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Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout

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ABSTRACT: Younger ages and smaller sizes at maturation have been observed in commercial fish stocks over the last century. We establish that age and length at 50% proportion mature (i.e. the proportion of mature individuals in a population or the probability that an individual is mature) decreased from the 1970s to the 2000s in North Sea cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus*, but not in Norway pout *Trisopterus esmarkii*. The potential contributions of demography, phenotypic plasticity and evolution to these trends were assessed. First, maturation trends were extricated from demographic effects and growth-dependent plasticity by estimating probabilistic maturation reaction norms (PMRNs). PMRN midpoints have significantly shifted downwards at most ages for cod, haddock and whiting, but not for Norway pout. Second, increased temperature and food abundance, loosened trophic competition and relaxed social pressure may also trigger growth-independent plasticity in maturation. Principal component regression of PMRN midpoints on annual estimates of relevant environmental variables exhibiting a temporal trend suggest that, despite some evidence of environmental effects, PMRN trends were mostly independent of growth-independent plasticity in haddock, whiting and male cod, but not in female cod. According to these findings, evolution of maturation, potentially in response to fishing, is plausible in haddock, whiting and male cod, but unlikely for Norway pout, and does not explain trends in female cod maturation. In agreement with life-history theory, the maturation response was larger in fast-growing, late- and large-maturing species exhibiting moderate reproductive effort.

KEY WORDS: Probabilistic maturation reaction norm · Demography · Phenotypic plasticity · Fisheries-induced evolution · Life-history strategy · Maturity · Growth · Reproductive investment

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INTRODUCTION

Trends towards younger ages and smaller sizes at maturation have been observed in commercial fish stocks over the last century (reviewed by Jørgensen et al. 2007, Sharpe & Hendry 2009, Audzijonyte et al. 2013). Maturing young and small implies smaller adult size because growth rate decreases markedly

after maturation owing to the trade-off between growth and reproduction (Stearns 1992). Consequently, fecundity is lowered due to size-dependence, and offspring survival may decrease due to parental age and body-size effects on the size and quality of eggs and larvae (Trippel 1995, Berkeley et al. 2004), which is counterbalanced by increasing survival until reproduction. Due to the effect of individual size on

reproduction, maturing younger and at a smaller size may be detrimental to population biomass and reproductive capacity, which in turn may reduce fishing yields (Law & Grey 1989, Heino 1998) and hamper population biomass rebuilding after collapse (Hutchings 2005, Enberg et al. 2009). Life-history traits could therefore serve as indices of the state of a population for management (Rochet 2000a), or early warning signals before stock collapse (Olsen et al. 2004).

Maturity ogives describe the proportion of mature individuals in a population (or the probability that an individual is mature) as a function of age and/or size. The age and size at 50% proportion mature, traditionally called A_{50} and L_{50} , are common indicators of age and size at maturity (Trippel 1995), and trends in maturity in exploited fish populations are primarily assessed through A_{50} and L_{50} . The proportion mature at a given age and size depends on maturation tendency according to age and size, but also on survival and growth until the focal age and size. Therefore, 3 main mechanisms can induce temporal changes in A_{50} and L_{50} : demography, phenotypic plasticity and evolution (Fig. 1).

The demographic mechanism influences maturity ogives whenever fishing induces a change in the maturity structure of the population. With size-selective fishing, the larger an individual within any age-class, the more likely it is to be mature but also the more vulnerable it is to fishing, which tends to reduce the proportion mature at any age, and increase A_{50} . Fishing may also be selective according to maturity status, targeting preferentially adults on the spawning grounds, which should increase A_{50} , or juveniles on the feeding grounds, which should decrease A_{50} , during the reproductive season. In short, the demographic mechanism induces changes in A_{50} and L_{50} , the direction of which depends on the fishing pattern.

The second mechanism involves phenotypic plasticity of age and size at maturation. In particular, age

and size at maturation are strongly influenced by somatic growth rate, which largely depends on environmental conditions such as food resources or temperature (Weatherley 1990); variations in growth may also be partly genetic (Kinnison et al. 2011). In harvested fish populations, earlier maturation can result from the relaxation of trophic competition due to reduction in population size, which accelerates growth (Reznick 1993, Trippel 1995). Furthermore, some environmental factors may induce maturation plasticity directly, i.e. without influencing growth. Body condition correlates positively with maturation propensity (Marteinsdottir & Begg 2002, Grift et al. 2007, Mollet et al. 2007, Uusi-Heikkilä et al. 2011): ecological factors enhancing body condition, such as food abundance (Siems & Sikes 1998), can therefore trigger trends in maturity ogives. Likewise, elevated temperature accelerates maturation (Dhillon & Fox 2004, Morita et al. 2009). In some fish species, maturation is also influenced by the social and/or size structure of the population (Hutchings et al. 1999) that fishing may alter by reducing the population's abundance or truncating its age and size structure: the resulting relaxation of the social pressure exerted by old and/or large dominant individuals may enable younger and smaller ones to mature (Sohn 1977, Hobbs et al. 2004, Kraak 2007).

As a third mechanism, maturation propensity per se may evolve in response to fishing-induced selection. Uniformly elevated mortality favours earlier maturation, which balances the decrease in survival by an increase in lifelong fecundity (Stearns 1992, Charlesworth 1994, Ernande et al. 2004, Gårdmark & Dieckmann 2006), and the selective pressure against large- and late-maturing individuals is strengthened when fishing is size-selective. Theoretical predictions suggest that species with late maturation and large adult size should be more

prone to evolutionary changes in age and size at maturation in response to fishing, because of higher cumulated mortality before maturation (Heino & Godø 2002). Moreover, species with fast growth rate, weak reproductive investment and low natural mortality should be particularly sensitive to harvest-induced evolutionary changes (Ernande et al. 2004).

Understanding which processes underlie maturity changes in wild populations therefore requires disentangling the influence of demographic, environmental and genetic factors.

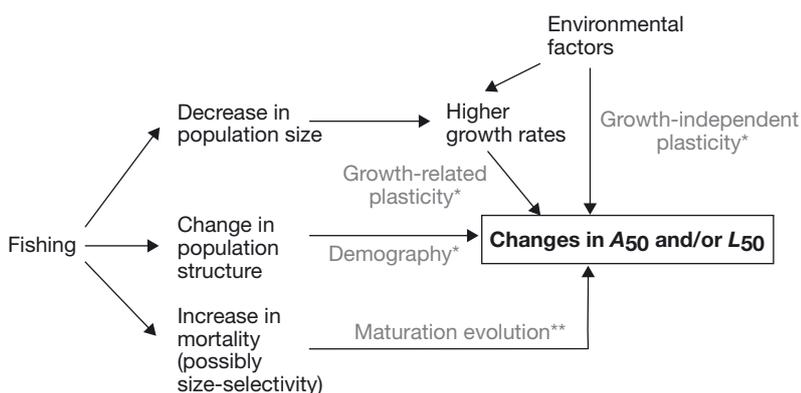


Fig. 1. Mechanisms potentially involved in maturation trends in exploited populations. *within-generation mechanism, **between-generation mechanism

Phenotypic plasticity of age and size at maturation in response to somatic growth variation can be described using the concept of the maturation reaction norm, defined as the combination of age and size at maturation that is expressed by a given genotype for different growth rates (Stearns & Crandall 1984, Stearns & Koella 1986). The probabilistic maturation reaction norm (PMRN) extends this deterministic concept to a probabilistic framework (Heino et al. 2002a) and describes the probability that an individual becomes mature according to age and size. This probability is conditional on the individual being immature and having reached the point defined by the focal age and size, which requires surviving and following a growth trajectory until this point. Consequently, by definition, PMRNs estimate maturation probability independent of the influence of survival and growth, whatever the source of variation in the latter (natural or anthropogenic, and genetic or plastic, respectively; Dieckmann & Heino 2007). Using PMRNs, changes in maturation propensity independent of demography and growth-dependent plasticity have been detected in many fish stocks (reviewed by Dieckmann & Heino 2007). However, the method cannot distinguish evolutionary changes from growth-independent plasticity due to environmental factors influencing maturation other than via growth; unless these factors are included as additional explanatory variables, they can drive plastic variations in PMRNs (Kraak 2007, Marshall & McAdam 2007, Uusi-Heikkilä et al. 2011).

The North Sea has been extensively exploited for centuries, with cod and haddock being major targets. Gadid stocks have been shown to be prone to fisheries-induced changes in their life history (Jørgensen 1990, Olsen et al. 2004, Pardoe et al. 2009, Vainikka et al. 2009, Devine & Heino 2011, Wright et al. 2011a). North Sea gadids therefore provide an adequate study system for a comparative analysis of fisheries-induced changes in maturation. In this study, we analysed 20 to 30 yr time series of maturity data in 4 North Sea gadid species: cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus* and Norway pout *Trisopterus esmarkii*. Earlier studies found shifts towards lower A_{50} and L_{50} in North Sea cod and haddock stocks from 1983 to 1995 (Rochet 2000b) and in North Sea Norway pout from 1983 to 2006 (Lambert et al. 2009). PMRN shifts have also been observed in similar direction for inshore haddock along the Scottish coast between the mid-1970s and the mid-1990s (Wright et al. 2011a) and for 3 subpopulations of North Sea cod (Wright et al. 2011b).

We start by analysing temporal trends in North Sea gadids' maturity ogives and then aim to disentangle the mechanisms responsible for these. To this end, we estimated time series of PMRNs in order to remove demographic and growth-dependent plasticity influences and time series of juvenile length-at-age to assess the potential role of growth rates. We further examined the effects of environmental variables that could influence maturation through growth-independent phenotypic plasticity, namely (1) summer water temperature, (2) food abundance, using the recruitment indices of sandeel *Ammodytes marinus* and Norway pout that are important prey of cod, haddock and whiting (Hislop 1997) and (3) competition for trophic resources and social structure, represented by recruitment indices of the 4 gadid species. Finally, since the 4 stocks belong to the same family and the same area, but have different life histories, we assessed whether the observed shifts in North Sea gadid PMRNs are in agreement with theoretical predictions about the influence of life-history strategy on the magnitude of evolutionary changes in maturation propensity due to fishing.

MATERIALS AND METHODS

North Sea gadids

Gadids form a family of marine fish species that are distributed in temperate to cold waters and show mainly benthic-demersal behaviour. Several gadids are of commercial importance, including our 4 model species. North Sea cod is widely distributed throughout the North Sea and is structured in many subpopulations (Hutchinson et al. 2001, Wright et al. 2006, Nielsen et al. 2009, Wright et al. 2011b). North Sea haddock usually occurs north of the Dogger Bank (a sandbank located at 54.5°N), with major spawning areas in the northern North Sea and off the Scottish east coast, possibly corresponding to 2 different subpopulations (Wright et al. 2011a). Adult whiting are widespread in the North Sea, whereas juveniles concentrate off the Scottish coast, in the south-eastern bight of the North Sea, and along the coast of the Netherlands. Three genetically distinct whiting subpopulations have been identified (Charrier et al. 2007). The distribution area of North Sea Norway pout is given as the northern North Sea (>57°N), at depths between 50 and 200 m (Sparholt et al. 2002).

All 4 stocks have high fecundity, spawn in winter and/or spring and have pelagic eggs and larvae (Hislop 1984), but they exhibit different growth and mat-

uration strategies: in the 1970s, cod reached maturity between 3 and 5 yr old at the largest size, i.e. between 50 and 70 cm, haddock between 3 and 4 yr old at a size between 30 and 40 cm and whiting around 2 yr old between 20 and 25 cm. In the 1980s, Norway pout reached maturity between 1 and 2 yr old at a size between 10 and 15 cm. Cod, haddock and whiting are long-lived species whose maximum lifespan reaches roughly 20 yr, whereas Norway pout usually die before age 5.

Data

Biological data

Biological data were collected during the North Sea International Bottom Trawl Survey (NS-IBTS; ICES 2010), which covers the North Sea, Skagerrak and Kattegat in order to provide recruitment indices of herring, cod, whiting, haddock, Norway pout, mackerel, sprat and saithe. The NS-IBTS has been conducted by 8 countries during the first quarter of each year since 1965 (as of more recently, the third quarter is also covered, but those data were not used in this study). The survey area is divided in statistical rectangles of 1° longitude × 0.5° latitude in which 1 to 6 hauls are towed using a Grande Overture Verticale trawl at a recommended ground speed of 4 knots. All fished species are sorted and numbered for further processing (ICES 2012). Individuals' total length is measured to the nearest cm or half-cm (depending on species), and their sex and maturity stage are determined by direct observation of gonads. Fish otoliths are sampled for aging using standard reading of growth rings. Otolith sampling is stratified into 9 RoundFish Areas (RFAs), with RFA 1 to 7 covering the North Sea and RFA 8 and 9 covering the Skagerrak–Kattegat, and according to length within each RFA. Age is then determined for 8 to 16 individuals (depending on species) per length class (1 cm width for all species) in each RFA.

Resulting sex-maturity-age-length keys (SMALKs) were extracted from the online database of trawl surveys (DATRAS, www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx) maintained by the International Council for the Exploration of the Sea (ICES), over the period 1974 to 2012 for cod, haddock and whiting, and 1983 to 2012 for Norway pout. We used data from the first quarter only (when gonads are ripe because individuals are prepared to or start spawning) to avoid confusion between spent gonads (empty gonads that have shrunk after spawning)

and immature ones. Catch per unit effort by length class (in number per trawl-hour) was used to estimate abundance indices per year, RFA and length class for the 4 stocks, assuming a constant trawl width and using RFA surfaces for the elevation. These indices were used to weigh individual data from SMALKs, in order to investigate average maturity and length-at-age at the scale of the entire North Sea for each stock, while eliminating the potential bias resulting from the spatial and length stratification of sampling and accounting for potential variations in growth and maturity between RFAs.

Skagerrak and Kattegat were excluded because sampling started later than in other areas. While cod, haddock and whiting were observed in all areas during the period considered, Norway pout was absent from areas 5 and 6. Ages 1 to 6 were used for cod, haddock and whiting, and 1 to 3 for Norway pout. Resulting sample sizes were: 27 784 female cod, 28 656 male cod, 46 909 female haddock, 46 193 male haddock, 54 369 female whiting, 47 282 male whiting, 9026 female Norway pout and 6519 male Norway pout.

Environmental factors

Environmental factors potentially affecting maturation via growth-independent plasticity were collected from different sources. Sea surface temperatures were extracted from the online OCEAN database (ocean.ices.dk/data/surface/surface.htm) maintained by ICES. As annual temperature variations were strongly correlated between the central area (Marsden subsquare 216;3, 55–60° N, 0–5° E) and adjacent areas (mean correlation of 0.74 with Marsden subsquares 216;1, 181;3, 216;4, 252;1, 217;1, 216;1, maximum 0.92, minimum 0.55), we selected data from the central area and left out stations at which depth was less than 20 m. We averaged the data monthly from June to August and then annually to obtain mean summer sea surface temperature. We focused on summer, as this is when vitellogenesis takes place (Kjesbu & Witthames 2007) and thus the maturation process starts. Summer sea surface temperature was strongly correlated (correlation of 0.8) to summer sea bottom temperature. Variations in sea surface temperature were thus considered as indicative of variations in temperature for the whole water column during the summer period despite stratification. Missing data for a given month (August 1973, June 1982, June 1985 and August 1986) were replaced by average temperature in the same month over the 2 preceding and following years (mean number of data per month: 470.7). Indices of food abundance, repre-

sented by sandeel and Norway pout recruitment indices, and indices of intra-specific competition and social structure, represented for each stock by its own recruitment indices at age 0 or 1, were estimated by the ICES Working Group on North Sea Skaggeiak and Kattegat using virtual population analyses. Recruitment estimates were available over the period 1974 to 2011 for cod and haddock, 1983 to 2011 for sandeel and Norway pout and 1990 to 2011 for whiting (ICES 2012).

Age and length at maturity

All statistical analyses were conducted separately for each species and sex. Maturity ogives o were estimated using logistic regression with a logit link function. The logit of the probability o_i of individual i of being mature was modelled as a function of its cohort c as a factor and (1) its age a_i as a continuous variable

$$\text{logit}(o_i) = \alpha_{0,c_i} + \alpha_{1,c_i} a_i \quad (1)$$

(2) its length l_i as a continuous variable

$$\text{logit}(o_i) = \alpha_{0,c_i} + \alpha_{1,c_i} l_i \quad (2)$$

or (3) both, with an interaction

$$\text{logit}(o_i) = \alpha_{0,c_i} + \alpha_{1,c_i} a_i + \alpha_{2,c_i} l_i + \alpha_{3,c_i} a_i l_i \quad (3)$$

Models (1) and (2) were respectively used to compute the age A_{50} and length L_{50} at which the probability of being mature reaches 50%, while model (3) was used for PMRN estimation (see below). Regardless of short-term variation, these annual estimates were used to investigate global temporal trends in age and length at maturity over the whole time period by means of linear regression. Predicted A_{50} and L_{50} were regressed linearly against cohort c as a continuous variable, weighted by the inverse of the standard error of each estimate,

$$\begin{aligned} A_{50,c} &= \alpha_0 + \alpha_1 c + \varepsilon_c \\ L_{50,c} &= \alpha_0 + \alpha_1 c + \varepsilon_c \end{aligned} \quad (4)$$

where ε here and in the following models is a normally distributed error term, and its subscript stands for the data point resolution, here 1 per cohort c .

Length-at-age

To compute maturation reaction norms (see below), the length-at-age l_i of individual i was estimated as a linear function of its cohort c_i and age a_i as factors

$$l_i = \alpha_{0,a_i} + \alpha_{1,c_i} + \alpha_{2,a_i \times c_i} + \varepsilon_i \quad (5)$$

To analyse temporal trends in juvenile length-at-age, individual length l_i was linearly regressed against age a_i as a factor and cohort c_i as a continuous variable, for ages 1 to 3 for cod, haddock and whiting, and for ages 1 and 2 for Norway pout

$$l_i = \alpha_{0,a_i} + \alpha_{1,a_i} c_i + \varepsilon_i \quad (6)$$

PMRNs

Estimation method

Since for our model species first-time and repeat spawners cannot be distinguished, PMRNs were estimated by the demographic method (Barot et al. 2004). The probability of maturing is given by

$$m(c, a, l) = \frac{o(c, a, l) - o(c, a - 1, l - \Delta l)}{1 - o(c, a - 1, l - \Delta l)} \quad (7)$$

with o , c , a and l as in model (3), and Δl the age-specific annual growth increment computed as $\Delta l(c, a) = l(c, a) - l(c, a - 1)$ using model (5). The probability of maturing at age a and length l is thus obtained as the ratio between the fraction of individuals which matured between age $a - 1$ and a , accounting for growth in length Δl between the 2 ages, and the proportion of immature individuals at age $a - 1$, to achieve a probability conditional on being immature (Barot et al. 2004).

This method assumes that mature and immature individuals have the same growth and survival rates within an age class and cohort. Barot et al. (2004) showed that the method is robust to violations of these simplifying assumptions when sample size is larger than 100 individuals per age class and cohort and when age is treated as a factor. Because sample sizes were low, age was treated as a continuous variable, which allows more robust estimation of PMRNs with small sample sizes, but implies the assumption that maturing probability varies linearly with age. PMRNs could be estimated for each cohort for cod, haddock and whiting, whereas for Norway pout, 3-cohort pools were necessary to obtain sufficient sample sizes.

Temporal trends in maturation propensity

To analyse temporal trends in maturation propensity, we used PMRN midpoints, i.e. the length $L_{p50,a}$ at which the probability of maturing is 50% at age a , determined by linear interpolation (Barot et al. 2004). Since PMRNs are obtained by combining several statistical analyses, confidence intervals are estimated

by bootstrapping (Manly 1997, Barot et al. 2004). Individuals in the original data set were resampled 1000 times with replacement while respecting sample size and the stratification by cohort, RFA and length class. Confidence intervals were estimated as the 95 % percentiles of the bootstrapped midpoint distribution.

Temporal trends in PMRN midpoints were tested by linear regression of $L_{p50,a,c}$ against age a as a factor and cohort c as a continuous variable, taking into account ages 1 to 4 for cod, ages 1 to 3 for haddock and whiting and ages 1 and 2 for Norway pout, weighted by the inverse of the bootstrap standard deviation of each midpoint to lower the influence of imprecise estimates on the regression

$$L_{p50,a,c} = \alpha_{0,a} + \alpha_{1,a}c + \varepsilon_{a,c} \quad (8)$$

Effects of environmental factors on maturation propensity

Growth-independent plasticity of maturation propensity in response to environmental variables was analysed through the effects on PMRN midpoints of summer water temperature (as an indicator of environmental fluctuations), sandeel and Norway pout recruitment indices (as indicators of food abundance) and the recruitment indices of each species, at age 0 for haddock and age 1 for cod and whiting (as indicators of social structure or intra-specific competition depending on cohort ages, see below).

Although short-term fluctuations in environmental factors may induce short-term variations in maturation, we were interested in long-term trends in maturation. Therefore, only environmental factors exhibiting a significant temporal trend, as assessed by linear regression against year, were selected for analysis.

PMRN midpoints $L_{p50,a}$ at age a were regressed against annual estimates of the selected environmental factors $e_{j,c+a-\Delta}$ and cohort c as continuous variables,

$$L_{p50,a,c} = \alpha_0 + \alpha_1c + \sum_j \sum_{\Delta=1}^a \alpha_{j,a-\Delta} e_{j,c+a-\Delta} + \varepsilon_c \quad (9)$$

where j denotes the environmental factor considered and $c + a - \Delta$ the year of the estimate with a time lag Δ varying from 1 to a yr. We thus estimated the effect of each environmental factor in each year from the birth of the cohort (age 0) until age $a - 1$. Recruitment of the cohort itself ($\Delta = a$, age = 0) is meant to account for trophic competition experienced by this cohort at any age because it was strongly correlated with cohort abundance at other ages (1 to $a - 1$). Recruitment of other cohorts of the species when the focal cohort c is

older ($\Delta < a$, age > 0) are included to represent social structure. A more natural indicator of the latter would have been spawning stock biomass, but it was strongly correlated with recruitment, which was included in the model for $\Delta = a$, and we therefore used recruitment at $\Delta < a$ as an indirect indicator of social structure. For temperature and prey recruitment indices, the time lag Δ allows determining at which ages the maturation process is critically affected by climate fluctuations and food abundance.

Because of their temporal trends, the explanatory variables were strongly correlated. To overcome any potential bias in the estimated effects via linear regression due to collinear explanatory variables, coefficients of model (9) were estimated using principal component regression (PCR), a method that estimates regression coefficients on principal components. Principal component analysis uses orthogonal transformation to convert a set of correlated variables into a set of uncorrelated ones, called principal components. L_{p50} estimates were then regressed against the principal components of explanatory variables in model (9), and the resulting PCR coefficients were transformed back to the original coordinate axes to obtain unbiased regression coefficients, standard errors and p-values associated with each explanatory variable (Coxe 1986, Fekedulegn et al. 2002). The family-wise Type I error rate was constrained to a probability of $\alpha = 0.05$ for each species by adjusting p-values according to the Holm-Bonferroni method (Holm 1979). We used all principal components for the PCR. For each environmental variable with a significant effect on L_{p50} , we further calculated the amount of change ascribable to this effect as the product of the regression coefficient of the environmental variable according to time, the regression coefficient of L_{p50} according to the environmental variable in the PCR and the duration of the time period.

These analyses were applied to the age at which L_{p50} was best estimated and weighted by the inverse of each L_{p50} estimate bootstrap standard deviation for male and female cod, haddock and whiting. For Norway pout, this analysis was precluded by the limited amount of L_{p50} estimates.

Effect of life-history parameters on the magnitude of maturation change

To examine whether the observed changes in North Sea gadid PMRNs were in agreement with theoretical predictions about the influence of life-history strategy on the magnitude of the evolutionary response of

maturation to fishing, we estimated several additional life-history parameters. To estimate juvenile growth rate and reproductive investment, we considered a 2-stage growth model in which individual growth is linear with age before maturation and declines afterwards to converge to an asymptotic length due to the trade-off between growth and reproduction (Kozłowski & Wiegert 1986, 1987, Kozłowski 1992). The model is given by

$$\begin{cases} l(a) = l_0 + ga & \text{for } 1 \leq a \leq a_m \\ l(a) = l(a_m) + \frac{g}{u} \{1 - \exp[-u(a - a_m)]\} & \text{for } a > a_m \end{cases} \quad (10)$$

with l_0 : length at age 0, g : juvenile growth rate, a_m : age at maturation and u : reproductive effort. a_m was estimated as the mean maturation age from age-based maturity ogives: $o(a)$ being the proportion of mature individuals at age a in the population, we estimated the proportion of individuals becoming mature at each age as $o(a) - o(a - 1)$, the mean age at maturation was then estimated as a weighted mean of age using the proportion of maturing individuals at each age as weights. l_0 , g and u were estimated by nonlinear least square fitting of model (10) to individual data on length, age and maturity status. Model (10) was fitted for each species and each sex separately, using data of cohorts 1974 to 1979 pooled for cod, haddock and whiting, and cohorts 1983 to 1986 for Norway pout. We focused on the earlier cohorts because the aim was to assess the influence of the original life-history trait values on subsequent changes in maturation. Mean maturation size l_m was estimated as the product of a_m and g . We then contrasted relative changes δL_{p50} in PMRN midpoints across species together with g , u , a_m and l_m , using Spearman correlation. Relative changes δL_{p50} were computed as $\delta L_{p50} = (L_{p50}(c_f) - L_{p50}(c_i)) / L_{p50}(c_i)$, where c_i is the initial and c_f the final cohort. We used the total change in L_{p50} instead of only the cohort contribution

estimated in PCR analyses because (1) environmental contributions were weak (see 'Results'), and (2) we wanted to include Norway pout for which no PCR analyses could be performed. All analyses were performed using R (R Development Core Team 2013).

RESULTS

Temporal trends in age and length at maturity

Age A_{50} and length L_{50} at 50% maturity decreased significantly over time from cohorts 1974 to 2007 for

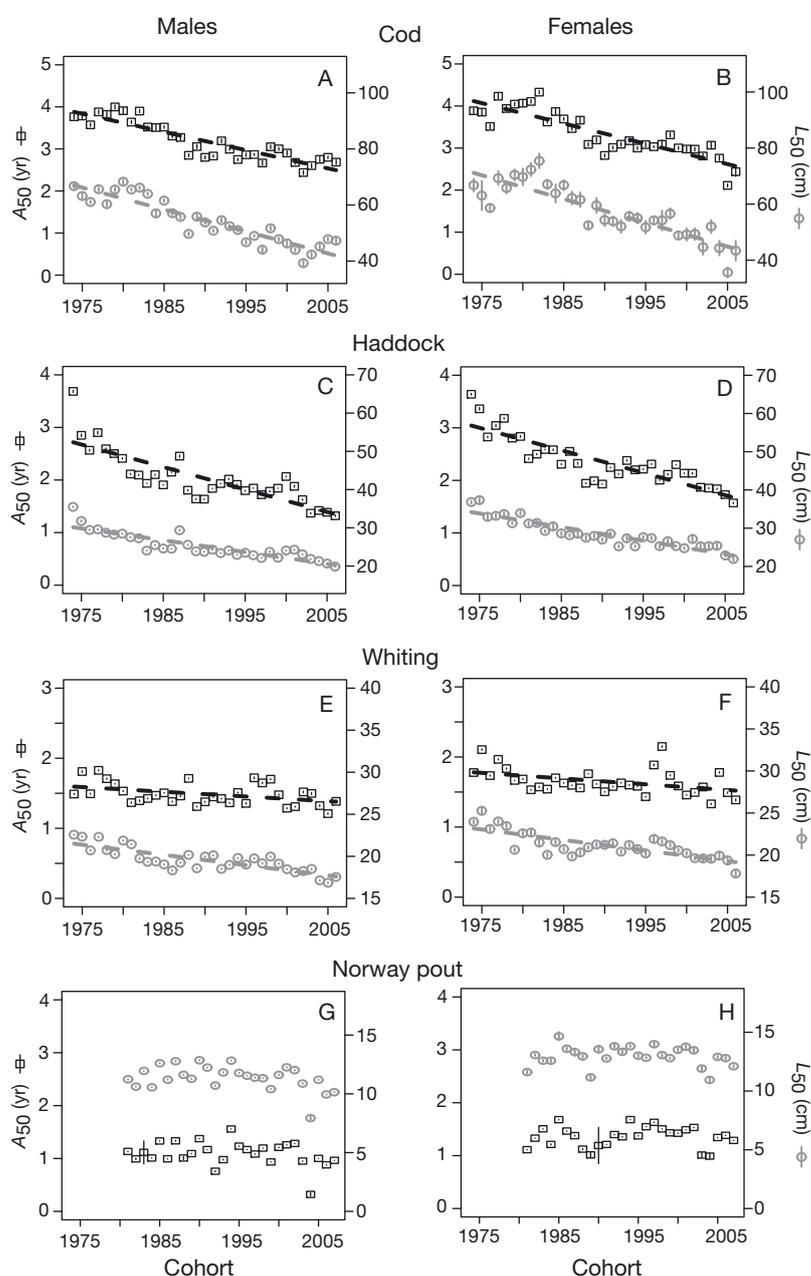


Fig. 2. Times series of age (A_{50} , black squares) and length (L_{50} , grey circles) at 50% maturity for (A, C, E, G) male and (B, D, F, H) female (A, B) cod, (C, D) haddock, (E, F) whiting, and (G, H) Norway pout. Vertical bars give the 95% confidence interval. Dashed lines give the regression line against cohort whenever significant at the 5% α -risk level

Table 1. Slopes of trends in age (A_{50}) and length (L_{50}) at 50% maturity, juvenile length (L_j) at ages 1 to 3, and probabilistic maturation reaction norm (PMRN) midpoints (L_{p50}) at ages 1 to 4. For each trait, the slope α_i estimated by the linear regression model (Eqs. 4, 6 and 8) against cohort and its standard error (in brackets) are given together with estimated trait changes over the time period (Δ). Within each species and each sex, p-values are adjusted to correct for multiple tests using the Holm-Bonferroni method and significant results ($p < 0.05$) are displayed in **bold**. Asterisks (*) denote results with p-values lower than 0.05 before the Holm-Bonferroni correction. NCE: ages that were not considered for estimation

Temporal trends coefficients (SE)	Cod 1974–2006 cohorts		Haddock 1974–2006 cohorts		Whiting 1974–2006 cohorts		Pout 1981–2007 cohorts	
	Male	Female	Male	Female	Male	Female	Male	Female
A_{50}	-4.3×10^{-2} (0.4×10^{-2})	4.8×10^{-2} (0.5×10^{-2})	-4.3×10^{-2} (0.5×10^{-2})	-4.3×10^{-2} (0.4×10^{-2})	-6.7×10^{-3} (3×10^{-3})	-8.2×10^{-3} (3×10^{-3})	-0.008 (0.006)	0.0005 (0.005)
Δ (yr)	-1.4	-1.5	-1.4	-1.4	-0.2	-0.3	-0.2	0.01
α_i (cm yr ⁻¹)	-0.78 (6.3×10^{-2})	-0.85 (0.09)	-0.31 (0.03)	-0.36 (0.03)	-0.12 (0.02)	-0.13 (0.02)	-0.05 (0.02)	-0.01 (0.02)
Δ (cm)	-25.1	-27.1	-9.9	-11.4	-3.9	-4.0	-1.3	-0.3
L_j age 1	-0.04 (9.0×10^{-3})	-0.02 (9.3×10^{-3})	6×10^{-3} (2.6×10^{-3})	0.02 (2.8×10^{-3})	-0.07 (0.003)	-0.05 (0.003)	-0.011 (0.003)	-0.012 (0.003)
Δ (cm)	-1.2	-0.7	0.2	0.7	-2.2	-1.8	-0.3	-0.3
α_i ,age2 (cm yr ⁻¹)	-0.21 (8.5×10^{-3})	-0.18 (9.0×10^{-3})	-0.037 (0.005)	-0.03 (0.004)	-0.15 (0.008)	-0.19 (0.008)	-0.051 (0.023)	-0.022 (0.023)
Δ (cm)	-6.9	-6.1	-1.2	-1.1	-5.0	-6.1	-1.2	-0.5
L_j age 3	-0.21 (0.016)	-0.2 (0.016)	-0.14 (0.014)	-0.2 (0.013)	-0.18 (0.02)	-0.23 (0.017)	NCE	NCE
Δ (cm)	-6.8	-6.7	-4.7	-6.7	-6.0	-7.5	NCE	NCE
L_{p50} age 1	-0.39 (0.18)	-0.38 (0.24)	-0.14 (0.05)	-0.22 (0.13)	-0.28 (0.04)	-0.15 (0.05)	-0.1 (0.15)	0.008 (0.05)
Δ (cm)	-12.6	-12.0	-4.5	-7.1	-8.9	-4.9	-0.8	0.07
L_{p50} age 2	-0.62 (0.16)	-0.69 (0.20)	-0.21 (0.05)	-0.45 (0.13)	-0.003 (0.05)	-0.14 (0.05)	-0.27 (0.3)	0.43 (0.28)
Δ (cm)	-19.8	-22.1	-6.9	-14.4	-0.1	-4.5	2.2	3.5
L_{p50} age 3	-0.88 (0.14)	-0.87 (0.21)	0.52 (0.10)	-0.70 (0.15)	0.22 (0.11)	0.14 (0.14)	0.85 (0.43)	1.2 (0.32)
Δ (cm)	-28.3	-27.8	-16.7	-22.2	7.1	4.5	6.8	9.6
L_{p50} age 4	-1.09 (0.16)	-1.14 (0.24)	NCE	NCE	NCE	NCE	NCE	NCE
Δ (cm)	-35.0	-36.5						

male and female cod, haddock and whiting (Table 1, Fig. 2A–F). No significant change was found for Norway pout over cohorts from 1983 to 2007 (Table 1, Fig. 2G,H). Species rank from the largest to the smallest magnitude of changes was the following: cod, haddock, whiting and Norway pout (Table 1). Short-term fluctuations in A_{50} and L_{50} were generally similar between sexes within species. For cod, A_{50} and L_{50} seemed steady (or even increasing) until 1983 and then steeply decreasing. For haddock, A_{50} steeply decreased between 1974 and 1990, followed by a partial rebound and subsequent steady period between 1991 and 2000, after which it decreased again until 2006, while L_{50} decreased more steadily over the study period. For whiting, the L_{50} temporal dynamic was roughly the same as for haddock A_{50} , except for the start of the rebound in 1986, while A_{50} decreased steadily with short-term fluctuations.

Temporal trends in juvenile length-at-age

Significant temporal trends towards smaller juvenile body length were found for male cod at ages 1 to 3, for female cod at ages 2 and 3, for male and female haddock and whiting at ages 1 to 3 and for male Norway pout at age 1 (Table 1, Fig. 3). Short-term fluctuations in length-at-age were roughly similar across ages and sexes within species. The strongest decline in cod and haddock juvenile length-at-age seemed to occur mainly after 1990. Regardless of species, the amplitude of the decline was lower at younger ages.

Temporal trends in PMRNs

PMRN isolines of 50% probability of maturing were estimated for each cohort independently and averaged over cohort decades (Fig. 4). These estimated PMRNs were close to linear

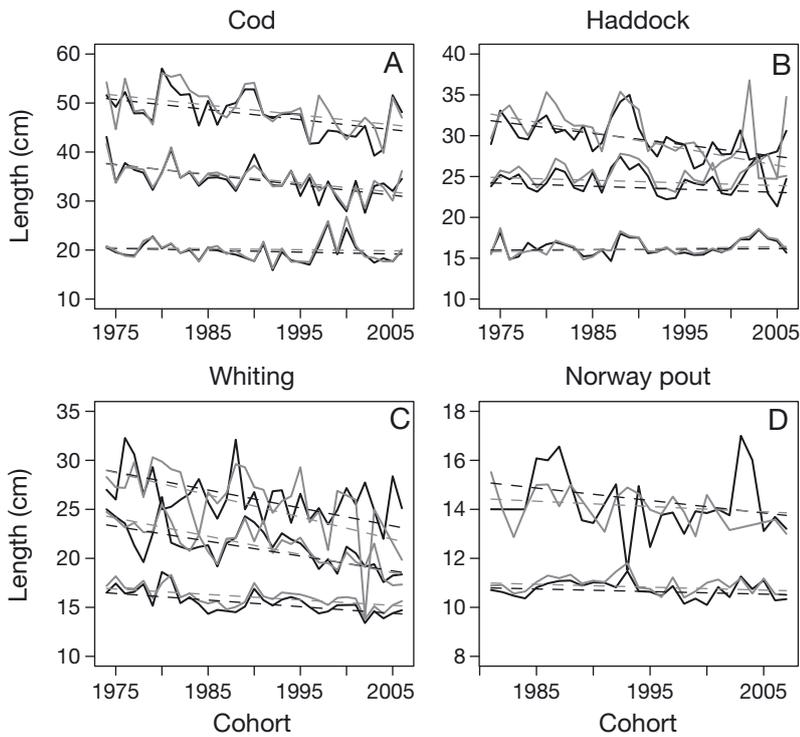


Fig. 3. Times series of mean juvenile length-at-age. Mean juvenile length estimated for male (black solid line) and female (grey solid line) (A) cod, (B) haddock, (C) whiting, and (D) Norway pout, from (bottom to top curve) age 1 to 3 for cod, haddock and whiting, and age 1 to 2 for Norway pout. Straight dashed lines, black for male, grey for female, give the regression lines of length-at-age against cohort

(partly as a consequence of using age as a continuous variable) and their slope varied from slightly positive to clearly negative so that the size at a certain probability of maturing was slowly increasing or decreasing with age, depending on species and/or time period. For male and female cod and haddock, the probability of maturing increased over time at each age and length, while PMRNs became more negatively sloped (Fig. 4A,B, C,D). This decrease in PMRN slopes was modelled through the interaction term between age and cohort in model (8), and was significant in all 4 cases (male cod: $F_{4,120} = 26.6$, $p < 0.0001$, female cod $F_{4,115} = 13.8$, $p < 0.0001$, male haddock $F_{3,83} = 17.7$, $p < 0.0001$, and female haddock $F_{3,84} = 29.9$, $p < 0.0001$). Meanwhile, cod and haddock average growth slowed down. Consequently, from the 1970s to the 2000s, the average age and size at which individual probability of maturing is 50% shifted from 3.9 yr and 67.8 cm to 2.7 yr and 44.6 cm for male cod, from 4.1 yr and 71.2 cm to

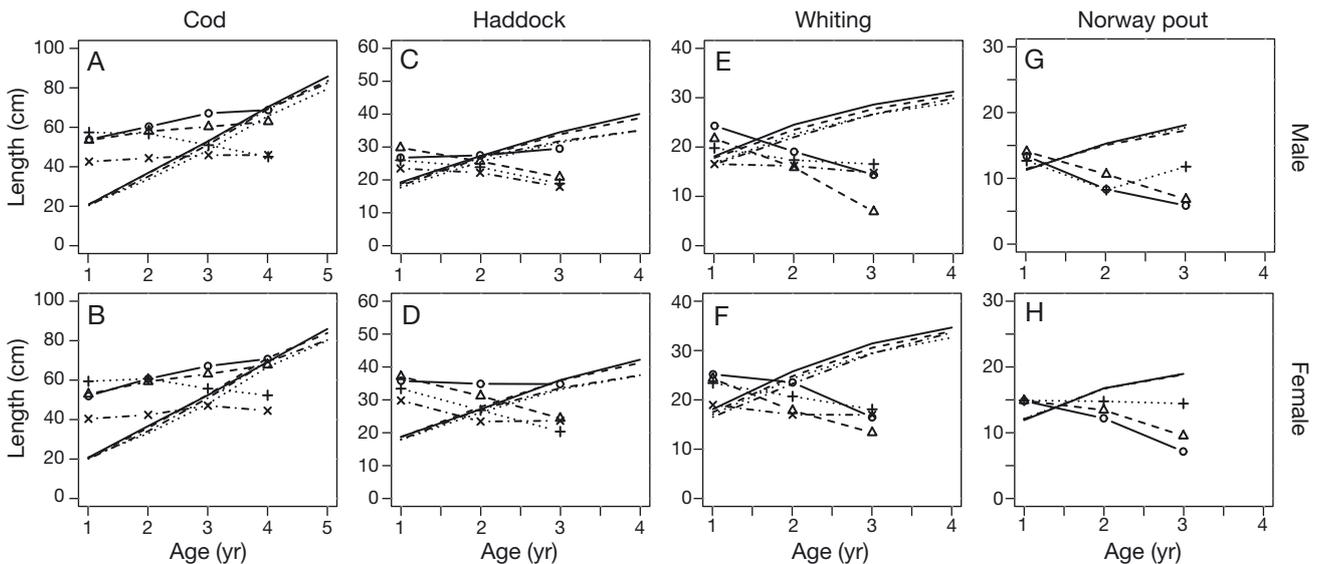


Fig. 4. Temporal trends in probabilistic maturation reaction norms (PMRNs). Probabilistic reaction norm isolines of 50% probability of maturing (= curve of PMRN midpoints L_{p50} at different ages) averaged over cohorts 1974 to 1980 (solid line, open circles), 1981 to 1990 (dashed line, open triangles), 1991 to 2000 (dotted line, + symbols) and 2001 to 2006 (dashed-dotted line, × symbols) for (A, C, E) male and (B, D, F) female (A,B) cod, (C, D) haddock, (E, F) whiting, and averaged over cohorts 1981 to 1989 (solid line, open circles), 1990 to 1998 (dashed line, open triangles), and 1999 to 2007 (dotted line, + symbols) for (G) male and (H) female Norway pout. L_{p50} averages are weighted by the inverse of their bootstrap standard deviations. Same line types without symbols: mean length-at-age of both immature and mature individuals for the corresponding cohorts

2.8 yr and 46.1 cm for female cod, from 2.1 yr and 27.2 cm to 1.3 yr and 22.7 cm for male haddock, and from 2.9 yr and 34.6 cm to 1.7 yr and 24.9 cm for female haddock. A weaker downward shift in whiting PMRN was observed, while growth decreased slightly as well (Fig. 4E,F). In contrast, female Norway pout, L_{p50} at age 2 (Fig. 4G,H) shifted upwards over the study period while male Norway pout L_{p50} at age 2 increased between the 1980s and 1990s, and decreased between the 1990s and the 2000s.

The shift in male and female cod and haddock PMRNs can also be seen through the significant downward trends in their midpoint L_{p50} at almost all ages (Table 1, Fig. 5A–D for the best age-wise estimate). Significant negative trends in L_{p50} were found at ages 1 and 2 for female and at age 1 for male whiting (Table 1, Fig. 5E,F). No trend was found for Norway pout PMRN (Table 1, Fig. 5G,H).

Environmental versus cohort effects on PMRNs

Not all environmental factors potentially affecting maturation propensity exhibited a temporal trend over the study period (Fig. 6). From 1974 to 2010, significant trends were found in summer water tem-

perature ($0.056 \pm 0.012^{\circ}\text{C yr}^{-1}$, $p < 0.001$), cod recruitment ($-3.8 \pm 0.6 \times 10^7$ recruits yr^{-1} , $p < 0.001$) and whiting recruitment ($-1.7 \pm 0.6 \times 10^8$ recruits yr^{-1} , $p = 0.012$). These were therefore selected for analysis of their effect on PMRNs. No significant trend was found in haddock, Norway pout or sandeel recruitment, which were left out from further analyses.

Male cod L_{p50} at age 3, male and female haddock L_{p50} at age 2, and male and female whiting L_{p50} at age 1 decreased significantly with cohort, while female cod L_{p50} at age 3 decreased significantly with temperature experienced at age 0 (Table 2). From cohort 1974 to 2006, the cohort effect explained a decrease of 20.8 cm in male cod L_{p50} at age 3, and of 8.7 cm and 14.3 cm, respectively, in male and female haddock L_{p50} at age 2. Despite being non-significant, the cohort effect accounted for a reduction of 17.8 cm in female cod L_{p50} at age 3 versus 5.9 cm for the significant temperature effect. From cohort 1990 to 2006, the cohort effect explained a decrease of 9.1 and 5.2 cm, respectively, in male and female whiting L_{p50} at age 1. These effects were stronger than the negative cohort effects previously found in male and female whiting L_{p50} at age 1 between cohorts 1974 and 2006 (Table 1).

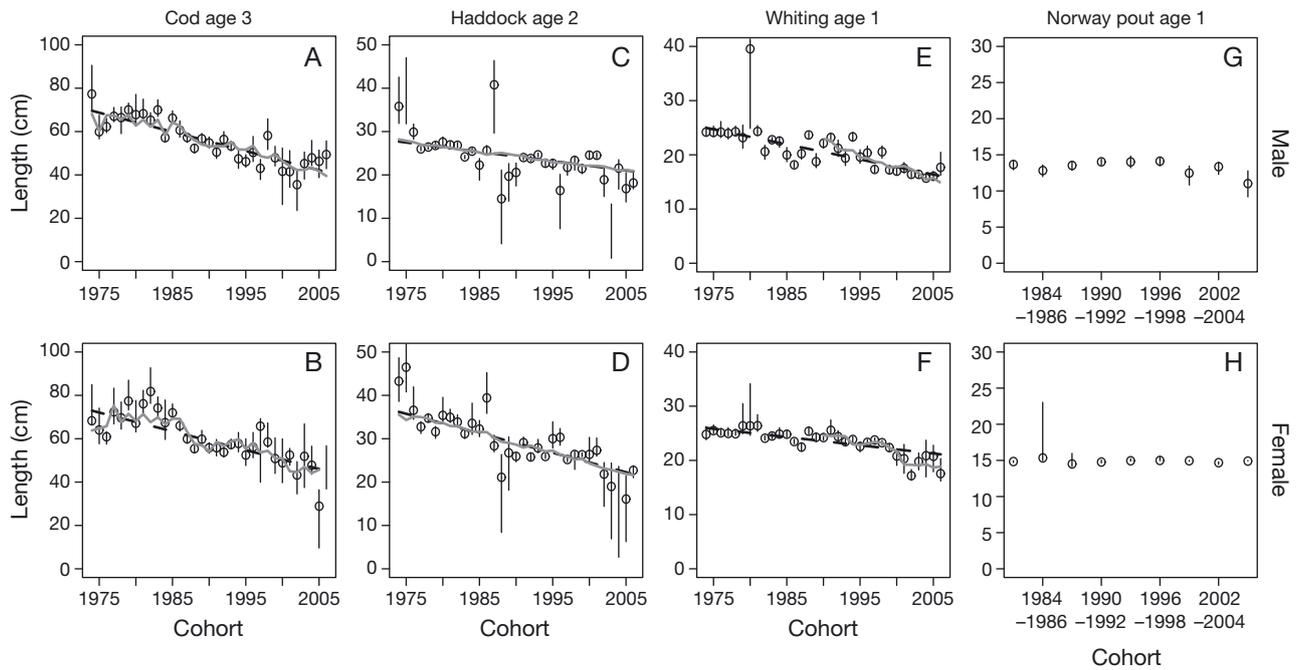


Fig. 5. Time series of PMRN midpoints (L_{p50}) at the ages they were best estimated for each species and sex: (A, C, E, G) male and (B, D, F, H) female (A, B) cod age 3, (C, D) haddock age 2, (E, F) whiting age 1, (G, H) Norway pout age 1. Vertical bars give the bootstrap 95% confidence interval. Dashed black lines give the regression line of L_{p50} estimates against cohort, weighted by the inverse of bootstrap standard deviations, whenever significant. Solid grey lines give the predicted L_{p50} from the principal component regression including cohort and environmental effects

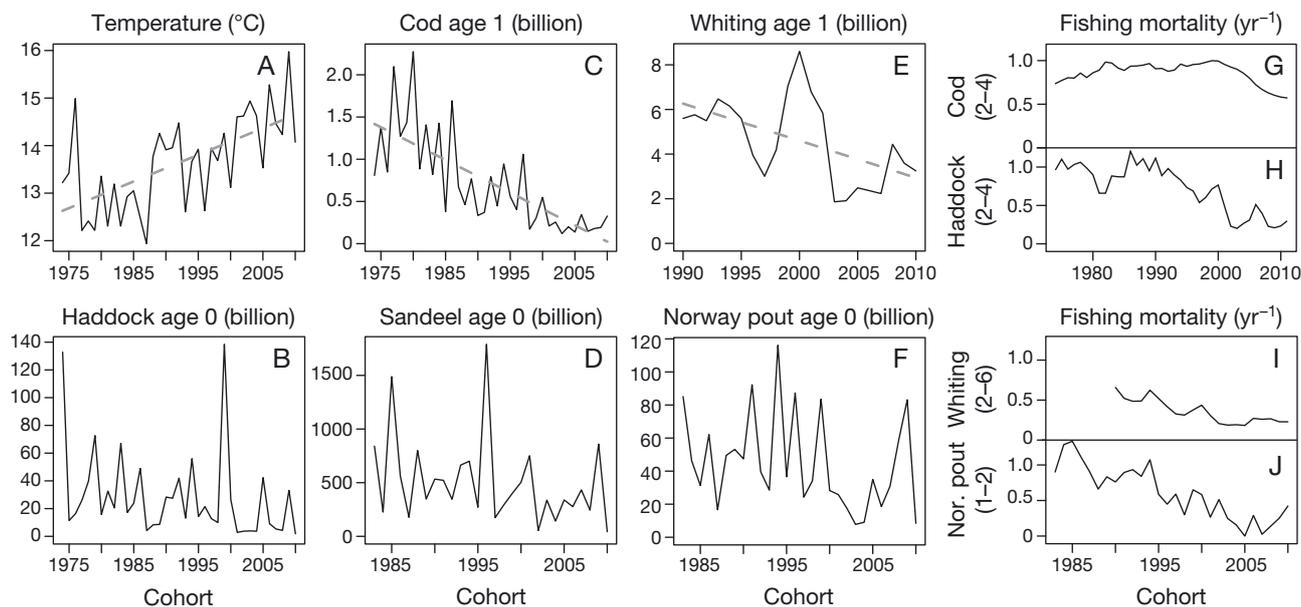


Fig. 6. Time series of environmental factors and fishing mortalities. (A) Summer sea surface temperature. Recruitment indices of (B) haddock at age 0, (C) cod at age 1, (D) sandeel at age 0, (E) whiting at age 1 and (F) Norway pout at age 0. Dashed grey lines are regressions lines whenever a significant time trend at the 5% α -risk is found. Average fishing mortality of (G) cod ages 2–4, (H) haddock ages 2–4, (I) whiting ages 2–6 and (J) Norway pout ages 1–2

Effect of life-history parameters on the magnitude of maturation change

Cod, haddock, whiting and Norway pout rank along a life-history strategy gradient from fast growth rate, low reproductive investment, and late maturation at large size to slow growth rate, strong reproductive investment and early maturation at small size, when the relative change in L_{p50} increases from strongly negative to no trend (Fig. 7).

DISCUSSION

Temporal trends in age A_{50} and length L_{50} at 50% maturity

From cohort 1974 to 2006, we detected temporal trends towards lower A_{50} and L_{50} in cod, haddock and whiting. Rochet (2000b) focused on the same stocks over the period 1983 to 1995 and found the same trends for cod and haddock, but no trend for whiting, and a significant increasing trend in age at maturity for Norway pout. These 2 discrepancies might arise from extending the time period considered. For whiting, the detected decrease was relatively slow over the period 1974 to 2001 and would have gone unnoticed over the period 1983 to 1995. For Norway pout, we also observed an increase in A_{50} from 1983 to 1995, but it decreased back to its

previous level afterwards, so that no trend was detectable over the whole period. In contrast, Lambert et al. (2009) found negative temporal trends in Norway pout age and length at maturity over cohorts 1983 to 2006. However, these trends were weak and driven by the last studied cohorts (2003 to 2005) that were characterized by low abundance and densities. The increase in the proportion of mature individuals at age 1 was no longer significant when removing these last cohorts. In accordance with this finding, our estimated age A_{50} and length L_{50} at 50% maturity for Norway pout both dropped around 2004, but they rebounded afterwards.

We accounted for the contribution of 3 non-mutually exclusive mechanisms to the temporal trends in maturity ogives: a demographic effect, a plastic response to temporal variations in individual growth rates and/or environmental factors, and an evolutionary change in maturation timing (Fig. 1). To this end, we identified trends in maturation propensity that are independent of demography and growth-dependent plasticity using PMRNs, and then investigated growth-independent plasticity in maturation by correlating PMRN midpoints with environmental variables. In the following, we will discuss these 2 points and interpret residual trends in maturation propensity related to a cohort effect as most likely evolutionary changes. Furthermore, we will retrospectively evaluate the impact of growth-dependent plasticity on A_{50} and L_{50} by qualitative reasoning.

Table 2. Regression coefficients and their standard errors (SE) for cod L_{p50} at age 3, haddock L_{p50} at age 2 and whiting L_{p50} at age 2, obtained from transforming back to the original set of axes the principal component regression coefficients and their SEs. For each coefficient, t -statistic value (t), uncorrected and corrected p -values associated with 25 degrees of freedom for cod, 29 for haddock, and 11 for whiting, and the amplitude (ΔL_{p50}) of the change in L_{p50} due to each effect over the study periods are given. Corrected p -values are adjusted to correct for multiple tests using the Holm-Bonferroni method and significant coefficients (corrected p -value < 0.05) are displayed in **bold**. Asterisks (*) denote results with p -values lower than 0.05 before the Holm-Bonferroni correction.

Effect	Sex	Coefficient (SE)	t	p	Corrected p	ΔL_{p50} (cm)
Cod Age 3 (cohort 1974–2006)						
Cohort (cm yr⁻¹)	M	-0.63 (0.23)	-2.76	0.009	0.037	-20.8
Temperature age 0 (cm °C ⁻¹)	M	-1.41 (1.02)	-1.38	0.098	0.451	-2.6
Recruitment age 0 (cm recruit ⁻¹)	M	2.24×10^{-9} (2.43×10^{-9})	0.92	0.812	1.000	-2.9
Temperature age 1 (cm °C ⁻¹)	M	-1.91 (1.1)	-1.74	0.055	0.279	-3.5
Recruitment age 1 (cm recruit ⁻¹)	M	-1.93×10^{-9} (2.44×10^{-9})	-0.79	0.222	0.870	2.5
Temperature age 2 (cm °C ⁻¹)	M	0.08 (1.20)	0.06	0.525	1.000	0.1
Recruitment age 2 (cm recruit ⁻¹)	M	1.19×10^{-9} (2.37×10^{-9})	0.50	0.687	1.000	-1.5
Cohort (cm yr ⁻¹)	F	-0.54 (0.26)*	-2.08	0.031*	0.119	-17.8*
Temperature age 0 (cm °C⁻¹)	F	-3.18 (1.18)	-2.69	0.010	0.043	-5.9
Recruitment age 0 (cm recruit ⁻¹)	F	-1.80×10^{-9} (2.80×10^{-9})	-0.64	0.266	0.525	2.3
Temperature age 1 (cm °C ⁻¹)	F	-2.50 (1.30)	-1.92	0.040	0.131	-4.6
Recruitment age 1 (cm recruits ⁻¹)	F	-2.77×10^{-9} (2.82×10^{-9})	-0.98	0.174	0.504	3.5
Temperature age 2 (cm °C ⁻¹)	F	-3.0 (1.38)	-2.16	0.270	0.119	-5.5
Recruitment age 2 (cm recruit ⁻¹)	F	1.18×10^{-9} (2.72×10^{-9})	0.43	0.663	0.666	-1.5
Haddock Age 2 (cohort 1974–2006)						
Cohort (cm yr⁻¹)	M	-0.25 (0.08)	-3.02	0.006	0.008	-8.6
Temperature age 0 (cm °C ⁻¹)	M	0.13 (0.63)	0.21	0.58	1.00	0.3
Temperature age 1 (cm °C ⁻¹)	M	0.31 (0.66)	0.48	0.68	1.00	0.6
Cohort (cm yr⁻¹)	F	-0.41 (0.09)	-4.48	<0.001	<0.001	-14.3
Temperature age 0 (cm °C ⁻¹)	F	-0.14 (0.72)	-0.20	0.424	0.497	-0.3
Temperature age 1 (cm °C ⁻¹)	F	-0.52 (0.75)	-0.69	0.253	0.497	-1.0
Whiting Age 1 (cohort 1990–2006)						
Cohort (cm yr⁻¹)	M	-0.54 (0.1)	-5.59	<0.001	<0.001	-9.1
Temperature age 0 (cm °C ⁻¹)	M	0.22 (0.56)	0.40	0.650	1.000	0.2
Recruitment age 0 (cm recruit ⁻¹)	M	-5.81×10^{-11} (2.54×10^{-10})	0.23	0.588	1.000	-0.2
Temperature age 1 (cm °C ⁻¹)	M	0.63 (0.57)	1.10	0.852	1.000	0.6
Recruitment age 1 (cm recruit ⁻¹)	M	-9.42×10^{-11} (2.50×10^{-10})	-0.38	0.357	1.000	0.3
Cohort (cm yr⁻¹)	F	-0.31 (0.08)	-3.99	0.001	0.005	-5.2
Temperature age 0 (cm °C ⁻¹)	F	-0.44 (0.42)	-1.04	0.160	0.640	-0.4
Recruitment age 0 (cm recruit ⁻¹)	F	-9.71×10^{-11} (1.83×10^{-10})	-0.53	0.304	0.640	0.3
Temperature age 1 (cm °C ⁻¹)	F	-0.43 (0.43)	-1.02	0.166	0.640	-0.4
Recruitment age 1 (cm recruit ⁻¹)	F	-4.01×10^{-10} (1.76×10^{-10})	2.28	0.978	0.978	-1.1

Processes at stake in temporal trends in maturity ogives

Temporal trends in PMRNs

Along with the changes in maturity ogives, PMRN midpoints significantly decreased over time in cod, haddock and whiting. A PMRN describes a conditional probability, i.e. the probability that an immature individual matures at a given age and size, conditional on having survived and grown until that age-size point. Under some assumptions about individual growth and survival against which the method is robust (see 'PMRNs: estimation method' above), PMRNs therefore allow depicting the maturation

process independently from the influence of survival and growth in contrast with maturity ogives. Since cod, female whiting and haddock PMRNs have varied, demography and growth-dependent plasticity cannot fully explain temporal changes in their maturity ogives: changes in maturation propensity due to growth-independent plasticity in response to environmental conditions and/or fisheries-induced evolution in maturation are likely to have also played a role. Negative temporal trends in PMRN midpoints have already been observed for inshore haddock along the Scottish coast (Wright et al. 2011a, but see Devine & Heino 2011) as well as for other cod stocks (Heino et al. 2002b, Olsen et al. 2004, 2005, Yoneda & Wright 2004, Pardoe et al. 2009, Vainikka et al. 2009).

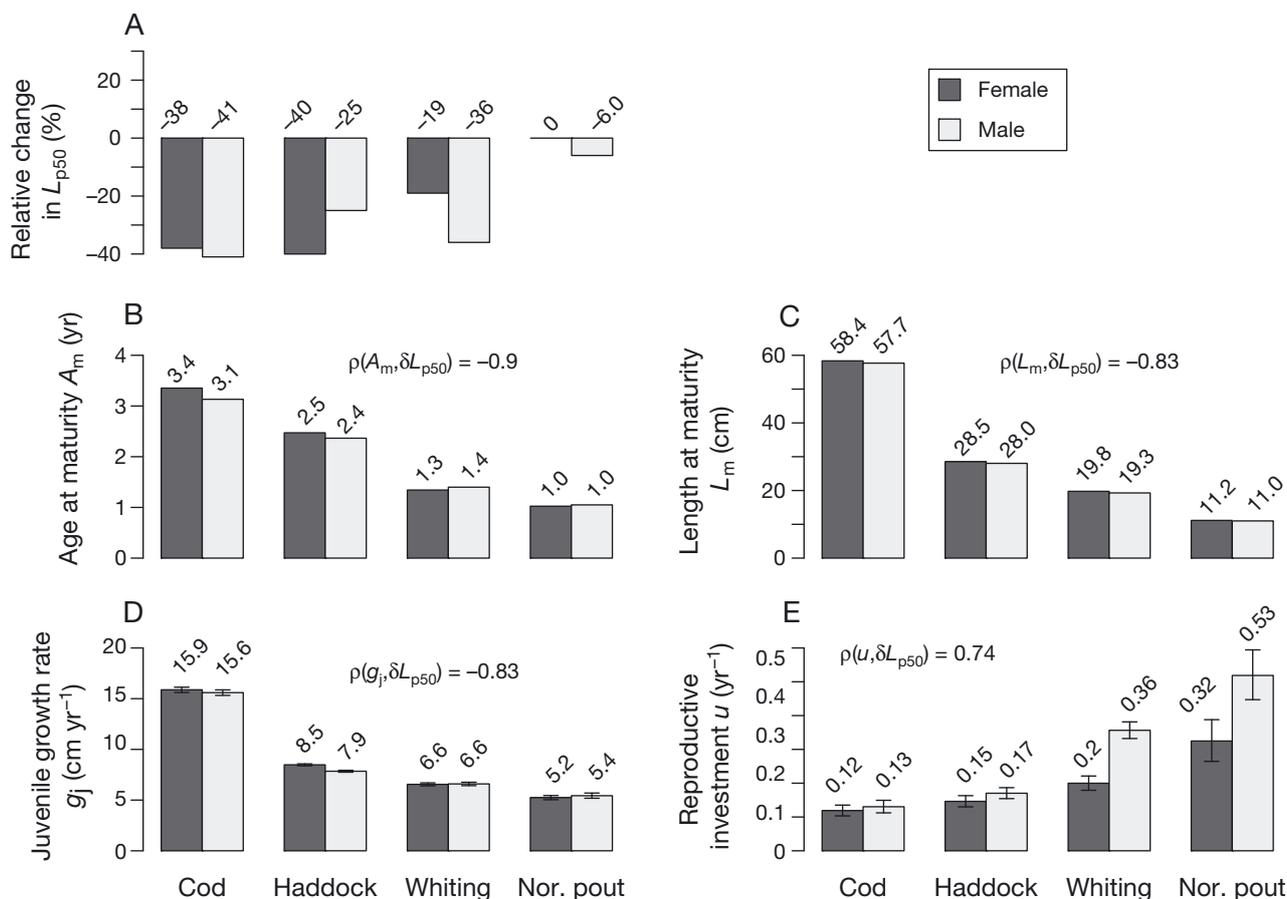


Fig. 7. Interspecies comparison of (A) relative change in L_{p50} (δL_{p50}) with life-history parameters estimated at the beginning of the study periods: mean (B) age A_m and (C) length L_m at maturity, (D) juvenile growth rate g_j and (E) reproductive investment u . Dark grey: females; light grey: males. ρ : Spearman correlation coefficient between (δL_{p50}) and the parameter. Error bars: 95% confidence intervals

More generally, most exploited stocks subject to PMRN analysis exhibited similar trends in maturation propensity (Jørgensen et al. 2007, Kuparinen & Merilä 2007, Hutchings & Fraser 2008). Therefore, the phenomenon is observed in phylogenetically different species located in different environments, suggesting that it is caused by a common and global driver. Increase in water temperature generated by global warming, decrease in population biomass due to fishing and fisheries-induced evolution are thus the most plausible explanatory factors.

Growth-independent plasticity versus fisheries-induced evolution

Rise in temperature, systematic increase in food abundance, release of trophic competition and relaxation of social pressure may all cause a direct plastic response of the maturation rate (Kraak 2007). Among the potential sources of growth-independent plasti-

city examined, only temperature had a significant effect on female cod maturation; temperature experienced at age 0 had a significant negative effect on female cod L_{p50} at age 3, in agreement with earlier work (Wright et al. 2011b, Neuheimer & Grønkvær 2012). Previous findings for North Sea plaice and sole have also shown that elevated temperatures may accelerate maturation (Grift et al. 2003, Mollet et al. 2007). Evidence of short-term temperature effects can also be found in the time series: around the years 1987 to 1989, temperatures exhibited a peak (Fig. 6A), which is concomitant with some drops in cod and haddock PMRN midpoints (Fig. 5A–D). Such a sudden shift in PMRN midpoints is more consistent with a plastic response of maturation to environmental fluctuations than with fisheries-induced evolution, which is more likely to operate gradually (Marshall & McAdam 2007, Heino & Dieckmann 2008).

Long-term negative temporal trends in male cod, haddock and whiting PMRNs were associated with a cohort effect in the PCRs despite the inclusion of the

most plausible environmental factors capable of generating growth-independent plasticity in maturation. Since these environmental factors cannot explain the totality of the temporal trends in PMRNs, this suggests fisheries-induced evolution, in agreement with Neuheimer & GrønkJær (2012) and Neuheimer & Taggart (2010) for haddock and Wright et al. (2011b) for male cod. For female cod, the cohort effect was no longer significant after the inclusion of the environmental variables in the analysis, although it was significant before correction for multiple testing and it explained the largest part of the temporal change in PMRNs. This could originate from overlooking North Sea cod population structure. Wright et al. (2011b) showed significant decreases of both male and female cod PMRNs in 3 subpopulations of the North Sea, with a much faster decline in the north-western and southern subpopulations than in the north-eastern one, which coincides with a near collapse of cod spawning stock biomass in the 2 first subpopulations. The trends in cod PMRNs estimated at the scale of the whole North Sea in this study are thus likely to be underestimated due to a bias towards the most abundant subpopulation, i.e. the north-eastern subpopulation, in which the decline in PMRNs has been slow. However, this does not explain the discrepancy in terms of cohort effect found between male and female cod. A possible answer lies in the potential effect of fishing mortality on sex ratio; in north-east arctic cod, fishing has been shown to increase the proportion of mature males (Jakobsen & Ajiad 1999). North Sea female cod in the less abundant subpopulations (north-west and south) could have been even scarcer than males due to fishing effects on sex ratio, thus resulting in PMRN trends at the scale of the whole North Sea more strongly biased for females than for males. For Norway pout, no analysis of the influence of environmental factors could be performed because of the lack of data, but the stability of the PMRNs can be qualitatively interpreted. Cod, haddock and whiting are important predators of Norway pout in the North Sea. The total biomass of these species decreased strongly over the last decades, which probably relaxed the predation mortality experienced by Norway pout (Sparholt et al. 2002). In addition, fishing mortality steeply declined over the study period for this species (Fig. 6J). Under lower mortality, individuals benefit from maturing later, so that age at maturation may have evolved towards older ages and counteracted fisheries-induced selection towards earlier maturation (Gårdmark & Dieckmann 2006).

In conclusion, for male cod, haddock and whiting, demography, growth-dependent plasticity and

growth-independent plasticity in response to environmental factors are not sufficient to explain the temporal trends detected in A_{50} and L_{50} . The residual trends in PMRNs associated with a cohort effect are compatible with the hypothesis of fishing-induced evolution for these species (Law 2007). For female cod, our results suggest that warmer temperature may have driven a plastic increase in maturation probability at age and size but should be treated with caution due to the potential influence of stock structure. Finally, for Norway pout, no change occurred either in maturity ogives or in PMRNs.

Further insights into the role of growth

The different processes affecting maturity ogives are not mutually exclusive, and all of them may have contributed to temporal trends in A_{50} and L_{50} . Notably, the intensity and the direction of the demographic effect and growth-dependent plasticity in maturation are not readily obtained from PMRN analyses, which only filter them out. It is, however, possible to outline qualitative expectations about the influence of growth on maturity ogives, based on the fact that the relationship between juvenile growth and observed individual ages and sizes at maturation in the population, and thus A_{50} and L_{50} , depends on the interplay between the geometry of the PMRNs and the length-at-age curves. For roughly linear PMRNs such as in our case, a negatively sloped PMRN implies that juvenile growth rate is positively correlated with observed length at maturation, whereas the correlation is negative for a positively sloped PMRN. The sign of the correlation between observed age at maturation and juvenile growth rate depends on how growth trajectories approach the PMRN: the correlation is positive when they approach the PMRN from above, negative from below (Fig. 8) (Heino & Dieckmann 2008, Marty et al. 2011).

Therefore, a compensatory response, that is earlier maturation and thus lower A_{50} related to faster growth favoured by the relaxation of trophic competition due to fishing, is possible if the PMRN is approached by juvenile growth trajectories from below, which was the case for all species. However, opposite to the compensatory response expectation, juvenile length-at-age decreased for the 3 stocks that exhibited changes in maturity ogives. Furthermore, as explained above, the direction of the related change in observed length at maturation depends then on the slope of the PMRN (Fig. 4). Slower juvenile growth should result in an increase in observed

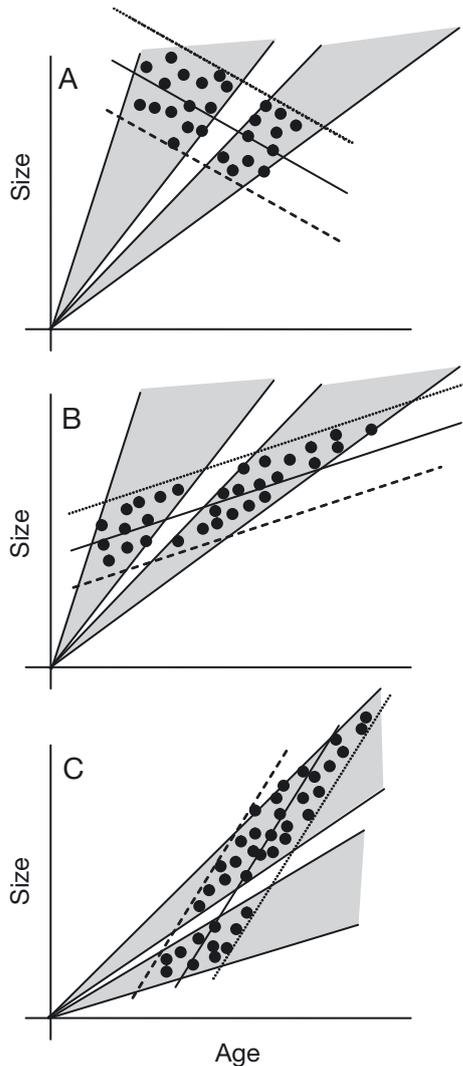


Fig. 8. Relationship between juvenile growth and observed ages and sizes at maturation (represented by black dots) resulting from the interplay between the geometry of the probabilistic maturation reaction norm (PMRN), illustrated by linear contour lines corresponding to 5% (dashed), 50% (continuous) and 95% (dotted) probability of maturing, and juvenile length-at-age curves (described by grey areas). (A) For a negatively sloped PMRN approached from below by length-at-age curves, faster growth rates (upper grey area) result in larger sizes at maturation and younger ages at maturation. (B) For a positively sloped PMRN approached from below by length-at-age curves, faster growth rates result in younger ages at maturation and smaller sizes at maturation. (C) When length-at-age curves approach the PMRN from above, which is possible for a positively sloped PMRN only, faster growth rates result in older ages at maturation and larger sizes at maturation

length at maturation when PMRNs are positively sloped, i.e. for cod and male haddock (Fig. 4, cohorts 1974 to 1980), and a decrease in observed length at maturation when PMRNs are negatively sloped, i.e. for whiting and female haddock (Fig. 4, cohorts 1974

to 1980). These expectations are inconsistent with the decrease in A_{50} and L_{50} in cod and male haddock, while they are consistent with the decreasing L_{50} in whiting and female haddock. Consequently, growth-dependent plasticity has probably counteracted the effect of other maturation determinants that drove A_{50} and L_{50} downwards in cod and male haddock. In contrast, growth-dependent plasticity probably contributed to trends towards lower L_{50} in whiting and female haddock. For the latter, this reasoning should be tempered, as the decline in L_{50} of female haddock occurred mainly during the period 1975 to 1990, whereas juvenile lengths at age mainly decreased after 1990. For Norway pout, the stability of A_{50} and L_{50} appears consistent with the weak change in length-at-age and the relative stability of PMRNs.

Strengths and limitations of the approach

Our findings should be interpreted with caution owing to the assumptions underlying our approach and the availability of data for potential relevant explanatory factors.

The PMRN approach

Firstly, age and size are proxies for the physiological determinants of maturation decision. Although the probabilistic nature of PMRNs can virtually encompass any within-cohort source of maturation variation, when it comes to between-generation variation and long-term PMRN trends, any physiological or environmental variables that underwent a temporal trend could be the causal agent (temperature, Morita & Fukuwaka 2007, Uusi-Heikkilä et al. 2011; social structure, Hutchings et al. 1999; body condition, Grift et al. 2007). The question then boils down to whether all potential drivers of maturation that steadily changed over time were considered. We considered all but one of these factors in our analyses, and thus it seems unlikely that we missed an environmental change as important as one able to drive the strong steady decrease in age and size at maturation detected in these stocks as well as in many other ones. However, we omitted body condition, which is known to affect maturation probability (Bernardo 1993, Uusi-Heikkilä et al. 2011). When adding it as a third dimension in PMRN estimation, empirical studies on North Sea sole and plaice showed that a temporal increase in condition had a significant negative effect on PMRN, although it could not explain the whole

temporal trend in maturation (Griff et al. 2007, Mollet et al. 2007). Unfortunately, we could not include such an index in our analyses because individual weights were not available. This may have resulted in underestimating the downward temporal trend in cod PMRNs, since body condition has significantly decreased in recent years (Yoneda & Wright 2004). It is worth noting, however, that our analyses included the influence of food (prey) abundance, which is one of the main drivers of body condition.

Secondly, we estimated juvenile growth trajectories using mean length-at-age for each cohort, implying that only 1 growth trajectory leads to a particular combination of age and length. Yet, different individual growth trajectories may lead to the same age and length combination. It has been shown that past individual growth history influences maturation probability independently from age and size, with most recent growth condition (just before the age at which probability of maturing is calculated) being the most determinant factor (Morita & Fukuwaka 2006). Individual growth trajectories can be back-calculated from scale or otolith reading (Engelhard et al. 2003, Baulier & Heino 2008, Mollet et al. 2010), but again this information was not available.

Finally, to investigate the contribution of growth-independent plasticity in PMRN shifts, the collinearity between explanatory variables was accounted for by using PCR. However, inferring firm causation from the significance of effects is not possible, since a correlation between 2 trended variables, here the PMRN midpoints and any explanatory factor, can always arise from a hidden confounding factor responsible for both trends. This issue holds for cohort effects as well as for environmental effects. In conclusion, PMRN analysis cannot provide direct evidence of evolutionary changes but can only assess whether, using the best available knowledge of factors influencing maturation and of environmental changes, it is compatible with the evolutionary hypothesis (Law 2007).

Temporal trends

Other statistical methods, such as generalized additive models, could have been appropriate to describe more precisely temporal variations in A_{50} , L_{50} , length-at-age, and L_{p50} . However, our aim was not to precisely describe how these estimates vary over time but to assess and statistically test the overall direction and amplitude of changes over the study period. Linear regression allows modelling variations

with a unique parameter that is easier to interpret than multiple parameters resulting from more sophisticated models. In addition, the trends we modelled were monotonous with small variations resulting in normally distributed residuals without any obvious pattern along the time axis, which justified using a linear model.

Population structure

We did not document within-stock variability in maturation trends potentially associated with population structure, and therefore possibly overlooked local specificities in terms of the responsible processes. Earlier studies have shown variations in trends in maturation probability among sub-populations of North Sea cod and haddock. Wright et al. (2011b) found a strong decline in L_{p50} in the southern and north-western subpopulations of North Sea cod, and a mild decrease in the north-eastern subpopulation, the difference being attributed to stronger selection for early maturing genotypes in the 2 former. Likewise, Wright et al. (2011a) showed that the magnitude of changes in maturation probability was greater in western than eastern North Sea haddock.

Extensions

Beyond the evidence for evolutionary changes, there is also a suggestion of fishing as the selective agent. Our analysis provides no direct evidence that fishing has generated the selective pressure responsible for the observed, potentially evolutionary, trends. In order to investigate this question more thoroughly, a complementary approach would be to estimate the strength of selection generated by fishing by comparing the age and size at maturation distribution before and after fishing, based on the selectivity of the fishery (Law 2000). Rowell (1993) estimated selection differentials for North Sea cod using a population model and showed that late-maturing fish were expected to be at a strong disadvantage. The body of evidence would be more complete with an empirical analysis of selection differential due to fishing for all 4 North Sea gadid stocks.

In addition, we estimated temporal changes in juvenile length-at-age to interpret temporal changes in maturation, but did not disentangle the potential mechanisms involved in growth long-term trends, which are the same as the ones considered for maturity: demography, plasticity and evolution.

Evolutionary sensitivity

Our comparison between relative changes in PMRN midpoints and life-history parameters across the 4 gadid stocks showed that species with late maturation at large size, fast growth rate and weak reproductive investment exhibited larger changes in maturation propensity. These results empirically corroborate the theoretical expectations about the influence of life history on fisheries-induced evolutionary changes in maturation (Heino & Godø 2002, Ernande et al. 2004). However, exploitation patterns can also influence the direction and strength of the maturation evolutionary response. Cod and haddock were exposed to fairly similar average fishing intensities at the beginning of the time series. Yet results from theoretical studies suggest that, at constant average intensity, exploitation patterns selecting for intermediate fish sizes protect against fishing-induced evolutionary impact. Such exploitation patterns can emerge from dome-shaped gear selectivity, such as gillnets, or spatio-temporal targeting of medium-size fish. In contrast, exploitation patterns selecting for large sizes might have stronger evolutionary impacts (Jørgensen et al. 2009). Cod, haddock and whiting are mainly targeted by mixed demersal fisheries using both trawls and gillnets (ICES 2009), and there is no major difference in selectivity pattern experienced by these 3 species. Norway pout is targeted by industrial trawlers for reduction purposes (fish meal and fish oil), but the state of this stock is not much affected by presently rather low fishing mortality levels. In other words, the temporal steadiness in Norway pout maturity could be a joint result of both weak fishing pressure from 1985 and weak intrinsic sensitivity to evolutionary changes. Therefore, even though our results corroborate theoretical expectations regarding sensitivity of maturation evolutionary response, a meta-analysis on more than 4 stocks would be necessary to significantly discriminate between sensitivity due to life-history strategy and exploitation regime.

Data archive. Data used for this study are held by the International Council for the Exploration of the Sea and available at https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx.

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