because the sampling does not adequately represent the abundance of pelagic fish relative to demersal. In addition, Heessen et al. (2015) were consulted to detect misidentifications or uncertainties in data reporting. Consequently, several taxa were either removed or combined at higher taxonomic levels (Table S1 in the Supplement at www.int-res.com/articles/suppl/m610p205_supp.pdf). Records of taxa at the genus or family level were set at the species level when only 1 species from this genus or family was present in the dataset. Other records of taxa that were only reported at the family or genus level and for which no grouping was done (Table S1) were removed from the dataset. Finally, to ensure that the data represented resident rather than occasional and infrequent taxa, taxa present in less than 7 out of 32 yr were removed, leading to the exclusion of 58 out of 136 taxa that corresponded to only 0.002 % of the total abundance. The resulting list consisted of 78 demersal fish taxa (henceforth referred to as species) that were retained in the analysis (Table S2 in the Supplement).

In order not to give a disproportionate weight to small and abundant species compared to larger and less abundant species, we converted the species abundance information to biomass. To obtain biomass estimates per species (in g), the number of individuals per length class and haul were converted from length (L) to weight (W) using the equation $W = aL^b$ where a and b are species-specific parameters. Parameter values were obtained from Fung et al. (2012), who calculated values from length-weight data collected during the NS-IBTS. Missing parameter values were extracted from Coull et al. (1989), Robinson et al. (2010), Verreycken et al. (2011) and Froese & Pauly (2017). The derived biomass of each species was averaged per year, per survey grid cell and per combination of year and survey grid cell.

2.1.2. Trait data

Eight traits representing body size (length), life history and reproduction (age and length at maturity, lifespan, fecundity, offspring size), growth (Von Bertalanffy growth coefficient K) and position in the

Table 1. Description and unit of the 8 fish traits chosen to characterize fish species in the North Sea

Trait	Unit	Description
Length	cm	Average length measured in survey; represents body size
Trophic level	No dimension	Calculated based on empirical observations of diet composition; represents position in the food web
Length at maturity	cm	Length at which 50 % of the population becomes mature; related to life history strategy, energy allocation and growth
Age at maturity	yr	Age at which 50 % of the population becomes mature; related to life history strategy, generation time and growth
Lifespan	yr	Maximum age; related to generation time and life history strategy
Growth coefficient K	yr ⁻¹	Rate at which maximum theoretical length is attained; based on Von Bertalanffy growth equation; proxy for individual growth rate
Fecundity	No. eggs yr ⁻¹	Mean number of eggs spawned female ⁻¹ yr ⁻¹ ; related to reproduction strategy and energy allocation
Offspring size	mm	Diameter size of eggs, length of egg case or body length of offspring; related to reproduction strategy and investment in offspring

food web (trophic level) were included (Table 1). These traits represent different morphological, physiological and life-history aspects of fish ecology, primarily in terms of reproduction, feeding and growth that are known to be responsive to environmental and/or anthropogenic stressors (Pauly et al. 1998, Jørgensen et al. 2007). The growth coefficient K (yr⁻¹) was chosen as a proxy for individual growth rate. It is a parameter of the Von Bertalanffy growth equation (VBGE) that expresses body length as a function of time, K and the theoretical maximum body length (length infinity; L_{∞}). The growth coefficient K determines how fast an individual approaches L_{∞} . In addition, an alternative growth parameter was calculated that is independent of size, namely the growth rate ω , proposed by Gallucci & Quinn (1979). It is calculated by multiplying K and L_{∞} , which is the initial slope of the VBGE, and thus primarily represents juvenile growth rate in cm yr⁻¹. The mean body length per species was calculated using body length measurements from the survey, which were averaged over all hauls conducted in the survey and weighted by the biomass of each length class. Other trait values originated from primary literature and FishBase (Froese & Pauly 2017). When available, values from the North Sea or adjacent regions were prioritized. When unavailable, trait values were inferred from closely related species present in the dataset. In cases where multiple trait values were reported, an average value was calculated. In addition, we used 1 trait value per species, despite the potential importance of intraspecific variation in traits (Alofs 2016, Ward et al. 2016). Trait values were also fixed throughout the study period, even though temporal changes in life history

traits have been demonstrated in North Sea fish (Jørgensen et al. 2007). A species list with trait values and references is provided in Table S2 in the Supplement.

2.1.3. Environmental and fishing effort data

To study potential anthropogenic and environmental drivers of fish community traits in space and time, data on fishing effort and 6 environmental variables were collected per grid cell and year. Monthly sea bottom temperatures (°C) and sea bottom salinities were extracted from Núñez-Riboni & Akimova (2015). Average temperature and salinity in the first quarter were calculated per year and survey grid cell. As a metric of seasonality, the difference between mean winter (January–March) and summer (July–September) bottom temperatures per grid cell was used. Depth was taken as the mean sampling depth per survey grid cell. As a proxy for phytoplankton biomass during the first quarter, the phytoplankton colour index (PCI) was used, which is a measure of greenness in water samples from the continuous plankton recorder (CPR) (SAHFOS 2016). Since the sampling scheme of the CPR consists of transects not covering the entire area, missing values were interpolated using a generalized additive model (GAM). Thereafter, a mean PCI was calculated per year and per survey grid cell. Seabed substrates were available through the European Marine Observation Data network Seabed Habitats project (EMODnet 2015). For each survey grid cell, the number of different substrates present was summed to represent substrate richness. Finally, 2 datasets of

international fishing effort in the North Sea for the periods 1990–1995 (Jennings et al. 1999b) and 2003–2012 (Engelhard et al. 2015) were used to calculate a mean beam trawl effort and otter trawl effort per survey grid cell. Trawl effort (in number of hours fishing) was estimated based on fishermen logbook data submitted to national administrations and the European Commission (Jennings et al. 1999b, Engelhard et al. 2015).

2.2. Data analysis

2.2.1. Community-weighted mean of traits

The community-weighted mean (CWM) of a trait is the average trait value in the community. It is based on the mass-ratio hypothesis, stating that dominant species are expected to have the largest impact on the structure and functioning of communities (Grime 1998, Garnier et al. 2004). When a CWM trait changes in either time or space, it typically indicates that the community has shifted in its structure, often as a response to changes in the environment or sudden disturbances (Mouillot et al. 2013). CWM traits are thus useful detectors of changes in structure by summarizing the overall response of a community based on the underlying species dynamics (Ricotta & Moretti 2011). The majority of traits in our dataset showed a skewed distribution. Consequently, we calculated the CWMs of each trait as a geometric mean weighted by species biomass:

$$\text{CWM} = \left(\prod_{i=1}^n \text{trait}_i^{p_i} \right)^{1/\sum_{i=1}^n p_i} \quad (1)$$

where n is the number of species, trait_i is the trait value of species i , and p_i is the relative biomass of species i . CWMs per trait were calculated according to 3 different spatial and temporal aggregations. First, to generate a time series of CWMs for each trait, CWMs were calculated based on spatially averaged species biomasses per year (i.e. averaged over all hauls per survey grid cell, and then averaged over all survey grid cells). Second, to get CWMs for each survey grid cell, CWMs were calculated using species biomasses averaged over all years. Finally, CWMs were calculated for each year in each survey grid cell. This last step allowed for examining spatio-temporal trends in CWM traits by constructing linear regression models for each time series of CWM traits in each survey grid cell using year as a predictor. The slope of the models indicated if there was a directional positive or negative change in the CWM trait

over time in the respective survey grid cell. Note that strong non-linear dynamics will give slopes close to 0, thereby indicating that over time no clear one-directional change has taken place. Finally, principal component analyses (PCAs) were used to assess the similarities in temporal trends, spatial patterns and spatio-temporal trends between the traits.

2.2.2. Assessing drivers of trait variation in space and time

Using a statistical modelling approach, we then assessed the degree to which the variation in the derived time series and spatial patterns of CWM traits could be explained by the environment and fishing effort. The spatio-temporal CWM traits were not further assessed for their drivers. We used GAMs and generalized additive mixed models (GAMMs), as these classes of models allow for non-linear relationships between response and predictor variables (Wood 2006). The basis dimension (k) for the smooth terms was restricted to 3 to limit the flexibility of model fitting and to reduce the risk of overfitting (Nogués-Bravo 2009). The temporal trends and spatial trait patterns were modelled separately, and the procedure for each is described below.

The time series of the 8 traits, consisting of 32 yr (1983–2014), were the response variables for the temporal models, i.e. 1 model for each trait. As predictor variables, we included sea bottom temperature, sea bottom salinity, seasonality in sea bottom temperature and the PCI as annual averages over all survey grid cells. All variables had a variance inflation factor (VIF) <10, deemed as an acceptable degree of collinearity between predictors (Borcard et al. 2011). Because of the short time series of beam and otter trawling effort (16 yr), these variables were not included. For each time series of traits, a GAM that included all 4 predictor variables was constructed as follows:

$$\text{CWM trait} \sim \beta + s(\text{Temperature}) + s(\text{Salinity}) + s(\text{Seasonality}) + s(\text{PCI}) + \varepsilon \quad (2)$$

where β is the intercept, s is a smooth function, and ε is the normally distributed error. We then tested for temporal autocorrelation of the model residuals. If present, a first-order autoregressive correlation structure (corAR1) was added to the model to account for temporal autocorrelation (Zuur et al. 2009). Since GAMs do not readily allow for correlation structures to be added, we therefore used a GAMM instead, including the corAR1 correlation structure with year as a

factor. A dummy variable was set as a random effect in order for the model to operate. Since temporal autocorrelation was detected for the model residuals of trophic level and the growth coefficient K , GAMMs were only constructed for these 2 traits.

The spatial models had the CWM traits per survey grid cell as response variables. The predictor variables were depth, sea bottom temperature, sea bottom salinity, seasonality in sea bottom temperature, the PCI, substrate richness, beam trawl effort and otter trawl effort. All variables were averaged over years for each survey grid cell. Beam and otter trawling effort data contained many small values, as well as 0s. Therefore, these data were $\log_{10}$ -transformed after having added a value of 1. The VIF of all predictors was <10 , indicating an acceptable degree of collinearity between variables (Borcard et al. 2011). A number of survey grid cells (22 out of 147) were excluded from the analysis, because they lacked data on substrate richness and/or contained low values of salinity (coastal areas) that, when included in the analysis, had a disproportionate influence on the modelled relationships. For each trait, a GAM was constructed that included all possible predictor variables:

$$\begin{aligned} \text{CWM trait} \sim & \beta + s(\text{Depth}) + s(\text{Temperature}) \\ & + s(\text{Salinity}) + s(\text{Seasonality}) + s(\text{PCI}) \\ & + s(\text{Substrate richness}) + s(\text{Bottom trawl effort}) \\ & + s(\text{Otter trawl effort}) + \varepsilon \end{aligned} \quad (3)$$

where β is the intercept, s is a smooth function, and ε is the normally distributed error. When testing for spatial autocorrelation of the model residuals using Moran's test (R package 'spdep'; Bivand et al. 2013, Bivand & Piras 2015), all 8 models showed spatial autocorrelation. Therefore, a GAMM was constructed for each trait instead, including all predictor variables as fixed effects, a dummy variable as a random effect and a Gaussian spatial correlation structure using the longitude and latitude of the survey grid cells. Six out of 8 spatial trait patterns (length, age and length at maturity, lifespan, fecundity and offspring size) were $\log_{10}$ -transformed to approach normally distributed residuals.

To assess the importance of the predictors of the temporal and spatial models, the relative variable importance (RVI) was computed for each predictor in each model. The RVI ranges from 0 to 1 and represents the probability of a variable ending up in the best fitting model. First, a set of models (with 1 to 4 predictors) was generated based on combinations of all predictor variables. The RVI for each predictor was then calculated as the sum of Akaike weights of the generated models that included the variable of

interest (Burnham & Anderson 2002). Model fitting and analysis were conducted using the 'mgcv' (Wood 2011) and 'MuMIn' (Barton 2016) packages in the R software, version 3.4.0 (R Core Team 2017).

3. RESULTS

3.1. Spatio-temporal patterns and trends in traits

The CWMs of length, age and length at maturity, lifespan and fecundity demonstrated similar decreasing temporal trends (Fig. 2i) until the early 1990s, after which length, length at maturity and fecundity levelled off (Figs 2a,b,g) and age at maturity and lifespan increased again (Figs 2c,d). Trophic level decreased slightly but constantly (Fig. 2f), whereas the growth coefficient K increased during the first 2 decades and fluctuated thereafter (Fig. 2e). Juvenile growth rate showed an opposite trend compared to K with a decrease in CWM during the first half of the study period and a slight increase again thereafter (Fig. S1 in the Supplement), hence similar to the trend of age at maturity. No temporal trend was observed for offspring size, which primarily showed strong inter-annual fluctuations throughout the period (Fig. 2h).

Similar spatial patterns were found for length, length at maturity and age at maturity (Fig. 3i), with high values along the Norwegian trench and the south-western British coast, as well as a small area of intermediate values in the central North Sea (Figs. 3a–c). High values were observed in the same areas for lifespan, although with a more pronounced west-to-east gradient of increase in the central North Sea (Fig. 3d). Fecundity also showed high values along the Norwegian trench, whereas its lowest values were observed in the south-western North Sea around the Wash and Thames estuaries (Fig. 3g). Offspring size followed an opposite pattern, with low values along the Norwegian trench and high values in the south-western North Sea (Fig. 3h). A distinct pattern was observed for the growth coefficient K , with peak values in the central North Sea (Fig. 3e). Juvenile growth rate showed a similar spatial pattern, but with additional high values along the Norwegian trench (Fig. S1). Trophic level generally followed a south-east to north-west gradient of increase, with high values along the Norwegian trench and in the south-western North Sea (Fig. 3f).

The spatio-temporal trait patterns revealed predominantly significant negative temporal trends for the majority of traits (length, length and age at maturity, trophic level and fecundity), except for the

Fig. 2. Time series of the community-weighted mean (CWM) traits between 1983 and 2014, and principal component analysis of the 8 time series. Trend of the CWMs of (a) length, (b) length at maturity, (c) age at maturity, (d) lifespan, (e) growth coefficient K , (f) trophic level, (g) fecundity and (h) offspring size. Grey line with shaded area is a loess-smoother with confidence interval to visualize the main trend. (i) Ordination plot demonstrating the relationships between the 8 time series. First and second principal components (PC1, PC2) explained 58 and 18% of the variation, respectively. A50: age at maturity; L50: length at maturity; Lifesp: lifespan; Lngt: length; Fec: fecundity

growth coefficient K , which mostly showed positive trends over time (Fig. 4). Most significant negative trends were found in the central North Sea, whereas most insignificant trends were located in the northern or eastern parts. Age and length at maturity and lifespan had several survey grid cells with significant increasing trends, particularly in the northern North Sea (Fig. 4b–d). Likewise, juvenile growth rate showed increasing trends in the north, but also decreasing trends in the south (Fig. S1). Length, trophic level, length at maturity, growth coefficient K and fecundity had the highest number of survey grid cells

with significant temporal trends in CWM traits. Relatively few were detected for offspring size, lifespan and age at maturity.

3.2. Drivers of fish community traits in time and space

The temporal models for length, and age and length at maturity demonstrated the highest degree of explained deviance (R^2) of all traits (Table 2). To a lesser extent, fecundity and lifespan were also well ex-

Fig. 3. Spatial distribution of the community-weighted mean (CWM) traits in 147 survey grid cells and principal component analysis of the 8 spatial trait patterns. Spatial patterns of the CWMs of (a) length, (b) length at maturity, (c) age at maturity, (d) lifespan, (e) growth coefficient K , (f) trophic level, (g) fecundity and (h) offspring size ($\log_{10}$ -transformed). (i) Ordination plot demonstrating the relationships between the 8 spatial trait patterns. First and second principal components (PC1, PC2) explained 46 and 24% of the variation, respectively. Offsp. size: offspring size; A50: age at maturity; L50: length at maturity

plained by the models. The total explained deviance was the lowest for the growth coefficient K , trophic level and offspring size. This indicates that their temporal variation was poorly explained by the environmental variables included and that their RVI scores should be interpreted with caution. The temporal trends in length, age and length at maturity, lifespan and fecundity were best explained by the PCI, as indi-

cated by RVI scores >0.8 (Table 2). These traits showed negative non-linear relationships with the PCI, indicating declining values with increasing PCI (Fig. S2 in the Supplement). Winter bottom temperature was another important predictor for length, and age and length at maturity ($\text{RVI} > 0.9$), where years with high CWMs of these traits generally corresponded to lower temperatures (Fig. S2). Lifespan and

Fig. 4. Slopes of the temporal linear regressions per survey grid cell performed on the community-weighted mean (CWM) traits, and principal component analysis of the slopes of the linear regressions. Linear regressions were performed on the time series of the CWM traits per survey grid cell to indicate spatio-temporal trait patterns. The slopes of the regressions are plotted for (a) length, (b) length at maturity, (c) age at maturity, (d) lifespan, (e) growth coefficient K , (f) trophic level, (g) fecundity and (h) offspring size. Red colours indicate a negative slope and blue colours indicate a positive slope. Circles indicate a significant temporal trend (small: $p < 0.05$, medium: $p < 0.01$, large: $p < 0.001$). (i) Ordination plot demonstrating the relationships between the slopes of the linear regressions performed for each CWM trait. First and second principal components (PC1, PC2) explained 49 and 18% of the variation, respectively. Lifesp.: lifespan; A50: age at maturity; L50: length at maturity

fecundity responded non-linearly to temperature (Fig. S2), which was also an important predictor of these traits (RVI = 0.65). Salinity obtained high RVI scores for age and length at maturity, lifespan and the growth coefficient K , where years with higher salinity corresponded to higher CWMs of these traits (Fig. S2).

Although the RVI of salinity was relatively high for fecundity (RVI = 0.65), no clear positive or negative relationship was detected (Fig. S2). Most traits did not reveal any strong relationships with seasonality in temperature (Table 2), except for a weak negative relationship with lifespan and fecundity (RVI = 0.42).

Table 2. Relative variable importance (RVI) values of the environmental predictors for each modelled time series of community mean traits. RVI ≥ 0.5 shown in **bold**. The bottom row presents the explained deviance, expressed as adjusted R^2 , of the full model of each trait (i.e. model including all predictors). The weighted mean RVI in the last column is the average RVI for each predictor over all modelled traits weighted by the R^2 -values of the full models. The environmental predictors were the phytoplankton colour index (PCI), winter bottom temperature and salinity, and seasonality (difference between summer and winter bottom temperature). For trophic level and growth coefficient K , generalized additive mixed models were performed to correct for temporal autocorrelation. The other traits without temporal autocorrelation were modelled using generalized additive models

Predictor	RVI								Weighted mean RVI
Traits:	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size	
PCI	1.00	1.00	1.00	0.88	0.04	0.48	0.88	0.23	0.97
Temperature	0.90	0.99	0.92	0.65	0.04	0.39	0.65	0.23	0.86
Salinity	0.22	0.76	0.95	0.65	0.73	0.15	0.65	0.22	0.65
Seasonality	0.19	0.16	0.26	0.42	0.05	0.08	0.42	0.31	0.25
R^2 full model	0.60	0.78	0.57	0.42	0.01	0.06	0.50	0.01	

The spatial models of trophic level, lifespan, fecundity and the growth coefficient K had the highest explained deviance of all traits (Table 3). The spatial patterns in offspring size, length, and age and length at maturity were only marginally explained. Therefore, their RVI scores should be interpreted with caution. Depth was an important spatial predictor for trophic level, fecundity, the growth coefficient K and lifespan (RVI > 0.8 ; Table 3). The first 3 of these traits increased with depth, although trophic level and the growth coefficient K levelled off at around 100 m. Inversely, lifespan decreased until approximately 100 m depth (Fig. S3 in the Supplement). Seasonality in temperature was an important predictor for

explaining the spatial trait patterns of lifespan and trophic level (RVI > 0.7). Lifespan decreased with seasonality, whereas trophic level showed a non-linear positive relationship with seasonality (Fig. S3). The spatial patterns of trophic level and fecundity were well explained by winter bottom temperature (RVI > 0.6), where the CWM of these traits increased with temperature (Fig. S3). Length and length at maturity were best explained by winter bottom temperature, showing positive relationships (Fig. S3), but note the low explained deviance of the models for these traits. Winter bottom salinity was of minor importance for all traits, except trophic level (RVI = 0.67) which decreased non-linearly with increasing

Table 3. Relative variable importance (RVI) of the environmental and fishing predictors for each modelled spatial pattern of community mean traits. RVI ≥ 0.5 is in **bold**. The bottom row presents the explained deviance, expressed as adjusted R^2 , of the full model of each trait (i.e. model including all predictors). The weighted mean RVI in the last column is the average RVI for each predictor over all modelled traits weighted by the R^2 -values of the full models. The predictor variables were depth, seasonality (difference between summer and winter bottom temperature), winter bottom temperature and salinity, phytoplankton colour index (PCI), substrate richness, otter trawl effort and beam trawl effort. All models were generalized additive mixed models

Predictor	RVI								Weighted mean RVI
Traits:	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size	
Depth	0.14	0.36	0.31	0.98	0.99	0.81	0.99	0.25	0.88
Temperature	0.84	0.58	0.30	0.29	0.24	0.85	0.68	0.12	0.51
Seasonality	0.12	0.16	0.48	0.96	0.06	0.71	0.10	0.21	0.46
Otter trawl effort	0.11	0.10	0.11	0.11	0.97	0.23	0.08	0.24	0.32
PCI	0.17	0.11	0.13	0.24	0.99	0.03	0.09	0.20	0.31
Salinity	0.18	0.19	0.26	0.08	0.12	0.67	0.28	0.14	0.30
Substrate richness	0.13	0.18	0.40	0.09	0.05	0.27	0.09	0.24	0.14
Beam trawl effort	0.19	0.10	0.10	0.15	0.09	0.03	0.08	0.14	0.09
R^2 full model	0.02	0.05	0.05	0.56	0.51	0.63	0.52	0.09	

salinity. The PCI was only an important predictor for the growth coefficient K ($RVI = 0.99$), where areas with higher PCI were associated with higher growth coefficients K . Neither substrate richness nor beam and otter trawl effort statistically explained a great deal of spatial variation in CWM traits, except for the growth coefficient K ($RVI = 0.97$), which had lower values in areas with higher otter trawl effort (Fig. S3).

4. DISCUSSION

4.1. Trait patterns in time and space

The long-term changes observed across traits indicate a pronounced change in fish community composition in the North Sea. More specifically, the community shifted from large, slow-growing, late-maturing, long-lived and highly fecund species feeding at high trophic levels towards smaller, faster-growing, earlier-maturing, shorter-living and less fecund species that feed at a slightly lower trophic level. These findings largely correspond to previous studies where the identified temporal changes in individual community mean traits of North Sea fish were attributed either to fishing, increasing sea temperatures or a combination of both (Jennings et al. 1998, 1999a, 2002, Greenstreet et al. 1999, 2012, Rogers & Ellis 2000, Nicholson & Jennings 2004, Piet & Jennings 2005, Engelhard et al. 2011, ter Hofstede & Rijnsdorp 2011).

Interestingly, the temporal changes in CWM traits were not uniformly distributed in space, but differed markedly between areas (Fig. 4). The majority of significant trends were located in the central North Sea, suggesting that the spatially averaged trends in traits (Fig. 2) are largely driven by changes in this area. Similarly, previous studies on the LFI demonstrated pronounced spatial variation and significant declines, primarily in the central North Sea (Engelhard et al. 2015, Marshall et al. 2016). These declines were partially explained by the northward shift of some large-sized species with high biomass, such as Atlantic cod, likely in response to both fishing and climate change (Engelhard et al. 2014, 2015). Since cod matures at an intermediate age and at a large size, its northward shift has likely also contributed to the community-wide changes in age and length at maturity presented in this study.

In addition to the marked temporal changes in traits, our results demonstrate considerable spatial structuring in trait composition throughout the area, following known spatial patterns in species composition in the North Sea (Daan et al. 1990, Callaway et

al. 2002). In general, sub-communities along the Norwegian trench were primarily composed of large, late-maturing, long-living and slow-growing species feeding at high trophic levels, while sub-communities in the southern parts of the area were dominated by smaller, faster-growing species feeding on lower trophic levels. While previous studies suggest a marked south-to-north gradient in fish biodiversity and species composition in the North Sea (Callaway et al. 2002, Dencker et al. 2017), the spatial patterns observed for individual traits did not show such a pronounced latitudinal gradient. Hence, areas with different richness and species composition (Daan et al. 1990, Callaway et al. 2002, Dencker et al. 2017) can comprise communities that are on average rather similar in terms of traits. Conversely, areas with similar biodiversity may have different trait compositions, thereby stressing the importance of studying the underlying trait patterns that make up a community (Weigel et al. 2016). For instance, sub-communities along the Norwegian trench are rather similar in trait structure compared to sub-communities around the Thames and Wash estuaries on the British coast. However, the similarity between these geographically distant areas is primarily visible in terms of size, length/age at maturation, lifespan and trophic level, while fecundity and offspring size show opposite patterns. This indicates that large-sized, higher trophic level species are abundant in both areas, while in the Thames and Wash estuaries these species are characterized by lower fecundity and larger offspring size compared to those in the Norwegian trench. This can largely be explained by differences in species composition, where in the vicinity of the Thames and Wash estuaries large elasmobranchs, that invest in only a few but large and high-quality eggs and offspring, are more abundant (Ellis et al. 2005, Sguotti et al. 2016).

4.2. Drivers of trait variation in time

The majority of temporal changes in CWM traits were explained by the PCI, winter bottom temperature and winter bottom salinity (ranked in order of decreasing importance). The pronounced increases in temperature and the PCI (Fig. S4 in the Supplement) were caused by large-scale changes in ocean-atmospheric forcing in the late 1980s leading to an increased flow of warm, nutrient-rich Atlantic waters into the northern North Sea, and subsequently to a higher phytoplankton biomass and a switch in the community composition of zooplankton

to smaller-sized species (Reid et al. 1998, 2001, Beaugrand 2009). Beaugrand et al. (2003) showed that this shift in zooplankton composition was a major cause of the low survival of larval and juvenile cod. Inversely, the recruitment of flatfish increased after the regime shift and was linked to changes in salinity and temperature (Beaugrand 2004, van Hal et al. 2010, Sparrevohn et al. 2013). The higher phytoplankton biomass and resulting increase in zooplankton production also led to an increase in small, planktivorous fish (Heath 2005). Hence, temperature and PCI have likely influenced the CWM traits indirectly through bottom-up processes, where higher temperature and phytoplankton biomass have favoured smaller and faster-growing species, leading to a decrease in the CWMs of length, age and length at maturity and an increase in the growth coefficient K . This is in accordance with previous studies showing community changes towards smaller body length during warm periods (ter Hofstede & Rijnsdorp 2011), largely resulting from an increase in smaller-sized and faster-growing Lusitanian species, like Mediterranean sculdbass *Arnoglossus laterna* and grey gurnard *Eutrigla gurnardus* and a decline in large-sized boreal species, like cod and Atlantic wolffish *Anarhichas lupus* (Beare et al. 2004, Engelhard et al. 2011). The opposite abundance trends of these groups of species have been primarily related to environmental effects acting on recruitment (Beaugrand et al. 2003, Beaugrand 2004, Rijnsdorp et al. 2009) and/or immigration/emigration processes (Perry et al. 2005, Engelhard et al. 2011). In particular, the distribution of Lusitanian species is expanding in the North Sea while large boreal species are expected to move further North in response to warming due to physiological constraints on their metabolism (Rijnsdorp et al. 2009, ter Hofstede et al. 2010, Engelhard et al. 2011).

Although not assessed in this study, the high fishing pressure in the North Sea and its decline since the early 2000s has also influenced the long-term changes in the species and trait composition of the North Sea fish community (Jennings et al. 1999a, Rogers & Ellis 2000, Wolff 2000, Daan et al. 2005, Bennema & Rijnsdorp 2015, Engelhard et al. 2015). The direct effect of fishing has been the removal of primarily large species and individuals. Indirectly, this has led to a release of predation pressure on smaller prey species and a subsequent increase in their biomass. Both effects have been argued to underlie the overall decrease in the LFI (Greenstreet et al. 2011, Engelhard et al. 2015), and hence, likely also to the decrease in the CWM of length observed

in this study. Because of the correlations in species traits, the decrease in the CWM of age and length at maturity and lifespan during the first part of the study period, as well as the increase in the CWM of the growth coefficient K could partially be understood in light of the direct and indirect effects of fishing (Jennings et al. 1998, 1999a, Greenstreet et al. 2012).

4.3. Drivers of trait variation in space

Out of the environmental drivers investigated, depth was one of the best predictors explaining the spatial variation in traits, including lifespan, the growth coefficient K , trophic level and fecundity. Depth is an important determinant of fish species distributions and community structure in the North Sea (Callaway et al. 2002, Dulvy et al. 2008, Fraser et al. 2008, Reiss et al. 2010). Similarly, studies from other regions have reported such trait–depth dependency (Macpherson & Duarte 1991, Smith & Brown 2002, Drazen & Haedrich 2012, Fernandez-Arcaya et al. 2016). The mechanistic understanding for why depth proves a good predictor is likely related to variables of more direct influence that co-vary with depth, e.g. temperature, seasonality, salinity and productivity (Fig. S5 in the Supplement). Indeed, none of the spatial trait patterns, except for offspring size, were best explained by depth alone, but always in combination with some of these variables (Table S3 in the Supplement). Other depth-related factors not accounted for in this study (e.g. light, wind stress and oxygen concentration) could also be of importance (Mindel et al. 2016) and merit future attention.

Winter bottom temperature was positively related to the spatial patterns of trophic level, length and fecundity. One could have expected the opposite, since colder temperatures have generally been shown to favour larger boreal species compared to smaller Lusitanian species (Engelhard et al. 2011, ter Hofstede & Rijnsdorp 2011). This discrepancy can largely be explained by high biomasses of predatory gadoids with high fecundity, e.g. cod and haddock *Melanogrammus aeglefinus*, particularly in the deeper northern North Sea, where during winter the bottom temperatures are considerably warmer compared to the shallow southern area (Fig. S5). In summer, however, the temperature pattern in the North Sea is reversed, with the warmest waters located in the shallow south. Hence, investigating potential seasonal shifts in trait distributions should merit attention in future studies.

Seasonality in bottom temperature was identified as one of the other key drivers explaining the spatial trait patterns. Seasonality generally decreases with depth because of stratification and less mixing of the water column in deeper waters. Hence, the deepest parts of the northern North Sea show temperature differences between summer and winter close to 0, whereas they reach $>10^{\circ}\text{C}$ in the shallow southern and eastern parts (Fig. S5). Seasonal environments favour small, fast-growing and short-lived species, because of their capability to quickly respond to environmental changes or disturbances (Winemiller & Rose 1992, Mims et al. 2010, Pecuchet et al. 2017). Contrary to these expectations, the spatial patterns in lifespan demonstrated predominately high values in the shallow, southern North Sea (Fig. 3d), illustrated by a negative relationship between lifespan and depth up to approximately 100 m (Fig. S3 in the Supplement). These spatial patterns are likely caused by high biomasses of flatfish with a long lifespan, particularly in the shallow southern area, e.g. European plaice *Pleuronectes platessa* and common sole *Solea solea*, as well as the exclusion of fast-growing, pelagic species in the analysis. Nevertheless, in addition to depth, seasonality was also included in the best fitting model for lifespan (Table S3), where it displayed a negative linear relationship (Fig. S3). This lends support to the previous findings showing that the proportion of species characterized by short lifespans is higher in seasonal environments.

Phytoplankton biomass, represented by the PCI, was positively related to the spatial variation in the growth coefficient K . Our findings are consistent with the work of Pecuchet et al. (2017) showing that highly productive environments select for small and opportunistic, and hence fast-growing, fish species. Phytoplankton biomass also varies with depth and is generally higher in coastal or shallow areas, especially on and around the shallow Dogger Bank located in the central North Sea (Fig. 1, Fig. S5). It has been suggested that the high observed primary production north of the Dogger Bank is caused by the presence of a frontal zone where deeper nutrient-rich waters are pushed by tidal forces onto the bank causing peaks in sub-surface primary production in front of the bank (Richardson et al. 2000, Heath & Beare 2008). This likely explains why this productive but less shallow area north of the Dogger Bank also harbours communities characterized by species with relatively high growth coefficients, such as lesser sandeel *Ammodytes marinus* and grey gurnard. It is therefore not surprising that both the PCI and depth

partially explain the spatial pattern in the CWM of the growth coefficient K .

Among the remaining drivers investigated in this study, salinity partially explained the changes in traits over time, but it was a poor predictor of trait variation in space. This is likely due to a narrow range of spatial variation in salinity, with rather high salinities throughout the area ($\sim 32\text{--}35$; Fig. S5). Hence, salinities do not reach critical levels below which physiological constraints on adults or early life history stages negatively affect individual species performance (e.g. through osmoregulation or egg buoyancy; MacKenzie et al. 2000, 2007) and community composition at large. Such effects of strong environmental filtering driven by low salinities have been demonstrated in the neighbouring Baltic Sea (Pecuchet et al. 2016), as well as in other brackish, estuarine ecosystems throughout the world (Henriques et al. 2017). Similar to salinity, substrate richness was a poor predictor of trait variation in space. Although greater taxonomic and trait diversity has been associated with substrate-rich areas, likely due to the higher availability of different habitats and niches allowing more species and traits to coexist (Tews et al. 2004, Dencker et al. 2017), substrate richness did not seem to explain any spatial variation at the level of individual community traits. Finally, we found only weak relationships between fishing and the variation of traits in space, with the strongest relationship being between the growth coefficient K and otter trawling. Empirical evidence shows that selective fishing leads to an increase in individuals (or species) with faster growth, smaller size and earlier maturation (Conover & Munch 2002, Heino & Godø 2002). However, the fitted spatial relationship was best described as negative (Fig. S3), which was contrary to our expectations and instead most likely suggests fishermen's preferences to fish in areas containing a high proportion of slow-growing species. Overall, the results suggest that the spatial trait composition of the community is more determined by the environmental heterogeneity of the area and that fishing has little additional impact (Szostek et al. 2016).

4.4. Future directions and conclusions

Understanding the responses of our oceans to multiple environmental and anthropogenic stressors poses a key challenge for marine ecologists and managers. In this study, we used a trait-based approach to demonstrate how fish community composition in a large and heavily exploited marine ecosystem is spa-

tially variable and how it has responded to marked changes in the environment in the past. Since the response of communities to environmental changes is mediated by the physiological, morphological and life-history traits of the constituent species, such a trait-based approach leads to a more mechanistic understanding of the impacts of environmental change and exploitation on community composition than when focussing on taxonomic identity alone. Community mean traits can also be used as ecological indicators to detect community-level responses and changes in community-level properties (Greenstreet et al. 2012, Beauchard et al. 2017). Yet, the low degree of variation explained by the models of some traits suggests that other biotic or abiotic drivers should be assessed as well and that not all traits are good candidates for ecological indicators. Expanding our study to other areas and to different spatial scales would be necessary to verify if the observed relationships between traits, the environment and fishing generally hold. Moreover, more attention should be paid to take into account intraspecific trait variation, as it could impact both the spatial and temporal CWM trait patterns. Spatial trait patterns can be affected by the fact that fish undergo large ontogenetic shifts in traits, such as size and diet, and that the spatial distribution of juvenile and adult stages may differ (Heessen et al. 2015). Temporal trends in CWM traits may also be affected by intra-specific variability, especially since several commercial fish species have lowered their age and/or length at maturity and increased their growth coefficient K in response to fishing (Jørgensen et al. 2007).

Besides the community mean, the community-weighted variance of traits may also shed light onto community dynamics, since a strong environmental filter or anthropogenic pressure may reduce the variation around the mean trait value rather than the mean itself (Spasojevic & Suding 2012, Enquist et al. 2015). Furthermore, trait-based ecologists recently argued for increasing the focus of how traits co-vary along environmental gradients (Poff et al. 2006, Laughlin & Messier 2015, Dwyer & Laughlin 2017a). Hence, covariation of traits in marine fish (e.g. length and age at maturity, size and growth rate) across environmental gradients should merit future attention using techniques such as structural equation modelling or joint trait models (Dwyer & Laughlin 2017b, Wüest et al. 2018).

This study illustrated a pronounced spatial structuring and dramatic long-term change in the trait composition of the North Sea fish community, largely explained by a number of key environmental drivers

acting in both space and time, notably depth, temperature, phytoplankton biomass and seasonality. Our findings emphasize the importance of taking both the spatial and temporal dimensions of traits into account when detecting and understanding trends and patterns in community composition and biodiversity, and stress the need for holistic ecosystem-based approaches, including multiple abiotic and biotic processes, to understand and sustainably manage our marine ecosystems in the future (Pikitch et al. 2004). We argue that a trait-based approach, broadened to account for multiple trophic levels, their interactions and responses to drivers, can readily inform and inspire such a development.

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