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Temporal stability of the maturation schedule of capelin *Mallotus villosus* in the Barents Sea

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Abstract – Capelin in the Barents Sea are primarily harvested in a terminal fishery that targets maturing individuals. Theory predicts that, in a semelparous population (i.e., one in which reproduction is seasonal, synchronous, and followed by parental mortality), an unselective, terminal fishery (i.e., one in which most of the fish that are not caught will not have a new spawning opportunity) does not generate strong selection for changed age and size at maturation. The probabilistic maturation reaction norm (PMRN) method was applied to test this prediction and to detect possible temporal changes in length at maturation of Barents Sea capelin between 1978 and 2008. Maturation reaction norms suggest that maturation is age-independent in capelin, but that males require a larger size to attain the same maturation probability as females. No temporal trends in length at maturation could be detected, thus confirming the theoretical prediction. Furthermore, none of the candidate environmental variables tested to explain the temporal variability in length at maturation (water temperature and capelin biomass) consistently showed a significant correlation with the PMRN midpoints.

Keywords: Probabilistic maturation reaction norms / Fisheries-induced evolution / Semelparous life-history / Forage fish / Osmeridae / Sub-Arctic fish

1 Introduction

Harvesting a fish stock, because it adds an extra source of mortality, usually leads to evolutionary selection with respect to age and size of sexual maturation. Increasing the mortality rate indiscriminately over a whole population increases the relative fitness of early-maturing individuals, even though their fecundity during a single spawning season is lower compared to their larger, late-maturing conspecifics. Provided that such precocious maturation is heritable, this trait will spread in the population and a reduction of the average age and size at maturation can be observed. Such evolutionary changes have been suggested for numerous fish species and populations (reviewed by Jørgensen et al. 2007; Heino and Dieckmann 2008; Sharpe and Hendry 2009). However, before concluding that fisheries-induced evolution has occurred, it is necessary to consider the influence of other factors acting on maturation through phenotypic plasticity. These may, for example, include water temperature (e.g., Kraak 2007), habitat characteristics (Morita et al. 2009) or food abundance (e.g., Trippel 1995; Uusi-Heikkilä et al. 2011). It is crucial to identify the nature of a maturation trend in order to predict the future development of a population. A change driven by phenotypic plasticity alone implies that the trend would be reversible were environmental conditions to become conducive to late maturation. If, however, a maturation trend includes a genetic component, then a return to late maturation would be expected to be slow (Law and Grey 1989; Conover et al. 2009; Dunlop et al. 2009; Enberg et al. 2009).

Probabilistic maturation reaction norms (PMRN) offer a methodology that helps disentangle the influence of growth-related phenotypic plasticity and evolutionary changes in age and size at maturation (Heino et al. 2002; Dieckmann and Heino 2007; Heino and Dieckmann 2008). Typically, a PMRN describes the probability for an immature individual to mature as a function of its age and size. The utility of this simple description of maturation tendency in disentangling plastic and genetic effects relies on the postulate that variation in growth is the single most important source of plasticity in maturation (Alm 1959), and that growth itself integrates many environmental influences on the maturation "decision" (Heino et al. 2002). However, this disentanglement can never be perfect, and PMRN results should be interpreted judiciously as they can show plastic changes. One reason is that other variables

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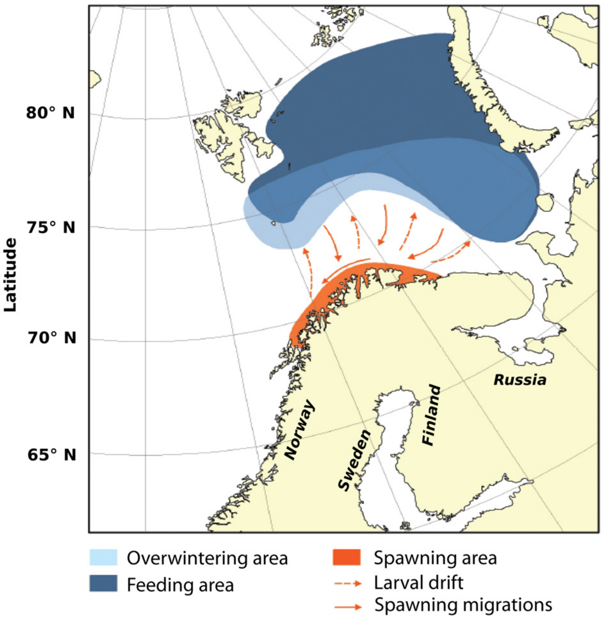

Fig. 1. The distribution area and migrations of Barents Sea capelin. Source: Institute of Marine Research, Norway.

than those included in the PMRN may also influence maturation. Another reason is that PMRNs may be influenced by growth: a recent experimental study conducted on zebrafish (*Danio rerio*) showed that PMRNs were unable to fully account for very large, experimentally-induced variations in somatic growth (Uusi-Heikkilä et al. 2011).

In this study, we use probabilistic maturation reaction norms to study maturation in Barents Sea capelin (*Mallotus villosus*).

Capelin is a short-lived pelagic fish inhabiting northern circumpolar latitudes in both the Atlantic and Pacific Oceans (Stergiou 1989; Dodson et al. 2007). The Barents Sea (Fig. 1) has several capelin populations: a number of small populations inhabiting fjords of the northern coast of Norway, and a large oceanic population with maturing individuals only migrating to the coast for spawning. Despite clear differences in life-history traits between coastal populations and the large oceanic population (Christiansen et al. 2008), no obvious genetic segregation between them has been detected (Mork and Friis-Sørensen 1983; Præbel et al. 2008).

The oceanic population in the Barents Sea potentially constitutes the largest capelin population in the world (Gjøsæter 1998). Capelin is also a forage fish that is a key component of the Barents Sea ecosystem. In particular, the size of this stock influences the abundance of other fish species in the Barents Sea, especially Atlantic cod (*Gadus morhua*), which predate on capelin (Dolgov 2002; Hjermann et al. 2004; Olsen et al. 2010). Capelin is also an important food source for other fish species (Dolgov 2002), as well as for marine mammals and sea birds (Gjøsæter 1998; Gjøsæter et al. 2009). Capelin is a major consumer of zooplankton (Panasenko 1981, 1984), competing with herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) where their distribution areas overlap (Huse and Toresen 1996; Dolgov et al. 2010). Since capelin consume much of the production in the area where the ice seasonally recedes (Wassmann et al. 2006), they play a crucial role in the transfer of energy to higher trophic levels, particularly during their spawning migration in late winter towards the coasts of northern Norway and Russia (Sætre and Gjøsæter 1975; Gjøsæter 1998).

Unlike coastal capelin populations, where at least females can survive to spawn more than once (Christiansen et al. 2008), virtually no capelin of the large oceanic population survive until a second spawning opportunity, even though females seem to remain physiologically capable of spawning a second time (Forberg 1982). Spent individuals usually die from exhaustion or wounds incurred during spawning (Møller and Olsen 1962; Sætre and Gjøsæter 1975; Christiansen et al. 2008) or are eaten by predators that have followed them during their spawning migration. The life history of this population can hence be considered as virtually semelparous.

The proportion of capelin maturing in a given year can be deduced mainly from the distribution of body length (Tjelmeland and Bogstad 1993; Gjøsæter 1999). Individuals having reached a minimum body length of 14 cm in September are usually assumed to spawn in the next spring (ICES 2009), and the proportion of individuals maturing at a given age appears to depend on the strength of the cohort considered (Gjøsæter 1998). Males caught on spawning grounds are usually larger than females at any given age. This is at least partly due to sexual dimorphism in body size (Møller and Olsen 1962; Vilhjálmsson 1994).

Growth fluctuates greatly in Barents Sea capelin, both temporally (Fig. 2) and spatially. It is affected, among other factors, by the abundance and distribution of zooplanktonic prey and by the size of the capelin population (Gjøsæter 1999; Gjøsæter et al. 2002b). Changes in growth also influence capelin dynamics by altering the age of sexual maturation. This metric has generally decreased over the period covered by the current study (−0.02 year/year in the data used here, ANCOVA $p = 0.02$ for males and $p < 0.01$ for females) and is usually similar in males and females for a given year (Fig. 3). Correspondingly, the contribution of the youngest age groups to the spawning biomass has gradually increased (Tereshchenko 2002).

The oceanic capelin stock in the Barents Sea has been exploited for centuries, initially mainly to provide bait for the cod fisheries (Møller and Olsen 1962). Starting in the 1920s, the fishery for industrial extraction of oil from capelin developed in Norway. The capelin fishery really took off toward the late 1950s, with an increase in size and modernization of the Norwegian fleet targeting the species. This development was facilitated by the decline and collapse of the Norwegian spring-spawning herring (Møller and Olsen 1962; Gjøsæter 1998). The Soviet fishing fleet experienced a comparable development, contributing to the strong increase in total capelin landings that peaked in 1977 (Gjøsæter 1998).

The Barents Sea capelin fishery is characterized by high fluctuations in landings. In the 1970s, it supported the largest single single-species fishery in Europe (Gjøsæter 1998; ICES 2009). In earlier times, the capelin fishery was essentially active in winter, during the spawning migration and on the spawning grounds. However, beginning in 1968, a summer offshore fishery developed (Gjøsæter 1998). This practically

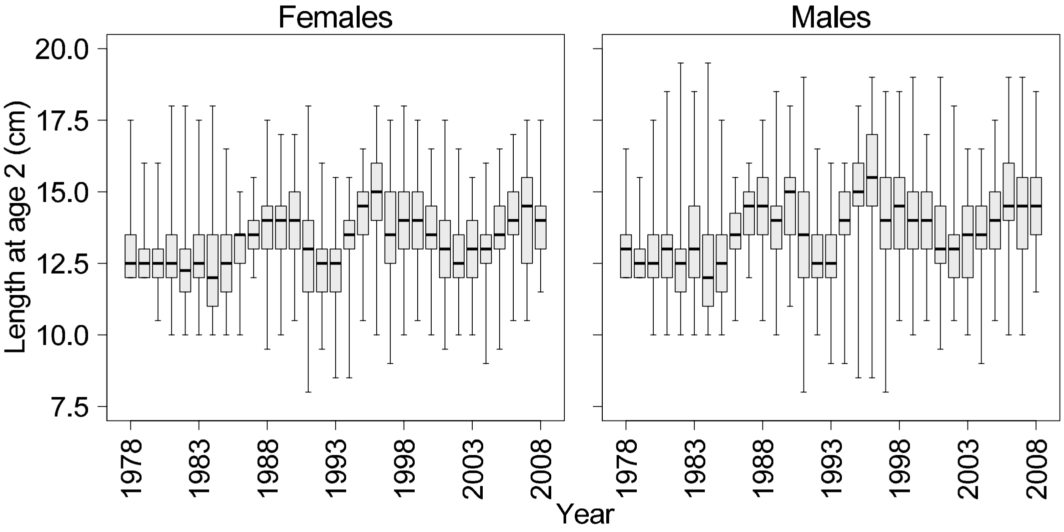

Fig. 2. Annual distribution of body length of Barents Sea capelin at age 2 years in samples from the IMR-PINRO autumn surveys. Horizontal lines represent the medians, grey boxes indicate the interquartile ranges and whiskers extend to the most extreme observations.

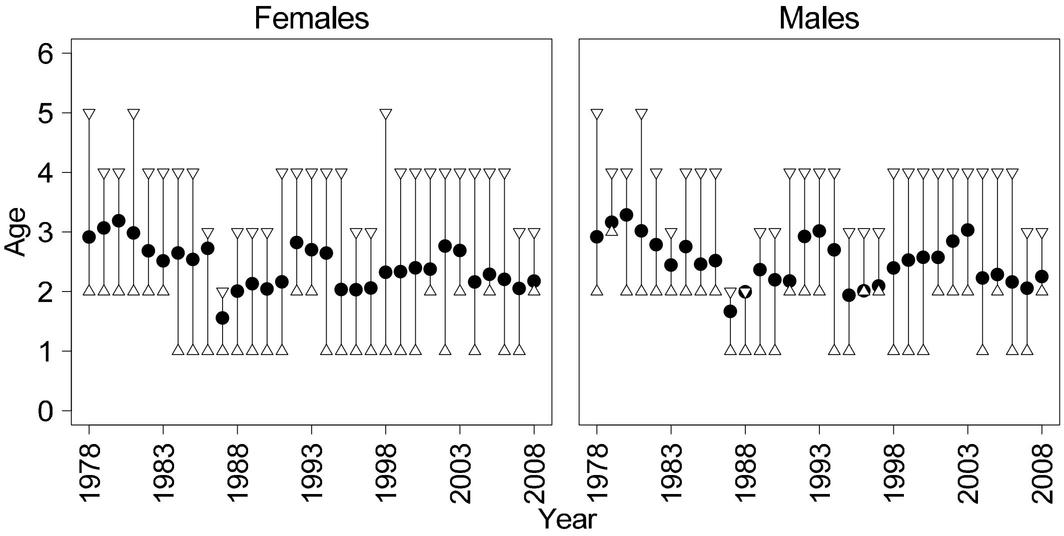

Fig. 3. Observed changes in the age of mature individuals through the study period, for females and males sampled during the IMR-PINRO autumn surveys. Black circles represent the mean age of sampled fish while minimum and maximum observed ages are shown as white triangles.

ceased from year 2003 on, despite small catches by Russian fishers in 2005 and 2008 (ICES 2009). Since 1978, when the first exploitation regulations were established by Norway and the USSR, the stock has been managed based on spawning biomass targets. A fishing moratorium has been enacted three times when the population collapsed below the target escapement. The influence of fishing pressure seems to have been negligible in explaining the stock collapses which were primarily attributed to natural predation instead (Gjøsæter 1998; Hallfredsson and Pedersen 2009; Hjermann et al. 2004, 2010). Indeed, the larval stage seems to be the most critical phase determining future capelin biomass (Gjøsæter and Bogstad 1998; Hjermann et al. 2010). Fishing mortality is low compared with natural mortality (Ushakov and Prozorkevich 2002), and most of the catch is realized in a terminal fishery (spent individuals have a very short life expectancy, even in the absence of harvesting).

We use probabilistic maturation reaction norms to assess whether the variations in age and size at maturation of Barents Sea capelin from 1978 to 2008 (Fig. 3) might have a genetic component. Barents Sea capelin make an interesting case study because (i) the dataset analyzed here begins soon after the start of the large-scale fishery, and (ii) we expect that selection on maturation was weak over the period considered and, therefore, that this stock would show only minor changes in its PMRN if any were shown at all. The reason for the latter prediction lies in the combination of the semelparous life history, the dominance of the winter fishery targeting maturing fish (ICES 2009, 2010), and the relatively low exploitation rate ($F/Z = 5\%$; Ushakov and Prozorkevich 2002): because Barents Sea capelin would die anyway after spawning, earlier sexual maturation will not reduce the mortality risk associated with the spawning migration, even when accounting for the terminal fishery targeting maturing capelin. Capelin have also been exposed to a summer fishery where immature capelin were caught, potentially favouring earlier maturation because exposure time to fishing could thus be reduced, but fishing mortality was relatively low compared to natural mortality: on average 0.04 y^{-1} over the period 1978–2000 (ranging from 0 to 0.14 y^{-1}) (Ushakov and Prozorkevich 2002). Furthermore, the minimum landing size of 11 cm has created an incentive to target schools of larger individuals (which increases the probability of including those that will mature in the following year), which are also more valued (Bogstad and Gjøsæter 2001), contributing to weak selection on maturation. At the same time, the high inter-cohort variability in growth in this population makes it a suitable case for evaluating whether the PMRN methodology is prone to show spurious patterns in presence of large growth variations (see Uusi-Heikkilä et al. 2011).

2 Material and methods

2.1 Sampling and data set

The data used for this study were collected during joint scientific surveys by the Institute of Marine Research (IMR, Norway) and the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia) in the Barents Sea, initiated in the early 1970s. The last available sampling year was 2008. In order to avoid bias in terms of sample representativeness, only autumn surveys were considered here – winter surveys were excluded because the mature and immature parts of the stock are segregated at that time of the year. The period from August to October, before the segregation of mature and immature individuals, is the most suitable for obtaining reliable estimates of population size (Gjøsæter et al. 1998). Although autumn surveys have been carried out since 1972 in order to estimate the size of the Barents Sea oceanic capelin stock, only the years from 1978 onwards were considered here, due to insufficient coverage of the population during the first surveys. The data analysed here constitute random samples collected using pelagic trawls only, as capelin are seldom found close to the bottom in autumn (Gjøsæter 1999). Moreover, the samples collected with bottom trawls are unlikely to reflect the composition of the capelin population encountered in a given area (Tjelmeland, IMR, pers. comm.), and no acoustic abundance estimation is available for capelin in or near the acoustic dead zone (Gjøsæter et al. 1998). Pelagic trawl hauls were carried out every 30 nautical miles or when the echograms suggested changes in the school composition. Details about the surveys and the sampling procedures can be found in Gjøsæter et al. (1998).

Sampled individuals were sexed, length-measured (total length down to the nearest 0.5 cm), weighed, aged by otolith reading, and their maturity stage was determined. The length of individuals in the samples ranged from 6.0 cm to 20.5 cm. Sexual maturation was described according to two different scales: a purely macroscopic five-stage classification based on the visual examination of gonads and, for females only, a more elaborate scale combining macro- and microscopic criteria, so-called Forberg maturity scale (Forberg 1982, 1983). Between 1989 and 2005, the maturity stage of each sampled female was defined on only one of the two scales. Outside this period, maturation stages were only identified macroscopically. On the purely macroscopic scale, individuals that had reached maturity stage 3 (“maturing”; opaque but developed gonads with distinct veins) were considered as maturing. On the Forberg scale, females in maturity stage 31 (“maturing”; fat vacuoles visible in the cytoplasm of at least 10% of the oocytes in the second growth phase) and more advanced maturity stages were considered as maturing.

2.2 The logistic maturation model

The essentially semelparous life history of Barents Sea capelin makes identifying first-time maturing capelin trivial, therefore allowing the use of the direct estimation method to derive probabilistic maturation reaction norms (Heino et al. 2002; Dieckmann and Heino 2007). The direct method amounts to a logistic regression to describe the maturation status of individuals as a function of their size and other attributes. In this study, the high number of individuals collected (108 396 individuals between age 1 and 4, 48% of which were females and 52% males), led to the statistical significance of all the explanatory variables tested (sex, age, cohort, body length) and their interactions. Models were hence fitted independently for males and females, as well as for each age (age 1 to 4 years) and cohort considered. The general formulation of the models is thus $\text{logit}(p_{mat}) \sim a + b \cdot length$, where p_{mat} is a binary response variable describing the maturity status (0 for immature, 1 for mature) and a and b are the parameters to be estimated. We did not use weight as an explanatory variable because only measurements of total weight, which is affected by gut content and gonad weight, were available.

The body length corresponding to a maturation probability of 50% at a given age, also called the PMRN midpoint (L_{p50}), was used to summarize the reaction norm, together with the width of the PMRN, measured here as the difference between body lengths at which maturation probability was equal to 25% (L_{p25}) and 75% (L_{p75}). The narrower this envelope width, the stronger the linkage between body length and maturation “decision” becomes. The body lengths corresponding to these specific maturation probabilities were derived by solving the equation $\log\text{it}(p_{mat}) \sim a + b \cdot length$ for length and replacing the term p_{mat} by the desired probability (i.e., 0.25, 0.50 or 0.75) and parameters a and b by their fitted values.

In order to focus on cases where the data were most informative (a combination of sex, age and cohort) and avoid very noisy and uncertain PMRN estimations, we dropped cases where either maturing or immature weighted individual numbers (calculated as explained below) constituted less than 5% of the total weighted numbers, or where less than three mature or immature fish were present. After this filtering, 30 565 females from age 1 to 4 years and 28 706 males from age 2 to 4 years remained.

2.3 The weighting of observations

Capelin are not uniformly distributed in the Barents Sea with regard to their age, size, and maturity (Gjøsæter 1999; Gjøsæter et al. 2002b). Samples therefore had to be weighted in order to obtain a representative picture of the population. Because catch per unit effort in a pelagic trawl is a poor quantitative indicator of capelin density, acoustic estimates of the capelin biomass were used to weight samples in the analyses. This weighting was done at the level of a spatial grid where each of the grid cells, here referred to as "divisions", usually extended one degree of latitude by two degrees of longitude (and hence had an area that declined with increasing latitude). The length distribution of capelin in each division is available from the acoustic estimations. Using a length-age key, estimates of biomass per length class were transformed into biomass estimates per age class. Each individual of a given sex and age sampled in a given division for a given year was first weighted by the total acoustic biomass of that age class and division. This weighting was then divided by the number of trawl hauls carried out that particular year in the division, and the number of fish of the same age in a sample. In other words, the sum of the weightings of the individuals sampled in a haul within a division was equal to the biomass of a certain age class in the division. By using this weighting, an assumption is made that the size distribution of mature and immature capelin in a trawl sample is representative of the division used in the acoustic biomass estimation. Because acoustic biomass estimation was only carried out by a subset of vessels taking part in the IMR-PINRO joint surveys, a number of trawl hauls were made outside divisions for which acoustic biomass estimates were available. In order to base the analyses on a larger number of samples, some of these hauls were allocated to a division for which acoustic biomass estimation had been made, provided their position was not too far from the centre of this same division. For this purpose, a maximum distance of 50 km was chosen. This corresponds to a distance slightly over half of the maximal longitudinal extension of a division (41.5 km) in the concerned area and below its maximal latitudinal extension (55.5 km). In cases of trawl hauls using multiple codends, an additional weighting was applied reflecting the proportion of the total catch caught in each individual codend.

2.4 Assessing model and data uncertainty

Bootstrapping with random draws of individuals within each sample (identified by a trawl haul or a bag, in the case of multiple codends, and an age class) was used to define confidence intervals around estimates of PMRN midpoints. The resampling was repeated 500 times.

To assess temporal changes in PMRN midpoints in the period considered and to identify correlates of their variability, linear regression models were applied, using the midpoint as the response variable. Capelin population biomass and two time series of water temperature data were considered as potential explanatory variables (Fig. 4). The temperature time series were the average annual temperature over the depth range 0–200 m along the Kola section (meridian 33° 30′ E) and the average temperature measured in August (the only month for which all years are available) along the Vardø-North transect (meridian 31° 13′ E); this second transect covers a more central part of the capelin distribution. Temperature and population biomass during the sampling year and the previous year (henceforth referred to as temperature and biomass series with one-year lag) were considered. The selection of explanatory variables was performed in a stepwise forward process, based on the outcome of the associated analyses of variance (ANOVA). The year of sampling, capturing possible temporal trends, was added to the models in a subsequent step after the inclusion of all significant environmental variables. A significant linear effect of time would be interpreted as support for evolutionary change in maturation. The reason why time was included last is that the possible effects of environment on age and size at maturation mediated through phenotypic plasticity have to be accounted for before considering potential evolutionary trends. In order to reduce the influence of low-precision PMRN estimates on the parameters of the linear regressions, PMRN midpoint estimates were weighted by the inverse of their standard deviation obtained by bootstrapping. The same weighting was applied to PMRN width when this was regressed against time.

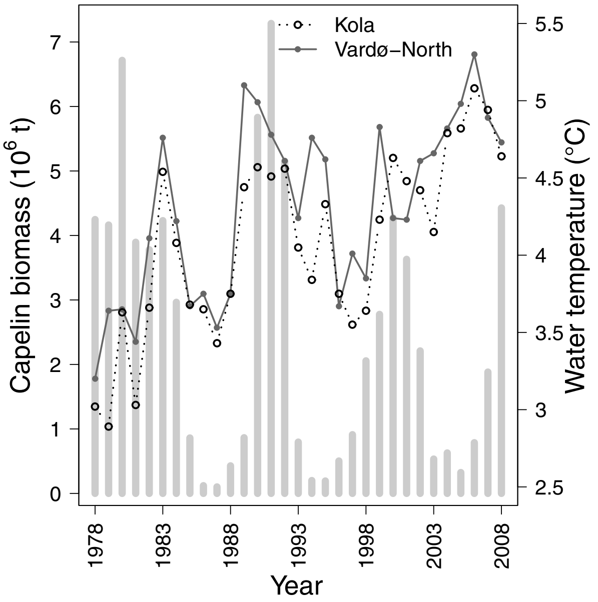

Fig. 4. Time series of environmental variables: capelin biomass (bars), water temperature in the Kola transect and water temperature in the Vardø-North transect.

In addition, because it is not known with certainty whether some females that have not reached Forberg maturity stage 31 at the time of the sampling (September–October) can still become mature by the next spawning season (March–April), the same regression analyses as presented above were also performed using Forberg maturity stage 21 ("early maturation I") as the threshold.

3 Results

The age range of maturing capelin in the data was from 1 to 5 years (Fig. 3). Because 1- and 5-year-old capelin were very infrequent, no estimates of maturation reaction norm midpoints were derived for these ages. Similarly, 4-year-old capelin were rare, and the computation of L_{p50} yielded estimates for three and six cohorts for females and males of this

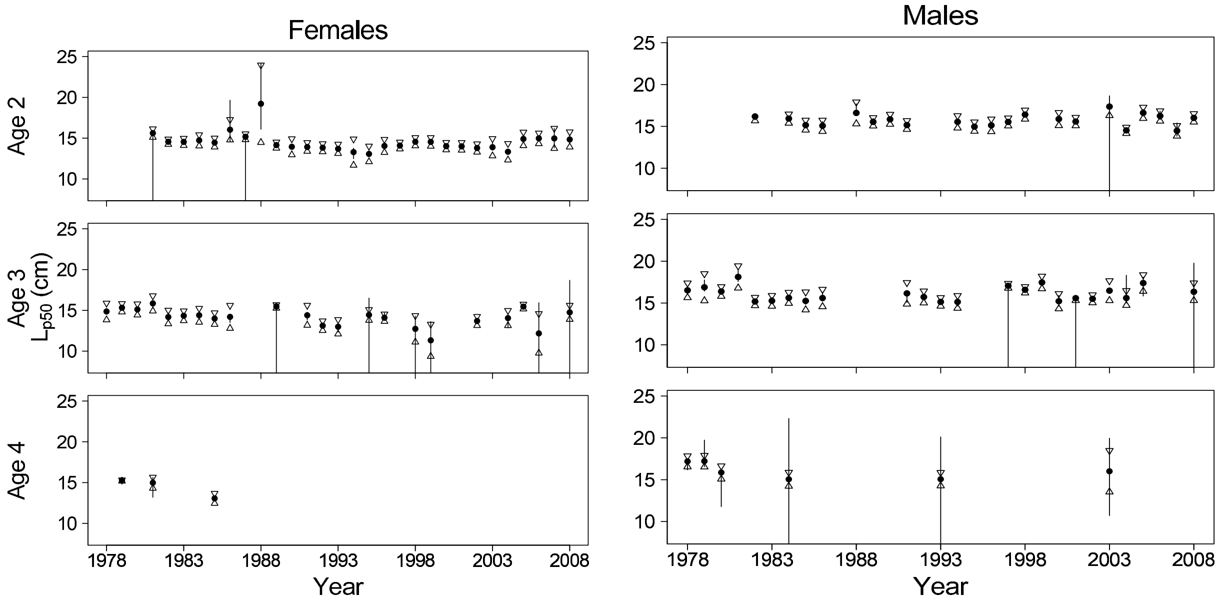

Fig. 5. Year-specific estimates of PMRN midpoints (L_{p50}) for maturation probabilities of 0.25 (L_{p25}) and 0.75 (L_{p75}) at age 2 (top panels) to 4 years (bottom panel) in females and males. Black circles are L_{p50} , upward and downward triangles are L_{p25} and $L_{p75,}$ respectively. Vertical bars indicate 90% confidence intervals obtained by bootstrapping around point estimates of L_{p50}.

age, respectively, usually associated with large errors. The series of midpoints at this age for females was hence not used in the regression analyses.

Male capelin in the Barents Sea exhibited higher reaction norm midpoints (L_{p50}) than females (Fig. 5) (two-sided paired Student's t-tests: $p < 0.001$ for both age 2 and 3): given the same growth trajectory, male capelin would, on average, mature at a larger size and an older age than females. Maturation was virtually age-independent in both sexes (Fig. 6): two-sided paired Student's t-tests comparing L_{p50} between two ages within a single sex revealed no significant differences either between ages 2–3 years in females or between ages 2–4 years in males ($p > 0.109$ in all cases). The probabilistic maturation reaction norms were narrow, with the envelope width (distance between L_{p75} and L_{p25}) less than 2 cm on average, except for fish maturing as four-year olds.

Table 1 summarizes the results from regressing PMRN midpoints for 2- and 3-year-old capelin against environmental variables. Of the six explanatory time series, only temperature measured along the Vardø-North section in the year preceding the sampling had a significant effect ($p \leqslant 0.05$), and only for females maturating at the age of 3 years. The analyses suggested a negative effect of temperature on maturation, if any. No influence of capelin biomass on maturation could be detected.

All environmental variables associated with a significance of $p < 0.1$ were retained in the models describing PMRN midpoints as a function of sampling year. This high significance threshold ensured that none of the potentially significant variables was omitted due to type-II errors. For both sexes and all ages, L_{p50} were relatively stable over time, without any apparent directional change (Fig. 5); the linear regressions on PMRN midpoints in models including the sampling year showed no significant temporal trends (Table 2). No significant temporal trends appeared in the regression of PMRN width against the sampling year either (results not shown), except for 4-year-old males ($p = 0.010$), although this result was caused by a single observation: the particularly wide PMRN in the last year (see Fig. 5).

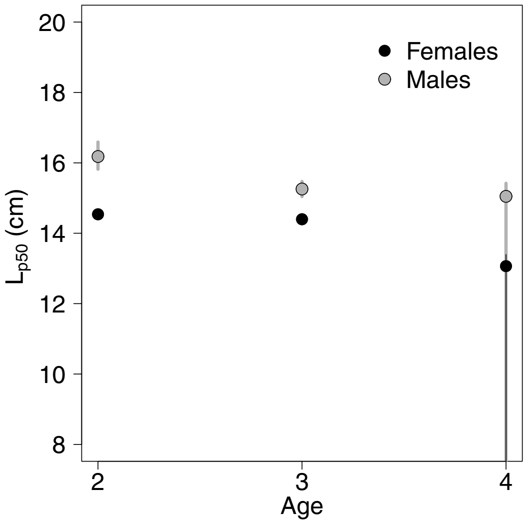

Fig. 6. Maturation reaction norms for females and males. Data allow the derivation of PMRN midpoints from age 2 to 4 for one cohort of each sex only. Females: 1981 cohort; males: 1980 cohort. Vertical bars indicate 90% confidence intervals obtained by bootstrapping around point estimates of L_{p50}.

In the period 1989–2005, Forberg maturity stages where routinely determined for female capelin. Using Forberg stage 21 to discriminate between immature and maturing females led to somewhat lower estimates of PMRN midpoints than when

Table 1. Summary of linear regressions of PMRN midpoints (in cm) on environmental variables (temperature and capelin biomass). The models for each explanatory variable were estimated independently. When available, Forberg stage 31 was used as the threshold maturity stage for females.

			Females				Males			
Age (y)			2		3		2		3	
			Slope	p	Slope	p	Slope	p	Slope	p
Temperature (°C)	Kola	no lag	−0.358	0.087	−0.399	0.195	−0.250	0.405	−0.692	0.051
		lag 1	−0.300	0.161	−0.534	0.060	−0.123	0.687	−0.531	0.064
	Vardø-North	no lag	−0.266	0.200	−0.208	0.501	−0.195	0.505	−0.400	0.303
		lag 1	−0.353	0.076	−0.658	0.039	−0.269	0.331	−0.655	0.056
Biomass (Mt)		no lag	−0.022	0.683	0.009	0.914	0.029	0.629	0.031	0.729
		lag 1	−0.005	0.918	−0.125	0.135	0.003	0.969	−0.121	0.184

Table 2. Summary of linear regressions of PMRN midpoints in models with the year of sampling alone and models including both year effect and environmental variables with $p < 0.1$. When available, Forberg stage 31 was used as the threshold maturity stage for females.

	Age (y)	Model	n	Slope α (cm y^{-1})	p
Females	2	$\alpha \cdot year$	28	–0.018	0.173
	2	$\beta \cdot T_{Kola} + \alpha \cdot year$	28	–0.010	0.506
	2	$\beta \cdot T_{Vard\_lag} + \alpha \cdot year$	28	–0.011	0.420
	3	$\alpha \cdot year$	22	–0.019	0.361
	3	$\beta \cdot T_{Kola\_lag} + \alpha \cdot year$	22	0.037	0.086
	3	$\beta \cdot T_{Vard\_lag} + \alpha \cdot year$	22	0.018	0.536
Males	2	$\alpha \cdot year$	21	–0.003	0.870
	3	$\alpha \cdot year$	23	0.023	0.242
	3	$\beta \cdot T_{Kola} + \alpha \cdot year$	23	0.038	0.078
	3	$\beta \cdot T_{Kola\_lag} + \alpha \cdot year$	23	0.037	0.086
	3	$\beta \cdot T_{Vard\_lag} + \alpha \cdot year$	23	0.023	0.242
	4	$\alpha \cdot year$	6	–0.095	0.158

using stage 31 (Fig. 7). None of the candidate environmental variables were significant at $p < 0.05$ when Forberg stage 21 was used as the maturation threshold (Table 3). This alternative classification did not change the sign of the temporal trends (Table 4) when compared to the results obtained with stage 31 above. However, unlike for the previous analysis, the temporal trend was significant in one of the two cases tested (females maturing at age 2, $p = 0.027$). The associated downward slope was, however, weak (Table 4).

Table 3. Summary of linear regressions of PMRN midpoints (in cm) in female capelin against environmental variables (temperature and capelin biomass) when using Forberg stage 21 as the threshold maturity stage for females for the period 1989–2005. The models for each explanatory variable were estimated independently.

Age (y)			2		3	
			Slope	p	Slope	p
Temperature (°C)	Kola	no lag	−0.322	0.465	−0.562	0.181
		lag 1	−0.417	0.325	−0.748	0.054
	Vardø-North	no lag	−0.091	0.836	−0.470	0.291
		lag 1	−0.329	0.427	−0.848	0.059
Biomass (Mt)		no lag	−0.031	0.768	0.048	0.675
		lag 1	−0.031	0.741	−0.159	0.188

Table 4. Summary of linear regressions of PMRN midpoints in models with the year of sampling alone and models including both year effect and environmental variables with $p < 0.1$. Forberg stage 21 was set as the threshold maturity stage for females. These estimates were only available for the period 1989–2005. However, the regression was made over the entire time series.

	Age (y)	Model	n	Slope α (cm y^{-1})	p
Females	2	$\alpha \cdot year$	26	−0.056	0.027
	3	$\beta \cdot T_{Kola\_lag} + \alpha \cdot year$	20	−0.030	0.272

4 Discussion

Despite large fluctuations in age at maturity (Tereshchenko 2002 and Fig. 3), we could not detect any significant temporal trends in maturation tendency of Barents Sea capelin, except when females at Forberg maturity stage 21 and later were assumed to be maturing. Instead, our results suggest that fluctuations in age at maturity primarily represented growth-driven phenotypic plasticity. In addition, the width of PMRN did not change, implying that the strength of the influence of body length on maturation was stable throughout the study pe-

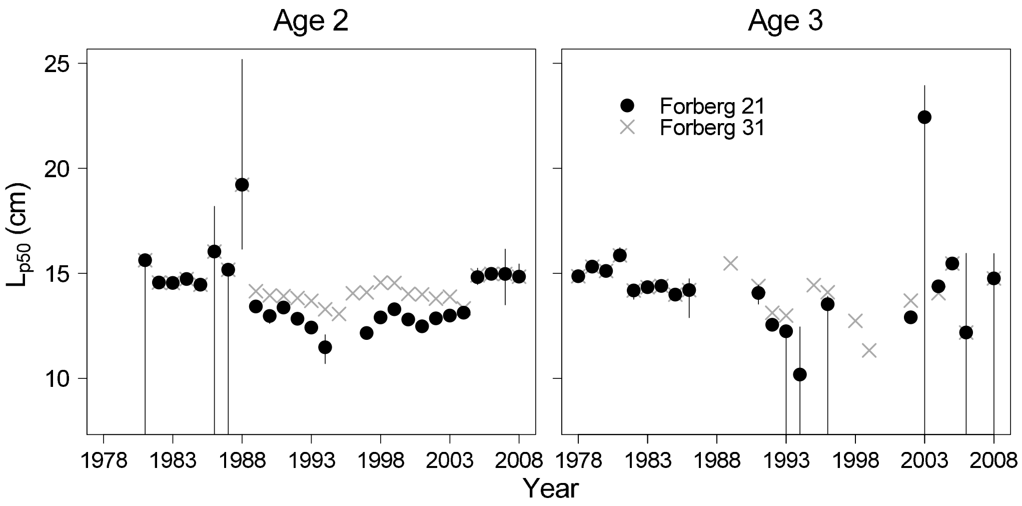

Fig. 7. Year-specific estimates of PMRN midpoints (L_{p50}) at age 2 and 3 years in female capelin when using Forberg stage 21 as the threshold maturity stage. These estimates are only available for the period 1989–2005; PMRN midpoints for the remaining years were derived based on the purely macroscopic maturity scale. Vertical bars indicate 90% confidence intervals obtained by bootstrapping around point estimates of L_{p50}. Midpoints obtained with Forberg stage 31 as the threshold maturity stage are displayed for comparison.

riod. These results are in line with what one would expect in a population that has not been subject to strong fisheries-induced selection.

Naturally, our results cannot prove that maturation tendency has not evolved in Barents Sea capelin during the period when large-scale fisheries were active. Indeed, there are several reasons for why we might have failed to detect evolutionary changes in age and size at maturation. First, evolution might have occurred before the period covered in this study. There is a gap of one decade between the start of the summer fishery in 1968 and the period covered in this study (1978–2008). This corresponds to about three generations, which would be enough, under strong selection, to produce significant evolutionary changes (see Conover and Munch 2002). However, given that fishing mortality in capelin is low compared to natural mortality, it is unlikely that the fishing selection was strong during this period. Second, the study period itself may have been too short to reveal significant fisheries-induced changes. However, our study period was of significant duration, covering about ten generations. Third, and most importantly, our results are influenced by the Forberg maturity stage that was used to distinguish the capelin that will spawn in the following year from those that will remain immature. When Forberg stage 21 (“early maturing I”) is used, the analysis suggests a significant trend in one occasion. However, we consider the results obtained with Forberg stage 31 (“maturing”) as the most reliable maturation threshold for the following reasons: using Forberg stage 21 led to fewer and more uncertain PMRN midpoint estimates (i.e., larger confidence intervals), and perhaps more importantly, to a more heterogeneous time series. Indeed, the large variations of PMRN midpoints at the boundaries of the period of routine use of the Forberg scale (1989–2005) suggest that Forberg stage 21 is less homologous to stage 3 on the macroscopic scale than Forberg stage 31. This interpretation is reinforced by the results of a comparison of the classification of female capelin according to the two different scales carried out by Forberg (1983), which indicates that the majority of individuals classified as Forberg stage 21 are identified as “immature” on the purely macroscopic scale (Forberg 1983).

Forberg and Tjelmeland (1985) developed a model for maturation in female Barents Sea capelin during the period 1978–1983, using the Forberg scale to characterise the maturation process. They constructed a length-based maturation function – essentially a PMRN, before the concept was formally introduced – that described the maturation fairly well, but found that length at 50% maturity (L_{50}) varied somewhat with age (3-year-olds matured at lower lengths than 2-year-olds) and with geographical area. The L_{50} was fairly constant from year to year. The estimated L_{50} lay in the range 12–15 cm, depending on which Forberg stage was used as the threshold (stage 21, 22, 31, 32 or 33). Hamre and Tjelmeland (1982) used a different length-based approach for splitting the total stock into immature and maturing parts. This approach normally gave a mean L_{50} around 14–15 cm. This is close to our cohort- and age-dependent estimates of L_{p50} based on Forberg stage 31 as the threshold (when available), suggesting that this threshold was a better choice than the alternative stage 21.

An additional reason for the lack of statistical significance of temporal trends in PMRN midpoints is the potential inadequacy of the approach used to detect evolutionary changes in age and size at maturation. This issue has been raised in several instances (see for example Kraak 2007; Kuparinen and Merilä 2007; Marshall and Browman 2007), based on different arguments. The most obvious one is that only evidence of changes at the genetic level can be considered as proof for evolution, which the PMRN approach, being solely based on the phenotypic expression of genes, does not provide (Kuparinen and Merilä 2007). Moreover, a limitation of the age- and length-based PMRN approach is the assumption that the main part of phenotypic plasticity in age and size at maturation is captured by accounting for average growth. This is acceptable if other factors acting on the maturation “decision” are stable in time or their influence is negligible. We considered two of these potentially influential factors in this study, namely water temperature and capelin biomass, but this did not challenge our conclusions. However, there were other potentially important factors that could not be taken into account due to the absence of relevant data. Among these are energetic condition (e.g., Rowe et al. 1991; Silverstein et al. 1997; Duston and Sanders 1999) and growth at critical times during the juvenile stage (e.g., Bromage et al. 2001; Morita and Fukuwaka 2006; Shearer et al. 2006). Because distinct growth rates during these stages can lead to identical average growth until maturation is detected, this factor is not accounted for in the classical two-dimensional PMRN approach. Additionally, the timing of observations traditionally associated with the derivation of PMRN has often been pointed out as non-relevant because age and size at maturation are distinct from the age and size at which the maturation "decision" is made (Wright 2007).

The absence of significant temporal trends in PMRN midpoints is in agreement with our prior expectations based on life-history theory, which suggests little or no fisheries-induced evolution in maturation tendency of semelparous fish that are unselectively harvested towards the end of their normal life, corresponding to the winter fishery in the case of Barents Sea capelin (e.g., Hard et al. 2008). A possible exception is females aged 2 years when the alternative maturation threshold was used (see Table 4), although, as discussed above, we consider these results as less credible. Nevertheless, selection pressures on maturation in Barents Sea capelin are not entirely clear-cut: some selection towards maturity at younger ages and at smaller body sizes might have occurred due to certain features of the Barents Sea capelin fisheries. First, the summer fishery between 1968 and 2002 caught both immature and maturing fish and, although this should have favoured earlier maturation, we noted that the landings from the summery fishery were usually lower than those from the winter fishery (ICES 2009, 2010). Second, if the winter fishery were size-selective, the prediction of evolutionary neutrality would no longer hold. Some size-selection is likely to have occurred because of the minimum size limit of 11 cm (total length) imposed on the capelin fishery since 1978. This is a lesser concern in the winter fishery (maturing capelin are generally larger than the limit). However, during the feeding season, capelin tend to form schools of individuals of similar body size (Gjøsæter and Korsbrekke 1990). In order to reduce the catches of under-sized fish, it was advantageous for fishers to target schools of large fish (Gjøsæter 1999; Bogstad and Gjøsæter 2001). Nevertheless, fishing mortality appears to be quite low compared with the mortality exerted by predators, particularly Atlantic cod (Dolgov 2002). Over the period 1973–2000, the fishing mortality was on average only 5% of the total mortality of capelin (Ushakov and Prozorkevich 2002). Our results are thus in agreement with the theory.

The current size at maturation of Barents Sea capelin has most likely been shaped by natural and sexual selection only. It has been influenced, among other things, by the positive effect of body size on fecundity in females (Huse and Gjøsæter 1997) the particular diet and feeding mode of the species (Panasenko 1981, 1984; Huse and Toresen 1996), competition with herring for food (Huse and Toresen 1996), male-male competition for mates (Vilhjálmsson 1994; Huse 1998), and the predation risk exerted mainly by cod late in life and from which capelin may have a higher chance to escape at a small size (Blanckenhorn 2000). Our results confirm that the maturation "decision" is primarily determined by body length and not by age in Barents Sea capelin, as previously shown by Forberg and Tjelmeland (1985); this is also an underlying assumption in the assessment model used for capelin (Gjøsæter et al. 2002a; ICES 2010). Accordingly, the PMRN for capelin is almost horizontal, as illustrated by Figure 6. Furthermore, our results suggest that male capelin have to grow to a larger size than female capelin to reach the same maturation probability. This is the first demonstration of such a sex difference in PMRNs: usually, there is no sex difference or males have a tendency to mature at a smaller size than females (Heino and Dieckmann 2008).

The effect of biomass on PMRN midpoints was never significant, its influence on maturation in Barents Sea capelin appearing to be mediated through growth instead (Gjøsæter et al. 2002b). The PMRN method thus appeared to effectively remove growth and density effects on sexual maturation. In contrast, the effect of water temperature measured during the summer of the year preceding the sampling reached the 5% significance level once (out of 16 cases), and was marginally significant (i.e., $0.05 < p < 0.1$) in four other instances. Considering further that the estimated relationships between water temperature and length at maturation were exclusively negative, whereas Carscadden et al. (1997) found a positive effect of temperature on the timing of spawning in Newfoundland capelin, we suggest that the influence of temperature on the maturation "decision" in Barents Sea capelin may not be a real one. This conclusion is reinforced by a known correlation between water temperature and abundance of krill (Eriksen and Dalpadado 2011), upon which large capelin predate. A positive relationship between PMRN midpoints and water temperature measured the same year could then be expected through the influence of krill abundance on capelin nutritional status. Moreover, even when statistically significant, temperature explained only little of the observed variability in length at maturation (18.7% in females maturing at the age of 3 years).

Capelin is an interesting case in the study of fisheries-induced evolution because here we did not expect to see marked evolutionary changes, despite a declining trend in age at maturation. This prior expectation was confirmed by our results, showing that the PMRN approach was successful in capturing growth-induced plastic variability in maturation. However, more generally, PMRNs might not capture all growth-related plasticity, at least when very large differences in growth occur, as in the zebrafish experiment by Uusi-Heikkilä et al. (2011). Nevertheless, growth in capelin has fluctuated substantially over the years (Fig. 2), suggesting that within the range of growth variability typically observed in the wild, the capacity of PMRNs to capture growth-related plasticity may well be sufficient. Our study thus supports the utility of probabilistic maturation reaction norms in assessing fisheries-induced evolution with phenotypic data.

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References

Alm G., 1959, Connection between maturity, size, and age in fishes. Rep. Inst. Freshw. Res., Drottningholm 40, 5–145.

Blanckenhorn W.U., 2000, The evolution of body size: what keeps organisms small? Q. Rev. Biol. 75, 385–407.

Bromage N., Porter M., Randall C., 2001, The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. Aquaculture 197, 63–98.

Bogstad B., Gjøsæter H., 2001, Predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) in the Barents Sea: implications for capelin stock assessment. Fish. Res. 53, 197–209.

Carscadden J., Nakashima B.S., Frank K.T., 1997, Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 54, 781–787.

Christiansen J.S., Præbel K., Siikavuopio S.I., Carscadden J.E., 2008, Facultative semelparity in capelin *Mallotus villosus* (Osmeridae) – an experimental test of a life history phenomenon in a sub-arctic fish. J. Exp. Mar. Biol. Ecol. 360, 47–55.

Conover D.O., Munch S.B., 2002, Sustaining fisheries yields over evolutionary time scales. Science 297, 94–96.

Conover D.O., Munch S.B., Arnott S.A., 2009, Reversal of evolutionary downsizing caused by selective harvest of large fish. Proc. R. Soc. B 276, 2015–2020.

Dieckmann U., Heino M., 2007, Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar. Ecol. Prog. Ser. 335, 253–269.

Dodson J.J., Tremblay S., Colombani F., Carscadden J.E., Lecomte F., 2007, Trans-Arctic dispersals and the evolution of a circumpolar marine fish species complex, the capelin (*Mallotus villosus*). Mol. Ecol. 16, 5030–5043.

Dolgov A.V., 2002, The role of capelin (*Mallotus villosus*) in the foodweb of the Barents Sea. ICES J. Mar. Sci. 59, 1034–1045.

Dolgov A.V., Johannesen E., Heino M., Olsen E., 2010, Trophic ecology of blue whiting in the Barents Sea. ICES J. Mar. Sci. 67, 483–493.

Dunlop E.S., Heino M., Dieckmann U., 2009, Eco-genetic modeling of contemporary life-history evolution. Ecol. Appl. 19, 1815–1834.

Duston J., Saunders R.L., 1999, Effect of winter food deprivation on growth and sexual maturity of Atlantic salmon (*Salmo salar*) in seawater. Can. J. Fish. Aquat. Sci. 56, 201–207.

Enberg K., Jørgensen C., Dunlop E.S., Heino M., Dieckmann U., 2009, Implications of fisheries-induced evolution for stock rebuilding and recovery. Evol. Appl. 2, 394–414.

Eriksen E., Dalpadado P., 2011, Long-term changes in krill biomass and distribution in the Barents Sea: are the changes mainly related to capelin stock size and temperature conditions? Polar Biol. 34, 1399–1409.

Forberg K.G., 1982, A histological study of development of oocyte in capelin, *Mallotus villosus villosus* (Müller). J. Fish Biol. 20, 143–154.

Forberg K.G., 1983, Maturity classification and growth of capelin, *Mallotus villosus villosus* (M), oocytes. J. Fish Biol. 22, 485–496.

Forberg K., Tjelmeland S., 1985, Maturity studies of Barents Sea capelin. Variation in length at maturity for female capelin. In: Gjøsæter H. (ed.). The Barents Sea capelin. Proc. 2nd PINRO-IMR Symp., Bergen, August 1984, pp. 213–222.

Gjøsæter H., 1998, The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia 83, 453–496.

Gjøsæter H., 1999, Studies on the Barents Sea capelin (*Mallotus villosus* Müller), with emphasis on growth. Ph.D. thesis, Department of Fisheries and Marine Biology, University of Bergen.

Gjøsæter H., Bogstad B., 1998, Effects of the presence of herring (*Clupea harengus*) on the stock-recruitment relationship of Barents Sea capelin (*Mallotus villosus*). Fish. Res. 38, 57–71.

Gjøsæter H., Bogstad B., Tjelmeland S., 2002a, Assessment methodology for Barents Sea capelin, *Mallotus villosus* (Müller). ICES J. Mar. Sci. 59, 1086–1095.

Gjøsæter H., Bogstad B., Tjelmeland S., 2009, Ecosystem effects of the three capelin stock collapses in the Barents Sea. Mar. Biol. Res. 5, 40–53.

Gjøsæter H., Dalpadado P., Hassel A., 2002b, Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. ICES J. Mar. Sci. 59, 959–967.

Gjøsæter H., Dommasnes A., Røttingen B., 1998, The Barents Sea capelin stock 1972–1997. A synthesis of results from acoustic surveys. Sarsia 83, 497-510.

Gjøsæter H., Korsbrekke K., 1990, Schooling-by-size in the Barents Sea capelin stock. ICES CM 1990/D:28.

Hallfredsson E.H., Pedersen T., 2009, Effects of predation from juvenile herring (*Clupea harengus*) on mortality rates of capelin (*Mallotus villosus*) larvae. Can. J. Fish. Aquat. Sci. 66, 1693–1706.

Hamre J., Tjelmeland S., 1982, Sustainable yield estimates of the Barents Sea capelin stock. ICES CM 1982/H:45.

Hard J.J., Gross M.R., Heino M., Hilborn R., Kope R.G., Law R., Reynolds J.D., 2008, Evolutionary consequences of fishing and their implications for salmon. Evol. Appl. 1, 388–408.

Heino M., Dieckmann U., 2008, Detecting fisheries-induced life-history evolution: an overview of the reaction-norm approach. Bull. Mar. Sci. 83, 69–93.

Heino M., Dieckmann U., Godø O.R., 2002, Measuring probabilistic reaction norms for age and size at maturation. Evolution 56, 669–678.

Hjermann D.Ø., Bogstad B., Dingsør G.E., Gjøsæter H., Ottersen G., Eikeset A.M., Stenseth N.C., 2010, Trophic interactions affecting a key ecosystem component: a multistage analysis of the recruitment of Barents Sea capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 67, 1363–1375.

Hjermann D.Ø., Stenseth N.C., Ottersen G., 2004, Indirect climatic forcing of the Barents Sea capelin: a cohort effect. Mar. Ecol. Prog. Ser. 273, 229–238.

Huse G., 1998, Sex-specific life history strategies in capelin (*Mallotus villosus*)? Can. J. Fish. Aquat. Sci. 55, 631–638.

Huse G., Gjøsæter H., 1997, Fecundity of the Barents Sea capelin (*Mallotus villosus*). Mar. Biol. 130, 309–313.

Huse G., Toresen R., 1996, A comparative study of the feeding habits of herring (*Clupea harengus*, Clupeidae, L.) and capelin (*Mallotus villosus*, Osmeridae, Müller) in the Barents Sea. Sarsia 81, 143–153.

ICES, 2009, Report of the Arctic Fisheries Working Group (AFWG). ICES CM 2009/ACOM:02.

ICES, 2010, Report of the Arctic fisheries Working Group (AFWG). ICES CM 2010/ACOM:05.

Jørgensen C., Enberg K., Dunlop E.S., Arlinghaus R., Boukal D.S., Brander K., Ernande B., Gårdmark A.G., Johnston F., Matsumura S., Pardoe H., Raab K., Silva A., Vainikka A., Dieckmann U., Heino M., Rijnsdorp A.D., 2007, Ecology: Managing evolving fish stocks. Science 318, 1247–1248.

Kraak S.B.M., 2007, Does the probabilistic maturation reaction norm approach disentangle phenotypic plasticity from genetic change? Mar. Ecol. Prog. Ser. 335, 295–300.

Kuparinen A., Merilä J., 2007, Detecting and managing fisheries-induced evolution. Trends Ecol. Evol. 22, 652–659.

Law R., Grey D.R., 1989, Evolution of yields from populations with age-specific cropping. Evol. Ecol. 3, 343–359.

Marshall C.T., Browman H.I., 2007, Disentangling the causes of maturation trends in exploited fish populations. Mar. Ecol. Prog. Ser. 335, 249–251.

Morita K., Fukuwaka M.A., 2006, Does size matter most? The effect of growth history on probabilistic reaction norm for salmon maturation. Evolution 60,1516–1521.

Morita K., Tsuboi J., Nagasawa T., 2009, Plasticity in probabilistic reaction norms for maturation in a salmonid fish. Biol. Lett. 5, 628–631.

Mork J., Friis-Sørensen E., 1983, Genetic variation in capelin *Mallotus villosus* from Norwegian waters. Mar. Ecol. Prog. Ser. 12, 199–205.

Møller D., Olsen S., 1962, Lodda og loddefisket. Fisken og Havet 1, 1–10.

Olsen E., Aanes S., Mehl S., Holst J.C., Aglen A., Gjøsæter H., 2010, Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES J. Mar. Sci. 67, 87–101.

Panasenko L., 1981, Diurnal rhythms and rations of capelin feeding in the Barents Sea. ICES CM 1981/H:6.

Panasenko L., 1984, Feeding of the Barents Sea capelin. ICES CM 1984/H:26.

Præbel K., Westgaard J.I., Fevolden S.E., Christiansen J.S., 2008, Circumpolar genetic population structure of capelin *Mallotus villosus*. Mar. Ecol. Prog. Ser. 360, 189–199.

Rowe D.K., Thorpe J.E., Shank A.M., 1991, Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci. 48, 405–413.

Sharpe, D., Hendry, A., 2009, Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evol. Appl. 2, 260–275.

Shearer K., Parkins P., Gadberry B., Beckman B., Swanson P., 2006, Effects of growth rate/body size and low lipid diet on the incidence of early sexual maturation in juvenile male spring Chinook salmon (*Oncorhynchus tshawytscha*). Aquaculture 252, 545–556.

Silverstein J.T., Shimma H., Ogata H., 1997, Early maturity in amago salmon (*Oncorhynchus masu ishikawai*): an association with energy storage. Can. J. Fish. Aquat. Sci. 54, 444–451.

Stergiou K.I., 1989, Capelin *Mallotus villosus* (Pisces: Osmeridae), glaciations, and speciation: a nomothetic approach to fisheries ecology and reproductive biology. Mar. Ecol. Prog. Ser. 56, 211–224.

Sætre R., Gjøsæter J., 1975, Ecological investigations on the spawning grounds of the Barents Sea capelin. Fiskeridirektoratets Skr. Ser. Havunders. 16, 203–227.

Tereshchenko E.S., 2002, The dynamics of population fecundity in Barents Sea capelin. ICES J. Mar. Sci. 59, 976–982.

Tjelmeland S., Bogstad B., 1993, The Barents Sea capelin stock collapse: a lesson to learn. Can. Spec. Publ. Fish. Aquat. Sci. 120, 127–142.

Trippel E.A., 1995, Age at maturity as stress indicator in fisheries. BioScience 45, 759–771.

Ushakov N.G., Prozorkevich D.V., 2002, The Barents Sea capelin – a review of trophic interrelations and fisheries. ICES J. Mar. Sci. 59, 1046–1052.

Uusi-Heikkilä S., Kuparinen A., Wolter C., Meinelt T., O'Toole A.C., Arlinghaus R., 2011, Experimental assessment of the probabilistic maturation reaction norm: condition matters. Proc. R. Soc. B: Biol. Sci. 278, 709–717.

Vilhjálmsson H., 1994, The Icelandic capelin stock: capelin, *Mallotus villosus* (Müller) in the Iceland-Greenland-Jan Mayen area. Rit Fiskideildar 13.

Wassmann P., Reigstad M., Haug T., Rudels B., Carroll M.L., Hop H., Gabrielsen G.W., Falk-Petersen S., Denisenko S.G., Arashkevich E., Slagstad D., Pavlova O., 2006, Food webs and carbon flux in the Barents Sea. Prog. Oceanogr. 71, 232–287.

Wright P.J., 2007, Understanding the maturation process. Mar. Ecol. Prog. Ser. 335, 279–283.