

Effects of temperature on life history set the sensitivity to fishing in Atlantic cod *Gadus morhua*

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ABSTRACT: Concern over sustainable fisheries resources has motivated investigations of possible synergistic effects of climate variability and fishing on marine populations. While many studies suggest that fishing increases population sensitivity to climate forcing, the effects of climate variability on the population response to fishing is relatively understudied. To fill this knowledge gap, we conducted a synthesis based on 20 Atlantic cod populations (11 in the Northeast and 9 in the Northwest Atlantic). These cod populations display considerable life-history variation and are exposed to different temperature regimes and differential harvest pressure throughout their broad geographical range. We hypothesized that the differences in life histories that result from the different temperature regimes determine the sensitivity of cod populations to fishing. Spatial correlations between life-history traits (growth, maturation, and natural mortality) and water temperatures confirmed that warmer temperatures lead to faster individual growth, earlier maturation, and higher natural mortality. Analysis of a population model revealed how temperature influences on life histories lead to differential population responses to fishing. We represented such population responses to fishing using a proxy for lifetime reproduction (fraction of unfished lifetime spawning biomass, FLSB). This index revealed that — all else being equal — populations in warmer regions in the Northeast Atlantic Ocean can sustain higher fishing rates than those in the cooler Northwest. Life history-mediated temperature effects on population dynamics provide a novel perspective on synergistic relationships between climate and fisheries. Understanding population life-history variation will enhance the capabilities for forecasting future fisheries production under climate change.

KEY WORDS: Fraction of unfished lifetime spawning biomass · FLSB · Atlantic cod · Life history · F_{35} · Natural mortality · Temperature variability

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INTRODUCTION

As one of the major aspects of climate change, changes in temperature can cause various effects that influence global fishery production both directly

and indirectly (Drinkwater 2005, Brander 2010). For example, temperature changes may affect growth, recruitment, spatial distribution, and inter- and intra-specific interactions (Brander 1995, 2007, Clark et al. 2003, Drinkwater 2005, Köster et al. 2005). Further,

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synergistic interactions between temperature changes and fisheries exploitation result in complex population dynamics (Brander 2010, Perry et al. 2010, Planque et al. 2010). For example, several authors have presented evidence that fishing can increase fish populations' sensitivity to environmental variability (Hsieh et al. 2006, Ottersen et al. 2006, Anderson et al. 2008, Wright & Trippel 2009, Worden et al. 2010, Botsford et al. 2011, Hidalgo et al. 2011, Rouyer et al. 2011). However, the effect of temperature variability on populations' responses to fisheries exploitation is relatively little studied. To achieve sustainable management of global fisheries resources, we must elucidate the complex interactions between temperature and fishing.

Life-history traits determine individual fitness under a given set of environmental and anthropogenic conditions, driving population growth rates and affecting a stock's sustainability under fishery exploitation. Fish species that exhibit 'fast' life histories (high growth rates, early maturity, and short life span) may sustain intensive harvesting while ones that exhibit 'slow' life-history strategies may not (Jennings et al. 1998, Fromentin & Fonteneau 2001, but see also Andersen & Beyer 2013). These findings suggest that the dependence of life history on temperature (e.g. Brander 1995, Drinkwater 2002) could mediate a differential population response to fishing. Such a relationship would have serious implications for fishery management under changing ocean temperatures.

In this study, we describe how temperature variability induces life-history variation that mediates differential population responses to fishing in Atlantic cod *Gadus morhua*, one of the most important commercially exploited fish species. Instead of tracking a population's response to a temperature time series, we assessed population response to temperature variability by evaluating spatial variation in population dynamic responses for 20 cod populations throughout the northern Atlantic Ocean (spanning 30° of latitude and >10°C in mean water temperatures; Fig. 1, Table 1). This broad distribution of cod populations covers a wide range of temperatures. In addition, these cod populations exhibit considerable variation in abundance, life-history traits, and exploitation history (McIntyre & Hutchings 2003, Olsen et al. 2004, Fudge & Rose 2008, Lilly et al. 2008).

Our objectives were to explore 2 questions: (1) how does temperature variability affect cod life-history variation, and (2) how does temperature-induced life-history variation change the sensitivity of population equilibria to fishing? We first examined correlations between temperature and life-history traits. We then used those life-history traits to calculate lifetime egg production, a metric related to the mathematical condition for persistence of marine fish populations (Sissenwine & Shepherd 1987, Botsford 1997). To compare the sensitivities to fishing among populations, we computed the level of fishing mortality that reduced lifetime egg production to an assumed critical threshold for sustainability.

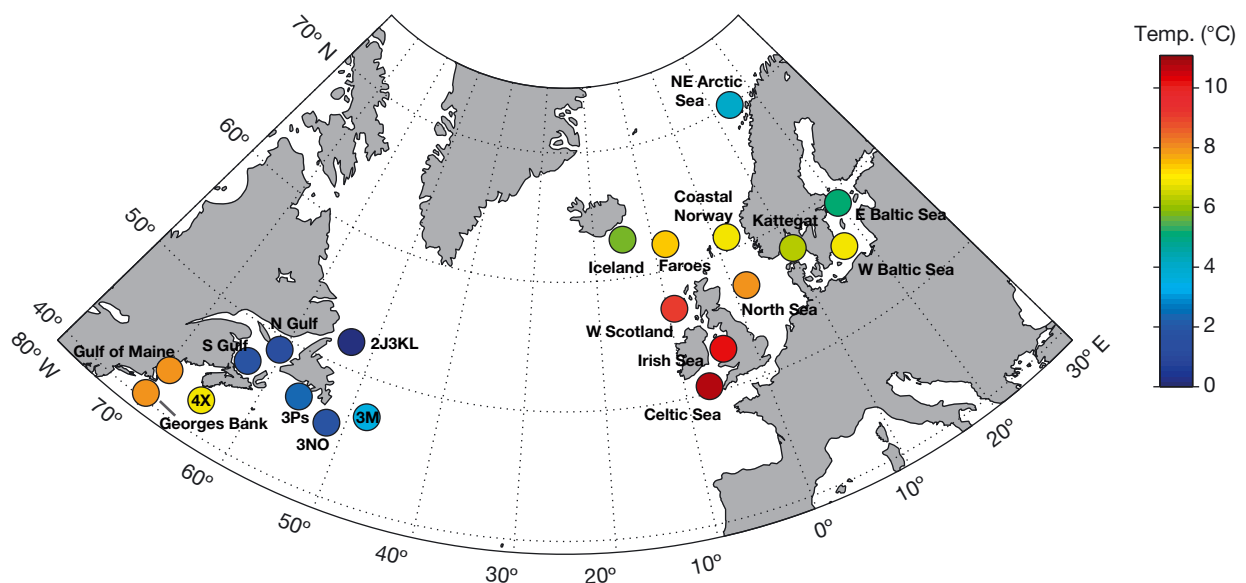


Fig. 1. Distributions and mean habitat temperatures of the 20 Atlantic cod *Gadus morhua* populations in this study

Table 1. Summary of cohort time-series and mean bottom temperatures for the 20 Atlantic cod *Gadus morhua* populations

| Population (abbreviation) | Cohorts | Temp. (°C) | Source |
|------------------------------|-----------|------------|--|
| Celtic Sea (Celtic) | 1970–2002 | 11.9 | ICES (2012a) |
| Irish Sea (Irish) | 1967–2006 | 10.56 | ICES (2012a) |
| North Sea | 1962–2001 | 8.4 | ICES (2012b) |
| West Scotland (W Scotland) | 1977–2005 | 9.57 | ICES (2012a) |
| West Baltic (W Baltic) | 1969–2001 | 7.00 | ICES (2012c) |
| Kattegat | 1970–2003 | 6.50 | ICES (2012c) |
| East Baltic (E Baltic) | 1964–2004 | 5.00 | ICES (2012c) |
| Coastal Norway (Coas N) | 1983–2001 | 7.13 | ICES (2012d) |
| Faroes | 1960–2002 | 7.40 | ICES (2011) |
| Iceland | 1954–1998 | 5.80 | ICES (2011) |
| NE Arctic | 1945–1999 | 4.00 | ICES (2012d) |
| Georges Bank (GB) | 1977–2000 | 8.00 | NEFSC (2012a) |
| Gulf of Maine (GM) | 1981–1999 | 8.00 | NEFSC (2012b) |
| 3NO | 1957–1997 | 1.75 | Power et al. (2010) ^a |
| S Gulf St. Lawrence (S Gulf) | 1947–1993 | 1.75 | Swain et al. (2009) ^b |
| N Gulf St. Lawrence (N Gulf) | 1971–1993 | 1.00 | Fréchet et al. (2009) ^b |
| 3M | 1987–2002 | 3.50 | González-Troncoso et al. (2012) ^a |
| 3Ps | 1956–1995 | 2.5 | Healey et al. (2011) ^b |
| 4X | 1979–1995 | 6.75 | Clark & Emberley (2010) ^b |
| 2J3KL | 1960–1989 | 0 | Bratley et al. (2011) ^b |

^aNortheast Atlantic Fisheries Organization, Scientific Council Research (NAFO SCR) Documents
^bFisheries and Oceans Canada, Canadian Science Advisory Secretariat (DFO CSAS) Reports

MATERIALS AND METHODS

Population dynamics approach

To assess the life history-mediated temperature effects on cod population dynamics, we calculated the responses of cod populations to fishing in terms of lifetime egg production (LEP, also known as eggs-per-recruit, EPR), a metric related to the mathematical condition for equilibrium for populations with age structure and density-dependent recruitment, both of which are characteristics of cod populations. The equilibrium condition for models of such populations is well known (Sissenwine & Shepherd 1987, Botsford 1997), and it has a convenient graphical interpretation based on the egg-recruit curve (a form of the stock-recruitment relationship; Fig. 2). Specifically, the equilibrium recruitment is the point at which a straight line through the origin with slope equal to the inverse of LEP intersects the egg-recruit curve. Thus,

if the egg-recruit relationship were of the Beverton-Holt form, the effect of increasing fishing, which diminishes LEP, would be to increase the slope of the straight line, moving the equilibrium to lower values of annual egg production and annual recruitment. The point at which LEP is reduced to the inverse of the slope of the egg-recruit curve at the origin would be the point at which the equilibrium would drop to zero, signifying population collapse. That is, persistence requires that LEP exceeds the inverse of the slope at the origin of the egg-recruit curve (Sissenwine & Shepherd 1987, Botsford 1997).

We used a proxy for this slope as a metric representing the relative population persistence of the various cod populations. As the nature of the egg-recruit relationship at low values is typically highly uncertain, our analysis does not depend on it. Rather we characterize the relative persistence of various cod populations in terms of the degree to which fishing has diminished LEP through truncation of their age structures. To avoid the confounding effects of differences in fecundities and larval survivals, we took the common step of representing LEP relative to its natural, unfished value, i.e. the fraction of lifetime egg production (FLEP, which is essentially equivalent to the spawning

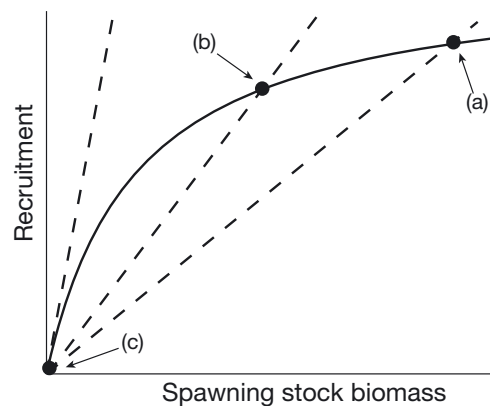


Fig. 2. Graphical representation of the equilibrium condition for age-structured populations with density-dependent recruitment. (Solid line) Dependence of recruitment on annual egg production (i.e. the stock-recruitment function) and (dashed lines) lines with slope $1/(\text{lifetime egg production})$, i.e. $1/\text{LEP}$. The unfished state is (a). With fishing, LEP is diminished and the equilibrium is at (b). Point (c) represents the maximum amount of sustainable fishing; for any greater values of fishing mortality (i.e. lower values of LEP), the equilibrium will be zero

potential ratio, SPR; Goodyear 1993, O'Farrell & Botsford 2006). Also, because fecundity relationships are not universally available for cod populations, we used biomass as a proxy for fecundity, resulting in lifetime spawning biomass (LSB) and the fraction of lifetime spawning biomass (FLSB). FLSB is a dimensionless quantity.

Datasets

We compiled time series data on age-specific estimates of weight, maturity probability, fishing mortality rates (F , units: yr^{-1}), as well as catch and population abundance for 20 cod populations. These data were compiled from the most recent publicly available sources, including the ICES (2011, 2012a–d) Reports, NEFSC (2012a,b) Reference Documents, DFO CSAS (2008, 2009–2011) Reports, and NAFO SCR (2010, 2012) Documents (see Table 1), covering 11 Northeast Atlantic and 9 Northwest Atlantic populations (Fig. 1). These time series represent a large number of cohorts for each of the populations (Table 1).

In order to calculate FLSB, we required several types of life-history information from each population: natural mortality rate, weight-at-age, the probability of maturity at each age, and the fishery selectivity (age-specific probability of being caught). The availability of these quantities varied among the populations, so we used a variety of procedures to obtain the necessary estimates.

Catch-based weight-at-age estimates were available for all 20 populations, but fisheries-independent weight-at-age estimates were not available in the cited documents for half of these populations.

Temporal data on age-specific probability of maturity (maturity ogives) were unavailable for most of the populations. Thus, we calculated population means of maturity ogives for those populations with time series of maturity ogives, and assumed a fixed maturity ogive for each population.

Some age-specific estimates for F and population abundance were unavailable for 3 populations (Kattegat, 2J3KL, and 3Ps). We restored these missing data using catch-at-age data with virtual population analysis (VPA, a.k.a. cohort analysis), based on available F for the terminal ages (Kattegat) or assuming F for the terminal ages was equal to the average F of the ages adjacent to the terminal ages ($F = 0.05$ and 0.4 yr^{-1} for 2J3KL and 3Ps, respectively). We assumed a constant natural mortality, $M = 0.2 \text{ yr}^{-1}$ in the VPA.

Average bottom temperature for each location was estimated using the ICES ocean climatology data of

the northwest European shelf (available at http://ocean.ices.dk/Project/OCNWES/clim_db_v01-2.zip) or taken from Myers et al. (2001, their Table 1). The ICES average bottom temperature data were estimated based on measurements taken at ≤ 15 m from the seabed (Berx & Hughes 2009).

Analyses

LSB for each population and each value of fishing mortality F is the sum over all ages of reproduction-at-age times the fraction surviving to that age (s_a). The survival probability is a function of both natural and fishing mortality at a given age. As we use biomass as a proxy for fecundity, the age-specific reproduction is calculated from the weight at age (w_a), and a maturity ogive (A_a),

$$\text{LSB}(F) = \sum_{a=1}^{40} w_a A_a s_a \quad (1)$$

As the distribution of spawning biomass declines to near zero before reaching the age of 40 yr for most cod populations (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m514p217_supp.pdf), we used maximum age = 40 yr to compute LSB. Due to the low abundance at this age, the presence of older age fish would not affect the result values of FLSB. The FLSB for each population is that value normalized by the value with no fishing for that population:

$$\text{FLSB} = \frac{\text{LSB}(F)}{\text{LSB}(F=0)} \quad (2)$$

We determined the logistic maturity ogive by logistic regression:

$$\text{logit}(A_i) = \ln\left(\frac{A_i}{1-A_i}\right) = \beta_0 + \beta_1 \times i \quad (3)$$

where i is age (yr), A_i is probability of maturity at age i , and β_0 and β_1 are coefficients.

Values of weight-at-age were determined from von Bertalanffy expressions for length-at-age using local values of L_∞ and K . Length was converted to weight by assuming the length (cm)-weight (kg) relationship was: $W_i = 0.00001L_i^3$. The value of the constant exponent here will have no effect on the resulting value of FLSB. Available values of the exponent are near the assumed value of 3 (e.g. 3, 3.02, and 3.16 for the populations in the North Sea, Coastal Norway, and NE Arctic; estimates derived from the stock assessment data; see Table 1).

Survival to each age, s_{ai} , included the effects of F , natural mortality M and a fishing selectivity function. We assumed the selectivity curve for cod followed a logistic form (Huse et al. 2000):

$$\text{logit}(S_i) = \ln\left(\frac{S_i}{1-S_i}\right) = \theta_0 + \theta_1 \times i \quad (4)$$

where S_i , selectivity, is the probability of being vulnerable to fishing at age i , and θ_0 , and θ_1 are the coefficients of the logistic regressions for the fishing selectivity ogive.

Given the historical changes in fisheries regulation of these populations (e.g. fishing closures), our estimation of population-specific selectivity took into account the temporal changes in fishing selectivity. That is, instead of fitting a selectivity curve to pooled data, we derived cohort-specific selectivity curves and calculated the average of these selectivity curves for a population. The protocol was: (1) For each cohort of a population we calculated the age-specific selectivity coefficients, S_i , which were the values of F -at-age, normalized to range from 0 to 1. (2) For each cohort we fitted a logistic regression to these selectivity coefficients, excluding the relatively old age data (age >10 yr) as the selectivity estimates for these age classes were likely underestimated due to relatively low abundance (e.g. a truncated age structure was observed for the NE Arctic cod; Ottersen et al. 2006). (3) After excluding the non-significant regression fits we then calculated mean slope (θ_1) and intercept (θ_0) of the cohort-specific regression coefficients to be the slope and intercept of the selectivity function of a population, and derived age-at-50% selectivity, S_{50} , as $-\theta_0/\theta_1$.

As there are 2 different published descriptions of the statistical dependence of natural mortality M on life-history parameters and temperature (Pauly 1980, Gislason et al. 2010), we used both of them, and compared results. The natural mortality function from model 2 of Gislason et al. (2010) depended on current size, L_i , in addition to L_∞ and K from the von Bertalanffy equation (from literature values; Table 2). The effect of temperature enters this relationship through the dependence of K on temperature (Gislason et al. 2010):

$$\ln(M_i) = 0.55 - 1.61 \times \ln(L_i) + 1.44 \times \ln L_\infty + \ln K \quad (5)$$

Pauly's (1980) natural mortality function is:

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T \quad (6)$$

Pauly's function depended on the von Bertalanffy parameters and temperature directly; T is the population-specific average bottom temperature (Table 1). For a direct comparison between these 2 models, we removed the length dependence from the Gislason model by assuming that L_i was the length at A_{50} , the age of maturity. Values for L_∞ were unavailable for 3 populations, so we substituted estimates of L_{\max} in those cases (Table 2).

Exploring temperature effects on cod life-history variation

It is clear from Eqs. (1) & (2) that temperature-dependent differences in individual growth (via w_a), maturation schedules (A_a) and mortality rate (via s_a) could have a substantial effect on the FLSB. We used linear regression to examine potential temperature effects on inter-population variation in the life-history traits involved in FLSB. To examine the

Table 2. von Bertalanffy parameters L_∞ and K , from various sources, and natural mortality estimates, M_P and M_{G_A50} , respectively, for the 20 Atlantic cod *Gadus morhua* populations. M_P is an age-invariant natural mortality based on the equation of Pauly (1980), whereas M_{G_A50} is the natural mortality associated with the population-specific age-at-50% maturity based on Eq. (2) of Gislason et al. (2010). NA = not available

| Population | L_∞ (cm) | K (yr ⁻¹) | M_P (yr ⁻¹) | M_{G_A50} (yr ⁻¹) |
|----------------------------------|-----------------|-------------------------|---------------------------|----------------------------------|
| Celtic Sea ^a | 99 | 0.390 | 0.450 | 0.719 |
| Irish Sea ^a | 99 | 0.390 | 0.440 | 0.844 |
| North Sea ^a | 126 | 0.217 | 0.252 | 0.427 |
| West Scotland ^b | 105 | 0.160 | 0.230 | 0.941 |
| West Baltic ^a | 103 | 0.150 | 0.192 | 0.584 |
| Kattegat ^b | 105 | 0.130 | 0.168 | 0.913 |
| East Baltic ^a | NA | NA | NA | NA |
| Coastal Norway ^b | 123 | 0.110 | 0.151 | 0.316 |
| Faroese ^a | 115 | 0.190 | 0.224 | 0.565 |
| Iceland ^a | 149 | 0.121 | 0.138 | 0.229 |
| NE Arctic ^a | 134 | 0.109 | 0.112 | 0.196 |
| Georges Bank ^a | 132 | 0.166 | 0.204 | 0.954 |
| Gulf of Maine ^a | 167 | 0.118 | 0.153 | 0.797 |
| 3NO ^a | 130 | 0.120 | 0.082 | 0.267 |
| S Gulf St. Lawrence ^a | NA | NA | NA | NA |
| N Gulf St. Lawrence ^a | 110 | 0.160 | 0.080 | 0.308 |
| 3M ^a | 98 | 0.150 | 0.142 | 0.489 |
| 2J3KL ^a | 81.3 | 0.243 | 0.014 | 0.307 |
| 3Ps ^a | 101 | 0.170 | 0.130 | 0.273 |
| 4X ^c | 117.5 | 0.220 | 0.234 | NA |

^aMagnussen (2007); ^bDenney et al. (2002); ^cTallack (2009)

dependence of these traits on temperature in a regression framework, we condensed each of those age-specific traits into a single point-estimate proxy value for each population. In total, we considered the age-4 mean weight (a proxy for growth; faster-growing fish will be larger at age 4), age-at-50% maturity (A_{50}), and 2 natural mortality indices (both Pauly-based M and Gislason-based M -at- A_{50}). We calculated a population's age-4 mean weight as the mean of age-4 weights for catch-based weight-at-age data from the available cohorts (Table 1). To derive A_{50} , we used the coefficients of the fitted logistic maturity ogive expressing A_{50} as $-\text{intercept}/\text{slope}$, i.e. $-\beta_0/\beta_1$.

Comparing the FLSB response to fishing at different temperatures (locations)

To determine the combined effects of fishing and temperature-induced life history variability on cod population dynamics, we used Eq. (2) to analyze the response of each cod population to different levels of fishing. By varying F from 0 to 2 yr^{-1} in 0.01 yr^{-1} increments, we calculated (1) fished LSB, representing the effects of size-selective F and natural mortality, and (2) unfished LSB, the same calculation with $F = 0$ in Eq. (2). To compare the values of F that would lead to a common collapse point, we determined the values of F that caused a decline of FLSB to 0.35. Hereafter we refer to this quantity as F_{35} . F_{35} is commonly used as a biological reference point representing collapse (Clark 2002). We then evaluated the relationship between the F_{35} and temperature using linear regression.

Due to the missing estimates of L_{∞} and K for the East Baltic Sea and Southern Gulf of St. Lawrence populations, as well as the missing maturity data for the 4X population, we were unable to model FLSB for these 3 populations. Consequently, the available data permitted our modeling analysis for 17 cod populations.

In these calculations, we were interested in how differences in life history, due to differences in temperature, cause differences in the way that FLSB (Eq. 2) responds to fishing. However, the age at which fishing

begins can influence that value in a way that would confound the effects of temperature. If fishing began before the age of maturity, the numerator and denominator of Eq. (2) would be multiplied by the same term reflecting survival up to the age of maturity, hence these effects would cancel. However, if fishing began after the age of maturity, this cancellation would not occur. To avoid this confounding effect of the age at which fishing began in our attempts to demonstrate the effects of temperature, we made the calculations in Eq. (2) for the case in which $S_{50} = A_{50}$, and used the maturation ogives to represent the selectivity curve.

RESULTS

Temperature effects on life-history variation of Atlantic cod

There was pronounced life-history variation among populations (Tables 2 & 3). For example, von Bertalanffy coefficients L_{∞} ranged from 81 to 167 cm and K from 0.11 to 0.39 yr^{-1} . Such variability in coefficients

Table 3. Logistic regression coefficients of maturity ogives (β_0 , β_1) and selectivity (θ_0 , θ_1), as well as age-at-50% maturity (A_{50}) and age-at-50% selectivity (S_{50}) for the 20 Atlantic cod *Gadus morhua* populations. Except for the maturation ogive functions for the Irish Sea population, all other regression fits are statistically significant ($p < 0.05$)

| Population | Maturity ogives coefficients (β_0 , β_1) | A_{50} (yr) | Selectivity coefficients (θ_0 , θ_1) | S_{50} (yr) |
|---------------------|--|-------------------|--|---------------|
| Celtic Sea | -5.22, 2.27 | 2.30 | -1.09, 0.67 | 1.63 |
| Irish Sea | - ^a | 1.97 ^a | -1.48, 1.05 | 1.41 |
| North Sea | -6.42, 1.72 | 3.73 | -1.84, 1.03 | 1.79 |
| West Scotland | -5.78, 2.73 | 2.12 | -2.42, 0.68 | 3.56 |
| West Baltic | -2.52, 0.85 | 2.96 | -1.23, 0.68 | 1.81 |
| Kattegat | -5.01, 2.20 | 2.28 | -2.22, 0.88 | 2.52 |
| East Baltic | -4.12, 1.30 | 3.17 | -2.94, 0.95 | 3.09 |
| Coastal Norway | -5.87, 1.11 | 5.29 | -4.24, 0.66 | 6.42 |
| Faroes | -4.88, 1.63 | 2.99 | -2.02, 0.43 | 4.70 |
| Iceland | -6.69, 0.99 | 6.76 | -1.28, 0.16 | 8.00 |
| NE Arctic | -7.45, 0.93 | 8.01 | -2.95, 0.48 | 6.15 |
| Georges Bank | -4.32, 2.15 | 2.01 | -7.06, 0.91 | 7.76 |
| Gulf of Maine | -3.98, 1.63 | 2.44 | -2.71, 0.71 | 3.82 |
| 3NO | -9.99, 1.65 | 6.01 | -2.34, 0.32 | 7.31 |
| S Gulf St. Lawrence | -6.36, 1.46 | 4.36 | -4.02, 0.50 | 8.04 |
| N Gulf St. Lawrence | -7.66, 1.45 | 5.28 | -3.47, 0.47 | 7.38 |
| 3M | -8.18, 2.28 | 3.59 | -2.33, 0.54 | 4.31 |
| 2J3KL | -10.99, 1.84 | 5.97 | -4.26, 0.57 | 7.47 |
| 3Ps | -9.21, 1.52 | 6.07 | -2.30, 0.32 | 7.19 |
| 4X | NA | NA | NA | NA |

^aThe fit of a logistic regression was not significant ($p = 0.99$) due to lack of variation in age-specific probability of maturity

also led to differences in estimates of M (Table 2). As noted by Gislason et al. (2010), Pauly-based estimates of M tended to be lower than Gislason-based estimates of M for a given population (Table 2).

A logistic form for maturation ogives fit well for all populations except the Irish Sea population. This exception was due to lack of variation in age-specific probability of maturity data (Table 3). Despite this, the A_{50} estimate for the Irish Sea population appeared reasonable (Table 3). A_{50} ranged from 1.97 to 8.01 yr among populations. Further, a logistic model for selectivity resulted in great variability in S_{50} among populations (1.41 to 8.04 yr). These values depend on management decisions, but, of course, are dependent on life histories.

There were strong linear relationships between temperature and population life-history traits. Populations in warmer water tended to grow faster (positive regression of $\ln(\text{age-4 weight})$ on T : $R^2 = 0.91$, $p < 0.001$; Fig. 3a), and mature earlier (negative regression of $\ln(A_{50})$ on T : $R^2 = 0.55$, $p < 0.001$; Fig. 3b). Both Pauly-based and Gislason-based M estimates were positively correlated with temperature (Pauly-based

M : $R^2 = 0.74$, $p < 0.001$; Fig. 3c; Gislason-based M -at- A_{50} : $R^2 = 0.50$, $p = 0.002$; Fig. 3d). There was also a strong correlation between the 2 sets of natural mortality estimates at each location ($R^2 = 0.56$, $p = 0.002$, not shown).

Modeling FL SB responses to the temperature and fishing mortality effects

We first note that for many of the populations, the value of S_{50} differed considerably from the value of A_{50} (see Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m514p217_supp.pdf). This confirms the fact that if we had used the empirical selectivity curves instead of setting $S_{50} = A_{50}$ there would have been a considerable confounding effect on estimation of FL SB.

These dependencies on temperature had a clear influence on the responses of the various stocks to fishing (Fig. 4). Fishing generally has a stronger effect on stocks in colder waters, causing a decline in FL SB to 0.35 at a lower value of F .

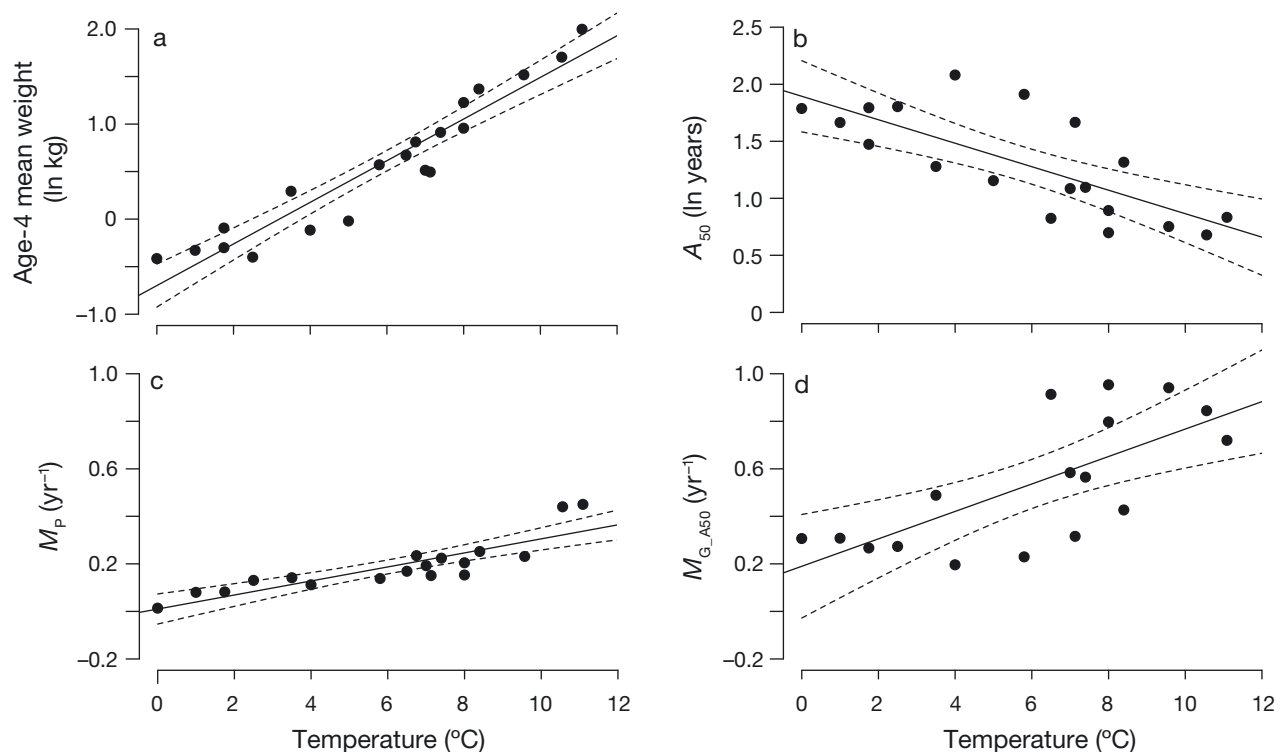


Fig. 3. Relationships between mean life-history traits and temperature for the 20 Atlantic cod *Gadus morhua* populations. The panels represent temperature effects on (a) natural log of mean weight at age 4, (b) natural log of age-at-50% maturity (A_{50}), (c) age-invariant natural mortality rates based on Eq. (11) of Pauly (1980; M_p), and (d) A_{50} -specific natural mortality rates based on Eq. (2) of Gislason et al. (2010; $M_{G_{A50}}$). Solid lines: linear regression fits; dashed lines: bootstrap 95% confidence intervals of the regression-predicted values

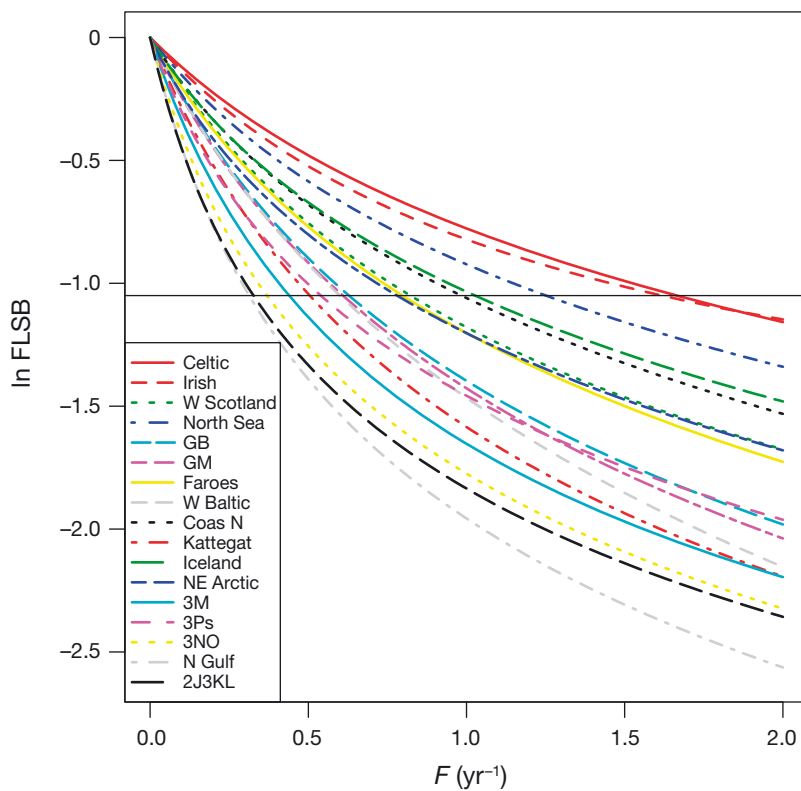


Fig. 4. Dependence of the natural log of the fraction of unfished lifetime spawning biomass, $\ln(\text{FLSB})$, on fishing mortality (F) for 17 Atlantic cod *Gadus morhua* populations (see Table 1 for population abbreviations). Black straight line indicates $\text{FLSB} = 0.35$. The data are based on simulations with equal selectivity and maturity curves and predicted natural mortality rates from the regression of temperature effect on M_{G_A50} (see Fig. 5c)

The values of F_{35} for each population were linearly correlated with temperature when calculated from the Pauly-based values of M ($R^2 = 0.46$, $p = 0.002$, Fig. 5a) but not when calculated from the Gislason-based values of M (Fig. 5b). Additionally, the choice of natural mortality functions had a strong effect on the overall magnitude of F_{35} . For a given population, Pauly-based values of M tended to produce lower values of F_{35} than Gislason-based values of M (Fig. 5a,b). We suspected that the lack of a clear relationship between Gislason-based M and temperature was an artifact of the relatively high variability in the relationship between Gislason-based M and temperature (Fig. 3d); in other words, the residual variability from the latter relationship could have been obscuring a potential relationship between FLSB and temperature. To avoid this extraneous variability, we simply extracted the temperature dependence by replacing the Gislason-based M for each population with a value of M obtained from the regression of Gislason-based values of M on temperature ($M\text{-at-}A_{50} = 0.2 + 0.058 \times$

temperature). Using these revised values of M to calculate FLSB resulted in a significant linear relationship between F_{35} and temperature ($R^2 = 0.61$, $p < 0.001$; Fig. 5c).

DISCUSSION

Our results demonstrate strong correlations between temperatures and life-history traits as others have shown (e.g. Brander 1995, Drinkwater 2002, Rätz & Lloret 2003). Consistent with the predictions of metabolic theory (Brown et al. 2004), higher temperatures were associated with faster growth, earlier maturation, and higher natural mortality. Such temperature-dependent life-history patterns led to a linear relationship between temperature and population response to fishing (F_{35}), all else being equal (i.e. if entry into the fishery coincided with maturity). Together, these results indicated prevalent temperature effects on fish population life history and fishery sustainability: populations in locations with warmer temperatures are less sensitive to fishing intensity, i.e. they can tolerate higher fishing mortality rates.

Temperatures influence cod life-history variation

It was evident that temperature variability strongly influenced cod growth rates, maturation schedules, and natural mortality. For natural mortality rates, we found significant dependence on temperature using 2 alternative formulas for estimating M (Pauly 1980 and Gislason et al. 2010). However, the residual variability was greater in the Gislason-based M versus temperature relationship (Fig. 3d). While temperature was not a parameter in the Gislason-based M function, previous research suggests that temperature exerts a linear effect on a population's von Bertalanffy growth parameters L_∞ or K (Taylor 1958, Brunel & Dickey-Collas 2010, Gislason et al. 2010, Cheung et al. 2013, but see Brander et al. 2013), which were included in the function. Potentially unaccounted-for temperature-dependent variability in these parameters led to the observed high residual

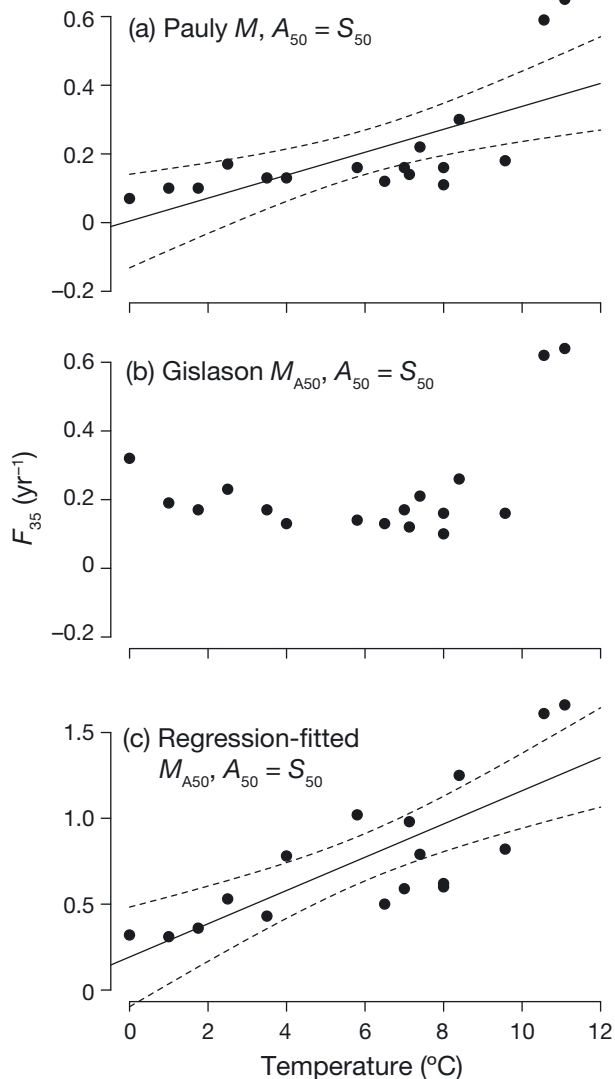


Fig. 5. Effects of temperature on the modeled fishing mortality rate F_{35} of Atlantic cod *Gadus morhua*, i.e. the point where lifetime spawning biomass (LSB) is 0.35 of the unfished value. F_{35} is calculated assuming that fisheries selectivity coincides with population-specific maturity ogives ($S_{50} = A_{50}$). The 3 panels represent 3 different parameterizations of natural mortality: (a) Pauly's (1980) temperature-dependent function; (b) Gislason et al.'s (2010) size-dependent function; (c) predicted natural mortality rates from the regression of temperature effect on $M_{G,A50}$ (see Fig. 3d). (Solid lines) Linear regression fits and (dashed lines) bootstrap 95% confidence intervals of the regression predicted values are shown

variability in the Gislason-based M vs. temperature relationship. Reduction of this variability by using the implied linear relationship to temperature was necessary to obtain a clear relationship between F_{35} and temperature.

Several cod populations in this study showed temporal changes in life-history traits (e.g. maturation

schedules have shifted over time for cod in North Sea, Iceland, and several Northwest Atlantic populations; Barot et al. 2004, Olsen et al. 2005, Pardoe et al. 2009, Wright et al. 2011, Neuheimer & Grønkjær 2012). However, because comparable temporal life history data (e.g. maturation ogives) for most populations are unavailable, we could not evaluate whether temporal changes in life-history traits would change our results.

Temperatures influence sustainable exploitation

In our results, high values of F_{35} were associated with relatively high temperatures, suggesting that in the warmer region these populations' life-history characteristics allow relatively high harvesting pressure. At a given latitude, the bottom-water temperatures are much lower in the Northwest than the Northeast Atlantic Ocean (Fig. 1). This difference in temperature patterns suggests differential fishery sustainability across the Atlantic Ocean. This phenomenon may extend beyond cod, so it may be useful to extend our current analysis to study other widely distributed fisheries species in the Atlantic Ocean (e.g. Durant et al. 2013). Given small variability in the exponent of the weight-at-length relationship, our estimation of population F_{35} should not be sensitive to the assumption of a constant exponent. Moreover, the inter-population responses to fishing do not depend critically on the choice of 35% (i.e. F_{35}); i.e. the declines in FLSB with increasing F occur in a more-or-less parallel fashion (Fig. 4). Thus a horizontal line drawn at any other critical value would approximate the same pattern of values of the critical value of F .

Our findings are consistent with previous results regarding the role of temperature in the spatial distribution of various measures of productivity of Atlantic cod (Dutil & Brander 2003). Together, these results demonstrate the pronounced importance of temperature on cod life histories and population dynamics, and suggest that environmental data should be included in modeling to predict spatial and temporal changes in cod life histories and population dynamics (e.g. Myers et al. 2001, Drinkwater 2005, Mantzouni & MacKenzie 2010).

Having demonstrated the relationships between temperature, life-history traits, and F_{35} for Atlantic cod populations, we suggest that the environmental dependence of life-history traits serves as a critical link to understanding climate effects on fish population dynamics. Such aspects of climate effects on

population dynamics of exploited species have been overlooked (e.g. most studies to date have focused on climate effects on lower trophic levels and fish recruitment variability; Brander 2010, Planque et al. 2010, but see recent contributions by Durant et al. 2013, Ottersen et al. 2013). An in-depth understanding of how temperatures affect life-history variation should offer insight into potential population responses to fishing. In cod, the long history of commercial fisheries exploitation depleted many populations in the Northwest Atlantic while most populations in the Northeast Atlantic persisted. This history may reflect the differential temperature effects on growth rates, maturation schedules, M , and productivity between populations on either side of the North Atlantic.

As our results depended on estimates of natural mortality rate from life-history variables (Pauly 1980 and Gislason et al. 2010), they are also related to ongoing research using metabolic scaling rules and life-history invariants (e.g. Andersen & Beyer 2013). Our population models also suggest F_{35} corresponds to L_{∞} , K , and natural mortality among the Atlantic cod populations. Our analyses differ, however, in that we do not specifically include the value of the slope at the origin of the stock-recruitment relationship in our analysis (Fig. 2), but rather we pose our question of sustainability in terms of collapse at a common fraction of unfished lifetime reproduction, i.e. 35%. These and other explorations may lead to the ability to estimate fishery reference points from life-history data in situations where detailed assessment data are unavailable.

While we suggest that the effects of temperature on life-history traits influence fishery sustainability, we note that this is an effect on equilibrium population levels, not on interannual variability, which has been attributed to temperature fluctuations in some cod populations (e.g. Drinkwater 2005, Durant et al. 2013, Ottersen et al. 2013). Temperature effects on recruitment may interact with population demographic structure and influence other aspects of population dynamics synergistically (Ottersen et al. 2006, Worden et al. 2010, Botsford et al. 2011, 2014, Rouyer et al. 2011, Durant et al. 2013). Such differential inter-population temperature effects on recruitment dynamics require further investigations; e.g. to understand the mechanisms through which spatial variability in mean temperature influences the sensitivity of recruitment to interannual variability and the consequence of that on sustainability of cod populations (Rouyer et al. 2014).

Fisheries management implications

The profound temperature effects on life histories and population resilience to fishing for Atlantic cod suggest that it may prove valuable to take into account spatial environmental differences in cod fisheries management, especially in the context of climate change. Previous studies suggest that changing climatic conditions alter cod population abundance and distribution (Nye et al. 2009, Perry et al. 2010). Together, these studies postulate that harvest regulations should account for climate-induced range shifts as well as changes in sustainability. While our present analyses and evaluation of fishing mortality rates are based on Atlantic cod, variability in environmental factors presumably influences other fisheries species or populations in a similar fashion. Thus, it may be useful to examine the environmental influences on life histories and fishing mortality rates for other fisheries species populations.

The variability in F_{35} suggests that different biological reference points are required for these cod populations. The temperature-dependent, spatial patterns of F_{35} suggest that different magnitudes of the biological reference points among populations should emerge, based on temperature and life-history characteristics. Current management of Atlantic cod uses local, population-specific life history to derive biological reference points such as F_{\max} (i.e. fishing mortality to maximize yield or spawning biomass per recruit) and F_{MSY} (e.g. ICES 2012e). Nonetheless, our analysis (1) explains some of the spatial variation in the success of management, and (2) suggests how the success of fishery management (and biological reference points) is likely to change with long-term trends in climate.

To further elucidate the synergies between climate and fisheries, we suggest extending our study to evaluate temperature effects on population life histories over time and synthesizing the effects of that variation on the population responses to fishing. Moreover, it is potentially useful to scale up observed environmentally induced changes in life-history variation to the population level in models that seek to project climate change effects on fishery production (e.g. Blanchard et al. 2012).

In conclusion, our analysis showed pronounced spatial variation in life histories among the cod populations. Temperature variability induces life-history variation and that in turn elicits differential responses to fishing. Thus, fisheries management could possibly be improved by taking into account spatial

variability in environmental conditions and population-specific life-history patterns. Fisheries management may be able to do this by managing a multi-population model with populations related to each other by the way temperature regimes influence population life-history traits. Such an approach would also enable a unified approach to the anticipation of differing effects of climate change among fish populations.

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