



Early life growth is affecting timing of spawning in the semelparous Barents Sea capelin (*Mallotus villosus*)

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ABSTRACT

Capelin (*Mallotus villosus*) is a forage fish and a key species in the Barents Sea (BS). The BS capelin are semelparous and hence only spawn once along the north coasts of Norway and Russia before they die. The age at spawning ranges from 2 to 5 years and the spawning season peaks in March/April but starts in February and lasts until June, and the causes of the variability in timing of spawning are not well understood. Here, we aimed to find out whether early growth is associated with the timing of spawning in BS capelin, both on the individual and population level, and if there is an association between early life growth and the spatial distribution at the nursery areas and feeding grounds. For the analysis, we used an extensive dataset comprising >150 000 otolith growth zone measurements carried out during surveys from 1976 to 2019 both from the spawning and feeding areas. The data from the feeding area showed that capelin with good first-year growth were found in the productive north-west part of the Barents Sea at both age 1 and 2, while capelin with relatively poor first-year growth were typically found in the south-east Barents Sea. The data from the spawning area showed on the individual level that capelin with good first-year growth tend to spawn both at a younger age and earlier in the season. The capelin spawning late in the season were also generally smaller than early spawners. On the population level, a contradictory pattern was observed where the proportion of maturing capelin at age 2 and 3 was negatively correlated with first-year growth indicating that the great variability in year-class strength masks the general effect found at the level of individual fish. Furthermore, first-year growth was positively associated with the abundance of 1-year-old capelin indicating that rapid growth early in life enhances recruitment. On the other hand, first-year growth was strongly negatively correlated with third-year growth suggesting an increased effect of density-dependent growth with age and/or compensatory growth, or reduced growth linked to earlier maturation. In sum, our results show that the first-year growth affects growth, maturation processes, and timing of spawning later in life, thus potentially strongly influencing capelin population dynamics.

1. Introduction

Plasticity in spawning time is very common in fish and may be critical in order to adapt the survival conditions for the progeny to a changing environment (Wright and Trippel, 2009). The seasonal timing has evolved in fish so that early life stages match the plankton bloom to ensure good feeding conditions for the larvae (Cushing, 1990) while minimizing larval predation risk (Bailey and Houde, 1989). For semelparous fish (i.e. they die after a single spawning event) the timing of spawning is not only important for seasonal timing, but essential in choosing the optimal time during their life span for the onset of

maturation and subsequent spawning (Huse, 1998).

Capelin is a small pelagic fish that may be both semelparous and iteroparous (i.e. die after two or more spawning events) depending on the population, and have been suggested to be facultative semelparous (Christiansen et al., 2008). The population of capelin in the Barents Sea is semelparous (Christiansen et al., 2008), which has likely evolved as a response to high adult mortality (Orzack and Tuljapurkar, 1989; Huse, 1998; Crespi and Teo, 2002). Barents Sea capelin (BS capelin) experiences heavy predation from piscivores fish, whales, seals, and seabirds and is considered to play a major role in the ecosystem transferring energy from zooplankton production to higher trophic levels (Gjøsæter,

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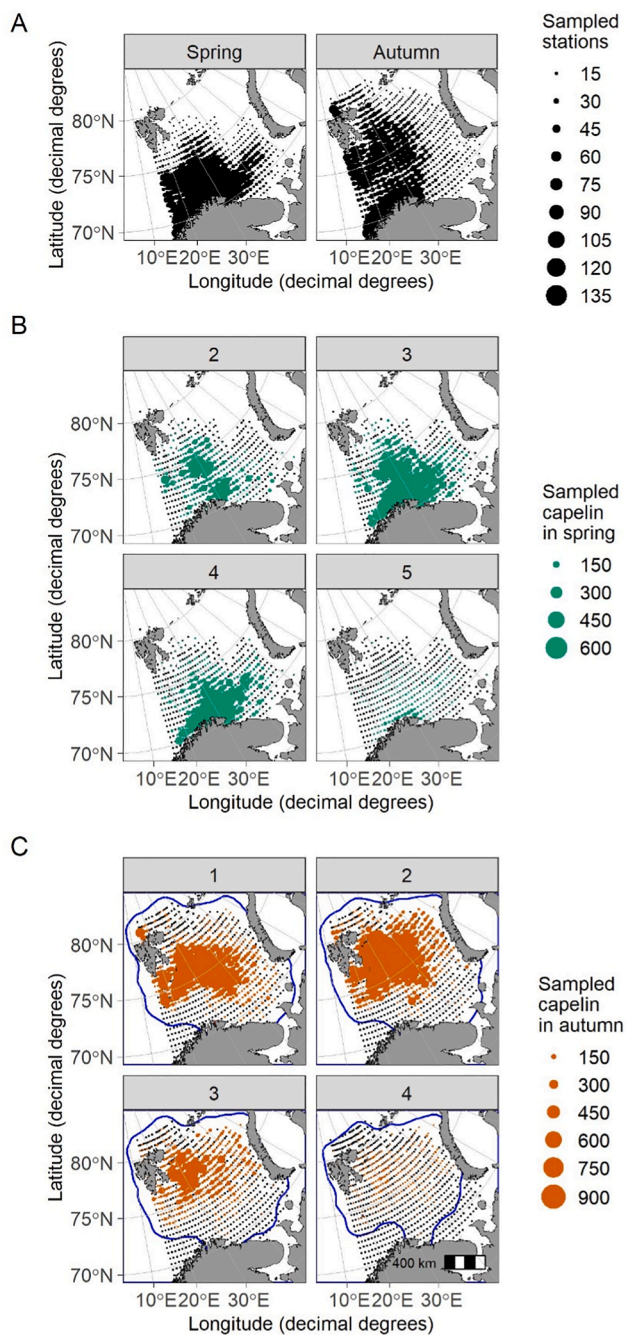


Fig. 1. A) Number of sampling stations included in the analysis per geographic rectangle (1° longitude \times 0.5° latitude). The included stations comprise sampling done with either shrimp trawl or pelagic trawl in the Barents Sea east of 15° E between 1976 and 2019. Number of capelin sampled per age including otolith growth zones analyzed during B) spring (February–June) and C) autumn (August–October). Black dots indicate sampled stations without capelin, and capelin age is shown on top of each panel. The blue line represents the interior edge used for the spatial model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1998; Ushakov and Prozorkevich, 2002). They have a life span of 2–5 years and the abundance of the short-lived BS capelin fluctuates strongly, sometimes causing severe cascading effects on the ecosystem (Gjøsaeter et al., 2009). BS capelin perform extensive migrations between feeding grounds north in the Barents Sea and wintering areas south of the winter ice edge, and to the spawning grounds along the coast of northern Norway and Russia (Gjøsaeter, 1998; Huse and

Ellingsen, 2008). They spawn demersal on sand and gravel, typically in current rich waters of 20–75 m depth. The capelin eggs hatch after an incubation period which decreases with increasing temperature but averages about 40 days at 4° (Gjøsaeter and Gjøsaeter, 1986). The larvae drift in the Barents Sea and have reached a mean total length of 35–58 mm by August (Loeng and Gjøsaeter, 1990). The larvae seem to be quite opportunistic feeders on small prey, such as phytoplankton, invertebrate eggs, nauplii, larvae, small copepods or bivalves (Fossheim et al., 2006; Pedersen and Fossheim, 2008). The capelin typically metamorphose during spring/summer the following year (Gjøsaeter, 1998). The onset of maturation and later spawning migration in BS capelin is strongly related to length (Forberg and Tjelmeland, 1985; Gjøsaeter, 1999; Baulier et al., 2012) and in the assessment, all capelin >14 cm are assumed to be maturing (ICES, 2020a). However, the proportion of maturing fish based on the assumption of constant maturity at length usually exceeds proportion based on the gonadal development (Jourdain et al., 2021). The age at maturation on the other hand is variable (Gjøsaeter, 1999; Baulier et al., 2012) and the seasonal timing of the spawning also varies. Even though peak spawning appears in March/April, historical records and results from larval monitoring surveys show that the spawning season of capelin may extend to the summer (Loeng and Gjøsaeter, 1990). Given that length is a reasonable proxy for predicting maturity in capelin, growth is expected to be an important driver for the variability in timing of spawning (Gjøsaeter, 1999), but no studies have investigated the importance of early growth for timing of spawning.

A common tool used for growth studies is calcified structures, such as otoliths, because they are characterized by continuous growth patterns which are usually linked to somatic growth (Black et al., 2019). Otolith growth increments are typically formed daily and annually allowing for estimation of age and growth of individual fish (Campana and Thorrold, 2001). Furthermore, measurements of annual increments allow for back-calculations of individual growth throughout a fish life by estimation of length at ages prior to capture (Francis, 1990; Vigliola and Meekan, 2009). Otolith measurements of BS capelin have systematically been carried out during scientific surveys conducted by the Institute of Marine Research (IMR) in the Barents Sea since the 1970s and are therefore well suited for elucidating causes and effects of variability in early growth.

In the present work, we aim to find out whether early growth is associated with the timing of spawning in BS capelin, both on the individual as well as population level. To address this, we take advantage of the large-scale biological sampling IMR has conducted on capelin for decades, including individual data of maturation, body length at age, and annual otolith growth. We first investigate whether early-life growth is affecting timing of spawning in capelin, both timing related to life span (age) and seasonal timing. Secondly, we investigate whether there is an association between early-life growth and the spatial distribution of capelin on the nursery areas and feeding grounds. Lastly, we explore if the variability in early-life growth can be linked to population dynamics measured as year class strength, such as recruitment or proportion of spawning individuals.

2. Material and methods

2.1. Biological data

Capelin were collected on scientific surveys in the Barents Sea (Fig. 1) conducted by the IMR during the period 1976–2019. Mainly shrimp trawl (Campelen 1800 bottom trawl) and pelagic trawl ('Harstad trawl') have been used for the sampling. Trawl hauls were carried out on fixed pre-selected stations as well as opportunistically on acoustic registrations (target hauls). Pelagic trawl captures in general smaller and younger capelin (Fig. S1–S2), but this most likely did not affect variable of interest (otolith size at 1st winter ring formation, Fig. S3). We limited the sampling region within the Barents Sea and included only samples north of 67.5° N and east of 15.0° E (Fig. 1).

Table 1

Total number of capelin with measured otolith growth zones sampled during the capelin spawning season (2–6, February – June) and feeding period (8–10, August – October) during scientific surveys from 1976 to 2019.

Year Months	Spring					Total	Autumn				Total
	2	3	4	5	6		8	9	10		
1976	182	52			817	1051	203	4583			4786
1977	257	149			1646	2052		3636	627		4263
1978	1160	209				1369					
1979	238				43	281		184			184
1980	51					51	177	113			290
1981		1912		3301	2117	7330	2488	6809			9297
1982	829	1054		938	538	3359	9				9
1983	1219	251		46	46	1516	938	689			1627
1984	913	134			1362	3064	1504	4282			5786
1985		81	794		1198	932	3005	903	4680	533	6116
1986	191		265		1466		1922		2185	109	2294
1987		195			75	22	292	10	1385	90	1485
1988		200					200		1820	568	2388
1989	852	949	245	149	62	2257	86	2322		50	2458
1990	339	190	49	4	434	1016	97	3710		209	4016
1991	190	1012			616	838		6726		273	6999
1992		320			28	58	406	98	5411	247	5756
1993	1748	344					2092		2840		2840
1994	823	277				200	1300	790	1948		2738
1995	479			267		2	748		1854		1854
1996	405	130				933	1468	25	1855	50	1930
1997	842					163	1005		3185		3185
1998	431						431		4314	347	4661
1999	838						838		5705	491	6196
2000	1667						1667		6281		6281
2001	2274						2274		5933	800	6733
2002	2233	976	108				3317		4449	348	4797
2003	1556	143					1699	836	1271		2107
2004	1370	468					1838	245	1636		1881
2005	1176	578		24	48		1826	479	2075		2554
2006	1483	618					2101	590	1709		2299
2007	843	303					1146	401	1888		2289
2008	1833	139					1972	196	2655		2851
2009	963	133					1096	561	2570		3131
2010	950	161					1111	342	3330		3672
2011	1046	123					1169	345	3021		3366
2012	508	192					700	1120	1902		3022
2013	859	221					1080	1250	1806		3056
2014	2302	662					2964	260	3558		3818
2015	144	46					190	959	2066		3025
2016		61					61	1182	965	73	2220
2017	71	443					514	20	4281		4301
2018	443	192					635	24	3683		3707
2019	140	1218					1358	963	1857	183	3003
Total	33,848	14,136	1461	9428	11,963	70,836	17,101	127,172	4998	149,271	

We used two datasets to address the questions of growth related to timing of spawning distribution during feeding. In the first dataset, we only included data collected

during the capelin spawning season from February to June (Table 1). Since 1-year-olds are too young to spawn, we only used capelin of age 2–5. In the second dataset, representing data from late in the feeding season, we included data from the capelin monitoring survey (1976–2002) and the Barents Sea ecosystem survey (2003–2019) which have both been conducted mainly in September but ranging from 1st of August to 30th of October (Table 1). This dataset was limited to capelin of age 1–4 which in terms of cohorts correspond to age 2–5 in the dataset from the spawning area. Older capelin were only sporadically sampled and were excluded ($N = 229$, 0.15%) as well as capelin with maturity stage categorized as ‘spawning’ in the feeding area dataset ($N = 93$, 0.06%).

For all capelin, total length (to the nearest 0.5 cm below) were measured. Maturity stages were determined by visual inspection of gonads according to the following scale: immature = 1–2, maturing = 3–5, spawning = 6 (Mjanger et al., 2019). For some analyses maturing and spawning capelin were combined as results for the two groups did not differ. Otoliths were extracted for age determination (counting winter

rings) and the annual growth radii (from the otolith core to the onset of the winter ring) and total otolith radius were measured along the longest axis. Most of the otoliths were measured with a 40x magnification resulting in a measuring precision of 0.024 mm (Mjanger et al., 2019). However, the magnification and precision might vary for some individuals. In this study, we used the size of the 1st annual otolith growth zone, hereafter 1st growth zone, as proxy for fish size at the end of the first year. For additional analyses, we also included the size of the 2nd and 3rd growth zone, represented by the increase from the 1st winter ring until the 2nd and from the 2nd to the 3rd, respectively.

2.2. Statistical analysis

All statistical analyses and plotting were conducted in the R software (R Core Team, 2020). For all tests, we used $p < 0.05$ as the level of significance. Capelin is known for its sexual dimorphism (Huse, 1998) and all analyses, therefore, included sex as factor.

We used a generalized additive model (GAM) with a cubic regression spline as smoother (s) of the otolith size (os) on body length with 5 knots (the number of knots was determined during the model fitting)

$$os = \alpha_1 + \beta_1 \times s(\text{bodylength})$$

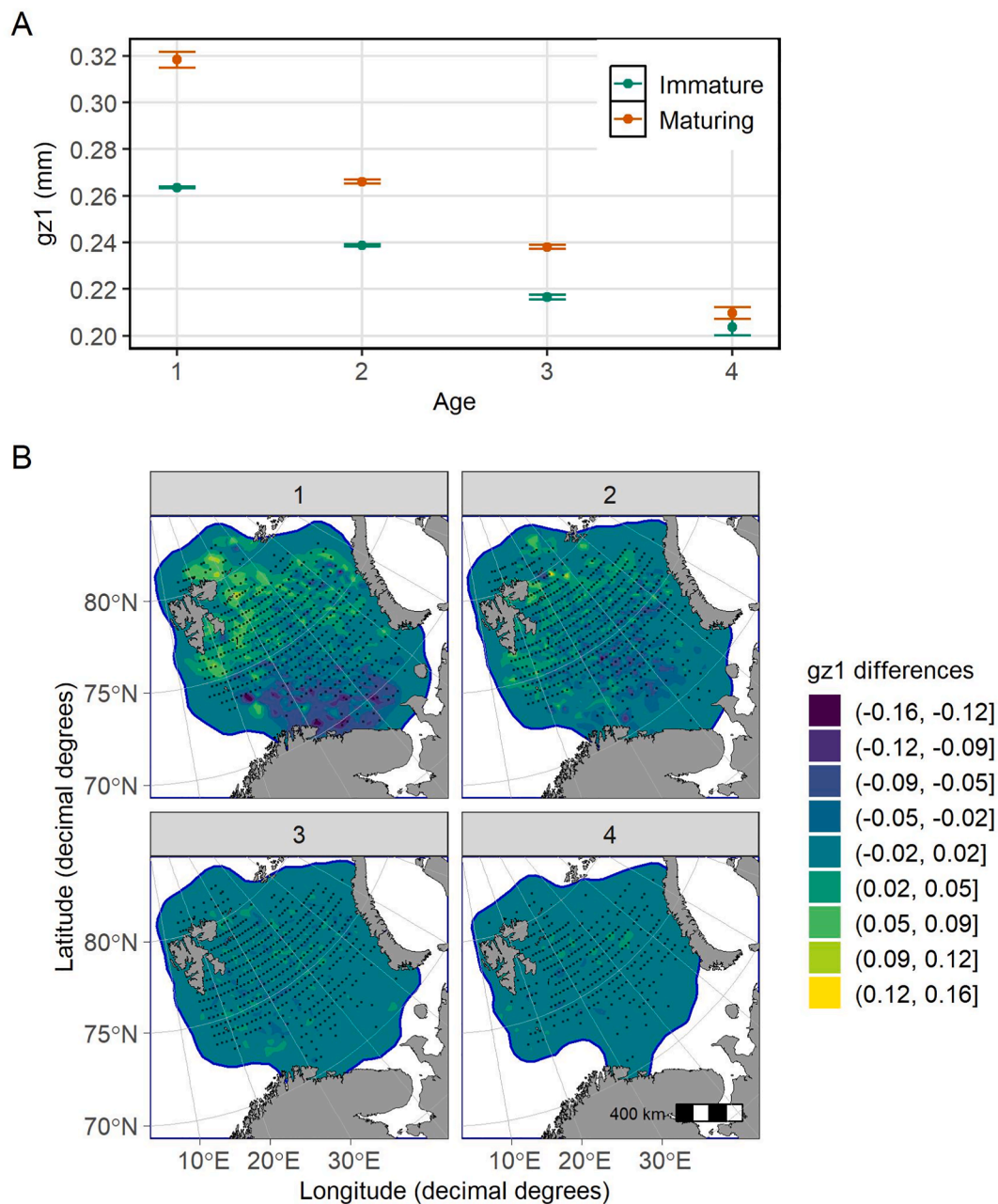


Fig. 2. A) Mean size of 1st growth zone (gz1) of immature (green) and maturing (brown) capelin of age 1–4 captured during autumn. Error bars represent 95% confidence intervals. B) Spatial distribution of capelin according to gz1 for ages 1–4. Contour plot shows the differences from the average gz1, see Table 2 for model outputs. Black points indicate locations of sampling stations. The blue line represents the geographical limit (interior edge) of the spatial model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

including only young-of-the-year (YOY) capelin, i.e. capelin of age 0. The otolith size of YOY capelin was clearly related to total length of YOY capelin, with average otolith size increasing with increasing average fish length (Fig. S4). Therefore, we used the 1st growth zone as proxy for fish size at the end of the first year, even though the relationship does not follow a linear trend and was best explained through a GAM (Table S1). Due to the strong seasonality, especially in terms of light, in the study area, we anticipated that the onset of a new growth zone will be relatively similar within age classes. Based on the deviance information criterion (DIC, Spiegelhalter et al., 2002), the model fit of the GAM (DIC = -15632) was more precise than for a regular linear and linear mixed-effect model (DIC = -10025).

Prior to fitting models, we followed the protocol of Zuur et al. (2010) for data exploration. We used the 1st growth zone of the otolith

representing the growth of YOY capelin during the feeding season until the onset of winter as response variable. Note that the size of the 1st growth zone can be an indication of different growth rates (i.e. when fish are born at the same time) or different hatching times resulting in different duration of the first growth season.

We constructed two separate models; the first model addressed the effect of nursery/feeding areas on early growth, and the second the effect of early growth on timing of spawning later in life. Both fitted models were Bayesian hierarchical spatiotemporal models, using the Integrated Nested Laplace Approximation (INLA) methodology implemented in the “R-INLA” package (Rue et al., 2009). This approach allows for the existence of spatial, temporal, and spatial–temporal correlation.

The first model investigating the effect of different nursery areas on the 1st growth zone (gz1) allowed for spatial correlation. The dataset

from the feeding period was used to fit the following full general structure:

$$gz1_i N(\mu_i, \sigma^2)$$

$$\mu_i = \alpha + \beta_1 \times month_i + \beta_2 \times maturity_i + \beta_3 \times month_i \times maturity_i + u_i + \varepsilon_i$$

$$\varepsilon_i N(0, \sigma_\varepsilon^2) \text{ and } u_i N(0, \sigma_u^2 \times GMRF)$$

where *month* was a continuous variable representing the month of capture for each *i*th capelin, *maturity* a factorial variable indicating if capelin were immature or maturing, and ε_i independent, identical, normal distributed noise. u_i is a spatial Gaussian Markov Random Field (GMRF) (Rue and Held, 2005) with a Matérn covariance function (Lindgren et al., 2011).

The second model investigating the effect of *gz1* on the timing of spawning later in life included a random walk and the full general structure for the model selection is described as:

$$gz1_{it} N(\mu_{it}, \sigma^2)$$

$$\mu_{it} = Intercept + Covariates_t + a_i + u_t + \varepsilon_t$$

$$u_t = u_{t-1} + \nu_t$$

$\varepsilon_t N(0, \sigma_\varepsilon^2)$ and $\nu_t N(0, \sigma_\nu^2)$ where u_t represents a trend for the year classes and ε_t independent, identical, normal distributed noise. The term a_i is the random intercept for the individual sample *i*. We compared the model including the random walk against a model where the year class was included as a random factor to check if the model would improve when allowing for temporal correlation between year classes. For the *Covariates*, we used the following fixed effects structure:

$$Covariates_{gz1} = month \times age \times maturity + sex$$

Due to non-linearity, month and age were included as factorial variables. Maturity stages were grouped into immature and mature capelin. The model accounted for the low numbers of sampled capelin in April-June for the last 20 years (1998–2019). The resulting trends were the same for different periods (high vs. low sample numbers in April-June). We could also not exclude that this was an artifact due to changes in sampling effort rather than a true observation. We, therefore, conducted the analysis on the full dataset. For model selection, the DIC was used as a metric of goodness of fit. In cases where the DIC difference was less than 10 the simplest model was chosen. We fitted the final model structure used for the estimates of the 1st growth zone, also to the 2nd and 3rd growth zone to obtain the temporal trends over the sampled year classes. The year class of each individual capelin was estimated by the year of capture subtracted by the age, thus each of the three growth zones was associated to the identical year class. The three different temporal trends showed the deviation from the overall mean of the corresponding growth zone (1st, 2nd, or 3rd) estimate based on the model for each year class.

To evaluate the effect of early growth on the dynamics of Barents Sea capelin at the population level, we used the assessment estimates of total number of capelin at ages 1–3, proportion of maturing capelin at age 2 and 3 (for the assessment individuals with a body size larger than 14 cm in the autumn are defined as maturing) and abundance at age 1 as recruitment index (ICES, 2020a; b). The assessment estimates are based on the capelin monitoring survey (1976–2002) and the Barents Sea ecosystem survey (2003–2019; ICES, 2020b). The population estimates were linked to their corresponding year class, e.g. the recruitment index (abundance at age 1) estimated in 2005 and the abundance at age 2 estimated in 2006 would both be linked to the year class of 2004. This allows a direct comparison of the temporal trends and the population estimates. We first performed correlation tests between the temporal trends of each of the three growth zones, one against the other. Then we tested the correlation between the growth zones and proportion of maturing capelin at ages 2 and 3. Finally, we tested log-transformed recruitment index and estimated total numbers at ages 2 and 3 against the growth zones for the corresponding year classes. Since we used

Table 2

1st growth zone of capelin captured during autumn: model parameter estimates (mean), standard deviation (sd) and 95% confidence interval (CI) of the estimates for fixed effects, and the precision parameter (σ) of the Gaussian distribution, the range (*r*; in km) and σ of each Gaussian Markov Random Field (GMRF). Results for the spatial distribution are given in Fig. 2B. Important covariates, i.e. zero is not included in the 95% confidence intervals, are shown in bold.

Fixed effects	Mean	sd	95% CI
Intercept	0.263	0.004	0.254 to 0.272
Age₂	-0.045	0.004	-0.048 to -0.034
Age₃	-0.070	0.004	-0.077 to -0.063
Age₄	-0.086	0.004	-0.094 to -0.079
Maturity_{Mature}	0.045	0.004	0.037 to 0.053
Age₂ : Maturity_{Mature}	-0.018	0.005	-0.028 to -0.007
Age₃ : Maturity_{Mature}	-0.022	0.005	-0.033 to -0.012
Age₄ : Maturity_{Mature}	-0.037	0.006	-0.048 to -0.026
σ	0.056	0.000	0.056 to 0.056
<i>r</i> GMRF	58.875	3.688	53.352 to 67.443
σ GMRF	0.040	0.001	0.039 to 0.043

multiple testing, we applied the Benjamini and Hochberg correction (Benjamini and Hochberg, 1995) to adjust the resulting p-values.

3. Results

3.1. 1st growth zone during the late feeding season (autumn)

The 1st growth zone was largest for maturing capelin at age 1 and decreased with age (Fig. 2A). The 1st growth zone was also larger for maturing than immature capelin at any given age (Fig. 2A and Table 2). Furthermore, the mean 1st growth zone of 1-year-old immature capelin was at the same level as for 2-year-old mature capelin. The same effect was observed for 2 vs. 3, and 3 vs. 4-year-old immature and mature capelin, respectively.

There was a strong relationship between the spatial distribution of capelin and the size of the 1st growth zone, especially for 1-year-old capelin (Fig. 2B). One-year-old capelin distributed in the northwest of the Barents Sea had the largest 1st growth zone, while fish in the southeast had the smallest 1st growth zone. For 2-year-old capelin, the trend was similar, but not as clear as for the 1-year-olds. There were no clear relationships between and size of the 1st growth zone for 3- and 4-year-olds. These older fish were more homogeneously distributed according to the size of the 1st growth zone but were not present in the south-easternmost areas (Fig. 2B).

3.2. Biological characteristics during spawning season (spring)

During the spawning season, there was no difference in age frequency distribution of immature capelin between the sampling months (Fig. 3A; Table S2), but immature capelin were on average larger in May-June than in preceding months (Fig. 3B). For the maturing and spawning capelin average age was lower and size was also smaller in May and June than in preceding months (Fig. 3B). Females were always smaller than males, but the seasonal trends in lengths were similar for both sexes (Fig. 4A).

Size of the average 1st growth zone clearly decreased with age for both immature and maturing/spawning capelin similar to what was observed for the data from the feeding season. The 1st growth zone also decreased by month for both immature and maturing/spawning capelin. The 1st growth zone was larger and the decrease in size was also more prominent for maturing and spawning capelin than for immatures (Fig. 4B, Table 3). Overall, the 1st growth zone was also larger for males than females (Table 3).

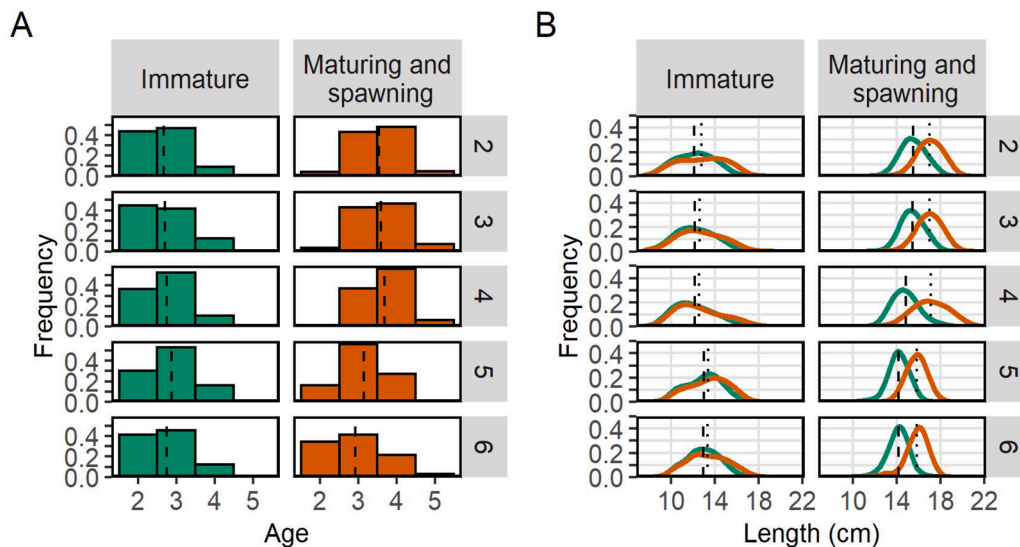


Fig. 3. A) Age and B) length distribution for capelin captured during spawning season. Different months are presented in the panels and separated into immature and maturing/spawning capelin. Green density curves represent females and brown males. Dashed lines represent mean age in A) and mean length for females in B) while dotted lines represent mean length for males. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Temporal growth trends and the population response

The temporal trend of the first-year growth improved the model fit and the negative trends in the mid-80s and –90s corresponded with the most marked collapse periods of capelin (Fig. 5). There was a clear positive correlation between the temporal trend and recruitment of BS capelin (Fig. 5B; Table S3). The temporal trend of the 1st growth zone was strongly negatively correlated with the temporal trend of the 3rd growth zone (Fig. 5C). There was no correlation between the temporal trend of the 1st and 2nd growth zones, or between the 2nd and 3rd growth zones (Fig. S5J, S5K). The temporal trend of the 1st growth zone was significant positively correlated with the abundance of BS capelin at ages 1–3 (Fig. S5A, D, G; Table S3). There was no correlation between the temporal trend of the 2nd growth zone and numbers of capelin for ages 1–3 (Fig. S5B, E, H), whereas the temporal trend of the 3rd growth zone was negatively correlated with the abundance of capelin at ages 1–3 (Fig. S5C, F, I).

At the population level, the temporal trend of the 1st growth zone was negatively correlated with the proportion of maturing capelin at age 2 (Fig. 5D), whereas the trends of the 2nd and 3rd growth zones were both positively correlated with the proportion of maturing individuals at age 2 (Fig. 5E; Fig. S5L). Similarly, the trend of the 1st growth zone was negatively correlated with the proportion of maturing capelin at age 3, and the trend of the 3rd growth zone positively correlated with the proportion of maturing individuals at age 3 (Fig. S5M, O), but there was no significant correlation between the trends of the 2nd growth zone and maturing individuals at age 3 (Fig. S5N).

4. Discussion

4.1. Summary of findings

This is, to our knowledge, the first study showing that the timing of spawning in the semelparous capelin, both within the season and within the life span (age), is clearly related to the first-year growth as estimated by the 1st growth zone. On the level of individual capelin, good first-year growth is associated with spawning both at an earlier age and earlier in the season, and the first-year growth is also highly associated with the spatial distribution at the nursery and feeding areas, particularly at age 1 but also age 2. On the population level, however, good

first-year growth was negatively correlated with the proportion of capelin maturing early, suggesting that the effects of density-dependent growth caused by highly variable year-class strength masks the signal found for individual capelin. Moreover, the first-year growth was positively correlated with abundance of capelin recruits (1-year-olds) while it was strongly negatively correlated with third-year growth. The results are based on an extensive material counting more than 150 000 measured otoliths from the period 1976–2019 and suggest that the first-year growth is influencing growth, maturation processes, and timing of spawning later in life with consequences for the population dynamics.

4.2. Individual first-year growth and timing of spawning

There was a clear trend in our results that individual capelin with good first-year growth start the maturation process earlier in life, and spawn both at an earlier age and earlier in the season than capelin with lower first-year growth. It is known that length is a strong predictor of capelin maturation (Gjøsaeter, 1999; Baulier et al., 2012), probably since initializing maturation and spawning at the earliest possible lifetime, i.e. when reached a given size, minimizes the cumulative adult mortality in a setting where the predation pressure on adults is high (Huse, 1998). The results from the present study indicate that the conditions experienced early in life are crucial for future life history in capelin.

The results in this study also show that both mean length and age of spawners were lower as the season progressed. Smaller fish have lower swimming capacity and might consequently reach the spawning areas later than bigger fish as has been shown for herring (Slotte and Fiksen, 2000). Gonadal development is also likely to be slower in small compared to big fish like it has been demonstrated for capelin in the north-west Atlantic (Flynn and Burton, 2003). The increasing proportion of young spawners with progressing season indicates that capelin just big enough to mature, migrate and spawn, prioritize to spawn early in the life span instead of spending another winter in the Barents Sea. The benefit of spawning early in life is reduced cumulative mortality risk, but spawning at smaller size comes at the cost of reduced fecundity. Huse and Gjøsaeter (1997) found that fecundity of female capelin increased exponentially as a function of length, and a 16 cm long capelin accordingly produced almost twice the amount of eggs compared to a 12 cm fish. A further cost of spawning late in the season is a shortened first feeding season for the larvae and possibly poor match with the

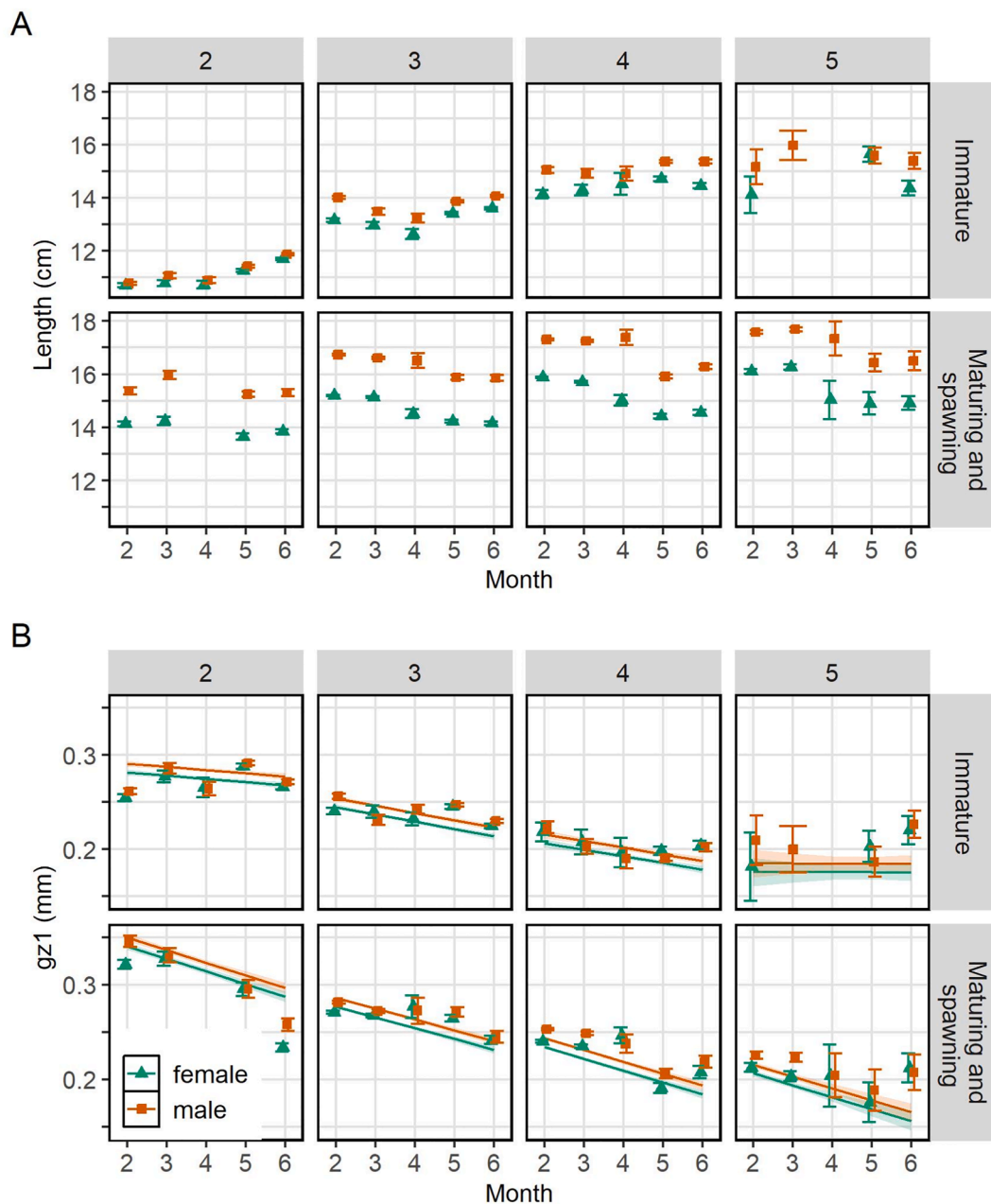


Fig. 4. A) Mean length and B) size of 1st growth zone (gz1) by month (February–June) for capelin captured during the spawning season. Different age groups are presented in the panels separated into immature and maturing/spawning capelin. Females are shown in green and males in brown. Error bars represent 95% confidence intervals. Lines indicate model predictions including 95% confidence interval. The otolith size was temporally correlated, and the trend is shown in Fig. 5A. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

spring plankton bloom, and a smaller size at first overwintering, potentially reducing survival (Cushing, 1990; Post et al., 1998). Late spawning of capelin can also increase the predation risk for capelin larvae since the overlap with their main predators like young herring and YOY-cod is large (Gjøsæter et al., 2016). Furthermore, it has been suggested that capelin spawning in summer belong to a separate population with life-history traits diverging from the main BS population. However, genetic investigations have not supported the concept of separate capelin populations in the east Atlantic including capelin in local fjords (Præbel et al., 2008), and our results with gradually decreasing trends in length, age, and first-year-growth with progressing season do not support the notion of a separate population of summer spawners.

4.3. Importance of nursery grounds

There was a strong relationship between capelin first-year growth and geographical distribution. Especially for age 1, but also to some extent for age 2, capelin with relatively poor first-year growth were distributed furthest to the south-east, and the ones with relatively good growth furthest to the north-west. A similar distribution pattern of slow growing capelin in the south was observed within a smaller area in a dedicated capelin summer survey in 1976 (Hamre, 1977). With our current data, we cannot determine whether a small 1st growth zone is due to a shorter growth season, poor growth conditions, or a combination of both. A shorter growth season would typically be the fact for the late spawned offspring having delayed drift out to the nursery areas compared to earlier spawned capelin. The wind and current systems also

Table 3

1st growth zone of capelin sampled during spring: model parameter estimates (mean), standard deviation (sd) and 95% confidence interval (CI) of the estimates for fixed effects, and the precision parameter (σ) of the Gaussian distribution, the random effect station and temporal trend for year classes (see Fig. 5A). Important covariates, i.e. zero is not included in the 95% confidence intervals, are shown in bold.

Fixed effects	Mean	sd	95% CI
Intercept	0.288	0.003	0.283 to 0.294
Month	-0.003	0.001	-0.005 to -0.002
Age₃	-0.028	0.003	-0.033 to -0.023
Age₄	-0.068	0.004	-0.076 to -0.06
Age₅	-0.113	0.012	-0.136 to -0.089
Maturity_{Mature}	0.079	0.004	0.072 to 0.086
Sex_{male}	0.009	0.000	0.008 to 0.01
Month : Age₃	-0.004	0.001	-0.005 to -0.003
Month : Age₄	-0.004	0.001	-0.005 to -0.002
Month : Age ₅	0.003	0.002	-0.001 to 0.008
Month : Maturity_{Mature}	-0.01	0.001	-0.012 to -0.008
Age₃ : Maturity_{Mature}	-0.04	0.004	-0.048 to -0.032
Age₄ : Maturity_{Mature}	-0.041	0.005	-0.05 to -0.031
Age ₅ : Maturity _{Mature}	-0.023	0.013	-0.048 to 0.002
Month : Age₃ : Maturity_{Mature}	0.006	0.001	0.004 to 0.008
Month : Age₄ : Maturity_{Mature}	0.004	0.001	0.002 to 0.007
Month : Age ₅ : Maturity _{Mature}	-0.003	0.003	-0.008 to 0.003
σ	0.052	0.000	0.052 to 0.052
σ for Year classes	0.017	0.001	0.015 to 0.020
σ for Station	0.022	0.001	0.020 to 0.022

change markedly from early to late spawning season in this area, with a tendency of reduced current strengths and slower larval drift away from coastal spawning grounds later in the season (Skagseth et al., 2011). Larvae hatched at peak season will tend to have a core distribution area in the central Barents Sea and as far north as 76–77 degrees by September in their first year of life (Eriksen et al., 2012). They will be positioned to overwinter close to the ice edge and take advantage of the early ice edge bloom in spring and follow the melting ice-edge northwards already as immatures at age 1 (Gjøsæter, 1998). These immatures will also be positioned to benefit from the predictable good feeding areas at the north-western banks (Gjøsæter, 1999; Aarflot et al., 2020) already at age 1. However, geographical differences growth rates showing up as wider annual growth zones in the otoliths would theoretically be influenced by both temperature and prey availability (Denechaud et al., 2020), as temperature dependent physiology sets an upper limit for growth of marine fish provided they have food in excess. The Barents Sea has two distinct climate regimes; a cold and harsh Arctic climate in the north, and a more Atlantic climate in the south (Smedsrud et al., 2013; Skagseth et al., 2020). Thus, it could be expected that the otolith growth of capelin in the southern region would benefit from higher temperatures. Our results, however, demonstrated a contradictory pattern making it difficult to detect a clear temperature signal given a possible strong interaction with food availability. As the most abundant planktivorous fish in the Barents Sea, adult capelin biomass can explain up to 50% of the variability in the abundance of plankton they are foraging upon (Dalpadado et al., 2020). Higher prey competition (Hamre, 1994) and predation risk (Fall et al., 2018) for young capelin in the southern Barents Sea, can be a major factor explaining the differences in first-year growth. Hence, it seems likely that prey availability has a stronger effect on the first-year growth of capelin in the Barents Sea than temperature. However, this overall picture might be more complex and future research is necessary to clarify the actual drivers of larval growth variability.

There is no longer a clear association between the first-year growth and geographical distribution of 3-year-old immature capelin at the feeding grounds in the Barents Sea. At this age, the fastest-growing fish will already have migrated to the coast to spawn as 2-year-olds. Our results showing that first-year growth decreases with age, especially among immature fish (see Fig. 2A and 4B) is probably a clear signal of

this – the fastest-growing individuals migrate to the coast to spawn and subsequently disappear out of the population.

Practically all the 3-year-old fish remaining in the population will now be large enough to perform migrations between the most beneficial feeding areas and wintering areas, blurring any geographical pattern according to first-year growth.

4.4. Temporal trend and population dynamics

We found a clear positive relationship between first-year growth and recruitment indicating that good early growth conditions enhance survival to age 1, in accordance with the theory predicting that faster larval growth gives survival benefits (Takasuka et al., 2003; Gagliano et al., 2007). It has previously been shown for Barents Sea cod, haddock, and herring that high pre-recruit growth rates are positively related to recruitment, with temperature as an underlying causal factor (Ottersen and Loeng, 2000). These authors hypothesized that at the high latitude end of their distribution range, environmental factors influencing growth are stronger than the impact of density-dependent factors limiting growth. Our results showed a negative correlation between third-year growth and abundance at ages 1–3 indicating an increased effect of density-dependent growth later in life. But compensatory growth may also partly explain these trends with capelin experiencing poor growth early in life accelerating growth under more favorable conditions later (Ali et al., 2003). A third explanation for the negative correlation could be that late maturing individuals (individuals with low first-year growth) have continued (higher) somatic growth compared to those that grew fast early and matured early. However, the maturation is rather age-independent while the length at maturity shows temporal stability (Baulier et al., 2012).

A higher first-year growth seems beneficial for individual capelin with higher survival (high recruitment) and early spawning and looking at these results alone one would expect age truncation at the population level. However, when analyzing the data at population level, high recruitment leads to a lower growth from age 1 to age 2–3, and a low proportion maturing at age 2. This is likely caused by density dependent growth (Hjermann et al., 2004). This interaction between individual and population response has consequences for the assessment of capelin in the Barents Sea, and future studies should investigate these mechanisms more thoroughly using for instance biochronology. Biochronologies based on growth patterns in calcified structures can be applied to elucidate long-term and ecological impacts on somatic growth (Morrongiello et al., 2012; Smoliński, 2019; Denechaud et al., 2020) or recruitment variability (Husebø et al., 2007; Morrongiello et al., 2014) at a fine-scale resolution. However, these chronologies are rather sensitive and non-random sampling may introduce biases into reconstructed time series (Smoliński et al., 2020)

4.5. Conclusion

Our study demonstrates that first-year growth of BS capelin strongly impacts maturation, timing of spawning and growth later in life, and influences the population dynamics including recruitment success. Capelin that have reached the productive north-western parts of the Barents Sea are characterized by good first-year growth, which again is associated with higher survival, an earlier maturation, and early return to the coast for spawning. These findings which apply at the level of individual capelin, are contrary to population level effects where strong inter-annual variability in year-class strength has a substantial effect on the timing of maturation likely caused by density dependent growth. Finally, the gradual change of size and age of spawners within the spawning season does not support the suggestion of two discrete spawning populations of Barents Sea capelin.

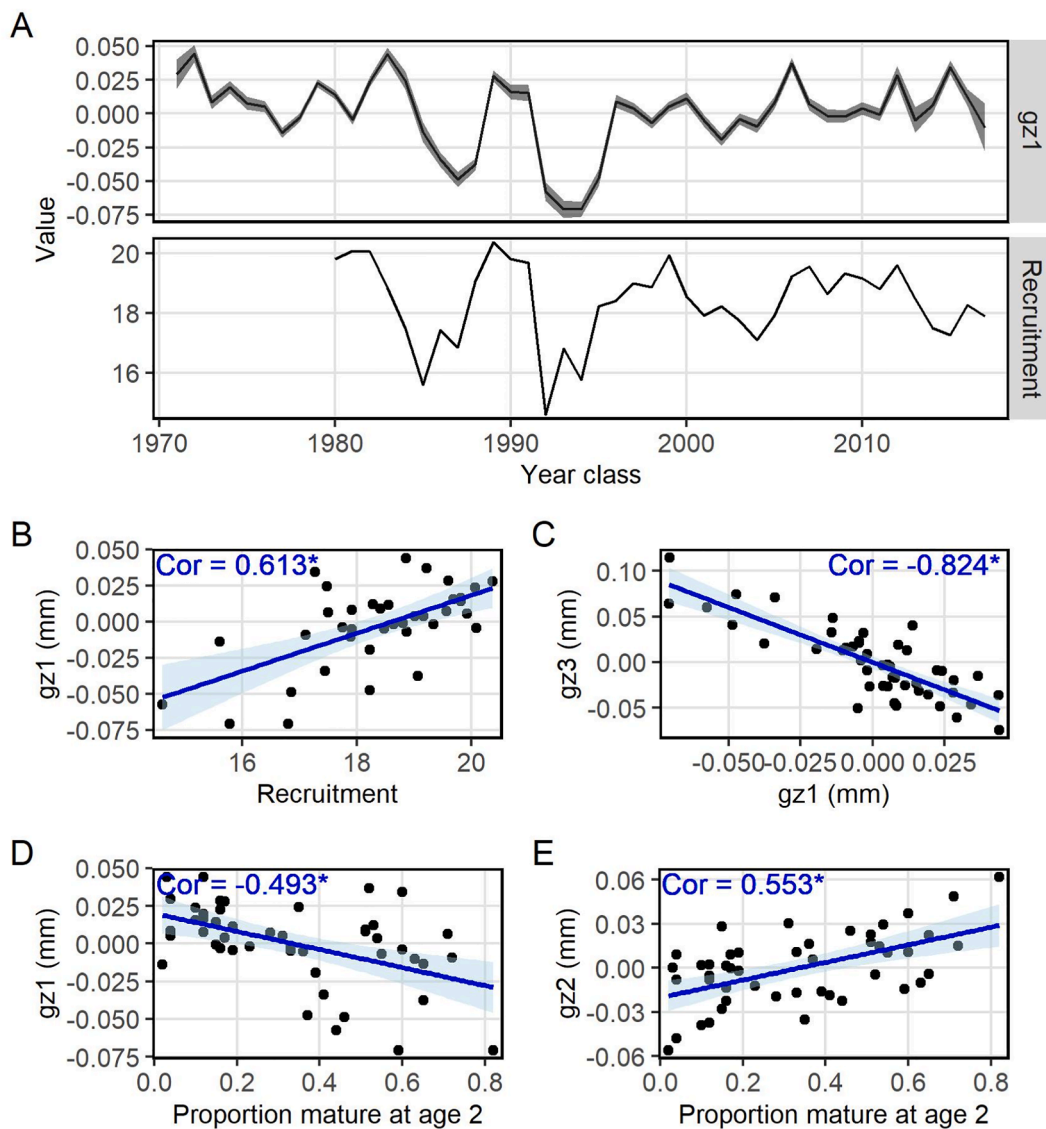


Fig. 5. A) Estimated temporal trend showing deviation from the overall mean of the 1st growth zone (gz1) estimate based on the model (upper panel) and recruitment (log-transformed numbers of age 1 capelin from the capelin assessment based on the autumn survey) per year class. Model estimates are shown in Table 3. Correlation (blue line) between B) temporal trend of gz1 and log-transformed number of recruits, C) temporal trend of the 3rd growth zone (gz3) and gz1, D) temporal trend of gz1 and proportion of maturing capelin at age 2, and E) temporal trend of gz2 and proportion of maturing capelin at age 2. The correlation coefficients are marked with asterisk (*) if significant after Benjamini and Hochberg adjustment. See Table S3 for p-values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2021.102614>.

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