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Functional responses of North Atlantic fish eggs to increasing temperature

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ABSTRACT: Temperature increase associated with global climate change can be expected to directly influence the spawning success of fish species, with implications for abundance and distribution. We conducted a meta-analysis to investigate and compare responses of development time, cumulative degree-days and survival of fish eggs from 32 populations of 17 species in the North Atlantic to different temperatures in order to determine potential consequences of global warming for these species. The response of development time exhibited a similar decreasing trend with respect to temperature across species. The similar slopes of regression lines relating ln-transformed development time and temperature indicate similar sensitivity to temperature changes. Across-species differences were mainly driven by intercept values, indicating up to 8-fold differences in development time at given temperature. There was an overall decrease, across species, in an index of thermal requirement (cumulative degree-days) for egg development with increasing temperature. Within an empirically derived optimal thermal range for egg survival, the thermal requirement was more variable in species adapted to cold waters compared to species adapted to warmer waters. Moreover, the sensitivity of survival of eggs from different species to increases in temperature differed, reflecting a pattern of sensitivity along a stenotherm-eurytherm gradient of vulnerability to temperature among species. The results quantify physiological effects of temperature on the eggs, and we propose that such effects are major factors leading to a close correspondence between the physiological optimal temperature for survival and observed temperature at spawning sites. Temperature during egg development appears to be a key evolutionary force affecting spawning time and location.

KEY WORDS: Degree-days · Development time · Fish eggs · Global warming · North Atlantic · Survival · Temperature effects

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INTRODUCTION

One of the most important effects of temperature on fish physiology is its influence on reproductive processes, including the development and survival rates of fish eggs (Pauly & Pullin 1988, Pepin 1991, Geffen & Nash 2012). In general, the early life stages of fish and other marine biota have relatively narrow thermal tolerance ranges compared to the adult stages (Helaouët & Beaugrand 2009, Pörtner & Peck 2010, Peck et al. 2013), making them more

sensitive to temperature changes. Therefore, temperature is likely a dominant factor to which fish species have evolved key life-history strategies and events, including the timing and location of spawning and migration behaviour. Given that climate change is likely to increase ocean temperatures in the coming decades (Hoegh-Guldberg et al. 2014), knowledge of how fish will respond to these changes will be needed to understand and predict climate change consequences for fish ecology, food webs and fisheries management. This knowledge

can also provide a stronger mechanistic basis for developing and interpreting statistical and correlative models of species distributions, habitat occupancy and range expansions and shifts.

A large body of literature exists that describes and quantifies how egg development rates are influenced by temperature (e.g. reviews and syntheses by Pauly & Pullin 1988, Pepin 1991, Geffen & Nash 2012, Peck et al. 2012b). The growth of this body of literature has been driven by 3 main requirements: to develop basic physiological and ecological knowledge of how temperature affects development rates; to apply the development rates in fish stock assessment via the daily egg production method; and to apply this knowledge in aquaculture settings (Geffen & Nash 2012). However, much of this literature can potentially be used to investigate other ecological and life-history concepts that to date have received less attention. These include understanding and comparing possible consequences of climate change on fish reproductive ecology, both within and among species (Peck et al. 2012b), and understanding how temperature via impacts on potentially inter-related species traits (i.e. egg development, survival and spawning time) has shaped fish life-history strategies.

For example, significant differences in development time per degree temperature among species, and/or in the cumulative degree-days required for development (Kamler 2002, Neuheimer & Taggart 2007, Geffen & Nash 2012, Neuheimer & MacKenzie 2014), would indicate differences in egg physiological performance among species and the potential sensitivity of different species to warming temperatures. In particular, the concept of degree-days (Neuheimer & Taggart 2007) can be a powerful tool for comparing physiological responses across many species under changing temperatures, particularly at temperature ranges well within physiological tolerance limits. Alternatively, shared reaction norms to temperature among species would indicate universal egg physiological responses to temperature changes and would suggest that the physiological and genetic mechanisms of egg development are conserved across species despite occupation of different thermal habitats.

Moreover, although fish egg development within a species can proceed at a wide range of temperatures, it is likely that survival rates are highest across a narrower range of temperatures than those that allow egg development, i.e. survival rates could be low at temperatures that could promote very fast or slow development (Kamler 2002, van der Have 2008). Because fish eggs produced by individual species can survive at only a limited range of temperatures,

adults must produce offspring in thermal conditions that allow moderate to high egg survival.

These observations suggest that adults should have evolved to spawn at times and locations when/where temperatures are similar to those that maximise egg survival based on the physiological response to temperature. However, spawning times and locations may have instead evolved to maximise fitness of individual spawners, i.e. producing at least 1 offspring during the spawner's lifetime that reaches maturity (Roff 1992). As a consequence, the time and location of spawning may be an evolutionary trade-off between many different (and potentially conflicting) processes and mechanisms that affect survival during the entire pre-adult life history. Processes influencing pre-adult stages would include predation, starvation, oceanographic transport processes affecting survival probability (Sinclair & Tremblay 1984, Leggett & DeBlois 1994, Bunn et al. 2000, Houde 2008), and the direct physiological effects of abiotic conditions, including temperature (Bailey & Houde 1989, Houde 2008). For example, it is possible that some species have evolved to spawn at times that are likely to minimise predation mortality of eggs and larvae, even though doing so might expose eggs to sub-optimal temperatures for their (physiological) survival. We will investigate this hypothesis by estimating the temperature range that optimises survival in (predator-free) laboratory experiments and comparing this with field estimates of spawning temperatures.

Here, we focus on several of the most abundant and commercially most important fish species in the North Atlantic Ocean. This area has a long history of exploitation of many fish stocks (Froese et al. 2012), and parts of the North Atlantic are some of the fastest warming regions in the global ocean (Belkin 2009, Hoegh-Guldberg et al. 2014). One consequence of the recent warming is change in distribution and range of many species, particularly those inhabiting the pelagic habitat (e.g. mackerel, herring and blue whiting). In this study, we conduct a meta-analysis to investigate patterns of sensitivity to temperature change, expressed in development time, cumulative degree-days and survival, of different fish species and populations. We anticipate that new analyses of interactions between temperature, development and survival rate will generate new insights into the thermal ecology of reproduction in North Atlantic fish species and the role of temperature in the evolution of their spawning strategies. The results may also provide additional perspectives regarding how future climate change might influence the reproductive success and ecology (e.g. spatial distributions) of these species.

MATERIALS AND METHODS

Data sources

Our investigation is based on data compiled from laboratory egg incubation experiments, in which eggs were artificially fertilised in the laboratory, using wild-caught adults, and were incubated at a wide range of temperatures. Studies with <3 experimental temperatures were excluded, as well as all field-derived estimates of development rates. We also excluded studies that used eggs produced from parents raised in aquaculture facilities because feeding and temperature conditions in such facilities may have affected overall condition of adults and thereby the survival and development rates of offspring in ways that may not be representative of such rates in nature (Geffen & Nash 2012). We collected data on development time (D) and survival (S) at different temperatures. Development data were extracted from tables and figures or, when the actual measurements were not available, we used the fitted regression lines between development time and temperature given in the articles. Development time refers to the number of days from fertilisation to 50% hatch, whereas survival is the total percentage of eggs that hatched successfully. The dataset and sources are described in Table 1.

All statistical and regression analysis were performed using R (R Core Team 2013).

Development time–temperature relationship

We assumed an exponential relationship between development time and temperature. Next, we used linear regression to describe the effect of temperature on development time (fitted on ln-transformed development time, as ln(days)) for each species and population. The slopes (b_d) represent the sensitivity of development time to temperature differences; for species or populations having similar slopes, intercepts (a_d) represent the offset of development time after having accounted for temperature differences. We ranked the slopes and intercepts from lowest to highest and plotted the data as bar charts to visualise trends and differences in a clear manner. Confidence intervals (95%) for the slopes and intercepts were approximated as being equivalent to 2 standard errors (SE), and species and populations were considered significantly different if confidence intervals failed to overlap.

We also assessed the generality of the egg development-temperature relationship for all species and populations in our dataset by constructing a linear regression model of ln(development time) vs. temperature without regard to species or population. We then identified which species or population produced eggs that developed faster or slower than rates predicted by the overall relationship; this was done by calculating the mean and $2 \times$ SE of the residual variation for each species or population in our dataset. Species whose confidence intervals excluded zero were considered to develop significantly faster (or slower) than the generalised prediction.

We evaluated the effect of egg size on development time by testing whether there is a significant linear relationship between egg weight (mg) or egg diameter (mm) and the slope b_d and the intercept (offset) a_d for a subset of species for which size data were available in the literature (Table 1).

Cumulative degree day analyses of egg development time

The overriding question we seek to address here is whether the thermodynamic constraints on egg development differ between species and populations. The cumulative degree-days is a metric that estimates the thermal requirements of an organism for the completion of a developmental stage (Kamler 2002, Neuheimer & Taggart 2007) and reflects the thermal history that the organism has experienced during a certain period, such as incubation period to hatching. It expresses a more physiologically relevant time scale, while taking into account a minimum threshold temperature, presumably species- and/or population-specific, below which biological activity does not take place (Kamler 2002, Neuheimer & Taggart 2007).

The cumulative degree-days (DD ; $^{\circ}\text{C} \times \text{d}$) required for egg development to hatch were estimated for each species and population by the following relation:

$$DD_T = D_T \times (T - T_{\text{th}}) \quad (1)$$

where D_T is the development time at temperature T , and T_{th} is the species/population-specific threshold temperature. The DD_T is therefore calculated by the accumulation of temperature experienced by an egg during its incubation period, after accounting for the threshold temperature. Eq. (1) is most suitable for the range of temperatures over which development rates are linearly related to temperature (Kamler 2002 and references therein). Therefore, development rate (d^{-1} ; $r(T)$) and temperature, within the optimal range

Table 1. Source of collated data for development period, survival and mortality of eggs. The regions and species codes that are used in the figures are shown. In data type, *D* refers to the developmental period (days) from fertilization to 50% hatched, *S* to survival percentage, and *M* to total mortality percentage (from which *S* was estimated)

Species	Common name	Species code	Region	Data type	Source
<i>Ammodytes americanus</i>	Sand lance	SL	NW Atlantic	<i>D, S</i>	Smigielski et al. (1984)
<i>Clupea harengus</i>	Baltic herring	H.b	Kiel Baltic Sea	<i>D</i> <i>D, S</i>	Blaxter & Hempel (1963), Peck et al. (2012c)
<i>Clupea harengus</i>	Herring Spring spawners	H.sC H.sN	Clyde Clyde, North Sea Norway	<i>D</i> <i>D, S</i> <i>D</i>	Blaxter (1956), Blaxter & Hempel (1963)
<i>Clupea harengus</i>	Herring Autumn spawners	H.a	Buchan, Downs, Minch North Minch, North Sea	<i>D</i> <i>D, S</i>	Blaxter & Hempel (1963) Blaxter (1956)
<i>Engraulis encrasicolus</i>	Anchovy	An	Bay of Biscay Gulf of Cadiz	<i>D</i> <i>D, M</i>	Ibaibarriaga et al. (2007a), Bernal et al. (2012)
<i>Mallotus villosus</i>	Capelin Beach spawning	c.nw	Trinity Bay and Notre Dame Bay, Newfoundland	<i>D, S</i>	Penton & Davoren (2013)
<i>Mallotus villosus</i>	Capelin offshore spawning	c.nw	Trinity Bay, Newfoundland	<i>D, S</i>	Penton & Davoren (2013)
<i>Mallotus villosus</i>	Capelin offshore spawning	c.Bs	Barents Sea	<i>D</i>	Gjosaeter & Gjosaeter (1986)
<i>Micromesistius poutassou</i>	Blue whiting	BW	NE Atlantic	<i>D, M</i>	Coombs & Hiby (1979)
<i>Sardina pilchardus</i>	Sardine	Sd	Portugal coasts	<i>D</i> <i>S</i> <i>D</i>	Miranda et al. (1990), Olmedo et al. (1990), Blaxter (1969) in Miranda et al. (1990)
<i>Scomber japonicus</i>	Chub mackerel	cm	Pacific	<i>D</i>	Hunter & Kimbrell (1980)
<i>Scomber scombrus</i>	Mackerel	M.s M.w M.ns M.nw	Biscay Bay-southern stock Biscay Bay/Celtic Sea-western stock North Sea NW Atlantic-Massachusetts	<i>D, M, S</i> <i>D, S</i> <i>D, M</i> <i>D^a, M</i>	Mendiola et al. (2006) Lockwood et al. (1977) Danielssen & Iversen (1977) Worley (1933)
<i>Sprattus sprattus</i>	Baltic sprat	Sp.b	Baltic Sea	<i>D, S</i> <i>D</i>	Nissling (2004), Petereit et al. (2008)
<i>Sprattus sprattus</i>	Sprat	Sp	English Channel German Bight, North Sea	<i>D, S</i> <i>D</i>	Thompson et al. (1981), Alheit et al. (1987)
<i>Trachurus trachurus</i>	Horse mackerel	hm	Celtic Sea NE Atlantic-Iberian region	<i>D, S</i> <i>D</i>	Pipe & Walker (1987), Cunha et al. (2008)
<i>Gadus morhua</i>	Atlantic cod	cod.Ir cod.NS cod.Norw cod.BtW cod.SD25 cod.SD27 cod.GeB cod.Nf cod.NWF	Irish Sea North Sea Norwegian Sea Baltic Sea, western Baltic Sea, SD25 Baltic Sea, SD27 Georges Bank Newfoundland Bay of Fundy, NW Atlantic	<i>D, S</i> <i>D</i> <i>D, S</i> <i>D</i> <i>D, S</i> <i>D, S</i> <i>D, S</i> <i>D</i>	Geffen et al. (2006) Thompson & Riley (1981) Iversen & Danielssen (1984) Wieland et al. (1994) and references therein Wieland et al. (1994) Nissling (2004) Laurence & Rogers (1976) Pepin et al. (1997) Peterson et al. (2004)
<i>Melanogrammus aeglefinus</i>	Haddock	hadd	Georges Bank	<i>D, S</i>	Laurence & Rogers (1976)
<i>Scophthalmus maximus</i>	Turbot	turbot	France	<i>D, S</i>	Devauchelle et al. (1988)
<i>Pleuronectes platessa</i>	Plaice	plaice	Irish Sea	<i>D, S</i>	Fox et al. (2003)
<i>Brevoortia tyrannus</i>	Atlantic menhaden	menh	Long Island, NW Atlantic	<i>D, S</i>	Ferraro (1980)
<i>Sparus aurata</i>	Gilthead seabream	gsb	France	<i>D, S</i>	Camus & Koutsikopoulos (1984)
<i>Merluccius merluccius</i>	European hake	hake	Norway	<i>D, S</i>	Bjelland & Skiftesvik (2006)

^aDevelopment period from fertilisation till first day of hatch

of a species, was described by the following linear regression:

$$r(T) = a_r + b_r \times T = b_r \times (T - T_{\text{th}}) \quad (2)$$

(Kamler 2002). The threshold temperature was calculated as the temperature at which development rate goes to zero, i.e. $T_{\text{th}} = -a_r/b_r$ (Kamler 2002). Mathematically, under assumed linearity expressed in Eq. (2) and because $r(T) = D_T(T)^{-1}$, Eq. (1) implies the following relation:

$$DD_T = \frac{1}{r(T)} \times (T - T_{\text{th}}) = \frac{(T - T_{\text{th}})}{b_r(T - T_{\text{th}})} = \frac{1}{b_r} \quad (3)$$

That is, the cumulative DD is directly related to the slope of the development rate – temperature regression (Bonhomme 2000). It follows from this that species with similar dr/dT values have similar degree days to development characteristics, irrespective of their threshold temperatures.

If the linear regressions of $r(T) \sim T$ for individual populations within a species were not significant (e.g. for capelin and herring), we estimated T_{th} using pooled data for the species. We estimated the degree-days at each available experimental temperature within the whole optimal temperature range T_{range} (see below) and calculated the mean DD and 95% confidence interval. We then evaluated the hypothesis that the mean numbers of DD were similar across species/populations using 1-way ANOVA and post-hoc Tukey HSD tests. We also evaluated whether DD for different species are adapted to different thermal conditions by estimating the correlation between the temperature that maximised survival, as estimated by T_{opt} from the fit of Eq. (4) (see below), and the species-specific degree-day sum.

Effects of temperature on egg survival rates

Survival of fish eggs under experimental conditions can be influenced by many different factors related to experimental design (e.g. egg density in the tanks, microbial infection and light intensity) and handling (e.g. mechanical damage, replacement of samples in the tanks, etc.) of eggs. An ideal experimental set up, for comparative purposes, would be to run the experiments at the same facilities, by the same person, under the same experimental conditions, which is beyond an institute's capabilities for various practical reasons. We recognise these limitations, but because we primarily assess the temperatures that produce high survival probabilities and not the absolute survival values, we instead filtered the available litera-

ture to obtain data with the most similar experimental protocols (Table 1 & Table S4 in the Supplement at www.int-res.com/articles/suppl/m555p151_supp.pdf).

Survival responses of fish eggs to temperature typically have complex nonlinear shapes. However, a common feature to nearly all is the presence of high survival at some intermediate range of temperatures and declines at lower and higher temperatures. Such a relationship can be quantified using different functions of varying complexity (e.g. number of fitted parameters), including 3-line segmented regression or a plateau type response (Peck et al. 2012a,c), a polynomial regression and a Gaussian equation. We used the latter because (1) there is much conceptual and theoretical support for such a shape (Helaouët & Beaugrand 2009, Pörtner & Peck 2010), (2) visual inspection showed that most of the scatterplots of survival vs. temperature in our data compilation resembled a Gaussian shape, (3) this equation can be fitted with a small number of parameters and (4) the parameters can be interpreted with biological meaning (see below). The low number of parameters in this equation is an important feature for our investigation because many of the experimental studies only contained survival measurements at a small number of temperatures (e.g. 30% of the experimental studies in our analysis had ≤ 5 temperature treatments). Consequently, models having many more parameters would likely be over-parameterised for such small datasets. Moreover, retaining these smaller datasets gave more geographic and taxonomic diversity to our analyses, making the results more generalisable to a wider variety of fish species.

The Gaussian equation we fitted (Eq. 4) to the survival and temperature (T) data for a given population/species is:

$$S = a_s \times e^{-\frac{(T-b_s)^2}{2c_s^2}} \quad (4)$$

The coefficient a_s is an estimate of the maximal survival at the peak of the fitted curve, and the coefficient b_s is an estimate of the optimal physiological temperature (hereafter referred to as T_{opt}) where egg survival peaks; c_s is the standard deviation and is used to estimate the spread of the optimal temperature range (T_{range}) where egg survival is highest as $T_{\text{opt}} \pm c_s$. Our interest in this investigation and analysis is focussed on how temperature affects survival and in particular the temperature range over which survival is highest. The absolute levels of survival can be affected both by internal egg physiological processes but also by many different aspects of experiments, the condition of the parents and viability of oocytes (Gef-

fen & Nash 2012). In addition, we assume that all eggs used for incubation experiments were fertilised, although this was not explicitly indicated in all studies. Consequently, the fitted values for a in Eq. (3) are difficult to interpret with certainty and have only secondary importance in this investigation.

Because c_s represents the spread of the Gaussian curve, it can be considered to be a measure of the sensitivity of egg survival to temperature changes: species with large values of c_s will have relatively high survival across a broad range of temperatures and could be considered to be eurythermic with respect to egg survival. In contrast, species with low c_s have survival rates that decline more rapidly as temperatures increase or decrease away from T_{opt} ; these species could be considered to have stenothermic egg survival responses. Therefore, the method of analysis used here provides parameters that we consider to be primary emergent traits related to the mean and spread (i.e. b_s and c_s) of the optimal thermal range for egg survival.

For the species/populations for which no statistically significant Gaussian fits were obtained, T_{opt} was estimated as a survival weighted average temperature: $T = \Sigma T \times S / \Sigma S$. T_{range} , for the species where no Gaussian fit was possible, was estimated as the temperature range where development was recorded.

Finally, using linear regression, we tested for significant correlations between the estimated threshold temperatures (T_{th} ; see 'Cumulative degree day analyses of egg development time' for definition) and T_{opt} or the average spawning temperature (T_{spw}).

Optimal survival temperature and spawning temperature

We investigated whether there was a correspondence between the egg T_{opt} and T_{spw} . We retrieved data from the literature referring to the prevailing temperature conditions during spawning (Table S2 in the Supplement at www.int-res.com/articles/suppl/m555/p151_supp.pdf) for all populations or species and compared T_{opt} and T_{spw} . Our null hypothesis was that temperatures that optimise egg survival are close to those at which spawning occurs (i.e. the 2 sets of temperatures would lie along the 1:1 diagonal).

We estimated the impact of a 2°C warming (Hoegh-Guldberg et al. 2014) of spawning areas on expected egg survival using the Gaussian fitted parameters for each species. Although absolute estimates of maximum survival rate, a_s , may be uncertain due to experimental artefacts (see above), we consider the relative change in maximum survival rate across a temperature range as a potential indicator of how temperature could affect egg survival. We calculated the difference in survival rate under present and future climates for each of the significant Gaussian fits by estimating survival at T_{opt} and at $T_{opt} + 2^\circ\text{C}$; the change (Ch_{opt}) was estimated as the ratio between future and present survival rates (i.e. survival ratio $Ch_{opt} = S_{T_{opt}+2} / S_{T_{opt}}$).

RESULTS

Development of eggs

We obtained egg development time for 32 populations of 17 species of fish in the North Atlantic over a temperature range of -1 to 26°C (mean = 10.4 , SE = 0.26). Egg development time was negatively related to temperature both across and within species and populations (Fig. 1; see Fig. S1, showing the species-specific scatterplots with fitted regressions, and Table S1 in the Supplement). A general relationship

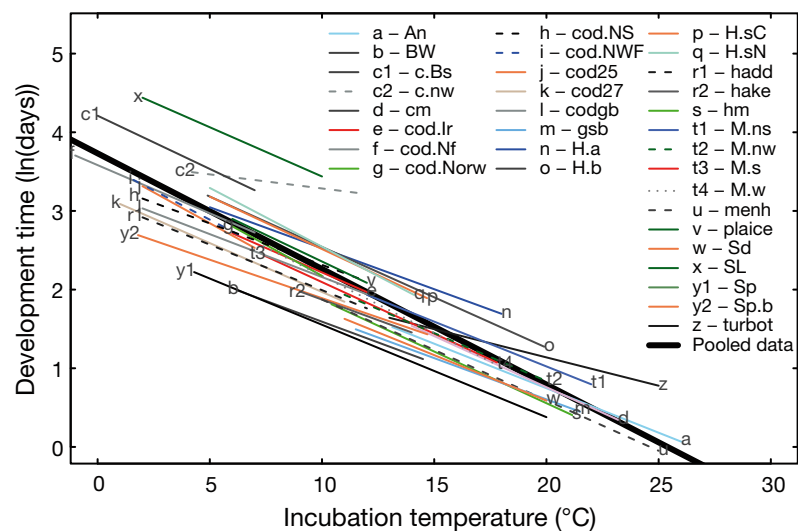


Fig. 1. Developmental period of eggs until 50% hatch, reared in laboratory conditions and at a wide range of temperatures. Time is given in days (ln-transformed) and temperature in $^\circ\text{C}$. Linear regression line fitted to the pooled data is shown with a thick black line. Species and population-specific regression lines are shown by different colours and line types and by letter symbols. The letter symbols $>10^\circ\text{C}$ are positioned at the right end, and letter symbols at temperatures $<10^\circ\text{C}$ are positioned at the left end of the regression line. The dataset is described in detail in Table 1

between development time and temperature across species was highly significant and associated with 80 % of the variability among stocks and species (\ln development time = $-0.15 \times$ temperature + 3.73; $p < 0.0001$; residual mean square error = 0.39). Residual analysis by species/stock showed clear differences among stocks/species in development time relative to the average development time-temperature response (Fig. 2c); 27 of 32 stocks contained confidence intervals that excluded 0. Some species were consistently below the fitted regression line, indicating faster than average development at a given temperature, whereas others were above the line, indicating slower than average development. The range in species-specific means was -0.6 to 1.1 in \ln -transformed development time units, which when back-transformed to arithmetic units corresponds to factors of 0.5- to 3-fold differences in development time at given temperatures. Most of the gadoid species had faster than average development (i.e. negative mean residuals). The 2 flatfish species (plaice and turbot), several herring stocks, the capelin stocks and sand lance had slower than average development (i.e. positive mean residuals).

Within individual species, temperature typically explained 90 to 98 % (mean $R^2 = 0.94$, $SE = 0.021$) of the variation in development time. Slopes (b_d) averaged -0.120 ± 0.004 for all species, and some differed significantly among species, based on non-overlapping 95 % confidence intervals (Fig. 2a, Table S1). The range of slopes was ca. -0.04 to -0.16 , and there was little taxonomic pattern among the slopes as species and stocks were often spread along the entire range of slope magnitudes. For example, some cod stocks were located at or near the high and low extremes of the range. Two stocks had significantly lower slopes than all others and appear as outliers (i.e. capelin in the northwest Atlantic and turbot). However, the low capelin slope may be due to slow development at the warmest temperature (11°C) used in the experiments for the NW Atlantic stock; the slopes for the 2 capelin stocks in the NW and NE Atlantic differed significantly. Excluding the rates measured at 11°C for the NW Atlantic stock and pooling the remaining data for both stocks resulted in a slope nearly identical (and not significantly different) to capelin data from the northeast Atlantic (-0.133 for pooled data and -0.135 for NE Atlantic data only).

Intercepts (a_d) averaged 3.4 (or 29 when back-transformed to arithmetic units) for all species, and there were some significant differences among stocks and species (Fig. 2b, Table S1). It should be

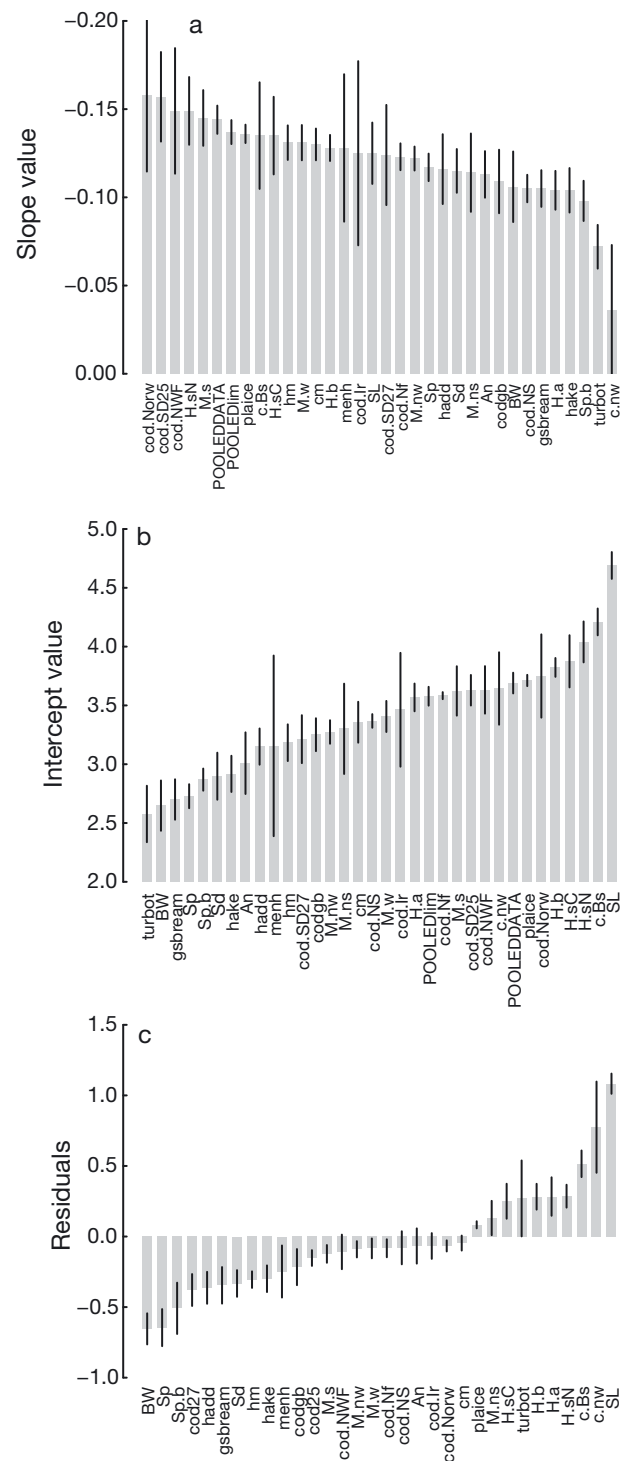


Fig. 2. Bar plots of mean values and error bars ($2 \times SE$) of the (a) slopes and (b) intercepts of the linear regression lines between development time ($\ln(\text{days})$) and temperature. The coefficients of the regression line to the pooled data (POOLEDDATA) and to the pooled data excluding capelin and sand lance (POOLEDLim) are also shown. (c) Bar plots of mean values and error bars ($2 \times SE$) of the residuals of the regression line fitted to the pooled data. See Table 1 for species codes

noted that differences in slopes also mean differences in intercepts. The difference in intercept range (2.58 to 4.69, or 13 to 109 d in arithmetic units) corresponds to a difference in multiplier effect of ca. 8-fold among stocks and species. These calculations suggest that differences in intercepts drive more of the variability in development time than differences in slope and that rates of change in development time per degree temperature are relatively similar across stocks and species.

Egg weight was significantly associated with some of the variation in intercepts (a_d) (intercept = 2.97 (SE: 0.15), slope = 3.12 (SE: 0.89), $R^2 = 0.52$, $p = 0.0052$) but not the slopes (b_d) ($p = 0.089$), whereas the egg diameter was not associated with significant variation in either b_d or a_d (Tables S3 & S4 in the Supplement). Similarly to egg weight, hatch length was significantly linearly related to a_d (intercept = 2.45, slope = 0.20, $R^2 = 0.67$, $p < 0.001$) but not b_d ($p = 0.059$).

Degree-day (DD) requirements for development differed significantly among species. The average DD for egg development of species/stocks from relatively warm regions ranged between 20 and 45 DD . In contrast, eggs of species from colder areas required 90 to 150 DD , with the exception of Newfoundland cod, capelin stocks and sand lance that required 196, 322–355 and 395 DD , respectively (Fig. 3a). The variation in DD within the optimal temperature range was narrower in warmer-adapted species (evident by the narrow confidence interval in Fig. 3 & Fig. S2 in the Supplement) but was more variable for the cold-adapted species (evident by the

wide confidence intervals in Fig. 3 & Fig. S2). ANOVA showed significant differences between cold and warm-adapted species plotted in Fig. 3b,c (post-hoc Tukey tests, $p < 0.001$), whereas within the cold-adapted species group, we found differences between cod and herring as well as between capelin and sand lance compared with all other species (post-hoc Tukey tests, $p < 0.001$).

Estimated threshold temperatures, T_{th} (Table S2), increased with the temperatures to which species are adapted and were significantly positively correlated with T_{opt} and T_{spw} (T_{th} vs. T_{opt} : slope = 0.792 (0.064), intercept = -7.11 (0.775), $R^2 = 0.83$, $p < 0.001$; T_{th} vs. T_{spw} : slope = 0.887 (0.069), intercept = -7.28(0.766), $R^2 = 0.84$, $p < 0.001$).

Optimal temperature range for survival

Maximal survival rates were highly variable within and between species (Fig. 4a–e). For example, maximum survival varied from 90 to 20% among 4 different mackerel studies. For some stocks and species, survival was relatively insensitive to temperature until critical values were reached, beyond which survival declined rapidly (e.g. western mackerel stock, blue whiting; Fig. 4a,b). In some cases, survival declined by only small amounts throughout the utilised temperature range. As a result, the survival–temperature relationship appears ‘truncated’ due to the temperature range employed in the experiments, which did not cover a wide enough range to impair survival. In these situations or those that used a lim-

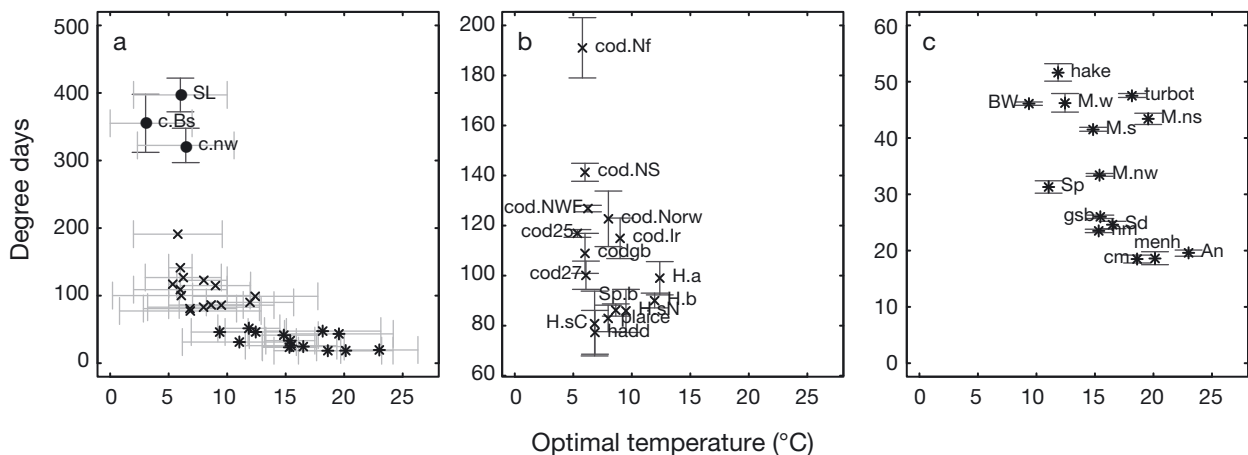


Fig. 3. Average number of degree-days ($^{\circ}C \times d$, DD) at the egg optimal temperature (T_{opt}). The confidence intervals of the DD as well as the range of the optimal temperatures are also plotted as bars around each data point and correspond to the y- and x-axis, respectively. (a) All species and population DD are shown in different symbols for comparison, with (b) the sub-group of species indicated with an 'x' and (c) the sub-group of species indicated with an asterisk (*) shown in more detail. Note the different ranges of the y-axes in the different panels. See Table 1 for species codes

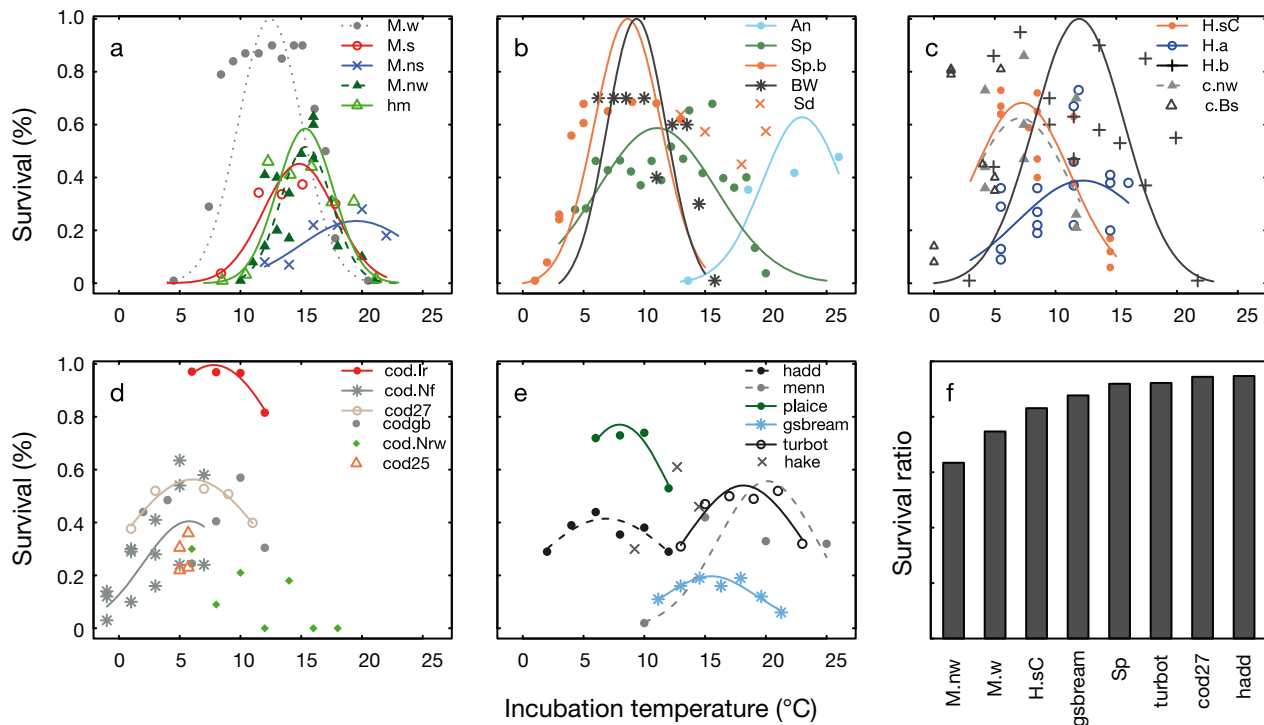


Fig. 4. (a–e) Survival curves based on the fitted Gaussian equation. Experimental data are also shown. Values of zero survival refer to temperature values where no hatching was observed. The survival curves of M.w, BW, H.b, Sp.b are normalised to fit the range of survival values (0–1). (f) Survival ratio, i.e. the change in survival at temperatures under future climate ($T_{\text{opt}} + 2^{\circ}\text{C}$) relative to T_{opt} under present climate. See Table 1 for species codes

ited number of experimental temperatures, Gaussian fit parameters could not be estimated.

In 21 species or stocks, significant ($p < 0.05$) estimates of the optimal temperature coefficient (b_s) could be derived, and in 12 cases, c_s could also be derived. In 8 stocks, all 3 parameters (a_s , b_s , c_s) could be estimated with significance ($p < 0.05$) (Table S3 in the Supplement). Because we are most interested in the b_s and c_s parameters, we present these results in some detail. In the subset of 12 Gaussian fits where both b_s and c_s were significant, the width of the optimal thermal range ($2 \times c_s$) for egg survival was on average 8°C ($c_s \sim 4^{\circ}\text{C}$) and was not related to whether species are adapted to warmer or colder temperatures.

Given the mean range of c_s (i.e. 4°C) for the statistically significant fitted Gaussian equations, a 2°C warming scenario at spawning sites would mean that future temperatures would be expected to be within 1 SD of the current spread of optimal temperatures for each of the species considered here. However, due to the shape of the function used to link survival to temperature (Gaussian model), any increase in temperature is expected to lead to a decline in survival rate, the magnitude of which will depend on

species-specific estimates of c_s . The decrease in survival ratio under a 2°C future warming scenario ranges from 34 to 2% (Fig. 4f). Similar results were obtained for the subset of the 8 species and stocks for which all 3 parameters of the Gaussian model were significant. The largest declines are expected in 2 mackerel stocks (southern/Bay of Biscay and north-west Atlantic stocks) and the smallest declines in the eastern Baltic cod and Georges Bank haddock stocks.

Estimated T_{opt} varied among species as could be expected for a selection of species from differing thermal environments. Moreover, there was a significant correspondence between T_{opt} and T_{spw} (Fig. 5; $R^2 = 0.81$, $p < 0.001$; slope and intercept not significantly different from 1 and 0, respectively; $p > 0.05$). Nearly two-thirds of the T_{opt} values (19 of 31) were above the line of equality, 9 were below, and 3 were on the line. The frequency of non-zero values that occurred above the line tended to be higher than expected by chance (chi-squared test; $p = 0.06$, $df = 1$). Therefore, these species and stocks spawn at temperatures that are lower than those that optimise egg survival. The species or stocks that were above the lines had T_{opt} on average 2.1°C warmer than the

for developing larvae. The consequences of such changes in phenology on early life survival are presently difficult to assess because of uncertainties and potential regional differences in how phyto- and zooplankton production will change under climate change (Edwards & Richardson 2004, Hollowed et al. 2013, Pörtner et al. 2014). In the past, temperature increases have been linked to decoupling of trophic interactions in North Atlantic plankton communities (Edwards & Richardson 2004). New field, laboratory and modelling investigations are needed to address these effects both for particular species and for resolving general responses.

The cumulative thermal requirements, known as degree-days (DD), are expected to remain constant within optimal temperature ranges for biological processes (Kamler 2002, Neuheimer & Taggart 2007, Neuheimer & MacKenzie 2014). The observed low variability in DD within the T_{range} of species and populations (confidence intervals in Fig. 3) indicates a lack of correlation between DD and temperature. However, when comparing DD requirements across species/populations, there was a decreasing trend in average DD as temperature increased, showing that eggs of species living in warmer environments require less thermal experience than eggs of species living in colder environments. This pattern has been observed in an earlier study on freshwater fish species (Kamler 2002) and for copepod species (our re-analysis of copepod egg development data collated from McLaren et al. 1969, 1989). The lower DD requirement for egg incubation of fish and copepod species in warm temperatures may indicate an evolutionary pressure to develop quickly in warmer environments, and that fast development could be a mechanism to counteract higher levels of predation mortality. The same mechanism has been suggested as an explanation for the higher growth rate of larval fish feeding stages in warm environments (Houde 1989, Pepin 1991).

The higher and more variable DD requirement (Fig. 3; average values among species) in cold environments may indicate that other events in early life, such as correct timing of larval emergence in the water, may be more important than fast egg development due to the limited period of available conditions favouring larval feeding and growth (Lowerre-Barbieri et al. 2011). Different mechanisms of thermal adaptation seem to prevail for different physiological processes in different life stages of fish. Neuheimer & MacKenzie (2014) studied the thermal requirements for gonadal development of 20 cod populations in the North Atlantic and observed that

the DD required for development decreased significantly with increasing latitude, i.e. colder environments. The reason for the latitudinal difference in thermal exposure required for gonadal development is unclear, but may be an adaptation to a shorter growing season in northern habitats (Neuheimer & MacKenzie 2014).

Among the studies reviewed here, DD were rarely estimated, and those that did assumed a threshold temperature equal to 0°C (Peck et al. 2012c). However, in comparative studies among species adapted to a wide range of temperatures or among populations locally adapted to their environment, this assumption is speculative and may lead to inaccurate results (Chezik et al. 2014). The differences we observed between cod and herring development times (shorter and longer incubation periods, respectively) were eliminated (almost reversed) when comparing the DD , partly because T_{opt} at which DD are estimated, was lower for cod than for herring and partly because cod populations had threshold temperatures (T_{th}) below zero (which are added to the temperature at which the DD are estimated; see Eq. 1). In comparison, herring populations had positive T_{th} . Here, we used a common method (Kamler 2002) to estimate T_{th} for all species and populations studied in order to obtain robust and comparative estimates of the thermal requirements of species and populations.

These comparative biogeographic examples based on fish egg and gonadal development illustrate that the thermal requirement for completion of developmental stages is a trait that can have adaptive potential at different scales of biological organisation (population or species). We hypothesise therefore that other rates in fish (e.g. growth rates) may also be locally adapted to regional temperature conditions and could differ from expectations based on species-wide generalisations (Conover et al. 2006, Hutchings et al. 2007, Hällfors et al. 2016).

Egg survival-temperature relationships

The survival rates compiled here are associated with predator-free environments and potentially represent physiological responses of egg survival to temperature, although we recognise that different kinds of experimental conditions can influence absolute levels of survival (Geffen & Nash 2012). For the subset of species where significant Gaussian relationships were defined, we found substantial variability in the sensitivity of survival to temperature difference among species. Some species (e.g.

mackerel stocks in the NE and NW Atlantic; lower c_s values leading to greater relative change in survival) were relatively more sensitive to temperature changes than others (e.g. haddock and Baltic cod). Given that climate change is expected to increase temperature in the North Atlantic by 1 to 3°C (Hoegh-Guldberg et al. 2014) and that the overall mean sensitivity of the survival response to temperature represents a range of 4°C (average c_s value), it is evident that egg survival in some of the species analysed here will be more vulnerable to global warming than others. The species-specific estimates of c_s will determine the magnitude of the decline in survival and therefore the vulnerability of species to future increasing temperatures.

The ranges of spawning temperatures for a given species throughout its geographic range and during the entire reproductive season can be quite large and probably represents a strategy to produce eggs (and subsequently larvae) over a wide range of abiotic and biotic conditions (Lowerre-Barbieri et al. 2011). We demonstrated that the physiological optimal temperature ranges for egg survival corresponded closely to the means of these wide spawning temperature ranges (here considered to represent conditions prevailing during final gonadal maturation and spawning). Hence, while interannual variability in biotic and abiotic conditions (e. g., abundances of predators and prey) affects offspring survival probability (Leggett & Deblois 1994, Houde 2008), at long time scales corresponding to those that affect the evolution of life histories, spawning at thermal conditions that maximise thermal-related early life survival, including successful development of gonads to ripening, appears to be a particularly important constraint on reproductive success.

However, some individual species had average T_{spw} lower than T_{opt} , which indicates spawning at the lower (colder) end of the egg optimal thermal range (T_{range}). Such a strategy could favour larval growth and survival, possibly by allowing larvae to grow fast as seasonal temperatures are rising or reaching annual maxima. This strategy also seems to be followed by many anuran species, which spawn at temperatures corresponding to the colder end of the optimal range for egg survival (van der Have 2008), favouring the match of the larval stages with their optimal environmental conditions.

Species responses to increasing temperature due to climate change are a major field of climate change studies (e.g. Pörtner & Farrell 2008, Petitgas et al. 2013). Regarding their spawning behaviour, species will have to adapt to ensure eggs continue to experi-

ence tolerable temperatures, possibly through spawning at different times or locations (Lowerre-Barbieri et al. 2011, Fincham et al. 2013, Petitgas et al. 2013). Alternatively, egg traits may have to evolve by attaining higher or wider temperature tolerances (see Angilletta et al. 2003 for the evolution of reaction norms) or for example by attaining different buoyancies to occupy colder depths. Adapting spawning time may be a more widespread response in northern latitudes where the seasonality is stronger and the favourable conditions for early life more restricted (Winemiller & Rose 1992, Lowerre-Barbieri et al. 2011) or in cases where early life stages are highly dependent on transport or retention mechanisms to nursery areas (Petitgas et al. 2013).

These results identify the relative sensitivity and vulnerability of key aspects of the egg ecology of several North Atlantic fish species to expected future temperature increases associated with climate change. The results could provide information that can be used to improve parameterisations of statistically based species distribution and habitat models. Our findings, though based on many species, nevertheless highlight the importance of conducting new experimental studies that can quantify the effect of temperature on egg survival in additional species and of identifying the functional shape of the survival responses (e.g. Gaussian, plateau-shaped with thresholds, etc.) as well as the species and population specific threshold temperatures. These values can prove useful for estimating the timing of spawning (Hamel et al. 1997) and its expected response due to warming waters. Priority should be given to those species and populations that have most functional and commercial importance in (North Atlantic) marine food webs. The generality of the patterns identified here should be extended further, within the fishes but also to other taxonomic groups (e.g. copepods, decapods and molluscs) and to other biogeographic regions. Identification and comparison of responses across a diverse range of taxa would not only give more generality and insight to our own findings and help clarify the specific impacts of future global warming on these other species but also identify potential similarities and differences in responses across species with very different life histories.

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