

Reproductive investment in the North Sea haddock: temporal and spatial variation

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ABSTRACT: Maturation and fecundity have been examined since the 1970s in 2 putative sub-populations of North Sea haddock *Melanogrammus aeglefinus*. Reproductive investment within the western North Sea haddock sub-population significantly increased between the 1970s and 2000s, as was evident from both a decline in maturation probability and an increase in fecundity with size. A decline in maturation probability was also evident in males from the east North Sea, although the length at 50% probability of maturing (Lp50) at the beginning and end of the study period was much higher than in the west North Sea. The changes in reproductive traits could not be explained as a compensatory response, since the trend for increasing reproductive investment was not reversed when the North Sea stock recovered over the past decade. Indeed increased reproductive investment was accompanied by a reduction in somatic growth rate. Temperature immediately prior to secondary gametogenesis could partially explain inter-annual variation in female maturation probability and may have influenced the difference in sub-population trends. However, declines in maturation probability with cohort were still highly significant after accounting for a temperature effect, and differences in potential fecundity could not be explained by changes in somatic condition. Overall, it appears that west North Sea haddock have increased their reproductive effort, following decades of high mortality, consistent with an evolutionary response.

KEY WORDS: Life-history theory · PMRN · Maturation · Fecundity · Haddock

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INTRODUCTION

Reproductive investment is an important fitness-related trait because it is closely associated with the quantity and quality of offspring produced (Roff 1992). In heavily exploited fish stocks, the reproductive life span can be substantially reduced relative to that in an unexploited stock (Dunlop et al. 2009). Hence exploitation is expected to select for early-maturing phenotypes and increased reproductive effort (Law 2000). Many changes in reproductive traits that have accompanied declines in exploited fish stocks appear consistent with selection for increased reproductive investment (Law 2000, Dieckmann & Heino 2007). However, reproductive traits vary due to an interaction between inherited and environmental factors and so it is difficult to distinguish between the effects of phenotypic plasticity and genotypic selection in the wild (Conover & Schultz 1995, Kokita 2003, Otterå et al. 2006, Heino et al. 2011). As plastic changes are likely to be easily reversible whilst genetic changes are not, it is impor-

tant to understand the causes of change in reproductive traits (Law 2000, Enberg et al. 2009). From the viewpoint of stock management, genetically induced selection for early maturation and higher reproductive investment should lead to a low yield stock (Law 2000) with a higher reproductive potential (Trippel et al. 1997a, Marshall et al. 1998, Scott et al. 1999). Thus, it is important to understand changes in reproductive traits for both medium term predictions of recruitment and long-term management plans.

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; Dieckmann & Heino 2007). For example, earlier and higher reproductive investment may 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 maturation reaction norm (PMRN) approach has

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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, and is independent of variations in growth and survival. Additional factors known to influence maturation such as condition (Marteinsdóttir & 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 its energetic state when the initial threshold physiological maturation switch was made (Wright 2007). Further, the PMRN method can be confounded by unaccounted for plastic effects influencing maturation. For example, experimental evidence for a direct effect of temperature on the maturation process (Dhillon & Fox 2004, Tobin & Wright 2011) demonstrates that this factor cannot be accounted for from just the resulting growth changes. Consequently, it is important to consider potential sources of phenotypic plasticity in the estimation of PMRNs (Morita et al. 2009).

Few studies have considered selection for reproductive traits other than maturation. As capital breeding fish tend to maintain size-specific fecundity, except under very poor feeding conditions (Hislop et al. 1978, Rijnsdorp 1990), temporal changes in fecundity in fish may reflect a genotypic response (Rijnsdorp et al. 2005). Life-history theory predicts that higher mortality on all ages would select for an increase in the intercept of the fecundity–size relationships (Gadgil & Bossert 1970), whilst lower adult survival would lead to an increase in the slope (Rochet et al. 2000). 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). Nevertheless, changes consistent with these predictions have been found in plaice *Pleuronectes platessa* (Rijnsdorp et al. 2005, van Walraven et al. 2010), Atlantic cod *Gadus morhua* (Yoneda & Wright 2004) and most convincingly in the whitefish *Coregonus lavaretus* (Thomas et al. 2009). As with maturation it is important to consider the effect of condition, as varying food intake can affect the fecundity–size relationship (Hislop et al. 1978).

The haddock *Melanogrammus aeglefinus* is a commercially important gadoid. In the North Sea the spawning stock biomass declined to very low levels in the early 1990s following a peak in the late 1960s and 1970s (ICES 2009). The total stock has since rebounded following a substantial reduction in fishing mortality combined with a few high years of recruitment. Haddock are concentrated north of the Dogger Bank with

major spawning areas in the northern North Sea and off the Scottish east coast (Saville 1959, Hedger et al. 2004). These 2 concentrations of spawning may reflect different sub-populations since differences in allozyme frequency have been detected between spawning haddock from either side of the Greenwich meridian (Jamieson & Birley 1989), tagged coastal haddock rarely move into the deeper north east waters (Jones 1959) and regional variation in growth characteristics have been reported (Jones & Hislop 1972).

In the present study, temporal changes in reproductive effort were considered from an analysis of maturation, growth and fecundity. Trends in maturation schedules from the 2 putative North Sea haddock sub-populations (W: coastal west; E: offshore east) were examined using the demographic PMRN approach (Barot et al. 2004). To account for the effect of temperature on maturation, trends were examined in relation to degree days during the summer period of maturation liability in haddock (Tobin et al. 2010). The biomass of haddock was also used as a covariate in order to consider competition for resources. Fecundity and body condition for haddock from the 2 North Sea sub-populations in the 1990s and 2000 were compared with similar data for the 1970s and 1980s. The possible causes of temporal and spatial trends are discussed with respect to predictions about environmentally and genetically induced changes in life-history traits.

MATERIALS AND METHODS

Sample data. Data on sex, maturity, age and length for the 1st quarter International Council for the Exploration of the Sea (ICES) International Bottom Trawl SMALK (Sex–Maturity–Age–Length Keys) were extracted from the DATRAS database. The bottom trawl surveys were undertaken between January and March, overlapping the February to May spawning period of haddock in the North Sea (Hislop 1984, Wright & Gibb 2005). In these surveys, data were collected conditional on length and ICES roundfish area, as the primary purpose was to produce age–length keys for raising length frequency data. This dataset was supplemented with additional research and commercial trawl sampling in years 1977, 1980, 1985, 1994–1996, 1999, 2003–2004, 2007–2008. Data from the 1970s for the west North Sea were from Hislop & Shanks (1981). All SMALK data were segregated into 2 regions corresponding to the main centres of the putative sub-populations from the W and E North Sea (Fig. 1). The SMALK data were total length (cm), age and maturity stage, as either 2 stages before 1990 (0, immature; 1, mature) or 4 stages after 1990 (1, immature; 2, developing; 3, spawning; 4, spent). In addition,

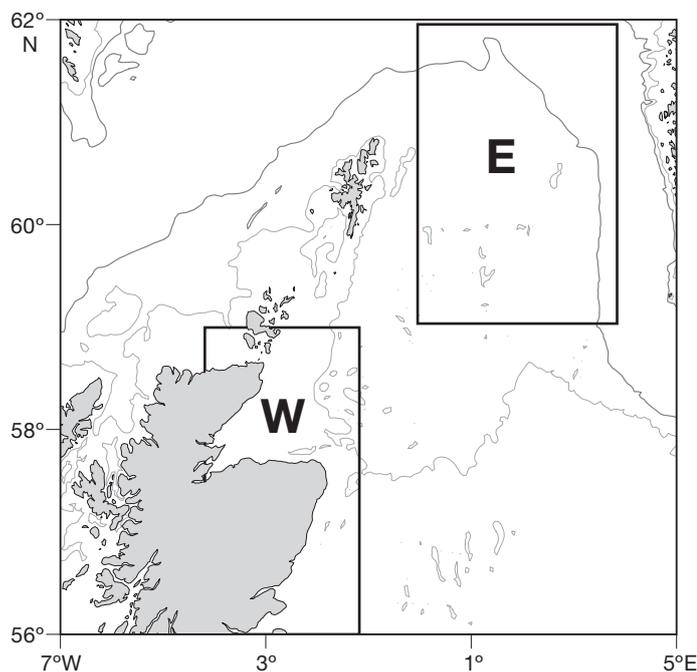


Fig. 1. *Melanogrammus aeglefinus*. Locations of sample collection in the North Sea. Sub-populations — W: coastal west; E: offshore east

supplementary data had information on total, eviscerated, gonad and liver mass measured to the nearest 0.1 g. Sagitta otoliths were collected for estimation of individual age. The incidence of *Lernaeocera branchialis* was also recorded as this parasite is known to affect fecundity in haddock (Hislop & Shanks 1981). A summary of the collected data by cohort, age and sub-population is shown in Table 1.

Probabilistic maturation reaction norm estimation.

As the data available for this study did not distinguish between first-time and repeat spawners, retrospective PMRNs were estimated using the demographic method of Barot et al. (2004), which relies on individual records of age (a), size (s ; in this case total length), and maturity (0/1). Estimation of the probability of maturing for the first time involved estimation of a maturity ogive, $o_{a,s,c}$ for a given age, size and cohort (c). Using the same ogive and decreasing size by the annual increment of a cohort gives the probability of being mature the preceding year, $o_{a-1,s-\Delta s,c}$. This allows consideration of only immature fish and the probability of maturing for the first time. The probability of having matured for the first time at age a size s in cohort c is thus:

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

Linear interpolation was used to estimate the size at which m is 50%, giving the PMRN midpoint or Lp50. The method assumes that immature and mature individuals within a given age- and size-class have the

Table 1. *Melanogrammus aeglefinus*. Number at age (1–4 yr) and percent that are female for each sub-population region (W: coastal west, E: offshore east) by data source (DS: dedicated research and commercial surveys, IBTS: International Bottom Trawl Survey).

| Data type, cohorts | No. at age | | | | Total | Female (%) |
|--------------------------------|------------|------|------|------|-------|------------|
| | 1 yr | 2 yr | 3 yr | 4 yr | | |
| E | | | | | | |
| DS 1990–98, 2000, 2003–05 | | | | | | |
| Total | 4 | 484 | 2568 | 1971 | 5027 | 54 |
| Mean per cohort | 4 | 97 | 428 | 246 | | |
| IBTS, 1975–2005 | | | | | | |
| Total | 664 | 2514 | 2040 | 1052 | 6270 | 47 |
| Mean per cohort | 26 | 90 | 70 | 36 | | |
| W | | | | | | |
| DS 1990–04, 1999–2001, 2003–05 | | | | | | |
| Total | – | 182 | 1604 | 1346 | 3132 | 76 |
| Mean per cohort | – | 36 | 267 | 192 | | |
| IBTS, 1975–2005 | | | | | | |
| Total | 2032 | 2015 | 1633 | 975 | 6655 | 52 |
| Mean per cohort | 88 | 81 | 60 | 36 | | |

same survival and growth rates, although this estimation is relatively robust to a relaxation of this assumption (Barot et al. 2004). PMRNs were estimated separately for males and females for each sub-population, age and cohort. Temporal trends were reported using PMRN midpoints. Analyses were limited to the 2 age-classes at which haddock first mature, i.e. 2 and 3, thus also requiring age 1 for estimation of growth increments and maturity. 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:

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

where age and cohort were treated as factors with individual maturity state as a binary response variable.

As SMALK data were from a length stratified sampling programme, annual length changes between ages 1 and 5 caught in research bottom trawls were estimated from the whole haul samples, using age stratified length frequency compositions raised to catch per hour from the DATRAS database. Mean length-at-age for each sub-population and cohort were estimated from a Generalized Linear Model (GLM):

$$\text{length} \sim \text{subpopulation} \times \text{cohort} \times \text{age} \quad (3)$$

where sub-population, cohort and age were treated as factors. Numbers at length were weighted by the catch per hour. The differences between predicted lengths-at-age were then used to estimate annual growth (Δs in Eq. 1) for a specific cohort from each sub-population.

Uncertainty in PMRN estimates was derived from the maturity ogive only. As the maturity data were sampled conditional on length and ICES roundfish area, bootstrap re-sampling of the data was not considered due to the complexity of the re-sampling design that would be required. Instead parametric bootstrapping was used. Using the ogive model parameter estimates and the estimated variance covariance matrix of these estimates, 9999 maturity ogives were simulated for each age and cohort combination, 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, sub-population 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 >10% 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 using inverse variance weighting (the variances were calculated directly from the simulated Lp50s). The magnitude of change was then calculated as:

$$(Lp_2 - Lp_1) / Lp_1 \quad (4)$$

where Lp_1 and Lp_2 refer to the Lp50 at the beginning (t_1) and end (t_2) of a data period, respectively. The apparent rate of evolutionary change, in the standard unit 'darwin', was calculated as:

$$\frac{\ln(Lp_2/Lp_1)}{\Delta t \times 10^{-6}} \quad (5)$$

Potential explanatory factors affecting the proportion mature. Since most haddock mature for the first time at age 2, trends in maturation probability of this age class were examined using logistic regression with temperature and competitive biomass as covariates. As the period of maturation liability in haddock occurs between the summer solstice and prior to September (Davie et al. 2007, Tobin et al. 2010), a prediction of degree days in July and August derived from the NORWECOM model was used (Skogen et al. 1995, Skogen & Soiland 1998; see ftp.imr.no/morten/WGOOFE_hindcast). There is a considerable overlap in the distribution and diet of different sized haddock as well as evidence for intra-specific competition between cohorts (Jones 1983). Therefore, a measure of competitive biomass, i.e. the biomass with which an individual fish has to compete for resources, was estimated for ages 1 to 3 from 1st quarter age stratified length frequency data, converted to weight frequency using the following relationship derived from all available years and specimens (N = 15835), inversely weighted by the number of samples within a year:

$$\text{mass} = 0.00622 \times \text{length}^{3.073} \quad (6)$$

where mass is eviscerated mass in g and length is total length in cm ($R^2 = 0.93$, $p < 0.001$). The temperature and biomass estimates were delimited to the same 2 sub-population regions as defined for the maturity data.

The full maturation model was:

$$\text{logit}(m) = (\text{sub-population} + \text{sex}) \times (\text{length} \times s[\text{cohort}] \times \text{temp} \times \text{biomass}) \quad (7)$$

where s denotes a spline with 4 degrees of freedom. The spline allows the probability of being mature to change smoothly with cohort within sub-population. The degrees of freedom were chosen based on model fit and the variation explained by this term. Model selection was through backwards stepwise selection of variables based on Akaike's Information Criterion (AIC). Due to a problem with over dispersion in the survey data a quasi-binomial link function was used.

Fecundity and condition. Variation in condition for the 4 decades, 1970s, 1980s, 1990s and 2000s, was examined for W haddock females sampled during the first quarter of the year from the supplementary data series. Similar data on E haddock females was only available for the 2 recent decades. The effect of decade on the eviscerated mass-length relationship was examined through the addition of this factor within a GLM. Length and mass was first log transformed to account for the allometry and increasing variance between these 2 variables. Only females with developing ovaries (vitellogenic oocytes) from the 2 ages at first maturity (2 and 3) were considered, as somatic condition can decline in spawning fish. In order to illustrate trends in mass for a given length, relative condition factor (K_n ; Le Cren 1951) was used to give an indication of somatic condition:

$$K_n = \frac{\text{mass}}{\hat{\text{Mass}}} \quad (8)$$

where mass refers to eviscerated mass (g) of an individual and $\hat{\text{Mass}}$ is the expected eviscerated mass calculated from the relationship for all specimens of females with developing ovaries (N = 2906):

$$\hat{\text{Mass}} = 0.0045 \times \text{length}^{3.17} \quad (9)$$

where length is total length in cm ($R^2 = 0.96$, $p < 0.001$).

Potential fecundity (F_p) was estimated from females with developing ovaries in 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. Gravimetric fecundity estimation was used in all of the studies, according to:

$$F_p = \frac{\text{mass}_{\text{ovary}}}{\text{mass}_{\text{sample}}} \times \text{number}_{\text{vitellogenic}} \quad (10)$$

where sample mass was around 0.3 g of ovary tissue. This method was used in order to compare with similar data from the 1970s (Hislop & Shanks 1981) and 1985 (J. Hislop unpubl. data). As the 1970s and 1985 studies did not consider pre-ovulatory atresia the temporal comparison was limited to F_p only.

Differences in potential fecundity–size relationships between decades of study were compared using a GLM according to the following model:

$$F_p = \text{length} \times K_n \times \text{age} \times \text{decade} \quad (11)$$

where age and decade were treated as factors, allowing a different intercept and slope for each age and decade. Eviscerated mass was also considered as an alternative to length. Specimens infected with *Lernaeocera branchialis* were not included in analyses. As with similar studies by Yoneda & Wright (2004), a gamma response distribution coupled with a log-link function 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, where deviance was analogous to the residual sums of squares (Swartzman et al. 1995).

RESULTS

Age, cohort and sub-population and the interactions between these factors all had a significant effect on length (GLM F -test, $p < 0.001$). W haddock were significantly larger than E haddock at age 1 (mean length W = 16.8 cm, E = 14.8 cm) and there was no significant trend in age 1 length with cohort. In contrast, length at age 2 was similar between the 2 sub-populations and so average annual growth increments between ages 1 and 2 were 8.1 and 11.0 cm in the W and E sub-populations, respectively. There was a significant decline in the length of ages 3 and 4 during the study period ($p < 0.001$), leading to a significant reduction in the annual growth increment between ages 2 and 3 and between ages 3 and 4 in both regions ($p < 0.001$; Fig. 2).

There were significant changes in the intercept and slope of the $\log(\text{mass})$ – $\log(\text{length})$ relationship for ages 2 and 3 W haddock over the 4 decades of sampling (GLM F -test, $p < 0.001$). This was due to the significantly lower mass for a given length by the 2000 decade. These changes in the mass–length relationship can be seen as a decline in K_n from above to below 1.0 (Fig. 3). Haddock from the E sub-population had a higher condition than those from the W in the 2000 decade ($F_{1,1903} = 149.6$, $p < 0.001$).

PMRNs

Between the 1976 and 2005 cohorts, the proportion of mature female age 3 haddock in samples increased from 0.71 to 1.0 in the E sub-population and from 0.86 to 1.0 in the W sub-population. At the start of the study period the Lp50 estimates for 3 year olds were 28.6 and 33.1 cm for male and female (respectively) W haddock. However, by the mid-1980s there was insufficient variation in maturity state to provide meaningful Lp50 estimates for this age-class. Therefore, only age 2 Lp50 trends are presented (Fig. 4). The initial and final Lp50 estimates for females from the E sub-population remained well above the mean length of this age-class (i.e. 26 cm) and the negative trend with cohort was not significant ($p = 0.06$). In contrast, the inverse variance weighted trend in Lp50s with cohort for males in the E sub-population was significant, declining by 6.6 cm between the 1976 and 2005 cohorts ($p < 0.001$). Similarly, there was a highly significant decline in Lp50 in age 2 males and females from the W sub-population of 7.4 and 7.6 cm, respectively. These declines in reaction norm midpoints mean that maturation at a given

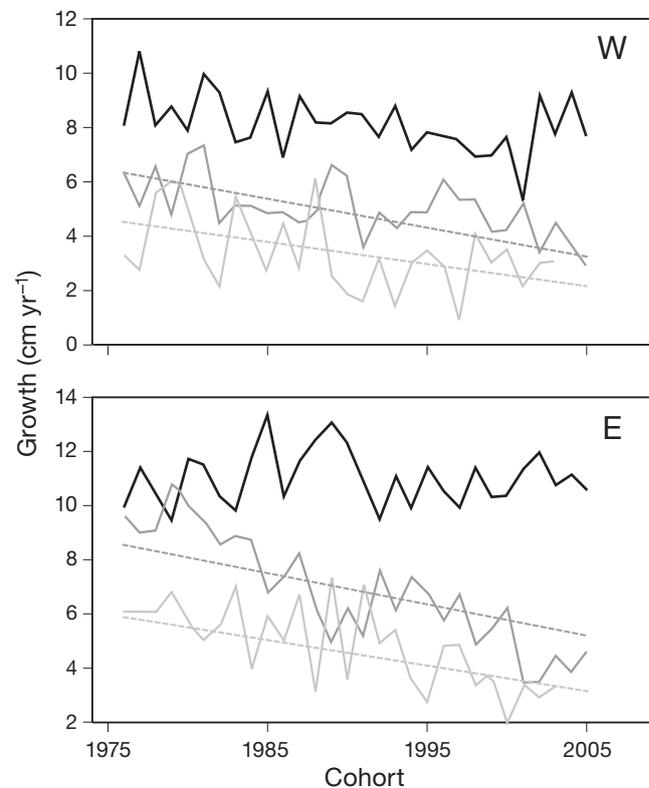


Fig. 2. *Melanogrammus aeglefinus*. Variation in annual growth increments with cohort for ages 1 to 2 (black lines), 2 to 3 (dark grey lines) and 3 to 4 (light grey lines) in the W and E North Sea sub-populations. Fitted regression to growth trends indicated by dashed lines

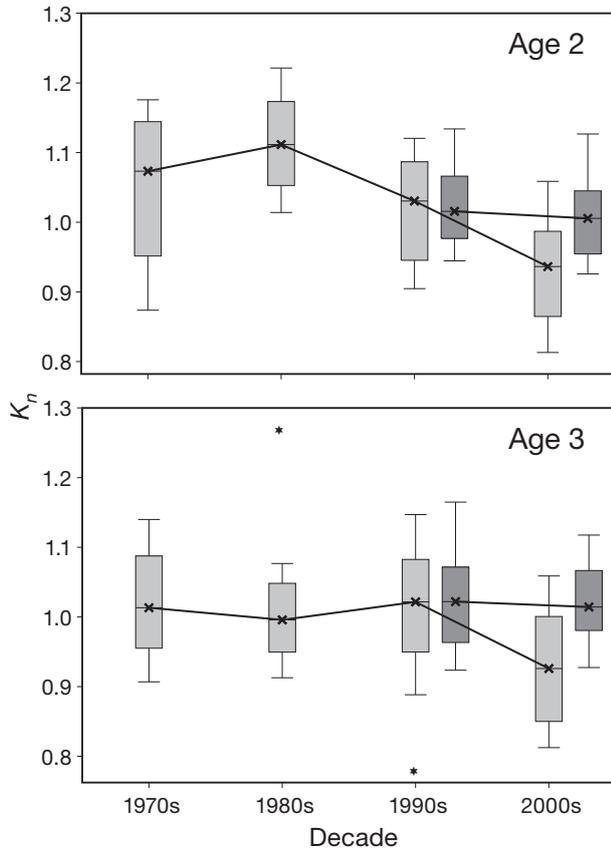


Fig. 3. *Melanogrammus aeglefinus*. Differences in condition (K_n) among decades 1970 to 2000 in the coastal W (light grey boxes) and offshore E (dark grey boxes) North Sea sub-populations, for ages 2 and 3. Mid-line: median; lower and upper box: 25 and 75th percentiles; error bars: 5th and 95th percentiles; asterisks: outliers

age shifted towards smaller body lengths. This decline corresponded to a magnitude of change in the order of 23 to 27 % within 29 yr. For males and females respectively, the changes in Lp50s corresponded to an estimated rate of 11 and 10 k Darwins in the W sub-population and 9.3 k Darwins for males in the E sub-population.

Trends in potential explanatory factors affecting the proportion mature

The significance of temperature to spatial differences in maturation probability was confounded by the lack of overlap in temperature ranges between the 2 sub-population regions (Fig. 5). There were weak but significant positive linear temperature trends in the E and W regions (t -test, $p < 0.05$) based on a GLM fit using gamma errors and an identity link function. There was no significant time trend in competitive bio-

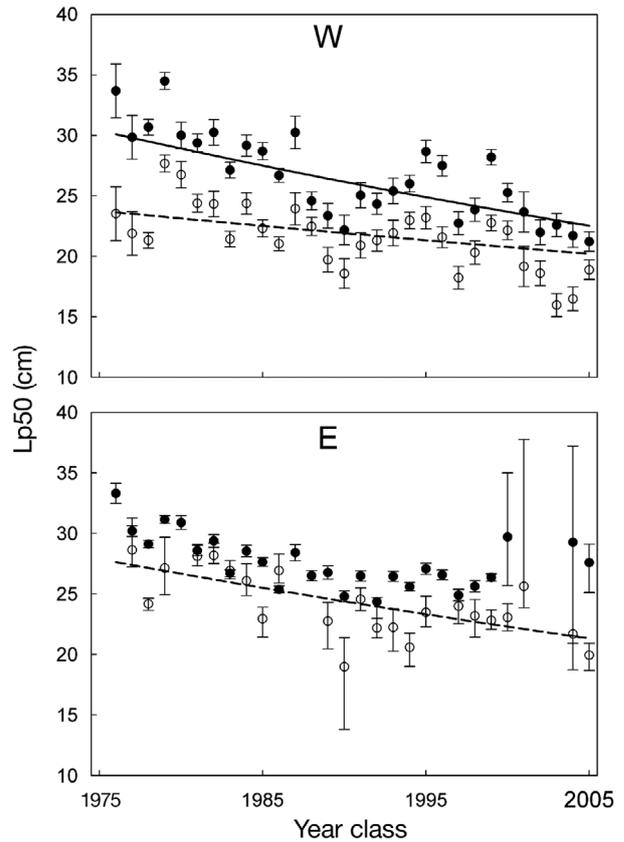


Fig. 4. *Melanogrammus aeglefinus*. Probabilistic maturation reaction norm midpoints (Lp50s) for age 2 females (●) and males (○) from the W and E North Sea sub-populations (cohorts 1976 – 2005). Error bars: 2.5 and 97.5 % parametric bootstrapped confidence limits. Lines: regression for females (solid line) and males (dashed line)

mass in the E region but a weak positive trend in the W region ($R^2 = 0.20$, $p = 0.01$). In order to remove time trends in the analysis, residuals from these relationships were used in the model of age 2 maturation probability.

The analysis of maturation probability in age 2 had-dock found a significant effect of sex, sub-population and cohort within sub-population at the 99 % level. Given the significant effect of sex and the difference in regional temperature, subsequent analyses were conducted on males and females and sub-population regions separately according to:

$$\text{logit}(m) \sim \text{length} + s(\text{cohort}) + \text{temperature} + \text{biomass} \quad (12)$$

All terms were significant in the model in females. However, the temperature and biomass terms only made a small contribution to reducing the model deviance in females (Table 2). The combined effect of temperature and biomass can be seen in Fig. 6 as additions to the cohort effect predicted for a 25 cm female.

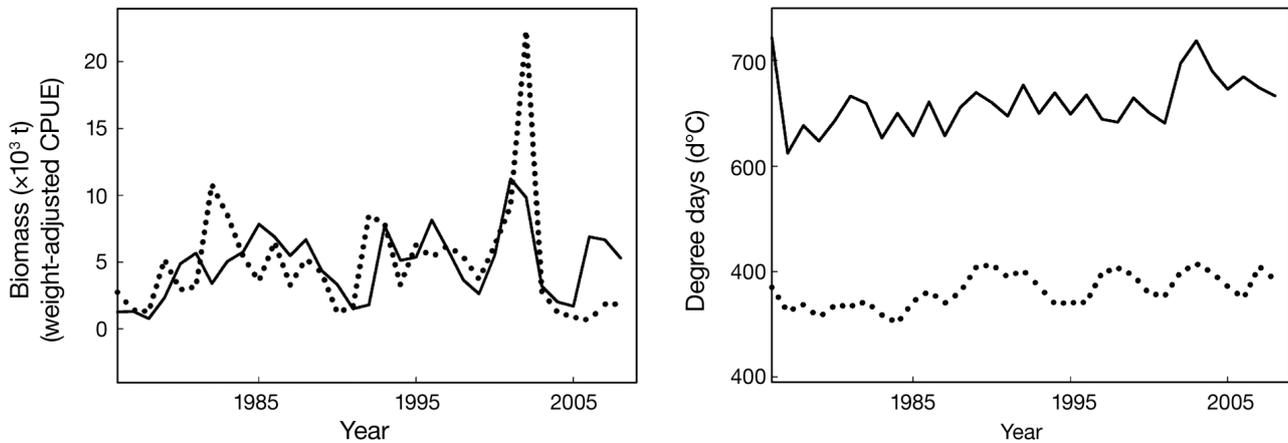


Fig. 5. *Melanogrammus aeglefinus*. Temporal changes in age 1 to 3 haddock biomass (left) and summer temperature (degree days; right) in the E (dotted lines) and W (solid lines) North Sea. CPUE: catch per unit effort

Temperature tended to have a consistent positive effect and accounted for a substantial addition to the positive cohort trend in the W haddock sub-population. However, neither temperature nor biomass effects

notably altered the rate of change in maturity in females from the E sub-population. Only biomass had a significant influence on the proportion of mature males from either sub-population (Table 2).

Table 2. *Melanogrammus aeglefinus*. Coefficients, standard errors, significance and pseudo- R^2 of effects of covariates on maturity relationship for female and male haddock from the west and east sub-populations. Cohort (modelled as a spline with 4 df), summer temperature and haddock biomass (ages 1–3)

| Explanatory variable | Residual df | Coefficient | SE | p | Deviance | R^2 |
|----------------------|-------------|-------------------------|------------------------|---------|----------|-------|
| Female | | | | | | |
| West | | | | | | |
| Null | 1329 | -13.01 | 1.643 | | 1883 | |
| Length | 1328 | 0.43 | 0.025 | <0.0001 | 397 | 0.211 |
| s(Cohort) | 1324 | | | <0.0001 | 241 | 0.128 |
| Temperature | 1323 | 5.18×10^{-3} | 2.22×10^{-3} | 0.02 | 6 | 0.003 |
| Biomass | 1322 | -5.92×10^{-8} | 2.88×10^{-8} | 0.04 | 3 | 0.002 |
| East | | | | | | |
| Null | 1234 | -4.128 | | | 1746 | |
| Length | 1233 | 0.244 | | <0.0001 | 352 | 0.202 |
| s(Cohort) | 1229 | | | <0.0001 | 126 | 0.072 |
| Biomass | 1228 | -1.447×10^{-7} | 3.8×10^{-8} | 0.0002 | 16 | 0.009 |
| Temperature | 1 | -0.0074 | 0.002995 | 0.014 | 6 | 0.003 |
| Male | | | | | | |
| West | | | | | | |
| Null | | -7.892 | 0.714 | <0.0001 | 1448 | |
| Length | 1 | 0.443 | 0.029 | <0.0001 | 196 | 0.14 |
| s(Cohort) | 4 | | | <0.0001 | 262 | 0.18 |
| Biomass | 1 | -1.405×10^{-7} | 2.934×10^{-8} | 0.025 | 18 | 0.01 |
| East | | | | | | |
| Null | 1488 | -7.452 | 0.560 | | 2767 | |
| Length | 1487 | 0.279 | 0.020 | <0.0001 | 604 | 0.22 |
| s(Cohort) | 1483 | | | <0.0001 | 379 | 0.18 |
| Biomass | 1482 | -5.97×10^{-8} | 2.66×10^{-8} | 0.025 | 8 | 0.004 |

Fecundity

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

$$F_p \sim \text{length} + \text{decade} + K_n + \text{age} \quad (13)$$

Length and K_n combined explained slightly more variation in F_p ($R^2 = 0.68$) compared to eviscerated mass 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; Table 3) but not when this age-class was excluded ($p > 0.05$ for age). For a given K_n , the slope of the F_p -length relationship was significantly higher in the 1990s and 2000s than in the 1970s and 1980s (GLM, $p < 0.01$; Fig. 7). A change in K_n from 0.8 to 1.2 resulted in about a 50% increase in F_p in both decades. Relative fecundity ($F_p/\text{eviscerated mass}$) similarly differed significantly over time for both age 2 (Kruskal-Wallis test; $H_{3,158} = 12.7$; $p = 0.005$) and age 3 ($H_{3,451} = 87.9$; $p < 0.001$) haddock, with the median rela-

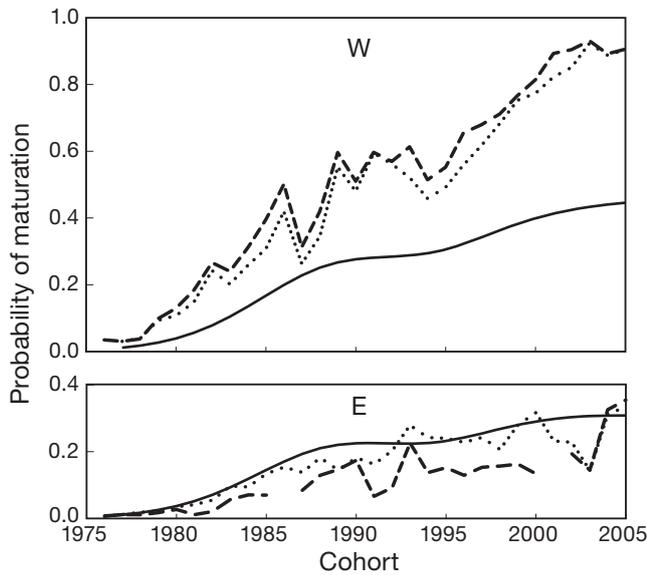


Fig. 6. *Melanogrammus aeglefinus*. Predicted maturation probability for haddock in relation to sub-population, cohort, summer temperature and biomass. Predictions are based on a 25 cm age 2 female. Solid lines: cohort effect alone (temperature fixed at 1976 or 1977 levels); dotted lines: predicted trend with the addition of varying temperature; dashed line: effect of biomass fixed at 1977 levels

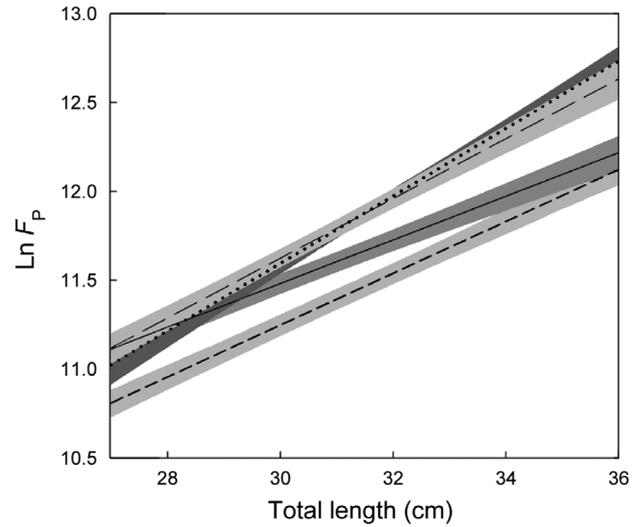


Fig. 7. *Melanogrammus aeglefinus*. Predicted potential fecundity–length relationships for W (age 3+) haddock fitted with condition factor (K_n) set at 1 for the 1970s (solid line), 1980s (short-dash line), 1990s (dotted line) and 2000s (long-dash line). Shading: lower and upper pointwise standard errors, respectively

Table 3. *Melanogrammus aeglefinus*. Coefficients, standard errors, significance and pseudo- R^2 of the effects of total length, age (2, 3), relative condition (K_n) and decade (1970, 1980, 1990 and 2000) on temporal changes in the potential fecundity of haddock from the W sub-population.

| Explanatory variable | Residual df | Coefficient | SE | p | Deviance | R^2 |
|----------------------|-------------|-------------|-------|---------|----------|-------|
| Null | 353 | 5.056 | 0.360 | | 159.0 | |
| Length | 352 | 0.148 | 0.008 | <0.0001 | 89.95 | 0.566 |
| Decade | 349 | | | <0.0001 | 9.54 | 0.060 |
| 1980 | | -0.206 | 0.069 | | | |
| 1990 | | 0.203 | 0.065 | | | |
| 2000 | | 0.150 | 0.069 | | | |
| Factor (Age) | 348 | 0.306 | 0.051 | <0.0001 | 4.66 | 0.029 |
| K_n | 347 | 1.08 | 0.217 | <0.0001 | 3.87 | 0.024 |

Table 4. *Melanogrammus aeglefinus*. Coefficients, standard errors, significance and pseudo- R^2 of the effects of total length, age (2, 3), relative condition (K_n), decade (1990 and 2000) and sub-population on potential fecundity of haddock

| Explanatory variable | Residual df | Coefficient | SE | p | Deviance | Residual deviance | R^2 |
|----------------------|-------------|-------------|-------|---------|----------|-------------------|-------|
| Null | 220 | 4.699 | 0.465 | | 72.05 | 72.05 | |
| Length | 219 | 0.135 | 0.012 | <0.0001 | 27.69 | 44.35 | 0.384 |
| Factor(Age) | 218 | 0.248 | 0.058 | <0.0001 | 3.15 | 41.20 | 0.044 |
| K_n | 217 | 1.867 | 0.263 | <0.0001 | 3.78 | 37.42 | 0.052 |
| Population | 216 | 0.210 | 0.061 | 0.0005 | 1.32 | 36.10 | 0.018 |
| Decade | 215 | 0.112 | 0.058 | 0.05 | 0.41 | 35.69 | 0.006 |

tive fecundity increasing from 249 to 341 in age 2 and 516 to 564 in age 3 fish between the start and end of the study period.

Differences in potential fecundity between the 2 sub-populations for ages 2 and 3 in the 1990 and 2000 decades were examined using the following model:

$$F_p \sim \text{length} + \text{age} + K_n + \text{population} + \text{decade} \quad (14)$$

The minimum adequate model excludes interactions (Table 4) because these did not reduce the AIC value. For a K_n of 1.0, the estimated fecundity of a 35 cm age 3 haddock was 171 758 and 192 196 for 1999 and 2007, respectively, in the E sub-population compared to 211 830 and 237 037 in the W sub-population.

DISCUSSION

By combining information on a range of reproductive and growth traits the present study provides one of the most comprehensive assessments of chang-

ing reproductive effort in a commercially important fish species. Reproductive investment within the W North Sea haddock sub-population significantly increased between the 1970s and 2000s, as evident from both a substantial downward shift in the maturation reaction norm of age 2 haddock and an increase in weight specific fecundity. A significant reduction in maturation probability at size was also seen in males from the E North Sea haddock but the magnitude of the decline was less than that seen in the west. Female haddock were found to reach 50% maturation probability at a larger size than males, as has been reported previously (Tormosova 1983). First maturing haddock from the W North Sea in this study were significantly smaller by the 1990s than that reported from studies in the early part of the last century and up to the 1970s (Tormosova 1983, Hislop 1984). Whilst studies of other haddock stocks have reported long term declines in length at maturity (Trippel et al. 1997b, Korsbrekke 1999) they did not consider maturity in relation to cohort and age and so did not account for variability in maturation state arising from demography and inter-annual differences in growth.

The recent recovery in the North Sea stock biomass did not affect the downward shift in maturation reaction norms. Between the 1970s and 1990s North Sea haddock spawning stock declined to less than a tenth of the maximum biomass, while fishing mortality in ages 2 to 4 remained close to 1.0 yr^{-1} , and year-class strength was generally below average (ICES 2009). Given these changes a reduction in intra-specific resource competition might have been expected, although this was not evident from competitive biomass estimates for the 2 study areas. The low variation in competitive biomass and the slight increase in the W in recent years probably reflect the importance of these areas as centres of North Sea distribution (Hedger et al. 2004). However, the PMRN has continued to decline since the 1990s and females continued to have high weigh-specific fecundity in the recent decade despite a substantial decline in fishing mortality and an increase in spawning stock biomass over the North Sea (ICES 2009). Moreover, the higher reproductive investment appeared to be at the cost of somatic growth as annual growth declined for maturing age haddock from the mid-1990s to the recent decade. Indices of somatic condition of mature fish were also lower in the 1990 and 2000 sampling periods than in previous decades. Hence there appears to have been an increase in reproductive effort, particularly in the W sub-population.

As with other PMRN studies, the field measurements of maturity used in this study were taken months after the fish made the physiological switch to continue gametogenesis through to spawning (Wright 2007,

Tobin et al. 2010). Consequently, the size measured may not reflect the energetic state that led to the fishes' maturity status. However, given that the decrease in L_{p50} of W haddock exceeded an annual length increment, the energetic state required to inhibit gametogenesis is very likely to have declined. Another proximate factor that was considered, summer temperature, could explain some of the variation in maturation probability in female age 2 haddock from the W North Sea. The positive effect of this factor on maturation trends is consistent with a recent experimental finding that a 2°C difference in summer temperature doubled the proportion of maturing female haddock for a given mass (Tobin & Wright 2011). The lack of a temperature effect on male maturation is unknown but may reflect their smaller size and energetic threshold for maturation. However, even after accounting for temperature, there remained a highly significant negative trend in maturation probability. Hence, the significant trend towards smaller size at maturity cannot just be explained by warmer summer temperatures.

The thermal environments inhabited by the 2 sub-populations differ by more than 2°C in the summer (Elliot et al. 1991). As the proportion of mature age 2 haddock was always lower in the deeper and cooler E North Sea, it is possible that the difference in maturation between sub-populations may partly reflect differences in thermal regime. However, due to this difference in summer temperature range between regions this explanation could not be formally tested in the present field based study. Only a common environment experiment, in which temperature was controlled for, could disentangle the potential genetic and thermal effects on maturation in the 2 sub-populations.

As applications of PMRN focus on a specific geographic region, it is important to distinguish between changes in life-history traits due to local selection rather than colonisation of differing genotypes. There is exchange of haddock between the west North Sea and Scottish west coast during the larval (Heath & Gallego 1998) and juvenile stages (Wright et al. 2010). Moreover, Dickey-Collas et al. (2003) reported an expansion of haddock to the west of the British Isles in the 1990s that appeared to be linked to favourable local conditions throughout this region. Between 1995 and 2000 the length at 50% maturity (L_{50}) of age 2 haddock was comparable (20 to 22 cm) to that observed in the W North Sea (Dickey-Collas et al. 2003). However, whilst there is no published information for years prior to this, the L_{50} of age 2 males and female haddock was 24 and 27 cm, respectively during the years 1978 to 1981 (J. Hislop unpubl. data). This is similar to estimates for W haddock which may reflect the inter-mixing of fish between coastal waters to the east and west of Scotland. However, a decline in the maturity-

size relationship has also been reported in coastal groups of Atlantic cod to the east and west of Scotland (Yoneda & Wright 2004). These coastal cod show much higher site fidelity than haddock (Wright et al. 2006). Consequently, either extensive exchange or a similar environment and exploitation history may explain the similar trend towards small size at maturity in both cod and haddock inhabiting the coastal waters around Scotland.

The age-specific difference in fecundity between 2 year old and older North Sea haddock is consistent with earlier evidence (Hislop 1988), although the relative fecundity of 2 year olds has increased since the 1970s. The increase in slope and intercept of the fecundity–size relationships over the 4 decades of study was consistent with the predicted life-history response to increasing mortality, particularly on adults (Rochet et al. 2000). Moreover, temporal differences in potential fecundity in W haddock could not be explained by higher somatic condition. This is important as poorer feeding conditions would be expected to reduce both condition and fecundity, as demonstrated in experiments on captive haddock (Hislop et al. 1978). As a consequence, whilst potential fecundity of E females in the 1990s and 2000 was within the range of historical reported relationships, that of W haddock was considerably higher (Raitt 1932, Alekseyeva & Tormosova 1979, Hislop & Shanks 1981).

Changes in haddock reproductive investment and somatic growth, particularly in the W North Sea, are consistent with phenotypic and genotypic changes in reproductive effort predicted to arise from intense periods of size-selective mortality (Law 2000, Rochet et al. 2000). The high level of fishing mortality on maturing ages between the 1960s to 1990s far exceeded estimated natural mortality (see ICES 2009). Such high levels of mortality may markedly increase the risk of reproductive failure for a cohort (Wright & Trippel 2009). Although there is no information on regional mortality rates, most demersal fishing effort in the northern North Sea was concentrated in the west coastal North Sea until recently (Jennings et al. 1999, Greenstreet et al. 1999, 2009). Consequently, it is highly likely that fishing mortality was historically much higher on the sub-population that has undergone the largest change. Assuming that genetic selection is involved, a downward trend in the maturation reaction norm is expected to stop once it falls below the size threshold where selection no longer has any effect (Ernande et al. 2004), i.e. below the minimum size of capture. Whilst the minimum landing length of haddock is 30 cm, discard rates of 20 to 30 cm fish have historically been very high (Ferro et al. 2008). In W haddock, the Lp50 of all age groups has recently come close to the selection threshold of bottom trawl gear

currently in use and therefore the trend might weaken in future years.

The spatial variation in post-maturation size, fecundity and condition of recent haddock may reflect population differences as proposed by Jamieson & Birley (1989) and the regional differences in thermal and historic exploitation patterns. The temporal and spatial differences reported here closely parallel the findings for cod from the same regions (Yoneda & Wright 2004). Given the evidence for regional variation within a stock, future studies should account for population structuring when attempting to detect temporal changes in life-history traits.

The results of the present study also have important implications for the assessed spawning stock biomass. Combining the average length of age 2 haddock from the assessment (ICES 2009) with the observed changes in maturation indicates that the proportion mature has increased from 0.14 in the early 1980s to 0.65 for the early years of 2000 in the W sub-population. In the E sub-population, the corresponding change in proportion mature was from 0.14 to 0.48. Around 70% of age 3 haddock were mature in the same 1980s period compared to around 97% in the recent period. These estimates are much higher than the maturity–age key currently used in the ICES North Sea haddock assessment and that reported by Raitt (1932) and Hislop (1984).

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