Review

Maturation in the Barents Sea capelin – Contrasting length- and gonad-based metrics

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ABSTRACT

It is assumed that maturation in the Barents Sea capelin is length-dependent, and that fish of at least 14 cm will potentially spawn. Current assessment and management models for the stock are based on this assumption of constant maturity at length (MaL). Using data from scientific surveys, this paper examines the validity of the constant MaL assumption, and contrasts it with maturation based on examination of fish gonads. Our analyses, based on time series of 16 years, show that MaL-based estimates of the proportion of maturing stock usually exceed gonad-based estimates. The difference varies consistently with time, and stock-size. We discuss the consequence of our results in the context of uncertainty associated with the current harvest rule.

1. Introduction

The Barents Sea capelin (Mallotus villosus Müller) – referred to hereafter simply as capelin – is a pelagic, planktivorous fish, with a maximum length of approximately 21 cm, and a maximum longevity of 5 years. It is generally accepted that the species is semelparous, with the spawning stock biomass dominated by fish of ages 3–5 (Hjermann et al., 2004). Capelin in the Barents Sea is central to the marine ecosystem, as it is a key forage species that dominate the diet of, for instance, the large stock of Northeast Arctic cod (Olsen et al., 2010).

Like most fish species with a short life history, the capelin stock size and spawning-age distribution fluctuate considerably. The annual acoustic survey (introduced in 1972) for abundance estimation of capelin stock size shows that the stock has experienced drastic fluctuations, with collapses occurring during 1985–1989, 1993–1997, 2003–2006 (Gjøsæter, 1998; Gjøsæter et al., 2007) and more recently, a mini-collapse in 2015–2016 (ICES, 2018). Associated with fluctuations in stock size are variations in capelin growth rates (Yndestad and Stene, 2002), age (Baulier et al., 2012; Carscadden et al., 2013; Ingvaldsen and Gjøsæter, 2013), and length (Gjøsæter, 1998; Tereshchenko, 2002) at maturation.

Changes in maturation (age or length) may be caused by several factors (environmental conditions, population size, mortality, food supply), and the result may represent a trade-off between reproductive (gonad development), and somatic growth (Engen and Sæther, 2016;

Stawitz and Essington, 2019). For species with unusual and/or complex life histories, the underlying factors that influence maturation may be difficult to untangle (Thorpe et al., 1998; Stokes et al., 2013; Folkvord et al., 2014; Hunter et al., 2015). This may be critical for short-lived species in a fluctuating environment as the probability of surviving multiple spawning seasons is low (Rideout et al., 2005; Rideout and Tomkiewicz, 2011; Engen and Sæther, 2016).

Ideally, both measurements (length and gonad-based) should be used when determining maturation stage of fish, and estimating the spawning stock biomass (Lassen and Medley, 2001, Ch. 9). In practice, however, this may be difficult due to the cost and logistics of data collection and processing (Rowell et al., 2017). There are also challenges with the method (macroscopic, histological techniques or gonadosomatic index) used to measure gonads (Saborido-Rey and Kjesbu, 2012; Flores et al., 2015; Balci and Aktop, 2019) and the time of year the survey is conducted (Chen and Paloheimo, 1994; Gjøsæter et al., 2002; Gjøsæter et al., 2012). Hence, for pragmatic reasons, either length- or gonad-based information is used to determine maturation (Gjøsæter et al., 2002; Gangl and Pereira, 2003; Saborido-Rey and Kjesbu, 2012).

For the Barents Sea capelin, both length- and gonad-based information are collected at a time when the gonad is still in development. The capelin stock is assessed in September of year Y (since 1972), giving estimates of abundance at age and length. Since full gonad-development is expected in March–April (in year $Y + 1$), projections of the spawning stock biomass are derived from length-based information (Gjøsæter

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et al., 2012). The length-based index is used to obtain a projection of the maturing stock biomass at January 1 (i.e., 3 months after assessment). The harvest control rule (HCR) uses this projected biomass to estimate the proportion of stock that can be fished (quota) when commercial fisheries commences in January. The goal is to ensure an escapement stock biomass of 200 kilo-tonnes by April 1 (i.e., commencement of spawning) (Gjøsæter et al., 2015; Tjelmeland and Bogstad, 1993). Currently, the Barents Sea capelin stock assessment model uses a cut-off of length 14 cm, that is non-sex-specific across years and age-groups, in calculating the proportion of maturing stock (Gjøsæter et al., 2002; IMR, 2011). Growth rates, age and maturation may fluctuate with, for example, stock size. Hence, this assumption of constant length at maturation could potentially bias estimates of spawning stock biomass which, subsequently, affect management decisions on total allowable catch (TAC) (Gjøsæter, 1986; Kraak et al., 2005; Carscadden et al., 2013).

Our goal is to assess maturation (level and trend) using gonad-based information and compare this with maturation based on the current (length-based) approach. We investigate existence of inconsistencies between the two maturation metrics, and discuss the effect in the broad context of managing short-lived species, whose growth and maturation rates are strongly influenced by temporal demographic and environmental variability.

2. Materials and methods

2.1. Data

The data set consists of 16 years (2003–2018 time series) of biological data from the Joint Norwegian/Russian Ecosystem Survey in the Barents Sea and adjacent waters that are carried out annually in the autumn. The survey, conducted just prior to the winter cessation of growth, monitors the status of abiotic and biotic factors and changes in these in the Barents Sea (IMR/PI, 2018). It provides extensive data from a grid of planned sampling stations (including pelagic, midwater and bottom trawls), and supplementary trawls based on acoustic registrations, with annual sampling effort varying between 320 and 599 trawl stations.

The biological measurements used in this manuscript are individual length measurements, maturation stage classifications, and estimated total number of age-2 capelin sampled at planned pelagic trawl stations only. The assumption is that the random samples are representative of the whole catch of capelin. Data samples from bottom trawl stations are unlikely to reflect the composition of capelin population since capelin occupy pelagic zones of the water column. These data are therefore, not used in annual fished stock assessment (ICES, 2019). The stock assessment process integrates uncertain information from many data sources, and modelling assumptions. Decoupling the effect of the various sources of uncertainty on the assessment results is non-trivial. Therefore, we have defined analysis that isolate effects of age on maturation by focusing on one age group (Hamre, 1985). This has the advantage that we can clearly ascribe differences to choice of maturation metric. However, this comes with the caveat that we cannot make quantitative considerations on the consequences for assessment. In addition, the abundance indices (both spawning and non-spawning) of age-2 capelin are much larger compared to age-3 capelin (Fig. 1, adapted from tables reported in ICES, 2019), because it generally has a relatively large number of length samples examined for various biological parameters. This is relevant as the proportion of individuals maturing at a given age may depend on the strength of the cohort considered (Gjøsæter and Bogstad, 1998, and Table 1). Finally, the proportion of capelin at age-2 is determined during the survey in autumn. This proportion is likely to change by the time of spawning, as fish would have crossed over to an older age-group. As is customary, age groups are separated by the 1st of January. We refer the reader to Gjøsæter (1999) and Eriksen et al. (2018) for detailed description of the survey design. In our analyses, we

use all age-2 capelin that were staged for maturity during the survey, with a sex-independent cut-off length of 14 cm for mature capelin, and gonad-based maturity classification following Tables 2 and 1, 1

2.2. Estimators of maturing fish

Pelagic trawl stations are the primary sampling units (PSUs) in the scientific survey of pelagic fish. Let $i = \{1, …, N\}$ represent a count index over the total of N trawl stations surveyed in a given year. Furthermore, let M_i and p_i represent respectively, the total number of fish sampled, and proportion of maturing fish at station i. Then an estimator for the proportion of mature fish, $\hat{p}$, for p, in a given year y is defined by

$$\hat{p}_{(j)} = \frac{\sum_i^N M_i \times \hat{p}_{i(j)}}{\sum_i^N M_i}, \quad j \in \{\text{Lb}, \ \text{Gb}\}, \tag{1}$$

where maturity is classified as: (i) length-based (Lb), such that Lb $\geq$ 14 cm, or (ii) gonad-based-inspection (Gb) following considerations in Table 2. Approximate 95% bootstrap confidence intervals are computed by applying the bias-corrected percentile bootstrap procedure in Magnusson et al. (2013), Jourdain et al. (2020) to the PSUs, in the following way:

(i) Sample the N PSUs with replacement.
(ii) Sample lengths from the sampled stations in step (i) and compute $\hat{p}_{i(\text{Lb})}$ and $\hat{p}_{i(\text{Gb})}$.
(iii) Calculate proportions mature in a given year, $\hat{p}_{(\text{Lb})}$ and $\hat{p}_{(\text{Gb})}$.
(iv) Calculate the difference between $\hat{p}_{(\text{Lb})}$ and $\hat{p}_{(\text{Gb})}$ in step (iii).
(v) Repeat steps (i)–(iv) B times, where $B = 1000$ is the number of bootstrap replicates.

To make inference about the difference, if any, between $p_{(Lb)}$ and $p_{(Gb)}$, we examine the nominal 95% confidence interval for $(p_{(Lb)} - p_{(Gb)})$. Several methods for testing whether the difference between two point estimates are statistically significant exist (Cole and Blair, 1999; Cromwell et al., 1996; Schenker and Gentleman, 2001). Some of which include the following

(i) the overlap procedure (Payton et al., 2003) – simple to use but potentially conservative and substantially deficient especially when associated standard errors of point estimates are not very different from each other (Schenker and Gentleman, 2001);
(ii) the "standard" method (see Schenker and Gentleman, 2001) – tests the hypotheses: $H_0 : \mu_x = \mu_y$ and $H_0 : \sigma_x = \sigma_y$, and assumes

Table 1
Column 2 (Total) includes only representative stations of the whole catch, and which are used in the stock assessment.

Year	Pelagic stations sampled		Biological measurements		Number mature	
	Total	With age-2 fish	Length	Staged	Length $\geq$14 cm	Gonads
2003	25	12	374	185	109	10
2004	35	14	328	223	130	78
2005	25	12	478	478	310	81
2006	21	12	372	372	308	122
2007	21	12	318	318	251	141
2008	30	21	726	726	514	186
2009	27	19	548	548	227	128
2010	45	30	505	504	213	68
2011	37	26	668	663	183	63
2012	27	22	317	317	84	32
2013	36	26	470	461	78	1
2014	26	21	461	461	103	11
2015	21	18	535	535	225	73
2016	31	14	283	278	221	17
2017	79	68	1898	1891	1272	713
2018	40	35	839	834	584	365

Table 2

Description and classification of macroscopic gonadal stages for Barents Sea capelin.

Stage	Condition	Description Female	Male	Classification
1	Immature	Juvenile phase. Gonads are band-like, thin, and totally transparent	Juvenile phase. Gonads are band-like, thin, and totally transparent	
2	Immature	Gonads are a little larger in volume, sex is relatively easy to see. Gonads are still transparent and colorless.	Gonads are a little larger in volume, sex is relatively easy to see. Gonads are still transparent and colorless.	
		Gonads opaque, but a little developed in volume. Visible blood veins. Ovaries	Gonads opaque, but a little developed in volume. Visible blood veins. Testes	Immature
3	Maturing	have yellow/white grains in the lamellae.	white or with white spots. Solid consistency.	
4	Maturing	Gonads larger in volume. Ovaries yellowish or white. The eggs can be easily seen and gonads begin to become transparent.	Gonads larger in volume. Visible blood veins. Testes light grey or white, the milt is viscous.	
5	Maturing	The ovaries fill the entire body cavity. Most eggs are transparent.	Testes grey or white. The milt is a thin liquid, but the gonads are still not running. Pressure applied to the abdomen will cause milt to run out.	Mature
6	Spawning	Running gonads. Light pressure on the abdomen causes eggs to come out.	Running gonads. Light pressure on the abdomen causes milt to come out.	
7	Spent	The gonads are slack, contains remaining eggs.	The gonads are slack, contains remaining milt.	
8	Resting	Gonads are small. Eggs are not visible. Difficult to distinguish from stage 2 or 3.	Gonads are small. Difficult to distinguish from stage 2 or 3.	
9	Abnormal	Gonad has developed abnormally, difficult to determine the stage	Gonad has developed abnormally, difficult to determine the stage	

estimates are consistent, asymptotically normal and asymptotically independent; and

(iii) nonparametric bootstrapping – flexible as it makes no assumptions about the distribution of $\widehat{p}_{Lb}$ and $\widehat{p}_{Gb}$.

Here, we use nonparametric bootstrapping to estimate associated standard errors σ_{Lb} and σ_{Gb} of p_{Lb} and p_{Gb}, respectively. By the duality between $100(1 - \alpha)$ confidence intervals and significance tests level α, we test the null hypothesis $H_0 : p_{(Lb)} - p_{(Gb)} = 0$ by examining whether the nominal 95% interval contains 0. The null hypothesis will be rejected if and only if the interval does not contain 0.

2.3. Estimator of overlap between juvenile and maturing fish

This section deals with quantifying the difference in length distributions of immature/mature fish, using a gonadal-based metric for
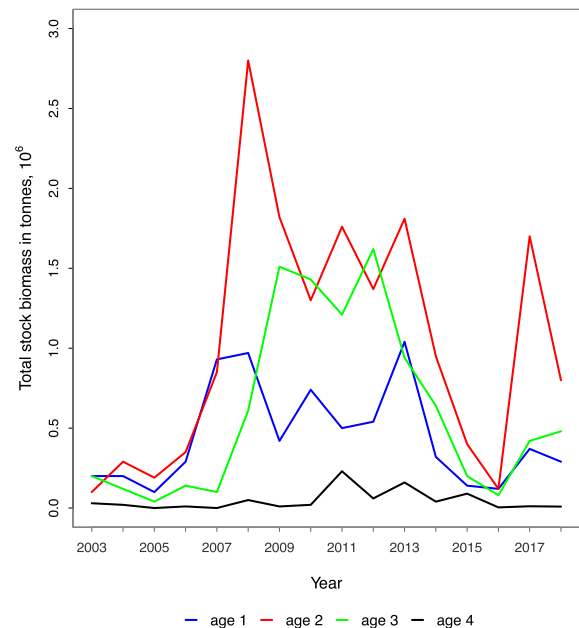

Fig. 1. Total stock biomass (in tonnes 10^6) by age (1–4 years) in years 2003–2018, where age-2 capelin are more dominant compared to maturing age-3 and age-4 capelin (IMR/PI, 2018, p. 55).

maturity. Our approach is based on quantifying the similarity in probability density functions of the length distributions.

Let $f_A(x)$ and $f_B(x)$ be the probability density functions (pdfs) over a continuous variable x, for sets A and B, respectively. We define the *overlapping coefficient* (see Weitzman, 1970; Ridout and Linkie, 2009), $\Delta \in [0, 1]$, as the common area under both f_A and f_B, i.e.,

$$\Delta(A, B) = \int_{R_n} \min[f_A(x), f_B(x)]\mathrm{d}x, \tag{2}$$

where $\Delta(A, B) = 1$ or $\Delta(A, B) = 0$ if and only if the densities are respectively, identical or have no overlap, for all values of x.

In practice, the density functions $f_A(x)$ and $f_B(x)$ are unknown. This paper derives the pdfs by applying a nonparametric density estimation technique to data. Nonparametric estimation of the overlapping coefficient has been studied in more detail by Schmid and Schmidt (2006), who proposed several estimators for $\Delta(A, B)$ that are based on Kernel Density Estimation (KDE). We adopt the distribution-free approximation technique by Pastore and Calcagnì (2019), where KDE estimates are used to approximate $f_A(x)$ and $f_B(x)$ and subsequently, $\Delta(A, B)$.

Let A and B represent immature, and mature fish, respectively, and let $L^a = (l_1^a, \ldots, l_i^a, \ldots, l_n^a)$ (similarly for B) be length realizations of fish that are classified as immature, based on gonad-inspection. The KDE approximation, $\widehat{f}_A(l)$, of $f_A(l)$ (and similarly for $f_B(l)$) is given by

$$\widehat{f}_A(l) = n^{-1} \sum_{i=1}^{n} K\left(\frac{l - l_i^a}{h}\right), \tag{3}$$

where K is the kernel and h is the bandwidth (Pastore and Calcagnì, 2019). The function `overlap` in the R package `overlapping` is used to estimate $\widehat{\Delta}(A, B)$ (Team, 2017; Pastore, 2018). We use the R function `boot.overlap`, with $B = 1000$ bootstrap replications, to estimate the variance of $\widehat{\Delta}(A, B)$ (Pastore, 2018; Pastore and Calcagnì, 2019) and approximate 95% confidence intervals. The nonparametric bias-corrected percentile bootstrap method is used to estimate confidence intervals (Gavaris and Ianelli, 2002; Magnusson et al., 2013).

3. Results

3.1. Evaluating maturity classification criteria

Temporal patterns in estimated proportions of maturing age-2 capelin show visible disagreement between the two maturity classification criteria (Fig. 2, upper panel). The estimates of the proportion maturing based on length consistently exceed those based on gonadal-inspection, with larger differences during periods of low capelin abundance (Fig. 2, lower panel). In addition, large variability exists in gonad-based estimates, particularly in the earlier years (2003–2008). We note that maturity stages of the capelin are determined by macroscopic examination of gonads. However, inference based on macroscopic examination can be highly uncertain, unless collaborated by microscopic examination of gonads. Even small amounts of error in the staging process of gonads can lead to profound variation in estimated proportions and decreased precision (Ferreri et al., 2009). An evaluation of the expected relative standard error $\{\mathrm{se}(\widehat{p}_{\mathrm{Gb}})/\widehat{p}_{\mathrm{Gb}}\}$ in gonad-based estimates of proportion mature lies in the range 16.3–122.3%, with at least 10 of the sampled years exceeding 25%. The results also show that the null hypothesis — there is no difference in estimated proportions between the two maturity criteria — can be rejected for all years, except 2012. We conclude therefore, that the disagreement between the two criteria is statistically significant (Fig. 2, lower panel). The non-significant difference between $\widehat{p}_{\mathrm{Lb}}$ and $\widehat{p}_{\mathrm{Gb}}$ in 2012 may therefore be merely coincidental. We also infer from Fig. 2 (lower panel) that in general, the occurrence of large differences in maturation metrics are coincidental with low capelin stock size. Thus, estimates of the proportion of the stock classified as maturing are expected to be biased during years of stock collapse (moratorium on fisheries), while consistent results are expected for years when the stock is open to commercial fisheries.

3.2. Estimating overlap indices

Fig. 3 (left panel) shows mixed results in variation of temporal overlap between immature and mature population of age-2 capelin. The 14 cm maturity criterion splits the region of overlap between the mature and juvenile population ($\sim$) equally for only three of the sampled years (2009–2010 and 2015). The overlap is, on average, larger in the earlier years (2005–2008), where growth rate of the juvenile population increased but not all have attained gonadal-maturity. The years (2005–2008) of increasing immature population growth rate are also marked by increase in both the total, and maturing stock biomass (Fig. 3, right panel). Furthermore, a significant number of fish that are classified as maturing based on gonad-inspection have lengths in excess of 14 cm; see Fig. 3, left panel. During the period 2011–2014, there seems to be a gradual shift towards an earlier onset of maturity (length <14 cm). Observe that this period marks a gradual decrease in the capelin biomass towards collapse (Fig. 3, right panel).

The lowest overlap values were in years 2016, 2011 and 2003, where, for two of these years, total capelin biomass was at its lowest (<0.60 million tonnes). These years with low overlap coefficients were part of, or immediately preceded, specific periods of drastic stock decline that resulted in fishing moratoria (2003–2007, 2016-2020) (Hjermann et al., 2004; Gjøsæter et al., 2016). Observe that analysis for year 2013 is excluded in this section. This is because only one mature capelin was sampled and the `overlap` R package requires at least two points in each input data set for automatic selection of bandwidth and, hence, the estimation of the pdf (Pastore, 2018, and Table 1).
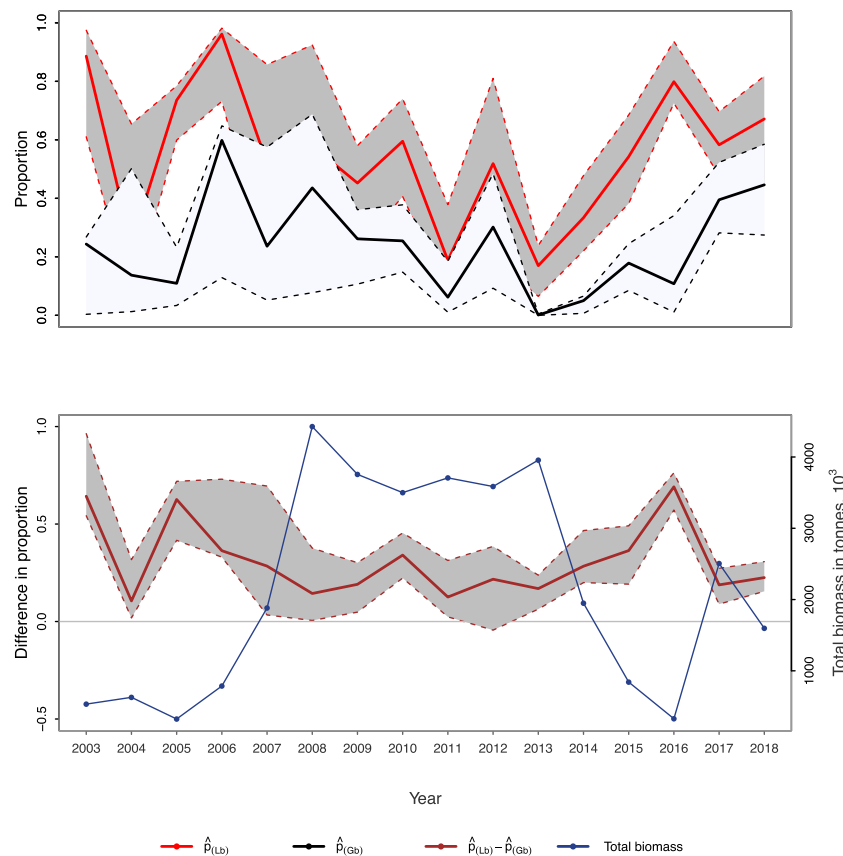

Fig. 2. Upper panel: Estimated proportion of mature age-2 capelin based on length $\{\widehat{p}_{(\mathrm{Lb})}\}$ and gonad-inspection $\{\widehat{p}_{(\mathrm{Gb})}\}$, Lower panel: Estimated difference in proportions $\{\widehat{p}_{(\mathrm{Lb})} - \widehat{p}_{(\mathrm{Gb})}\}$ with total biomass (in tonnes 10^3) in years 2003–2018, with approximate 95% bias-corrected bootstrap confidence intervals for 1000 bootstrap replications.
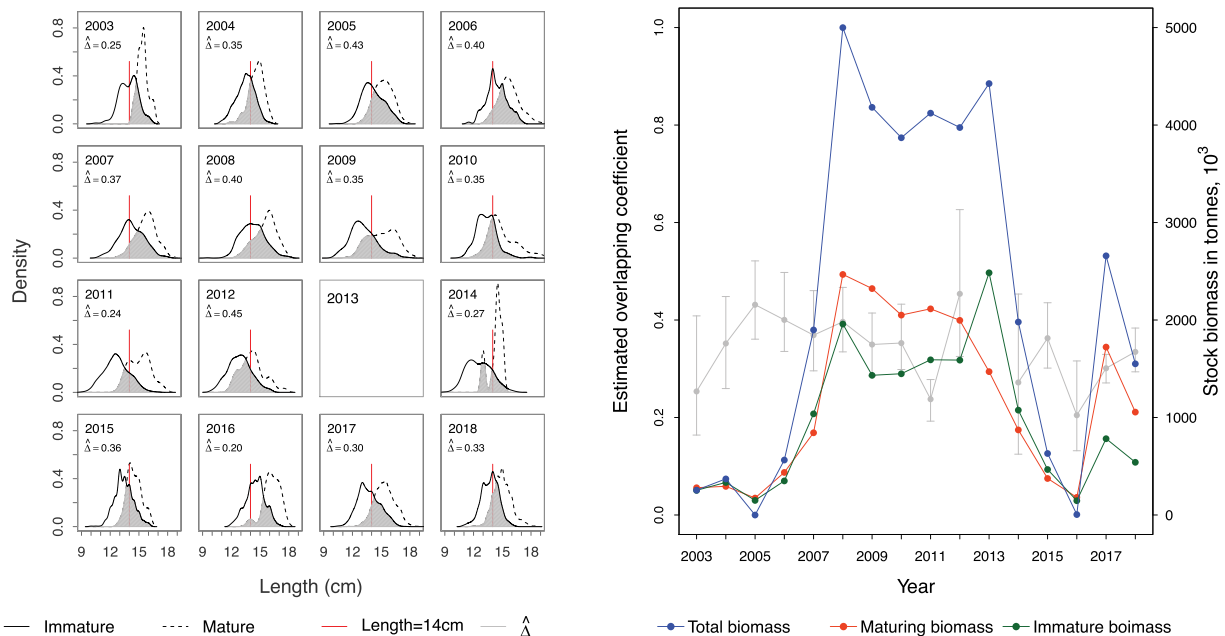
Fig. 3. Left: Estimated kernel densities of immature and mature age-2 capelin based on gonad-inspection, Right: Estimated overlap coefficients with approximate 95% bias-corrected bootstrap confidence intervals, and biomass of maturing and immature capelin (in tonnes, 10^3) (ICES, 2019) for years 2003–2018.

4. Discussion

Both individual length and gonad-based classifications in the fall are proxy indicators of the propensity to spawn in the spring. We have compared the two criteria using selected trawl stations that mimic those typically used in abundance index estimation. However, because abundance indices are derived from acoustic surveys, our estimates of total catch proportions cannot be extrapolated to population parameters. This notwithstanding, the estimates provide a solid basis for comparing criteria and investigating temporal trends. In order to isolate effects, we have focused on age-2 capelin, which constitutes the largest fraction of the stock biomass, and also have a good mix of mature and immature individuals for almost all years.

Our analysis shows variability in the proportion of stock maturing (for length-based maturation cut-off) that depends on whether the maturing stock proportion is being calculated for a low (collapse) or high-to-moderate biomass state. There is a high propensity for underestimating the maturing stock biomass for the former, while an over-estimation is more likely for the latter scenario. These findings are consistent with those in Jokar et al. (2021).

While length-based and gonad-based classifications systematically trend in the same direction, we find that these criteria yield different estimates of the proportion of mature age-2 capelin, with the former consistently providing higher estimates. The most likely errors in macroscopic inspection would be those of not detecting all maturing individuals, rather than misclassification of those immature, as mature. Using microscopic gonad investigation, Forberg and Tjelmeland (1985) showed that for most years, L_{50} for age-2 capelin were somewhat higher than for age-3 female capelin. Precisely for this reason, we have sought to isolate the age-effect by focusing on age-2 capelin. We note that the difference between the two maturation criteria does not seem to be invariant of stock size (Fig. 2, lower panel), with large differences in years of low total capelin abundance, and vice versa.

In order to more directly assess how the two maturation criteria differ, we have also analysed the overlap of the length distributions of sampled fish that are classified as mature or immature, based on gonad-inspection. Our results indicate that thresholds for optimal separation differ from year to year, depending on stock size (Fig. 3, right panel).

The years with less individual growth, and less visible maturation

provides a better length-separation between the mature and immature parts of the age-group, and hence a better agreement between the two criteria. The signal seems to be driven by variation in the length of immature fish (Fig. 3, left panel), with modes clearly shorter in years with large stock size.

Interestingly, this tendency is not evident until the halt in increasing stock biomass (year 2009), but continues almost throughout the period of decline in stock biomass (2014–2015). If one assumes systematic bias in the macroscopic gonad inspections, these observations may be indicative of how stock size is linked to individual growth and maturation conditions.

There is a limitation in inferring the potential impact of our results on stock assessment. However, we have documented the existence of bias (length- or gonad-based) when estimating the proportion of the stock that can be classified as mature. Minimizing bias within each metric (length-, and gonad-based), and across metrics is relevant to sustainable management of the capelin stock, as the annual TAC is based on estimates of the maturing stock biomass. This consideration also extends, in general, to other short-lived fish stocks (including forage fish). Such species are usually characterized by volatile population dynamics and rates of maturation may be influenced by confounding events of changing biotic and abiotic conditions. A special relevance of our results applies to those short-lived species that are managed by escapement strategies, and for which combining information from different data sources may be attractive in helping reduce uncertainty in management decisions.

5. Conclusions

The fraction of total capelin biomass that can be considered as maturing can be determined either based on length measurements or on gonad inspections. Results presented in this paper show that for each of these methods, estimates of maturing stock proportion exhibit a temporal trend that is influenced by stock size. The average length at maturation (using a length-based metric) is much higher during periods of commercial fisheries than during fisheries moratorium times. This, in turn, means that the maturation intensity (i.e., the change in maturation proportion with respect to length, measured at the median length) will be higher when stock numbers are low, than for cases when the stock

size is high. In comparing estimates from the two metrics, we observe that the level of temporal discrepancy is determined by stock size.

While direct gonad inspections at an early (pre-maturation) stage are not necessarily better indicators of maturation than length, the assumption of constant length at maturation is rather strong, and significant inter-annual variation in maturation at length is supported by previous microscopic analysis. The strong co-trending of the difference in predicted mature proportion between maturation criteria and the size of the stock, strongly suggest that this inter-annual variation is not due to random fluctuation, but reflect density effects. The assumption of constant maturation length may, therefore, introduce a stock-size dependent bias in the assessment of spawning stock biomass. Gonad and length measurements are taken during the same survey. Hence both measurements can be used to estimate bounds for the spawning stock biomass in a transparent manner that is reflective of the inherent uncertainty in determining fish maturation.

The results in this paper are also significant from an ecological perspective. The large discrepancies in maturation metrics at low stock size may be reflective of different scenarios by which capelin allocates energy to metabolism, growth, and reproduction. Further research is required to help understand the link between energy allocation and population density in capelin, as well as the subsequent effect on maturation scheduling.

Declaration of Competing Interest

The authors report no declarations of interest.

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