

OPINION

Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes

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Abstract

Decreasing body size has been proposed as a universal response to increasing temperatures. The physiology behind the response is well established for ectotherms inhabiting aquatic environments: as higher temperatures decrease the aerobic capacity, individuals with smaller body sizes have a reduced risk of oxygen deprivation. However, empirical evidence of this response at the scale of communities and ecosystems is lacking for marine fish species. Here, we show that over a 40-year period six of eight commercial fish species in the North Sea examined underwent concomitant reductions in asymptotic body size with the synchronous component of the total variability coinciding with a 1–2 °C increase in water temperature. Smaller body sizes decreased the yield-per-recruit of these stocks by an average of 23%. Although it is not possible to ascribe these phenotypic changes unequivocally to temperature, four aspects support this interpretation: (i) the synchronous trend was detected across species varying in their life history and life style; (ii) the decrease coincided with the period of increasing temperature; (iii) the direction of the phenotypic change is consistent with physiological knowledge; and (iv) no cross-species synchrony was detected in other species-specific factors potentially impacting growth. Our findings support a recent model-derived prediction that fish size will shrink in response to climate-induced changes in temperature and oxygen. The smaller body sizes being projected for the future are already detectable in the North Sea.

Keywords: climate change, dynamic Factor Analysis, ectotherms, fish growth, fisheries, temperature size rule, von Bertalanffy

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Introduction

Aquatic environments pose inherent challenges for ectothermic organisms respiring underwater (Graham, 2006). Warming temperatures compound these challenges by increasing anabolic oxygen demand while decreasing oxygen solubility. Any imbalance between oxygen demand and oxygen supply will constrain aerobic scope, thereby impairing individual performance (Pörtner & Knust, 2007). In warming environments, small-sized individuals are better able to balance demand and uptake because of their larger surface area to volume ratio (Pauly, 2010). These physiological constraints lead to the expectation that individuals experiencing higher temperatures will have smaller body sizes, an outcome known as the temperature size rule (TSR) (Atkinson, 1994). The physiological basis underpinning the TSR (Pörtner & Knust, 2007; Forster *et al.*, 2011) combined with cross-taxa support (Gardner *et al.*,

2011; Forster *et al.*, 2012; Edeline *et al.*, 2013) has led to smaller body size being proposed as a universal outcome of warming temperatures (Daufresne *et al.*, 2009). In marine ecosystems, which include a high proportion of ectothermic species, the implications of the TSR are profound. A recent simulation integrating this ecophysiological understanding with temperature projections predicted that by 2050 the assemblage-averaged maximum body weight of fish species would shrink by 14–24% globally due to the combined impacts of small-sized species replacing large-sized species and the TSR (Cheung *et al.*, 2013a). This conclusion, which garnered global press coverage upon publication, has been challenged on the grounds that both the scale and the speed of the change are not credible (Brander *et al.*, 2013). Criticism of the projection model was refuted by the authors (Cheung *et al.*, 2013b). This debate highlights the need for an ecosystem-level test of whether body sizes of fishes have synchronously decreased in regional seas that have undergone warming in order to retrospectively support model projections of climate impacts on productivity. While the importance of TSR

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has been shown in laboratory conditions (Forster *et al.*, 2012), empirical evidence is needed (Ohlberger, 2013). Statistical analyses of long-term data series are required to provide the most direct evidence for changes in body size caused by climate warming (Daufresne *et al.*, 2009).

Over the past 30 years, water temperatures in the North Sea have increased by 0.2–0.6 °C per decade with the rates of warming being rapid relative to other regional seas (Belkin, 2009). During this period, declining body sizes have been observed in haddock (*Melanogrammus aeglefinus*) (Baudron *et al.*, 2011), herring (*Clupea harengus*) (Brunel & Dickey-Collas, 2010), and plaice (*Pleuronectes platessa*) (van Walraven *et al.*, 2010). The fact that three species differing in their life histories, trophodynamics and vertical distribution in the water column (Table S1) exhibited smaller body sizes concomitant with a warming environment is consistent with the claim that the TSR is a universal response and suggests that temperature is an ‘omnibus’ factor impacting fish species synchronously. A complication in establishing direct causality between warming temperatures and decreasing body sizes in commercial species is disentangling the effect of temperature from other factors possibly affecting body size (Table S2): (i) large fluctuations in abundance may affect growth rates via density-dependent competition for resources (Taylor & Stefánsson, 1999); (ii) fisheries-induced evolution may result in body size reduction via non-random genetic selection (Enberg *et al.*, 2012); (iii) positive size-selective fishing mortality will reduce the number of large old individuals and may lead to a non-genetic size artifact (Sinclair *et al.*, 2002). Disentangling the relative effects on growth of these three factors and temperature on a species-specific basis can prove extremely challenging when two or more factors are confounded. Unlike temperature, it is difficult to see how these three factors could impact growth uniformly across species. Density-dependent growth would likely be species-specific given the variety in habitat and diet of North Sea fish species (Table S1). Similarly, the scale and speed of an evolutionary response would also be unique to each species given the differences in exploitation history and life history traits affecting the selection differential. Finally, size artifacts would likely be species-specific given the differences in pattern and degree of fishing selection. Although density-dependence, fisheries-induced evolution and size artifacts seem unlikely to vary synchronously across species, all three factors must be examined for synchronicity. If no synchronous trends across species are detected in any of these three factors, then logically they are unlikely to be responsible for generating a synchronous trend in body size across species, although species-specific contributions to temporal variability in size cannot be excluded.

Establishing that declines in body size are, firstly, synchronous across a range of species, and secondly, concurrent with temperature would strongly imply the ‘omnibus’ effect of temperature.

Our aim was to test whether the North Sea fish assemblage exhibited synchronous declines in asymptotic body size that were concurrent with increases in temperature and consistent with TSR, rather than explaining body size variation individually for each species. We used the von Bertalanffy growth function (VBGF) (Pauly, 2010) to estimate L_{∞} , the asymptotic body length, on a cohort-by-cohort basis for eight North Sea fish species for which age and size data were available at least annually over the past four decades. Statistical analyses were performed to test for a synchronous trend in L_{∞} across species and to compare this trend with the temperature trend. Annually resolved indices of density, fishing mortality and mean cohort age were also examined for synchronicity across species to determine the potential for density-dependence, fisheries-induced evolution and size artifact to generate a synchronous trend in L_{∞} . The implications for yield were examined for species exhibiting a synchronous component in variability of L_{∞} .

Methods

Sea bottom temperatures (SBT) from 1970 to 2008 were obtained from the NORWECOM model (Skogen & Søliland, 1998) which gives monthly mean values averaged over 0.25° latitude by 0.5° longitude rectangles. SBT values were averaged per roundfish area (Figure S1a) and per year to match the spatial and temporal resolution of the biological data. SBT time series showed identical temporal trends in northern (areas 1 and 2) and southern (areas 5 and 6) regions with a ca. 3 °C gradient (Figure S1b). Age-length keys (ALKs) generated from data collected during annual International Bottom Trawl Surveys (IBTS) of the North Sea are available for demersal and pelagic species from the DATRAS database (<http://datras.ices.dk>) maintained by the International Council for the Exploration of the Sea (ICES). ALKs for benthic flatfish species are estimated from a combination of commercial samples, survey samples and otolith back-calculations (Rijnsdorp *et al.*, 2010). Our analysis was restricted to commercial species having long time series of otolith-derived age estimates that are essential for modeling growth. Demersal (distributed nearer bottom) species were haddock, cod (*Gadus morhua*), whiting (*Merlangius merlangus*) and Norway pout (*Trisopterus esmarkii*). Pelagic (distributed nearer surface) species were herring and sprat (*Sprattus sprattus*). Benthic (distributed on the bottom) flatfish species were plaice and sole (*Solea solea*). Collectively, these eight species (hereafter referred to as stocks) span a range of habitats, body sizes, and life-history traits that are representative of the North Sea fish assemblage.

Age-length keys give the number of sampled fish in a given 1-cm length class that were assigned through otolith reading

to age t in year y . For IBTS surveys conducted in quarter 1, age values remained as integers (t) while ages used for quarter 2, 3 and 4 were $t + 0.25$, $t + 0.5$ and $t + 0.75$, respectively. Because ALKs are generated through length-stratified sampling of the catch, they do not accurately represent the true length distribution-at-age. To correct for this bias, ALKs for each ICES round fish area were raised by the catch-per-unit-effort per length class for the area except for the two flatfish species where ALKs were raised by length distributions instead. To account for the strong spatial gradient in temperature (Figure S1), data for cod, whiting and herring were split into northern and southern substocks and the raised ALKs were combined for ICES roundfish areas 1 and 2 and for areas 5 and 6 to represent the northern and southern North Sea, respectively. Haddock and Norway pout are only found in the north, whereas sprat is only found in the south. Plaice and sole are mostly found in the south but were split by sex to account for known differential growth that gives rise to large phenotypic differences between males and females (Rijnsdorp *et al.*, 2010). Splitting gave a total of 13 substocks and accounted for known sources of variation in temperature (by region) and growth (by gender) that would otherwise have confounded the analysis. For each substock, the growth of a cohort spawned in year y was modeled by fitting the VBGF to the length distribution-at-age represented by the raised ALKs:

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)}).$$

where L_t is the length (cm) at age t , K is the Brody growth parameter (yr^{-1}), and t_0 is the hypothetical age (year) at length equal to 0. As cohort-specific values of L_{∞} and K are strongly negatively correlated (Pauly, 2010) (Figure S2) examining temporal variation in one of the two parameters is sufficient to describe growth. Examining variation in L_{∞} by cohort assumes that the shape of the growth curve of a cohort is highly impacted by the early stages of life, an assumption supported experimentally (Forster *et al.*, 2011; Scott & Johnston, 2012). For each substock, the VBGF was fit for cohorts 1970–2008; cohorts 1970–2001 were modeled with data for ages 1 to 10 while cohorts 2002–2008 were modeled with 9–3 years of data. Outliers in the L_{∞} time series (>2 * average or L_{∞} having standard errors $>10\%$ of the value) owing to poor VBGF fits were omitted from subsequent analysis (Table S3). For all other cohorts, estimated parameters (L_{∞} , K and t_0) had P -values <0.05 . A Dynamic Factor Analysis (DFA) (Zuur *et al.*, 2003) was used to objectively estimate common trends in the L_{∞} time series of the substocks considered. DFA is a multivariate time series analysis that allows the estimation of underlying common trends in short, nonstationary time series containing missing values. The aim of DFA is to model as few common trends as possible while giving a reasonable model fit. Prior to inclusion in the DFA model, L_{∞} time series for all substocks were standardized by subtracting the mean and dividing by the standard error (Zuur *et al.*, 2003). The 13 L_{∞} time series were each modeled as a combination of common trends (x), factor loadings (Z) plus some offset (a) as follows:

$$L_{\infty,s}(t) = Z_{1,s}x_{1,t} + \dots + Z_{i,s}x_{i,t} + a_s + e_{s,t},$$

where $e_t \sim \text{MVN}(0, R)$ with MVN standing for Multivariate Normal. R is the error covariance matrix, s is the considered substock and i is the number of common trends identified in the data. The magnitude and sign of Z indicate to what extent the common trends are related to the original times series. DFA models with 1–6 common trends and with either a diagonal and equal or a diagonal and unequal error covariance matrix were tested. The best of the 12 candidate models was selected using the Akaike's Information Criterion (AIC). Correlation tests between the predominant common trend (Trend 1) and SBT were performed using different time windows for temperature impacts: SBT experienced at age 0 (no lag), at age 1 (lag 1), at age 2 (lag 2), during the first 2 years of life (average SBT from age 0 to 1) and during the first 3 years of life (average SBT from age 0 to 2). Correlation tests between Trend 1 and the common trend in density were performed to test for intra-cohort (no lag), inter-cohort (lag 1 and lag 2), and cumulative (sum of densities at lags 0–1, and lags 0–2) density-dependent growth. As the purpose of these tests was to assess the correlation between underlying trends rather than short-term, high-frequency variations, the P -values presented do not account for autocorrelation as this would have involved detrending the time series. Correlations were summarized by Pearson product-moment correlation coefficients. As multiple tests were conducted, a sequential Bonferroni correction was applied to adjust the level of significance of the multiple inferences.

To test for synchronicity in density, fishing mortality and mean cohort age across species, the DFA and correlation tests were repeated for these three factors. Abundance-at-age one indices were used as a proxy for density (no sex-specific abundance indices were available for plaice and sole substocks). For stocks distributed across the northern and southern North Sea, the survey abundance-at-age one indices were split by area. For other substocks, XSA abundance-at-age one indices given in the 2012 ICES assessment reports were used (ICES, 2012a, b). For Norway pout North and sole South, recruitment time series from the assessment were used as no abundance-at-age 1 indices were available. Data were available from 1970 to 2011 for all species apart from whiting, Norway pout and sprat for which indices were available from 1990, 1983 and 1984, respectively. Average fishing mortalities were obtained from 2012 ICES assessment reports (ICES, 2012a, b). Assessment data were available from 1970 to 2011 for all species apart from whiting, Norway pout and sprat that assessments began, respectively, in 1990, 1983, and 1991. For stocks distributed across the northern and southern North Sea (whiting and herring), a survey-based assessment (SURBA) model (Needle, 2012) was used to obtain local estimates of total mortality in order to capture spatial gradients in fishing pressure. Assuming a constant natural mortality, total mortality times series for these two stocks were used as proxies for fishing mortalities. For each species, the mean age of each cohort used in estimating L_{∞} time series was computed and employed as an index to investigate whether the number of old individuals varied synchronously across species.

Comparative yield-per-recruit analyses were performed as a proxy for changes in yield prior to and after changes in individual body size. Yield-per-recruit was approximated by simulating a fishery on a single cohort composed of eleven year classes (from age 0 to age 10), and with an initial recruitment (abundance-at-age 0) of 10 000 individuals. 5-year means of L_{∞} and K prior and after changes in growth were used to compute length-at-age values, assuming $t_0 = 0$ for all substocks. Length values were converted into weights-at-age using length-weight relationships obtained from Marine Scotland and IMARES. Fishing mortality-at-age was estimated by the mean over the last three historical years (2009–2011), while natural mortality-at-age and proportion mature-at-age were assumed to be constant. For plaice and sole, the fishing mortality was assumed to be equal for both sexes. All estimates were obtained from the 2012 ICES assessment reports (ICES, 2012a, b). The cumulative contribution to yield of the successive year classes of the cohort were then summed and divided by the original number of recruit to obtain approximations of yield-per-recruit.

All statistical analyses were performed using the R software (version 2.15.1; <http://www.r-project.org/>). DFA was performed using the MARSS package (Holmes *et al.*, 2012).

Results and discussion

A decrease in L_{∞} (expressed as difference between average 1973–1977 and average 1993–1997) was observed for haddock North (29%), whiting North (13%), whiting South (29%), herring North (10%), Norway pout North (19%), sprat South (16%), male sole South (13%), female sole South (1%) and male plaice South (12%), averaging 16% (Figure S3c–f and h–l). These nine substocks also exhibited narrow 95% confidence intervals (95%CI) around L_{∞} estimates. The four remaining substocks (cod North, cod South, herring South and female plaice South) showed divergent trends in L_{∞} (Figure S3a, b, g and m). Cod North, cod South and herring South time series showed an increase in L_{∞} but had high proportions of outliers (Table S3). The wide 95%CI for the two cod substocks indicate that the VBGF was a poor fit to the data and the high (>200 cm) values of L_{∞} reflect near-linear growth rather than the asymptotic growth assumed by the VBGF. Herring South showed an increase in L_{∞} from the 1990s onwards (Figure S3g) while female plaice South showed an increase from 1970 to 1990 followed by a recent decrease (Figure S3m).

The best model identified by DFA to describe temporal variation in L_{∞} included two common trends (Table S4). Fitted values for all substocks showed that the model succeeded in describing L_{∞} time series (Fig. 1). The DFA model captured the decrease in L_{∞} for the nine substocks identified above and exhibited narrow 95%CI apart from the most recent cohorts which have

fewer sampled age classes (Fig. 1c–f and h–l). The first common trend (Trend 1) showed a steep decline from 1978 to 1993 after which it remained stable (Fig. 2a). The second common trend (Trend 2) increased slightly until the early 1990s after which it showed a sharp decline (Fig. 2c). Fitting a DFA model restricted to one common trend returned a trend almost identical to Trend 1 (Fig. 2a), which indicates that Trend 1 is predominant in describing the common trend in L_{∞} (Zuur *et al.*, 2003). The nine substocks showing a decrease in L_{∞} from the mid-1970s to the mid-1990s (Fig. 1) were all positively related to Trend 1 (Fig. 2b). Six of these substocks (haddock North, whiting North, whiting South, herring North, Norway pout North and male sole South) had similar factor loading values (Z) on Trend 1, indicating that the stock-specific trends in L_{∞} were equally well described by Trend 1 (Fig. 2b). These substocks also showed small Z s on Trend 2 (Fig. 2d). Female sole South and male plaice South, although positively related to Trend 1, showed larger Z s on Trend 2 (Fig. 2d).

Cod North, cod South, and female plaice South were negatively related to Trend 1 but positively related to Trend 2 (Fig. 2b and 2d). Herring South was negatively related to Trend 2 and showed a different temporal trend (Fig. 1g). The high Z of female plaice South on Trend 2 (Fig. 2d) suggested that Trend 2 was mainly driven by this substock. Because the L_{∞} time series for the two cod substocks and herring South included many outliers (Supplementary Table S3), it is difficult to describe decadal-scale trends for these substocks with confidence. Flatfish substocks showed mixed trends, with males of both species conforming to Trend 1, whereas the decrease in L_{∞} was small in female sole South and absent in female plaice South. Differences between males and females in their growth response to temperature have been detected in fish (Kuparinen *et al.*, 2011) although the physiological basis for dimorphic growth is unknown.

The common trend in L_{∞} represented by Trend 1 describes only the synchronous component of the total variability in the L_{∞} time series. Residual variation around Trend 1 for any given stock reflects the influence of stock-specific factors and estimation error. Our aim was to isolate this synchronous component across stock. Assessing the impact of stock-specific factors is beyond the scope of this study. Trend 1 showed concurrent and opposite variations with sea bottom temperature (SBT) and the temperature increase through the 1980s was concurrent with the decline in L_{∞} described by Trend 1 (Fig. 2e). This is consistent with the TSR prediction that higher temperatures result in smaller body sizes. Furthermore, this cross-stock synchronicity was detected when

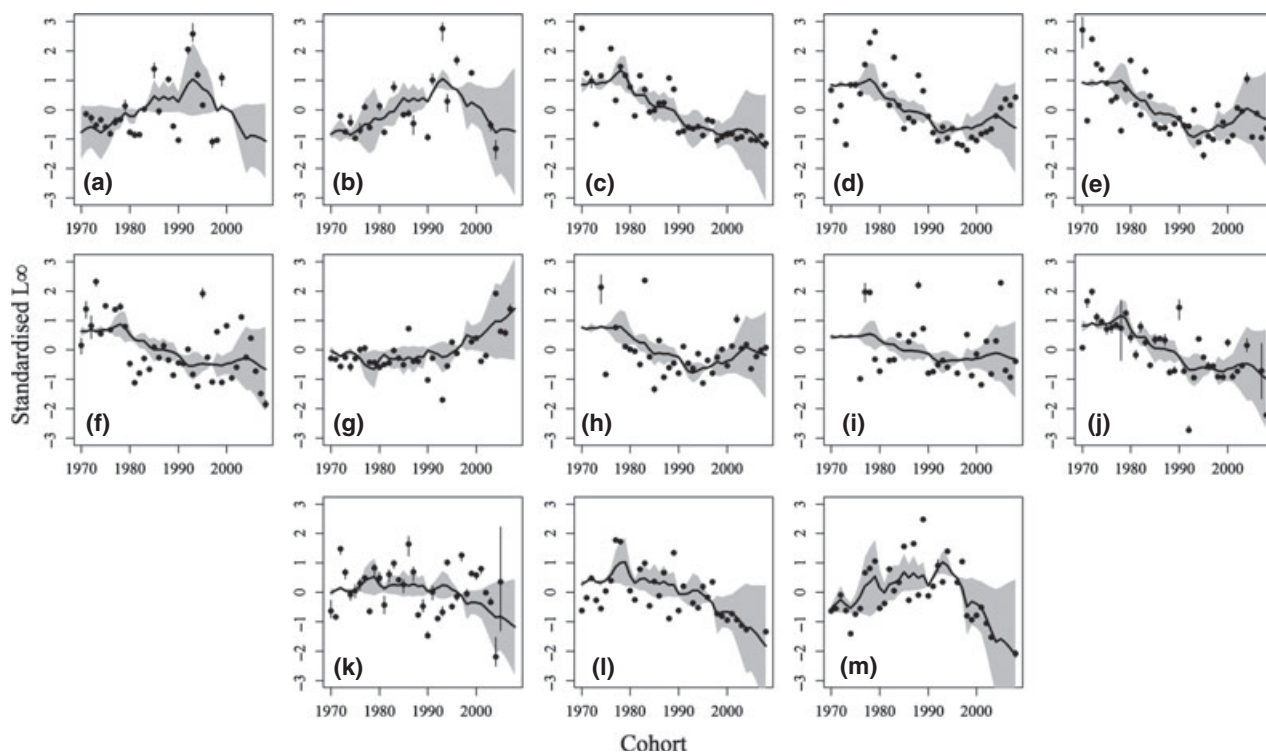


Fig. 1 Standardized L_{∞} time series for the 13 substocks considered in the analysis (filled circles) with their 95% confidence intervals (vertical segments), along with the fitted values from the selected Dynamic Factor Analysis model (line) and their corresponding confidence intervals (shaded areas). (a) cod North; (b) cod South; (c) haddock North; (d) whiting North; (e) whiting South; (f) herring North; (g) herring South; (h) Norway pout North; (i) sprat South; (j) male sole South; (k) female sole South; (l) male plaice South; (m) female plaice South.

growth was examined by cohort suggesting that temperatures experienced early in the life of the cohort are critical in determining L_{∞} , a result also consistent with current physiological understanding of growth (Forster *et al.*, 2011; Scott & Johnston, 2012). Trend 1 was significantly, negatively correlated ($P \leq 0.05$) with the average monthly SBT experienced at age 0, age 1, age 2 as well as during the first two years and the first three years of life (Table 1). The possibility that the synchronous trend in L_{∞} could have been generated by a driver other than temperature was rejected for all three factors investigated (Table S2). Although a common trend in density was detected by DFA, it was not equally strongly supported by all nine substocks (Figures S4 and S7). No significant correlations were observed between Trend 1 in L_{∞} and the common trend in density (Table S5). The nine substocks exhibiting the synchronous decline in L_{∞} described by Trend 1 represent six species with different life-history characteristics and asynchronous trends in fishing mortalities (Figures S5 and S7) ruling out the possibility that non-random genetic selection is responsible for inducing cross-stock synchronicity in L_{∞} . No synchronous trend was observed in the mean cohort age

of the nine substocks conforming to Trend 1, ruling out the possibility that size artifacts could have elicited a synchronous signal in L_{∞} (Figures S6 and S7). Therefore, the TSR is a plausible and parsimonious explanation for the synchronous reduction in L_{∞} detected in the majority of North Sea substocks and species examined here.

The nine substocks exhibiting a detectable degree of synchrony had fewer outliers and less uncertainty in L_{∞} estimates than the four substocks that did not conform to Trend 1. They included fast-growing/early-maturing species as well as slow-growing/late maturing ones and their habitats encompassed pelagic, demersal and benthic regions. This suggests a uniformity of the response to warming temperature which is consistent with current physiological (Pörtner & Knust, 2007; Forster *et al.*, 2011; Scott & Johnston, 2012) and ecological (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011; Ohlberger, 2013) understanding. It is not possible to infer direct causality from our analysis due to the comparative shortness of the L_{∞} time series used here (<40 years) and the intrinsically 'uncontrolled' nature of ecosystems. Support for inferring a causal relationship between temperature

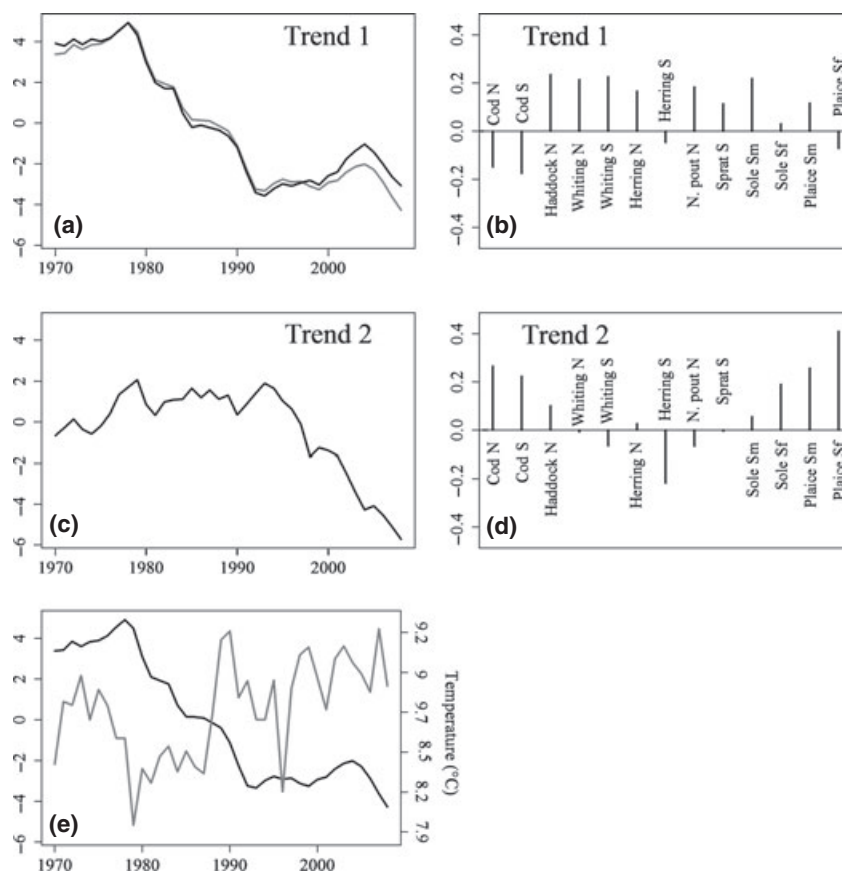


Fig. 2 Common trends given by the best candidate model (panels a and c) to describe L_{∞} time variations over time and the corresponding factor loadings for the thirteen sub-stocks (panels b and d). In panel a, the grey line corresponds to the common trend given by a model fitted with one common trend. In panel e the Trend 1 is plotted along with the sea bottom temperature (grey line) averaged across the round fish areas 1, 2, 5, and 6.

Table 1 Estimated correlations between sea bottom temperature SBT and Trend 1 and their corresponding P -values. The age interval included in the estimation of mean temperature is indicated (see Methods). Significance was adjusted by a sequential Bonferroni correction: the ordered P -values were compared with the inequality, $P_i \leq \alpha(1 + k - i)^{-1}$, where α is the confidence level to test for significance (0.05), K is the number of correlation tests carried out and i is the rank of the correlation considered. Correlations for which the inequality is met are significant (*).

Age interval	Correlation	P -value	$\alpha(1 + k - i)^{-1}$
0 to 2 years	-0.54	0.00064	0.010*
0 to 1 years	-0.49	0.00182	0.013*
2 years	-0.49	0.00200	0.017*
1 year	-0.45	0.00510	0.025*
0 years	-0.43	0.00640	0.050*

and growth would be provided if ecosystems showing strong warming consistently showed evidence of synchronous changes in growth rates across species

while ecosystems with little to no warming were asynchronous. For example, juvenile growth rates (proportional to the VBGF parameter K) were correlated with temperature for six of eight long-lived commercial fish species in the temperate southwestern Pacific (Thresher *et al.*, 2007). The intrinsically negative correlation between K and L_{∞} (Pauly, 2010) (Figure S2) suggests that there may have been a corresponding reduction in asymptotic body size in the Pacific species, a hypothesis that is difficult to test due to their longevity. The two studies, undertaken in temperate regions of the northern and southern hemisphere, confer a degree of verisimilitude on the inference that temperature is responsible for imposing a detectable, synchronous signal on temporal variation in asymptotic body size that is consistent with TSR.

If the synchronous decline in L_{∞} observed in several species was driven by temperature, as the reasoning above suggests, then this study can be considered to support the prediction that the future assemblage-averaged maximum body weight of species may be

Table 2 Yield-per-recruit (YPR) values (kg) prior (1978) and after (1993) the observed decline in L_{∞} with corresponding individual yield loss in value (kg) and percentage. 1978 and 1993 were years in which the standardized common Trend 1 reached its maximum and minimum values prior and after the decline in L_{∞} . For sole and plaice, the low natural mortality estimates (0.1 at all ages) resulted in high YPR values for these two species compared to other species.

Substock	YPR 1978	YPR 1993	Individual yield loss	% loss
Haddock North	0.00473	0.00290	0.00183	38.7
Whiting North	0.00089	0.00086	0.00003	3.1
Whiting South	0.00116	0.00060	0.00056	48.1
Herring North	0.00514	0.00450	0.00063	12.3
N. Pout North	0.00171	0.00133	0.00038	22.2
Sprat South	0.00075	0.00072	0.00003	4.0
Sole male South	0.10458	0.08600	0.01858	17.8
Sole female South	0.14949	0.12571	0.02377	15.9
Plaice male South	0.12375	0.06664	0.05711	46.2
Average				23.1

substantially smaller (Cheung *et al.*, 2013a). This model-derived projection of future shrinkages (14–24% smaller by 2050) reflects both temperature impacts on individual growth and biogeographic shifts towards communities having a higher proportion of small-sized species. Considering only impacts on individual growth resulted in 10% shrinkage (Cheung *et al.*, 2013b). Our study showed that a relatively small increase in temperature (<2 °C) over a 40-year period was concurrent with reductions in L_{∞} that were variable across species (1–29%) but surprisingly large (average 16%) and comparable in scale to the Cheung *et al.* projection. The speed and scale of Cheung *et al.*'s prediction about body sizes in future oceans appear more reasonable than critics claim (Brander *et al.*, 2013). In our opinion, the projections of Cheung *et al.* have merit. In combination with our empirical observation of synchronous growth trends in North Sea fishes, it is clear that a comprehensive analysis of available data on individual growth is required.

Our results also provide empirical support for a recent simulation study showing that shrinking body sizes impact fisheries yield (Audzijonyte *et al.*, 2013). Comparing two years before and after the decline in L_{∞} (1978 and 1993, respectively) shows that, under several assumptions, yield-per-recruit, i.e., the catch in weight per recruit entering the fishery (Beverton & Holt, 1957) for the affected North Sea stocks decreased by 3.1–48.1% with an average reduction of 23.1% (Table 2). Despite the many assumptions required to estimate yield-per-recruit, it is self-evident that smaller body sizes will decrease *per-capita* estimates of produc-

tivity. The magnitude of these declines seems both substantial and underappreciated relative to the well-documented impacts of fishing over recent decades (Fernandes & Cook, 2013). Given that seasonal mean surface temperatures in the North Sea are predicted to increase by 2.42–3.27 °C by the end of the century (MCCIP, 2010) future synchronous reductions in yield-per-recruit are probable.

Warming temperatures are generally associated with faster growth rates (higher K) for temperate stocks (Thresher *et al.*, 2007; Neuheimer & Grønkgjaer, 2012). However, it has not been fully appreciated that, given the negative relationship between L_{∞} and K , the downside of fast early growth is smaller adult body size. Consequences of smaller adult body size include reduced *per-capita* reproductive rates (Rijnsdorp *et al.*, 2010), decreased resilience (Hsieh *et al.*, 2006) and altered ecosystem function and services (Sheridan & Bickford, 2011; Edeline *et al.*, 2013). If individual growth rates change directionally in response to warming then management strategies that assume productivity can be restored to levels observed when temperatures were cooler must be re-considered.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Data availability, distribution and life-history traits of the species considered in the analysis. Mean length-at-age 1 was calculated from the age-length keys obtained from the DATRAS database (<http://datras.ices.dk>), except for plaice and sole which calculated length-at-age 1 using the von Bertalanffy equation. A_{50} (age at 50% maturity) values were averaged across time series and were estimated by fitting maturity ogives to sex maturity age-length keys obtained from the DATRAS database except for plaice where proportion of mature-at-age values were used. For sole, the value 2.5 was chosen as A_{50} is reached between age two and age three. The selectivity (age classes targeted by the fishery) values were obtained from ICES assessment working group reports and correspond to the age ranges used to estimate the average fishing mortality (F). Main preys were estimated from diet data given in Pinnegar *et al.* (2011) and Greenstreet (1996).

Table S2. Summary table listing the candidate factors considered to explain the synchronous decline in body size observed for a majority of substocks, their effects on body size, and the conclusions from the analyses regarding their possible links with the synchronous trend.

Table S3. Summary table of the cohorts considered as outliers for each substock, with their L_{∞} values and associated standard errors (SE). Unrealistically high values of L_{∞} reflect growth trajectories that are more linear than asymptotic.

Table S4. Selection table of candidate models tested in the Dynamic Factor analysis including log-likelihood, Akaike criterion (AIC) and the difference (Δ_{AIC}) between the AIC of the considered model and the best candidate model (minimum AIC observed).

Table S5. Estimated correlations between Trend 1 and the trend in density for the substocks related to Trend 1, with their corresponding P -values. The lag included in the estimation of the density is indicated (see Methods). Significance was adjusted by a sequential Bonferroni correction: the ordered P -values were compared with the inequality, $P_i \leq \alpha(1 + k - i)^{-1}$, Where α is the confidence level to test for significance (0.05), K is the number of correlation tests carried out and i is the rank of the correlation considered. Correlations for which the inequality is met are significant (*).

Figure S1. (a) the International Council for the Exploration of the Sea (ICES) standard round fish areas for the North Sea used for the International Bottom Trawl Surveys; (b) Overall average annual sea bottom temperature (thick continuous line) between the average of round fish areas 1 and 2 (lower continuous line) and the average of round fish areas 5 and 6 (upper continuous line). The two lower dashed lines correspond to areas 1 and 2, the two upper dashed lines to areas 5 and 6.

Figure S2. Log-scaled relationships between the K and L_{∞} parameters for the substocks considered in the analysis (triangles: cod, straight crosses: haddock, circles: whiting, squares: herring, diagonal crosses: Norway pout, stars: sprat, F and M: female and male plaice, f and m (in grey): female and male sole). Filled symbols stand for substock in northern North Sea, empty symbols for substocks in the southern North Sea. Lines correspond to linear models fitted to the data points.

Figure S3. Time series of L_{∞} estimates (line) with their corresponding 95% confidence intervals (shaded areas) of the thirteen substocks considered in the analysis. (a) cod North; (b) cod South; (c) haddock North; (d) whiting North; (e) whiting South; (f) herring North; (g) herring South; (h) Norway pout North; (i) sprat South; (j) male sole South; (k) female sole South; (l) male plaice South; (m) female plaice South.

Figure S4. Abundance-at-age 1 indices (filled circles) used as a proxy for density for the substocks related to Trend 1 (for both plaice and sole substocks the abundance index stands for the males and females together as no sex-specific abundance index were available) plotted along the fitted values from the best Dynamic Factor Analysis model (line) and their corresponding 95% confidence intervals [(a) haddock North; (b) Norway pout North; (c) Sprat South; (d) plaice South; (e) sole South; (f) whiting North; (g) whiting South; (h) herring North].

Figure S5. Fishing mortality (filled circles) for the substocks related to Trend 1 [fishing mortality was assumed to be equal for both male and female sole South] plotted along the fitted values from the best Dynamic Factor Analysis model (line) and their corresponding 95% confidence intervals [(a) haddock North; (b) Norway pout North; (c) Sprat South; (d) plaice South; (e) sole South; (f) whiting North; (g) whiting South; (h) herring North].

Figure S6. Mean age of each cohort (filled circles) used in estimating L_{∞} for the substocks related to Trend 1 plotted along the fitted values from the best Dynamic Factor Analysis model (line) and their corresponding 95% confidence intervals [(a) haddock North; (b) Norway pout North; (c) Sprat South; (d) plaice male South; (e) sole male South; (f) sole female South; (g) whiting North; (h) whiting South; (i) herring North].

Figure S7. The common trends (black line) identified by the best-fitting Dynamic Factor Analysis (DFA) model to describe temporal variation in density (panel a), fishing mortality (panels c and e) and mean cohort age (panels g, i and k) for the eight substocks that were positively related to Trend 1 (grey line) and their corresponding factor loadings for each substock (panels b, d, f, h, j and l, respectively). For fishing mortality and mean cohort age, the best model identified by DFA included more than one trend suggesting that there is no synchrony in the fishing mortality time series and the mean age of sampled individuals for these eight substocks. For density, although the best model identified by DFA included a single trend, haddock North and sprat South did not conform to it while whiting North showed the highest factor loadings of all substocks, suggesting that the trend was mainly driven by this substock only.