

Climate effects on size-at-age: growth in warming waters compensates for earlier maturity in an exploited marine fish

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Abstract

Over the past 3 decades, North Sea Atlantic cod (*Gadus morhua*) have exhibited variable length-at-age along with declines in spawning stock biomass and timing of maturity. Multiple factors affecting growth and development in fish acted on this economically important stock over the same period including warming waters and an intensive fishery. Here, we employ North Sea cod as a model population, exploring how a physiologically relevant temperature metric (the growing degree-day, GDD; °C day) can be used to compare year-classes on a physiologically relevant time-scale, disentangling influences of climate (thermal history) on observed length-at-age trends. We conclude that the trends in North Sea cod length-at-age observed during the last three decades can be explained by a combination of temperature-dependent growth increases and a trend toward earlier maturation, the latter likely induced by the intensive fishing pressure, and possibly evidence of fisheries-induced evolution.

Keywords: Climate, fish, fishing, growing degree-day, growth, length, maturation, production, size, temperature

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Introduction

Animal size-at-age is determined by the interaction between growth and development rates (e.g., maturation), and associated environmental and genetic effects. Thus, the size of a mature animal not only depends on immature and mature growth rates (the latter partially determined by reproductive investment), but also the age at which the animal matures. Maturity often marks a switch from the relatively high-growth immature phase to relatively low-growth mature phase where a portion of resources becomes diverted to reproduction. In addition to environmental and genetic components of growth and development, anthropogenic influences can also play a role in determining size-at-age, particularly for resource populations including exploited fish stocks.

Because size-at-age influences the fecundity of the individual (Trippel, 1995; Hislop, 1996; Hedeholm, 2010) and individual fecundity is integrated to determine production (Barot *et al.*, 2004a), explaining changes in size is necessary to explain variability in population production. Thus, to explain past trends in size and stock production, as well as make predictions concerning production in a changing climate, it is necessary to disentangle climate effects on growth and developmental rates.

Although North Sea Atlantic cod (*Gadus morhua*) has been an economically important species for centuries, the population has been estimated below the precautionary approach biomass (150 000 t) since 1984 (Blanchard *et al.*, 2005; ICES, 2011). These biomass declines have been accompanied by variability in length-at-age (LaA; Rindorf *et al.*, 2008), as well as declines in both size and age at maturity (Wright *et al.*, 2011). Disentangling factors that influence LaA and maturity timing (e.g., temperature and fishing) can be difficult (Brander, 2007a,b) but is imperative to the development of successful conservation strategies (Sinclair *et al.*, 2002; Olsen *et al.*, 2011). As ectotherms, environmental temperature is a controlling factor for fish regulating the fish's metabolism and resulting physiological and demographic rates (e.g., Fry, 1971). Thus, temperature-dependent variability in growth and development must be examined foremost to accurately quantify the effects of other, temperature-independent factors (Brander, 1995; Neuheimer & Taggart, 2007). Disentangling temperature-dependent variability in fish growth and development requires (1) observations of temperature ambient to the fish (Brander, 2000) and (2) estimates of temperature on a physiologically relevant time scale (Neuheimer & Taggart, 2007). For over two centuries in other areas of ectotherm research (Seamster, 1950; Atkinson, 1994; Bonhomme, 2000) and recently for fish (e.g., Neuheimer & Taggart, 2007; Righton *et al.*, 2010; Venturelli *et al.*, 2010) the physiologically relevant metric employed is the growing degree-day (GDD) – the

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time integral of daily temperature above a threshold temperature. The GDD (°C day) represents the thermal history of the fish and has proven success in disentangling temperature-dependent variability in length-at-age among stocks, year-classes (YCs), etc., with strong linear relationships between LaA and GDD within a developmental stage (i.e., while the energy-budget of the fish remains unchanged; Neuheimer & Taggart, 2007) and when temperatures remain within the tolerance limits of the fish (Neuheimer *et al.*, 2011). When life history transitions (e.g., smoltification, maturation) are marked by changes in the amount of energy allocated to growth, an abrupt change in the relationship between LaA and GDD occurs (Neuheimer & Taggart, 2007, 2010). Such a change identifies a thermal constant – the amount of heat (GDDs) needed to achieve some aspect of development (Campbell *et al.*, 1974; Day & Rowe, 2002). The thermal constant has been employed to determine a physiologically meaningful development time to stage (e.g., emergence, maturation) in agriculture and entomology (Trudgill *et al.*, 2005) and is equally applicable to fish development timing (Lange & Greve, 1997) including egg hatching time, smoltification (Neuheimer & Taggart, 2007) and maturation (Neuheimer & Taggart, 2010; Venturelli *et al.*, 2010).

In particular, GDD can be used to extend the explanation of maturation variability via probabilistic maturation reaction norms (PMRNs). PMRNs describe the probability of a fish maturing at a certain age and size (Heino *et al.*, 2002). By incorporating both age and size (unlike common maturity ogives, e.g., age-at-50%-maturity), PMRNs remove the influence of survival and average juvenile growth on the maturation schedule, the latter helping to disentangle plastic- vs. genetic-based variation in maturation (Barot *et al.*, 2004a; Dieckmann & Heino, 2007). In traditional PMRNs, environmental effects on maturation are represented through the range in observed growth rates, acknowledging that most factors affecting growth will also affect maturation (Barot *et al.*, 2004a). However, it is possible that environmental factors will act on maturation independently of growth (Grift *et al.*, 2003; Dhillon & Fox, 2004) prompting recent endeavors to extend the PMRN to include these factors directly (e.g., condition, Grift *et al.*, 2007; Dieckmann & Heino, 2007; Vainikka *et al.*, 2009; Uusi-Heikkilä *et al.*, 2011). Using GDD to incorporate the thermal constant of maturity into PMRN analyses would improve the extrication of environmental (temperature) effects on maturation that may act independently of growth (e.g., Tobin & Wright, 2011).

Here we employ GDD to estimate LaA variability among YCs of North Sea cod that is attributable to differences in climate (i.e., temperature). First, we use GDD to explain what role temperature has played in

shaping temporal variation of growth of North Sea cod. Second, we extend the PMRN method with GDD to examine temperature (thermal history) influences on maturation timing for these fish. Finally, we discuss residual, temperature-independent variability in growth and maturation with respect to other factors affecting this population. Trends in size and maturation for this population, along with rapid warming and intensive fishing pressure, make it an ideal model population with which to test our ability to disentangle climate effects from observed time series of size variability. Moreover, as conservation strategies will differ depending on the sources of variation in size-at-age, our study aims at extricating temperature effects on the observed trends in North Sea cod LaA to allow for more predictive models and successful conservation strategies in the face of a changing climate.

Methods

The North Sea (confined within 51°N and 62°N latitude and 4°W and 9°E longitude, International Council for the Exploration of the Sea (ICES) Subarea IV; Fig. 1) is a continental shelf sea in the northeastern Atlantic ranging in average depth from 30 m in the south to 200 m in the north and maximizing in depth at the Norwegian Trench (~725 m). Circulation is influenced by Atlantic waters mainly through the north and to a lesser extent through the English Channel. Most areas remain vertically mixed with some stratification occurring in the south and central North Sea in May–June, deepening through the summer, and mixing again in November (Blanchard *et al.*, 2005; Pilling *et al.*, 2007).

Length, age, maturity, and sex data were obtained from the ICES co-ordinated North Sea International Bottom Trawl Survey (NS-IBTS) with data downloaded from the ICES DATRAS database. Fish were sampled from 1983 through 2010 using bottom trawls with a small mesh cover (nets standardized among nations by 1983; ICES, 2010) in the first quarter (January through March, approximated as day-of-year = 45), coinciding with spawning time and likely minimizing any effect of immigration from other stocks into the North Sea. Total length (to 1 cm) of all fish (for samples > 75 fish, a representative sub-sample was chosen) was determined and otolith samples were taken ($n = 76\,675$ fish; minimum of 8 fish per 1 cm length-class per roundfish area when available; Fig. 1; ICES, 2010). Maturity stage was recorded for each aged fish and we considered mature fish those designated as stage 2 (“maturing”) or greater (NS-IBTS finfish maturity key; ICES, 2010).

Cod are widespread over the North Sea (Brander, 1994) with a low rate of immigration and emigration from other areas (Houghton & Flatman, 1981). While there is some evidence for substock structure among North Sea cod (Jamieson & Birley, 1989; Hutchinson *et al.*, 2001), the inclusion of micro-satellite loci under selection (Nielsen *et al.*, 2009) and evidence for variable mixing among groups (Blanchard *et al.*, 2005; Horwood *et al.*, 2006; Holmes *et al.*, 2008) makes substock structure description ambiguous. There is evidence that the

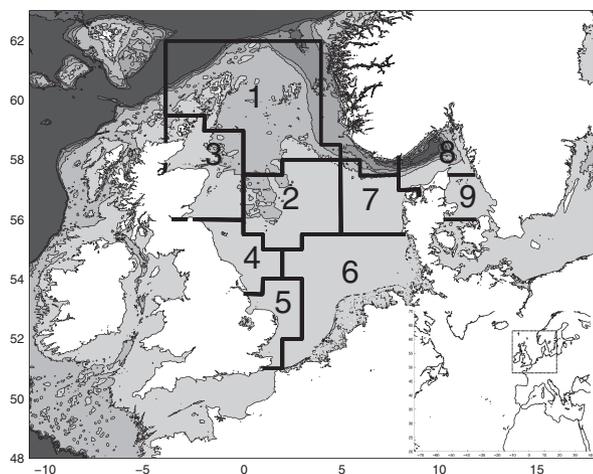


Fig. 1 Chart showing the North Sea in the northeast Atlantic (inset) with North Sea International Bottom Trawl Survey roundfish areas (black lines) and 100 m depth contours.

distribution of cod in the North Sea shifted to more northern waters in the 1990s (Hedger *et al.*, 2004; Perry *et al.*, 2005). To include inter-annual variations in cod distribution, annual mean LaA (cm) for North Sea cod aged 1–8 years were estimated from age-stratified length-frequency estimates weighted by age-, year-, and area-specific catch per unit effort (CPUE; for ages 1 through 6 years extracted from ICES DATRAS database; cod aged 7 and 8 years were assumed uniformly distributed due to no available CPUE data; Wright *et al.*, 2011). Here we assume intra-annual movements are small as compared to the roundfish area scale (Fig. 1), an assumption supported by tagging studies of cod in the North Sea (Turner *et al.*, 2002; Righton *et al.*, 2010). Length-at-age outliers were considered those ± 4 standard deviations of the mean length-at-age for the study period, and were removed.

Temporal variation in LaA 1 through 8 years over the study period was examined for discontinuities (Legendre & Legendre, 1998; See Supporting Information) and trends were quantified through Model 1 linear regression. LaA was further examined by year-class (YC) to examine YC-specific variations in growth and maturity. Timing of maturity varied over the study period with age-at-50%-maturity declining from 4.5 to 3 years between 1980 and 1995 (Cook *et al.*, 1999) and further declines more recent (Wright *et al.*, 2011; this study). YC-specific analyses were restricted to LaA of mature fish (ages 4 through 8 years), with implications for immature fish discussed, to determine external (e.g., temperature, fishing) vs. internal (energy budget of the fish changing upon maturation) factors affecting LaA. YC-specific time-series of LaA for ages 4 through 8 years were well explained by a linear relationship and were examined for the 1979 through 2001 YCs. To allow for measurement error in both the response and explanatory variables, correlations were first assessed for significance ($P < 0.05$) and significant correlations were described using a Model 2 linear regression (Legendre & Legendre, 1998):

$$\text{LaA} = \beta' \cdot \text{Time} + \alpha', \quad (1)$$

where LaA is length-at-age (in days, for comparison with GDD metric, see below), β' is the slope, $\text{cm} \cdot (\text{day})^{-1}$ (an estimate of growth rate), and α' is the intercept, cm (possibly correlated with maturation size, see Discussion) of the LaA-at-Time relation.

Estimates of bottom temperature (within 5 m of bottom; 1979 through 2010) for the North Sea were extracted from the ICES Oceanographic database sampled by CTD casts over the North Sea (Hedger *et al.*, 2004; Blanchard *et al.*, 2005; Wright *et al.*, 2011). To ensure temperature estimates matched the cod distributions (i.e., best estimates of temperatures ambient to the fish), temperature data were averaged monthly in each roundfish area and weighted by the age-, year- and area-specific CPUE to get an average (and YC specific) monthly temperature experienced by cod in the North Sea.

The GDD at day n ($^{\circ}\text{C}$ day) was calculated for each YC as:

$$\text{GDD}(n) = \sum_{i=1}^n (T_i - T_{\text{Th}}) \cdot \Delta d, \quad T_i \geq T_{\text{Th}}, \quad (2)$$

where T_i is the interpolated mean daily temperature experienced by the YC at day i where $i = 1$ at hatching (i.e., day-of-year 60 representing the mid-point of spawning, Blanchard *et al.*, 2005), T_{Th} is the predetermined threshold temperature ($T_{\text{Th}} = 0$ $^{\circ}\text{C}$, Neuheimer & Taggart, 2007) and Δd is a set time-step (sampling frequency, i.e., 1 day).

LaA (cm; ages 4 through 8 years) as a function of GDD ($^{\circ}\text{C}$ day) was determined for each YC by assessing correlations for significance ($P < 0.05$) and describing significant correlations using a Model 2 linear regression according to:

$$\text{LaA} = \beta \cdot \text{GDD} + \alpha, \quad (3)$$

where β is the slope, $\text{cm} \cdot (\text{C day})^{-1}$ (an estimate of temperature-independent and physiologically relevant growth rate), and α is the intercept, cm (a possible indicator of maturation size, see Discussion) of the LaA-at-GDD relation.

Age-at-50%-maturity was estimated for females and males of each YC using logistic regression. GDD-at-50%-maturity (i.e., GDD at which 50% of the fish were mature) was estimated for females and males of each YC using integrated temperature from spawning to age-at-50%-maturity (Neuheimer & Taggart, 2010; Venturelli *et al.*, 2010). Proportions mature at age (or GDD) were weighted with distribution estimates (CPUE) as above.

Variability in maturation among YCs was explored by estimating sex-specific PMRNs on two time-scales, calendar age (years; PMRN-age) and thermal history of the individual (i.e., physiological age; $^{\circ}\text{C}$ day; thermal constant of maturity; PMRN-GDD). The PMRNs or probability of maturing at age a and size s , $m(a,s)$, are given by

$$m(a,s) = \frac{o(a,s) - o(a-1, s - \Delta s)}{1 - o(a-1, s - \Delta s)}, \quad (4)$$

where $o(a,s)$ is the probability of being mature at a and s , $a-1$ is the previous age and Δs is the size increment from age $a-1$ to age a (Barot *et al.*, 2004a). Eqn (4) assumes iteroparity, and that immature and mature individuals have the same survival and growth rates within the same age-class, with probability estimation robust to these latter assumptions (Barot *et al.*,

2004a; Grift *et al.*, 2007). We also consider a model that uses GDD as the time-scale:

$$m(\text{GDD}_{a,s}) = \frac{o(\text{GDD}_{a,s}) - o(\text{GDD}_a - \Delta\text{GDD}_{a,s} - \Delta s)}{1 - o(\text{GDD}_a - \Delta\text{GDD}_{a,s} - \Delta s)}, \quad (5)$$

where s and Δs are defined as in Eqn (4) and GDD_a is the GDD to age a and ΔGDD_a is the GDD increment from age $a-1$ to age a .

Estimating the YC-specific PMRNs required four steps: (1) $o(a,s)$ and $o(\text{GDD},s)$ were estimated through logistic regression as (Grift *et al.*, 2003; Barot *et al.*, 2004a):

$$\text{logit}(o) = \log_e\left(\frac{o}{1-o}\right). \quad (6)$$

Two o give models were explored for their ability to explain maturation:

$$\text{logit}(o) \sim y + a + s + (y \times a) + (y \times s) + (a \times s), \quad (7)$$

$$\text{logit}(o) \sim y + \text{GDD} + s + (y \times \text{GDD}) + (y \times s) + (\text{GDD} \times s), \quad (8)$$

where y , a , s (length, cm) and GDD are variates (continuous variables, Barot *et al.*, 2004b). Models were selected using likelihood ratio tests ($P < 0.05$) between competing models using forward and backward stepwise model selection procedures for first-order interactions (Vainikka *et al.*, 2009). The interaction between age and length was omitted to prevent “swapping” of the reaction norm (i.e., a higher probability of maturing at smaller sizes, Pardoe *et al.*, 2009). 2) Δs and ΔGDD were estimated as the difference in cohort-specific mean LaA and GDD for two consecutive ages. 3) YC-specific $m(a,s)$ and $m(\text{GDD},s)$ were estimated from Eqns (4) and (5). 4) Results were summarized as L_{P40} , L_{P50} , and L_{P60} , describing the 40, 50, or 60% probability that the fish will mature at a given size and age or GDD (Barot *et al.*, 2004a). L_{P40} , L_{P50} , and L_{P60} were estimated by linear interpolation between the sizes that lead to the probabilities of maturing immediately lesser and greater than 40, 50 or 60% (Barot *et al.*, 2004b). PMRNs were also formulated for cod restricted to the northwest (Area 3; Fig. 1) and south (Areas 4, 5 & 6) of the North Sea to examine identified spatial variability (sub-stock structure) in maturity changes (Harrald *et al.*, 2010; Wright *et al.*, 2011).

Where appropriate, regression parameters are estimated with explanatory variables normalized (i.e., relative to the mean of the explanatory variable). The result is a more meaningful intercept estimate, where the intercept represents the value of the dependent variable when the explanatory variable is equal to the mean (vs. e.g., an estimate of the dependent variable at year 0). Statistical significance was evaluated at a significance level of 0.05.

Results

Distribution-weighted mean monthly temperature within the North Sea exhibited a mean of 8.4 ± 2.1 °C (mean \pm standard deviation) over the study period with a significant increase in temperature over time (1979 through 2010; 2-year smoothed temperature series: Linear regression with normalized Year: Tempera-

ture = $(0.052 \text{ °C yr}^{-1}) \text{ Year} + 8.4 \text{ °C}$; $r^2 = 0.61$; $P < 0.001$; Fig. 2). All subsequent results were similar using the smoothed and un-smoothed series, with the un-smoothed mean monthly temperature series used in all further analyses to ensure small variations in the YC-specific thermal histories were incorporated.

Over the entire study period, North Sea cod showed a significant decline in LaA 6 years from 1983 to 2011, while more recently (1996–2011, break-point determined using discontinuity analysis, see Supporting Information), LaA 1 through 4 years has increased (Fig. 3; Table 1). No significant trend was observed for LaA 5, 7 and 8 years. (Fig. 3; Table 1). All trends in LaA analysis were similar among males and females.

Changes in growth and development among cohorts were explored by examining trends in LaA by YC in both calendar time (year) and physiological time (GDD). YC-specific regressions of length on age for mature fish plotted in calendar time showed significant variation among YCs (Fig. 4a) with an increase in slope (i.e., growth rate, cm day^{-1} ; Correlation: $P = 0.010$; Model 2 regression with normalized YC: Slope = $(0.00031 \text{ cm day}^{-1}\text{YC}^{-1}) \text{ YC} + 0.026 \text{ cm day}^{-1}$; $r = 0.51$; Fig. 4c) and decrease in intercept (cm; Correlation: $P = 0.0093$; Model 2 regression with normalized YC: Intercept = $(-0.73 \text{ cm YC}^{-1}) \text{ YC} + 28 \text{ cm}$; $r = -0.52$; Fig. 4e) with increasing YC. Thus, YCs exhibit trends toward faster growth (slope) and possibly earlier

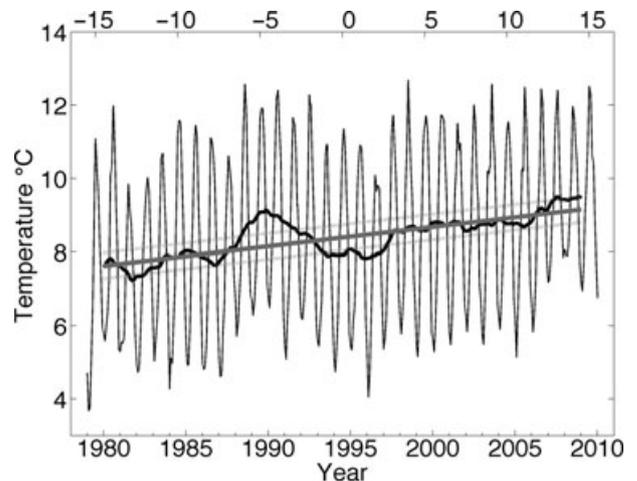


Fig. 2 Interpolated monthly mean (black thin line) and smoothed (2-year moving average, black thick line) bottom temperature (°C) samples obtained from the ICES Oceanographic database weighted by the spatial distribution of cod in the North Sea (via CPUE data). Smoothed temperatures demonstrate an increase over time (gray solid line, linear regression with normalized year; dashed line, 95% confidence intervals around the prediction; Temperature = $(0.052 \text{ °C yr}^{-1}) \text{ Year} + 8.4 \text{ °C}$; $r^2 = 0.61$; $P < 0.001$). Upper axis is normalized year used in regression analysis.

maturation (intercept, see Discussion) but how much of this variation might be due to temperature is unclear until they are examined on a thermal time-scale (GDD).

No trend was found among slopes (growth rate, cm (°C day)⁻¹), when examined on a thermal (GDD) time-scale (Fig. 4b), suggesting that differences in thermal history explain much of the trend in growth rate among YCs (No correlation, $P = 0.58$; Fig. 4d). However, a significant decline in intercepts was maintained when GDD is used as the time-scale (cm; Correlation: $P = 0.023$; Model 2 regression with normalized YC: Intercept = $(-0.75 \text{ cm} \cdot \text{YC}^{-1}) \cdot \text{YC} + 30 \text{ cm}$; $r = -0.46$; Fig. 4f). Thus, differences in thermal history (GDD) among YCs was able to explain major variability in

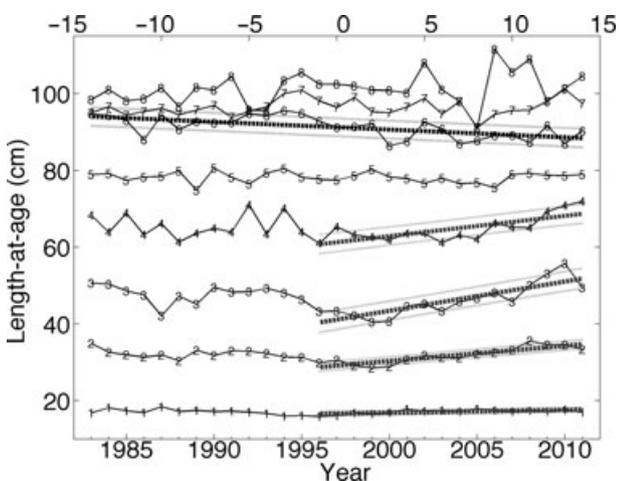


Fig. 3 Variation in mean length (cm) at age (year, labels) for North Sea cod for ages 1 through 8 years, from 1983 through 2011 (black solid lines; ICES North Sea International Bottom Trawl Survey). Significant trends are given as linear regression (dashed lines) and 95% confidence intervals around the prediction (dotted lines) for 1983 through 2011 (black) and 1996 through 2011 (gray, see Methods). Upper axis is normalized year used in regression analysis. Parameterization of trends are given in Table 1.

Table 1 Parameters of linear regression length-at-age (cm) of North Sea cod as a function of normalized year from 1983 through 2011

Age (year)	1983 through 2011				1996 through 2011			
	Slope (cm yr ⁻¹)	Intercept (cm)	r^2	P -value	Slope (cm yr ⁻¹)	Intercept (cm)	r^2	P -value
1				0.86	0.07	17	0.38	0.012
2				0.42	0.39	32	0.77	<0.001
3				0.69	0.76	46	0.72	<0.001
4				0.51	0.53	65	0.57	<0.001
5				0.59				0.69
6	-0.20	91	0.37	<0.001				0.13
7				0.31				0.82
8				0.11				0.67

growth of mature fish but not that of the intercepts of the LaA vs. time relations, the latter possibly indicative of maturation changes, which we explored next.

Comparing fish from all YCs, mature fish in each age received statistically higher GDD than immature fish of that age (ages 1 through 4 years; see Supporting Information Fig. S1), possibly indicating the influence of thermal time (GDD) on maturation. However, this result may simply be GDD acting through the size of the fish to influence maturation (vs. GDD influencing maturation directly); a possibility we examine in our PMRN analysis below by simultaneously quantifying effects of GDD and length on maturation probability. Consistent with previous literature (Cook *et al.*, 1999), declines in age-at-50%-maturity were found for both female (see Supporting Information Fig. S2a) and male (Fig. S2c) fish (from approximately 4.5 to 2.5 years), with abrupt shifts over 1990–1995 (see Supporting Information). Declines were maintained when examined on a thermal time-scale where GDD-at-50%-maturity declined from approximately 13 000–8000 °C day over the time period (Fig. S2bd).

In general, PMRNs estimated for the entire North Sea exhibited a negative slope with declining L_{P50} with increasing age when accessed as calendar time (PMRN-age, Figs 5ac) or using the thermal constant of maturity (PMRN-GDD, Fig. 5b and d). Patterns were similar among males and females (Fig. 5). Elevation of L_{P50} declined with increasing YC such that L_{P50} for a specific age was lower for more recent YCs (i.e., declining length- and age-at-maturity; Fig. 5). In addition, the slope of the PMRNs became steeper (more negative, Fig. 5) indicating an acceleration of the decline in age-at-maturity with increasing YC. These trends were consistent when examining the sub-areas of the North Sea, though slopes of the PMRNs varied by sub-region and fish in the southern areas matured at a larger size than those in the northwest (see Supporting Information Fig. S3 & S4).

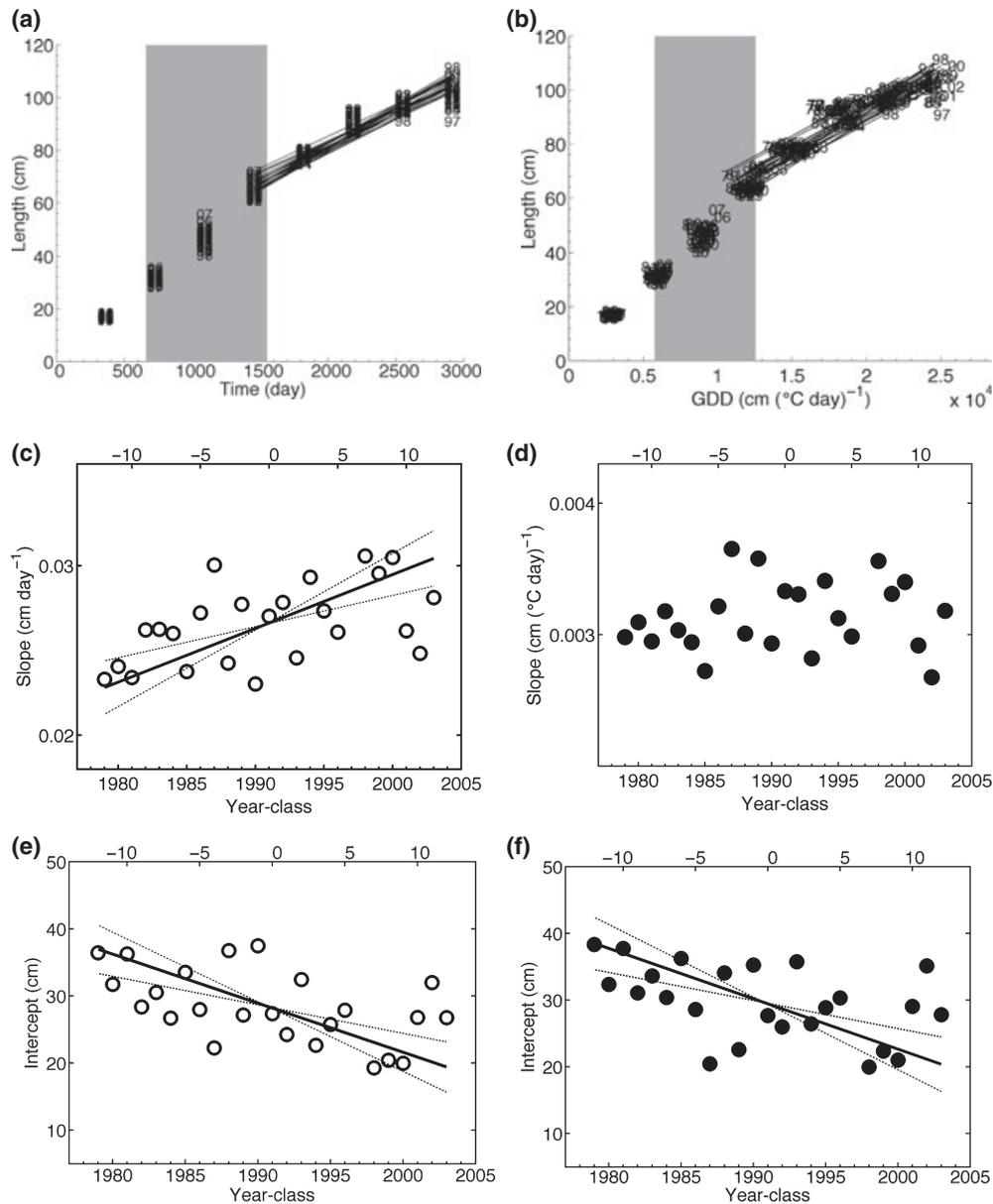


Fig. 4 Length-at-age analysis among North Sea year-classes. (a,b): Length for North Sea cod ages 1 through 8 years as a function of (a) calendar time (day) and (b) growing degree-day (GDD; °C day). Lines indicate a significant linear relationship among LaA 4 through 8 years and (a) calendar time or (b) GDD (correlation $P < 0.05$; Model 2 regression $P < 0.05$). The shaded area is variability in (a) age- or (b) GDD-to-50%-maturity. Data-labels denote YC decade and year. (c-f): Parameters of the (c,e) LaA-at-Time and (d,f) LaA-at-GDD linear relations for North Sea cod year-classes (YCs). Slopes of LaA-at-Time relations (c), cm day^{-1} , demonstrate a significant increase with increasing YC (solid line, linear regression; dashed line, \pm standard deviation; Correlation coefficient: $P = 0.010$; Model 2 regression with normalized YC: Slope = $(0.00031 \text{ cm day}^{-1} \text{ YC}^{-1}) \cdot \text{YC} + 0.026 \text{ cm day}^{-1}$; $r = 0.51$) while slopes of the LaA-at-GDD relations (d), $\text{cm } (^\circ\text{C day})^{-1}$, show no trend over YCs (correlation coefficient; $P = 0.58$). Intercepts of LaA-at-Time relations (e) and the LaA-at-GDD (f) relations, cm, demonstrate significant declines with increasing YC (solid line, linear regression; dashed line, \pm standard deviation; e: Correlation coefficient: $P = 0.0093$; Model 2 regression with normalized YC: Intercept = $(-0.73 \text{ cm YC}^{-1}) \cdot \text{YC} + 28 \text{ cm}$; $r = -0.52$; f: Correlation coefficient: $P = 0.023$; Model 2 regression with normalized YC: Intercept = $(-0.75 \text{ cm YC}^{-1}) \cdot \text{YC} + 30 \text{ cm}$; $r = -0.46$). Upper axis is normalized YC used in regression analysis.

As GDD scales calendar time with temperature to provide a physiologically relevant time-scale, assessing PMRNs on thermal time will explain variability in

PMRNs that can be attributed to temperature differences among YCs. This effect is apparent in the North Sea cod PMRNs as the analysis including GDD results

in the PMRNs becoming noticeably (though not significantly) similar among YCs (e.g., the difference in slopes of the 1993- and 2003-PMRNs is reduced in Fig. 5, S3cd and S4ab; horizontal shifts bring the near-parallel PMRNs of the 1993- and 2003-YC closer in Figs S3ab and S4cd). Still, overall trends of declining age and length at 50% probability to mature remain (e.g., declining elevation of PMRN), suggesting that temperature-independent factors underlie the decline in maturation timing (Figs 5, S3 and S4). As individuals of the same YC are assumed to have the same thermal history, variability in maturation within a YC does not change when examined on the GDD time-scale (i.e., envelope width between L_{P40} and L_{P60} , Figs 5, S3 and S4).

Discussion

Fish size-at-age is determined by the interaction between stage-specific growth rates, and the timing of developmental shifts, such as maturity. Over the last

three decades, we show North Sea cod exhibit variability in both traits with an increase in mature growth (slope of LaA-at-Time relation, Fig. 4c) and decline in age-at-maturity (Fig. S2 and possibly Fig. 4e) combining to produce observed variability in LaA. How much of the trends in growth and maturity are explained by temperature becomes apparent when we compare YCs on a physiologically relevant time-scale. First, we examine YC-specific LaA with YC-specific thermal history (GDD) to find GDD variation is able to explain the increase in slopes of the LaA-at-Time relations (Fig. 4c) and no significant trend among slopes of the LaA-at-GDD relations remains (Fig. 4d). Thus, the trend toward increased slope (growth) of the mature North Sea cod can be explained by differences in the thermal history among YCs.

Investigations such as the present require identification of temperatures ambient to the fish (Brander, 1999; Neuheimer & Taggart, 2007), which can present a challenge to studies over short time periods as well as in

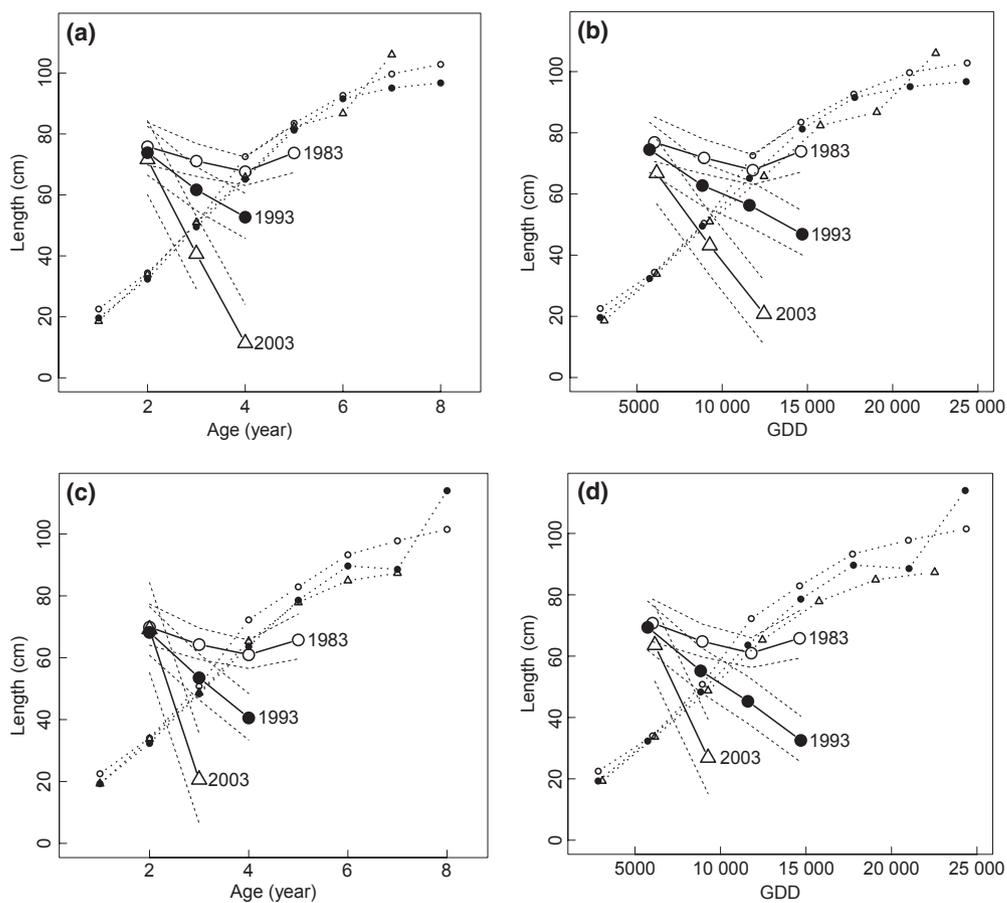


Fig. 5 YC-specific PMRNs (solid lines) assessed on (a,c) calendar time (years) or (b,d) physiological time [thermal constant of maturity, growing degree-day (GDD), °C day] for females (a,b) and males (c,d) across the North Sea. Lines are reaction norm mid-points where there is a 50 (solid line), 40 or 60 (dotted lines) % probability to mature at the given time (age or GDD) and size. Data labels and symbols denote year-class (open circles: 1983; closed circles: 1993; triangles: 2003). Dashed lines are mean LaA for each year-class.

populations exhibiting highly migratory behavior and/or experiencing fine spatial variability in temperatures. The physical characteristics of the North Sea system result in temperature that is highly correlated among regions (Cook & Heath, 2005), simplifying the estimation of relevant temperature series, and we also attempt to include effects of distribution changes on the temperature series estimates by including age-specific information on spatial distribution in CPUE. However, finer temporal and spatial resolution of the YC-specific thermal histories including horizontal (i.e., at scales less than that of the roundfish areas) and vertical (e.g., ontogenetic variations in depth) distribution of the stock may explain some remaining variation in LaA and/or maturation timing among YCs (i.e., scatter in Fig. 4d and f). In particular, tagging data may offer a means to assess how representative temperatures observed from large-scale survey programs are of ambient temperatures experienced by the fish. Previous such tagging studies indicate that cod in the North Sea are not yet seeking out cooler waters (Neat & Righton, 2007).

A decline in intercepts remains among YCs when examined as LaA-at-GDD relations (Fig. 4f). Though a change in intercepts could be due to other factors (e.g., variation in immature growth rate), the decline in the intercept of the LaA-at-GDD relation could also be explained by a switch to earlier maturity. In addition, this interpretation is consistent with our estimates of age- and GDD-at-50%-maturity (Fig. S2) as well as the PMRN analysis, where declines in size and age at 50% probability of maturing are evident in both calendar time (Figs 5a and c, S3ac and S4ac) and physiological time (i.e., thermal constant to maturity; Figs 5b and d, S3bd and S4bd). Our results are consistent with previous estimates of maturation changes in this stock where declines in age- and size-at-50%-maturity were found (Cook *et al.*, 1999; Wright *et al.*, 2011).

While traditional age-based PMRNs attempt to capture phenotypic influences on maturation through effects on growth, factors such as temperature may affect the probability of maturing directly, independent of effects via growth (Grift *et al.*, 2003; Dembski *et al.*, 2006; Tobin & Wright, 2011). The influence of temperature on maturation timing has been found in other areas and species (e.g., Rijnsdorp, 1993; Grift *et al.*, 2003; Kraak, 2007). In our study, a higher GDD-at-age was associated with mature individuals (Fig. S1), indicating the possible influence of GDD on maturation directly through the thermal constant concept. The thermal constant of maturity represents the thermal energy required to achieve maturation (Neuheimer & Taggart, 2010; Venturelli *et al.*, 2010) and can describe temperature effects on maturation that may act independently of growth (e.g., modifying activity of pro-

teins regulating maturation; Pankhurst & Porter, 2003). The thermal constant of maturity will explain shifts in PMRNs calculated on calendar time (PMRN-age), when such shifts are due to differences in the thermal history of the YCs. Evidence of this is found in the North Sea data where PMRNs among YCs become closer together when calculated on thermal time (Figs 5, S3 and S4). Still, changes in the elevation of the PMRNs remains in both calendar and GDD time, indicating trends toward smaller length- and earlier age-at-maturity remain unexplained by temperature.

Major trends in declining age- and length-at-maturity were consistent between sub-areas examined. However, PMRNs varied in the degree of decline in maturity size and timing (Figs S3 and S4), with those fish in the southern North Sea maturing at a larger size than those in the northwestern areas; results similar to those of previous studies (Harrald *et al.*, 2010; Wright *et al.*, 2011). Due to this within-stock variability in maturity (Wright *et al.*, 2011 & Figs S3 & S4), sub-stock structure of life history and growth characteristics should be incorporated into models of how maturation and production trends will change in the future.

In general, GDD may represent a more relevant time-scale with which to examine changes in the timing of maturity, rather than calendar age, the ultimate significance of which has been questioned (Dieckmann & Heino, 2007). Moreover, the thermal constant of maturation could easily be included in many life history models including energy allocation models (e.g., Jørgensen & Fiksen, 2006; Jørgensen *et al.*, 2006) to help shape the "decision" process of maturation.

Variability in PMRNs remaining when assessed on thermal time (PMRN-GDD) could be indicative of two, not mutually exclusive, possibilities. First, though we go further than traditional PMRNs by including possible temperature-dependent effects on maturation itself (similar to 3D reaction norms, e.g., Kraak, 2007), other environmental factors may be acting on maturation independent of growth (Grift *et al.*, 2003; Barot *et al.*, 2004a). Food availability may vary, changing the condition of the cod and the probability the fish will mature (Grift *et al.*, 2003, 2007; Uusi-Heikkilä *et al.*, 2011). Condition estimates are not possible with our current data set due to a lack of energy reserve (e.g., liver weight, hepatosomatic index; Pardoe *et al.*, 2008) or even weight data for the majority of individuals. Though no direct measures are available, the decline in North Sea cod biomass (ICES, 2011) may indicate a release of density-dependent resource limitation, better condition, and earlier maturation. However, evidence for such density-dependent effects on growth are mixed both in the North Sea (e.g., Bromley, 1989; Rindorf *et al.*, 2008) and other cod populations (e.g., Sinclair *et al.*, 2002;

Armstrong *et al.*, 2004; Barot *et al.*, 2004a) with declines in maturation timing and size often remaining after possible condition effects are removed (e.g., Baulier *et al.*, 2006; Vainikka *et al.*, 2009).

Second, it is possible that the remaining variability in PMRNs (Figs 5bd, S3bd and S4bd) represents a genetic shift in the maturation schedule for the stock (Heino *et al.*, 2002; Barot *et al.*, 2004a). In North Sea cod, it appears that the physiologically relevant thermal time, and thus heat energy, needed for a fish to reach maturity has reduced. Consequently, there has been a shift in the fundamental maturation characteristics of the population, a shift that may be indicative of fishing effects on this stock. Such declines in PMRNs have been found in other Atlantic cod stocks (e.g., Heino *et al.*, 2002; Barot *et al.*, 2004a; Olsen *et al.*, 2004), in other exploited fish (e.g., plaice, Grift *et al.*, 2003), and in numerical models of fishing effects on maturation (Ernande *et al.*, 2004), making a shift toward maturation earlier and at smaller size a common feature of many exploited stocks (Barot *et al.*, 2004a; Dieckmann & Heino, 2007; Neuheimer & Taggart, 2010). High fishing mortality such as that experienced by North Sea cod (Hislop, 1996; Cook *et al.*, 1997; Blanchard *et al.*, 2005; ICES, 2011), can induce changes in maturity timing as late-maturers risk the chance of being harvested before first spawning (Roff, 1992; Heino & Kaitala, 1999; Conover, 2000; Jørgensen *et al.*, 2009). This is of particular concern for fish that mature at a relatively late age, such as cod, resulting in high cumulative fishing mortality prior to first spawning (Heino & Gødo, 2002; Armstrong *et al.*, 2004). Such declines in maturity timing are predicted to occur in heavily exploited populations (Nelson & Soulé, 1987; Brander, 2007b; Sattar *et al.*, 2008) and have been noted in other stocks where fishing is intensive (e.g., Reznick *et al.*, 1990; Rijnsdorp, 1993; Rochet, 1998; Heino & Gødo, 2002; Barot *et al.*, 2004a; Neuheimer & Taggart, 2010) including collapsed western Atlantic cod stocks (Myers *et al.*, 1996; Olsen *et al.*, 2004; Neuheimer, 2007).

Changes in mature fish LaA has resulted from a combination of (i) temperature-dependent growth, encouraging higher LaA, and (ii) earlier maturation (possibly fisheries-induced), encouraging lower LaA. Whether future temperature increases (e.g., a 2–3 °C predicted rise by 2100 for the North Sea; Drinkwater, 2005) will continue to compensate for the likely fisheries-induced decline in LaA depends on the nature of that increase, as well as the physiological limitations and age-structure of the stock (Mantzouni *et al.*, 2010). First, further temperature increases would need to remain within the tolerance limits for North Sea cod. For most species within their normal temperature range, a slight increase in temperature is beneficial to

physiological rates, resulting in more energy and higher reaction rates for growth, maturation, etc. (Higley *et al.*, 1986; Neuheimer *et al.*, 2011). However, higher temperatures eventually exceed tolerance limits resulting in negative impacts to an individual's physiology, as cardiac output cannot keep pace with increased metabolic demands (Pörtner & Knust, 2007; Wang & Overgaard, 2007). Indeed, an assumption of the GDD method in predicting fish length is that temperatures remain within the tolerance limits of the fish, where the interaction between temperature and growth is near linear (Neuheimer & Taggart, 2007). Further research into the tolerance limits (and how they vary with fish size, etc.; Björnsson & Steinarsson, 2002) of the North Sea cod population is needed, particularly as the average temperature in the area approaches 10–14 °C, thought to be the optimum temperature for growth and feeding performance for cod (Jobling, 1988; Pörtner *et al.*, 2001). Such estimates of cod tolerance limits (and how they vary in space) would allow for the formulation of more general, non-linear relationships between GDD and LaA, including temperature-sums (GDD), and estimates of growth, at temperatures beyond tolerance limits. Second, future LaA will depend on whether maturation timing continues to decline. Maturation may have reached a physiological limit for how early maturation can occur (Trippel, 1995), or size at maturation may have fallen below the threshold where selection by the fishery has an effect (Ernande *et al.*, 2004). Third, fish must be able to reach older ages to allow for enough time integrating the increased temperature (increased growth rate) to counteract the decreased age-at-maturity and reach previous LaA. The influence of the increased growth predicted by the warming temperatures is more prominent as the fish ages (e.g., slope of increase for LaA 1 through 3 years, Table 1; Fig. 3), requiring fish to achieve an older age before the integrated effects of growth at higher temperature are measurable in LaA.

Here we echo the call for reduced exploitation of the North Sea cod stock (Hislop, 1996; Mantzouni *et al.*, 2010), and, most importantly, the need for improved exploitation patterns (Hislop, 1996) that are better able to preserve the genetic (Reed & Frankham, 2003), age, size (Carlson & Stenseth, 2008), and life history (Harrald *et al.*, 2010; Petitgas *et al.*, 2010; Wright *et al.*, 2011) diversity of the stock; characteristics that mark the difference between a collapsed stock and one that is simply depleted (Petitgas *et al.*, 2010). Such diversity allows a population to fully exploit suitable habitat (Petitgas *et al.*, 2010) and will confer a population's best chance to successfully respond to a changing climate. Finally, Brander (2000; p. 493) states 'It is disappointing that few simple, credible relationships have emerged

which can be used to provide better prognostics for fisheries conservation, even when, as in the case of temperature and growth, such relationships clearly exist'. The use of the GDD metric offers one such tool, that allows for the assessment of stock status/recovery in the natural environment and, when used in conjunction with climate (*sensu* Clark *et al.*, 2003) and recruitment (Olsen *et al.*, 2011) modeling, could allow for predictions on how fish size and the productivity of fish stocks will change in the future.

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Supporting Information

Additional Supporting Information also includes supporting methods may be found in the online version of this article:

Material S1. Supporting Methods and Results.

Figure S1. GDD-to-maturation.

Figure S2. Age- and GDD-to-50%-maturity.

Figure S3. Probabilistic maturation reaction norms for southern North Sea.

Figure S4. Probabilistic maturation reaction norms for north-western North Sea.

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Climate effects on size-at-age:**Growth in warming waters compensates for earlier maturity in an exploited marine fish****Anna B. Neuheimer and Peter GrønkJær****Supporting Information****Supporting Methods – Discontinuity Analysis**

Discontinuity analysis was performed on LaA and maturity time-series via Webster's Method as described in Legendre and Legendre (1998). In Webster's Method, a sample window with two equal halves is moved along the equispaced data in time. Differences in mean values of the points on the left-hand (x_1) and right-hand (x_2) portion of the window are determined via a t-

statistic = $\left(\frac{|\bar{x}_1 - \bar{x}_2|}{s_x} \right)$, where s_x is the standard deviation of the whole series (with

homoscedasticity assumed). Significant discontinuities are determined by comparing the t-

statistic to that value at $P < 0.05$ using degrees of freedom = $\left(\frac{window}{2} \right) - 1$.

In our analysis, varying window widths were employed (e.g. 8, 12 yrs), to ensure results were robust. In the case of determining discontinuities in the LaA analysis, a significant discontinuity was found at 1996 for LaA-2, -3 and -6 yrs and this was used to govern the choice of examining trends in LaA for all ages over 1996-2011, as well as the entire study period.

Supporting Methods – GDD-at-Maturation Analysis

The influence of thermal time (GDD) on maturation was first examined by pooling fish of all year-classes and comparing the thermal time accumulated (i.e. GDD-to-age) by immature vs. mature female and male fish at each age. The median GDD-to-age of immature vs. mature fish was compared using nonparametric Kruskal-Wallis tests for medians for ages 1 through 5 yrs. Comparisons were made by first subtracting the age-specific mean estimate (\overline{GDD}_a) from each individual GDD estimate ($GDD_{i,a}$) to better illustrate differences among ages.

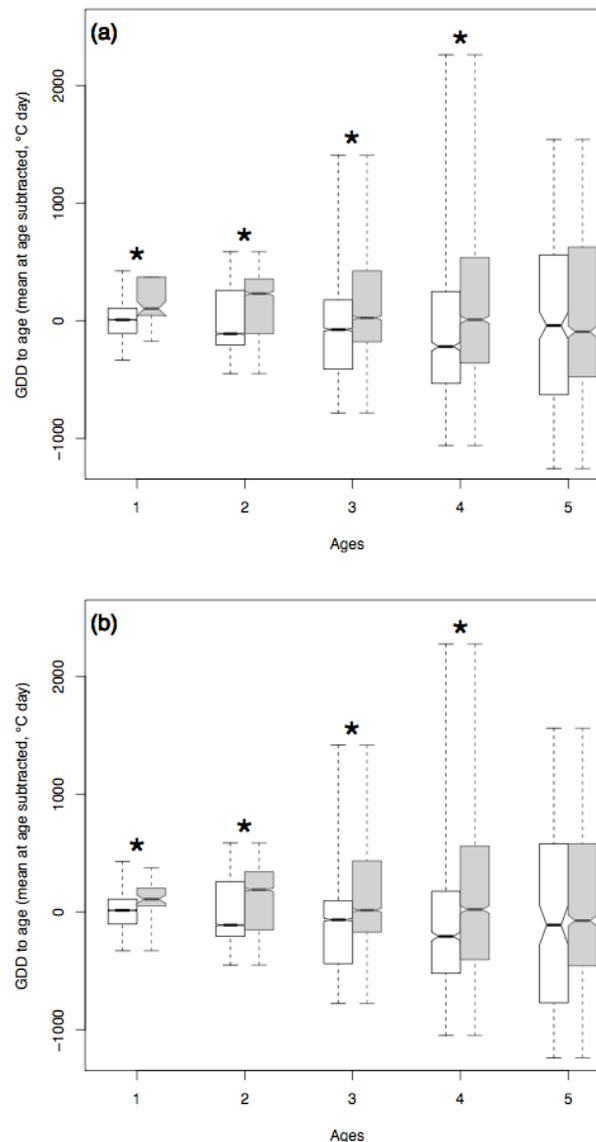
Supporting Results:

Fig. S1: Comparison of GDD to age among immature (white) and mature (grey) individuals at each age (1 through 5 yrs.) for a) female and b) male fish. Boxes extend from the lower to upper quartiles and show the median (horizontal line), uncertainty around the median (notch), and range of data (dashed whisker lines). * denotes statistically different median GDD between immature and mature fish (Kruskal-Wallis test, $P < 0.05$). Comparisons were made by first subtracting the age-specific mean estimate from each individual GDD estimate to better illustrate differences among ages.

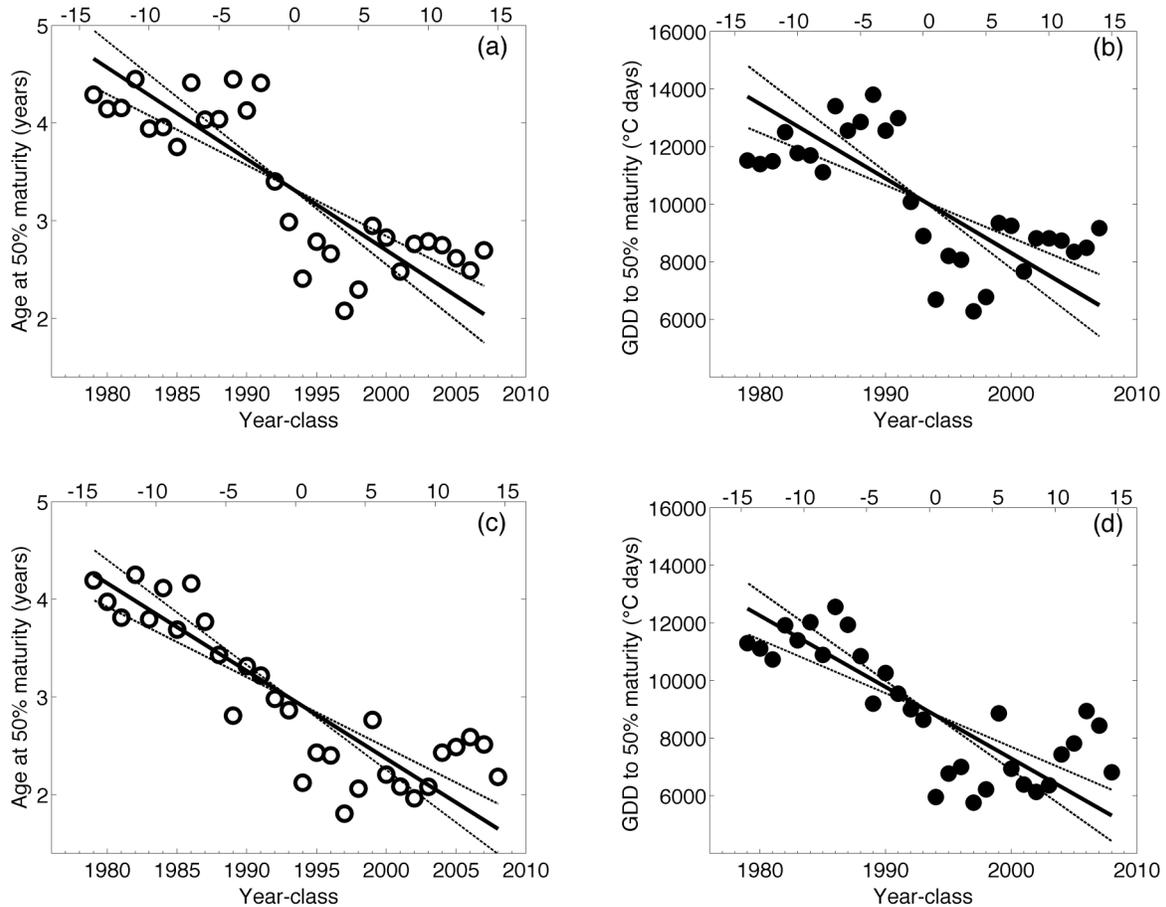


Fig. S2: Changes in maturity with year-class (YC) in (a,c) calendar and (b,d) thermal time for females (a,b) and males (c,d). (a,c) Age-at-50%-maturity, yrs., (solid line, linear regression; dashed line, \pm standard deviation; a, females: Correlation coefficient: $P < 0.001$; Model 2 regression with normalized YC: age-at-50%-maturity = $(-0.094 \text{ Year YC}^{-1}) \text{ YC} + 3.4 \text{ years}$; $r = -0.83$; c, males: Correlation coefficient: $P < 0.0001$; Model 2 regression with normalized YC: age-at-50%-maturity = $(-0.090 \text{ Year YC}^{-1}) \text{ YC} + 3.0 \text{ years}$; $r = -0.86$). (b,d) The thermal constant of maturity (i.e. GDD-to-50%-maturity), $^{\circ}\text{C}\cdot\text{day}$, (solid line, linear regression; dashed line, \pm standard deviation; b, females: Correlation coefficient: $P < 0.0001$; Model 2 regression with normalized YC: GDD-at-50%-maturity = $(-259 \text{ }^{\circ}\text{C}\cdot\text{day YC}^{-1}) \cdot \text{YC} + 1.0 \times 10^4 \text{ }^{\circ}\text{C}\cdot\text{day}$; $r = -0.70$; d, males: Correlation coefficient: $P < 0.0001$; Model 2 regression with normalized YC: GDD-at-50%-maturity = $(-247 \text{ }^{\circ}\text{C}\cdot\text{day YC}^{-1}) \cdot \text{YC} + 9.1 \times 10^3 \text{ }^{\circ}\text{C}\cdot\text{day}$; $r = -0.78$). Upper axis is normalized YC used in regression analysis.

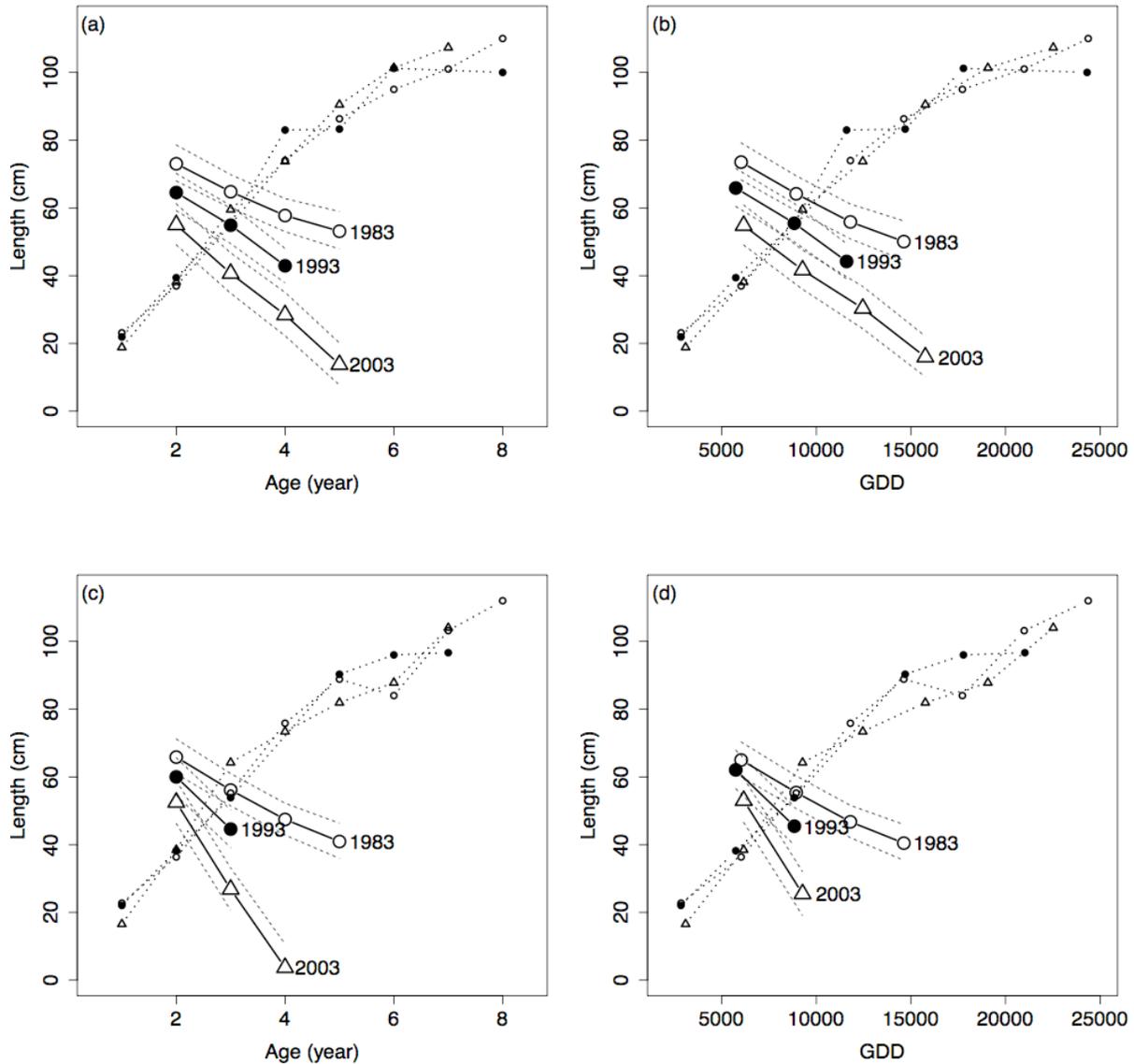


Fig. S3: YC-specific PMRNs (solid lines) assessed on (a,c) calendar time (yr) or (b,d) physiological time (thermal constant of maturity, GDD, °C day) for females (a,b) and males (c,d) for fish in the southern North Sea (roundfish areas 4, 5 & 6; Fig. 1). Lines are reaction norm mid-points where there is a 50 (solid line), 40 or 60 (dotted lines) % probability to mature at the given time (age or GDD) and size. Data-labels and symbols denote year-class (open circles: 1983; closed circles: 1993; triangles: 2003). Dashed lines are mean LaA for each year-class.

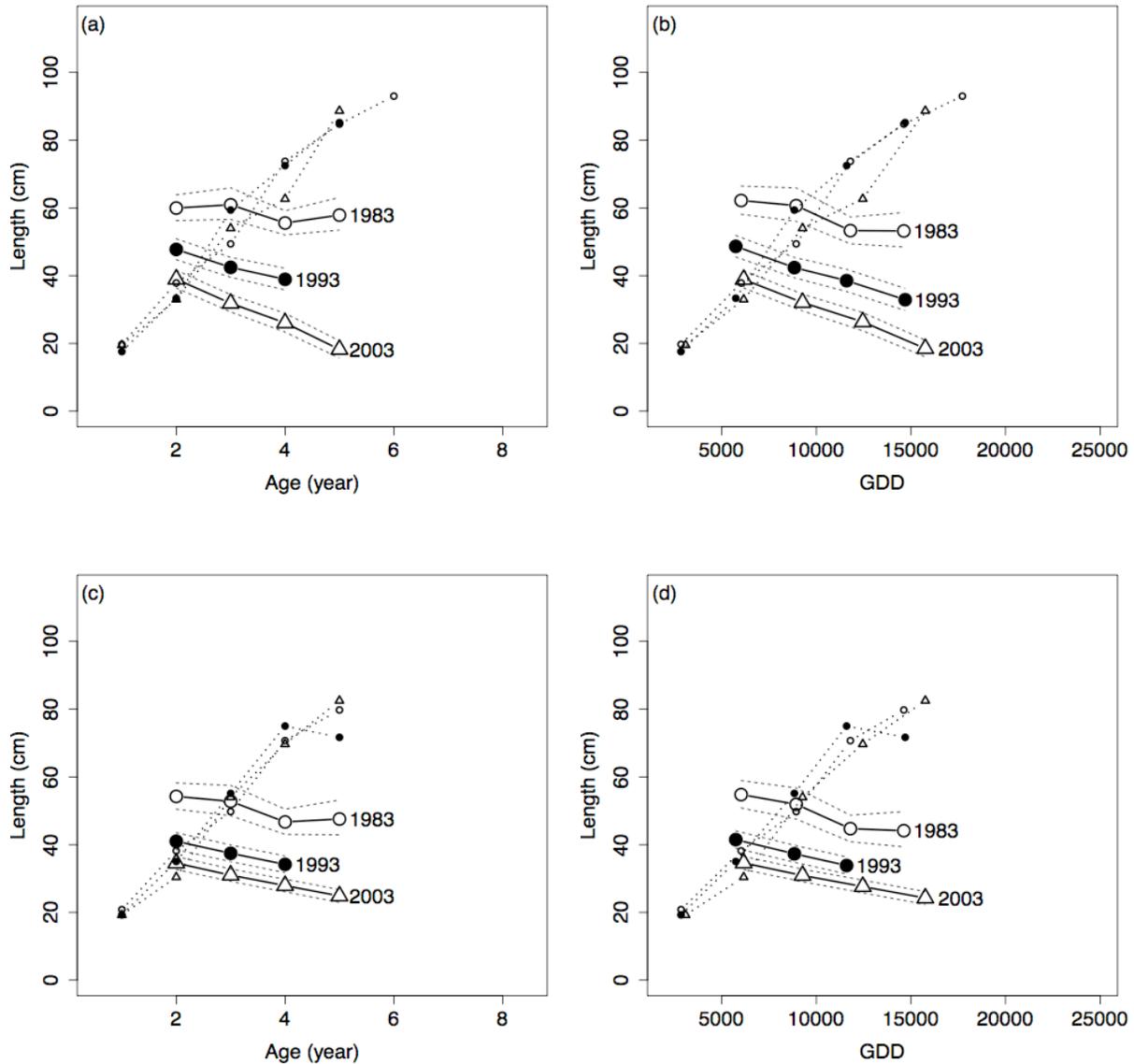


Fig. S4: YC-specific PMRNs (solid lines) assessed on (a,c) calendar time (yr) or (b,d) physiological time (thermal constant of maturity, GDD, °C day) for females (a,b) and males (c,d) for fish in the northwest North Sea (roundfish area 3; Fig. 1). Lines are reaction norm mid-points where there is a 50 (solid line), 40 or 60 (dotted lines) % probability to mature at the given time (age or GDD) and size. Data-labels and symbols denote year-class (open circles: 1983; closed circles: 1993; triangles: 2003). Dashed lines are mean LaA for each year-class.

Supporting References

Legendre P, Legendre L (1998) *Numerical ecology. Developments in Environmental Modelling*, 2nd edn. Netherlands: Elsevier.