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Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference

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ABSTRACT: In exploited fish stocks, long-term trends towards earlier maturation have been interpreted as an evolutionary response to sustained, high fishing mortality. The evidence used to support this diagnosis consists of directional shifts in probabilistic maturation reaction norms (PMRNs) that are consistent with the expectation that high fishing mortality favours the genotype for early maturation. Most PMRNs describe the probability of becoming mature solely as a function of age and length. Because they do not fully account for several physiological aspects of maturation (including growth effects on maturation, critical time windows for maturation decisions and developmental thresholds for maturation), it is possible that the observed shifts in PMRNs that are currently being attributed to changes in genotype actually reflect environmental effects on maturation. In this study, a comparative approach was used to interrogate the historical database for Northeast Arctic cod *Gadus morhua* in relation to 2 contrasting but not mutually exclusive hypotheses: (1) that there is a significant effect of food availability on the probability of being mature, using condition as a proxy for food availability; and (2) that there has been a long-term shift in the PMRN for maturation in a direction that is consistent with a diagnosis of fisheries-induced evolution. The results show that the maturation trends in Northeast Arctic cod could be variously interpreted as showing a strong environmental effect, no genetic effect, or a strong genetic effect. If the scope of the analysis had been restricted to testing a single hypothesis related to either an environmental effect or a genetic effect, then the study could very easily have made a Type I error of inference. A more integrated view of maturation, incorporating key aspects of the physiological processes that culminate in maturation, is therefore required to avoid incorrect inferences about the underlying causes of earlier maturation.

KEY WORDS: Cod · *Gadus morhua* · Maturation · Probabilistic maturation reaction norms · Condition · Plasticity · Simulation · Fisheries-induced evolution

INTRODUCTION

In human populations, the age at puberty in females has declined steadily in several different countries (Parent et al. 2003). An association between increased adiposity and early maturation has been consistently shown (Kaplowitz et al. 2001). Other environmental factors that could have contributed to earlier maturation include increased exposure to pollutants (Denham et al. 2005), improved prenatal nutrition (Adair 2001) and higher levels of stress (Bellis et al. 2006). Because these factors are not mutually exclusive, it is proving difficult to unambiguously identify the causes (Herman-Giddens et al. 2004, Anderson & Must 2005). Identifying the factors that contribute to earlier maturation in exploited fish stocks is proving equally challenging. As is the case for human populations, environmental factors are important in determining when individual fish mature. For example, large reductions in stock size can increase per capita food availability, thereby enhancing individual growth and condition and leading to earlier maturation (Reznick 1993, Bigler et al. 1996, O'Brien 1999, Engelhard & Heino 2004). An additional complication for exploited fish stocks is that there is a plausible genetic explanation for trends towards earlier maturation. Because fishing mortality

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is size-selective, the individuals who mature and reproduce prior to capture will make a disproportionately large contribution to the gene frequencies of subsequent generations (Law 2000). This phenomenon is considered to be an example of fisheries-induced evolution and it is of concern to managers because of the potential for substantial reductions in yield that could be difficult to reverse.

In recent years, fisheries-induced evolution has been reported in maturation rates of several commercial fish stocks (Grift et al. 2003, Barot et al. 2004a, 2005, Olsen et al. 2004, 2005). These diagnoses of fisheries-induced evolution have been made on the basis of directional shifts in probabilistic maturation reaction norms (PMRNs) that are consistent with a selective mortality favouring a genotype for earlier maturation. For a cohort (or group of cohorts), the PMRN describes the maturation probability at each age and length combination. If there is no change over time in cohort-specific PMRNs, then it is generally inferred that there has been no evolution; if the PMRN midpoints decline in time then fisheries-induced evolution is diagnosed. Obviously, this does not constitute prima facie evidence of a change in the gene frequencies for maturation rates. Rather, a diagnosis of evolution is made on the basis of changes in phenotype that are suggestive of genetic adaptation in maturation schedules. Many studies of fisheries-induced evolution acknowledge the inherently circumstantial nature of the evidence provided by directional shifts in the PMRN with the caveat that the evidence is consistent with but not unequivocal proof of evolution. It is also argued that, given the deleterious consequences that can potentially result from irreversible genetic change, strict application of the precautionary approach should draw the worst-case conclusion, i.e. that fisheries-induced evolution has occurred.

In any analysis, failing to consider the full range of plausible explanations for trends in maturation increases the likelihood that conclusions are confounded by factors that were not included. For example, studies that are primarily interested in genetic effects on maturation typically assume that environmental effects on maturation are accounted for by the PMRN and that any resulting directional shifts in the PMRN across cohorts reflect an evolutionary response. However, it is increasingly clear that many of the current generation of PMRN do not fully account for growth (Morita & Fukuwaka 2006) or condition effects, and have thus misrepresented environmental effects on maturation. It is possible that studies that have concluded that directional shifts in the PMRN are consistent with fisheries-induced evolution have made a Type I error of inference by rejecting the null hypothesis 'that there is no genetic effect' when it is correct. Similarly, studies that investigated time trends in maturation exclusively from the perspective of density- or environmentally-driven changes in food availability failed to consider the degree to which directional genetic selection could also be contributing to the observed long-term trends in maturation. If the environmental factor covaried with the intensity of genetic selection (e.g. high fishing mortality resulted in both improved feeding conditions and selection for early maturation), then the confounding of these 2 factors would increase the risk of a Type I error of inference.

Another approach would be to entertain several mutually exclusive explanations simultaneously, in comparable detail and using the same dataset. Such an approach is often used in geology where it is common for a single study to test 2 or more highly contrasting hypotheses (termed 'end-member hypotheses' in the geological literature) using a single, comprehensive suite of empirical observations (e.g. Lizarralde et al. 2004). All of the observations are evaluated as being either consistent or inconsistent with the highly contrasting hypotheses with the expectation that the observations would, on balance, provide stronger support for the more correct hypothesis. The success of the approach depends on having well-resolved databases that can be used to interrogate different facets of the complex phenomenon under scrutiny. Examples of this comparative approach to hypothesis testing are rarer in fisheries science but include McQuinn (1997), who undertook a comprehensive review of the literature pertaining to metapopulation structure of herring to determine whether there was greater support for the hypothesis that metapopulation structure was a plastic response to variable environmental conditions (the 'adopted migrant' hypothesis) compared with the hypothesis that the metapopulation structure of herring had a strong genetic basis that was partly maintained by persistent environmental features (the 'member-vagrant' hypothesis). An important advantage of this comparative approach is that it minimizes the possibility of selecting approaches and evidence that supports a particular hypothesis (Hilborn 2006).

Applying a similar approach, this essay will test 2 contrasting but not mutually exclusive hypotheses for interpreting the long-term trends in maturation that have been observed in the Northeast Arctic cod *Gadus morhua* stock (Jørgensen 1990, Marshall et al. 2006). The first analysis tests whether there is a significant effect of food availability on the probability of being mature, using condition as a proxy for food availability. Positive correlations between condition and the probability of being mature at a given age or length have been found for Icelandic cod (Marteinsdottir & Begg 2002), walleye (Henderson & Morgan 2002), American plaice (Morgan 2004) and sardine (Silva et al. 2006).

The second analysis uses the same database to test whether there have been long-term shifts in the PMRN of Northeast Arctic cod that could be interpreted as being consistent with a diagnosis of fisheries-induced evolution such as has been made for other cod stocks (Barot et al. 2004a, Olsen et al. 2004, 2005). The purpose of presenting both analyses, albeit briefly, is to illustrate both the limitations of having a narrow focus on complex phenomena such as maturation and the advantages of investigating maturation from a more integrated, physiological perspective.

VALIDITY OF THE COMPARISON

A direct comparison of the 2 analyses of maturity trends would be problematic if the maturity data underlying them differed. This is not the case for the 2 analyses presented here. The first analysis uses estimates of the probability of being mature at a given age (m_a) that are estimated annually by the International Council for the Exploration of the Sea Arctic Fisheries Working Group (ICES AFWG). The second analysis uses the same m_a values (aggregated by cohort rather than by year) in combination with the observed age-length keys (Marshall et al. 2004) for individual cohorts. The simulation-based approach (B. J. McAdam & C. T. Marshall unpubl. data) to estimating PMRNs was then applied using both the m_a and age/length keys for the cohort. The underlying maturity-at-age (m_a) data are the same in both analyses (obtained from the ICES AFWG), making for a like-with-like comparison. The most important distinction between the 2 analyses is in their principal dimensions: the first analysis is year-specific because environmental effects on maturation will be more strongly manifested on that dimension, whereas the second analysis is cohort-specific because genetic effects on maturation are only relevant for that dimension.

NORTHEAST ARCTIC COD

The Northeast Arctic cod stock has been fished by both Russia and Norway; consequently, both countries have well-resolved time series for many key biological variables. Since the end of WWII there has been a large increase in fishing mortality (Fig. 1a), which has resulted in the size composition of the spawning stock being shifted towards smaller sizes (Fig. 1b). Over the same time period the mean length at which 50% of the spawning stock are mature has decreased by approximately 40 cm (Fig. 1c); however, this trend could partly be an artefact of there being fewer large fish. A trend towards mature fish being heavier for their length is also evident (Fig. 1d). The direction of this trend suggests that changing abundance and a shift in size composition towards smaller fish has increased the per capita food consumption, resulting in higher condition. Higher condition is likely to result in earlier maturation (Henderson & Morgan 2002, Marteinsdottir & Begg 2002, Morgan 2004). Thus, a cursory analysis of the historical trends in the exploitation history and stock dynamics of Northeast Arctic cod suggests that there could be both genetic and plastic effects on maturation.

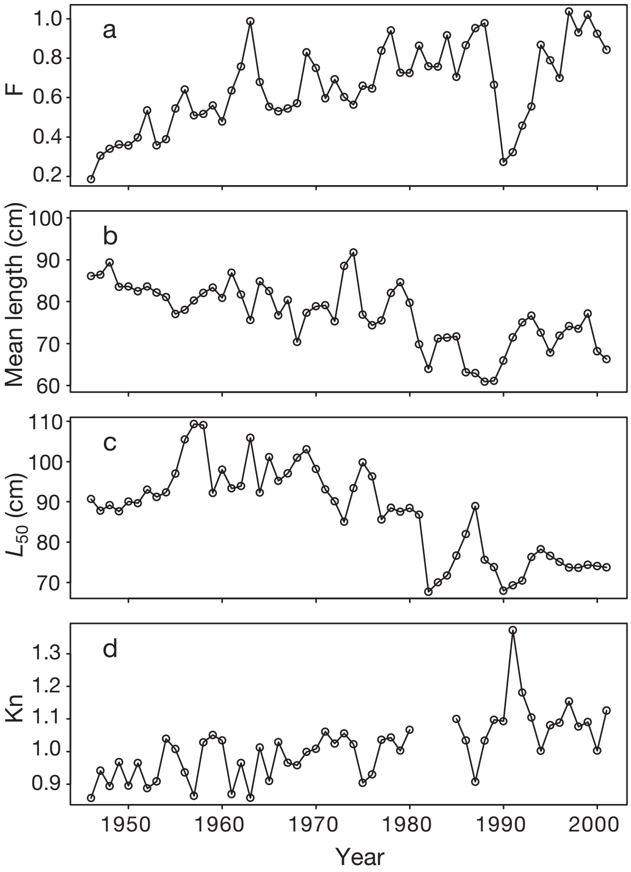

Fig. 1. *Gadus morhua*. Time trends in key population indicators for Northeast Arctic cod. (a) Average fishing mortality (F) of Ages 5 to 10 yr (from ICES Advisory Committee on Fishery Management 2002). (b) Mean length of the spawning stock (estimated from abundance-at-length data described by Marshall et al. 2006). (c) Length at 50% maturity (L_{50}) as estimated from length-based maturity data described by Marshall et al. (2006). (d) Relative condition index (Kn) estimated for the mean length at 50% maturity shown in (c). Kn was estimated as predicted weight at mean length at 50% maturity that year (estimated using the year-specific weight-length relationships in Table 3 of Marshall et al. 2004) divided by the weight at that length predicted using Eq. 10 in Marshall et al. (2006). Thus, Kn expresses weight at length in a given year as a proportion of the long-term (1946–2001) mean weight at that length. Estimates of Kn for 1980–1984 are missing owing to data quality problems described by Marshall et al. (2004)

Evidence of environmental effects on maturation of Northeast Arctic cod

Time series for both the m_a and weight-at-age (w_a) are updated annually by the ICES AFWG because they are used to estimate spawning stock biomass. It should be noted that Norwegian observations for the period 1980 to 1984 (inclusive) are unreliable and thus preclude accurate estimation of the m_a and w_a values for those years (Marshall et al. 2004). Bivariate plots of w_a versus m_a (both time series were obtained from ICES ACFM 2002) suggests that for the pre-1980 time period, there is a significant ($p < 0.05$) positive correlation between m_a and w_a for Ages 7 to 10 yr (Fig. 2). This correlation implies that in years when cod are heavy for their age, they are more likely to be mature. Interestingly, there is a distinct discontinuity between 2 time periods in the nature of the relationship. Observations pre-1980 show lower proportions to be mature and a positive relationship between m_a and w_a, whereas observations post-1984 show fish to have higher m_a but no overall relationship between m_a and w_a. The timing of the discontinuity is synchronous across these age classes; in other words, it affects several cohorts simultaneously. This suggests that the underlying cause of the discontinuity is non-genetic.

A difficulty with using w_a as a proxy for condition is that it combines length-at-age (l_a) with weight-at-length (w_l) into a single value (w_a). Consequently, a short, heavy fish could have the same value of w_a as a long, starved fish. To develop a more sensitive index of condition, age-based estimates of weight and maturity were converted to length-based equivalents, as is described by Marshall et al. (2006). Values of w_l were assumed here to be proxies for condition, which is a reasonable assumption given that the results that are reported here using w_l as a proxy for condition are consistent with the positive relationship between a more refined index of condition (liver weight for a given length). The lengths that were used here for estimating proportion mature-at-length (m_l) and w_l were 72.5, 82.5, 92.5 and 102.5 cm, which correspond to the midpoints of four 5 cm length classes (70–74.9 cm to 100–104.9 cm) that are representative of the length range over which the majority of Northeast Arctic cod are becoming mature. For the post-1984 period there is a significant ($p < 0.05$) positive correlation between m_l and w_l for all 4 of the lengths (Fig. 3). This indicates that in years when cod were heavier for their length, a higher proportion were mature. This result is consistent with the interpretation that the probability of being mature de-

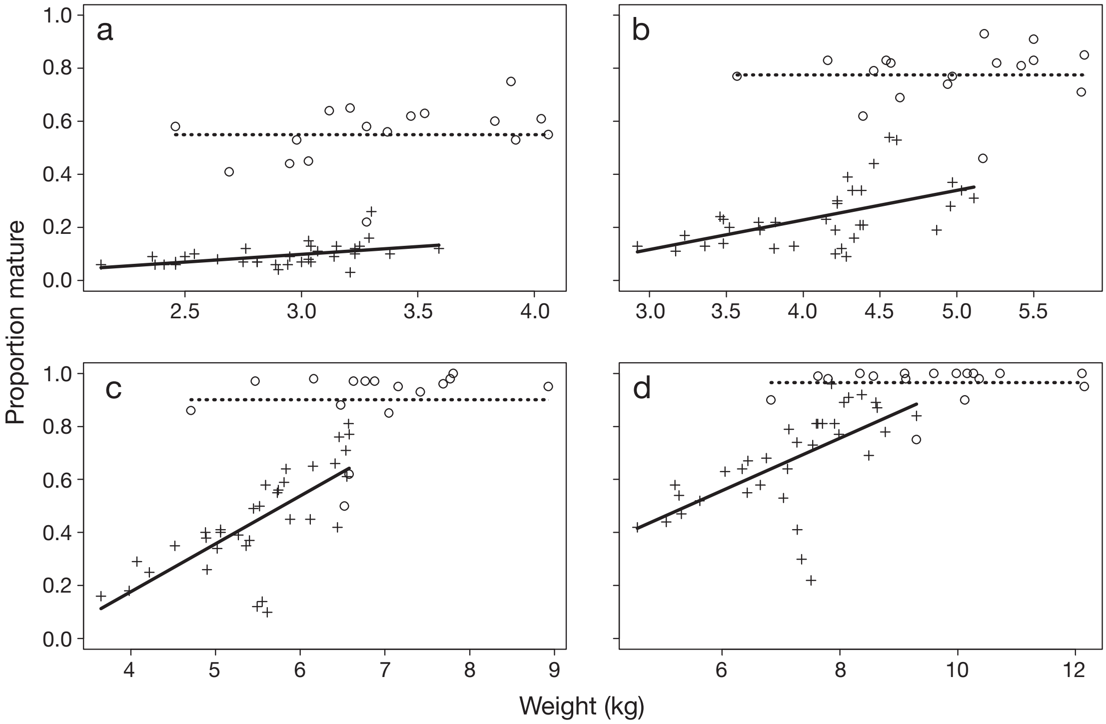

Fig. 2. *Gadus morhua*. Relationship between weight-at-age (w_a) and proportion mature-at-age (m_a) for different ages. Data are from ICES Advisory Committee on Fishery Management (2002). Circles denote data from 1984 to 2001 (inclusive); crosses denote data from 1946 to 1979 (inclusive). Solid line indicates significant ($p < 0.05$) linear relationship; dashed line indicates non-significant ($p > 0.05$) linear relationship. (a) Age 7, (b) Age 8, (c) Age 9, (d) Age 10 yr

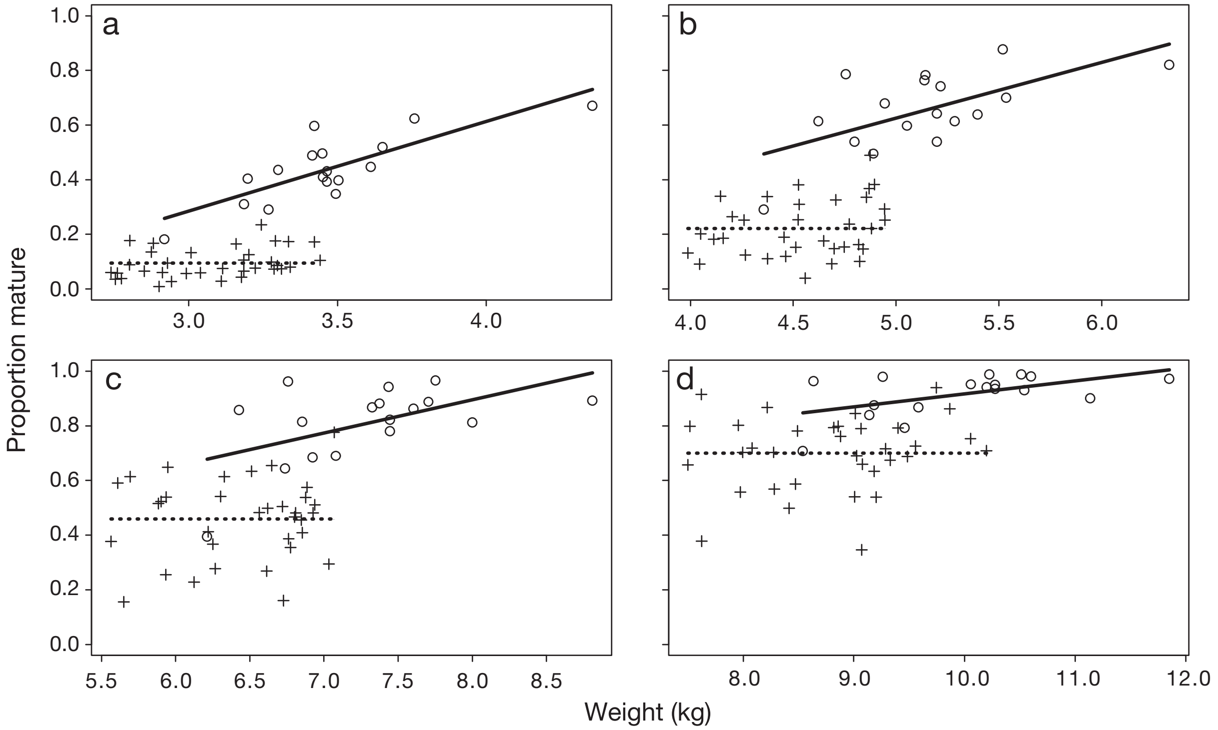

Fig. 3. *Gadus morhua*. Relationship between weight at length (w_l) and proportion mature-at-length (m_l) for different lengths. Data were converted from age-based values in Fig. 2 using the age/length keys described by Marshall et al. (2004). Lengths used for estimating both m_l and w_l were the midpoints of four 5 cm length classes. (a) 70–74.9 cm, (b) 80–84.9 cm, (c) 90–94.9 cm, (d) 100–104.9 cm. These length classes roughly approximate the age classes used in Fig. 2 (Ages 7 to 10 yr). Circles denote data from 1984 to 2001 (inclusive); crosses denote data from 1946 to 1979 (inclusive). Solid line indicates significant ($p < 0.05$) linear relationship; dashed line indicates non-significant ($p > 0.05$) linear relationship

pends on the amount of stored reserves. Therefore, factors such as population density and the environmental conditions that contribute to feeding success are impacting maturation rates in Northeast Arctic cod in this time period.

The discontinuity between the 2 time periods (1946 to 1979 and 1985 to 2001) that was evident in Fig. 2 is also evident in Fig. 3. Cod in the pre-1980 time period are generally leaner for their length compared with the post-1984 time period, which suggests that feeding conditions were poorer in the early time period, perhaps owing to decreased prey abundance and/or higher densities of cod resulting in increased competition. The positive relationship between m_l and w_l is evident only for the post-1984 period, possibly because cod span a larger gradient in w_l in this time period. The mechanisms responsible for generating a discontinuity in the maturation dynamics are beyond the scope of this study. However, other aspects of stock dynamics shifted abruptly around 1980, including the relationship between spawning stock biomass and recruitment (Marshall et al. 2006).

Evidence of fisheries-induced evolution in Northeast Arctic cod

The second hypothesis being tested here is that the phenotypic changes in maturation that were observed for Northeast Arctic cod (Fig. 1c) were the result of fisheries-induced evolution. Because Russia and Norway sample slow- and fast-growing portions of the stock, respectively, any analysis of changes in life history traits that are linked to growth (e.g. maturation) must use data from both countries. However, it is not possible to fit PMRN using individual-level data because historical data for individuals are not accessible for both Russia and Norway. Consequently, B. J. McAdam & C. T. Marshall (unpubl. data) have developed a simulation-based method that uses the age-length keys that are available for each year (Marshall et al. 2004) and the values of m_a to fit PMRNs for individual cohorts of Northeast Arctic cod stock over a long time period (1946 to 1989 cohorts). These 2 types of data (Fig. 4a) are readily available for many stocks, making the simulation-based method used here applicable to a wide range of stocks. The simulation-based method of fitting a PMRN from a combination of age-length keys and m_a data was validated by comparing the PMRN fit using this method to published PMRNs estimated for North Sea plaice by Grift et al. (2003) using the method of Grift et al. (2003) and Barot et al. (2004b). On the basis of this validation exercise, the simulation-based PMRNs were judged to provide a description of long-term trends that was consistent with the approach of Barot et al. (2004b).

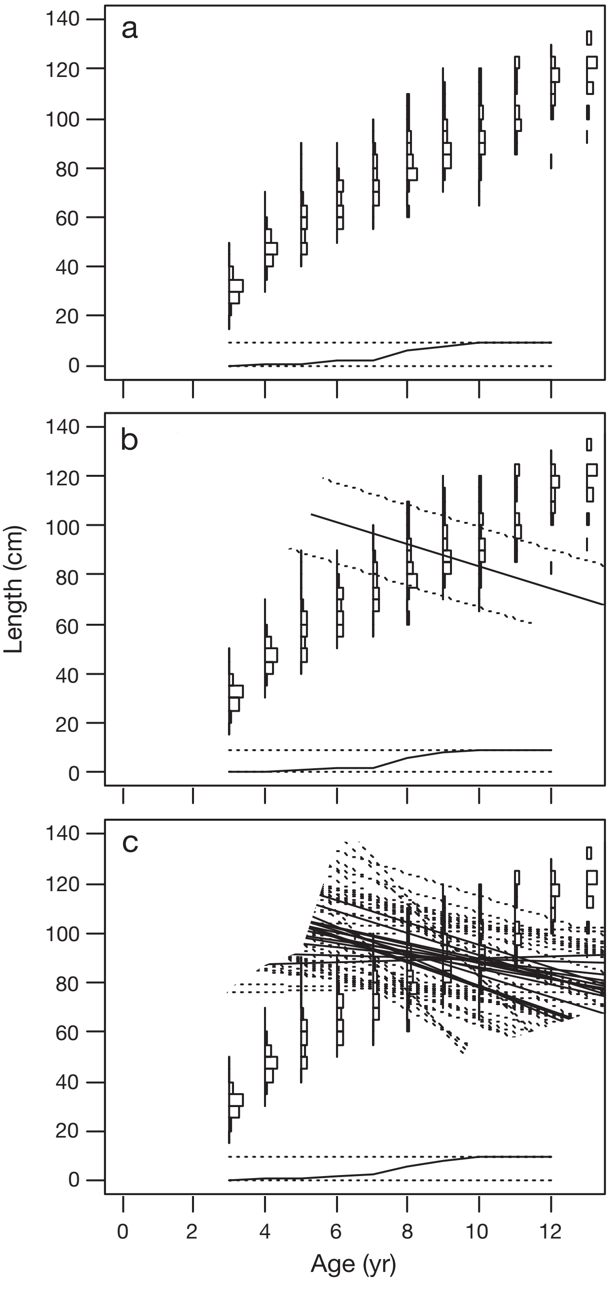

Fig. 4. *Gadus morhua*. Data for a single cohort (1980) and the fitted probabilistic maturation reaction norms (PMRNs). (a) Proportion of cod at each size class for each age shown as histograms. Cohort-specific values of the fraction mature-at-age (m_a) are shown beneath. These 2 data sources were used to fit the simulation-based PMRN shown in the subsequent 2 panels. (b) As above and with contour lines for the single best-fit PMRN. Solid line indicates 50 % probability of maturation; dotted lines indicate 25 % and 75 % probabilities. (c) As above and with the subset of PMRNs that all have a 95 % posterior probability

The PMRNs presented here for Northeast Arctic cod have the advantage of being fit using data representing the whole stock (see Marshall et al. [2004] for a description of how Russian and Norwegian age-length keys are combined; see ICES Advisory Committee on Fishery Management [2006] for a description of how Russian and Norwegian maturity data are combined to give m_a). Unlike other formulations for PMRNs (e.g. Barot et al. 2004b), the contours are constrained to be straight and parallel, as illustrated for the 1980 cohort in Fig. 4b. The linear PMRN models have 3 parameters: S_0, the intercept of the 50 % probability of maturation contour with the length axis (i.e. the length that a hypothetical Age 0 yr fish would have to be to be mature); S', the slope of the contours; and W, the width between contours (i.e. the length difference between a fish with 25 % probability of maturation and one with 50 % probability). In the model fitting, a candidate PMRN is tested by repeatedly simulating the maturity status of fish and recording the fraction of simulations that match the actual observations of m_a for all ages in the cohort. The fraction of simulations that match observations is the probability of obtaining the observations, given that the PMRN model is correct: p(*observations*|*model*). After assessing a subset of possible models, Bayes' law can be used to calculate the relative probability of each model being correct, given the observations that were made, i.e. p(*model*|*observations*). Of the suite of possible PMRNs, one is identified as the most probable (Fig. 4b) on the basis of having the highest value of p(*model*|*observations*) relative to the other candidates. A subset of PMRNs (Fig. 4c) can be identified as having a 95 % probability of explaining the observations in Fig. 4a.

Emulating the graphical approach used in Fig. 3 of Olsen et al. (2004) in their diagnosis of fisheries-induced evolution in Northern cod, the length for 50 % maturation probability (L_{p50}) at Age 6 yr was plotted for the 1946 to 1989 cohorts (Fig. 5). Similar trends are observed in other age classes; however, Age 6 yr is presented here because it represents an age class for which the transition to maturity could be expected for a variable and occasionally large fraction of the stock (cf. Fig. 2). Over the full time period there has been a large decrease in L_{p50} (Fig. 5a), indicating that Age 6 yr cod are likely becoming mature at smaller lengths. The temporal trend in L_{p50} could be interpreted as being consistent with fisheries-induced evolution. Indeed, there are few qualitative differences between Fig. 5a and Fig. 3 of Olsen et al. (2004).

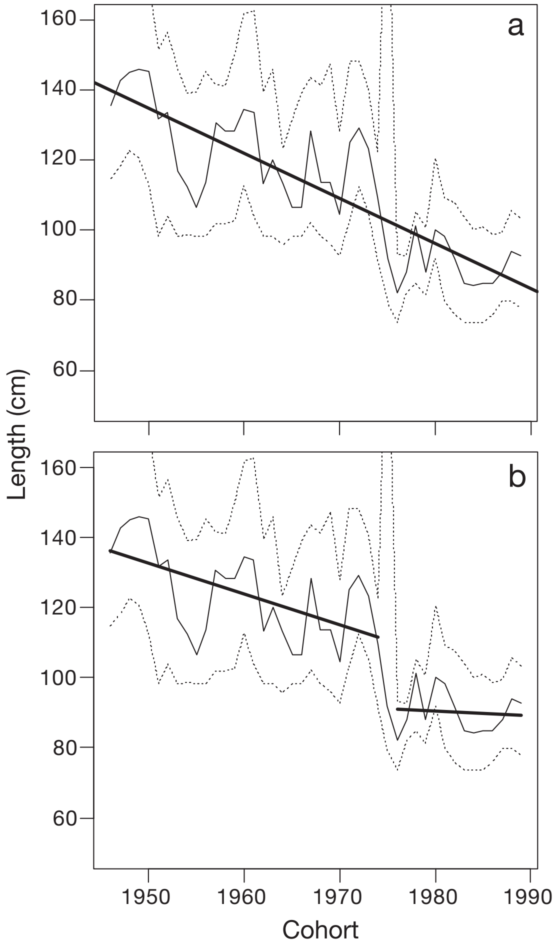

Fig. 5. *Gadus morhua*. Trend in the probabilistic maturation reaction norms (PMRNs) over time (1946 to 1989 cohorts shown). Solid line indicates length for 50 % maturation probability (L_{p50}) at Age 6 yr for each cohort; dotted lines indicate 95 % confidence interval for this value. (a) Bold line indicates linear trend in L_{p50} over time for the whole time series. (b) Time series for L_{p50} is divided into 2 parts: up to and including 1974, and 1976 and onwards. Bold line indicates linear trend in L_{p50} over the 2 time periods

Having undertaken the first analysis, there are several aspects of the PMRN analysis that are inconsistent with the tentative diagnosis of fisheries-induced evolution. Firstly, the rapidity of the changes in L_{p50} is striking. Specifically, there is a sudden shift to lower values in the 1975 and 1976 cohorts. This discontinuity is evident in a plot of S_0 versus the corresponding S' for all of the fitted PMRN for the 1973 to 1979 cohorts. The parameter space (i.e. the cluster of points that represent values of S_0 and S' of the fitted PMRN for a single cohort) for the 1973 and 1974 cohorts is non-overlapping with the parameter space for S_0 and S' for subsequent cohorts, indicating a sharp discontinuity in coefficients of the PMRNs between the 1974 and 1975 cohorts. Given that cod begin to mature around Age 5 and 6 yr, this abrupt shift corresponds to the discontinuity noted in the year-specific analysis (Fig. 2) around 1980. Secondly, the first analysis (Fig. 2) showed that the discontinuity happened simultaneously across age classes, suggesting that the cause is not genetic. Thirdly, the first analysis indicated that cod were more likely to be mature in years when they were heavy for their length (Fig. 3). Because condition of Northeast Arctic cod is dependent on the abundance of Barents Sea capelin (Yaragina & Marshall 2000), this is consistent with an environmental effect on maturation. Fig. 1d indicates that the condition of cod has increased over the full time period, and the post-1984 time period in particular is characterized by better condition. The effect of condition is not adequately represented in PMRNs that consider maturation as a function of only age and length. Length is an integrated measure of growth history but it is not a sensitive index of condition, either at the onset of maturation or in the critical periods in the run-up to maturation when the fish is ‘deciding’ whether to initiate maturation. Thus, by using length-based PMRNs to diagnose fisheries-induced evolution in Northeast Arctic cod, condition effects on maturation are being confounded with genetic effects.

Without the perspective provided by the first analysis, it would be possible to interpret the downward trend in L_{p50} (Fig. 5a) as being consistent with, though not direct proof of, fisheries-induced evolution. The null hypothesis of no directional shift in phenotype attributable to a genetic effect could have been rejected, with appropriate caveats, in favour of the alternative hypothesis (directional shift in phenotype is due to evolution). However, the additional perspective provided by the first analysis suggests that the long-term trend in maturation is distinctly discontinuous (Fig. 5b). This discontinuity contributes to the perception of a downward trend in L_{p50} (Fig. 5a). There is a downward trend in L_{p50} for the early time period, driven largely by high values in the post-WWII years, but no overall trend in L_{p50} for the more recent time period (Fig. 5b). The cause of the discontinuity is unknown but it is most likely non-genetic given that it was observed to be synchronous across age-classes.

This dual-pronged analysis has shown that part of the phenotypic variability in maturation that could be inferred by PMRNs to result from genetic change could instead be a consequence of the confounding influence of proximate cues, such as feeding and condition. The PMRN approach has recently been extended to 3 dimensions to account for variation in condition by including this as an additional dimension in the PMRN for plaice (Grift et al. 2007). However, it is also important to consider that the condition effect on maturation is likely to occur well in advance of maturation itself (Morita & Fukuwaka 2006, Skjaeraasen et al. 2006). If the PMRNs are fit using observations for age, length and condition data that were measured at the point of maturation, then the true nature of the age, length and(or) condition effect on maturation could be obscured.

DEVELOPING MORE INTEGRATED PERSPECTIVES ON MATURATION

The comparative approach used here, which interrogated the same database in relation to 2 contrasting but not entirely mutually exclusive hypotheses, indicated that trends in maturation could variously be interpreted as showing a genetic effect (PMRNs show downward trend across cohorts; Fig. 5a), no genetic effect (PMRNs characterized by a pronounced discontinuity of non-genetic origin; Fig. 5b), or an environmental effect (positive relationship between condition and probability of being mature; Fig. 3). If the scope of the analysis had been restricted to testing for either a genetic or an environmental effect, then a Type I error of inference could very easily have been made. It is dangerous to interpret the temporal trends in PMRNs for the early cohorts (e.g. Fig. 5b) as evidence of genetic change when the model does not properly account for environmental effects on condition (Fig. 3).

Our results illustrate that disentangling phenotypic plasticity in maturation remains a challenge for fisheries science. A recent study into the potential for shifts in reaction norms for reproductive investment in plaice (Rijnsdorp et al. 2005, p. 841) similarly concluded that, 'although the weight loss during the spawning period is in agreement with the expected fisheries-induced change in reproductive investment, the alternative explanation of a phenotypic response to an environmental change cannot be excluded and is even more likely'. Such ambiguity is disconcerting for managers, who are increasingly being called upon to adopt Darwinian fisheries management strategies (Conover & Munch 2002). It is somewhat reassuring that the factors responsible for shifts in maturity schedules for humans are proving to be similarly elusive despite intensive research (Herman-Giddens et al. 2004, Anderson & Must 2005). Intriguingly, a recent longitudinal study tracking the body mass index of girls born in 1991 concluded that the most significant factor in predicting early puberty was the body mass index at age 36 months, a time point 'well before the onset of puberty' (Lee et al. 2007). The compatibility between this result for humans and the model of fish maturation proposed for salmonids by Thorpe et al. (1998) is striking. The attainment of sexual maturity must be regarded as the culmination of a sequence of physiological events and the precise nature of those events must be described before the genetic basis of maturation can be established with confidence.

The development of the PMRN approach (Heino et al. 2002) has greatly stimulated investigations into the genetic aspect of maturation dynamics. However, environmental effects on maturation have not as yet been adequately represented in this approach. The next generation of PMRNs should strive towards incorporating knowledge from applied areas of fisheries science. For example, the results of field- (Englehard & Heino 2004, Yoneda & Wright 2004) and laboratory-based (Rowe et al. 1991, Silverstein et al. 1998, Shearer & Swanson 2000) studies on maturation can be used to identify what proximate cues are important and how they should be parameterized. Accurate models of maturation clearly require a detailed knowledge of the environmental and endocrinological cues that trigger physiological responses in fat, blood hormones and gonad development (Okuzawa 2002, Campbell et al. 2006). Given that the decision to mature is made well in advance of maturation itself (Morita & Fukuwaka 2006, Skjaeraasen et al. 2006), PMRNs for maturation should be developed using data measured during the critical period preceding maturation. PMRNs could be made more realistic if maturation was dependent on attaining a critical size or physiological state (Thorpe et al. 1998, Day & Rowe 2002). The development of physiologically based reaction norms has been advocated for describing the developmental times of insects (Davidowitz & Nijhout 2004), and this line of research would be worth following as it could be a useful analogue for developing physiologically based reaction norms for fish maturation. Finally, the literature on trends in human maturation provides much relevant information regarding the heritability of maturation (Towne et al. 2005), gene polymorphisms associated with early maturation (Xita et al. 2005) and the inheritance pattern of maturation (de Vries et al. 2004).

CONCLUSIONS

Quantifying the degree to which selective harvesting changes the life-history traits of exploited species is a central task for ecology. It is both intuitive and logical that genetically based changes in life-history traits should be occurring in response to selectively applied mortality (Law & Grey 1989). Life-history traits in fish have sufficient heritability to evolve, and micro-evolutionary changes occur within a few generations in controlled experiments (Reznick et al. 1990, Conover & Munch 2002). While these arguments are appealing, they should not predispose researchers towards believing in fisheries-induced evolution to such an extent that the inherent limitations of the PMRN approach are downplayed (sensu Hilborn 2006). A more integrated view of maturation, incorporating key aspects of the physiological processes that culminate in maturation, can be developed by critically evaluating highly contrasting hypotheses using databases having a high degree of biological resolution. This will lead to more accurate inferences about the underlying causes of early maturation in exploited fish stocks.

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