Ecology, 95(12), 2014, pp. 3364–3375

Explaining life history variation in a changing climate across a species' range

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Abstract. Timing of reproduction greatly influences offspring success and resulting population production. Explaining and predicting species' dynamics necessitates disentangling the intrinsic (genotypic) and extrinsic (climatic) factors controlling reproductive timing. Here we explore temporal and spatial changes in spawning time for 21 populations of Atlantic cod (*Gadus morhua*) across the species' range (40° to 80° N). We estimate spawning time using a physiologically relevant metric that includes information on fish thermal history (degree-days, DD). First, we estimate spawning DD among years (within populations) to show how recent changes in spawning time can be explained by local changes in temperature. Second, we employ spawning DD to identify temperature-independent trends in spawning time among populations that are consistent with parallel adaptive evolution and the evolutionary history of the species. Finally, we use our results to estimate spawning time under future climate regimes, and discuss the implications for cod ecology across the species' range.

Key words: Atlantic cod; climate change; evolutionary biology; Gadus morhua; *macroecology; North Atlantic Ocean; phenology; temperature.*

INTRODUCTION

Environmental change affects many aspects of a species' physiology and ecology, including changes in size and life history phenology. While these changes are thought to include both genetic and plastic components, the ability to disentangle adaptive (genetic) changes from plastic responses is difficult (Hansen et al. 2012, Merilä 2012). However, identifying plastic vs. genetic diversity is a necessary step in defining the capacity of a species to tolerate and/or adapt to changing conditions. It is this level of diversity that governs the long-term response of a species to environmental change, including possible abundance and distribution changes as well as species' resilience (Hilborn et al. 2003, Wright 2013).

Among influencing factors in the environment, temperature is a controlling factor for ectotherms (e.g., reptiles, amphibians, insects, most fish), regulating the ectotherm's metabolism and resulting physiological rates (Fry 1971, Neuheimer and Taggart 2007, 2010). For most species within their normal temperature range, a slight increase in temperature results in higher reaction rates for growth, maturation, et cetera (Neuheimer et al. 2011). Thus temperature acts to "scale" time in ectotherms; warmer days result in an increased capacity for growth and development relative to colder days. A more physiologically relevant measure of time will then include a measure of the organism's thermal history as integrated temperature, or degree-days (DD, °C × d). The DD metric has proven utility in identifying responses of ectotherm growth and development that are due to temperature (e.g., Trudgill et al. 2005, Neuheimer and Grønkjær 2012). In the case of development, DD can be used to estimate "thermal constants" or the thermal time (i.e., amount of DD) needed to reach a particular developmental stage (Neuheimer and Taggart 2007). By comparing thermal constants of development timing both within and among populations, one can identify changes in the organism's phenology that may be due to temperature-independent factors, including genetic diversity within a species.

One life history character of particular interest is the timing of reproduction, because the success of offspring under changing conditions has a strong influence on fitness (e.g., Opdal et al. 2011). Reproductive timing is largely heritable (e.g., fish; Otterå et al. 2006, Kjesbu et al. 2010, Wright 2013) and is thought to evolve to allow early life stages to exist under beneficial conditions (Cushing 1969, Sinclair and Tremblay 1984, Platt et al. 2003), with photoperiod and temperature often acting as proximate factors determining reproductive timing in ectotherms. Of these, photoperiod, a relatively noise-free signal, is thought to initiate the process leading to reproduction in temperate species (i.e., between tropic and polar circles), while temperature acts to determine the pace of process development (e.g., Kjesbu et al. 2010, Migaud et al. 2010, Wright 2013). Thus an estimate of the DD required for reproduction (e.g., a "thermal

Manuscript received 22 December 2013; revised 28 April 2014; accepted 1 May 2014; final version received 23 May 2014. Corresponding Editor: L. Ciannelli.

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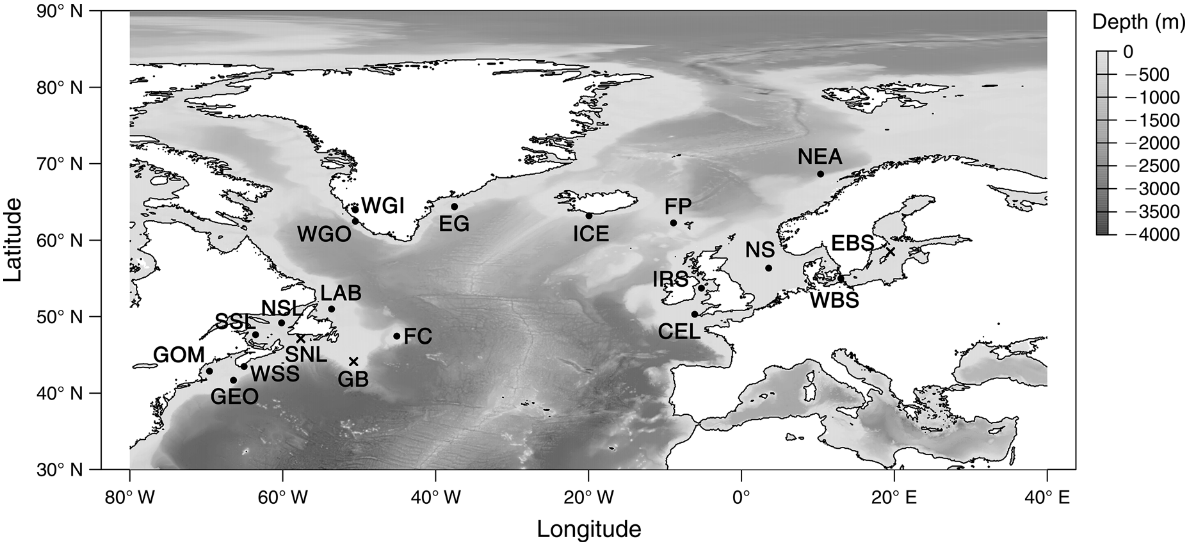

FIG. 1. Atlantic Cod (*Gadus morhua*) populations across the North Atlantic. The chart shows the North Atlantic Ocean, with locations of cod populations used in the analysis of spatial variability in time to spawning at Georges Bank (GEO), Gulf of Maine (GOM), western Scotian Shelf (WSS), southern Gulf of St. Lawrence (SSL), northern Gulf of St. Lawrence (NSL), south Newfoundland (SNL), Grand Bank (GB), Flemish Cap (FC), southern Labrador and eastern Newfoundland (LAB), west Greenland offshore (WGO), west Greenland Inshore (WGI), east Greenland (EG), Iceland (ICE), Faroe Plateau (FP), northeast Arctic (NEA), eastern Baltic Sea (EBS), western Baltic Sea (WBS), North Sea (NS), Irish Sea (IRS), and Celtic Sea (CEL) (Appendix C; positions approximated from Drinkwater [2005]). Populations marked with an "x" denote those also used to examine within-population, temporal variability in time to spawning (see *Methods: Estimating spawning date*).

constant of spawning") can be made by summing the temperature from the onset of gonadal maturation (governed by photoperiod) to the time of reproduction. Degree-days represent the overall thermal time required to complete the many processes involved in gonadal maturation, each dependent on temperature. Comparing variation in DD vs. calendar days (CD) to spawning estimates how much variation in spawning time both within and among populations is due to temperature vs. other (possibly genetic) factors. Moreover, identifying temperature-dependent variability in life history timing using DD aids in the prediction of species dynamics in a changing climate, particularly as changes in one main factor (temperature) are expected while the other (photoperiod) will remain relatively constant.

Here we employ Atlantic cod (*Gadus morhua*) as a model species to assess the hypothesis that major patterns in reproductive timing both in time (within populations) and space (among populations) can be attributed to changes in the amount of thermal history the ectotherms are experiencing. Atlantic cod is an exploited and highly fecund marine fish with determinate spawning (Miller et al. 1995). Cod populations surround the North Atlantic (Fig. 1), spanning large (and largely parallel) latitudinal (40° to 80° N) and temperature (−1° to 20°C) gradients on both sides of the ocean basin (Drinkwater 2005, Bradbury et al. 2010). Growth and developmental diversity (including spawning time) has been identified previously among cod populations (e.g., Mieszkowska et al. 2009), but the level of plastic vs. genetic change is still unclear. In this study we examine time to spawning both within and among cod populations using the physiologically relevant DD metric. We identify the portion of temporal and spatial variability in spawning time that is explained by temperature and explore the remaining variation in the context of other possible factors affecting spawning, including the species' genetic structure. Finally, we exploit our results to estimate possible spawning time changes under future climate conditions and assess the implication of these for the species.

METHODS

Spatial (among populations) and temporal (within population) variability in time to spawning was examined using both calendar time (calendar days to spawning, CD [d]) and thermal time (degree-days to spawning, DD [°C × d]). Both CD and DD require information on the onset of gonadal maturation and the average spawning day to determine the respective start and end of the temporal or thermal integrations. In addition, DD requires information on the temperature experienced by the fish (Appendix A).

Estimating onset of gonadal maturation

Gonadal maturation refers to the yearly maturation of gonads that occurs once a cod has matured, rather than the once-in-a-lifetime development from juvenile to adult fish. In fish, photoperiod is thought to be the primary cue for gonadal development in cold-water species (e.g., Lowerre-Barbieri et al. 2011), with the change in day length thought to trigger the seasonal gonad development in temperate fish (e.g., Bromage et al. 2001, Norberg and Brown 2004, Davie et al. 2007*a*, *b*). For cod, the start of gonadal development is linked to the decline in day length from the summer solstice (e.g., Cyr et al. 1998, Davie et al. 2007*b*), which acts by stimulating the hypothalamus–pituitary–gonadal axis that regulates gonadal development (Migaud et al. 2010). Other studies indicate that temperature dependency in gonadal development happens later, during secondary gametogenesis following the autumnal equinox (Norberg and Brown 2004, Skjæraasen et al. 2004, Davie et al. 2007*a*, Kjesbu et al. 2010). In either case, the trigger for the onset of gonadal maturation (i.e., changing day length) appears similar among populations, with evidence from wild cod in the southern Gulf of St. Lawrence (48°51′ N, 67°32′ W; Cyr et al. 1998) and reared cod originating in the United Kingdom (55°44′ N, 5°44′ W; Davie et al. 2007*b*), as well as from wild and reared Norwegian coastal cod (60°25′ N, 5°20′ E; Norberg and Brown 2004, Skjæraasen et al. 2004, Kjesbu et al. 2010). These populations cover much of the latitudinal range of cod, and the results indicate a similar photoperiod trigger for gonadal maturation across the species' range. Such a result is not surprising as day length changes occur consistently in time over ~45° to 66° N, though the intensity of light varies. We used the autumnal equinox timing as the start-date for our CD and DD estimates (Appendix A). We explored the implications of a summer solstice start-date in our analyses (Appendix B).

Estimating spawning date

We used mean or peak spawning date as the end date for our CD and DD estimates (Appendix A). Though other spawning metrics (e.g., spawning duration) are of interest, the influence of population-specific factors (e.g., the size- and/or age-structure of the population; Hutchings and Myers 1993) make them beyond the scope of this study. Mean spawning date (day of year) information was obtained for each cod population ($n = 21$) from a review of cod populations across the North Atlantic (Fig. 1, Appendix C; International Council for the Exploration of the Sea [ICES] 2005). Mean spawning date was estimated as either the day of 50% spawning, peak spawning, or the midpoint of the range, depending on reporting. While the majority of cod populations spawn in the first half of the year (February to July; Appendix C), a few localized populations spawn in the autumn (Miller et al. 1995). We included autumn-spawning western Scotian Shelf cod (WSS2) to assess autumn spawning within the context of spawning variability across the species range.

We examined temporal variation in spawning time for three populations across the species range. Temporal variation in mean spawning time was obtained for the southern Newfoundland (SNL, 1953 through 1987; Hutchings and Myers 1994) and Grand Bank (GB, 1947 through 1992; Hutchings and Myers 1994) populations as the time at which 50% of reproductive females had spawned, and the eastern Baltic Sea (EBS, 1969 through 1996; Wieland et al. 2000) population as day of peak egg abundance; we chose the time series based on the availability of data and the presence of trends in temporal variability of spawning.

Estimating ambient temperatures

Ambient temperature was represented (at least relatively; see *Discussion*) by bottom temperature to reflect the cod's demersal habitat. Bottom temperature estimates (within 5 m of bottom, 1940 through 2011) were obtained from measurements available in the International Council for the Exploration of the Sea (ICES) and Fisheries and Oceans Canada (DFO) databases. Additional inshore Greenland temperature estimates were obtained for Nuuk fjord (R. Hedeholm, *personal communication*). The influence of bottom temperature definition (i.e., within 5 m of bottom) on analyses was explored by varying the definition to include temperatures within 25 m of bottom. A population-specific temperature time series (monthly temperature) was estimated for each population from temperature samples in the relevant management area (Appendix C: Fig. C1). Monthly temperature estimates were linearly interpolated to approximate daily temperature estimates. For the temporal analysis, SNL and GB temperature measurements were restricted to depths of 150–200 m to reflect cod distribution within the management areas (Cohen et al. 1990). In addition, temperatures for the temporal analysis were smoothed using a 2-yr (731-d) uniformly weighted, centered moving average to reduce any noise introduced by variations in sampling location and extent among years (Neuheimer et al. 2008). Due to availability, temperature for analysis with the EBS time series was estimated as mean temperature from the 40–60 m depth range over 54°20′–56°10′ N and 14°30′–18°00′ E as in Wieland et al. (2000).

Estimating time to spawning

Calendar days were estimated for each population (and each year for within-population analyses) as the number of days from the autumn equinox to mean spawning date (Appendix A). Degree-days were estimated for each population (or each year for within-population analyses) as

$$DD_j = \sum_{\text{autumnal equinox}}^{\text{spawning}} (T_{i,j} - T_{\text{Th}})\Delta d, \qquad T_{i,j} \geq T_{\text{Th}} \qquad (1)$$

where $T_{i,j}$ is the temperature (°C) at day i and population (or year) j, T_{Th} is a predetermined threshold temperature ($T_{\text{Th}} = 0°\text{C}$; Neuheimer and Taggart 2007), and Δd is a set time step (i.e., one day; Appendix A). For the spatial analysis, estimates of the mean and standard deviation of DD to spawning were made for each population.

Trends in time to spawning

Trends of CD and DD in space and time were examined using linear regression. Regression parameters were estimated with standardized explanatory variables (i.e., standardized relative to the mean of the explanatory variable), resulting in a more meaningful intercept estimate, where the intercept is then an estimate of the dependent variable when the explanatory variable is equal to the mean (Neuheimer and Grønkjær 2012). We ensured data conformed to assumptions of statistical methods (e.g., normality) before trends were reported. Outliers to observed trends were determined using Cook's distance, with outliers defined as those with a Cook's distance $> 4/(\text{sample size} - 2)$ (Fox 2002). Statistical significance was evaluated at a significance level of 0.05.

Predicting spawning time in a changing climate

Finally, we explored the possible implications of warming waters for spawning time of cod populations across the species' range. Here we increased the long-term seasonal temperature climatology to reflect projected bottom warming in the North Atlantic that is predicted to occur by 2100 (Appendix D).

Ensemble model projections (based on 19 models) predict temperature increases varying between 0.3° and 3.0°C in North Atlantic subsurface (200–500 m) waters (Yin et al. 2011). Areas near the continental shelf habitats of Atlantic cod show similar predicted increases of 1.5° to 2.0°C across the basin and species' range (Yin et al. 2011), but higher resolution, population-specific predictions are not available. Based on these results, we explored the impact of a projected bottom warming of 0.5° to 2.0°C by 2100 on cod spawning time. It should be noted that future climate changes are expected to vary seasonally, bathymetrically, and geographically, and this analysis represents a preliminary estimate of possible climate effects on cod reproductive timing. We employed the DD estimated for each population as a thermal constant of spawning (i.e., the number of DD needed to reach spawning). We applied this thermal constant estimate to the elevated temperature series by estimating the time (days) it would take to reach the thermal constant under the new temperature regime. This gave us an estimated CD under the future climate regime, and thus an estimate of how much the spawning time of the different populations would advance under predicted warming (assuming no further adaptation; see *Discussion*).

RESULTS

Within population: temporal variation in spawning time

Calendar days to spawning (CD) showed a significant decline over 1953 through 1987 for the southern Newfoundland population (Fig. 2a; $\text{CD} = (-1.5\ \text{d/yr}) \times \text{year} + 231\ \text{d}$, $r^2 = 0.39$, $P < 0.001$, root mean square error [RMSE] = 18.5 d). For the Grand Bank population, a significant increase in CD was observed from 1947 through 1992 (Fig. 2c; $\text{CD} = (0.44\ \text{d/yr}) \times \text{year} + 235\ \text{d}$, $r^2 = 0.13$, $P = 0.033$, RMSE = 14.8 d). Calendar days to spawning increased from 1969 through 1996 for the eastern Baltic population (Fig. 2e; $\text{CD} = (1.8\ \text{d/yr}) \times \text{year} + 248\ \text{d}$, $r^2 = 0.53$, $P < 0.001$, RMSE = 14.2 d). Trends in all populations were removed when examined in thermal time using degree-days (DD) (Fig. 2b, d, f; southern Newfoundland $P = 0.94$, Grand Bank $P = 0.12$, eastern Baltic $P = 0.11$). In general, temporal results were robust to assumptions of gonadal maturation start-date (Appendix B: Fig. B2) and bottom temperature definition.

Among populations: spatial variation in spawning time

For the among-population analysis, temperature variation among populations (~10°C range in mean temperatures among populations) was greater than within (average 3.4°C range in mean annual temperatures within a population), allowing long-term average bottom temperature estimates to capture relative changes in thermal history among populations.

Long-term, average calendar days to spawning increased with latitude on the west side of the Atlantic, but no significant trend for the eastern Atlantic populations was observed (Fig. 3a; west Atlantic $\text{CD} = (14\ \text{d/°N}) \times \text{latitude} + 181\ \text{d}$, $r^2 = 0.40$, $P = 0.05$, RMSE = 45 days; east Atlantic $P = 0.99$). The autumn-spawning western Scotian Shelf population (WSS2) was an outlier to the linear relationship in the west (based on Cook's distance; see *Methods: Trends in time to spawning*). The eastern Baltic Sea population (EBS) appeared as an outlier relative to populations living at similar latitudes (Fig. 3a).

When thermal history was included in the estimate of time, populations on both sides of the Atlantic demonstrated significant declines in DD with latitude (Fig. 3b; west Atlantic $\text{DD} = (-107(\text{°C} \times \text{d})/\text{°N}) \times \text{latitude} + 873\text{°C} \times \text{d}$, $r^2 = 0.67$, $P = 0.007$, RMSE = 187°C × d; east Atlantic $\text{DD} = (-68(\text{°C} \times \text{d})/\text{°N}) \times \text{latitude} + 1057\text{°C} \times \text{d}$, $r^2 = 0.74$, $P = 0.001$, RMSE = 249°C × d; Appendix C). In addition, linear relationships of the west and east Atlantic populations were similar in slope but not intercept (ANCOVA; slopes $P = 0.29$; intercepts $P < 0.001$). The autumn-spawning western Scotian Shelf population (WSS2) and northeast Arctic (NEA) were outliers to their respective western and eastern relationships (based on Cook's distance). In contrast, the eastern Baltic Sea (EBS) population that appeared as an outlier in calendar time (Fig. 3b) was consistent with the among-population trend in thermal time (Fig. 3b). Spatial analysis trends were robust to assumptions, including gonadal maturation start-date (Appendix B: Fig. B3) and bottom temperature definition.

Spawning time in a warming climate.

Long-term mean DD to spawning was used as a thermal constant of spawning to determine implications

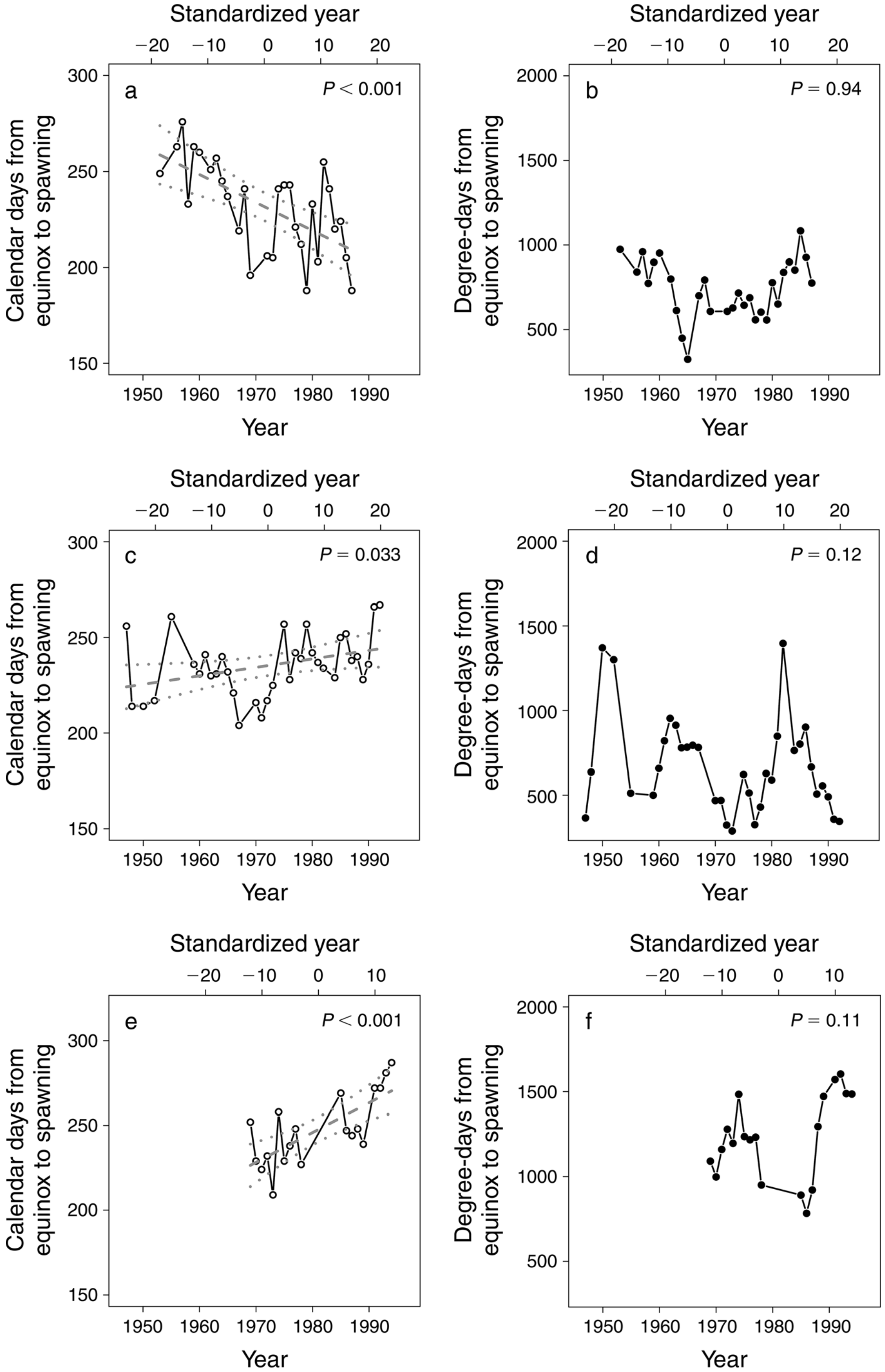

FIG. 2. Temporal variation in spawning. A comparison of yearly time to mean spawning as (a, c, e) calendar days (CD), and (b, d, f) degree-days (DD; °C × d) for (a, b) south Newfoundland, (c, d) Grand Bank, and (e, f) eastern Baltic Sea, using the autumnal equinox as a gonadal maturation start-date. Dashed lines indicate a significant linear trend in CD to spawning with standardized year; dotted lines show the 95% confidence interval around the prediction; see also *Results: Within population: temporal variation in spawning time*). Degree-days to spawning showed no significant trend with time. The upper axis is standardized year used in regression analysis.

for observed spawning time under climate-change conditions for the different populations (see *Methods: Predicting spawning time in a changing climate*). The result is an estimated advance in spawning time ranging from 1 to 73 days and 6 to 129 days with a temperature rise of 0.5° to 2.0°C, respectively (Fig. 4). In general, cold-water populations showed the most dramatic change in time to spawning (e.g., Labrador, 73 to 129 days for 0.5° to

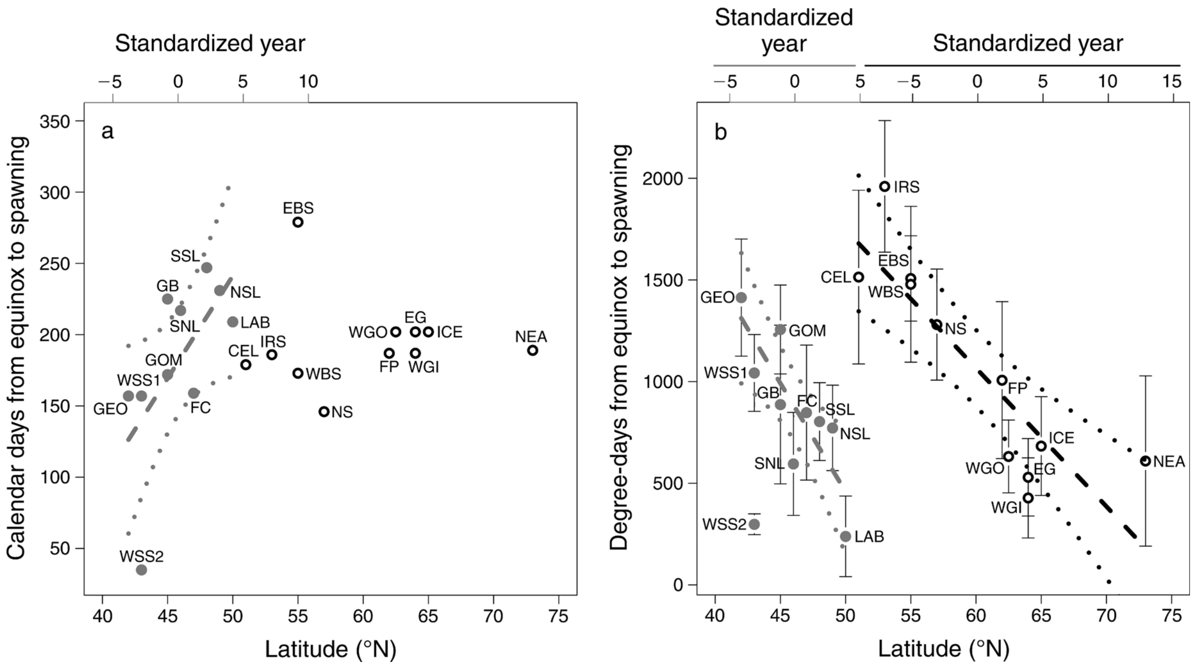

FIG. 3. Spatial variation in spawning. A comparison of time to mean spawning as (a) calendar days (CD), and (b) degree-days (DD; °C × d) with latitude. Western Atlantic populations (Canada and USA) are solid gray circles and eastern Atlantic populations (Greenland, Iceland, and Europe) are open black circles. (a) The dashed line indicates marginal linear trends in CD to spawning with standardized latitude for the west Atlantic populations (gray $P = 0.05$; the dotted lines show 95% confidence interval around the prediction; see also *Results: Among populations: spatial variation in spawning time*). There was no significant trend in CD with to spawning for the east Atlantic populations ($P = 0.99$). (b) The dashed line indicates a significant linear trend in DD to spawning with standardized latitude (gray $P = 0.007$, black $P = 0.001$; the dotted lines show the 95% confidence interval around the prediction; see also *Results: Among populations: spatial variation in spawning time*). Error bars denote standard deviation in DD to spawning among years. The WSS2 and NEA populations are outliers to their respective western and eastern DD relationships (based on Cook's distance). Linear DD relationships of the west and east Atlantic populations are similar in slope but not intercept (based on nonstandardized latitude; ANCOVA slopes $P = 0.29$, intercepts $P < 0.001$). The upper axes are standardized year used in regression analysis. See Fig. 4 and Appendix C for population information and codes.

2.0°C warming, respectively). In contrast, warm-water populations showed the smallest change with predicted warming (e.g., North Sea, 10 to 34 days for 0.5° to 2.0°C warming, respectively). Predicted spawning time estimates in warming waters using the summer solstice as the start-date showed similar spatial patterns, with spawning times estimated earlier relative to estimates employing the autumnal equinox (Appendix B: Fig. B4).

DISCUSSION

Temperature is thought to be a physiological regulator of gonadal maturation in fish due to the aerobic demands of their relatively large reproductive organs (Pörtner and Farrell 2008), with rate of transport (e.g., of protein, vitellogennin) to the oocytes governed by environmental temperature (Kjesbu et al. 2010). Links between increased temperature and earlier spawning times have been noted in a number of species (Teal et al. 2008, Fincham et al. 2013). Indeed, the link between temperature and spawning timing is such that spawning time may "be used to indicate the temperatures that adult cod have been experiencing, i.e., the ovaries of cod could be used as a 'biological thermometer.'" (Kjesbu et al. 2010:622). Though temperature as a regulator of spawning time has been identified previously (e.g., Hutchings and Myers 1993, 2010, Wieland et al. 2000, Fincham et al. 2013), few have employed a degree-day approach to examine spawning variability on a thermal time scale (but see Wieland et al. [2000], Grabowski et al. 2011, Morgan et al. 2013).

Here we employed the integrated temperature metric to identify temperature-dependent variability in time to spawning for a wide-ranging marine fish. We began by examining interannual changes in time to spawning within the southern Newfoundland (SNL), Grand Bank (GB), and eastern Baltic Sea (EBS) populations. In all cases, populations demonstrated trends in time to spawning when examined on calendar time. In all cases, these trends were removed when the time to spawning was estimated on a degree-day (DD) scale, with differing calendar-day (CD) trends among the populations explained by differing thermal environments. This is consistent with previous work finding positive correlations between earlier spawning time and DD during the period of gonadal maturation for Baltic cod (Wieland et al. 2000). The GB results are in contrast to those found

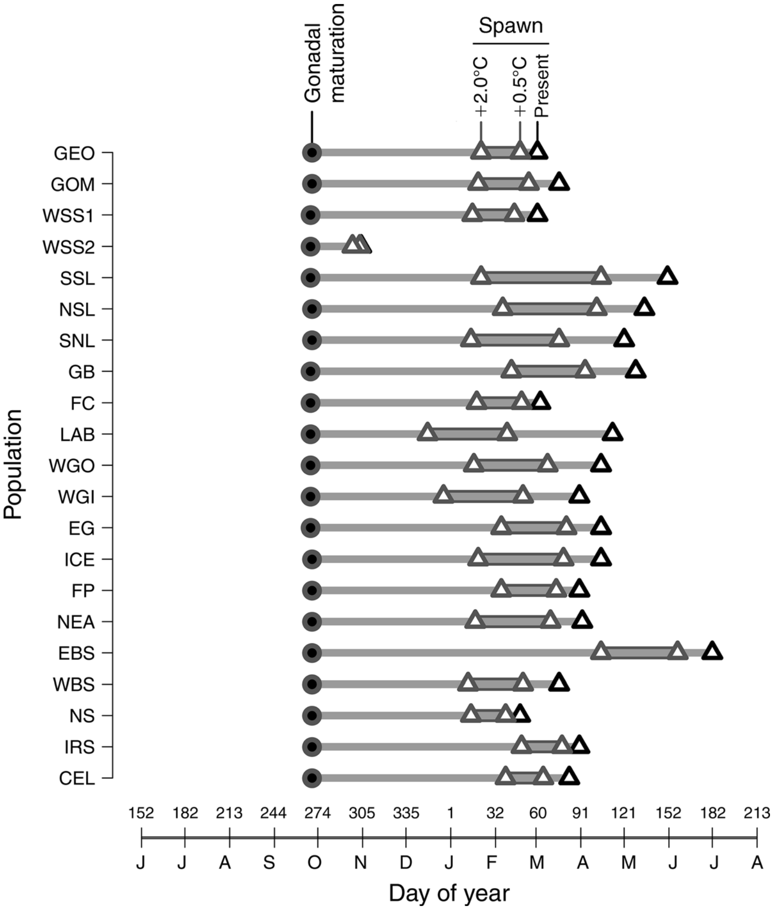

FIG. 4. Spawning time in a warmer climate. Shown are the results of warming analysis for each population demonstrating the onset of gonadal maturation (solid circles) and spawning time (triangles) under present (black) and future (gray, 0.5° to 2.0°C) warming. The horizontal axis is day of year and abbreviated month of year. Population codes are Georges Bank (GEO), Gulf of Maine (GOM), spring-spawning western Scotian Shelf (WSS1), autumn-spawning western Scotian Shelf (WSS2), southern Gulf of St. Lawrence (SSL), northern Gulf of St. Lawrence (NSL), south Newfoundland (SNL), Grand Bank (GB), Flemish Cap (FC), southern Labrador and eastern Newfoundland (LAB), west Greenland offshore (WGO), west Greenland Inshore (WGI), east Greenland (EG), Iceland (ICE), Faroe Plateau (FP), northeast Arctic (NEA), eastern Baltic Sea (EBS), western Baltic Sea (WBS), North Sea (NS), Irish Sea (IRS), and Celtic Sea (CEL).

by Morgan et al. (2013), where temperature was unable to explain the trends in GB spawning time. It should be noted that Morgan et al. (2013) define DD over a fixed period (October to May) rather than as a thermal constant where temperature is integrated over the development period of interest (i.e., gonadal maturation), and the end point of the integration is allowed to vary with the spawning date of the fish (i.e., as we do here). When we examined the thermal constants of spawning for the three populations, we found that major spawning-time trends could be explained by changes in the amount of thermal history the fish experienced over time rather than by any adaptive changes (i.e., spawning-time evolution).

The estimation of thermal history for any species requires estimates of temperature ambient to the animal (Brander 1999, Neuheimer and Grønkjær 2012). This can present a challenge to species that show changes in distribution over time or space. The validity of any assumptions made in estimating ambient temperature will depend on the question. Here we were concerned with relative changes in DD to spawning and assumed that relative differences in ambient temperature are captured by relative differences in bottom temperature estimates among years or populations when confined to areas inhabited by the cod population. This allowed us to estimate temperature influences on trends in spawning time through relative estimates of the thermal constant, while the actual absolute value of the thermal constant may vary. The highest degree of uncertainty regarding this assumption lies in the within-population analysis. Here we confined population-specific temperature estimates to reflect the available area-specific information of fish distribution. The accuracy of this method could be tested using the wealth of storage tag data that has been collected for a number of cod populations (e.g., Righton et al. 2010), if individual spawning time was observed in concert.

Remaining temperature-independent variability in time to spawning was observed as variation in DD to spawning among years (Fig. 2b, d, f) and is evidence that the thermal constant of spawning fluctuates over time. Changes in the thermal constant of spawning among years may be due to age- and size-structure changes (e.g., Hutchings and Myers 1993, Wieland et al. 2000, Kjesbu et al. 2010, Lowerre-Barbieri et al. 2011), subpopulation structure (though variable among populations; e.g., Eiríksson and Árnason 2013), experience (e.g., presence of first-time spawners; Wieland et al. 2000), food availability (Wieland et al. 2000), and condition of the population (though the latter two are thought to be permissive rather than rate-determining factors governing time to spawning [Pankhurst and Porter 2003], and effects of food condition and fish size on spawning could be disregarded for at least one population [Kjesbu et al. 2010]). Of these, the influence of fish age on spawning time has been well studied (e.g., Morgan et al. 2013), with findings including both advanced (Hutchings and Myers 1993) and delayed (Wieland et al. 2000) spawning time associated with younger fish. Because of this, changes in spawning time may accompany changes in age structure associated with exploitation in fish populations (Wright 2013). Information on temporal variability in average spawner age within populations was limited to bottom-trawl surveys that cover the last half of our study period (1975 through 1987–1992) and to the SNL and GB populations (Morgan et al. 2013). Restricting our spawning time data to correspond with this average spawner age data (SNL: 1975 through 1987; GB: 1975 through 1992), we found no trends in time to spawning of the shortened time series (SNL $P = 0.58$; GB $P = 0.41$), while the average spawner age increased over time (data analyzed from Morgan et al. [2013]; linear regression, SNL mean spawner age $= 0.087 \times \text{yr} - 164$ yr, $r^2 = 0.30$, $P = 0.052$; GB mean spawner age $= 0.085 \times \text{yr} - 162$ yr, $r^2 = 0.52$, $P = 0.00073$). It is unclear if these trends toward older-aged spawners extend to the first half of our time series. If so, increased spawner age has been correlated with later spawning time in western Atlantic populations (Hutchings and Myers 1993), and an increase in spawner age may explain the trend toward later spawning time in GB cod (Fig. 2b) but not the trend toward earlier spawning time in the SNL (Fig. 2a) population. Though age- and size-structure changes will undoubtedly influence spawning time, thermal influences on time to spawning remains the most parsimonious explanation for spawning-time changes in all three populations examined. In addition to possible environmental and demographic effects, remaining variation in DD to spawning among years may occur due to genetic changes (Otterå et al. 2006, Mieszkowska et al. 2009). Possible evidence of the genetic contribution to spawning-time variation became clearer when we examined spawning time on a macroecological scale and variability in spawning among populations (Merilä 2012).

By examining spatial variability in time to spawning across the species range, we found parallel trends in decreasing DD with increasing latitude among cod populations on the west and east sides of the Atlantic, trends not revealed using CD. The EBS population was consistent with the DD trend for the eastern populations (Fig. 3b), though EBS appeared as an outlier when time to spawning was measured in CD (Fig. 3a), and the population is often noted as an outlier with respect to the species due to the unique environment and resulting physiology of the Baltic Sea and Baltic Sea cod (Kjesbu et al. 2010). In contrast, the autumn-spawning western Scotian Shelf (WSS2) population was an outlier when examined in either CD or DD time. Autumn-spawning cod may have different environmental cues for gonadal maturation and/or differing sensitivities of development rate, allowing them to increase the pace of gonadal maturation relative to spring spawners (after Migaud et al. [2010]). Our among-population analyses were restricted to comparisons of long-term mean spawning date but on a thermal time scale. By exploring spawning time on a thermal time scale, we implicitly included much of the year-to-year variability that is due to temperature changes (i.e., as shown in the within-population analyses). Moreover, such comparisons of the mean are particularly warranted when made among populations over a wide spatial (and temperature) range where variability in the thermal environment (and spawning time) among populations is greater than that within (see *Results: Among populations: spatial variation in spawning time*).

Assuming relative differences in thermal history have been captured, as discussed in this section, the west and east trends in DD to spawning as a function of latitude represent shifts in the thermal constant of spawning among populations and may be evidence of spawning time adaptation. Trends in DD were similar in slope but different in intercept between the west and east populations (Fig. 3b). This is consistent with parallel adaptation to an environmental gradient of two groups long separated. Previous studies indicate populations in the western Atlantic (Canadian and U.S.) diverged from those in the eastern Atlantic approximately 100–150 thousand years ago (Bigg et al. 2008). In contrast, eastern Atlantic populations, including European, Greenlandic, and Icelandic populations, have diverged from each other more recently (<21 thousand years ago; Bigg et al. 2008, Therkildsen et al. 2013), a finding consistent with our results, which place the Greenlandic and Icelandic populations well within the eastern Atlantic grouping (Fig. 3b; based on Cook's distance). Indeed, recent work examining genomic regions of elevated divergence among cod populations show that populations around Iceland and Greenland (Davis Strait) are most similar to eastern Atlantic populations (e.g., Ireland, Barents Sea, Baltic Sea; Bradbury et al. 2013).

Further, the parallel nature of the spatial trends of the west and east Atlantic are consistent with current theories regarding genetic variability among the populations. Parallel clines in allele frequencies have been observed for cod populations on both sides of the Atlantic (Nielsen et al. 2009, Bradbury et al. 2010). Such clines were correlated to temperature differences among populations even when allowing for effects due to latitude and geographic distance (Bradbury et al. 2010). Indeed, links between temperature and polymorphism of genes controlling oxygen binding (i.e., hemoglobin gene b1) have been found (Andersen et al. 2009). As well, genetic variability was found over smaller spatial scales (e.g., Therkildsen et al. 2013) and has been linked to spawning variability of coastal Norwegian cod (Otterå et al. 2006, 2012). Though the marine environment offers few obvious boundaries to encourage the development of genetic differentiation (particularly in broadcast spawners such as cod), a high degree of population discreteness is maintained both by nonmigratory populations and high fidelity to discrete spawning locations (Skjæraasen et al. 2004, Bradbury et al. 2010, Therkildsen et al. 2013).

The occurrence of parallel, independent clines among populations is strong evidence of adaptation in many species (Samis et al. 2012). In this case, we have declines in DD to spawning with increasing latitude on both sides of the ocean basin. Such patterns may be adaptation to the shorter growing season (light availability and temperature) of high-latitude environments. By systematically reducing the thermal constant of spawning (i.e., thermal energy needed before spawning) with latitude, the cod populations are able to experience remarkably similar life histories despite dramatic environmental variation along the latitudinal gradients. Genetic compensation to achieve similar phenotypes over a range of conditions is often termed countergradient variation (CGV; e.g., Conover and Schultz 1995, Marcil et al. 2006). Countergradient variation has been noted in many plant and animal species distributed over an environmental cline (e.g., with altitude or latitude; Conover and Present 1990, Kokita 2004) and is expected to be a common pattern in latitudinally widespread fishes (Kokita 2004). Indeed, evidence for CGV has been observed in growth rates for western Atlantic cod populations across a temperature gradient (Purchase and Brown 2000) and egg buoyancies for a number of marine fish species spanning salinity ranges (MacKenzie and Mariani 2012). While comparative life history data can provide valuable information regarding CGV, a combination of common garden experiments (e.g., Otterå et al. 2006) and quantitative genetic analyses is the only method to confirm CGV (e.g., Hansen et al. 2012, Merilå 2012). Our biogeographic evidence of among-population trends in DD to spawning suggests that CGV may be a mechanism that cod employ to compensate for the lack of light, shorter growing season, and less thermal energy available with increasing latitude.

Due to temperature dependence, ectotherm life history processes are expected to respond to warming (e.g., advanced flowering with warming; Anderson et al. 2012). Here, we can use population-specific DD to spawning as estimates of population-specific thermal constants of spawning. In so doing, we can use the thermal constants to estimate what could happen to spawning time under climate change. As a first approximation, we considered a bottom temperature increase of between 0.5° and 2.0°C by 2100 (Yin et al. 2011), though it should be noted that future climate changes are expected to vary seasonally, bathymetrically, and geographically (see *Methods: Predicting spawning time in a changing climate*). We found the magnitude of advancement in spawning due to predicted bottom water warming was population specific (Fig. 4). For warmer areas, the predicted increase in temperature is small relative to the thermal constant of spawning, and we saw a small advancement in spawning time (e.g., GEO in Fig. 4). In contrast, the predicted increase in temperature is large relative to the thermal constant of spawning for cod in colder areas, and a large advancement in spawning time was estimated (e.g., WGO in Fig. 4). Thus we projected changes in the spawning time of the cod populations such that by 2100, for example, the WGO population (63° N) could be spawning at the same time as the current spawning time for the GEO population (42° N), i.e., an advance of 37–88 days from mid-April to January–March.

Such analyses assume constant age structure and size structure of the populations, no further genetic adaptation in spawning time, and sufficient food quantity and quality to allow for gonadal development. In addition, these analyses assume that the predicted temperature increase remains within the thermal tolerance limits of the fish. The DD approach (in the form presented here) assumes temperatures are in the midrange where there is a near-linear increase in development rate with temperature. Outside of this range, the interaction between development rate and temperature becomes nonlinear, and at some point negative (Neuheimer et al. 2011). As the thermal niche appears narrower during spawning than during other periods of the year (Righton et al. 2010), and maximum reproductive rate has a relatively narrow thermal range (Mantzouni et al. 2010), it is possible that temperatures will eventually surpass those tolerated by a specific cod population. Further research in this area requires information on cod temperature tolerance limits and how these may vary over the range of the species (e.g., Bolton-Warberg et al. 2013).

A predicted advancement in spawning time may change the overlap between cod larvae and their food. Reproductive timing of many species is thought to be such to allow offspring to overlap in time and space with beneficial conditions for growth, development, and survival (Bromage et al. 2001, Kristiansen et al. 2011). Spatial or temporal mismatch between food and larval timing may result in high larval mortality and reduced population productivity (Platt et al. 2003, Mieszkowska et al. 2009, Kristiansen et al. 2011). The degree of mismatch will depend on the differing magnitudes of responses to climate by predator and prey species, including potential mitigative mechanisms such as adaptation or shifts in geographical distributions. At some point, the seasonal temperature may change in such a way as to decouple thermally timed ecological processes from those governed primarily by the other major cue for ectotherm development: photoperiod. In such cases, we might expect higher trophic levels (e.g., zooplankton, fish) to become decoupled from primary producers (e.g., phytoplankton; Thakeray et al. 2013), particularly considering the apparent limited ability for cod to rapidly adjust spawning time to temporal variability in prey species (Beaugrand et al. 2003, Mieszkowska et al. 2009). Alternatively, cod may alter their distribution to maintain spawning time in the face of temperature changes (e.g., moving to higher latitude, moving deeper; Engelhard et al. 2011). Distributional shifts have been correlated with temperature (e.g., west Greenlandic cod [Drinkwater 2005]; bluefish *Pomatomus saltatrix* [Sabatés et al. 2012]), including changes in cod spawning grounds (Opdal et al. 2011).

In summary, this study exploits the thermal history concept to identify meaningful variability in reproductive timing in a wide-ranging species. The pace of physiology for ectotherms is governed by environmental temperature, such that temporal and spatial variability of all manner of life history timing can begin to be elucidated by comparing groups on a thermal and physiologically relevant time scale. In so doing, we can identify trends among groups that may be independent of temperature, including effects due to demographics, food, and genetic variability. Here we use DD to show that major trends in spawning time within populations can be attributed to plastic responses to changing temperature. Similar to other ectotherms (e.g., Phillmore et al. 2010), among-population spawning time variability remains unexplained by DD, and it is consistent with adaptation to an environmental cline and the evolutionary history of the species. By disentangling these plastic vs. (possibly) genetic responses, we can begin to predict how a species' life history timing, and subsequent production and distribution, may react to a changing climate. The ability to identify relevant life history variability is a necessary step to managing and preserving a species' adaptive diversity (Bradbury et al. 2010, Grabowski et al. 2011), with survival and productivity of the species relying on how much biocomplexity is maintained (e.g., life history variability, age structure, and size structure, Hilborn et al. 2003).

Acknowledgments

We thank all those involved in the International Council for the Exploration of the Sea and Fisheries and Oceans Canada research surveys. We thank R. Hedeholm for providing Greenland temperature data. We thank K. Brander, E. Nielsen, and two anonymous reviewers for comments on previous versions of this manuscript. We thank the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/13-2370.1.sm