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Fishing impacts on age structure may conceal environmental drivers of body size in exploited fish populations

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Using analysis of field survey size-at-age data, we examine responses of European plaice (*Pleuronectes platessa*) to spatial differences in environmental variables in the North Sea.
Using available samples of plaice aged 1–7, northern and southern migrating groups of males and females grew differently. However, length-at-age growth patterns were not corroborated by complementary otolith-based estimates. Southern females and males were smaller than their northern counterparts until age 3. Southern males remained smaller up to age 7; by contrast southern and northern females reached similar size-at-age by year 4.
Due to covariation, the influence of spatially variable environmental conditions was equivocal. However, temperature, depth, fishing pressure, phosphate levels, distance from shore, and conspecific density were all significant predictors of size for plaice aged 1–7.
Our results suggest that fishing impacts on age structure limit the potential to examine the role of environmental variation on body size. For fish that rarely reach their full potential age and size, expected metabolic responses to warming may remain unexpressed, challenging predictions in a changing climate.

Keywords: European plaice, growth, North Sea, otolith, Pleuronectes platessa, size.

Introduction

Understanding fish growth responses to environmental variation is vital when assessing the impacts of human activities, particularly in relation to climate change. Opportunities to utilize field data from populations, across a breadth of environmental conditions both in time and space, enable a greater understanding of fish growth and adaptive capacity. Across the Northeast Atlantic, long-term fisheries surveys have identified several species with sub-stocks or groups that have experienced differing levels of exploitation (Hutchinson *et al.*, 2003; Harrald *et al.*, 2010; Zimmermann and Werner, 2019), and characteristically different environmental conditions (Hunter *et al.*, 2003; Ottersen *et al.*, 2006; Keating *et al.*, 2014). Understanding the impacts of different environmental conditions and levels of exploitation on species sub-groups, including inherent genotypic and phenotypic diversity, can help us to understand how species may respond to future changes (Hurst and Abookire, 2006; Baudron *et al.*, 2014; Romo-Curiel *et al.*, 2015; Kuparinen *et al.*, 2016; Rindorf *et al.*, 2016). Management that accounts for, and supports, intraspecific diversity and species sub-groups could help to sustain species into the changeable future (Hilborn *et al.*, 2003; Schindler *et al.*, 2010; Lindegren *et al.*, 2013).

Sub-groups of mature north-east Atlantic European plaice (*Pleuronectes platessa*, hereafter "plaice") are known to maintain geographical separation in the western, eastern, and central North Sea through the summer feeding period. These separated sub-populations experience markedly different environmental conditions during the season that determines annual growth (Hunter *et al.*, 2004a). Due to a north–south summer gradient of environmental conditions (Figure 1), plaice migrating to feeding grounds in the central North Sea experience markedly cooler waters compared with individuals that migrate towards the south-east and south-west. Studies using archival tags have shown strong feeding site fidelity across sub-groups (Hunter *et al.*, 2003), and recent analyses of otolith chemistry from the same fish suggest that these spatial patterns are maintained during adult life (Darnaude and Hunter, 2018). However, during the winter, plaice migrate back from these different summer feeding grounds to form non-segregated southerly located spawning aggregations (Bolle *et al.*, 2005; Hunter *et al.*, 2009), with no evidence to date of genetic isolation between the different sub-groups (Hoarau *et al.*, 2002).

Environmental conditions across the central North Sea vary on a roughly north–south gradient (Figure 1). Northern plaice will experience deeper, colder summer bottom temperatures, largely due to seasonal stratification (Figure 1a, b), and lower phosphate levels, with increasing distance from anthropogenic influxes (Figure 1d; Menesguen *et al.*, 2018). The northern
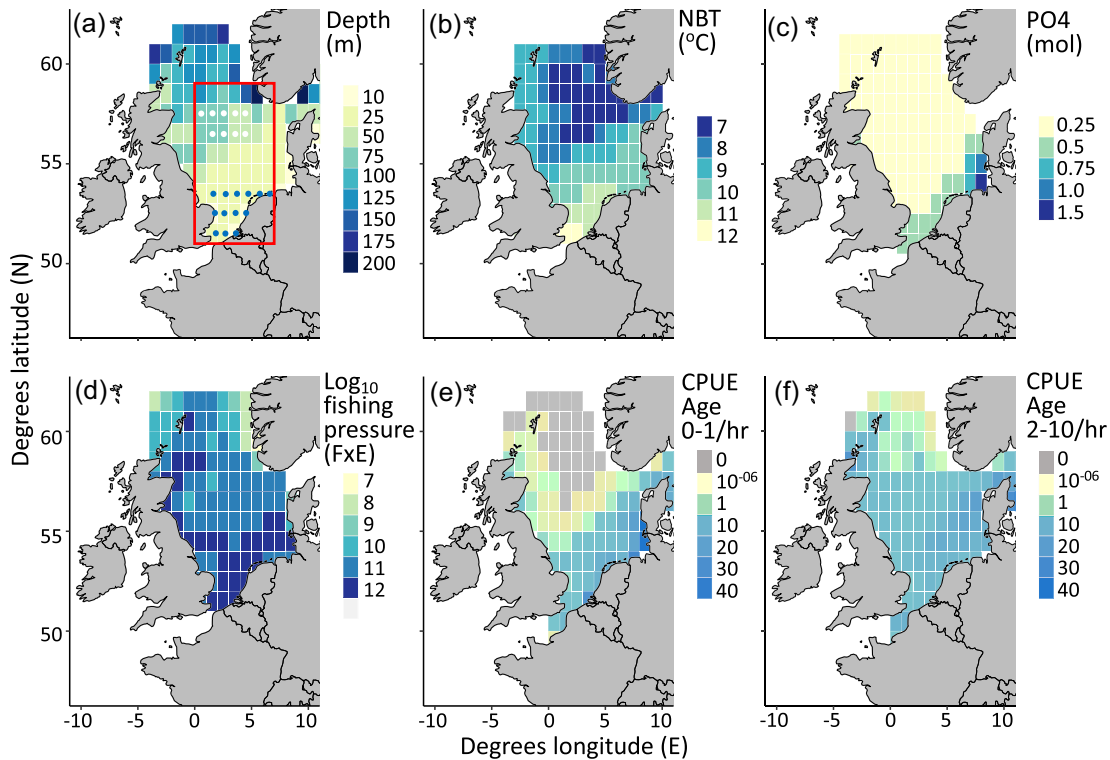
Figure 1. Study region and environmental data on a one degree latitude and longitude cell scale. (a) Average cell depth in metres, from survey haul data. The red rectangle marks the overall study area. The white and blue spots indicate northerly and southerly sub-sample cells, respectively. (b) Mean annual cell near bottom temperature (NBT) (2004–2013), from Copernicus Marine Environment Monitoring Service (CMEMS) . (c) Mean molar concentration of phosphate in seawater (1991–2011) from CMEMS. (d) Log_{10} mean fishing pressure combining annual fishing mortality for plaice (f) (1998–2008) with mean otter and beam trawling effort (e) (1990–1995) for each cell based on hours of fishing. (e) Mean catch per unit effort (CPUE) per hour per cell (1991–2013) of 0-group and age 1 plaice. (f) Mean CPUE per hour per cell for plaice aged 2–10, both from North Sea International Bottom Trawl Survey (IBTS-ICES) survey data and age estimates.

North Sea also experiences lower fishing pressure (Figure 1d) and there are lower densities of younger plaice (Figure 1e). The differences in environmental conditions through the central North Sea are of sufficient magnitude to expect that plaice growth to the north would be different to plaice growth towards the south. As the North Sea has also experienced warming of 0.30–0.45°C/decade between 1985 and 2014 (Hughes et al., 2017), there is also potential to use the available datasets to assess the impacts of temporal warming on this cold-adapted species.

Plaice are a sexually dimorphic species, male fish being smaller and investing more energy in reproduction relative to growth than females (Rijnsdorp and Ibelings, 1989). Body size and distribution of plaice in the North Sea have already been shown to be influenced by a range of anthropogenic, environmental, and demographic variables. Fishing pressure across the North Sea selects for individuals that mature early at smaller sizes and at younger ages (Grift et al., 2003; van Walraven et al., 2010; Mollet et al., 2016a; Mollet et al., 2016b), particularly for males (Rijnsdorp, 1994). Yet trawling may also yield more accessible prey and, therefore, concurrently increase the size of individuals (Engelhard et al., 2011), which may make it difficult to identify the role of fisheries-induced evolution (FIE) on plaice size. Higher intraspecific competition amongst juveniles has been shown to have a negative impact on plaice growth (Rijnsdorp and van Leeuwen, 1996; Rijnsdorp et al., 2004; Ciotti et al., 2013), whilst habitat quality at places of settlement has an influence

on distribution (Lauria et al., 2011) and size in young fish (Fox et al., 2014). Higher temperatures are implicated in increased growth in juveniles (Fonds et al., 1992; Rijnsdorp et al., 2004; Teal et al., 2008), and result in reduced growth in adults (Fonds et al., 1992), although this is not evident in trawl data between 1950 and 1995 (Rijnsdorp and van Leeuwen, 1996). The influence of higher temperatures resulting in faster early growth but ultimately smaller individuals is supported by wider analysis on males (Baudron et al., 2014), and by otolith growth increment analysis (van der Sleen et al., 2018) and future predictions (Cheung et al., 2013). Various studies have also suggested that plaice distributions are shifting as conditions change, to optimize their experienced environmental conditions (van Keeken et al., 2007; Dulvy et al., 2008; Engelhard et al., 2011). The movement of plaice could be driven by: (i) high temperatures limiting recruitment success (Fox et al., 2000; Hermant et al., 2010); (ii) elevated metabolic demand exceeding local food availability (Fonds et al., 1992; Teal et al., 2012); (iii) a possible reduction in competition from larger plaice offshore and/or a potentially higher number of predators inshore (van Keeken et al., 2007); (iv) fish deepening their distribution to access temperatures lower than those in shallower waters (Perry et al., 2005; Dulvy et al., 2008; van Hal et al., 2016); and (v) a reduction in predators (van Keeken et al., 2007). However, not all studies identify temperature as a key driver of plaice distribution (Lauria et al., 2011) or distribution shifts (Perry et al., 2005). Variable survey effort and limited replication may also confound

the results of distribution change studies (Moriarty *et al.,* 2017).

The North Sea groundfish surveys (ICES-BTS, 2017; ICES-IBTS, 2017) provide a multidecadal plaice dataset enabling analysis of both spatial and temporal variation in growth for both male and female plaice, with the potential to explore temperature-mediated impacts on growth at a relatively fine spatial resolution. An otolith archive for surveyed North Sea plaice further enables a potential comparison between length-at-age data and otolith increments, to determine whether comparable growth patterns across space can be extracted.

In the present study, we aimed to deepen our understanding of the drivers of fish growth by utilizing spatial analysis to test specifically for drivers of dimorphic growth between the sexes. We also used high-resolution environmental and survey data to identify key drivers of plaice growth over time. We use fish length data and otolith records of growth to test the hypothesis that environmental variation, especially temperature, influences species growth and maximum size.

Methods

Initially, we explored size variation between northern and southern plaice feeding sub-groups (sub-group data). For this analysis, we also tested whether otolith increment analysis could be used as a reliable proxy for fish length when analysing fine-scale growth variation. Having identified variations in growth in plaice sub-groups, we explored the drivers of size variation in place across a wider continuous area of the North Sea (continuous data).

Size variation between northern and southern plaice sub-groups

The initial analysis in this study used samples from northern and southern plaice feeding groups (sub-group data, see Figure 1a) as identified in Hunter *et al.* (2004a) to explore spatial variations in growth of this exploited fish species. We used mark-recapture tagged plaice to confirm that plaice demonstrate fidelity to distinct areas, and their associated environmental conditions (detailed in the supplementary methods, results, and Supplementary Figure S1). The distinct feeding groups experience different environmental conditions (Figure 1a), providing an opportunity to see if growth is influenced by the environment in different feeding group areas. The southern group covered 51–54°N and 0–6°E, whilst the northern group covered 56–58°N and 0–5°E.

The differences in size between sub-groups, were compared using both fish length-at-age data and otolith increment measurements at age, using samples and measurements collected in the North Sea IBTS-ICES. Otolith-based estimates of fish size were compared to fish size at capture to explore whether both fish length data and otolith estimates of length could be used together when analysing fish size variation. Otolith increment analysis was also used to test the potential for extending the time period captured in the analysis. There was potential to use otoliths to explore growth throughout the lifespan of older fish caught at the beginning of the survey timeseries and therefore increase the timescale captured. Otoliths also integrate the environmental influences on growth rate experienced during the lifetime of the specimens, with the potential to provide detail not available in single mature fish length measurements.

Full otolith width and fish length relationship

Firstly, to validate the use of otolith increments as a proxy for fish size, the relationship between otolith size (width) and fish size (length) was tested. For details of otolith selection, see the otolith data methods in the supplementary materials. The total width of otoliths from 323 fish aged 0–7 were measured (Supplementary Figure S2) and compared to fish length data from the IBTS-ICES survey records at the point of capture (described below). The relationship between $\log_{10}$ fish length (cm) and $\log_{10}$ increment width (μm) was explored using Pearson's product moment correlation; results are shown in Supplementary Figure S2. $\log_{10}$ fish length and $\log_{10}$ otolith width had a strong linear relationship and so both datasets were used to explore variations in growth between plaice sub-groups. The linear model describing the relationship between $\log_{10}$ fish length (L) and $\log_{10}$ otolith width (w) was used to estimate the length of fish from otolith measurements in subsequent analyses (Supplementary Figure S2):

$$L = 1.225w - 2.3049$$

Fish length at age data for sub-group analysis (sub-group data)

Plaice length at age data for the sub-group analysis were extracted from both the North Sea IBTS-ICES and beam trawl surveys (ICES-BTS, 2017) undertaken in August of 2012 and 2013. Data used included age, standardized length, sex, and haul data (see supplementary methods). Lengths at capture of each age group (1–7 years old) were averaged for each sex in each region to identify differences in size between these groupings. See Supplementary Table S1 for details of the number of samples available for each age group, sex, and area. See supplementary methods for survey data extraction and quality control processes.

Otolith increments for sub-groups analysis

To assess fish size patterns between sub-groups using otoliths, annual increments of 215 fish aged 4–7 were measured. Male and female samples aged 4–7 were selected for the northern and southern regions in as equal proportion as were available. For detailed sample selection and processing, see the supplementary methods, and Supplementary Table S1 for sample numbers. Each annual increment was measured and was used as a replicate in the appropriate age group. Mean fish lengths from otolith measurements were estimated, using the linear model described above, for each sex in each region to identify variations in size between these groupings.

Fish length estimated from otolith increment width measurements were compared to direct fish length measurements, to confirm whether otolith increments would adequately capture fine-scale variation in fish size. Pairwise ANOVA tests of size variation between areas for each age and sex were used for otolith length estimates and fish length measurements separately and then compared. Back calculated lengths from otolith increments captured discrete annuli formation whilst the fish length measurements represented age at capture plus months to August. Therefore, the absolute size of the plaice was not directly comparable. As the analysis explored the difference between otolith and direct length measurements between area and sex this approach
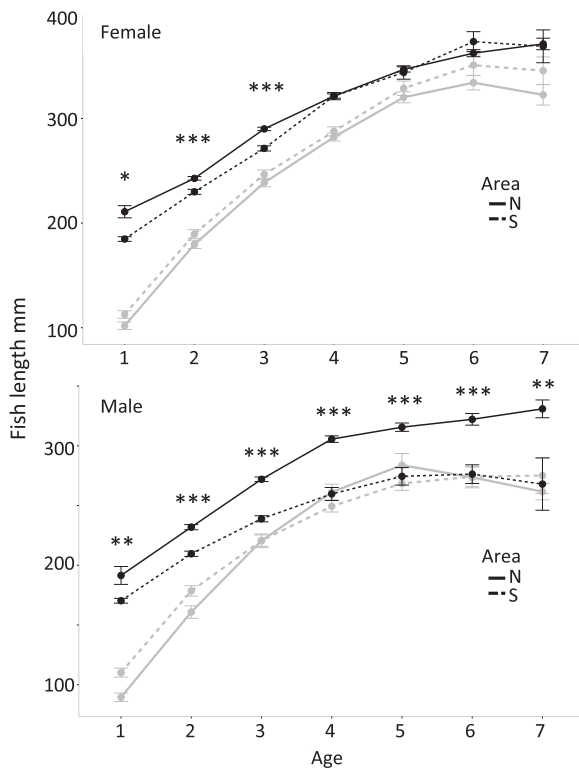
Figure 2. Average length-at-age of female and male plaice. Black: mean (±SE) length of fish (mm) caught at age in the North Sea in 2012 and 2013 in August, grouped by sex and area (as defined in Figure 1a), representing age plus months to August. Significant differences identified by pairwise ANOVA tests of size between areas for each age and sex are marked (∗ $p < 0.05$, ∗∗ $p < 0.01$, and ∗∗∗ $p < 0.001$). Grey: mean length of fish estimated from otolith increments, for each annulus formation, from fish collected in 2012 and 2013 (see methods for detail).

enabled clear interpretation and visualization of the variation analysed.

Environmental variables determining size for continuous plaice dataset

Continuous data selection

Having identified variations in size between sub-groups of plaice we then used all available survey length data from the southern-central area of the North Sea to explore the drivers of size variation. Samples were selected from August surveys to ensure similar seasonal growth was captured, as August was the best sampled month between 1996 and 2013. 1996 was the earliest year available with adequate replication of all age groups of plaice for analysis (Supplementary Table S1). Only length at capture data was used for this analysis, as otolith measurements did not corroborate the fine-scale growth variation over space (see initial results). This analysis extending from 51 to 58°N and 0 to 6°E, covering the main plaice spawning areas (Harding et al., 1978) and feeding grounds (Hunter et al., 2004a), whilst avoiding areas with extreme thermal inputs such as the Baltic Sea winter influx (Figure 1a) (see red box Figure 2.1a). The continuous spatial coverage captured a continuous range of environmental and effort variables for analysis. Including all plaice across the area had the added benefit of increasing the number of individuals included in the analysis. For fish length data details, see the supplementary methods "Survey data extraction and quality

control process" section. Forty-nine one-degree latitude and longitude grid cells (hereafter 1 × 1° cells), where wider environmental data were also available, were selected.

Environmental variation across the study area

Environmental parameters within the study area vary across a general north–south gradient, with deeper water, lower phosphate levels, and colder bottom temperatures found in the north due to summer stratification. There is also lower fishing pressure and evidence of lower catches, particularly for younger plaice, in the north (Figure 1c, e, and f). In addition to this spatial temperature variation, the North Sea is also experiencing warming, with temperatures in recent decades increasing by an average of 1.31°C (Sherman and Hempel, 2008).

Plaice lifetime experience of environmental drivers

Lifetime sea temperature

Sea surface temperature (Rayner et al., 2003) and NBT from Copernicus Marine Environment Monitoring Service (CMEMS, 2017) were averaged monthly across 1 × 1° cells. Growing degree-months (the monthly equivalent of growing degree-days; e.g. Neuheimer and Taggart, 2007) experienced over the lifetime of each individual were calculated for both the cell of capture and across the whole North Sea sample area (see Figure 1), to test whether the feeding area or wider thermal experience best explained the size of individuals. As mature plaice return to similar areas for summer feeding each year, the cumulative lifetime experience is assumed to capture the variation experienced by fish caught in different areas. It is acknowledged, however, that some temperature variation, particularly during the juvenile life phase, may not be fully captured using this approach. Individuals were assumed to be settled and experiencing NBT by March of the year of hatching. The mean temperature for each month after March of the year hatched was summed up to and including the August of capture.

Lifetime salinity, chlorophyll, nitrate, and phosphate data

Data to 2013 were accessed from monthly estimates on a 1 × 1° latitude and longitude cell scale (CMEMS, 2017) for: salinity (psu) at surface; chlorophyll (mg C m^{-3}) at surface; nitrate (mmol m^{-3}) at 10 m depth; and phosphate (mmol m^{-3}) at 10 m depth. The mean lifetime experience of salinity, chlorophyll, nitrogen, and phosphate for each individual in the cell of capture was calculated from annual averages per cell from the year of birth to the year of capture. As individuals are expected to return to similar areas to feed each year, it was assumed that this fixed location approach captured some of the likely and persistent variation in the variables that individuals experience.

Lifetime average fishing pressure

We calculated a spatially explicit metric of fishing pressure for each year to test whether available fishing pressure data was a predictor of fish size. To do this we combined annual information on North Sea plaice fishing mortality (F), weighted by spawning-stock biomass, from annual ICES stock assessments (ICES, 2022), with spatial information on otter and beam trawling effort (annual number of hours fishing, averaged over 1990–1995; Jennings et al., 1999a) (following Rutterford et al., 2015), for each 1° × 1° cell. We calculated a spatially explicit metric of fishing pressure by allocating the total

mortality across the North Sea in each year to each cell relative to the mean effort reported in Jennings *et al.* (1999a) for each cell. The 1990–1995 relative effort in each cell (Jennings et al., 1999a) was assumed to appropriately reflect the relative effort across 1° × 1° cells during the time period of our study. We then calculated the average annual fishing pressure in the cell of capture for the lifetime of each fish. Through combining temporal trends in fishing mortality and spatial distribution of fishing effort, we were able to test whether available fishing pressure data were a predictor of fish size.

Average location based 1° × 1° cell conspecific density

An indicator of conspecific density was estimated from survey-based CPUE records, measured as catch per hour. Conspecific density was estimated for two age groups (0–1 and 2–10), as younger fish are likely to experience more competition from similarly aged conspecifics, and older fish likely to be more affected by competition with older conspecifics. CPUE data (catch per hour) from the North Sea IBTS survey quarters 1 and 3 from 1990 to 2013 for each 1 × 1° cell was used. Average CPUE per year for each 1 × 1° cell was calculated from all available haul records. Age 1 fish were considered to coincide with 0-group and age 1 fish, whilst 2–7 year old fish were expected to overlap with 2–10 year olds. A single average CPUE was calculated from the 1990–2013 data for all ages in the category (0–1 and 2–10). Conspecific density was averaged to provide a long term estimate of competition at the 1 × 1° cell scale. This approach was used to avoid additional assumptions regarding the competitive experience of individual fish when they are not in the cell of capture. As there is no available data about the movements of individual fish, we used the location of capture as the most appropriate location to represent competition for individuals. Density was assessed from random survey locations whereas most other variables were extracted from standardized monthly or annual datasets on a 1 × 1° latitude and longitude cell scale. Therefore, the metric used to assess competition only explores spatial variation in competition in the analysis.

Nearest neighbour distance

The *sp* package in R (Pebesma and Bivand, 2005) was used to calculate the nearest neighbour distance to land (in km) from the point of capture. This variable was included to explore whether coastal influences, not captured in the available variables, were driving plaice size.

Generalized additive model (GAMs) using the continuous fish length at age dataset

GAMs were used to assess the importance of different environmental variables on the size of plaice across the North Sea study area.

Biologically meaningful environmental variables already recognized as mechanistically influencing fish size were explored alongside additional speculative variables that could conceivably represent proxies for additional variables, the data for which were not directly available. The biologically meaningful variables were temperature, nutrients (phosphate and nitrate), salinity, fishing pressure, and chlorophyll. Due to the limited and equivocal role of the biologically meaningful variables in influencing size (Supplementary Figure S3), we further explored distance from shore (to capture potential anthropogenic influences such as pollution), and depth (to capture potential variation in community composition and

likely driven by wider environmental conditions such as pressure and light levels) (Brown and Thatje, 2014).

To identify variables that explained the most variance in plaice size, Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) values, and R^2 values (Table 1 and Supplementary Figure S1) were assessed. Consistent models for all ages were selected where both the AIC and BIC ranks were low. BIC scores were used to ensure the final selection favoured the simplest model ($\Delta > 4$ was used as the criteria for model simplification). To keep the model variables consistent between age groups, only nitrate, chlorophyll, and salinity were removed (Table 1).

The relationship between selected predictor variables was assessed through visualization of the variable plots and the Variance Inflation Factor (VIF). Values of VIF of around 5 and under were considered only moderately correlated, and these variables were therefore included in the analysis. The identified covariation between variables was taken into account when the model output was interpreted, alongside consideration of the relative importance of different variables for each age group. Variations in size between sex and survey were captured and controlled for through inclusion as factors (fixed effects) in the model.

The equation for the selected gam model is:

$gam(fish\ length\ at\ age) \sim s(lifetime\ degree\ month\ temperature\ of\ 1 \times 1°\ cell, k = 3)$
$+ s(log10(distance\ from\ shore), k = 3)$
$+ s(log10(mean\ lifetime\ fishing\ pressure), k = 3)$
$+ s(log10(mean\ lifetime\ phosphate), k = 3)$
$+ s(depth, k = 3) + s(competition, k = 3)$
$+ Sex\ Survey,\ family = gaussian$

The GAMs, were coded using the *mgcv* package in R (Wood, 2011), with k = 3 to limit the degrees of freedom in line with the number of data points.

Results

Sub-group plaice size variation

Male plaice were consistently and significantly smaller than females from the same area and age group ($p < 0.01$ or $p < 0.001$, see Figure 3 for sample numbers), except for the age 1 sample from the northern group. Female southern plaice were smaller at age than their northern counterparts until age 3, but at ages 4–7 years at capture, they were not significantly different in size. Males were smaller at age in the south compared to the north at all ages 1–7 (Figure 2).

North-western areas of the North Sea are predominantly visited by low numbers of relatively small, older, and female plaice (Figure 3). Larger mature females (age 3+) tend to be found across the eastern side of the study area whilst the larger mature males are mainly found to the north east of the study area.

The use of back-calculated estimates of plaice size, from otolith increment measurements, did not provide results consistent with plaice length measurements for the same area (Figure 2).

Broader environmental drivers of size

To identify likely drivers behind the differences in the size of males and females of different ages across the North Sea, the sample set was increased to include all individuals aged 1–7 across a central band of the North Sea (Figures 1 and 3). An analysis of drivers of size relied on the continuous range of environmental and effort variables over continuous spatial coverage, and had the added benefit of increasing the number of

Table 1. Model fits and significance for all candidate variables examined explaining plaice size at age.

Age	Metric	Sex	Survey	Chlorophyll	Cell of capture degree days	North Sea degree days	Distance from shore	Fishing pressure	Depth	Phosphate	Nitrate	Salinity	CPUE (0–1 or 2–10)	Deviance explained by full model	R-sq (adj)
1	a	0.147	0.151	0.151	0.152	0.148	0.138	0.139	0.149	0.147	0.147	0.131	0.136	15.50%	0.151
	b	***	***	***	**	***	***	***	***	***	***	***	***		
2	a	0.162	0.210	0.225	0.224	0.207	0.224	0.210	0.228	0.225	0.225	0.224	0.225	22.80%	0.227
	b	***	***	***	***	***	***	***	NS	***	***	***	***		
3	a	0.144	0.253	0.264	0.260	0.251	0.266	0.252	0.267	0.259	0.265	0.264	0.267	26.70%	0.265
	b	***	***	***	***	***	*	***	NS	***	***	***	NS		
4	a	0.105	0.274	0.271	0.265	0.268	0.275	0.276	0.271	0.266	0.274	0.275	0.273	27.60%	0.273
	b	***	***	***	***	***	**	NS	***	***	***	**	***		
5	a	0.104	0.306	0.307	0.295	0.308	0.310	0.309	0.302	0.302	0.309	0.309	0.306	31%	0.306
	b	***	***	**	***	*	NS	**	***	***	NS	NS	***		
6	a	0.108	0.312	0.313	0.303	0.312	0.316	0.315	0.308	0.307	0.314	0.316	0.312	31.60%	0.311
	b	***	***	**	***	***	NS	NS	***	***	NS	NS	**		
7	a	0.111	0.315	0.316	0.306	0.314	0.319	0.319	0.310	0.312	0.319	0.319	0.316	31.90%	0.314
	b	***	***	**	***	***	NS	NS	***	***	NS	NS	**		
Notes				Uneven replication/sampling over variable range		Uneven replication/sampling over variable range	Significance in young fish warrants inclusion				Strong co-variation with phosphate and a significant predictor in least age groups so excluded	Uneven replication/sampling over variable range			

(a) Adjusted R^2 values of predicted compared to observed fish size—representing the explained deviance when the covariate was left out of the full GAM model for each age group. (b) Significance of variables in the full GAM model for each age group with deviance explained and adjusted R^2 values (NS–not sig., $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$). Survey and sex are factorial variables, other variables are smoothed with $k = 3$ in the model. For age 1, the variable CPUE (catch per unit effort, representing conspecific density) was based on catches of plaice aged 0 and 1 combined, whilst for ages 2–7, this was based on the catches of plaice across all ages 2–10 combined. Grey cells show variables that, when excluded, did not alter the BIC value by > 4. Variables highlighted in bold were used across all age groups for the GAMs used in the study.
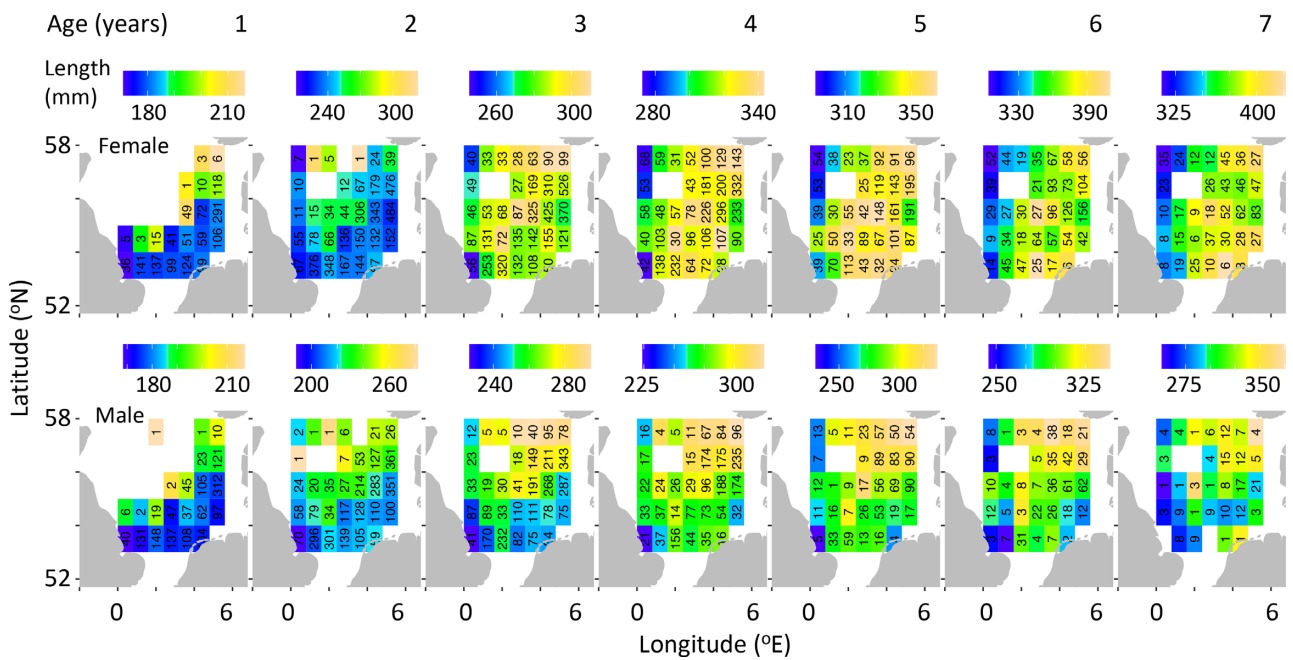
Figure 3. Mean size-at-age (indicated by colour shading) for female and male plaice across ages 1–7 years, as sampled in BTS and IBTS surveys during August across an area where both surveys had at least 20 hauls each year (therefore, 53–58°N, 0–7°E; excluding 53°N,6°E, 56°N,1°E, and 56°N,2°E). To ensure > 10 fish samples per survey per year for each age group, the following years were sampled: age 1: 2003 onwards; ages 2–4: 2000–2013; ages 5 and 6: 2002–2013; age 7: 2006–2013). The total number of individuals per cell is detailed within the cell.

individuals included in the analysis. The variables considered as potentially important drivers of size [mean lifetime salinity, depth at capture, mean lifetime chlorophyll, distance from shore at capture, mean lifetime fishing pressure, mean lifetime nitrogen, mean lifetime phosphate, lifetime degree-month temperature, conspecific density (from CPUE) in the cell of capture, sex, and survey] showed no clear linear relationships with plaice size when explored for separate age groups. Thus, a non-linear GAM approach was applied to test the role of all variables for each age group.

When exploring environmental variables that explained variations in plaice size. we found differing levels of covariance between variables (Supplementary Figure S6). We only explored variables that were not strongly correlated (assessed using VIF analysis) to limit misinterpretation of the drivers of variation. However, we acknowledge that covariation challenges the interpretation of size patterns in North Sea plaice. The variables that best explained size trends for all ages were selected, in order, as: sex, temperature (degree months in cell of capture), depth, phosphate, survey, conspecific density (from CPUE), distance from shore, and spatially explicit fishing pressure. The influence of each selected variable on model fit varied depending on the age group, but overall patterns were similar (Table 1). Within the GAM, temperature explained significant amounts of variation and showed a similar bimodal peak for all age groups with both lower and higher degree-month values associated with larger individuals. Fish aged 1–3 showed a positive relationship between fish size and greater distances from shore, and increased fishing pressure accounted for an increase in size for younger fish. Whilst conspecific density showed a negative relationship with young fish size, this was not seen in older fish. Phosphate levels generally have a negative relationship with fish size. In plaice aged four and above, fish size was also negatively associated with deeper water (Figure 4).

Discussion

Our study provides evidence that both environmental conditions and anthropogenic influences affect plaice. Annual migrations between central spawning grounds and separated feeding areas play a role in driving variation in length. However, the predicted growth benefits of cooler temperatures were not seen in this study. The limited effect of temperature is likely due to FIE, whereby individuals that mature early and at a smaller size than those targeted by fishers are selected for, limiting the size of individuals overall. The study region is also centrally located in the known spatial and thermal distribution of the species (point data map, Fishbase, 2019). We also find that otolith increments may not reliably reflect fine-scale variation in fish length.

Inferring spatial distributions from tagging data

Previous studies have shown that migratory sub-groups of plaice consistently return to different northern and southern feeding grounds after spawning (Hunter et al., 2004a). In this study, we assessed all available Cefas-collected mark-recapture data to gauge the level of fidelity to specific feeding and spawning grounds between seasons. These data show a regular pattern aligning with repeated annual migrations between consistent feeding and spawning locations, as shown in previous studies (Hunter et al., 2003; Darnaude and Hunter, 2018). However, the study by Hunter et al. (2004a) focused primarily on large, mature females (99% of individuals), and the data in the current study highlight that feeding groups are not as spatially distinct when the aggregations are considered in their entirety. We note that the detailed archival tag records for plaice in the studies by Hunter et al. (2003; 2004b) are heavily weighted towards mature females, and that the movements of maturing juvenile plaice are less well
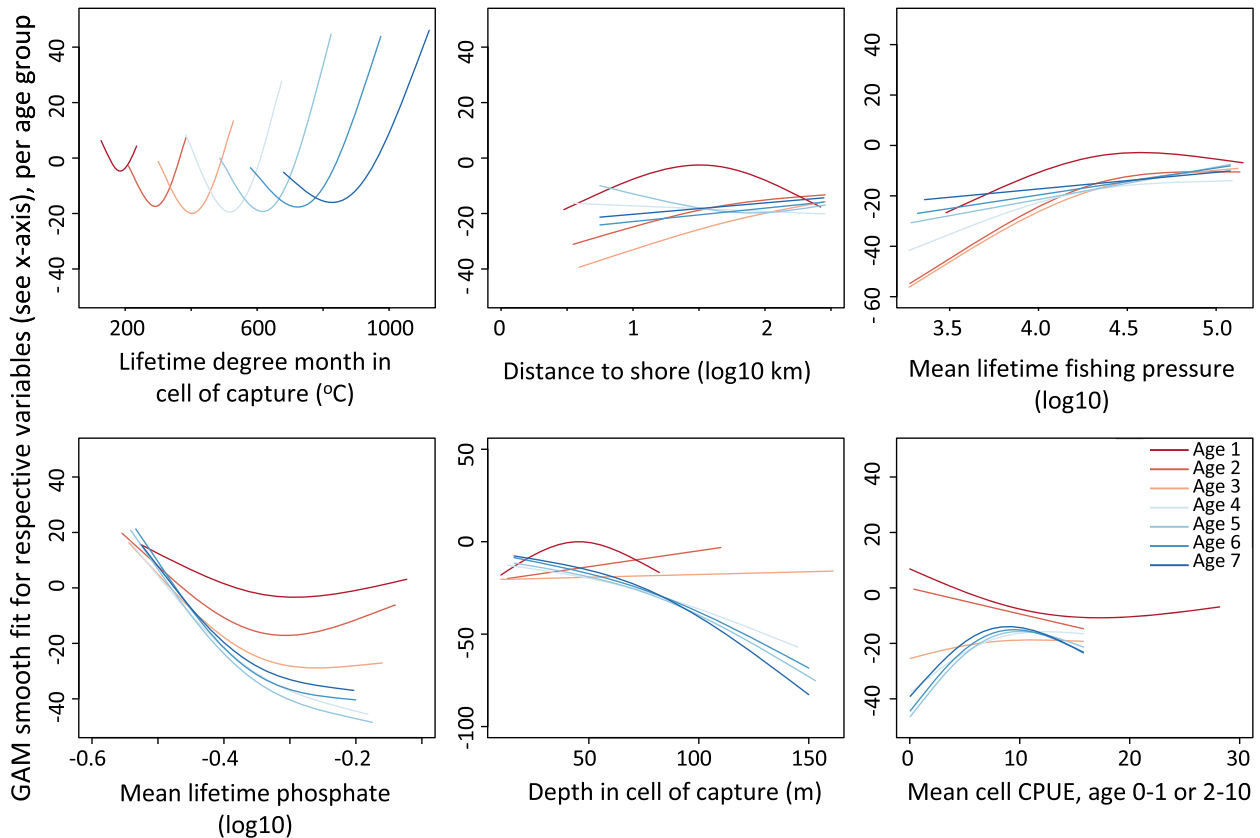
Figure 4. GAM model output, for selected model variables, for each age group (see legend) showing model fit of smoothed variables. Y-axis captures the length response of individuals to the x-axis variables in the model. Fish length at age data was collated from surveys undertaken between 1996 and 2013.

known (e.g. Poos *et al.,* 2013) and may not align with the geographically discrete mature groups. It seems likely, therefore, that the environmental conditions experienced within different sub-groups are likely to be more variable than previously suggested (Hunter *et al.,* 2004a), complicating our ability to test for environmental drivers behind variations in size. Archival tag data further demonstrate that plaice travel further and faster than shown by mark-recapture tags (Metcalfe and Arnold, 1997), rapidly traversing environmental thresholds (Hunter *et al.,* 2003), and potentially diverging further from predicted environmental experiences. Consequently, the degree to which plaice caught in geographically discrete areas experience different environmental conditions is still partially equivocal, and requires further study. Furthermore, the illustration of the spatial pattern of length at age of males and females presented in this study (Figure 3) showcases the lifetime distribution changes that occur in the plaice population. The spatial pattern reflects the total combined possible differences in growth rate during ontogeny as well as the consequences of different patterns of behaviour (notably migration patterns) related to body size.

Whilst the available evidence from archival tags (Hunter et al., 2003) and otolith chemistry (Darnaude and Hunter, 2018) suggest that mature plaice follow specific migration pathways, and the environmental conditions experienced on the feeding grounds should largely reflect conditions over their adult lifetimes, more uncertainty is likely to apply during the first 3 years in life. Settlement locations of juveniles from

mixed spawning grounds depend on larval settlement following a long (3–4 month) planktonic phase, which may result in plaice settling far from spawning locations (ICES, 2014) and depends on the offshore dispersion rate (van Keeken et al., 2007). Therefore, larvae may settle in different areas to their parents and in quite different environmental conditions. Whilst we know that nursery grounds are concentrated in the southern and German Bights and along the eastern coast of Britain (ICES, 2014), where local conditions will influence early growth and development, it was not possible to capture variability in these conditions for the individuals in our analysis. From nursery grounds, juveniles then gradually migrate from shallow coastal nursery grounds out to deeper water as they grow (ICES 1992, van Keeken et al., 2007). Data suggests that body size may affect migration distance (van Keeken et al., 2007), so the length-at-age of adult plaice in offshore areas may also be influenced by their ontogenetic growth rate. Whilst we have been unable to disentangle these life-stage specific influences in the current study, we have started with the assumption that cumulative lifetime ambient experience between north and south sub-groups would present significant differences. Advances in otolith chemistry, particularly oxygen isotope ratios, show promise when exploring the lifetime thermal experience of plaice. Recent analysis of isotope ratios in plaice otoliths demonstrates the potential to provide insights into intra- and inter-annual migratory patterns that are not readily obtained by conventional means (Darnaude and Hunter, 2018).

Environmental drivers of plaice size over time

The results of our North Sea wide analysis suggest that environmental variation influences the size of plaice. However, the relationships presented are not straightforward, likely due to a combination of covarying environmental factors and the truncated age structure due to high exploitation. Our study shows that larger fish (at age) are found at both the lower and upper limits of the study area's temperature range, particularly in younger age groups. This pattern was observed both in the outputs from our models limited to the most directly mechanistic variables and in the more speculative models capturing wider variation. For the younger age groups, this could be due to the larger fish occurring in deeper, cooler waters further offshore, due to developmental changes, or potentially exploitation driving deepening (Frank et al., 2018). It is also likely that the size distribution seen is a result of environmental variation not fully captured in the models. For example, spawning grounds for plaice are located both in the northern (cooler) and southern (warmer) areas of our study (Fox et al., 2000), so it seems likely that habitat (Lauria et al., 2011) or other local environmental variables that favour settlement and growth are driving a bimodal size pattern more than the experienced temperatures. For the largest fish in our study, the lack of a clear thermal limit on size due to oxygen limitations in warmer waters is perhaps unsurprising given the narrow age and size range of plaice now regularly caught in the North Sea. Whilst plaice have the potential to reach 1 m in length and to live to 40 years (ICES, 2014), very few fish older than 7 years or at lengths of over 40 cm were caught in the fisheries surveys sampled in this study. These relatively small individuals are far from reaching asymptotic size, so physiological size limits in relation to temperature are unlikely to be reached (Atkinson, 1994; Neuheimer et al., 2011). Furthermore, the study area is located at the centre of the plaice distribution range, and so the thermal variation experienced may be well within the species physiological tolerance limits (e.g. Kerby et al., 2013). However, existing analysis (Teal et al., 2012) does indicate that larger plaice in the southern North Sea may be affected by higher temperature, if plaice reach sizes above the current norm. Additionally, the relationship between fish length and environmental conditions in the $1 \times 1°$ cell of capture will not fully capture the cumulative growth in response to environmental conditions across various locations during the life time of individuals. However, fidelity of individual fish to relatively distinct feeding areas does mean that the approach used should capture environmental variation experienced between individuals from maturity.

The study period also follows a reported regime shift across the North Sea (Spencer et al., 2012) and relatively rapid warming, that has been suggested as a driver of size reductions (Baudron et al., 2014). Our sampled plaice therefore may already have, or have been, adapted physiologically or evolutionarily to warmer conditions. A similar study drawing on more localized survey data has suggested that increasingly high temperatures are limiting adult female plaice size (van der Sleen et al., 2018), however, the analysis applied relied solely on growth-increment data, which may not accurately reflect fish size. The van der Sleen et al. (2018) study also highlights that fishing pressure and other environmental variables, not assessed in their study, may have played a role in reducing increments over recent decades. This provides further evidence that the

mechanism or mechanisms driving the size variation may not be limited to temperature alone.

The GAM used in this study indicates that whilst the size of young fish is limited by conspecific density, older plaice are larger at mid-range densities. However, we acknowledge that our use of an average location-based competition metric across full $1 \times 1°$ cells may not adequately capture the experienced competition that might significantly influence size variation. Existing studies have provided some insight into the mechanism by which competition may play a role in size variation. Given that conspecific density is likely a proxy for competition, this indicates that growth may be constrained in young fish due to high intraspecific competition [also seen in Ciotti et al. (2013) and van der Sleen (2018)]. Older fish can travel further and faster (Rijnsdorp and Pastoors, 1995), enabling dispersal of individuals to the most suitable habitats and feeding grounds, where higher densities can potentially be sustained. However, the GAM model results also suggest that high levels of interspecific competition for older plaice (ages 6 and 7) result in limits to growth (as previously reported by Rijnsdorp and van Leeuwen, 1996). Fine-scale detail of localized plaice movements and matching intraspecific competition data at the same scale would be required in order to explore this further. Additionally, North Sea plaice are part of complex multispecies communities therefore, competition for resources will depend on both inter and intraspecific competition.

Also of note here is the recent significant increase in plaice stocks across the North Sea, increasing dramatically from a very low spawning stock biomass (SSB) in 1999 to a relatively high biomass in 2013, likely as a response to a pronounced reduction in fishing pressure (ICES, 2022). It is possible that this increase in conspecific SSB may have resulted in increased competition, although not to the levels of historic maxima (Rogers and Ellis, 2000), as high fishing pressure has been recorded since the 1890s (Rijnsdorp and Millner, 1996).

The GAM outputs from our study further suggest that plaice are smaller at high phosphate levels. As high phosphate is generally expected to correlate with increased growth in young fish (Rijnsdorp et al., 2004), this result may suggest a mismatch between the granularity of our data ($1 \times 1°$ cell averages) and a highly localized impact of nutrient levels (Menesguen et al., 2018) influencing plaice growth. We propose that the observed co-variance of high near-coast plaice densities, high coastal phosphate inputs, and lower latitude temperatures (identified as moderately correlated with phosphate in the VIF analysis for some ages) likely complicates growth trends.

The role of fisheries in driving dimorphic size between the sexes

The North Sea has experienced high exploitation for centuries (Barrett et al., 2011) and continues to experience widespread fishing pressure (Couce et al., 2020), resulting in reduced total fish biomass (Jennings and Blanchard, 2004), altered abundances (Lynam et al., 2017), truncated age structures (Rouyer et al., 2011), and fisheries-induced changes in individual size, alongside changes to habitats through mobile demersal fishing (van Denderen et al., 2015; Kenny et al., 2018; Couce et al., 2020).

When considering the size of male plaice across the North Sea, we suggest that FIE has played a role in both reducing

abundance and average size, especially in heavily fished southern waters (Grift *et al.,* 2003). Previous studies show that males spend more time at spawning grounds than females (Arnold and Metcalfe, 1996), and are more susceptible to capture during spawning periods (Beverton, 1964; Rijnsdorp, 1993), thus amplifying the effects of fishing on males compared to females. Beyond increased vulnerability to fishing pressure, males also mature younger and at a smaller size than females (Rijnsdorp and Ibelings, 1989). Higher mortality rates in males are also predicted due to the higher costs of their "all or nothing" spawning strategy (Swain, 2011). The combined likely outcome of fishing effects and the male reproductive strategy is a disproportionate reduction in the number of males compared to females. Yet the high gamete production in males also at small size may dilute or remove any overall impact on the reproductive success of the species. Fishing pressure is also implicated in accelerating size-based selection to favour males that mature below the minimum catch size of 27 cm. Historic and current heavy fishing pressure continues in the southern North Sea (Figure 1), including the use of small-mesh sole (*Solea solea*) nets (Engelhard, 2008; Engelhard *et al.,* 2011), potentially driving the overall reduction in southern male size (Figure 3). Another possibility is that the genetic variation upon which selection can act may be broader in males than in females. For example, male guppies have been shown to respond more rapidly to changes in selection pressures than females due to higher genetic variance for age and size at maturity (Reznick *et al.,* 1997). In line with the results presented here, a study of southern North Sea plaice between the 1970 and 1990s found only males reduced in size, providing further evidence of sex-specific impacts of fishing pressure (Baudron *et al.,* 2014). If males are indeed experiencing more rapid evolutionary change than females, efforts to restore stocks of plaice could actually increase the size difference between the sexes. Females may be able to rebound faster when released from fishing pressure, since recovery from evolutionary change is slower than more plastic phenotypic changes (Rijnsdorp *et al.,* 2010), and males may have a smaller genetic pool than the females from which to breed.

Although fishing pressure tends to reduce the overall size of fish, it has also been shown to encourage faster growth in younger fish. When analysing plaice across the North Sea as a whole, the data suggest an increase in fish size with increasing current fishing effort, particularly in fish aged 1–3. The mechanism for faster growth is hypothesized to be fishing pressure resulting in reduced competition, fewer predators, and more accessible prey enabling faster growth (Engelhard *et al.,* 2011). Previous studies support the following framework; that with faster growth in younger plaice under high fishing pressure, fish reach maturity at a smaller size (Sharpe and Hendry, 2009) and grow faster to optimize their reproductive output (Jennings *et al.,* 1999).

Reliability of otolith size as a proxy for fish size variation

The use of otoliths to estimate size-at-age by sex to extend the available data series did not corroborate the fish size-at-age size patterns based on fish length measurements observed in this fragmented North Sea population. This may be due to survival ability in older fish being determined by early growth characteristics, potentially affecting the comparisons between

early growth increments from older fish to fish caught, and measured, at young ages (i.e. "Lee's phenomenon": Lee, 1912; Morrongiello *et al.,* 2012). Spatially variable environmental conditions also have the potential to affect the relative relationship between otolith increments and fish length (Morrongiello and Thresher, 2015). To produce a reliable relationship between otolith width and fish length in the context of this study, we would have required greater replication from all age groups and areas, with the potential for different relationships to be calculated for separate sub-groups and sexes (Morrongiello and Thresher, 2015). Our work highlights some of the challenges of using sclerochronology as a proxy for fish size variation in samples experiencing fine-scale environmental variation, as differing conditions have the potential to influence growth trajectories between different sampled groups. The relationship between fish size and otolith increment widths to analyse growth under different environmental conditions should be considered when using otoliths to explore fish size variation over environmental gradients (Rountrey *et al.,* 2014; Ong *et al.,* 2015). Given the observed disparity between otolith fish size-at-age estimates and fish length-at-age, we used only direct length measurements in our wider analyses to arrive at the conclusions drawn in this study.

Conclusion

Whilst the spatial separation of plaice provides a prime opportunity to investigate the impact of different conditions on plaice size, our results highlight that in heavily fished stocks, fish may not respond as predicted. For example, the narrow age distribution for plaice has resulted in limited opportunities for individuals to reach a size at which temperature becomes limiting. However, other accepted drivers of growth are seen to influence plaice size, with average location-based conspecific density and fishing effort both appearing to play a role. The growth responses to variability in the physical environment seem to be influencing the distribution of young (to age 7) plaice, in line with the movement of larger individuals offshore into deeper and preferred habitats.

As the North Sea continues to warm, and innovative survey and monitoring techniques broaden data availability, further opportunities will arise to investigate how environmental and anthropogenic influences affect key commercial fish stocks. Better historic growth trends may also be identified if adequate otolith records for both sexes from across the full spatial and environmental range are collated and tuned. Robust otolith-derived size estimates at age will enable the gap filling of more disparate historic length-at-catch data. Given the relatively fixed summer/autumn North Sea survey season, there may be value in collating available data from wider surveys, potentially including commercial records, across the full year. More comprehensive spatio-temporal coverage of plaice movements, especially for the less studied males, may be driving some of the variations in size and abundance. In addition to fish data, access to more granular environmental data such as habitat types and coastal temperatures, alongside details of changes to stratification, may provide insights that are not yet possible at a less-refined spatial scale.

Acknowledgements

International Council for the Exploration of the Sea (ICES) International Bottom Trawl Survey (IBTS) and Beam Trawl Survey (BTS) for collecting and providing survey data and otolith samples. We would like to particularly thank the survey data and otolith archive team at Cefas, including Mark Etherton, Sally Songer, Glenn Saunders, Suzy End, Jo Smith, and Gary Burt.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Funding

Author contributions

S.D.S., E.H., and L.A.R. conceived the research; S.D.S., M.J.G., E.H., L.A.R., and G.H.E. contributed to project development; L.A.R. pre-processed fisheries agency and climate data and otolith samples; M.J.G., L.A.R., E.H., and G.H.E. designed the analysis; L.A.R. conducted the analysis; L.A.R., and E.H. prepared the initial manuscript and all authors contributed to revisions.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Handling Editor: Jan Jaap Poos