



Growth as a measure for environmental conditions and relatedness of North Sea fish stocks

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ABSTRACT: Information about the ecological connections between species is needed to make the shift from fisheries management strategies centred around single species to ecosystem-based fisheries management. Growth rates of fish strongly depend on the environment. Individual growth curves could therefore contain valuable information about the environmental conditions experienced by an individual throughout its life. In this study, we explored whether estimated growth curves contain information about the competition within and between species. We estimated growth curves for 10 species in 10 North Sea roundfish areas based on length-at-age data from the North Sea International Bottom Trawl Survey (NS-IBTS) fish survey by fitting a von Bertalanffy growth model with varying asymptotic length. From these model fits, we extracted a relative measure for the temporal variation in growth in body size of a stock, which can be used as an indicator of the experienced environmental conditions. We found signs of density-dependent growth in at least 6 out of the 10 species for some specific areas as well as all North Sea areas combined. In addition, we used cluster analysis to explore the relatedness in ecological growth conditions between species and areas. Ecologically related species tended to show more similar temporal variation in ecological growth conditions than ecologically more distant species. Likewise, areas that were geographically closer showed more similarity in ecological growth conditions compared to geographically more distant areas. This suggests that information on ecological conditions derived from growth curves provide a useful way to distinguish ecological groups or regions without the need for additional stomach sampling or ecological studies.

KEY WORDS: Environmental factors · Growth limitation · Ecological niche · Fish ecology · North Sea · von Bertalanffy · North Sea International Bottom Trawl Survey · NS-IBTS

1. INTRODUCTION

About 3 decades ago, general concern about the sustainability of large-scale fisheries arose. Most of the commercially exploited fish stocks were in decline and showed clear signs of overexploitation (Cook et al. 1997, Beverton 1998, Pauly et al. 2002). The widespread fear of aquatic ecosystem collapse and stock overexploitation led to a consensus about the need to reform fisheries management. The intensified management of fish stocks seems to be paying off, as numerous stocks

show signs of recovery (Worm et al. 2009, Hutchings et al. 2010, Cardinale et al. 2013, Fernandes & Cook 2013, Zimmermann & Werner 2019, Rindorf et al. 2020, Wang et al. 2020). Due to improvements in fisheries management, estimated stock biomass for several stocks has reached sufficient numbers to produce maximum sustainable yield, which is considered a low-risk scenario (Froese et al. 2018, Zimmermann & Werner 2019).

The positive trend in the recovery of fish stocks does not mean that the current fisheries management practices cannot be improved further (Zimmer-

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mann & Werner 2019), especially because a substantial number of global fish stocks are still over-exploited (FAO 2020). In addition, commonly used stock assessment models fail to predict large temporal changes in the dynamics of the abundance, structure and yield from fish stocks (Hilborn et al. 2020, Britten et al. 2021). This mismatch between predictions and reality can be partly explained by the lack of data on the dynamics of some stocks, but is likely also a result of the ecological context in which stocks are considered (Jardim et al. 2021). Most management models consider fish stocks in isolation and only use stock quantities such as the spawning stock biomass to predict the ecological dynamics of a stock. This assumption conveniently simplifies the calculation of reference points, but it is clear that environmental conditions and ecological interactions between species are important drivers of the dynamics of exploited fish stocks (Andersen et al. 2015, Säterberg et al. 2019). Based on this insight, ecosystem-based management starts to gain importance in the consideration of fishing quotas.

Ecosystem-based approaches to fisheries management have in common that they require some level of information about the ecological connections between species (May et al. 1979, Birkenbach et al. 2020). Most of the current knowledge on interactions between fish species is based on stomach samples, physiological similarities and occurrence patterns (Rice & Kronlund 1997, Rochet et al. 2011, Matley et al. 2018). Studying ecological relatedness in these ways is often time-consuming and based on limited data. In addition, the results from these studies are often inconclusive or very spatial or population-specific (Amundsen & Sánchez-Hernández 2019, Cadrin 2020). A more general measure of the response of species to the environment is needed to understand the ecological relatedness between co-occurring species. The body size of individuals might contain important information about the environment experienced by a stock, because fluctuations in the environment often affect the growth of individual fish (Croll & van Kooten 2022). In this article, we explore to what extent temporal variations in growth curves of fish species contain information about the experienced environment and the interactions within and between populations.

Growth in body size is an important life history process. Growth requires a substantial amount of the assimilated resources of an individual and eventually determines the size of an individual. In this way, growth is strongly linked to other life history processes such as consumption, reproduction and mor-

talidity. Growth curves of fish generally show a high degree of variation and a strong link to the environment. For example, changes in growth rates of fish are linked to changes in temperature and stock biomass (Pauly 1980, Lorenzen & Enberg 2002, Lorenzen 2008, Tu et al. 2018, Rindorf et al. 2022). The link between growth rates and temperature arises because temperature affects the metabolic rates of an individual (Kooijman 2000). In contrast, the link between growth rates and stock biomass is likely to emerge through competition. A higher stock biomass increases competition and reduces the resource availability per individual, which could be a limiting factor for individual growth. In addition, an interaction between temperature effects and competition might arise because changes in temperature might affect the food requirements of an individual, while it might also have a direct effect on the food source itself. Growth rates are even argued to respond to harvesting pressure through evolution, although similar patterns could also emerge through the effects of harvesting on the competition and food availability within a stock (Enberg et al. 2012, Heino et al. 2015). The growth curves of individuals in a stock thus contain valuable information about the environment that individuals experienced.

In this article, we explore what information about ecological similarities and competition within and between exploited North Sea fish stocks can be obtained from growth curves. The von Bertalanffy growth curve is a classic way to describe growth of fish species and assumes that growth is a balance between energy assimilation and catabolism for processes other than growth (von Bertalanffy 1938). The link of assimilation and catabolism rates with the von Bertalanffy growth rate is well established in energy budget theory, which suggests that the asymptotic length of the von Bertalanffy growth rate is mainly connected to environmental factors through anabolism, while the von Bertalanffy growth scalar is mainly linked to internal processes through catabolism (Kooijman 2000). The growth curves were fitted to fishery survey data of 10 exploited North Sea fish stocks using the method developed by Croll & van Kooten (2022). This method is tailored to fit von Bertalanffy growth curves to length-at-age observations from fisheries surveys and accounts for variation in growth between cohorts and individuals as well as temporal variation. By applying this technique, all temporal variation in growth curves is summarized in a yearly varying asymptotic length, which we used as an indicator of the effects of environmental conditions on individual growth. We scale and

normalize the asymptotic length such that it is comparable between areas and species and use this as a corrected measure of the environmental growth conditions (EGCs). To gain insight into the asymptotic length as a measure for the impact of competition on growth, we first explored trends in the corrected EGCs with time and stock biomass. In addition, we performed cluster analysis on the normalized EGCs to explore whether these growth curves contain information about the overlap of the environment experienced by the fish stocks.

2. METHODS

2.1. Data collection

We used the sex-maturity-age-length-key (SMALK) data and the catch per unit effort (CPUE) per length per haul per hour data from the North Sea International Bottom Trawl Survey (NS-IBTS) to fit growth curves and estimate stock density, respectively. The data were downloaded from the ICES DATRAS database in January 2022 (<https://datras.ices.dk>). The NS-IBTS is a broad-scale survey conducted in the North Sea region between the British Isles, The Netherlands, Denmark and Norway. The survey uses standardized bottom trawl gear to target demersal stocks. The survey has been conducted since 1965 and is performed throughout the year. In this study, we focused on data collected in the first quarter of each year (January to March), because this quarter includes the largest number of data points and covers the largest number of years. Growth periods in this study therefore spanned from the first quarter of a year to the first quarter of the following year. We performed our analysis for 10 species which are labelled as the target species of the NS-IBTS (ICES 2020): plaice *Pleuronectes platessa*, witch *Glyptocephalus cynoglossus*, Atlantic herring *Clupea harengus*, European sprat *Sprattus sprattus*, Atlantic mackerel *Scomber scombrus*, Norway pout *Trisopterus esmarkii*, saithe *Pollachius virens*, whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua*. The data were split and analysed separately for every spe-

cies and the 10 roundfish regions (Fig. 1), which are commonly used to analyse length and age relations for the NS-IBTS species (ICES 2020).

The SMALK data report individual specific combinations of length and age measurements, represented as the number of individuals observed with a specific age-length combination in every year and area. Lengths are recorded in 5 or 10 mm intervals and ages are recorded in years. Individuals above a pre-determined, species-specific age are recorded as a plus-group. To make the SMALK data suitable for our analysis, the data of every species and area were processed in several steps. First, all observations with missing age or length values were removed. Second, all plus-groups were removed from the data, because the exact age of these individuals was unknown, which could have introduced biases when fitting growth curves. Third, early years were discarded until the number of individual age-length observations in the first year exceeded the number of age groups in the analysis for the specific species and area combination. Similarly, low and high age classes were discarded until the number of individual age-length observations in the youngest and oldest age

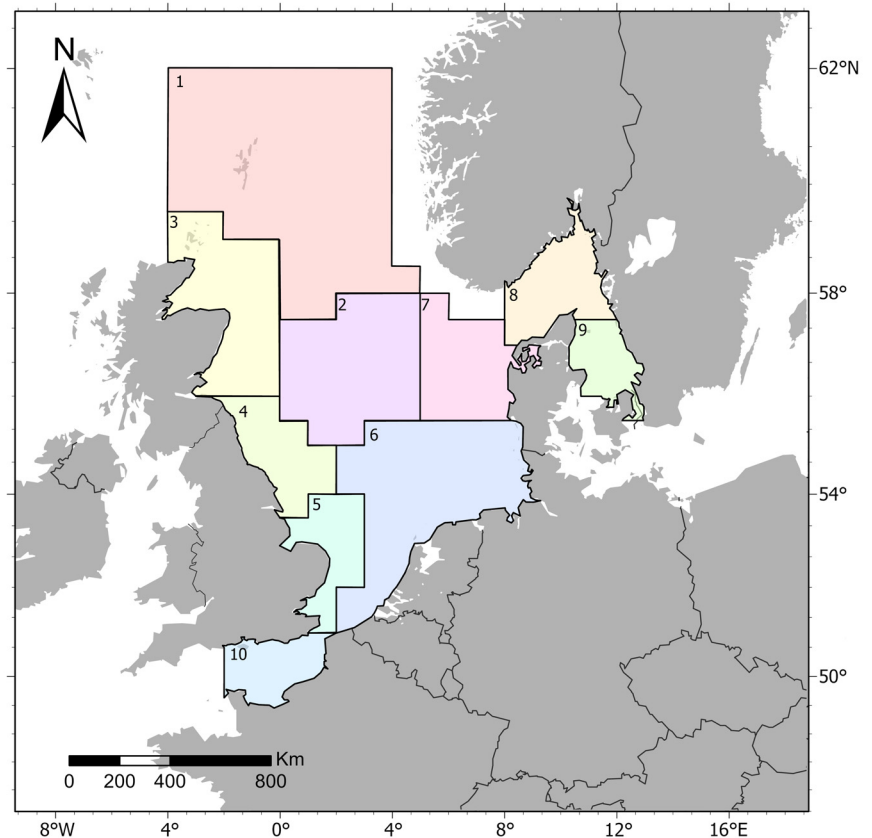


Fig. 1. Roundfish areas used for the North Sea International Bottom Trawl Survey (NS-IBTS) data

groups exceeded the number of years in the analyses for the specific species and area combination. Last, areas in which the number of age and year combinations exceeded the number of observations were excluded from the analysis entirely (see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m725/p057_supp.pdf, for all supplements).

The CPUE data contain a relative measure of the number of individuals caught per hour in every 5 or 10 mm length class for every haul for every species and area combination in the survey. We used this metric to derive a relative proxy for the population biomass. Every length class was represented by the length midway between the length class boundaries. This length was converted to individual mass using a power scaling between individual length (ℓ , mm) and mass (M , g):

$$M = a\ell^b \quad (1)$$

The values of a and b are species-specific scalars which are derived from FishBase (Froese & Pauly 2021) (Table 1). We used the length–weight relationships from FishBase because the NS-IBTS data lacked sufficient information to construct an accurate length–weight relationship for some species. The use of the length–weight relationship from FishBase also minimizes the relationship between the length-at-age data used to fit the growth curves, which are used as a dependent variable in the analysis, and the estimated stock biomass, which is used as an independent variable in the analysis. The individual mass was multiplied with the CPUE per length and summed per haul to obtain the total biomass per unit effort (BPUE). The separate values of the BPUE were averaged over all hauls within a year for every area and species. This quantity was used as a relative

Table 1. Species-specific scalars for the individual length-to-mass conversion following a power scaling ($M = a\ell^b$; M = mass, ℓ = length). Values are taken from FishBase (Froese & Pauly 2021)

Species	a	b
Plaice	0.00794	3.07
Witch	0.00490	3.09
Herring	0.00562	3.09
Sprat	0.00575	3.06
Mackerel	0.00646	3.06
Norway pout	0.00589	3.06
Saithe	0.00636	3.06
Whiting	0.00617	3.06
Haddock	0.00646	3.08
Cod	0.00676	3.08

proxy of the population biomass in a given area for a given year. The biomass in terms of BPUE was used as a measure for potential environmental impact, instead of the abundance in terms of CPUE, because we expect the environmental impact of an individual to increase with body size. This is in line with the derivation of the von Bertalanffy growth curve from energetic theory which assumes that the link with the environment through assimilation scales with body size (Kooijman 2000, Croll & van Kooten 2022).

2.2. Fitting growth curves

The von Bertalanffy growth curve can be described by the following recursive equation:

$$\ell_{(T+1,a+1)} = \ell_{(T,a)}e^{-r_B} + \mu_T\ell_\infty(1 - e^{-r_B}) \quad (2)$$

which describes the length of an individual at a given time and age ($\ell_{(T,a)}$) using the asymptotic length ($\mu_T\ell_\infty$) and the von Bertalanffy growth scalar (r_B). The asymptotic length is determined by the limitation of the environment at a given time (μ_T) and the asymptotic length without environmental limitation (ℓ_∞). By assuming the environmental limitation follows a Gaussian distribution with a varying mean ($\bar{\mu}_T$) and variance ($\bar{\sigma}_T^2$), Croll & van Kooten (2022) derived recurrence relations describing the length-at-age distribution of a cohort in terms of the expected value or mean ($E[\ell_{(T,a)}]$) and variance ($V[\ell_{(T,a)}]$) of the length-at-age distribution:

$$E[\ell_{(T+1,a+1)}] = E[\ell_{(T,a)}]e^{-r_B} + \bar{\mu}_T\ell_\infty(1 - e^{-r_B}) \quad (3a)$$

$$V[\ell_{(T+1,a+1)}] = V[\ell_{(T,a)}]e^{-2r_B} + \bar{\sigma}_T^2\ell_\infty^2(1 - e^{-r_B}) \quad (3b)$$

The model described by Eqs. (3a) & (3b) was fitted separately to the SMALK data for every species and area combination following the procedures outlined by Croll & van Kooten (2022) and using the ‘VBGfit’ package in R (Croll 2022). In the fitting procedure, Eqs. (3a) & (3b) were used to predict the length-at-age distribution for every cohort in every year, characterized by the expected value ($E[\ell_{(T,a)}]$) and variance ($V[\ell_{(T,a)}]$) of the distribution. The likelihood of the individual length-at-age measurements from the SMALK data were calculated using these predicted distributions. The likelihood of the model with a set of parameter values was calculated by the product of the likelihoods of the individual length-at-age measurements. For every species and area combination, the model was fitted separately by minimizing the log of the likelihood of the model using the Sbxpl algorithm from the ‘NloptR’ package (Johnson 2021).

This resulted in the values of the model parameters consisting of 1 value for the von Bertalanffy growth scalar (r_B), the mean and variance in length at the youngest age for every year ($E[\ell_{(T,a_{\min})}]$, $V[\ell_{(T,a_{\min})}]$), the mean and variance in length at all ages in the first year ($E[\ell_{(T_{\min},a)}]$, $V[\ell_{(T_{\min},a)}]$) and the mean and variance in asymptotic length for every year ($\bar{\mu}_T \ell_\infty$, $\sigma_T^2 \ell_\infty^2$). The von Bertalanffy growth scalar thus applies to all individuals in all years but might differ between areas because the model is fitted separately for every area and species combination. The mean asymptotic length varies between years and areas but applies to all cohorts of a species in a given area and year. We used this mean asymptotic length as a general indicator of the impact of the environment on the growth of individuals of a species in an area and year. An increase in the asymptotic length indicates that the environment of an individual becomes more favourable and the individual therefore grows faster and bigger.

2.3. Correcting the fitted asymptotic length

The fitted asymptotic length is an indicator for the impact of the environment on the growth of an individual, but because these values were fitted separately for every species and area combination, the values cannot be directly compared between species and areas. Therefore, we processed the time series of the mean asymptotic length in 3 steps as described below to obtain a value of the EGC that is suitable for comparison between areas and species.

First, the asymptotic length fitted by the model is not reliable in years without sufficient data points (Croll & van Kooten 2022). A lack of data points affects the fitted asymptotic length in the year before and after the survey period with lacking data. Because the effects in those 2 years cancel each other out, the effect of missing data does not propagate to other years. Therefore, the fitted asymptotic length of the year before and after an observation period with fewer than 2 data points per age class were excluded from further analysis. This results in a gap in some of the time series for the mean asymptotic length. These gaps did not contribute to further analysis.

Second, the asymptotic length ($\bar{\mu}_T \ell_\infty$) and the von Bertalanffy growth scalar (r_B) cannot be estimated separately, which results in a spurious relationship between the estimated asymptotic length and the von Bertalanffy growth scalar between areas (Pilling et al. 2002, Eveson et al. 2007). This could result in a pattern in which the value and variation of the esti-

mated asymptotic length is high in areas with a low estimated von Bertalanffy growth scalar and low in areas with a high estimated von Bertalanffy growth scalar. We used a series of linear regressions to correct for this spurious relationship using the linear model functions in R (R Core Team 2023) (see Supplement 2 for the statistical formulas). The first linear regression was used to quantify the correlation between the asymptotic length ($\bar{\mu}_T \ell_\infty$) and the inverse of the growth scalar ($1/r_B$). This correlation was significant for several species. The spurious relationship between the value of the asymptotic length and the growth scalar was corrected by taking the residuals of this linear regression model for all species. This removes the effect of the growth scalar on the value of the asymptotic length. We therefore continue the analysis with the residual asymptotic length.

We expressed the variation in the residual asymptotic length within an area as a fraction of the standard deviation of the residual asymptotic lengths in every area. A second linear regression was used to quantify the spurious correlation between standard deviation of the residual asymptotic lengths and the inverse of the growth scalar. This relationship was significant for several species. For all species, we divided the residual asymptotic length by the predicted values of the second regression to correct for the effect of the growth scalar on the amplitude of the fluctuations in the asymptotic length. These corrections resulted in a quantity of which the value and standard deviation are independent of the von Bertalanffy growth scalar and can be compared between areas. This quantity is still related to the estimated mean asymptotic length and contains the same information about the environment experienced by the individuals in a stock, but has different absolute values. We will therefore refer to this quantity as the corrected EGC.

Third, the corrected EGC still differs in value and variance between species. These absolute differences emerge from the physical differences between species. To enable comparison of the general patterns in corrected EGC between species, we normalized the corrected EGC of all species by subtracting the mean and dividing by the standard deviation of the corrected EGC per species. This resulted in a normalized value of the EGC. This value can be used for comparison between areas and species, because it is corrected for the possibly spurious relationship between the estimated asymptotic length and the von Bertalanffy growth scalar as well as the physical differences between species that are not caused by the environment.

2.4. Analysis of EGCs

We first analysed general trends in the corrected EGC with respect to time and BPUE using linear regression in which the corrected EGC is the dependent variable and either time or BPUE is the independent variable. This was done separately for every area and species combination as well as all areas combined for every species.

In addition, we explored the relatedness of the normalized EGC between species and between areas. Dissimilarities between species were calculated as the mean squared difference between the normalized EGC in a given year and area because the mean square difference eliminates the sign of the difference and is comparable between species combinations with various numbers of overlapping year and area combinations. Likewise, the dissimilarities between areas were calculated as the mean squared difference between the normalized EGC for a species in a year. Dissimilarities were only calculated for pairs of species or pairs of areas if they contained EGC values for at least 5 overlapping area–year or species–year combinations, respectively. This resulted in dissimilarity matrices for the dissimilarity between all species pairs in each area and between areas for each species separately. If overlap in the time series of normalized EGC between 2 species or areas was insufficient, the dissimilarity between these species or areas was set to the average dissimilarity in the dissimilarity matrix. This additional step was only necessary for the dissimilarity between witch and mackerel due to several data-lacking years for these species. These dissimilarity matrices were analysed using several clustering methods (complete linkage, average [unweighted pair group method with arithmetic mean, UPGMA] and McQuitty [weighted pair group method with arithmetic mean, WPGMA]). These clustering procedures cluster pairs of species or areas with the lowest dissimilarity, after which the species or area in the cluster is replaced with a single entry for the cluster in the dissimilarity matrix. This is repeated until all initial species or areas are part of the same cluster. The 3 clustering methods differ in the way the dissimilarities between the new cluster and the other species, areas or clusters are calculated. All 3 clustering methods consider the dissimilarity between all members of a cluster and another species, area or cluster. The complete linkage method uses the largest of these dissimilarities, the UPGMA method takes the unweighted average of these dissimilarities, and the WPGMA method takes the weighted average of these dissimilarities as the dissimilarity to the new cluster.

Multiscale bootstrapping with 10000 repeats was performed on the normalized EGC to calculate the probability of appearance of clusters using the 'pvclust' package in R (Suzuki & Shimodaira 2006). In this bootstrapping procedure, the normalized EGC data were resampled with replacement in which the number of samples taken varied between repeats (Shimodaira 2002). Because the results of the various clustering methods were very similar, we only show the results from the average (UPGMA) clustering in the main text and include the results of the other clustering methods as supplementary figures (Figs. S14 & S15 in Supplement 3).

3. RESULTS

3.1. Estimating EGCs

We fitted growth curves of 10 fish species in 10 roundfish areas based on the length-at-age data from the NS-IBTS (Fig. 2a–c; Figs. S1–S10 in Supplement 1). In total, 78 out of 100 of the species–area combinations contained sufficient data to fit the von Bertalanffy growth model (Fig. 2d; Fig. S11 in Supplement 1). This resulted in time series of the estimated asymptotic length which differed strongly in time span, ranging from only 1 or 2 yr to the full time span of 50 yr (Table S1).

Eight out of the 10 species (plaice, haddock, herring, sprat, Norway pout, saithe, whiting and cod) showed a significant positive relationship between the estimated mean asymptotic length and the inverse of the growth scalar ($p < 0.05$). This relationship accounted for a substantial amount of the variation in the estimated mean asymptotic length between areas for some of the species ($0.8287 > R^2 > 0.0205$) and resulted in large differences in the estimated mean asymptotic length between areas (Fig. 2e; Fig. S12 in Supplement 2). Five of these species (plaice, Norway pout, whiting, haddock and cod) showed a significant positive relationship between the standard deviation in the estimated mean asymptotic length and the estimated growth scalar as well ($p < 0.05$, $0.9681 > R^2 > 0.608$) (Fig. 2f; Fig. S13 in Supplement 2). We obtained the corrected EGC by correcting the fitted asymptotic length for the spurious relationship with the von Bertalanffy growth scalar. After this correction, the corrected EGC values and the standard deviation herein did not correlate with the inverse of the growth scalar anymore, except for cod, which showed a slight positive relationship between the corrected EGC and the inverse growth scalar. This remaining relationship for cod explained a neg-

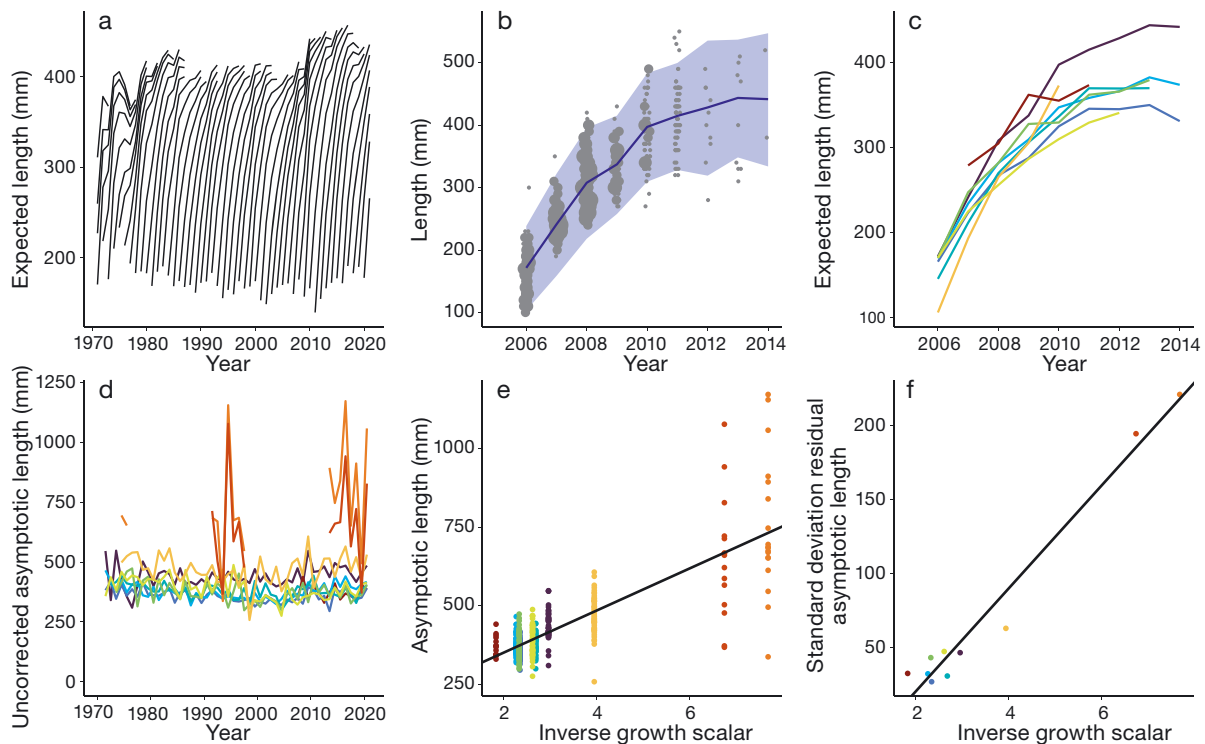


Fig. 2. Model predictions, model output and corrections for whiting. (a) Expected length of every cohort in area 1 predicted by the model. (b) Expected length and region in which 95% of the individuals are expected for the cohort born in 2005 in area 1 predicted by the model. For comparison, grey dots indicate the datapoints from this cohort used in fitting the model. (c) Expected length for all cohorts born in 2005 as predicted by the model. (d) Uncorrected asymptotic lengths as fitted to the data. (e) Spurious relationship between the fitted asymptotic size and the inverse of the fitted growth scalar. (f) Spurious relationship between the standard deviation in the fitted asymptotic size and the inverse of the fitted growth scalar. Similar figures for the other species are included in Figs. S1–S10 in Supplement 1

ligible amount of variation in the corrected EGC between areas ($R^2 = 0.0156$ after correction against $R^2 = 0.8287$ before correction).

In general, the corrected EGC is centred around zero due to the corrections made (Fig. 3). Most values of the corrected EGC fall between -2.5 and 2.5 , which is roughly 2 times the standard deviation of the corrected EGC for all species. Nonetheless, the corrected EGCs for the analysed species show some extreme values between -7.5 and 7.5 , which usually occur in a series of years with limited data. The time-series of the corrected EGC show large year-to-year fluctuations, which makes it difficult to distinguish patterns in specific areas by eye (Fig. 3). The general patterns over time and similarities between species will be explored further in the following sections.

3.2. General trend in environmental growth conditions

Seven of the 10 species (plaice, herring, sprat, mackerel, whiting, haddock, cod) showed a negative

trend in the corrected EGC in at least one ICES roundfish area (Table 2, Fig. 4). This indicates that the environmental conditions deteriorated over time, resulting in a decrease in the length-at-age over time. For 5 of these species (plaice, herring, sprat, haddock, cod), the negative trend in corrected EGC was also apparent on a larger scale when the corrected EGC data from all areas were combined (Table 2, Fig. 4). This significant negative trend over all areas remained for plaice and sprat when only the corrected EGC from 2000 onward was considered and remained for herring, haddock and cod when only the corrected EGC before 2000 was considered (data not shown). Interestingly, mackerel and Norway pout only showed a significant negative trend over all areas when only the corrected EGC before 2000 was considered and whiting even showed a negative trend in corrected EGC before 2000 and a positive trend in EGC from 2000 onward (data not shown). This might suggest there is a change in the trend in corrected EGC for these species.

In total, 78 out of 100 species–area combinations contained sufficient data to analyse the effect of the

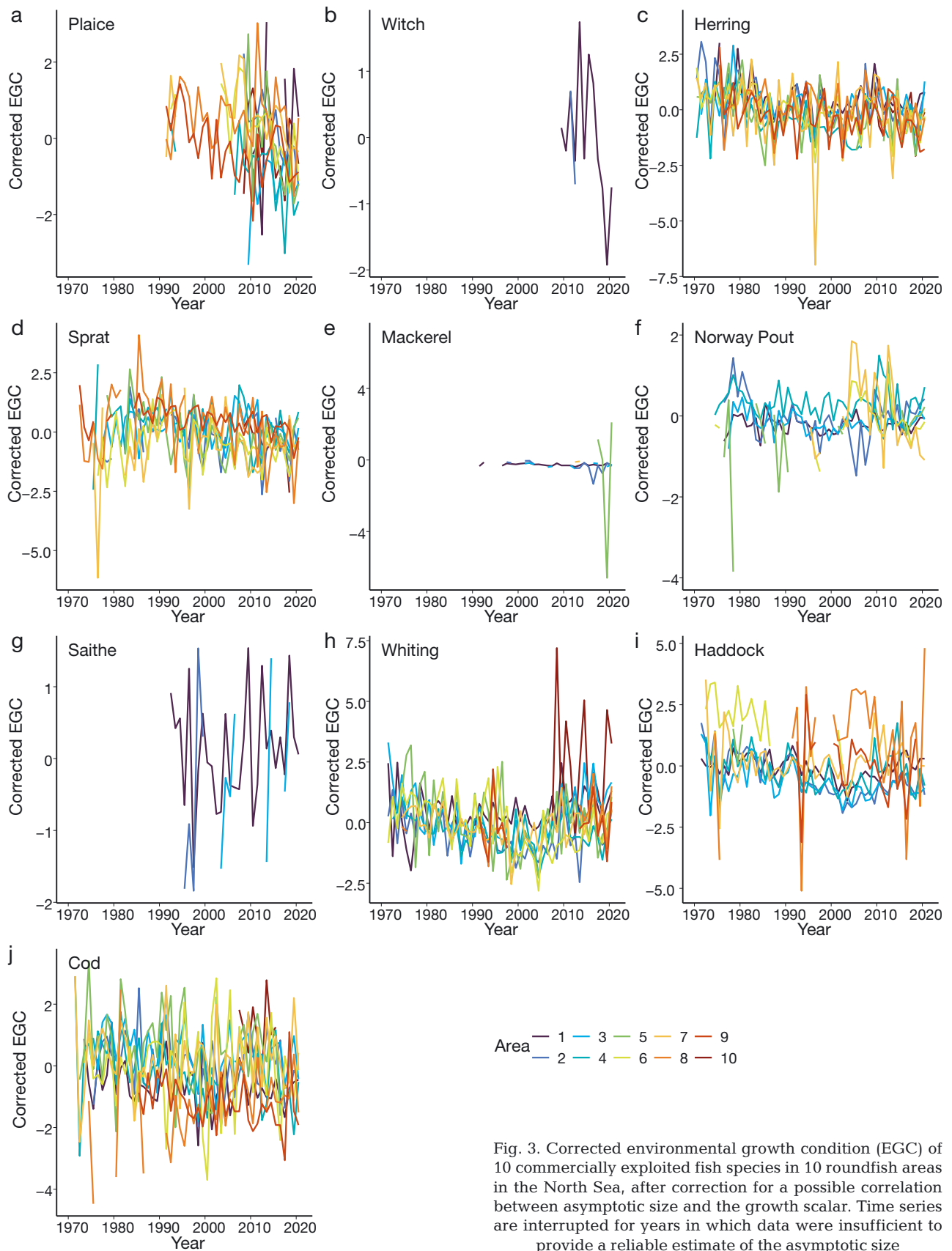


Fig. 3. Corrected environmental growth condition (EGC) of 10 commercially exploited fish species in 10 roundfish areas in the North Sea, after correction for a possible correlation between asymptotic size and the growth scalar. Time series are interrupted for years in which data were insufficient to provide a reliable estimate of the asymptotic size

Table 2. Linear relationship between the corrected environmental growth conditions (EGCs) and the years for which the EGCs are calculated for 10 North Sea fish species. Slopes of the relationship are presented for the analysis including data from all 10 roundfish areas. *Significance of the slope (** $p < 0.01$, *** $p < 0.001$). In addition, we indicate the areas in which the slope of the relationship is negative as well, when only considering data from 1 area. **Bold** font highlights important results

Species	Slope	Individual areas with a significant slope
Plaice	-0.0430***	4/10 (areas 2, 4, 6, 9)
Witch	-0.1196	0/2
Herring	-0.0189***	6/10 (areas 1, 2, 4, 5, 6, 9)
Sprat	-0.0162***	3/10 (areas 5, 9, 10)
Mackerel	-0.0003	1/6 (area 3)
Norway Pout	0.0023	0/7
Saithe	0.0151	0/3
Whiting	-0.002	2/10 (areas 4, 6)
Haddock	-0.0186***	4/9 (areas 2, 3, 4, 6)
Cod	-0.0130**	3/10 (areas 3, 4, 9)

BPUE on the corrected EGC (Table 3, Fig. 5). The corrected EGC was negatively correlated with BPUE for 5 species (herring, Norway pout, whiting, haddock, cod) when considering all areas together. For 4 of these species (herring, Norway pout, whiting, haddock), a negative relationship between corrected EGC and BPUE was found in at least one area. These negative correlations all occurred in roundfish areas 1 to 4, which are the more north-western areas in the North Sea. Sprat also showed a negative relationship between the corrected EGC and BPUE in area 3, but this relationship did not persist when all areas were analysed together. In contrast to the negative correlation when all areas were analysed together, cod showed a positive correlation between the corrected EGC and BPUE in area 5.

3.3. Clustering

We clustered the 10 species based on the normalized EGC in all areas and years with 3 cluster methods. This resulted in several consistent species clusters, occurring with every clustering method. Here we only show the results using the average (UPGMA) clustering. The first cluster consists of plaice and witch, which are the 2 flatfish species in our analysis (red cluster, Fig. 6). These flatfish species cluster together with 2 small forage fish species, herring and sprat, although with a relatively low bootstrap probability (green cluster, Fig. 6). Mackerel and Norway pout are pelagic species of intermediate length and

cluster together with saithe, which is a somewhat larger pelagic species (blue cluster, Fig. 6). The last cluster consists of whiting and haddock, which are both larger species that partly forage on smaller fish species (purple cluster, Fig. 6). Cod is the largest predatory fish in the data and does not cluster with the other species.

Likewise, we clustered the 10 roundfish areas in this analysis based on the normalized EGC (Fig. 7). This resulted in a big cluster of the north-western roundfish areas 1 to 4, with a relatively high bootstrap probability (red cluster, Fig. 7). Another cluster consists of areas 5 and 6, which are 2 large adjacent regions in the south of the North Sea (green cluster, Fig. 7). Areas 8 and 9 form the Skagerrak and Kattegat areas between Denmark, Norway and Sweden which cluster together as well (blue cluster, Fig. 7). Geographically, area 7 is connected to all above-mentioned clusters, but it is unclear to which cluster area 7 belongs. This might suggest that there are some strong links between the clustered areas. Lastly, area 10 does not cluster well with any of the other areas. This is likely because area 10 is only present in the survey from 2009 onward and is relatively isolated geographically.

4. DISCUSSION

We fitted von Bertalanffy growth curves for 10 exploited North Sea fish stocks in 10 roundfish areas over a period of 50 yr. The temporal variation in these growth curves was summarized in the fitted mean asymptotic length. We corrected the fitted mean asymptotic length for a possibly spurious relationship with the estimated von Bertalanffy growth scalar and used these quantities as a corrected measure for the EGC. The EGC is a summary statistic for the environmental factors that limit growth, such as food availability. Seven out of the 10 species showed a negative trend in the corrected EGC over time in at least one area. In addition, corrected EGC showed a link with BPUE in at least one area for 6 out of 10 species. More interestingly, clustering based on the normalized EGC resulted in 4 distinct clusters of species. These clusters consisted of the flatfish species and the forage fish species on one side and the small to intermediate pelagic species and the predatory species on the other side. Similarly, clustering of the roundfish areas resulted in 3 distinct clusters, consisting of a large cluster covering the northern areas, a cluster with the southern areas and a cluster covering the Skagerrak and Kattegat.

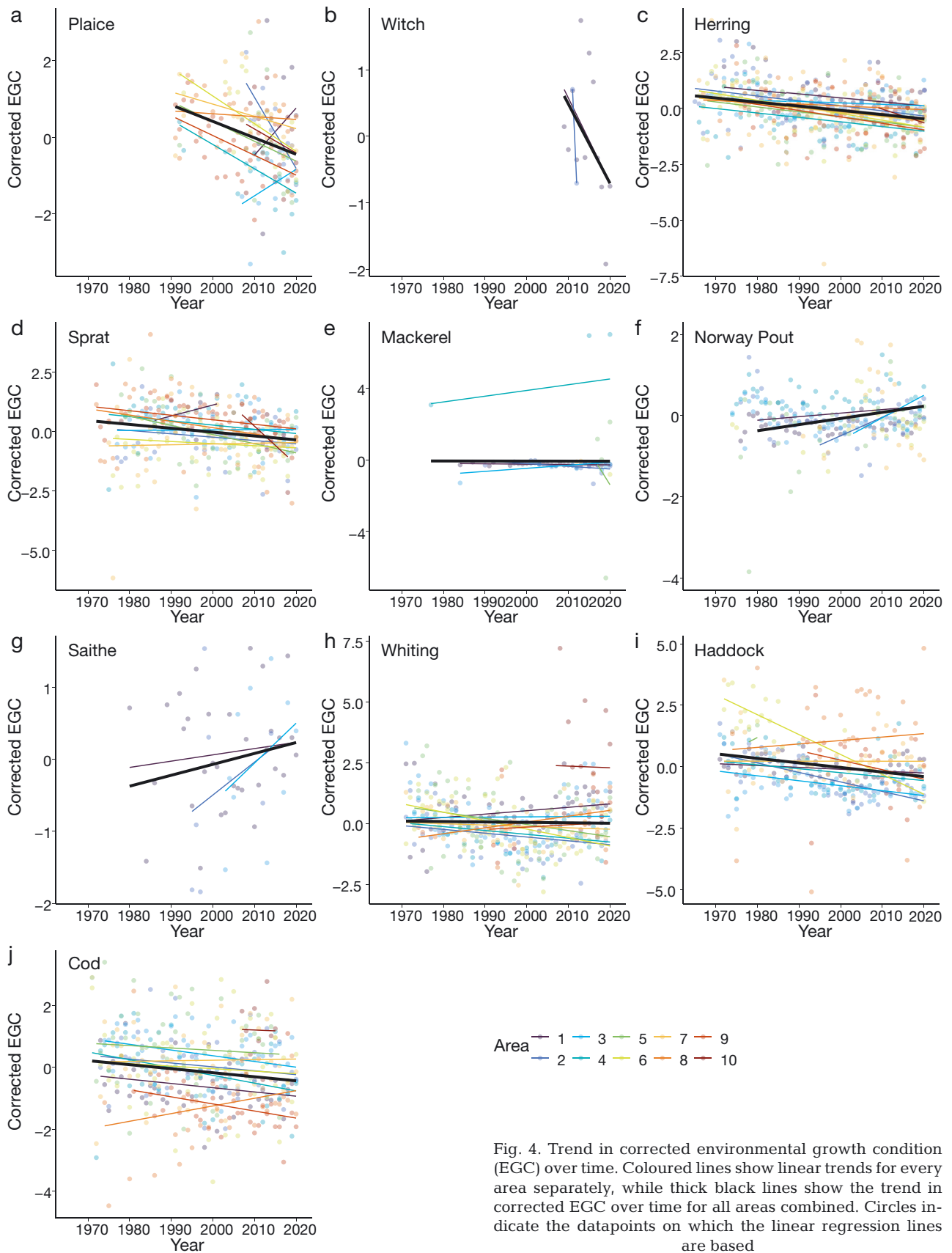


Fig. 4. Trend in corrected environmental growth condition (EGC) over time. Coloured lines show linear trends for every area separately, while thick black lines show the trend in corrected EGC over time for all areas combined. Circles indicate the datapoints on which the linear regression lines are based

Table 3. Linear relationship between the corrected environmental growth conditions (EGCs) and the biomass per unit effort (BPUE) for 10 North Sea fish species. Slopes of the relationship are presented for the analysis including data from all 10 roundfish areas. *Significance of the slope (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). In addition, we indicate the areas in which the slope of the relationship is negative as well, when only considering data from 1 area. **Bold** font highlights important results

Species	Slope	Individual areas with a significant slope	
Plaice	-6.90×10^{-6}	0/10	
Witch	1.14×10^{-4}	0/2	
Herring	$-4.17 \times 10^{-7**}$	2/10	(Negative in areas 2, 4)
Sprat	-1.12×10^{-6}	1/10	(Negative in areas 3)
Mackerel	-1.67×10^{-6}	0/7	
Norway pout	$-2.21 \times 10^{-6***}$	2/7	(Negative in areas 1, 4)
Saithe	-3.79×10^{-6}	0/3	
Whiting	$-9.73 \times 10^{-7*}$	1/10	(Negative in area 3)
Haddock	$-3.06 \times 10^{-6***}$	1/9	(Negative in area 3)
Cod	$-5.36 \times 10^{-6**}$	1/10	(Positive in area 5)

By fitting a von Bertalanffy growth curve in which the asymptotic length varied between years, we were able to summarize the temporal variation in growth with this asymptotic length (Croll & van Kooten 2022). Using this fitted asymptotic length as a basis for a measure of growth condition has several advantages over other indicators for growth. Firstly, our model only needs observations on length and age of individuals and does not need additional measurements or estimates. Many common environmental indicators based on size such as the length at maturity or the length at the maximum age need additional estimates such as maturity status or maximum achievable age (Shin et al. 2005, Kantoussan et al. 2018). Similarly, indicators such as the mean length or the size spectrum of a stock require estimates of the stock density at various sizes, which are also not needed for our fitting procedure (Shin et al. 2005, Kantoussan et al. 2018). Secondly, our model, and with it the fitted asymptotic length, is insensitive to fluctuations in recruitment. Indicators which require information on abundance such as the mean length or the size spectrum of a stock are strongly influenced by fluctuations in recruitment because this strongly affects the abundance of small and young individuals (Shin et al. 2005, Kantoussan et al. 2018). Because our model fits size distributions for every year and cohort, the estimated parameters, including the asymptotic length, are insensitive to differences in density between years and cohorts. Thirdly, the fitted asymptotic length is age independent and equally applies to all cohorts in a year. As a consequence, the fitted asymptotic length does not depend on the growth history of a cohort, in contrast to indicators such as the length at

a given age. The major constraint for using the asymptotic length as an indicator for environmental condition is the spurious relationship between the growth scalar and the asymptotic length when fitting the von Bertalanffy growth curve to multiple data sets (Pilling et al. 2002, Eveson et al. 2007). We corrected for this spurious relationship using a series of linear regressions to obtain the corrected EGC. This correction might affect the uncertainty of the corrected EGC because it is based on the estimates of 2 parameters, the asymptotic length and the von Bertalanffy growth scalar. Nonetheless, the uncertainty of these 2 parameters is likely to be strongly linked as they are estimated simultaneously by the same

model. In addition, the applied corrections mask whether differences between areas occur due to an effect in the growth scalar or the asymptotic length. Despite these downsides, it is very important to correct for the spurious relationship between the growth scalar and the asymptotic length to compare between areas and species.

Because the EGC is used as a summary statistic for the environmental impact on growth, it is likely that the EGC is determined by multiple environmental factors such as food availability and temperature. Quantitatively, every environmental factor is likely to influence growth in a distinct way, but qualitatively these effects can be separated in 2 mechanisms. Some environmental factors such as food availability directly affect the anabolism rate of an individual. According to metabolic theory, these environmental factors only affect the asymptotic length of the growth curves (von Bertalanffy 1938, Kooijman 2000). In contrast, some environmental factors, such as temperature, directly affect the catabolism rates of an individual. According to metabolic theory, these processes affect the asymptotic length and the von Bertalanffy growth scalar in opposite directions (von Bertalanffy 1938, Kooijman 2000). As a consequence, factors affecting the catabolism rates of an individual will result in a negative correlation between the estimated asymptotic length and the estimated von Bertalanffy growth scalar. This relationship is indistinguishable from the spurious relationship that might arise from the fitting procedures. Consequently, differences between areas caused by an environmental factor that affects catabolism rates will not be present in the data corrected for the spu-

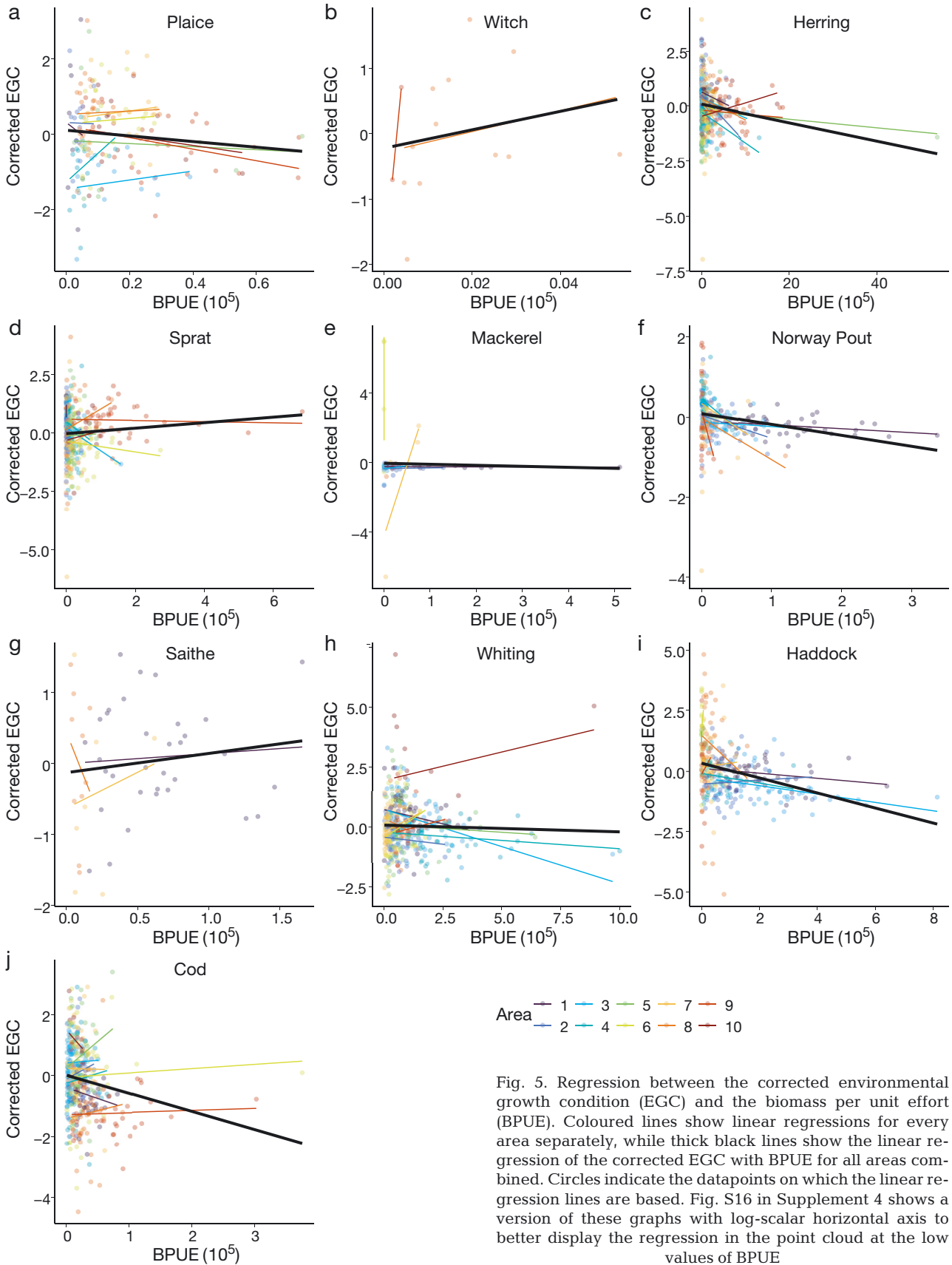


Fig. 5. Regression between the corrected environmental growth condition (EGC) and the biomass per unit effort (BPUE). Coloured lines show linear regressions for every area separately, while thick black lines show the linear regression of the corrected EGC with BPUE for all areas combined. Circles indicate the datapoints on which the linear regression lines are based. Fig. S16 in Supplement 4 shows a version of these graphs with log-scalar horizontal axis to better display the regression in the point cloud at the low values of BPUE

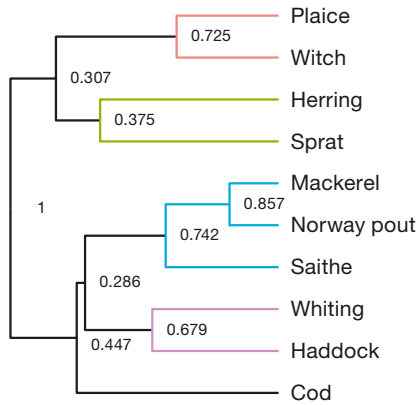


Fig. 6. Clustering of 10 North Sea fish species based on the normalized environmental growth condition (EGC) for the average (unweighted pair group method with arithmetic mean [UPGMA]) clustering method. Small digits show the bootstrap probability, which is the fraction of bootstrap repeats in which a branch contained the depicted species. Coloured branches show clusters which arise in all clustering methods

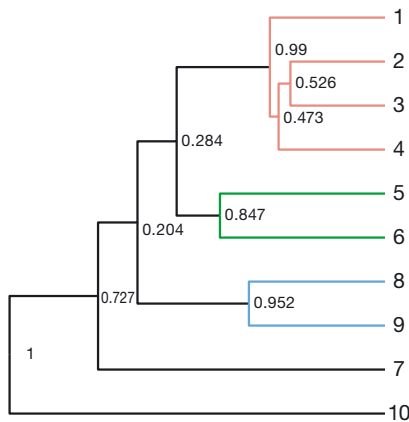


Fig. 7. Clustering of 10 roundfish areas based on the normalized environmental growth condition (EGC) for the average (UPGMA) clustering method. Small digits show the bootstrap probability, which is the fraction of bootstrap repeats in which a branch contained the depicted areas. Coloured branches show clusters which arise in all clustering methods

rious relationship arising from the fitting procedures. Before this correction, environmental factors affecting catabolism rates would result in a very distinctive pattern in which the estimated mean asymptotic length is negatively correlated with the estimated von Bertalanffy growth rate, and both are correlated with the environmental factor but with opposite slopes. We did not observe this pattern for the BPUE as a predictive variable in our study. This suggests that BPUE, as a measure of population density, only affected individuals' anabolism rates but not catabolism rates. The correction for the methodological artefact does not affect the dynamics of the estimated

asymptotic length within an area because the von Bertalanffy growth scalar is estimated as a constant parameter for every area. The corrected asymptotic length can therefore be used as a relative proxy for the EGC within an area.

Seven out of the 10 analysed stocks showed a decreasing trend in EGC over time in at least one area. For 5 of the species, this trend was even present when all areas were analysed simultaneously. This negative trend in EGC might seem counterintuitive, as most of the North Sea fish stocks have been recovering over the last decades (Worm et al. 2009, Hutchings et al. 2010, Cardinale et al. 2013, Fernandes & Cook 2013). The counterintuitive decrease in EGC observed in this paper can have various causes. Firstly, it could be that in the linear regressions, a constant or increasing EGC in the last part of the timeseries was overshadowed by a strong decrease in EGC in the first part of the timeseries. We did a rough test for this pattern by performing linear regressions over time for all species with all areas combined for the corrected EGC before and after the year 2000. Only whiting showed a significant negative trend in corrected EGC before 2000 and a positive trend in corrected EGC after 2000. For some of the species with an overall negative trend, the negative trend in corrected EGC was only significant before or after 2000. This could indicate that the trend in corrected EGC is changing, but could also be caused by a lack of data in the non-significant periods. Longer timeseries might be necessary before changes in trends of the corrected EGC become visible. Secondly, the negative trend in corrected EGC might be caused by a decrease in individual size due to fisheries-induced evolution, which is suggested to decrease the size of individuals because fisheries mainly target large individuals (Enberg et al. 2012, Heino et al. 2015). In general, fisheries-induced evolution is slow (Andersen & Brander 2009), and the NS-IBTS data set only contains a limited number of generations. Even if fisheries-induced evolution would cause the decrease in corrected EGC, it would do so through selection, also causing a decrease in the variance of the asymptotic length. Although not tested statistically, we did not observe such a trend in variance in asymptotic length fitted in our model. Thirdly, the pattern of decreased EGC could be caused by density dependence in the recovering stock. The recovery of a stock is commonly reported based on an increase in stock biomass and not in a change in stock structure or individual growth curves. Stock recovery therefore indicates that the density or biomass of the stock increased. An increase in sock biomass could lead to

higher consumption or increased use of space, which can result in a decrease in EGC. However, we also reported a decrease in EGC for cod in the North Sea, while this cod stock is still heavily overfished and does not display a clear increase in biomass (Cardinale et al. 2013, Fernandes & Cook 2013, Blöcker et al. 2023). In this situation, the decrease in EGC is unlikely to be caused by competition, but is likely linked to a change in some other environmental factor such as temperature. This might be a worrying signal about the status of the stock, as both the biomass and the environment of the stock seem to be deteriorating. This is in line with the suggestion that the cod stock has failed to recover from overfishing due to a regime shift caused by a combination of high fishing pressure, internal stock dynamics and environmental change (Blöcker et al. 2023). A clear trend in EGC might therefore be an interesting addition to stock biomass as an indication of stock status.

Six of the 10 analysed species showed a link between EGC and BPUE in at least one area, which suggests that growth in these species is density dependent. Density dependence in individual growth has been shown for numerous fish stocks (Lorenzen & Enberg 2002, Schram et al. 2006, Lorenzen 2016, Zimmermann et al. 2018, Rindorf et al. 2022), including herring, sprat, whiting, haddock and cod, for which we found this pattern as well. A common explanation for this pattern is that an increase in stock biomass results in an increase in competition for food and space and thus a decrease in resources for individual growth. Density-dependent individual growth has previously been shown for plaice (Rijnsdorp & Van Leeuwen 1996), mackerel (Jansen & Burns 2015) and saithe as well (Cormon et al. 2016). We did not find an indication of density dependence in growth for these species in our analysis, even though we found a decreasing trend in EGC for these species. It is likely that we were not able to detect density dependence in these species due to a lack of data or an inaccurate estimate of the stock biomass. For example, we were only able to estimate growth curves for plaice in most areas from 2010 onward, while the major recovery and fluctuations in stock biomass of plaice occurred before this period (ICES 2021). In addition, it is important to consider that stocks live in a diverse environment with many interactions. The impact of a stock on the environment could therefore be overshadowed by other factors such as competing species or human activities. This would reduce the relative impact of the stock density on the environmental conditions, thus reducing density dependence in growth. This could also explain the apparent

positive relation between BPUE and growth of cod in roundfish area 5. An unknown confounding factor could lead to an increase in environmental conditions along with an increase in both growth and recruitment, resulting in an apparent positive relationship between individual length and stock density (Rindorf et al. 2022). The relationship between individual growth and stock density is therefore an interesting indicator for the relative impact of a stock on its own environmental conditions.

We performed cluster analysis on the fish species and the roundfish areas based on EGC estimated from population growth curves. This resulted in 4 distinct clusters of species that differentiated between forage fish species and flatfish species on one side and predatory species on the other side. Interestingly, Norway pout and mackerel clustered together with other predatory species, although only large individuals of these species feed on other fish. These clusters could be explained by a partly overlapping diet. Mackerel and Norway pout mainly forage on crustaceans (copepods or euphausiids), while saithe, whiting and haddock feed on a mixed diet of crustaceans and forage fish (Mehl & Westgård 1983, Hislop et al. 1991, Bromley et al. 1997). For the size range included in this study, cod are rarely associated with foraging on crustaceans, which corresponds with the result that cod clustered farthest away from mackerel and pout (Bromley et al. 1997, Floeter & Temming 2003, Link et al. 2009). This clustering could indicate that the non-piscivorous part of the diet from saithe, whiting and haddock has the largest impact on the experienced growth conditions of a stock, possibly because most individuals within these stocks are young and not (yet) piscivorous. Another possibility is that the patterns in the growth curves of the predatory species are caused by environmental factors other than food availability, such as a similar reaction towards shifting temperatures or fishing regimes within the Gadidae family. Nonetheless, the clustering of fish species based on growth curves was very similar to the clusters expected based on ecological and geographical similarities. This shows that growth curves contain valuable information about the environmental conditions encountered by a species in a specific area.

Clustering of the roundfish areas resulted in a northern cluster, a southern cluster and a cluster for the Skagerrak and Kattegat. This suggests that the EGC in geographically adjacent areas is similar. The high connectivity between the roundfish areas is further emphasized by the result that further clustering of these 3 clusters was inconclusive. Yet, the more

global clustering of the North Sea in 3 regions is very clear and suggests that geographic differences in EGC are present. The distinct clustering of the roundfish areas might be linked to habitat preference and movement patterns of stocks. Areas with similar habitat types or seascapes are likely to have similar species compositions and show similar patterns in the dynamics of the biomass density of stocks (Rademaker et al. 2021). Likewise, some habitat structures might cause an environmental barrier between clusters of areas for specific species due to specific morphological characteristics or habitat preferences. Similarly, fishing pressure is linked to specific habitat structures, which might indirectly drive similarities in the population dynamics of stocks in similar areas (van der Reijden et al. 2018). As a consequence, changes in habitat structure or ecological conditions in an area are likely to cause changes in EGC, which might cause a shift in the growth and size of individuals in an area and might even result in a shift in the geographical distribution of a stock, such as observed in sole and plaice (Engelhard et al. 2011, Teal et al. 2012).

Fisheries management is slowly shifting from a single-species perspective to a multi-species and ecosystem-centred perspective (May et al. 1979, Birkenbach et al. 2020). Information about the ecological overlap of species is needed to facilitate this shift. Generally, such information is collected using labour-intensive methods such as stomach sampling, physiological similarities and expert knowledge (Matley et al. 2018, Amundsen & Sánchez-Hernández 2019, Cadrin 2020). In this study, we show that reconstructed growth curves can reveal relevant information about the ecology of a stock as well. Growth of individual fish is strongly affected by the environment (Lorenzen 2008, Kooijman 2000, Tu et al. 2018). Growth curves therefore contain valuable information about the ecological conditions and limitations experienced by a stock. It is likely that ecologically similar species are affected in a similar way by the environment, and that environmental conditions are similar in geographically and physically similar areas. Environmental conditions derived from growth curves could therefore provide valuable insight in the ecological relatedness between stocks and areas, based on straightforward length and age measurements. This could be further tested by comparing the results of diets and stomach samples of species with similar growth curves. Similarly, the clusters could be compared to reconstructions of the North Sea food web. In addition, estimated growth curves and EGC could be correlated to densities of

other stocks to show additional ecological relationships between species such as competition and predation. Overall, growth curves appear to contain valuable information about the ecological conditions and relatedness of fish stocks and are a promising method to provide additional information about the state of a stock.

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