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Intra-stock variability in reproductive investment strategies: consequences for the estimation of fisheries induced evolution

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The stocks of many marine fishes comprise several spawning components that differ with respect to life history traits. Recent field studies indicate that the maturity and fecundity – size relationships of both cod and haddock differ among putative sub-populations in the North Sea. In this paper we report on how these differences in reproductive characteristics have developed over the last decades, in terms of the change in probabilistic maturation reaction norms and weight specific fecundity. Sub-populations inhabiting the most heavily depleted and climatically variable region have undergone the largest declines in size and age at maturation, with cod and haddock from the north west inshore region now maturing at much smaller sizes and at a year younger than those from the north east region. Maturation differences between these sub-populations persisted when juveniles were raised under a common environment, suggesting that present differences were not solely reflective of local environment. Nevertheless, warming during the summer maturation decision phase may also have contributed to the rapid decline in maturation reaction norms. Fecundity at size has also increased in the inshore north west North Sea in haddock. Over the same time, somatic condition and post-maturation growth of these haddock has declined. Take together these observations are consistent with a fisheries induced adaptive change in reproductive effort. Further, this study demonstrates that a failure to account for sub-stock structuring can lead to erroneous conclusions about the magnitude of such changes within a stock.

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INTRODUCTION

Marked declines in size and age at maturity have been widely reported in many exploited fish stocks (Law, 2000, Trippel & Mork, 2003; Jorgensen *et al*., 2007). Such changes in maturation schedules may arise from the reduced intra-specific competition associated with a declining stock, since faster growing individuals will attain the size and condition required for maturation at an earlier age (Trippel, 1995; Grift *et al*., 2007). However, such a compensatory response does not explain why there is often a downward shift in the size at age trajectory of maturity. Indeed, in some cases earlier maturation has been associated with a reduction in growth and condition (Baird *et al*., 1992; Morgan *et al*., 1994). Genetic selection has been implicated in such shifts in the size and age at maturity, as there is a heritable component to the age at maturity (Gjerde, 1984; Tipping 1991). Fishing is probably an important contributory factor to this genetic change (Trippel 1995; Law 2000; Jørgensen *et al*., 2007; Heino and Dieckmann, 2008) since the mortality it imposes can be considerably greater than natural mortality (Mertz and Myers, 1998) and may even change the pattern of selection from juveniles to adults (Carlson *et al*., 2007; Conover, 2007). Life history theory predicts that such changes in mortality schedules should select for increased reproductive effort, with earlier maturation, increased reproductive investment and a reduction in post-maturation growth rate (Roff, 1992; Stokes *et al*., 1993; Law, 2000).

The present study examines changes in reproductive effort in two commercially important gadoid species found in the North Sea, the Atlantic cod, *Gadus morhua* and the haddock, *Melanogrammus aeglefinus.* The North Sea total stock biomass of both species declined to very low levels in the early 1990s following a peak in the late 1960s and 1970s (ICES, 2009), but whilst that of haddock has recovered following a reduction in fishing mortality, the North Sea cod stock is still below precautionary biomass limits. For North Sea cod, Yoneda and Wright (2004) demonstrated that since the last period of high spawning-stock size, spatial differences in reproductive investment had developed by the early 2000s, with those from the north west inshore region maturing at a smaller size and having a higher fecundity than those in the deeper north east North Sea waters. Maturity at size differences have also been detected between cod from this north west inshore region and the southern North Sea in both the field and under a common environment (Harrald *et al*., 2010). These regional differences in maturity reflect spatially (Wright *et al*., 2006a, b; Righton *et al*., 2007) and genetically segregated spawning populations of cod within the North Sea (Hutchinson *et al*., 2001; Nielsen *et al*., 2009). Whilst evidence for population structuring is less clear in haddock, there tends to be two major spawning areas in the North Sea; in the north west inshore region and the north east North Sea (Saville 1959; Hedger *et al*., 2004). These spawning concentrations may reflect sub-populations since differences in transferrin allozyme frequency have been detected between spawning haddock from either side of the Greenwich meridian (Jamieson & Birley, 1989) and coastal haddock tend not to move into the deeper north east waters (Jones, 1959; Wright & Tobin, unpubl. data). Similar, to cod, spatial differences in reproductive investment were found in haddock from the north west inshore and north east North Sea in the 1990s (Wright, 2005).

Given regional differences in sea temperature and its recent rate of warming in the North Sea (Elliot *et al*., 1991; Sharples *et al*., 2006), the spatial pattern of maturation may reflect counter-gradient selection, as fish tend to mature at a smaller size in order to compensate for a less favourable environment (Conover *et al*., 2006). Conversely, as North Sea fisheries targeting both species of gadoids have tended to move from coastal to offshore waters over the last five decades (Greenstreet *et al*., 1999, 2009; Jennings *et al*., 1999) the current spatial variability in life history traits could reflect divergent responses to local selective pressures. Any analysis of temporal changes in reproductive investment must therefore be considered in relation to population structure and environmental forcing, since failure to account for an appropriate spatial scale could lead to erroneous conclusions about the magnitude of change.

As there is currently little direct evidence for genetic changes in maturation schedules, attempts to identify such a response have looked for trends in traits that appear to counter that predicted from plastic responses alone (i.e. counter trend variation; Dieckman & Heino, 2007). For example, earlier and higher reproductive investment can be linked to individuals growing fast and having high condition as a result of reduced intra-specific competition associated with a stock decline (Trippel, 1995). The development of the probabilistic reaction norm approach for maturation (PMRN) has helped to disentangle such a compensatory plastic response from possible genetic variation (Heino *et al*. 2002). This approach models the probability that individuals mature, having reached a given age and size. The method is not affected by variations in growth and survival that influence conventional maturity ogives. Additional factors know to influence maturation such as condition (Marteinsdottir & Begg, 2002) can be

included in the estimation of maturation probability (Grift *et al*., 2007). However, as field applications are limited by the need to characterise gonad development macroscopically, estimated maturation probability at age and size reflect the outcome of the fish's continued investment in gonadal development rather than it's energetic state when the initial physiological maturation decision was made (Wright, 2007). Further, the PMRN method can be confounded by unaccounted for plastic effects influencing maturation. For example, experimental studies suggest that temperature can have a direct effect of temperature on the maturation decision process, for a given body size (Adams & Thorpe, 1989; Dhillon & Fox, 2004; Tobin & Wright, in review). Further, as field applications are limited by the need to characterise gonad development macroscopically, reported maturation size (Lp50) mid-points reflect the energetic outcome of the fish's continued gonadal development rather than it's state when the initial physiological maturation decision was made (Wright, 2007).

One way of separating the genetic and environmental components of current spatial variation in maturation is by taking a ‘‘common-environment’’ experimental approach (Purchase & Brown, 2001). This rests on the assumption that if extrinsic factors can be controlled for and remain equal, any emergent variation between fish from different regions can be attributed to intrinsic population factors rather than the environment. The common-environment approach differs from a common- garden approach in that it does not control for maternal effects (Marteinsdottir & Steinarsson, 1998) and effects generated by post hatching differences in the early environment (Johnston, 1993). Although control of such factors can be desirable, cultured fish may contain fish that only survived because of the relatively favourable laboratory conditions and hence may not be representative of fish that have survived the early

phase of high mortality to settlement in the wild. In the context of studying maturation, it is important to control for conditions during the time of year when fish make the physiological ‘‘decision’’ to continue gametogenesis through to spawning (Wright, 2007). In the case of cod and haddock this “decision” period occurs in the summer preceding the year of spawning (Kjesbu *et al*., 2010; Tobin *et al.,* in press).

In addition to changes in maturity, size specific fecundity may also increase in response to high juvenile mortality. Given that fecundity is related to body size, an early spawning small individual would have to invest more heavily in egg production with age if it is to compensate for the initial low fecundity (Rochet *et al*., 2000). This trade-off between current and future reproduction means that the lower fecundity at first maturity, the greater it will be at later reproductive events (Rochet, 1998). As such, the slope of fecundity – size relationships may be expected to increase in response to high adult mortality. Life history models generally predict that evolution for fecundity-size relationships will be weaker than that for maturation probability and size (Dunlop *et al*., 2009). However, there has been an increase in fecundity at size in North Sea cod between cohorts from the 1960s and 2000 (Yoneda & Wright, 2004). Moreover, this increase in fecundity could not be explained by changes in the fish’s condition, as would be expected from a compensatory response. Changes in the slope of the fecundity – size relationship have also been found in plaice (Rijnsdorp, 1991) and Thomas *et al* (2009) found an effect of harvesting on the inter-annual variation in fecundity of whitefish, *Coregonus lavaretus*, after having accounted for the effects of changing lake productivity.

This study integrates a number of approaches in order to consider temporal and spatial differences in reproductive effort in putative sub-populations of North Sea cod and haddock. The demographic PMRN approach (Barot *et al*., 2004a) was applied to data on pre-spawning fish. As the physiological decision to continue maturation probably occurs in the summer preceding spawning in haddock (Kjesbu *et al*., 2010; Tobin *et al*., in press), maturation trends were examined in relation to bottom sea temperature at this time. Competitive biomass, the biomass of juvenile conspecifics in an area, was used as a covariate in order to consider competition for resources at the time of maturation. Fecundity and body condition for haddock from coastal west and offshore east regions of the North Sea in the 1990s and 2000 were compared with similar data for the 1970s and 1980s (Hislop & Shanks, 1981) to complement earlier work on cod by Yoneda & Wright (2004). Finally, the relative contributions of environmental and intrinsic factors to recent spatial differences in maturity were examined in a series of common environment experiments. The possible causes of temporal and spatial trends were discussed with respect to predictions about compensatory and genetically induced changes in life-history traits.

MATERIALS AND METHODS

Sample data

Data on sex, maturity, age and length were extracted from the 1st quarter ICES (International Council for the Exploration of the Sea) International Bottom Trawl SMALK database (DATRAS), for the years 1971-2009. These bottom trawl surveys were undertaken between January and March, which is usually within one month of spawning (Hislop, 1984). This data was supplemented with additional research and

commercial trawl sampling in years 1999, 2002-2004 and 2008 for cod and 1977, 1980, 1985, 1994-6, 1999, 2007-8 for haddock. Total length was measured to the nearest 1 cm and maturity stage was determined macroscopically as either 2 stages before 1990 or 4 stages after 1990: 1, immature; 2, developing; 3, spawning; 4, spent. All data were segregated into three regions corresponding to putative sub-populations from the southern (S), north west inshore (NW) and north east offshore (NE) North Sea (Figure 1). As SMALK data were from a length stratified sampling programme, annual length increments were estimated from age stratified length frequency compositions raised to catch per hour from the DATRAS data base.

Probability maturation reaction norm estimation

As the data available do not distinguish between first-time and repeat spawners the retrospective demographic PMRN approach was used (Barot *et al.*, 2004a). Estimation of the probability of maturing for the first time involved estimation of a maturity ogive, $o(s)$, for a given age, size and cohort. Decrementing age and decreasing size by some annual increment (depending on age and cohort) gives the probability of being mature the preceding year, $o_{a-1,s-\Delta s_{a,c},c}$, equivalently if size the preceding year can be directly estimated this can be written $o_{a-1,s_{a-1,c},c}$. This allows consideration of only immature fish and the probability of maturing for the first time. By subtracting from and scaling the original ogive the probability of having matured for the first time at age a size s in cohort c is:

(1) $$m_{a,s,c} = \frac{o_{a,s,c} - o_{a-1,s-\Delta s,c}}{1 - o_{a-1,s-\Delta s,c}}.$$

Linear interpolation was used to estimate the size at which m is 50%, giving the PMRN midpoint (or Lp50). This method assumes that immature and mature individuals have the same survival and growth rates, however, PMRN estimates are relatively robust to a relaxation of this assumption (Barot *et al*., 2004a).

PMRNs were estimated separately for males and females for each sub-population, age and cohort. Temporal trends were reported using Lp50s. Analyses were limited to ages of first maturity, i.e. 2 – 4, thus also requiring cod of age 1 for estimation of growth increments and maturity. In the majority of cases, the final age- and cohort-specific sample sizes fulfilled the minimum recommended sample size (100) for PMRN analysis (Barot *et al*. 2004a). However, for some ages and cohorts with very low sample sizes, it was not possible to compute the Lp50.

Maturity ogives were estimated by logistic regression. Individual maturity state (immature or mature) was regressed against age and length, separately for each sex and sub-population. To facilitate comparison between sub-populations and sex the same model formulation was used:

(2) $$\text{logit}(o) \sim (age + length) \text{ x } cohort$$

where age and cohort were treated as factors. Since the age-specific sample sizes were sometimes too low no age:length interaction was considered. Cohort, sub-population and sex effects were tested by simulating the distribution of the Lp50s and constructing tests based on confidence intervals about appropriate test statistics. Sampling from the distribution of the ogive and growth model paramters was achieved by MCMC sampling, hence intervals should be considered credible intervals

and significance in these tests should be interpreted in terms of probability. Test statistic distributions were compared to zero and if zero was outside the ellipsoid that contains 95% of the probability density, the test was considered significant.

Mean annual age-specific changes in size were calculated as the differences in mean length of individuals belonging to the cohort of interest in two successive years.

Cohort-specific growth increments for ages 1 to 4 were estimated by predicting average length at age *a* using the model:

$$E(length)_{a,r,c} = \alpha_{r,c}(age)^{\beta_{r,c}}, \quad (3)$$

where a different α and β for each cohort, c, and sub-population region, r, was fitted. Numbers at length were weighted by the catch per hour and a lognormal error distribution was assumed. Effectively a normal linear model was used to regress log length against log age. The effect of age, cohort and region on length was examined using standard F tests. The difference between predicted lengths at age a in year y and at age a – 1 in year y – 1 was used to calculate annual growth.

Uncertainty in PMRN estimates was derived from the maturity ogive only. Since interest lies in making inferences about a function of the ogive parameters, simulation of the model parameters was used. As the maturity data were sampled conditional on length, and for certain ages and years no mature cod were present, bootstrap re-sampling of the data was not considered appropriate. Parametric bootstrapping could be used, however this should lead to similar results as direct model simulation. Using the parameter estimates and the covariance matrix from these estimates, 9999 maturity ogives were simulated, and from each an Lp50 was calculated. Confidence intervals (CI) were estimated as the 2.5 and 97.5 percentiles of the 9999 simulated

Lp50 estimates for each age and cohort, region and sex. Poorly defined Lp50s, particularly for those ages where few individuals mature, can result in wide CIs. In some cases parameter sets resulted in undefined Lp50s. If Lp50s were undefined in < 90% of the 9999 simulated samples, that age/cohort was removed from further analyses.

To test for a trend in the Lp50 at a given age, the reaction norm midpoints were regressed against cohort and weighted by the inverse of the simulated variance of each mid-point. The apparent rate of evolutionary change, in the standard unit 'darwin', was calculated as:

$$d = \frac{\ln\left(Lp_2 / Lp_1\right)}{\Delta t \times 10^{-6}} \quad (4)$$

where Lp_1 and Lp_2 refer to the Lp_{50} at the beginning (t_1) and end (t_2) of a data period,

Incorporating explanatory variables in the estimation of maturation probability

Factors such as temperature (Tobin & Wright, *in review*) and competitive biomass (Mollet *et al*., 2007) could directly affect maturation decisions. Where first maturation is generally restricted to a single age class, as in North Sea haddock, these factors can be considered as covariate terms within a logistic model of maturation probability. However, a development of the PMRN approach is required for species that may mature over several age classes, such as cod. Past PMRN studies have considered the significance of potential explanatory factors from an analysis of residuals from the Lp50 – cohort regression (e.g. Mollet *et al*., 2007). However, incorporating environmental factors into the estimation of PMRN, in addition to year class, is the only statistically sound approach to the identification and disentanglement of additional plastic effects on maturation (Dieckmann & Heino, 2007). One solution to

this problem is to model the probabilities of maturing directly, hence the PMRN directly, and use these estimates to build a cumulative probability of maturation to test against data. Defining the probability of maturing as π, then the probability that a fish matures for the first time at age a is:

(5) $$\phi_a = \pi \prod_{j=0}^{a-1} (1-\pi),$$

where $a = 1$ is the youngest observed age class. Counts of mature fish at age a contain those maturing for the first time but also fish that have previously matured. The probability of a fish being mature at age a is given by

(6) $$p_a = \sum_{i=1}^{a} \phi_i$$

which results in a binomial likelihood for the data with probabilities, p_a.

The simplest model for the probability of maturing is

(7) $$\text{logit}(\pi) \sim 1.$$

This base model assumes that the probability of maturing is constant for all ages, lengths and year classes. Assuming that the logistic link function is appropriate, further covariates can be added and their significance tested using F-tests based on changes in deviance and degrees of freedom. In order to correctly incorporate covariates, estimates back to the youngest age in the data set have to be supplied. The covariates used in this study were length, summer temperature, preceding length and competitive biomass. Factor covariates included age, year class, sex and region. Importantly, this model of maturation probability could account for the conditions that the fish experiences at every period of maturation liability, rather than at one time point.

The number of degree days in July and August were derived from monthly mean North Sea bottom temperatures predicted from the NORWECOM model (Skogen *et al*., 1995; Skogen & Soiland, 1998; see ftp.imr.no/morten/WGOOFE_hindcast). Data on competitive biomass were estimated from numbers at age by length in the 1st quarter IBTS survey, raised to biomass using a length – weight relationship for cod aged 1-4 and haddock aged 1-3. The temperature and biomass estimates were delimited to the same regions as defined for the maturity data, for the years 1970-2008.

The length-history of a fish was estimated by assuming that the mean length followed a power relationship with age as in equation (3). This results in predicted lengths of:

$$l_{a-i} = \left(\frac{i}{a}\right)^{\beta} l_a, \tag{8}$$

where a is the observed age, l_a is the observed length of the fish and i is the age at which length is being predicted. A different β was estimated for each region and year class.

By incorporating length in the model Lp50s can be estimated. For a given set of covariate values (age, cohort, region, temperature) the probability of maturing can be written in the form $\text{logit}(\pi) \sim \alpha + \beta\, length$. The Lp50 estimate for this covariate set is then $-\frac{\alpha}{\beta}$, and its standard error can be computed by simulation, as before, from the covariance matrix of the parameters. The covariance matrix is estimated from Fishers information matrix. Model selection was by forward and backwards step wise selection of variables based on changes in deviance using F-tests.

Haddock fecundity and condition

The following biometric indices were calculated for the supplementary data series: relative condition factor (K_n; Le Cren, 1951) was used to give an indication of somatic energy:

(9) $$K_n = \frac{M_s}{\hat{M}}$$

where M_s is somatic mass ($M_s = M - M_g$, where M_g is gonad weight) and $\hat{M}$ is the expected eviscerate mass calculated from the relationship for all available years and samples (N = 15835) inversely weighted by the number of samples within a year: $M_e = 0.00622.L^{3.073}$ ($r^2 = 0.93$; $p < 0.001$). A Kruskal-Wallis test followed by Dunn's multiple-comparison test or the Mann-Whitney U-test (U-test) was used to compare K_n among decades.

As the liver is the main source of lipid accumulation in haddock (Shevchenko, 1972), a measure of relative liver weight (H_r) was used to consider liver energy on maturity:

(10) $$H_r = \frac{H_w}{\hat{H}_w}$$ where H_w is liver weight and

$\hat{H}_w = 0.0081.\ M_e^{\ 1.2623}$ ($r^2 = 0.62$; $p < 0.001$; based on all (N = 15410) individuals.

Fecundity was estimated from a subset of the supplementary data set. Oocyte size distribution in the ovary is homogenous during vitellogenesis (Robb, 1982), therefore the middle portions of the ovarian lobe were excised and fixed in 4% neutral buffered

formalin for fecundity estimation. A gravimetric fecundity estimation was used in all of the studies, according to:

(11) $$F_p = \frac{M_{ovary}}{M_{sample}} \cdot N_{vitellogenic}$$

where N = number and M = mass and sample mass was around 0.3 g. This approach was used in order to compare with similar data from the 1970s (Hislop & Shanks, 1981) and 1985 (J. Hislop, unpubl. data) for the west North Sea region. Previous studies also included information on L, M, age. However, as the previous study did not consider pre-ovulatory atresia the temporal comparison was limited to PF only.

Differences in potential fecundity - size relationships between the 4 decades of study were compared using Generalized Linear Models (GLM) according to the following model:

(12) $$F_p = L * Kn * factor(A) * factor(D)$$

Where L is length, A is age and D refers to the decade of sampling. Eviscerated weight was also considered as an alternative to length. Specimens infected with *Lernaeocera branchialis* were not included in analyses. As with similar studies by Yoneda and Wright (2004), a gamma response distribution coupled with a log-link function ($Y = e^{ax+b}$) was chosen to account for the increased predictor variance with increasing response variable. An additional measure of model fit was based on a pseudo-coefficient of determination (R^2), which was the fraction of the total variation explained by the model

$$R^2 = 1 - \left[\frac{Residual \quad deviance}{Null \quad deviance} \right]$$

where deviance was analogous to the residual sums of squares (Swartzman *et al.*, 1995).

Common environment experiments

Experiments were conducted on individually marked individuals, raised under identical conditions, in order to be able to compare final maturation state with size and growth history around the time of the maturation decision. The influence of sub-population, length, mass, and relative liver index on proportion mature was examined using a generalized linear model, with maturity (immature or mature) modelled using a binomial logit-link function with sub-population set as fixed factor and size terms as continuous variables. Tank was treated as a fixed factor nested within sub-population. A 'full' model was first fitted with the main effects and interactions which were then simplified by removing non-significant terms (at the 5% level) based on Wald tests. The contribution of explanatory variables was considered using a pseudo-coefficient of determination (R^2).

Cod

Common environment experiments were conducted on the 2005 year-class from the 3 sub-populations at the Marine Laboratory in Aberdeen. The original intention was to maintain cod under the same ambient thermal range which required them to begin maturing at the same age. However, due to differences in age at first maturity among sub-populations different years had to be considered, with those from the southern

and north west North Sea being studied in 2006 and 2007 whilst those from the north east were studied in 2007 and 2008. Full details of rearing experiments for Southern and North west North Sea cod are given in Harrald *et al*. (2010). In this study, size data from August monitoring of individuals was used to consider size around the maturation decision.

Haddock

Haddock from the north east and north west North Sea were established under constant conditions around 6 months of age in October 2008. Due to difficulty in returning live 0-group from the north east North Sea, eggs and sperm were stripped from running haddock. Thirteen females were cross-fertilised with twenty six males to generate 26 half-sib families. The resulting offspring were reared under aquacultural conditions at Ardtoe hatchery until transfer to the Marine Laboratory in August (see Treasurer *et al*., 2006 for further information). Wild caught 0-group from the north west North Sea were caught off the east coast of Scotland (56°58′N 2°12′W) in August 2008. All fish were acclimatised for a minimum of 2 months in cylindrical tanks (2 m diameter x 1.2 m depth) and were fed on a pelleted marine diet (14%) prior to commencement of the experimental trials.

The experimental trial was conducted between December 2008 and November 2009. A total of 223 (north east n = 109; north west n = 114) fish were internally PIT tagged (Trovan Ltd., UK) at the beginning of the experiment and assigned to replicate rectangular tanks (7 x 3 x 1 m). Fish were size-matched between tanks to eliminate the risk of any potential size effects. Photoperiod was adjusted to ambient (latitude 57°N) using artificial fluorescent green lighting, mimicking a natural annual

photoperiod cycle. Using temperature control units, water temperature was maintained at 10°C during the course of the experiment. This was representative of the average annual bottom temperature at the sampling site over the course of the experiment (3553°C.day^{-1}) and was known to lead to a high rate of maturation in the NW haddock (Tobin & Wright, in review). The fish were fed 1.0% body mass.day^{-1} using a wet-feed diet over two daily feed sessions, seven days a week, following a similar feeding regime to Treasurer *et al*. (2006). Each tank was monitored daily to ensure that all feed had been consumed. All work was carried out in accordance with the U.K. Animals Scientific Procedures Act 1986.

Somatic body mass (M_S), gonad (M_G) and liver mass (M_L) were measured on 94 (45 inshore and 49 offshore) 1-year old females at the end of the experiment in November. Relative liver mass (H_r) was calculated as above. Maturation state was based on histologically determined ovarian development according to Tobin *et al*. (in press). Ovaries only containing peri-nucleolar and circum nuclear ring stage were considered immature whilst cortical alveolus and vitellogenic oocytes indicated maturing females.

RESULTS

Cod

Length-at-age

Age, cohort, sub-population and the interaction between cohort and sub-population all had a significant effect on length (ANOVA, $P < 0.001$). Cod from the NE sub-

population were the smallest at age whilst those from the S were the largest. There was significant positive temporal trend in length at age in the S sub-population, but a negative although small decline in the two other sub-populations. The average annual growth increment for ages 2-3 was 15.8, 16.0 and 18.0 cm in the NE, NW and S sub-populations respectively (Figure 2).

PMRNs

Despite short-term variation in the Lp50s and wide CI for some cohorts, there were clear negative trends in two of the three sub-populations. Based on tests of sex and sub-population effects from MCMC sampling, the effect of sex was highly significant with females having a larger Lp50 than males ($P<0.01$). Sub-population differences were also highly significant ($P<0.001$). As NE cod only begin to mature by age 3 and most NW and S cod were mature at this age by the end of the study period, only trends in Lp50 for this age-class are presented (Figure 3). However, as a very high proportion of age 3 cod from the NW and S were mature in the final years of the study the Lp50 estimates were subject to generally wide confidence intervals. The negative trend in Lp50s in age 3 cod with cohort, weighted by the inverse simulated variance, was significant for both sexes in the NW and S sub-populations ($P<0.05$; Table 1). These trends corresponded to a magnitude of change in the order of 29 – 51% within 26 - 29 years. In contrast, there was no consistent trend in Lp50 with cohort in the NE cod. As a result, although the Lp50 for NE cod was approximately 7 cms greater at the start of the study than other sub-populations, by the end of the study this difference had increased to between 27 and 42 cms. Additionally, whilst a high proportion of age 2 cod became mature in the S and NW sub-populations by the 2005 cohort, there was virtually no age 2 cod mature in the NE. For males and females

respectively, the changes in Lp50s of age 3 cod corresponded to an estimated of 11.7 and 22.2 k darwins in the S sub-population and 27.5 and 20.7 k darwins in the NW sub-population.

Trends in potential explanatory factors

The significance of temperature to the spatial differences in maturation probability was partially confounded by the lack of overlap in ranges between the three sub-population regions (Figure 4). There were significant positive linear temperature trends in the NE and NW region (F-test; $P<0.05$) and a highly significant trend in the S region ($P<0.001$). Biomass of ages 1-3 in the first quarter survey also differed among regions, although the only sub-population with a significant declining trend with year was the NW sub-population ($r_S = -0.54$; $P <0.01$).

The non-parametric permutation analysis of maturation probability found a significant ($P<0.05$) effect of sex, and sex interacting with sub-population, age and cohort within subpopulation. Given the significant effect of sex, subsequent analyses were conducted on males and females separately. The following base model was used to define average trends in Lp50 with cohort (c) and sub-population (p);

(r1) $\text{logit}(\pi) \sim l + a + p + p{:}l + p{:}a + p{:}s(c)$

where s(.) denotes a spline with 4 degrees of freedom and : denotes an interaction. On the logistic scale, this allows the probability of maturation to have a different slope for each sub-population; while the level can change with age, region, age within region and cohort within region. A spline was used rather than treating cohort as a factor because many interaction terms were significant due to a few extreme cases where all where all fish were either mature or immature.

The additional effect of preceding summer temperature and competitive biomass on trends in cohort was fitted in which s(cohort) in the base model (r1) was replaced by linear effects of temperature (t) and cod biomass(b):

(r2) $p_a \sim$ l + a + p + p:l + p:a + p:t + p:b

All terms in the model were significant, however, model (r2) had 6 less parameters than model (r1) and the deviance was ~ 1000 less, indicating a significantly poorer fit. Hence, temperature and cod biomass fail to adequately explain the trend in maturation probability. Within sub-populations, linear effects of temperature and cod biomass were significant additions to the base model (r1) and were selected as the final models for both males and females (see Tables 2a and b). The Lp50s from these models are shown in Figure 5, along with estimated cohort effects. Maturation probabilities were greater for ages 3 and 4 than at age 2. The average Lp50 was higher in the NE sub-population, followed by NW then S. The effect of length on maturation probability followed the same pattern. Temperature had a consistent significant positive effect in all sub-populations and sexes, except for females in the NE. Cod biomass did not have a consistent effect across region but was consistent across sexes, having a positive effect in NE and negative effect in the NW and S sub-population. The combined effect of temperature and cod biomass can be seen in Figure 5 as deviations from the cohort effect. This shows that the addition of temperature and cod biomass explain some of the decline in Lp50s; this is due to a positive effect of temperature along with a generally increasing temperature trend experienced by the sub-populations. Figure 5 also shows neither covariate explains the increasing positive trend in maturation probability but temperature increases the apparent magnitude of the trend.

Common environment experiment

Maturity–size relationships

As stated in the methods there were qualitative difference in age at onset of maturation. Some fish from the NW and S were ready to spawn at age 2. Even between these two sub-populations there were qualitative differences in the range in mass of mature cod just prior to spawning in January-February, i.e. NW: M_s = 550 to 757 g compared to > 1027 g in SNS individuals. The mass of mature pre-spawning cod was even greater in the NE with all maturing fish being > 1300 g. The length at 50% first maturity was 36.5, 46.5 and 49.5 cm TL in NW, S and NE cod, respectively just prior to spawning. August length (R^2 = 0.33; P <0.01) and population (R^2 = 0.14; P <0.01) was significantly related to maturation probability with cod from the NE maturing at largest size whilst those from the NW maturing at the smallest size (Figure 6).

Haddock

Length at age differed significantly between the two sub-populations and over time (ANOVA, $p < 0.001$). In NW haddock, length at age declined significantly with cohort in ages 2 and 3 after the mid 1990s but not in age 1. In contrast there was no significant trend in NE haddock length at age, except for a weak positive trend in age 2 haddock. The average annual growth increment for ages 1-2 was 5.1 and 6.3 cm in the NW and NE sub-populations, respectively (Figure 7). There was no significant difference in L-GW regression between W haddock from recent years and the 1970s

or among regions in 1990 (GLM p> 0.05). Relative condition factor was significantly lower in mature W haddock sampled in the 1990 and 2000 decades compared with that in the previous two decades (Kruskal-Wallis χ_3 = 75.05, P<0.001). Median Kn was 1.06, 1.10,1.0, 0.96 in age 2 fish and 1.03, 1.0, 0.97 and 0.94 in age 3 fish, for the decades 1970, 80, 90 and 2000.

PMRNs

There has been a substantial change in the proportion of age 2 and 3 female haddock between the early 1980s and 2000s. Based on the average size/length of ages 2 and 3 in the North Sea assessment (ICES, 2009) and maturation probability estimated from this study, the proportion of age 2 mature haddock in both the east and west sub-population would have averaged around 0.14 between 1980 and 1985 compared to approximately 0.48 and 0.65, respectively for the period 2000 - 2005. Around 70% of age 3 haddock were mature in the same 1980s period compared to around 97% in the recent period. Given that the main change in maturation affected 2 year olds and for many years nearly all age 3 haddock have matured, only the Lp50s for age 2 age-class are presented in Figure 8. The negative trend in Lp50s in age 2 haddock with cohort, weighted by the inverse simulated variance, was significant for both sexes in the W and males in the E sub-populations (P<0.01; Table 3). This decline in reaction norm midpoints with age means that maturation at a given size and age shifted toward smaller body lengths. The trends corresponded to a magnitude of change in the order of 23 – 27% within 26 - 29 years. However, there was a substantial difference in the Lp50 at the start of the time series, with E haddock having a higher Lp50. Indeed, the Lp50 was close to the maximum length of age 2 in E haddock from 1976 to 1980. As such, the estimates of Lp50s during the 1970s and 1980s were often close to the

maximum length at age 2 and may therefore be unreliable. For males and females respectively, the changes in Lp50s corresponded to an estimated of 11 and 10 k darwins in the W sub-population and 9.3 k darwins in the E sub-population.

Maturation probability in relation to temperature and biomass

The analysis of maturation probability was restricted to age 2 haddock. A significant effect of sex, sub-population and cohort within subpopulation was found at the 99% level. Given the significant effect of sex, subsequent analyses were conducted on males and females separately. The following base model was used to define average trends in Lp50 with cohort and sub-population;

(r3) $$\log it(m) = \beta_0 + \beta_2 l + \beta_3\, factor(c) + \beta_4 p + \beta_5 p : l + \beta_5 p :\, factor(c)$$

where : denotes an interaction. Due to the larger sample sizes for haddock and the single age-class.

The additional effect of preceding summer temperature and competitive biomass (see Fig. 8) on trends in cohort was fitted in which cohort, as a continuous linear variable in the base model (r3), was replaced by linear effects of temperature and cod biomass:

(r4) $$\log it(m) = \beta_0 + \beta_1 l + \beta_2 p + \beta_3 p : l + \beta_4 p : t + \beta_5 p : b$$

All but biomass terms were significant in the model. However, the explained deviance of model (r3) was higher, improving the R^2 by >4% for males and females, indicating that (r4) was a significantly poorer fit. Hence, variation in maturation probability was better explained by cohort than other potential explanatory measures. However, the interaction between sub-population and temperature in (r4) did explain more deviance

than any other interaction with sub-population, probably because of the qualititative difference between sub-populations. Within sub-populations, linear effects of temperature were significant additions to the base model (r3) in females but not males. The maturation probabilities from these models are shown for a 25 cm female in Figure 9, along with estimated cohort effects. Temperature had a consistent significant positive effect and accounted for some of the year to year variation around the positive cohort trend. Thus the addition of temperature may explain some of the decline in Lp50s but does not account for the overall trend.

Fecundity

Length, condition, age and sample decade all had a significant effect on potential fecundity in west haddock. As the only significant interaction was between length and period, the minimum adequate model was:

$$F_p = L + Kn + factor(A) + factor(D) + L : factor(D)$$

Length and relative condition factor (Kn) combined explained slightly more variation in *Fp* ($R^2 = 0.68$) compared to eviscerated weight alone ($R^2 = 0.67$). The addition of age to the relationship was significant when age 2 females were included ($p < 0.001$ for age) but not when this age-class was excluded ($p > 0.05$ for age). As such this confirms earlier evidence for an age-specific difference in fecundity between 2 year old and older North Sea haddock (Hislop, 1988). For a given Kn the slope of the *Fp* – length relationship was significantly higher in the 1990s and 2000s than in the 1970s and 1980s (Figure 10). A change in Kn from 0.8 to 1.2 resulted in about a 50 % increase in *Fp* in both periods.

Common environment

There was no effect of tank on maturity (Wald statistic = 1.55; $P = 0.46$). More than 95% (2/45) of females had cortical alveoli or vitellogenic oocytes in November in the NW group compared to 75% (12/49) in the NE. Maturity was significantly related to sub-population ($t = 2.53$; $P = 0.01$), residual liver weight ($t = 2.11$; $P = 0.04$), and total length ($t = 1.92$; $P = 0.06$). Figure 11 illustrates the estimated combined effects of length and sub-population on maturation probability for a relative liver index of 1.0.

DISCUSSION

Declines in Lp50s were evident within North Sea cod and haddock stocks but the magnitude of change differed markedly among putative sub-populations. Cod from the NE sub-population currently mature around a similar size to that found in the 1970s and even more than a century ago (see Holt, 1893). However, in the coastal western North Sea maturation probability declined markedly in both cod and haddock. The magnitude and rate of Lp50 change found in the NW and S cod sub-populations is comparable to that found in Georges Bank stocks (Barot *et al*., 2004b) and stocks found off Newfoundland (Olsen *et al*., 2004), being close to the highest reported for cod and indeed any other fish species (Jorgensen *et al*., 2007). The North West Atlantic cod stocks have declined substantially, as have the two affected North Sea sub-populations (Holmes *et al*., 2008). In contrast, the lack of detectable change in the

NE cod sub-population is more in line with the low rates of change in the North east Arctic (Heino *et al*., 2002) and Icelandic cod stocks (Pardoe *et al*., 2009). Whilst a compensatory response might have been expected for cod given the decline in the total stock and particularly the north west and south regions (Holmes *et al*., 2008), the downward shift in reaction norms indicates that the change in maturation timing was not linked to competition and growth. Moreover, a compensatory mechanism cannot explain why the trend for lower maturity at age and decreasing Lp50 in haddock was not reversed when the North Sea stock recovered. In the case of haddock, the higher reproductive investment appeared to be at the cost of somatic growth as annual growth declined for maturing age (age 2 and 3) fish from the mid 1990s to the recent decade and condition was lower in the 1990s and 2000s. Yoneda & Wright (2004) also found that the somatic condition of NW cod declined between the 1960s and 2000.

A genetic difference does appear to underlie recent differences in Lp50 estimated from the field, since spatial differences in maturation probability were found to persist in fish held under a common environment. The similarity between field and experimentally derived size-at-maturation estimates in the North Sea is reassuring because the maturation decision takes place many months before field measurements of maturity status are made and little is known about the proximate factors, such as lipid reserves, that influence this decision (Wright, 2007). Indeed, smaller female size at maturity has been found to partly reflect higher relative liver weight in cod (Harrald *et al*., 2010) and the maturation decision phase in haddock coincides with a peak in liver condition (Tobin *et al*., in press).

The intrinsic difference in maturation probability between the east and west North Sea may be enhanced by thermal differences, as the deeper eastern waters are consistently colder in the summer. Annual temperature variability within regions did explain some of the variation around the declining trend in maturation probability with cohort. Summer temperature preceding the year of spawning, i.e. during the maturation 'decision' phase can partly explain the trend in maturation probability and regional differences. This is consistent with recent experimental evidence that a 2°C difference during this period can double the proportion of haddock maturing for a given weight (Tobin & Wright, in review). The positive influence of sea temperature when combined with the positive cohort effect is to strengthen the apparent rate of decline in Lp50's in the NW haddock sub-population and southern North Sea cod.

Potential fecundity of NW haddock in the 1990s and 2000 was considerably higher than that reported previously in North Sea haddock (Raitt, 1932; Alekseyeva & Tormosova, 1979; Hislop & Shanks, 1981). Food availability during the period of vitellogenesis can influence the condition and fecundity of haddock (Hislop et a;. 1978). However, by controlling for somatic condition effects, it does appear that the higher fecundity at size found in this study is unlikely to be related to poorer feeding conditions. Thus the temporal changes in fecundity at size found in this study and in cod from the same region (Yoneda & Wright, 2004), provides further evidence for an increase in reproductive investment.

Whilst we do not have information on regional mortality rates, the rapid decline in maturation probability in the NW and S cod sub-populations occurred following the near collapse of spawning biomass in these regions during the 1980s (Holmes *et al*.,

2008). In the preceding two decades, fishing mortality on ages 2-10 exceeded 1.0 and nearly all demersal fishing effort was concentrated in the coastal NW and southern North Sea (Jennings *et al*., 1999). Conversely, until the current decade, spawning biomass remained high (Holmes *et al*., 2008) and fishing effort was low (Greenstreet *et al*., 1999; 2009) in the one region where the change in PMRN mid-points has been low or negligible. Consequently, it is highly likely that fishing mortality was historically much higher on the sub-populations that have undergone the largest change and hence selection for early maturing genotypes would be expected to have been higher.

The different trends in maturation probability among North Sea sub-populations highlight the need to account for population structuring in assessing changes. Stock level sampling may become biased towards the most abundant sub-population, as fish from declining areas become too scarce to maintain stratified sampling programmes. Consequently, if rapid declines in PMRN reflect a collapsing stock component, as found in the present study, stock level estimates will tend to underestimate the magnitude of change. A previous study has considered population structure in their application of PMRN by weighting samples from different stock components (Pardoe *et al*., 2009). However, weighting could still give a misleading trend if life history responses to environmental change or selective pressures diverged between different sub-populations.

In conclusion the combined results on maturation, fecundity and post-maturation somatic growth indicate that reproductive effort has increased since the 1970s in some sub-populations of North Sea cod and haddock. Whilst we cannot be certain of the

causes of the observed changes in maturation probability it is possible to rule out some explanations. The slowest growing sub-population matured at a larger size which is contrary to expectations from counter-gradient selection (Conover *et al*., 2006). Neither, regional temperature nor conspecific biomass could fully explain the highly significant negative trends in Lp50s. Therefore, given the likely intense periods of size-selection mortality in the NW cod and haddock sub-populations and the S cod sub-population, selection for early maturing genotypes appears to be the most parsimonious explanation for the temporal changes in reproductive effort. The present study does however, highlight that the combined effects of phenotypic responses to temperature and genetic selection for earlier and smaller size at aturation could lead to bias in the estimate of evolutionary rates based on PMRN alone.

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Tables

Table 1. Estimated change (weighted linear regression) of estimates in cod PMRN midpoints (Lp50s) between 1976 and 2005 cohorts and significance of trend.

Sub-population	Sex	cm	P
NE	F	-1.7	0.49
NE	M	-0.1	0.12
NW	F	-32.6	0.04
NW	M	-17.4	0.03
S	F	-25.2	<0.0001
S	M	-30.6	0.01

Table 2. Coefficients, standard errors and significance (* 0.05, ** 0.01, ***<0.001) of effects on PMRN covariate model for cod from the NE (p1), NW (p2) and S (p3) sub-populations.

Female				Male			
	Estimate	Std. Error			Estimate	Std. Error	
(Intercept)	-7.28	0.6	***	(Intercept)	-3.27	0.47	***
length	0.08	0.01	***	length	0.07	0.01	***
factor(age)3	1.2	0.16	***	factor(age)3	0.9	0.15	***
factor(age)4	1.23	0.35	***	factor(age)4	0.72	0.36	*
p1	9.58	1.82	***	p1	8.08	1.65	***
p2	2.18	1.06	*	p2	0.8	0.67	
length:p1	0.07	0.01	***	length:p1	0.12	0.01	***
length:p2	0.04	0.01	***	length:p2	0.05	0.01	***
factor(age)3:p1	-1.65	0.33	***	factor(age)3:p1	-2.24	0.32	***
factor(age)4:p1	-2.4	0.48	***	factor(age)4:p1	-2.73	0.48	***
factor(age)3:p2	-0.57	0.27	*	factor(age)3:p2	-0.74	0.25	**
factor(age)4:p2	-1.9	0.61	**	factor(age)4:p2	-0.5	0.55	
p3:b	-0.03	0.04		p3:b	-0.14	0.04	***
p1:b	0.38	0.07	***	p1:b	0.42	0.07	***
p2:b	-0.43	0.12	***	p2:b	-0.13	0.08	
p3:t	2.17	0.33	***	p3:t	0.32	0.28	
p1:t	3.9	0.74	***	p1:t	4.14	0.69	***
p2:t	0.12	0.49		p2:t	0.39	0.38	

Table 3. Estimated change (weighted linear regression) of estimates in haddock PMRN midpoints (Lp50s) between 1976 and 2005 cohorts and significance of trend.

Sub-population	Sex	Length change (cm)	P
NE	Female	-7.6	0.06
NE	Male	-7.4	<0.0001
NW	Female	-7.6	0.0001
NW	Male	-6.6	0.0001

Figures

Figure 1. Location of the three regions corresponding to putative sub-populations of cod and haddock from the southern (S; cod only), north west inshore (NW) and north east offshore (NE) North Sea.

Figure 2. Time series trends by cohort in annual growth in cod between the ages a) 2-3 and b) 3-4 (stippled line S, solid line NW and dotted line NE).

Figure 3. Probabilistic maturation reaction norm midpoints (Lp50s) for age 3 female (closed circles) and male (open circles) North Sea cod from the NE (cohorts 1976 – 2005), NW (cohorts 1979 – 2005) and S (cohorts 1976 – 2005) sub-populations.

Figure 4. Time series trends by and degree days in the summer by year by sub-population region (stippled line S, solid line NW and dotted line NE). Comparable trends in cod biomass and haddock biomass are also given.

Figure 5 Covariate Lp50 estimates for 3 year old cod plotted against cohort for each sex and sub-population. The blue line shows the model fit in which temperature and cod biomass were used in addition to the smooth trend in cohort; the green line shows the model fit in which only temperature is used in addition to the cohort trend with biomass fixed at 1976 level whilst the red line shows the cohort effect with both temperature and conspecific biomass fixed at 1976 levels.

Figure 6. Predicted relationship between maturation and length in August for cod (age 2 – NW and S; age 3 – NE) reared under a common environment. Solid line is fit, stipled lines indicates ±1 standard error.

Figure 7. Annual growth increments for ages 1 to 2 in the NW (solid line) and NE (dotted line) North Sea sub-populations of haddock.

Figure 8. Probabilistic maturation reaction norm midpoints (Lp50s) for female and male North Sea haddock from the west and east North Sea sub-populations (cohorts 1976 – 2005). Closed circles represent females, open circles represent males. Lines denote significant regressions for females (solid line) and males (dotted line).

Figure 9. Predicted probability of maturation for a 25 cm age 2 haddock showing estimated cohort trends. The stipled line is based on model r3 with the addition of a temperature term, whilst the solid line illustrates cohort effect alone when temperature is fixed at 1976 (NE) or 1977 (NW) levels.

Figure 10. Relationship between potential fecundity and total length in the west North Sea haddock sub-population at age 3. Prediction lines for GLM fitted to potential fecundity at length and Kn, with Kn. set at 1 for the 1970s (dashed line), 1980s (solid dark grey line), 1990s (solid light grey line) and 2000s (solid black line). Dotted lines represent lower standard errors.

Figure 11 Predicted relationship between maturation and length in August for haddock reared under a common environment for a relative condition of 1.0. Solid line is the fit, stipled lines refer to ±1 standard error.

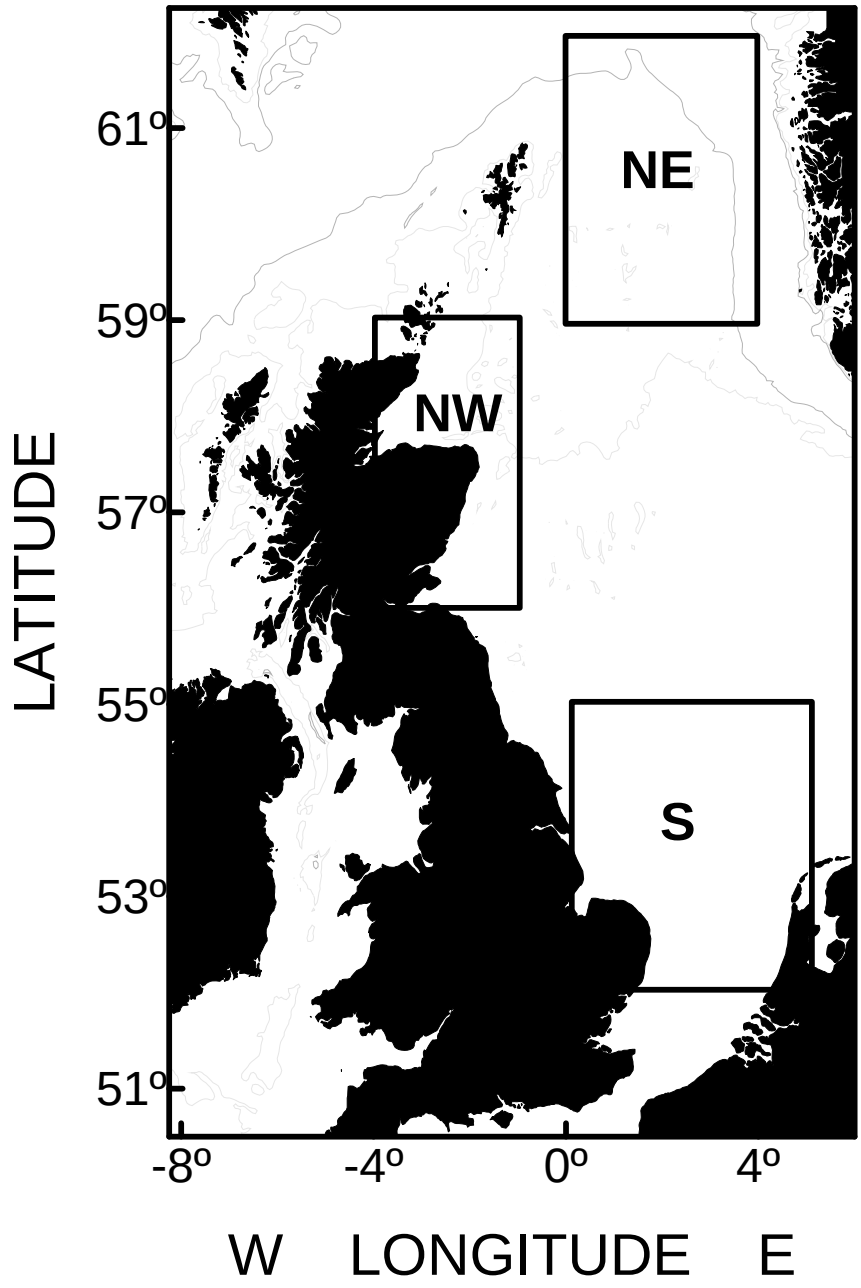
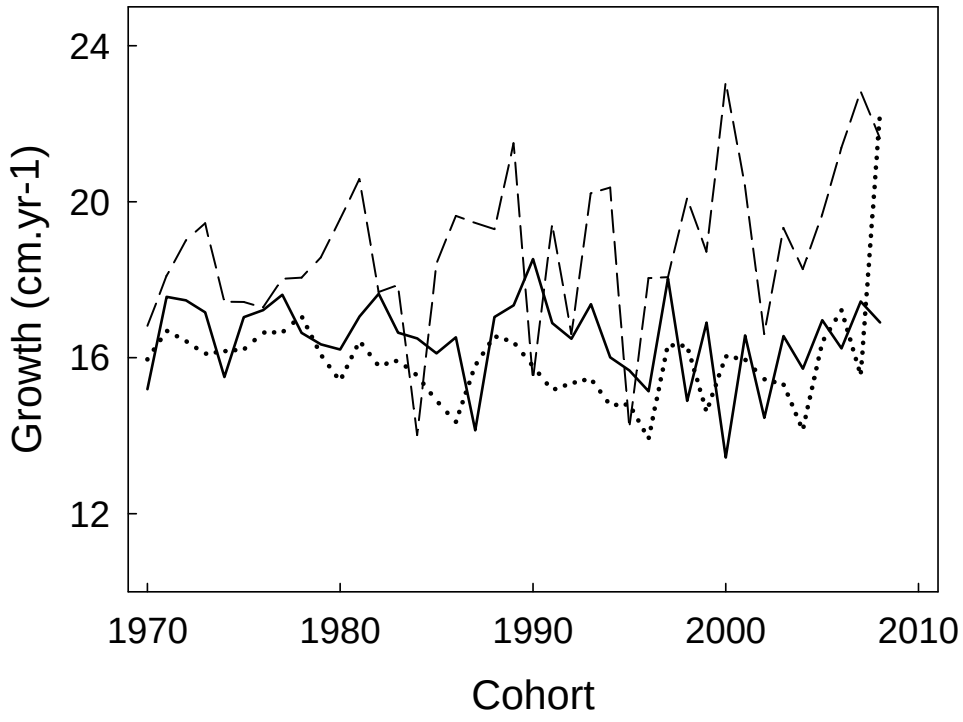
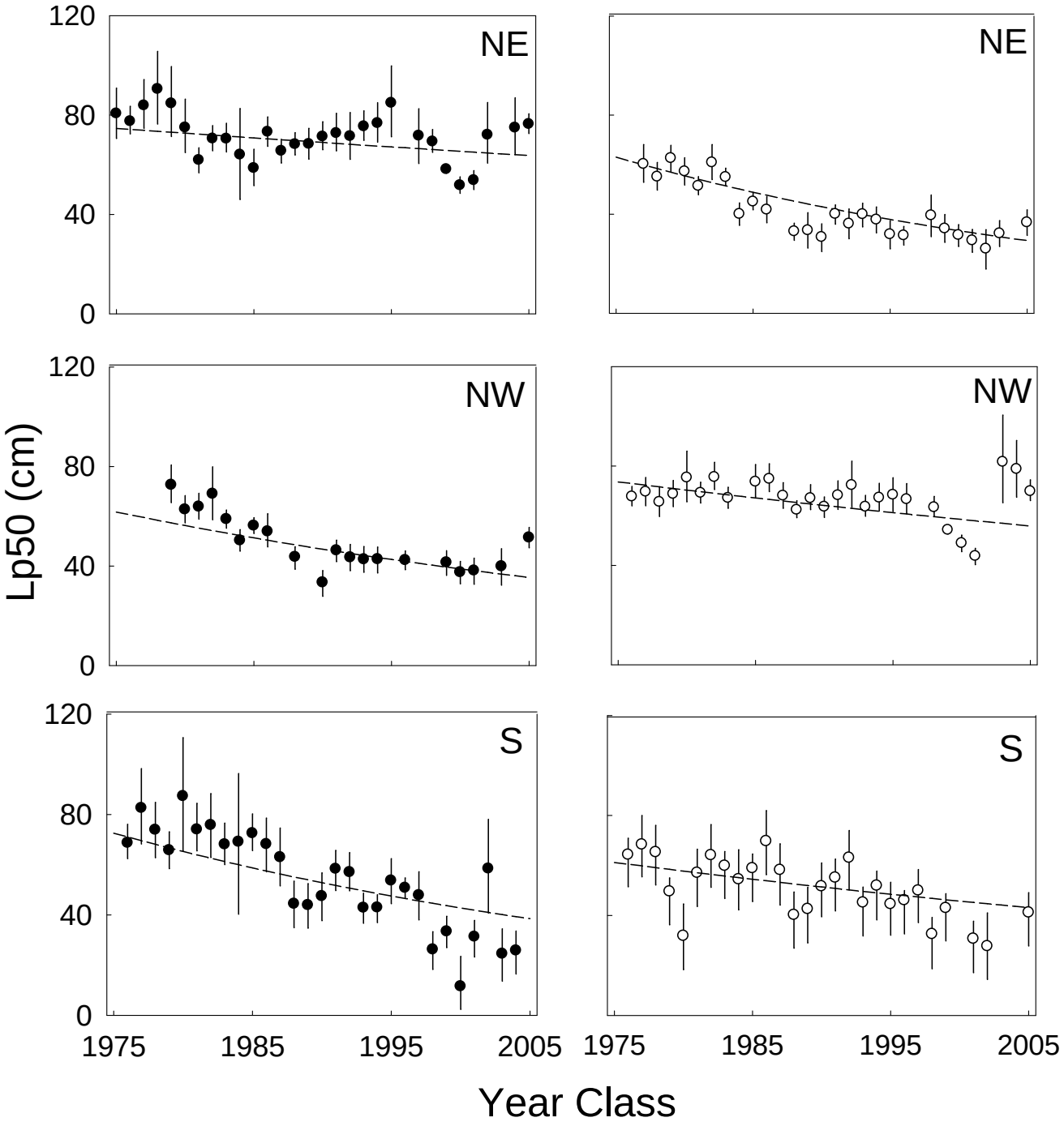
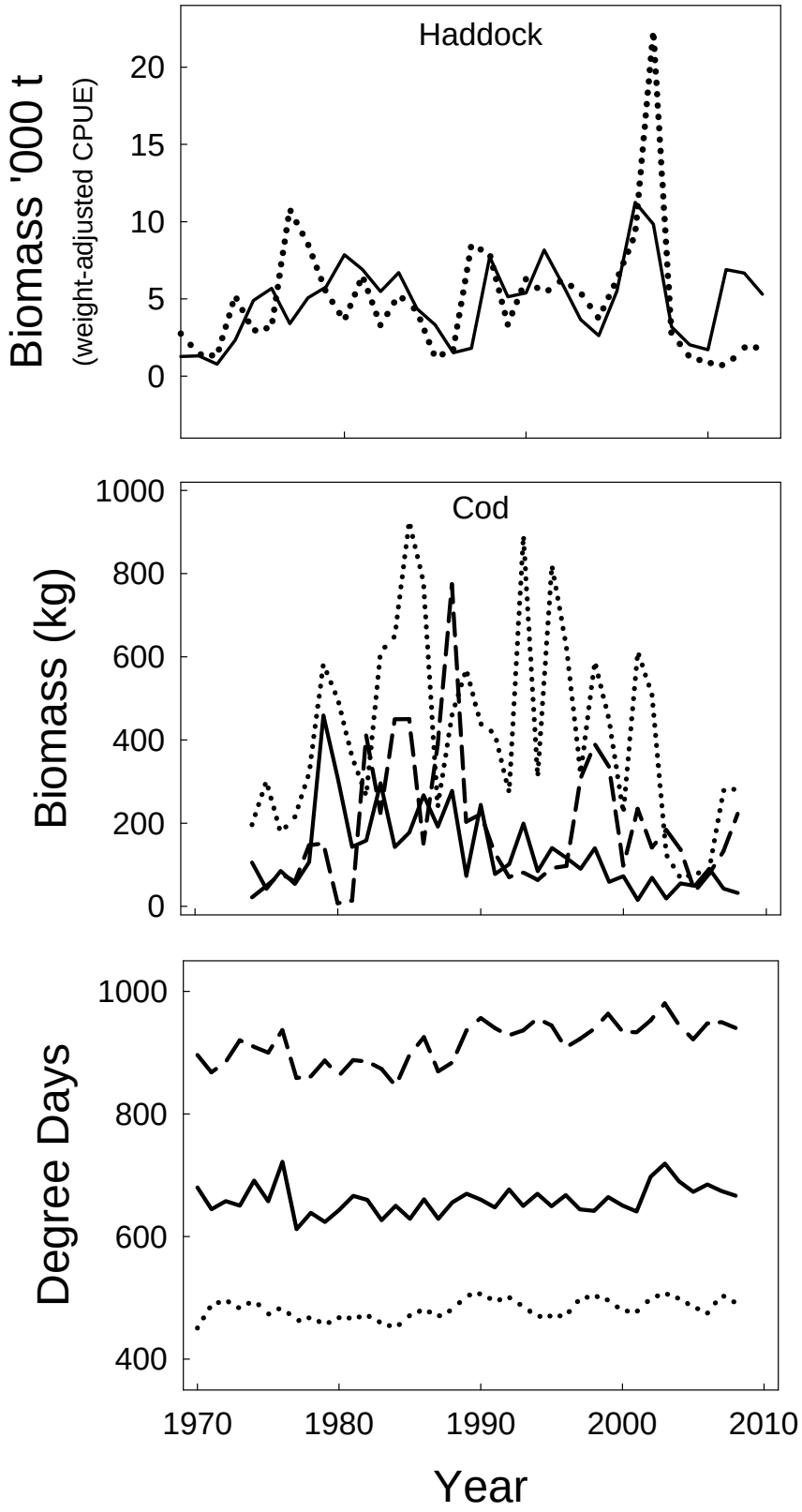
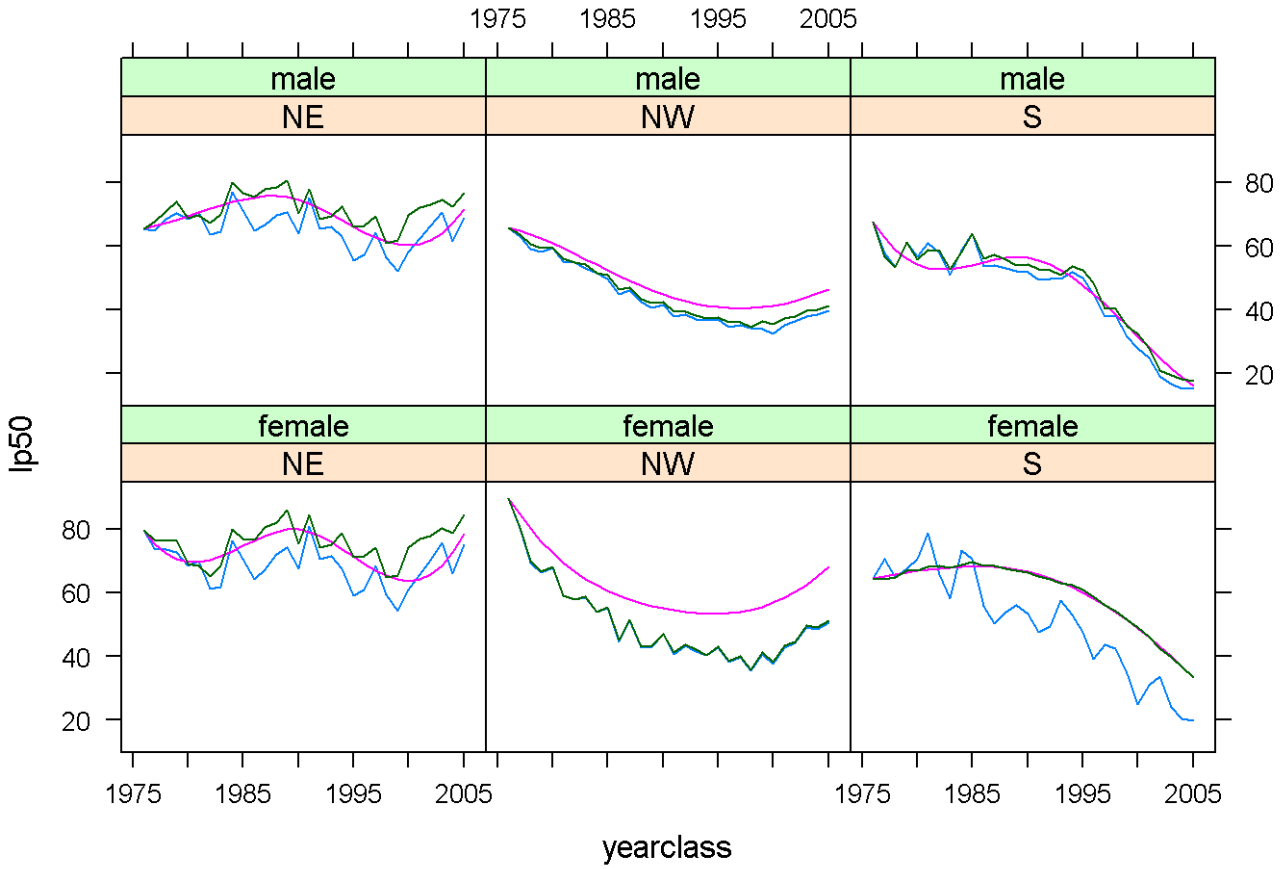

NE
NW
S
61º
59º
57º
55º
53º
51º
LATITUDE
-8º
-4º
0º
4º
W LONGITUDE E

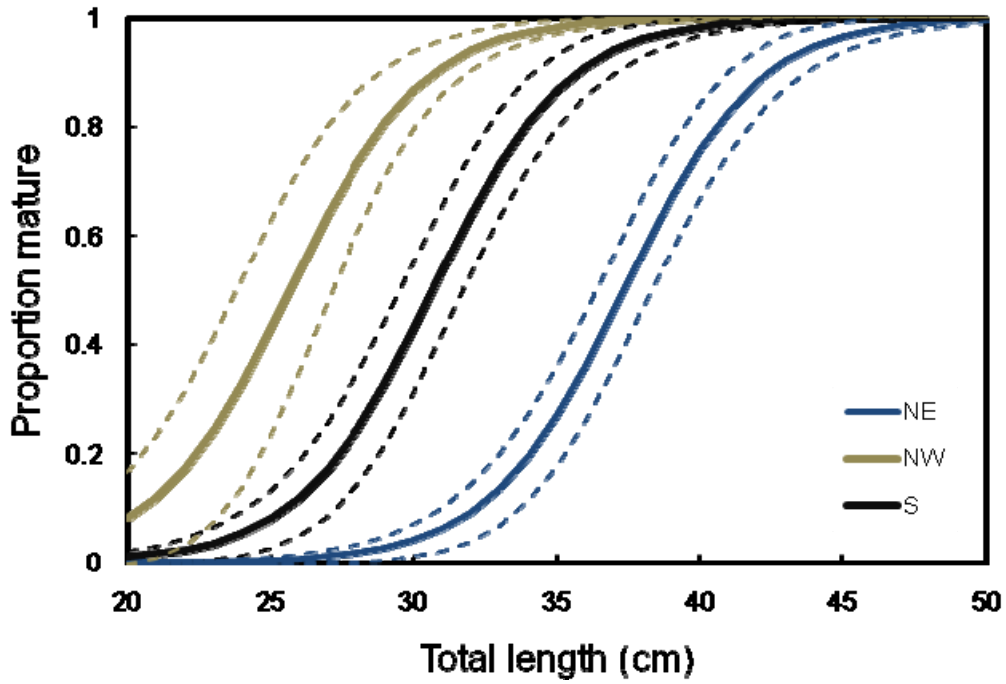
Fig. 1

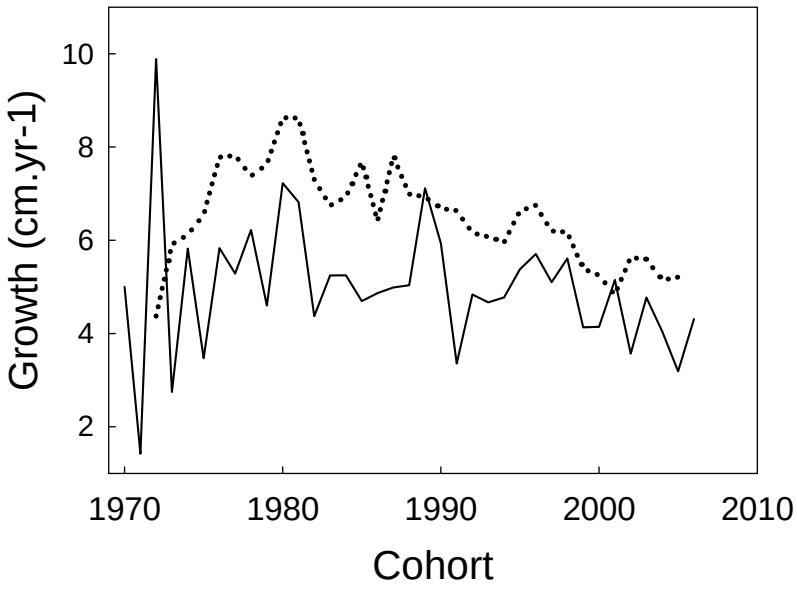

24
20
16
12
Growth (cm.yr-1)
1970
1980
1990
2000
2010
Cohort

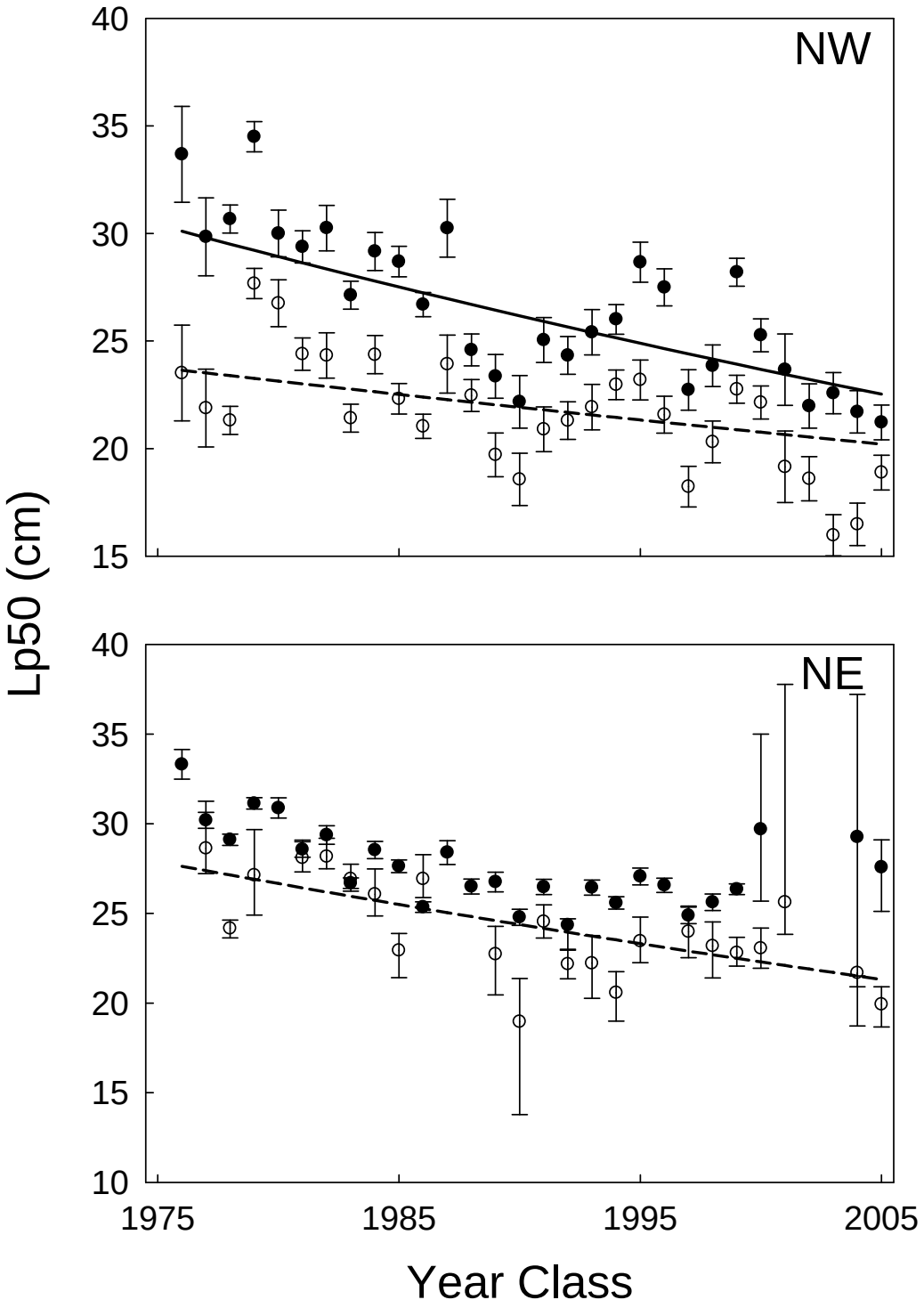

NE
NE
NW
NW
S
S
Lp50 (cm)
120
80
40
0
1975
1985
1995
2005
Year Class


Haddock
Biomass '000 t
(weight-adjusted CPUE)
20
15
10
5
0
Cod
Biomass (kg)
1000
800
600
400
200
0
Degree Days
1000
800
600
400
1970
1980
1990
2000
2010
Year


male
NE
male
NW
male
S
female
NE
female
NW
female
S
lp50
yearclass
1975
1985
1995
2005
20
40
60
80


Proportion mature
1
0.8
0.6
0.4
0.2
0
20
25
30
35
40
45
50
Total length (cm)
NE
NW
S


Growth (cm.yr-1)
10
8
6
4
2
1970
1980
1990
2000
2010
Cohort


NW
NE
Lp50 (cm)
Year Class
40
35
30
25
20
15
10
1975
1985
1995
2005

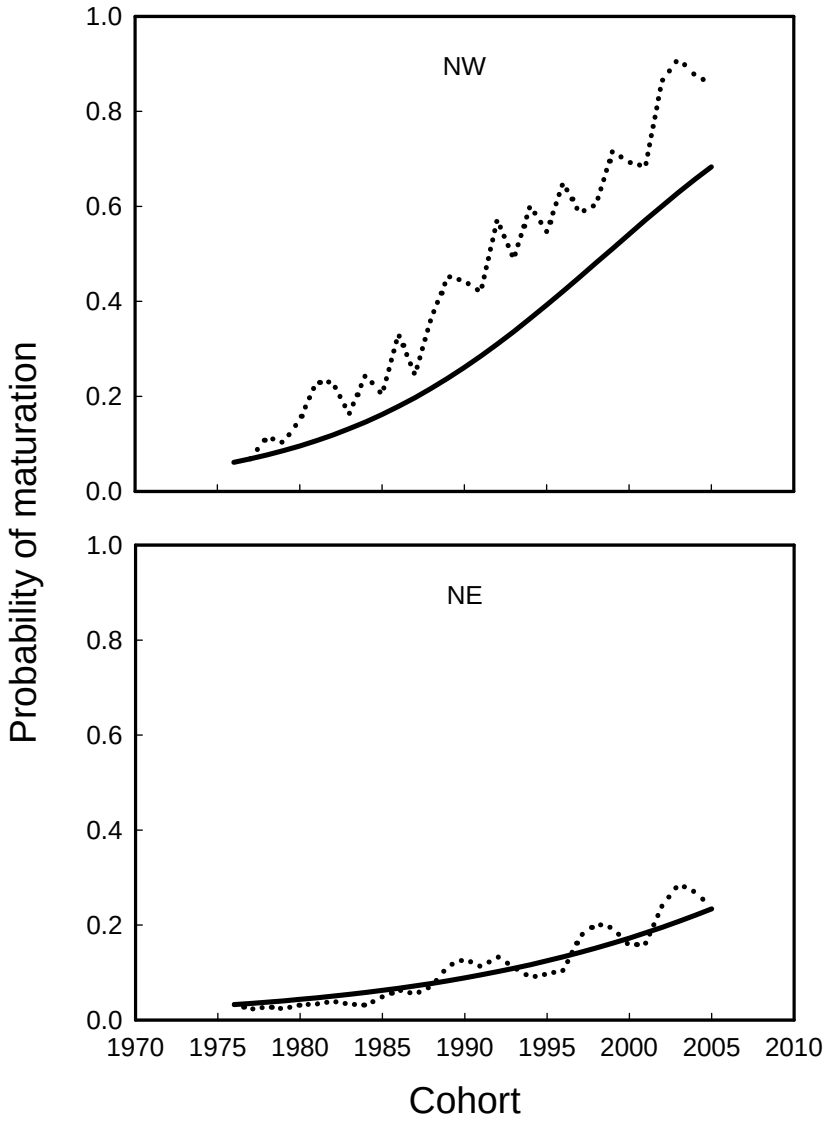

NW
NE
Probability of maturation
Cohort
0.0
0.2
0.4
0.6
0.8
1.0
1970
1975
1980
1985
1990
1995
2000
2005
2010

Figure 9.

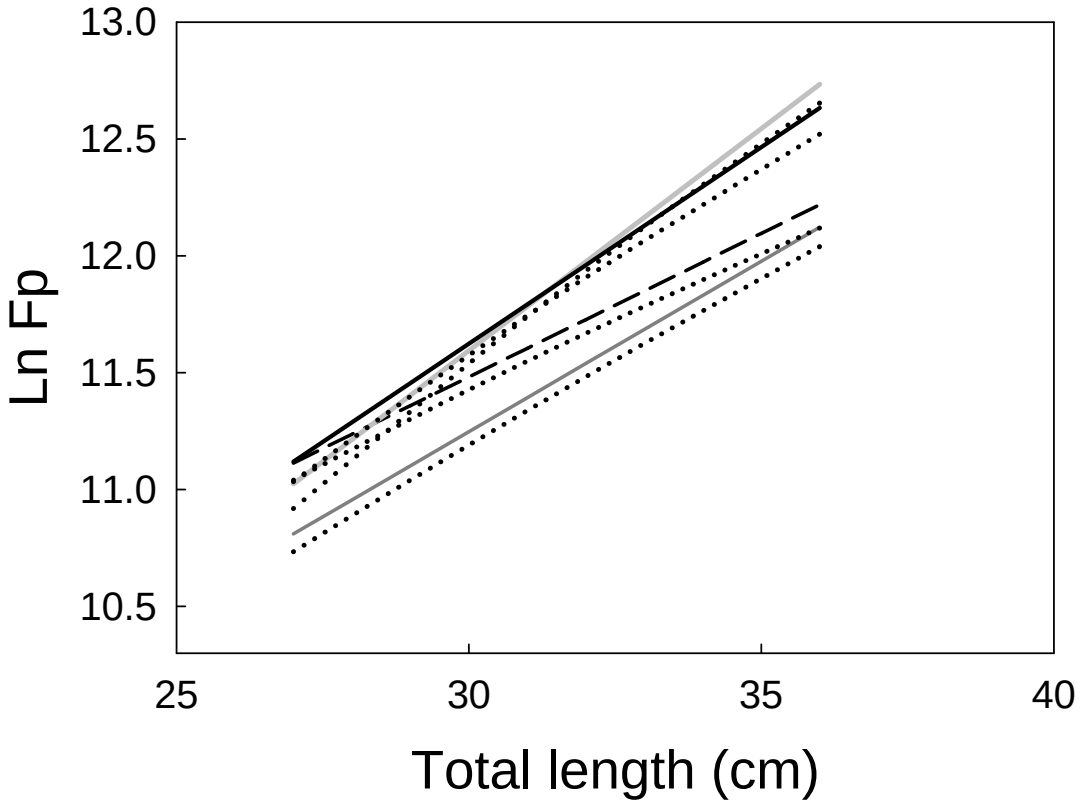
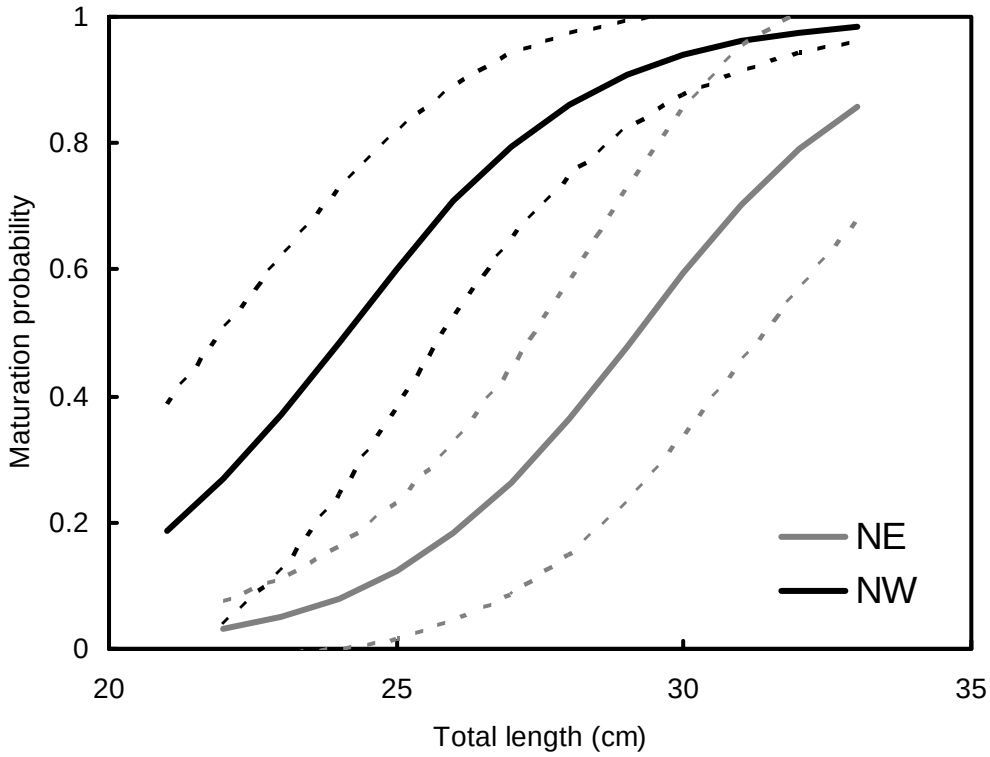


Figure 10


1
0.8
0.6
0.4
0.2
0
Maturation probability
20
25
30
35
Total length (cm)
NE
NW