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Cultivation and Growth Dynamics of Capelin (*Mallotus villosus*) from Hatch to Adulthood

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Abstract: This study describes the first successful rearing of capelin from hatch to adulthood in a laboratory setting using intensive culture methods. Over the span of about two years, the capelin were reared in aquaculture tanks under a constant temperature of 7 °C. The capelin demonstrated a robust linear growth during their first year of life, with a mean length increment of 0.36 mm per day. Due to their accelerated growth, some of the capelin became sexually mature as early as one year post-hatch. The first year was characterized by a rapid increase in condition factor (CF) while the second year showed a plateau. The von Bertalanffy growth equation effectively described the two-year growth of the cultivated capelin, predicting an asymptotic length (L∞) of 18.4 cm, similar to the 18.6 cm median L∞ of wild Icelandic capelin (1981–2018 cohorts). The cultivated capelin were projected to reach this length in 2.6 years, compared to about 6 years for wild capelin. This study provides new insights into the growth dynamics of capelin and although the species is sensitive to handling, it demonstrates that intensive culture methods can be used to investigate biological aspects of this important forage species.

Keywords: *Mallotus villosus*; laboratory rearing; growth; condition factor; feeding; asymptotic length

Key Contribution: This study is the first to monitor the growth of capelin from hatch to adulthood under laboratory conditions. It provides information on the husbandry practices required to rear this species and presents new insights into their growth dynamics.

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1. Introduction

The capelin (*Mallotus villosus*) is a small pelagic fish with a circumpolar distribution in the northern hemisphere and a principal prey item for many species of predatory fish, whales, and seabirds. Beyond its ecological significance, the capelin is also highly valued by the fishing industry in the North Atlantic region, where it is commercially exploited [1]. Four genetically distinct regional groups have been identified within the circumpolar capelin population, i.e., the West Pacific, East Pacific, Newfoundland, and Northeast Atlantic/West Greenland regional groups [2]. All capelin populations undertake extensive feeding, overwintering, and spawning migrations, facilitating massive energy transfer from deep, cold waters to warmer coastal ecosystems [3].

Capelin populations in the Northeast Atlantic Ocean (Iceland and Barents Sea) are demersal spawners, except for beach spawning populations in local fjords [3,4]. On the other hand, capelin populations in the Northwest Atlantic are predominantly beach spawners [5]. While females in beach spawning populations may spawn more than once during their lifetime, very few capelin in the large demersal spawning populations (e.g., Icelandic capelin and Barents Sea capelin) survive first spawning and are thus classified as semelparous [4].

As capelin approach maturity, a noticeable size difference is observed between males and females. Generally, males exhibit faster growth and tend to be 1–3 cm longer than females at maturity [3,6]. The attainment of maturity in capelin is primarily determined

by size, with a maturity threshold of approximately 14 cm in total length [3,7–9]. Capelin show significant spatial and temporal variation in growth rates [10–12] and rapid early growth has been shown to be strongly related to early sexual maturity [13,14].

The asymptotic length ($L\infty$) of capelin varies across different populations and locations. In the Northwest Atlantic Ocean, it is generally estimated to be around 20 cm [12,15,16], while smaller $L\infty$ have been observed in Icelandic waters and the Barents Sea [3,17]. The underlying factors contributing to these variations, whether genetic or environmental, remain uncertain. Due to the high mortality rate after first spawning, capelin larger than 20 cm make up a very small fraction of the population, and specimens exceeding 22 cm in total length are only occasionally found [18].

Research on small pelagic fish has predominantly been based on field studies, with relatively few controlled laboratory studies. The paucity of laboratory studies on small pelagic fish can be attributed to the practical challenges of rearing these species from hatch to adulthood. Laboratory studies have been performed on all life stages of Atlantic and Pacific herring (*Clupea harengus* and *Clupea pallasii*), providing valuable insights into their biology [19]. There is also a growing number of laboratory studies on species such as the European sardine (*Sardina pilchardus*) and European anchovy (*Engraulis encrasicolus*) (e.g., [20,21]) and, recently, the Japanese anchovy (*Engraulis japonicus*) has been described as a promising species for use as a model organism for marine teleosts [22].

Studies on captive capelin have a relatively long history, beginning with the successful spawning in captivity in Russia in 1958 [23]. Since then, research on capelin has been conducted in laboratory settings and outdoor enclosures, covering a wide range of topics. These include growth, development, feeding, behavior, endocrinology, metabolism, spawning, responses to abiotic factors, and reactions to toxic substances [4,23–47].

These previous studies are, however, limited to the use of capelin of wild origin and have only been performed during egg and larval stages or with captive adults. There is currently a lack of research involving capelin reared beyond the larval stage. The longest study to date reared capelin larvae in large outdoor enclosures for four months, during which the larvae reached a length of up to 32 mm by feeding on natural zooplankton [26]. Additionally, laboratory studies have employed traditional intensive cultivation methods, including the use of rotifers as initial feed, but these studies have been limited to the early larval stages [34,47].

This study presents the first successful cultivation of capelin from hatch to adulthood. The primary objectives of the study were to establish a foundation for future laboratory studies on all life stages of the capelin and present new insights into the growth dynamics of this species.

2. Materials and Methods

2.1. Egg Collection

Capelin eggs and sperm were collected from newly caught fish on board a commercial fishing vessel (Vikingur AK 100, Brim hf, Reykjavík, Iceland) at the height of the spawning season on 6 March 2021. The fish were caught with a purse seine in Faxaflói, close to the southwest coast of Snæfellsnes (approximately 64.4° N, 23.4° W). A volume of about 1 L of capelin eggs was manually stripped into two 5 L plastic buckets. Sperm from about 50 males were then collected the same way and gently mixed with the eggs. The mixture rested for approximately five minutes before the buckets were filled up with clean 5 °C seawater. Shortly after contact with seawater, the eggs hardened and glued together, forming egg clusters (2–3 cm in diameter) on the bottom. The eggs remained in the buckets at 4 °C in a dark cooling room until the ship docked in Akranes on 12 March. During the time on-board, the water was changed daily by ~90%. Upon landing, the eggs were transported to the MFRI Aquaculture Research Station (ARS), which is located on the Reykjanes peninsula near Grindavík, southwest Iceland.

2.2. Incubation

Upon arrival at the research station, the glued egg clusters were broken down into smaller pieces and disinfected with Pyceze™ (1 mL/10 L) for 30 min, during which the temperature was gradually increased from 5 to 7 °C and maintained at 7 °C throughout the incubation period. As the egg clusters were broken down into smaller pieces, some of the eggs were freed, but most remained glued to other eggs in relatively small clusters (<2 cm in diameter). After disinfection, the small clusters and individual eggs were evenly distributed over the bottom of a 3.2 m^3 circular black fiberglass tank (2 m diameter, 1 m height).

2.3. Rearing Conditions

The capelin were reared indoors in a flow-through system. The station's seawater comes from 50 m deep boreholes. It is naturally filtered through lava bedrock and has a relatively stable temperature (6.7–7.9 °C), salinity (31 ppt), and pH (7.7), all year round. During the embryonic and early larval stages, the waterflow was kept at 5 L/min and increased gradually as the fish developed, so that the oxygen saturation was maintained above 90% without adding pure oxygen. During the first and second years of the study, the mean temperatures were 7.4 ± 0.30 and 7.2 ± 0.29 °C, respectively. The fish were always fed in moderate excess.

Three days post-hatch (3 dph), live rotifers (Reed Mariculture Inc., Campbell, CA, USA) were introduced into the tank as a potential prey item for the capelin larvae. The rotifers were cultivated in 250 L silos at 26 °C and fed S.parkle Selco® (INVE Ltd., Leeds, UK) every four hours, following the manufacturer's instructions. Rotifers were enriched with Larviva Multigain (BioMar A/S, Aarhus, Denmark) and added to the nursery tank two times per day (9:00 and 15:30) along with 30 mL of microalgal paste (Rotigreen® omega, Reed Mariculture Inc., Campbell, CA, USA). During the first 10 dph, the larvae were fed small rotifers (*Brachionus rotundiformis*, S-type, 85–150 µm), before a larger strain of rotifers (*Brachionus plicatilis*, L-type, ~210 µm) was introduced in a 1:1 ratio to the S-type on 11 dph. At the start of exogenous feeding, surface light intensity was set at 150 Lux and gradually increased to 650 Lux by 24 dph, after which it remained at 650 Lux throughout the live feeding and weaning process (Table 1).

The S-type was taken off the menu at 38 dph, and at the same time, newly hatched artemia nauplii (*Artemia salina*, AF artemia, INVE Ltd., Salt Lake City, UT, USA) were introduced as prey. The artemia were incubated in 250 L silos at 28 °C. Each morning, before being fed to the capelin larvae, the artemia were condensed to 20 L and disinfected over 10 min with 6 mL of Pyceze™. After rinsing, half of the artemia were offered to the larvae in the morning, while the other half were stored at 10 °C for the second feeding in the afternoon. The artemia nauplii were replaced with EG artemia (INVE Ltd., Salt Lake City, UT, USA) on 60 dph. The EG artemia were enriched at 28 °C for ~20 h in 250 L silos with Easy DHA Selco® (INVE Ltd.). The procedures for disinfection, storage and feeding of EG artemia to the larvae remained the same as those used for the artemia nauplii.

Feeding with rotifers ceased at 45 dph when weaning onto dry feed began (Larviva Prostart, Biomar AS, initial particle size 200 µm). During the first week, the larvae were hand-fed first thing in the morning, when prey levels were low. Thereafter, dry feed was added continuously (24 h) using an automatic belt feeder (FIAP GmbH, Ursensollen, Germany). No live feed was provided after 99 dph.

With live feed added only twice daily, prey density peaked after the afternoon feeding. Despite decreased prey retention with increased water flow, some rotifers and artemia remained in the tank by morning.

Until 255 dph, the young capelin were kept in the 3.2 m^3 circular black hatchery tank under simulated annual variation in day length. The tank was equipped with an automatic cleaning arm that gathered feces and leftover feed, which were siphoned out each morning and afternoon. At 255 dph, approximately a quarter of the fish (n = 267) were randomly selected and moved to a 4 m^3 green rectangular fiberglass tank (measuring

2 m × 2 m × 1 m). From that day onwards, these fish were reared under continuous light, and the daily cleaning of the tank was conducted manually using a broom.

Table 1. Summary of temperature, surface light intensity, flow rate, and feeding schedule from the start of exogenous feeding (3 dph) through the live feed and weaning phases in a 3200 L tank. Although shown weekly, adjustments were made on specific days. Total live feed is given in millions, with algae paste and live feed added in the morning and afternoon. During the first week of weaning, the larvae were hand-fed dry feed, after which the feed was continuously dispensed using an automatic belt feeder.

dph	T °C	Light Intensity (Lux)	Flow Rate (L/min)	Algae Paste (mL)	S-Rotifer (m)	L-Rotifer (m)	Artemia Nauplii (m)	Enriched Artemia (m)	Dry Feed (g)
3	7.2	150	5	2 × 30	2 × 15				
10	7.2	350	5	2 × 30	2 × 20				
17	7.2	420	7	2 × 30	2 × 10	2 × 10			
24	7.2	650	7	2 × 30	2 × 13	2 × 13			
31	7.2	650	10	2 × 50	2 × 13	2 × 13			
38	7.2	650	10	2 × 50	2 × 25	2 × 15	2 × 3		
45	7.2	650	15	2 × 50		2 × 23	2 × 5		
52	7.2	650	15	2 × 50			2 × 7.5		5
59	7.2	650	15	2 × 30			2 × 9		15
66	7.2	650	15	2 × 30				2 × 8	20
73	7.2	650	25	2 × 30				2 × 8	25
80	7.3	650	25	2 × 30				2 × 5	40
87	7.3	650	25	2 × 30				2 × 2.5	60
94	7.3	650	30	2 × 30				2 × 1	70
101	7.3	650	30	2 × 30					90

Only the fish that were transferred to the green tank on day 255 were subjected to regular measurement. This group will henceforth be referred to as group A. The remaining fish were split between three black hatchery tanks. The cultivation of the fish in one of those tanks, referred to as group B, is briefly described below.

At 527 dph, the fish in group A were transferred back to a 3.2 m^3 circular black hatchery tank for cultivation until the end of the study. The transfers between tanks were conducted carefully using a soft and fine-meshed fishnet (Laguna Pond Net, HAGEN group®, Montreal, QC, Canada). After being netted, the fish were released into 20 L buckets, moved a distance of 12 m, and gently poured into the new tanks.

Group B

After transferring the experimental fish to the 4 m^3 green tank on day 255, the remaining fish were divided among three 3.2 m^3 black tanks. One of these tanks contained approximately 300 fish (group B), which were cultivated under similar conditions as the experimental group (7 °C and LD 24:0) until 942 dph. Group B was mainly used to provide eggs and larvae for subsequent hatching experiments and was therefore mostly left undisturbed from measurements. After being separated from group A on day 255, however, group B was subjected to measurements at three time points: at 526 dph (27 fish), and subsequently at 806 and 942 dph, where all remaining fish (126 and 43, respectively) were measured. Since group B was cultivated some nine months longer than group A, the measured TL of the fish in group B was incorporated into the dataset to improve the

accuracy of the growth parameter estimates in the von Bertalanffy growth analysis for the cultivated capelin (see subsubsection in Section 2.4).

2.4. Measurements and Data Analysis

Temperature and oxygen of the rearing water were measured daily throughout the study. Dead fish were collected and counted daily from day 255 until the end of the study. Over the course of the nearly two-year study, the mean body size of the fish in group A was estimated 34 times. A random sample of 5–35 fish was collected for each measurement, but all the remaining fish were measured on the last day of the study. The sample sizes and intervals between measurements (1–100 days) increased with the size of the fish.

Up until day 504, the sex of the measured fish was not determined, but in subsequent measurements, the gender was identified through visual inspection of external appearances. Based on a visual inspection, the presence of skeletal deformities was documented for each fish on the last day of the study. The deformities were broadly classified based on their location as either head or trunk deformities.

Body length was measured as standard length (SL) up to 260 dph, with only 48 larvae measured for both SL and total length (TL). After 260 dph, all fish were measured for both SL and TL. Before 260 dph, SL was converted to TL using a relationship between TL-SL Ratio and SL of larvae and juveniles measured for both SL and TL. The dataset used to establish this relationship comprised 154 fish with SL ranging from 0.68 to 9.8 cm. Of these fish, 87 were sourced from unpublished research conducted at the ARS (Figure 1).

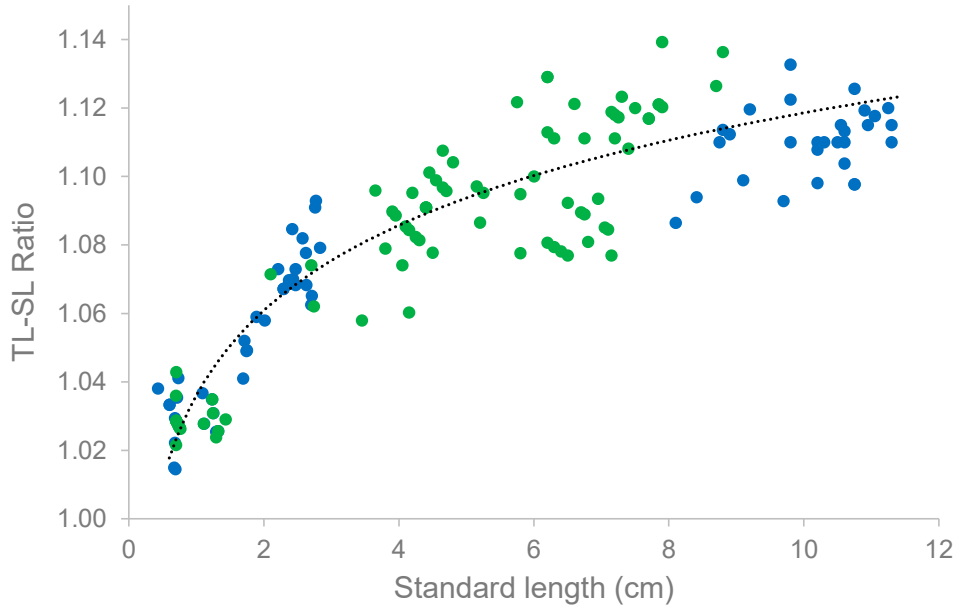

Figure 1. The relationship between the TL-SL Ratio and SL in cultivated capelin below the age of 260 dph. The regression line is expressed as TL-SL Ratio = αln(SL) + β, with a calculated slope (α) of 0.036, an intercept (β) of 1.036, and a coefficient of determination (R^2) of 0.85. Blue dots depict data from the current study and green dots represent data from other laboratory studies at the ARS.

From the relationship presented in Figure 1, TL was calculated using the following equation:

$$TL = SL \times (0.036 \ln(SL) + 1.036) \quad (1)$$

During the first 58 dph, the larval length was measured using ImageJ software (version 2.1.0/1.53c) and photographs taken with an iPhone 8 (Apple, Cupertino, CA, USA) attached to the eyepiece of a Wild M3Z stereomicroscope (Wild Heerbrugg AG, Gais, Switzerland) using a NexYZ DX smartphone adapter kit (Celestron®, Torrance, CA, USA). From 67 dph, the length was visually measured to the nearest millimeter with a ruler, and from 81 dph, individual body weights (W) were measured to the nearest 0.01 g. Before 81 dph, the larvae

were euthanized before being photographed or measured, but thereafter, all measurements were performed under tricaine methane sulfonate anesthesia (0.05 g/L, Finquel®, Intervet International B.V. Boxmeer, The Netherlands), and the fish were returned to the tank after measurements. During the final measurement, all fish were humanely killed with an overdose of tricaine methane sulfonate and measured as described before.

The growth performance of the capelin during the first 351 days of the study was assessed based on their SL. The absolute daily incremental growth rate during this period is expressed in mm/day, as determined through a linear regression analysis. The growth performance over the entire 681-day study period was evaluated using TL.

The condition factor (CF) was calculated as follows:

$$CF = (W/TL^3) \times 100 \quad (2)$$

The standard allometric equation $W = aTL^b$ was used to establish the relationship between W and TL. Females with CF greater than 0.7 and external features suggesting the retention of ovulated eggs were excluded from the weight–length relationship.

Growth Comparison Between Cultivated and Wild Icelandic Capelin

The long-term growth performances of the hatchery-reared capelin were compared with growth data for wild Icelandic capelin from year-classes 1981–2018. This comparison was carried out utilizing von Bertalanffy growth curves (VB), which were fitted to length-at-age data for both the cultivated capelin and each year-class of wild capelin using non-linear least squares regression as follows:

$$La = L\infty(1 - e^{-K(a-t_0)}) \quad (3)$$

where La is total length (cm) at age a (years), $L\infty$ is asymptotic length, K is the growth coefficient, with a dimension of year^{-1}, expressing the rate at which $L\infty$ is approached, and t_0 is theoretical age at which length is zero. For all VB model estimates, the initial values for the model fitting process were $t_0 = 0$, and $L\infty$ and K were estimated via the concept of the Ford–Walford plot [48].

Only metamorphosed capelin (TL > 8 cm) [49,50] were included in the VB analysis. Growth data for wild capelin were extracted from the MFRI database containing all available individual capelin measurements from samples collected 1981–2023 during assessment surveys, other research surveys, and from fisheries. Inclusion criteria were that each individual had to have a valid estimate of TL, W, and age, while obvious errors were removed. Acoustic and pelagic trawl assessment surveys have in general taken place biannually, i.e., autumn surveys in September–November and winter surveys mainly in January–February. Capelin fisheries have historically taken place in summer (June–August), autumn (September–November) and winter (January–March), while in most of the recent years, the catches have mainly been taken during winter. Catches have been taken in varying proportions by seine and pelagic trawl, which may suggest that there is usually not continuous sampling from all seasons for each year-class. However, to obtain as coherent an evaluation of the growth pattern of each year-class as possible, all available survey and fishery measurements were used. This resulted in a total of more than 582 thousand individual measurements from the 1981–2018 year-classes.

2.5. Statistical Analysis

For the cultivated capelin in group A, data for TL, W, and CF are presented as means ± standard deviation (SD). The significant deviation of the sex ratio from 1:1 was assessed using the χ^2 goodness-of-fit test. Shapiro–Wilk tests were conducted to evaluate whether TL, W, and CF for males and females followed a normal distribution. Levene's tests were applied to assess the homogeneity of variances between sexes. Subsequently, Welch's *t*-tests were used to examine sex differences in TL, W, and CF at a significance level of $p = 0.05$.

Additionally, Shapiro–Wilk tests were used to evaluate whether the VB parameters of the wild year-classes deviated from normality [51]. The VB parameters of the cultivated capelin were then compared with those of the wild populations. For t_0 and $L\infty$, one-sample *t*-tests were used, while the *K* parameter, due to its non-normal distribution, was analyzed using the Wilcoxon signed-rank test. All statistical and VB analyses were conducted using R version 4.3.0 (R Core Team, 2023).

3. Results

3.1. Hatching

The fertilization rate was highly variable among the small egg clusters, as contamination from rotting unfertilized eggs caused high or total mortality in some clusters. Fertilized and unaffected eggs hatched over a one-week period from 30 March to 6 April 2021 (25 to 31 days after fertilization). However, most of the eggs hatched synchronously on 5 April after the eggs were siphoned from the tank bottom through a plastic tube into buckets. During the few minutes they remained in the buckets, many eggs were seen hatching and most of them hatched within a few hours after being returned to the tank. The remaining fertilized eggs hatched after the procedure was repeated on the next day (6 April). As most of the eggs hatched on 5 April, this day will hereafter be considered the hatching day for the whole group.

3.2. Feeding

Most of the larvae ingested the S-type rotifers within a few hours after start-feeding was initiated on 3 dph on 8 April 2021. This was clearly observed as the larvae displayed a prominent white streak on their underside, indicating their ravenous appetite for live rotifers. Due to the translucent nature of the capelin larvae, foraging success was easy to inspect (Figure 2).

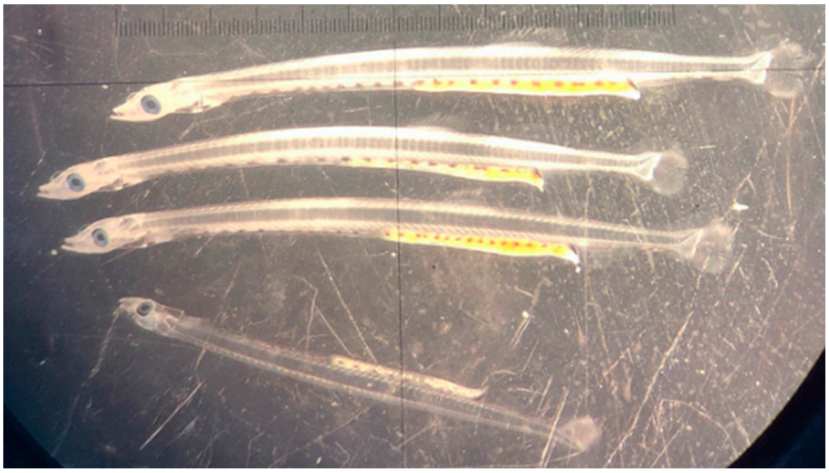

Figure 2. Capelin larvae 39 days post-hatch. The three largest larvae are approximately 21 mm in length, while the smallest is 16 mm. The larger larvae fed on artemia, whereas the smallest larva fed exclusively on rotifers, as it could not yet handle larger prey.

The weaning process, commencing on 45 dph, proved to be successful. Dry feed was observed in the digestive tract of a few translucent larvae on the first day of feeding, and most of the larvae were consuming dry feed within a week after its introduction.

3.3. Early Growth Performance

During the first year post-hatch (351 dph), the capelin exhibited a linear growth trajectory with a mean length increment of 0.36 mm in SL per day (Figure 3a). The weight increase from 81 to 219 dph was adequately described by a second-order polynomial, although the weight increase was approximately linear during the last 4–5 months (Figure 3b).

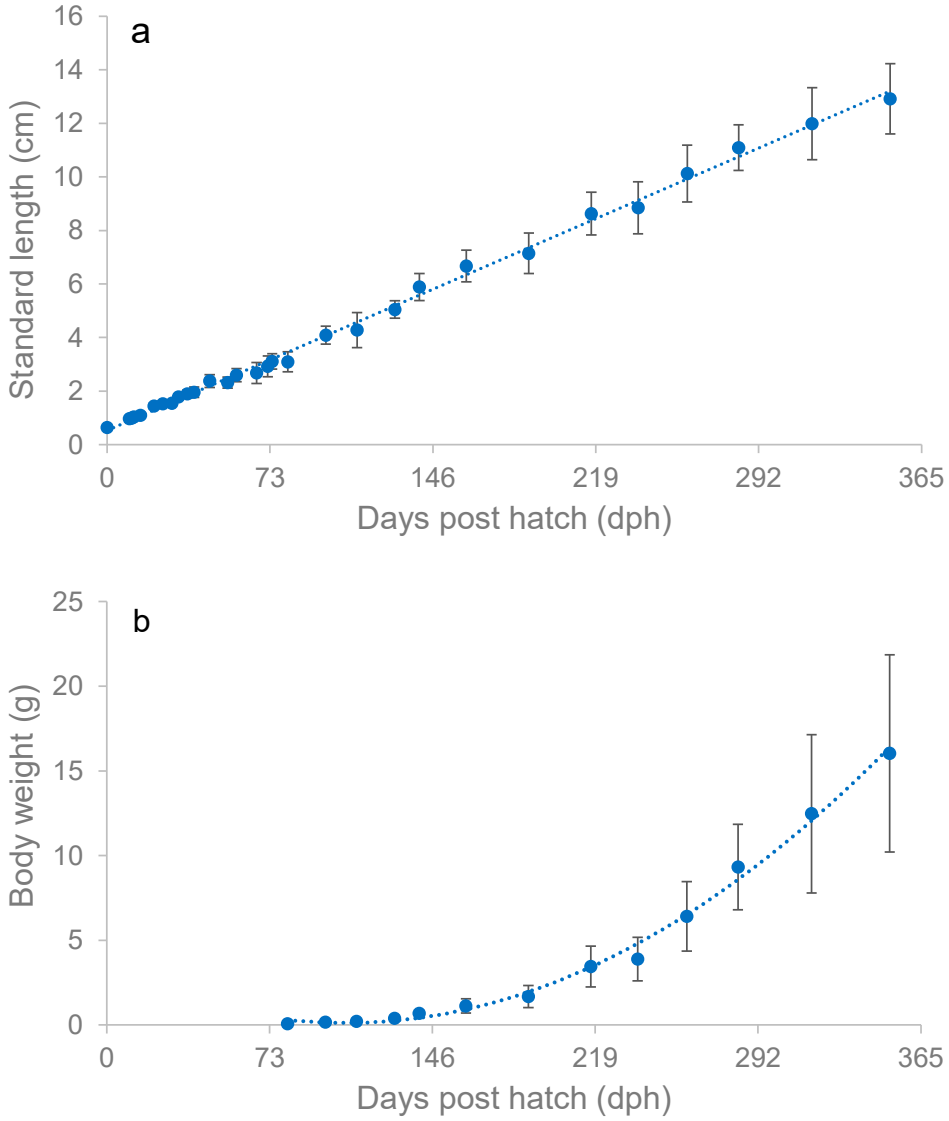

Figure 3. The progression in average total length ± SD from hatching to day 351. The dotted line represents the regression line: SL = 0.0361dph + 0.5374 (**a**) (modified from Árnason et al. [52]). The growth in weight from day 81 to 351. Weight data are fitted with a second-order polynomial: $W = 0.0003dph^2 - 0.0588dph + 3.274$ (**b**).

3.4. Adult Growth Performance

During the second year post-hatch, the post-larval length trajectory deviated from linearity and gradually approached $L\infty$. The final measurement on day 681, which included all remaining fish, showed an average TL of 17.7 ± 1.7 cm (Figure 4a). A subgroup (Group B) reared under identical conditions in a separate tank had a slightly higher mean TL of 18.0 ± 1.7 cm on day 942.

For most of the study, the capelin exhibited relatively rapid weight gain. However, during the last 3–4 months, growth performance plateaued, with the average W remaining relatively stable, decreasing slightly from 30.9 ± 10.0 g to 30.5 ± 10.6 g (Figure 4b). The plateau in W was accompanied by a noticeable decrease in appetite during that period of the study.

At the last measurement, the experimental group exhibited a wide variation in size, with TL ranging from 13.8 to 22.0 cm and W ranging from 13 to 63 g. The largest fish in the sibling subgroup B was a male with a TL of 22.7 cm and weighing 89.0 g.

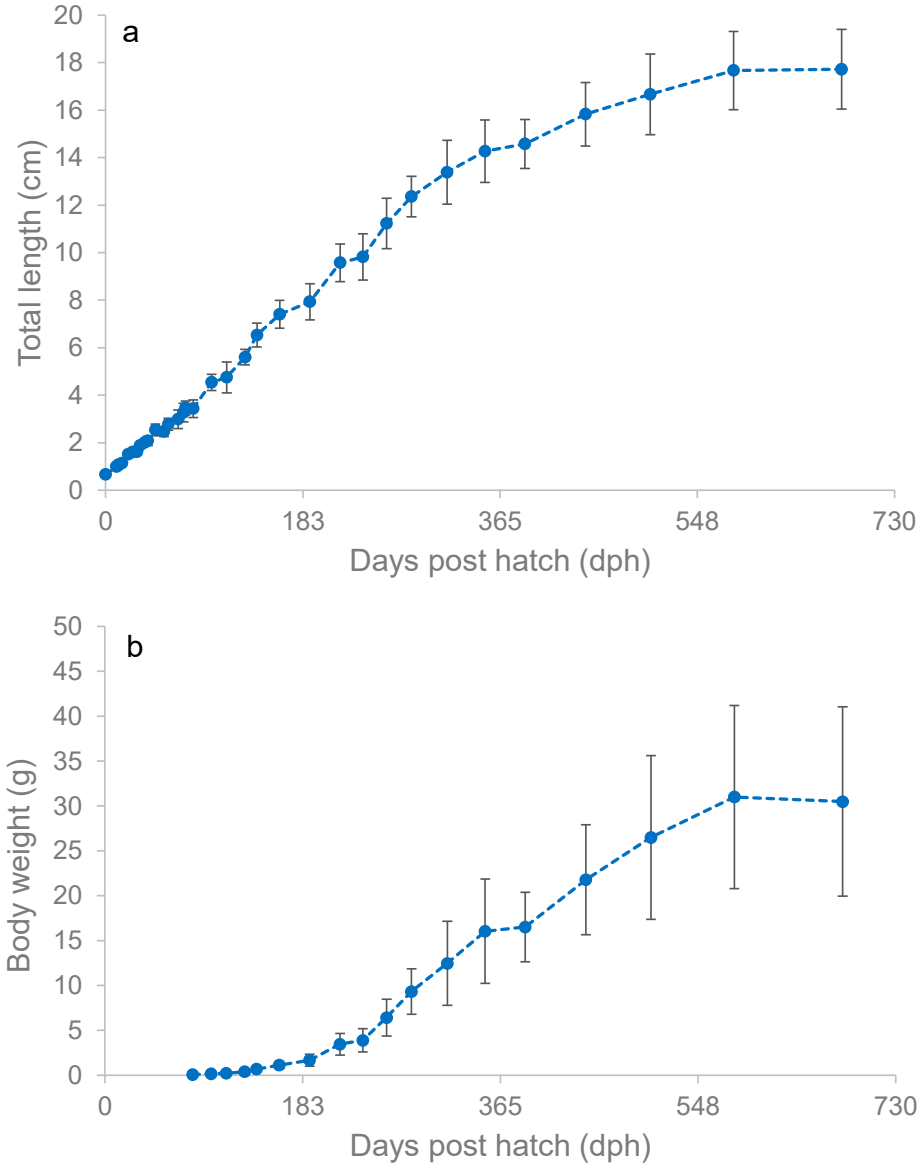

Figure 4. The progression in average total length ± SD (**a**) (modified from Árnason et al. [52]) and body weight ± SD (**b**) of cultivated capelin.

3.5. Sexual Size Dimorphism

The sexing of fish began at 504 dph. Observations showed that males were significantly longer and heavier than females for the remainder of the experiment (Welch's *t*-test, $p < 0.05$). However, the relative size difference between the sexes decreased over time. Between 504 and 681 dph, the relative size difference decreased from 9% (17.5 vs. 16.0 cm) to 6% (18.2 vs. 17.2 cm) in TL and from 38% (32 vs. 22 g) to 16% (33 vs. 28 g) in W. At 504 dph, males had a higher condition factor (CF) compared to females (Welch's *t*-test, $p < 0.05$), but not for the rest of the study period (Welch's *t*-test, $p > 0.05$).

3.6. Body Condition

The frequent sampling of length and weight allowed for a detailed analysis of the capelin's length–weight relationship between 81 and 681 dph (Figure 5a). The relationship was closely described by a power equation ($W = aTL^b$), and a high weight exponent (b) of 3.75 reflects the strongly allometric growth rate over the studied size range. The cultivated capelin exhibited two distinct growth stanzas. The growth was characterized by a rapid

rise in CF (positive allometric growth), before reaching a plateau at a value of ~0.53 when the fish were approximately 14 cm (TL) and one year old (Figure 5b).

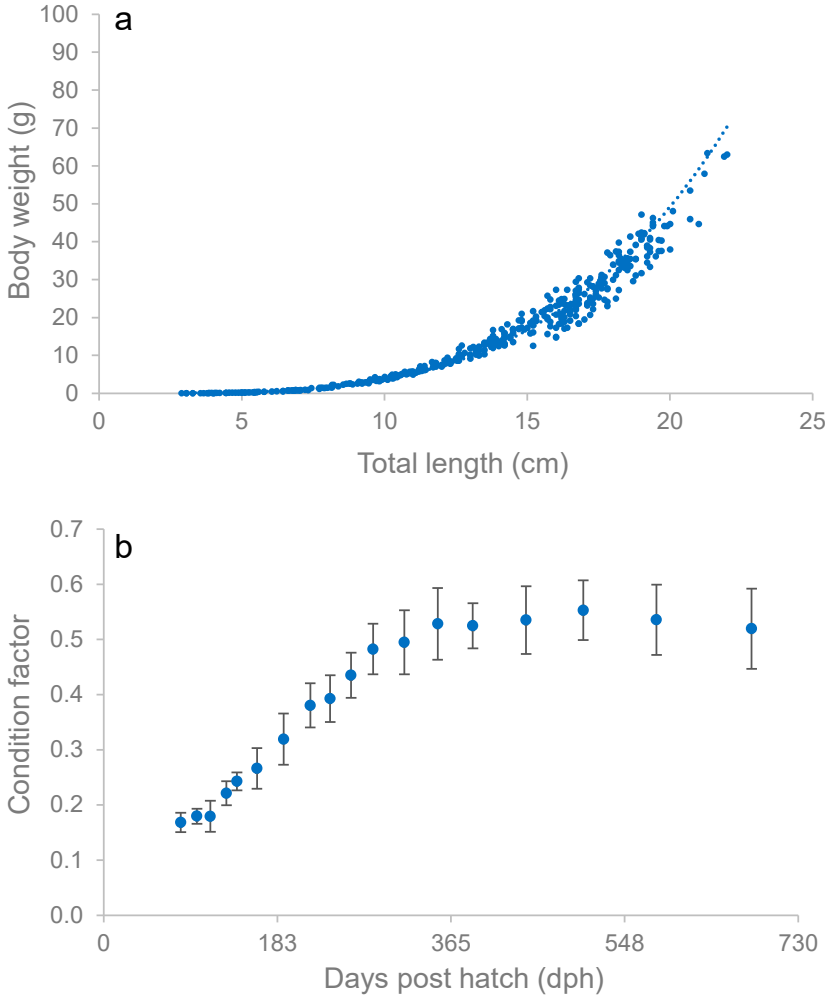

Figure 5. The relationship between total length and body weight of cultivated capelin (**a**). The overall regression line is described by $W = 0.0006TL^{3.751}$, with n = 428, $R^2 = 0.967$. The average condition factor ± SD of the cultivated capelin during the study period (**b**).

3.7. Wild Stock Comparison

The comparative VB analysis shown in Figure 6 reveals a striking difference in the growth performance and growth dynamics of wild and cultivated capelin. Among the different cohorts of wild capelin, the growth factor (K) spanned from 0.51 to 1.30, $L\infty$ from 17.2 to 20.7 cm, and t_0 from −0.1 to 0.75. The cultivated capelin grew much faster and had significantly higher K when compared with the mean K of wild capelin from year-classes 1981–2018 (Wilcoxon rank test, $p < 0.01$), with values of 2.06 and 0.74, respectively. Thus, the cultivated capelin were estimated to reach 99% of their $L\infty$ in about 2.6 years, compared to about 6 years for the wild capelin. However, there was no significant difference in $L\infty$ between the cultivated and wild capelin (one-sample t-test, $p > 0.05$) and the same applied for the parameter t_0 (one-sample t-test, $p > 0.05$).

After the genders were identified from day 504 and onwards, the number of males and females did not differ significantly from a 1:1 ratio at any time point in the experimental group, nor in group B ($\chi^2 < 3.84$, $p > 0.05$).

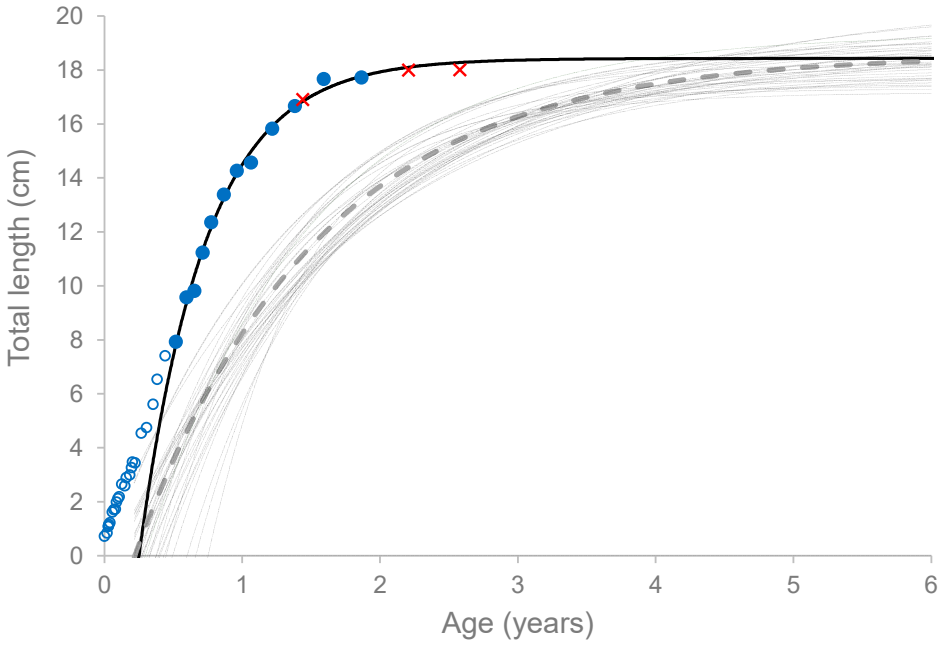

Figure 6. The von Bertalanffy growth analysis of cultivated capelin (black line) with the mean total lengths of metamorphosed capelin in groups A (•) and B (×). The model was exclusively fitted to the growth of metamorphosed capelin, excluding translucent capelin (o). The cultivated capelin's growth curve parameters t_0, K and $L\infty$ were 0.25, 2.06, and 18.4, respectively. Thin grey lines represent wild Icelandic capelin from year-classes 1981–2018, while the dashed line shows the growth curve derived from the median von Bertalanffy parameters of these wild cohorts (median t_0 = 0.24, K = 0.75, $L\infty$ = 18.6).

3.8. Behavior, Survival, and Deformity

Observations revealed that the newly hatched larvae exhibited positive phototaxis by gathering near the surface and tank walls. After introducing shading algal paste into the nursery tanks at 2 dph, the larvae descended and dispersed uniformly around the tank. The capelin were highly sensitive to disturbances and exhibited erratic swimming behavior in response to routine maintenance activities such as cleaning the tank bottom. This behavior often resulted in collisions with the tank walls, leading to head injuries among the fish. At the end of the study, all the capelin exhibited deformities in the head region. These head deformities were characterized by a compressed or swayed snout, a protruding lower jaw, and lower jaw papilloma. Out of the 103 fish examined, only one had a noticeable spinal deformity.

In the period from 255 to 681 dph, 38.6% of the fish survived. Of the fish that died during this period, 69% died within one week after measurements or following the transfer between tanks.

4. Discussion

In this study, the growth and development of capelin reared under laboratory conditions is described from hatch to adulthood for the first time. The study has helped elucidate the growth dynamics of capelin and provides information about the husbandry practices required to rear this delicate species in a laboratory.

4.1. Cultivation of Capelin

The experimental fish used in this study originated from artificially fertilized eggs collected aboard a commercial fishing vessel. The larvae hatched over a one-week period, with the majority hatching immediately after being subjected to mechanical stress from being siphoned from the nursery tank into a bucket. This phenomenon is in line with

observations made by Frank and Leggett [53], who noted that the emergence of capelin larvae from beach gravel is triggered by the mechanical actions of wind and waves.

One of the main challenges in intensive cultivation of marine teleosts is the development of first feeding strategies that can provide the larvae with feed of the right size and necessary nutrients for growth and development [54]. Wild first feeding capelin larvae eat a variety of prey but seem to base their foraging on small organisms such as *Acartia* spp. and *Temora longicornis* [55]. The prey size for first-feeding capelin in a large outdoor enclosure ranges from 40 to 300 µm in length [26]. However, based on Frank and Leggett [29], the optimal prey size for growth and survival of first feeding capelin larvae is at the lower end of this range, or between 40 and 51 µm. In the present study, enriched S-type rotifers (*Brachionus rotundiformis*, 85–150 µm) were used as first feed for the capelin larvae. While the prey sizes were within the range reported by Moksness [26], Frank and Leggett [29] suggest that first feeding capelin may prefer even smaller prey. However, in this study, most larvae had started ingesting the S-type rotifers on 3 dph at 7 °C, which is consistent with Morgan et al. [34] and about one day earlier than reported by Moksness [26]. This indicates that prey size in the current study was sufficiently small.

The early onset of exogenous feeding and high growth rates during the early developmental stages in the present study may be largely attributed to the light characteristics in the nursery tank. Because most fish larvae are visual feeders, the conspicuousness of the prey is vital for successful foraging. The addition of live algae or algae concentrate to nursery tanks (green water technique) is widely used in the intensive farming of marine fish. In addition to increasing growth and survival by improving visual contrast for foraging, the green water technique can provide direct nutrition through active ingestion, and indirectly by the enrichment of live prey in the nursery tank [56,57]. While the nutritional benefits of adding phytoplankton to the nursery tank in the present study are unknown, the green water technique clearly influenced behavior, as the larvae were observed to swim down from the surface and away from the tank walls directly after the algae were added to the tank water. Similar behavior was seen in black 150 L cylindrical tanks (unpublished results). However, in an otherwise similar environment, this behavior was not observed among capelin larvae reared in white 0.5 m^3 tanks. Furthermore, in these white tanks, the larvae did not ingest rotifers and died from starvation (unpublished results). This underlines the importance of light conditions during the early development and suggests that dark-colored tanks may be more suitable than light-colored tanks for the intensive cultivation of capelin. Similarly, prey ingestion, larval growth and survival of other species have been found to be influenced by tank color due to background contrast against live feed [58–60], or due to phototaxis to light-colored tank walls [61].

In the present study, 38.6% of the capelin in group A survived from day 255 to day 681. The mortality observed during measurements indicated a significant impact of handling stress, as 17–70% of randomly selected fish died within a day after being measured. It was established that mechanical stress was not the cause of mortality, as no skin injuries were observed. However, the capelin displayed signs of lethargy, such as swimming upside down, when temporarily placed in a bucket containing approximately 7 L of seawater prior to measurement. It can therefore be hypothesized that the mortality after the measurements was to some extent caused by high levels of physiological stress. Other factors, such as exposure to air during length measurements and the absence of a starvation period prior to handling, may also contribute to the observed high mortality rates. Overall, the study highlights the delicate nature of capelin and the challenges it may pose in future laboratory studies. Additionally, the present study is relevant to fishery management, as the small and fragile capelin may be more likely to suffer escape mortality from trawling than larger and more robust species. Previous studies have shown that escape mortalities of small pelagic fish can be substantial and may be caused by stress, exhaustion, and contact with netting [62,63]. Given the observed handling-related mortalities, studies on capelin survivability after contact with fishing gear are warranted.

Although the laboratory-reared capelin in the present study exhibited good appetite and rapid growth, the occurrence of craniofacial deformities, such as a compressed or swayed snout, protruding lower jaw, and lower jaw papilloma, raises questions about the husbandry practices employed. While skeletal malformations in fish can result from various factors, including nutritional deficiencies [64], previous studies have shown that repeated contact or collisions with tank walls can induce jaw injuries in captive adult capelin and other fish species [35,65,66]. In this study, craniofacial deformities appeared relatively late and were not observed during the larval stages. Given that all 103 fish examined at the final measurement had craniofacial deformities, with only one fish displaying vertebral deformity, it seems likely that the craniofacial malformations were caused by mechanical injuries as the fish became agitated and swam erratically during the daily cleaning process.

To mitigate this issue and improve the welfare of adult capelin, the use of large tanks (>3 m^3) and/or tanks with self-cleaning ability is recommended. Tank size has been shown to influence wall collisions and schooling behavior in capelin. For instance, captive adult capelin kept in a 7 m^3 tank collided less frequently with the walls and formed a tight school, whereas no schooling behavior and frequent wall collisions were observed in a 0.5 m^3 tank [35].

While previous studies have shown that wild-caught adult capelin display courtship behavior and spawning when kept in aquariums and tanks (e.g., [4,23,25,37]), the hatchery-reared capelin in the present study did not spawn in the tanks. Further investigation is needed to determine the reason for this, but it is possible that stable environmental conditions during the maturation process and the lack of suitable substrate, such as sand or gravel, may have contributed to the absence of spawning.

It has generally been assumed that wild male capelin have a 100% post-spawning mortality rate, while females in some populations may survive to spawn again the following year [3,67]. However, Christiansen et al. [4] found that a small proportion of captive male capelin can survive spawning and resume growth after a period of growth depression. In the present study, it was observed that 28% and 33% of males exhibited prominent secondary sex characteristics on days 581 and 681 post hatch, respectively. Despite this, the mortality rate among mature males during this period was low. These findings show that, in the absence of the mechanical stress associated with copulation and spawning, a significant proportion of mature males survive maturity. It is also noteworthy that, in group B, males with distinct spawning ridges were alive, approximately one year after they developed secondary sex characteristics (observed in June 2023).

4.2. Growth Dynamics

During the first year in the present study, the hatchery-reared capelin exhibited remarkable linear growth, with a mean SL increment of 0.36 mm per day. This growth rate by far surpasses the growth observed in previous studies where capelin larvae were fed cultured rotifers, which reported either negligible or slightly positive growth rates [34,47]. In a series of mesocosm experiments conducted by Ivarjord et al. [40], it was observed that capelin larvae feeding on natural zooplankton exhibited a mean SL increment of 0.25 mm over periods ranging from 35 to 79 days. Under similar conditions, Frank and Leggett [29] reported larval growth of 0.23 mm per day. These experiments were conducted under comparable or higher temperature conditions compared with the present study. In another study, Moksness [26] reported a mean SL increment of 0.29 mm per day at approximately 8 °C for capelin larvae released into a large basin with self-sustaining natural populations of phyto- and zooplankton, with a mean prey density ranging from approximately 11 to 16 organisms per liter. Moksness [26] also mentioned growth rates in a similar experiment with prey density ten times higher. In that experiment, daily increments of 0.31 and 0.44 mm were observed over 15 and 26 days from hatching, respectively. In comparison with wild capelin larvae, the daily growth rates in the present study were within the range of calculated values for Icelandic larvae (0.3–0.4 mm/day) [68], as well as values documented in Canadian waters (0.11–0.49 mm/day) [69,70] and the Barents Sea (0.33 mm/day) [71]. In

summary, these growth comparisons strongly suggest that the feed and rearing conditions in the current study supported rapid growth of the cultivated capelin.

Studies have demonstrated that fast-growing capelin tend to mature earlier than slower-growing capelin [14]. In capelin, the onset of spawning is highly size-dependent and for the fishery management of capelin in the Barents Sea, all capelin > 14 cm are assumed to be maturing [8]. Given the high and steady growth rate of the hatchery-reared capelin in the present study, it is not surprising that some of them developed secondary sex characteristics and mature gonads as early as one year post-hatch, or two years earlier than most of their wild counterparts in Icelandic waters [3]. Under the constant light and temperature in the present study, the timing of maturation was asynchronous, and capelin displaying secondary sex characteristics and mature gonads were observed among immature fish during the period from one year post-hatch until the termination of the study. This made it possible to collect eggs and sperm from the cultivated capelin at any time of the year. In May 2022, the first attempt to produce larvae from 14-month-old, cultivated capelin broodstock proved to be successful.

Under the stable environmental conditions provided in the present study, the growth trajectory of metamorphosed capelin (>8 cm) closely followed the growth trajectory predicted by the VB equation. Over the course of the study, it was observed that the growth of the cultivated capelin in group A decelerated in the second year after hatching, suggesting that the fish were nearing their threshold $L\infty$. This observation was further supported by the growth trajectory of group B, which exhibited a similar pattern. Between 806 and 942 dph, group B showed no growth in length, and at these time points, it only exhibited a slightly higher mean TL (18.0 cm) compared to group A (17.7 cm) at day 681.

To provide additional context to the results of this study, the growth performance of the cultivated capelin was compared to the measured growth data of 38 year-classes of wild Icelandic capelin (year-classes 1981–2018). Based on the VB growth model, the cultivated capelin in this study exhibited an $L\infty$ of 18.4 cm, which aligned with the median $L\infty$ of 18.6 cm of the wild capelin cohorts. However, in the absence of seasonal variation in temperature and daylength experienced by wild capelin, the cultivated capelin showed a K of 2.06 year^{-1}, or almost three times higher than the mean K of the wild Icelandic capelin (K = 0.75). As a result of the higher growth rate, the cultivated capelin were projected to reach their $L\infty$ in approximately 2.6 years, whereas the wild capelin would take about 6 years to reach their $L\infty$. This suggests a correspondingly shorter lifespan and generation time for the cultivated capelin compared to their wild counterparts. These findings align with previous studies showing that capelin inhabiting colder waters tend to reach sexual maturity and achieve maximum length at a later stage of their life cycle, resulting in an extended lifespan [12,15].

In the current study, the cultivated capelin had essentially the same $L\infty$ and t_0 compared to the median $L\infty$ and t_0 of the 38 wild Icelandic cohorts. Among the wild Icelandic cohorts, there was a distinct variation in the VB parameters. While it is beyond the scope of this study to elucidate these observed variations, it is worth noting that previous studies have suggested regional differences in $L\infty$ of capelin. Populations in the West Atlantic Ocean have usually been reported to have $L\infty$ at around 20 cm [12,15,16]. In contrast, the mean $L\infty$ of 16 year-classes of Barents Sea capelin was found to be 17.0 cm [17], and 18.6 cm for the 38 year-classes of the Icelandic capelin presented in this study. These regional differences may suggest that $L\infty$ could be influenced by environmental factors, either through slow evolutionary divergence and/or through phenotypic plasticity. To further understand the impact of environmental variations on capelin growth dynamics, future studies could be conducted under controlled laboratory conditions.

While the $L\infty$ of the cultivated capelin was predicted to be 18.4 cm, there was considerable variation in body size among the fish at the final measurement. In group A, the smallest fish measured approximately 14 cm, while the largest male reached 22.0 cm in length and weighed 63 g. It is worth noting that even larger fish were found in group B at 806 dph, with the largest male measuring 22.7 cm and weighing 89 g. These sizes, although

remarkable, fall short of the longest recorded capelin, a 10-year-old female measuring 25.2 cm [18].

In the present study, the length–weight relationship over the entire studied size range (from 2.6–22.0 cm) was strongly allometric, with a weight exponent (*b*-value) of 3.75. A more detailed examination revealed the presence of at least two distinct growth phases, roughly corresponding to the first and second year of the study period. The first one started at approximately 5 cm in TL (112 dph) and is reflected as a steady increase in CF. This coincides with profound morphological changes observed in wild capelin between 5 and 8 cm in TL. These changes include a rapid thickening of the body musculature and a transition from a translucent juvenile morphology to the adult form [50]. After the fish had completed metamorphosis to the adult form, the CF continued to rise towards the end of the first year. This may largely be attributed to the accumulation of adipose tissue as the capelin approached maturation. This phenomenon has been previously observed in wild capelin during the feeding months as they prepare for spawning the following year [3]. As a result, the CF of the capelin increased linearly with age during the first year, until it approached a plateau at a value of approximately 0.53 when the mean TL was about 14 cm. The observed plateau in body condition during the second year of the study may suggest isometric growth following the initial period of rapid growth. However, capelin in group B demonstrated a notable increase in appetite as they entered their third year of life. At 806 days post-hatch (dph), group B exhibited a mean CF of 0.61 $\pm$ 0.07, TL of 18.0 $\pm$ 1.72 cm, and W of 37.9 $\pm$ 12 g. These measurements indicate that the fish in group A would likely have also gained weight if the study had been extended beyond day 681.

5. Conclusions

This study presents the first successful rearing of capelin from hatch to adulthood using intensive aquaculture methods. During the larval stages, the cultivated capelin exhibited growth rates comparable to those of wild Icelandic capelin larvae. However, under the stable environmental conditions provided in this study, the growth of the cultivated capelin eventually surpassed that of their wild counterparts. The cultivated capelin are predicted to reach a projected L∞ of 18.4 cm after 2.6 years from hatch, while wild Icelandic capelin are expected to reach an L∞ of 18.6 cm after about 6 years. This study provides valuable insights into the growth dynamics of capelin, as well as the husbandry practices necessary for successful cultivation under laboratory conditions. While capelin are sensitive to handling, their short lifespan makes them a promising species for laboratory research.

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References

1. Carscadden, J.E.; Vilhjálmsson, H. Capelin—What Are They Good For? Introduction. *ICES J. Mar. Sci.* **2002**, *59*, 863–869. [CrossRef]
2. Præbel, K.; Westgaard, J.I.; Fevolden, S.E.; Christiansen, J.S. Circumpolar Genetic Population Structure of Capelin *Mallotus villosus*. *Mar. Ecol. Prog. Ser.* **2008**, *360*, 189–199. [CrossRef]
3. Vilhjálmsson, H. *The Icelandic Capelin Stock. Capelin, Mallotus villosus (Müller) in Iceland–Greenland–Jan Mayen Area*; Rit Fiskideildar; Marine Research Institute: Reykjavík, Iceland, 1994; Volume XIII, 281p.
4. Christiansen, J.S.; Præbel, K.; Siikavuopio, S.I.; Carscadden, J. 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.* **2008**, *360*, 47–55. [CrossRef]
5. Carscadden, J.E.; Frank, K.T.; Miller, D.S. Capelin (*Mallotus villosus*) Spawning on the Southeast Shoal: Influence of Physical Factors Past and Present. *Can. J. Fish. Aquat. Sci.* **1989**, *46*, 1743–1754. [CrossRef]
6. Vandeperre, F.; Methven, D.A. Do Bigger Fish Arrive and Spawn at the Spawning Grounds Before Smaller Fish: Cod (*Gadus morhua*) Predation on Beach Spawning Capelin (*Mallotus villosus*) from Coastal Newfoundland. *Estuar. Coast. Shelf Sci.* **2007**, *71*, 391–400. [CrossRef]
7. Baulier, L.; Heino, M.; Gjøsæter, H. Temporal Stability of the Maturation Schedule of Capelin *Mallotus villosus* in the Barents Sea. *Aquat. Living Resour.* **2012**, *25*, 151–161. [CrossRef]
8. ICES. *Arctic Fisheries Working Group (AFWG)*; ICES Scientific Reports; ICES: Copenhagen, Denmark, 2021; Volume 3, 817p. [CrossRef]
9. Jourdain, N.O.A.S.; Fuglebakk, E.; Subbey, S. Maturation in the Barents Sea Capelin–Contrasting Length- and Gonad-Based Metrics. *Fish. Res.* **2021**, *237*, 105880. [CrossRef]
10. Gjøsæter, H. The Population Biology and Exploitation of Capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia* **1998**, *83*, 453–496. [CrossRef]
11. Hedeholm, R.; Grønkjær, P.; Rosing-Asvid, A.; Rysgaard, S. Variation in Size and Growth of West Greenland Capelin (*Mallotus villosus*) Along Latitudinal Gradients. *ICES J. Mar. Sci.* **2010**, *67*, 1128–1137. [CrossRef]
12. McNicholl, D.G.; Davoren, G.K.; Reist, J.D. Life History Variation Across Latitudes: Observation Between Capelin (*Mallotus villosus*) from Newfoundland and the Eastern Canadian Arctic. *Polar Biol.* **2018**, *41*, 643–651. [CrossRef]
13. Magnaye, M.; Rideout, R.M.; Davoren, G. Irregular Growth Patterns in the Otoliths of a Short-Lived Forage Fish Do Not Reliably Indicate Reproductive History. *Fish. Res.* **2019**, *218*, 120–126. [CrossRef]
14. Berg, F.; Shirajee, S.; Folkvord, A.; Godiksen, J.A.; Skaret, G.; Slotte, A. Early Life Growth Is Affecting Timing of Spawning in the Semelparous Barents Sea Capelin (*Mallotus villosus*). *Prog. Oceanogr.* **2021**, *196*, 102614. [CrossRef]
15. Winters, G.H. Life History and Geographical Patterns of Growth in Capelin, *Mallotus villosus*, of the Labrador and Newfoundland Areas. *J. Northwest Atl. Fish. Sci.* **1982**, *3*, 105–114. [CrossRef]
16. Friis-Rødel, E.; Kanneworff, P. A Review of Capelin (*Mallotus villosus*) in Greenland Waters. *ICES J. Mar. Sci.* **2002**, *59*, 890–896. [CrossRef]
17. Hamre, J.; Johnsen, E.; Hamre, K. A New Model for Simulating Growth in Fish. *PeerJ* **2014**, *2*, e244. [CrossRef]
18. Winters, G.H. Record Size and Age of Atlantic Capelin, *Mallotus villosus*. *J. Fish. Res. Board Can.* **1970**, *27*, 393–394. [CrossRef]
19. Peck, M.A.; Alheit, J.; Bertrand, A.; Catalán, I.A.; Garrido, S.; Moyano, M.; Rykaczewski, R.R.; Takasuka, A.; van der Lingen, C.D. Small Pelagic Fish in the New Millennium: A Bottom-Up View of Global Research Effort. *Prog. Oceanogr.* **2021**, *191*, 102494. [CrossRef]
20. Dorval, E.; Appel, P.; Human, M.H.; Macewicz, B.J.; Watson, W. Rearing and Inducing Spawning in Captive Pacific Sardine (*Sardinops sagax*). *Calif. Coop. Ocean. Fish.* **2019**, *60*, 123–134.
21. Garrido, S.; Saiz, E.; Peters, J.; Ré, P.; Alvarez, P.; Cotano, U.; Herrero, D.L.; Martínez de Murguía, A.; Irigoien, X. Effects of Food Type and Concentration on Growth and Fatty Acid Composition of Early Larvae of the Anchovy. *J. Exp. Mar. Biol. Ecol.* **2012**, *434*, 16–24. [CrossRef]
22. Sakaguchi, K.; Yoneda, M.; Sakai, N.; Nakashima, K.; Kitano, H.; Matsuyama, M. Comprehensive Experimental System for a Promising Model Organism Candidate for Marine Teleosts. *Sci. Rep.* **2019**, *9*, 4948. [CrossRef]
23. Pozdnyakov, Y.F. Spawning of Capelin in the Aquarium. *Izv. Karel. Kolsk. Fil. SSSR* **1959**, *3*, 145–147. (In Russian)
24. Pozdnyakov, Y.F. Materiali o Razvitii Moivi Barentsevo Morja. *Tr. Murm. Morsk Biol. Ins.* **1960**, *2*, 211–225. (In Russian)
25. Friðgeirsson, E. *Observations on Spawning Behaviour and Embryonic Development of the Icelandic Capelin*; Rit Fiskideildar; Hafrannsóknastofnunin: Reykjavík, Iceland, 1976; Volume 4, 35p.
26. Moksness, E. Food Uptake, Growth and Survival of Capelin Larvae (*Mallotus villosus* Müller) in an Outdoor Constructed Basin. *Fisk. Dir. Skr. Ser. HavUnders.* **1982**, *17*, 267–285.
27. Zenzerov, V.S. Morphofunctional Changes in the Thyroid Gland of the Capelin, *Mallotus villosus villosus*, Under Experimental Conditions. *Vopr. Ihtiol.* **1982**, *22*, 93–96.
28. Gjøsæter, J.; Monstad, T. Primary Growth Rings in Otoliths of the Barents Sea Capelin. *Fisk. Dir. Skr. Ser. HavUnders.* **1985**, *17*, 521–528.
29. Frank, K.T.; Leggett, W.C. Effect of Prey Abundance and Size on the Growth and Survival of Larval Fish: An Experimental Study Employing Large Volume Enclosures. *Mar. Ecol. Prog. Ser.* **1986**, *34*, 11–22. [CrossRef]

30. Gjøsæter, H.; Gjøsæter, J. Observations on the Embryonic Development of Capelin (*Mallotus villosus* Müller) from the Barents Sea. *Fisk. Dir. Skr. Ser. HavUnders.* **1986**, *18*, 59–68.
31. Davenport, J.; Stene, A. Freezing Resistance, Temperature and Salinity Tolerance in Eggs, Larvae and Adult Capelin, *Mallotus villosus*, from Balsfjord. *J. Mar. Biol. Assoc.* **1986**, *66*, 145–157. [CrossRef]
32. Davenport, J. The Effects of Salinity and Low Temperature on Eggs of the Icelandic Capelin *Mallotus villosus*. *J. Mar. Biol. Assoc.* **1989**, *69*, 1–9. [CrossRef]
33. Paine, M.D.; Leggett, W.C.; McRuer, J.K.; Frank, K.T. Effects of Hibernia Crude Oil on Capelin (*Mallotus villosus*) Embryos and Larvae. *Mar. Environ. Res.* **1992**, *33*, 159–187. [CrossRef]
34. Morgan, M.J.; Anderson, J.T.; Brown, J.A. Early Development of Shoaling Behavior in Larval Capelin (*Mallotus villosus*). *Mar. Behav. Physiol.* **1994**, *24*, 197–206. [CrossRef]
35. Christiansen, J.S.; Siikavuopio, S.I. Survival and Growth of Post-Spawning Capelin (*Mallotus villosus*)—An Introductory Report from a Laboratory Study. ICES CM, 1998, CC, 1–11. Available online: https://www.ices.dk/sites/pub/CM%20Doccuments/1998/CC/CC0898.pdf (accessed on 10 November 2024).
36. Burton, M.P.M.; Flynn, S.R. Differential Postspawning Mortality Among Male and Female Capelin (*Mallotus villosus* Müller) in Captivity. *Can. J. Zool.* **1998**, *76*, 588–592. [CrossRef]
37. Karamushko, L.I.; Christiansen, J.S. Aerobic Scaling and Resting Metabolism in Oviferous and Post-Spawning Barents Sea Capelin *Mallotus villosus villosus* (Müller, 1776). *J. Exp. Mar. Biol. Ecol.* **2002**, *269*, 1–8. [CrossRef]
38. Behrens, J.W.; Præbel, K.; Steffensen, J.F. Swimming Energetics of the Barents Sea Capelin (*Mallotus villosus*) During the Spawning Migration Period. *J. Exp. Mar. Biol. Ecol.* **2006**, *331*, 208–216. [CrossRef]
39. Karamushko, O.V.; Christiansen, J.S. Some Aspects of the Feeding and Behavior of Larvae of the Barents Sea Capelin *Mallotus villosus villosus* (Salmoniformes, Osmeridae) in Experimental Conditions. *J. Ichthyol.* **2006**, *46*, 322–327. [CrossRef]
40. Ivarjord, T.; Pedersen, T.; Moksness, E. Effects of Growth Rates on the Otolith Increments Deposition Rate in Capelin Larvae (*Mallotus villosus*). *J. Exp. Mar. Biol. Ecol.* **2008**, *358*, 170–177. [CrossRef]
41. Frantzen, M.; Falk-Petersen, I.B.; Nahrgang, J.; Smith, T.J.; Olsen, G.H.; Hangstad, T.A.; Camus, L. Toxicity of Crude Oil and Pyrene to the Embryos of Beach Spawning Capelin (*Mallotus villosus*). *Aquat. Toxicol.* **2012**, *108*, 42–52. [CrossRef]
42. Penton, P.M.; Davoren, G.K. A Common Garden Experiment on Capelin (*Mallotus villosus*) Early Life History Stages to Examine Use of Beach and Deep-Water Spawning Habitats. *J. Exp. Mar. Biol. Ecol.* **2013**, *439*, 54–60. [CrossRef]
43. Præbel, K.; Christiansen, J.S.; Kettunen-Præbel, A.; Fevolden, S.-E. Thermohaline Tolerance and Embryonic Development in Capelin Eggs (*Mallotus villosus*) from the Northeast Atlantic Ocean. *Environ. Biol. Fish* **2013**, *96*, 753–761. [CrossRef]
44. Beirão, J.; Baillon, L.; Litt, M.A.; Langlois, V.S.; Purchase, C.F. Impact of Crude Oil and the Dispersant Corexit™ EC95004 on Capelin (*Mallotus villosus*) Embryo Development. *Mar. Environ. Res.* **2019**, *147*, 90–100. [CrossRef]
45. Tairova, Z.; Frantzen, M.; Mosbech, A.; Arukwe, A.; Gustavson, K. Effects of Water Accommodated Fraction of Physically and Chemically Dispersed Heavy Fuel Oil on Beach Spawning Capelin (*Mallotus villosus*). *Mar. Environ. Res.* **2019**, *147*, 62–71. [CrossRef]
46. Shadrin, A.M.; Makhotin, V.V.; Eriksen, E. Incubation Temperature Effect on Qualitative and Quantitative Composition of Abnormalities and Mortality Rate in Embryogenesis of the Barents Sea Capelin *Mallotus villosus* (Osmeridae). *J. Ichthyol.* **2020**, *60*, 79–89. [CrossRef]
47. Nahrgang, J.; Granlund, C.; Bender, M.L.; Sørensen, L.; Greenacre, M.; Frantzen, M. No Observed Developmental Effects in Early Life Stages of Capelin (*Mallotus villosus*) Exposed to a Water-Soluble Fraction of Crude Oil During Embryonic Development. *J. Toxicol. Environ. Health A* **2023**, *86*, 404–419. [CrossRef]
48. Ogle, D.H.; Doll, J.C.; Wheeler, A.P.; Dinno, A. *FSA: Simple Fisheries Stock Assessment Methods*; R Package Version 0.9.4. 2023. Available online: https://CRAN.R-project.org/package=FSA (accessed on 2 February 2024).
49. Bailey, R.F.J.; Able, K.W.; Leggett, W.C. Evidence for the Presence of a Metamorphic Check in Capelin (*Mallotus villosus*) in Otoliths and Implications for Age Determination. *J. Fish. Res. Board Can.* **1977**, *34*, 2008–2014. [CrossRef]
50. Vesin, J.-P.; Leggett, W.C.; Able, K.W. Feeding Ecology of Capelin (*Mallotus villosus*) in the Estuary and Western Gulf of St. Lawrence and Its Multispecies Implications. *Can. J. Fish. Aquat. Sci.* **1981**, *38*, 257–267. [CrossRef]
51. Royston, P. Remark AS R94: A Remark on Algorithm AS 181: The W Test for Normality. *J. R. Stat. Soc. Ser. C Appl. Stat.* **1995**, *44*, 547–551. [CrossRef]
52. Árnason, T.; Bárðarson, B.; Steinarsson, A. Cultivation of Capelin in the Aquaculture Research Station in Grindavík. In *Capelin in a Changing Environment*; Haf-og vatnarannsóknir, HV 2023-43; Singh, W., Ólafsdóttir, A.H., Jónsson, S.Þ., Óskarsson, G.J., Eds.; Marine and Freshwater Research Institute: Hafnarfjörður, Iceland, 2023; pp. 27–30.
53. Frank, K.T.; Leggett, W.C. Wind Regulation of Emergence Times and Early Larval Survival in Capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* **1981**, *38*, 215–223. [CrossRef]
54. Yúfera, M.; Darias, M.J. The Onset of Exogenous Feeding in Marine Fish Larvae. *Aquaculture* **2007**, *268*, 53–63. [CrossRef]
55. Fossheim, M.; Tande, K.S.; Semenova, T.; Timonin, A. Capelin Larvae (*Mallotus villosus*) and Community Structure of Zooplankton of the Coast of Northern Norway. *J. Plankton Res.* **2006**, *28*, 585–595. [CrossRef]
56. Muller-Feuga, A.; Robert, R.; Cahu, C.; Robin, J.; Divernach, P. Use of Microalgae in Aquaculture. In *Live Feeds in Marine Aquaculture*; Støttrup, J.A., McEvoy, L.A., Eds.; Blackwell Publishing: Oxford, UK, 2003; pp. 253–299.

57. van der Meeren, T.; Mangor-Jensen, A.; Pickova, J. The Effect of Green Water and Light Intensity on Survival, Growth, and Lipid Composition in Atlantic Cod (*Gadus morhua*) During Intensive Larval Rearing. *Aquaculture* **2007**, *265*, 206–217. [CrossRef]
58. Downing, G.; Litvak, M.K. The Effect of Photoperiod, Tank Color, and Light Intensity on Growth of Larval Haddock. *Aquacult. Int.* **2000**, *7*, 369–382. [CrossRef]
59. McLean, E.; Cotter, P.; Thain, C.; King, N. Tank Color Impacts Performance of Cultured Fish. *Ribarstvo* **2008**, *66*, 43–54.
60. Bera, A.; Kailasam, M.; Mandaal, B.; Sukumaran, K.; Makesh, M.; Hussain, T.; Sivaramakrishnan, T.; Subburaj, T.; Thiagarajan, G.; Vijayan, K.K. Effect of Tank Color on Foraging Capacity, Growth, and Survival of Milkfish (*Chanos chanos*) Larvae. *Aquaculture* **2019**, *515*, 734347. [CrossRef]
61. Planas, M.; Cunha, I. Larviculture of Marine Fish: Problems and Perspectives. *Aquaculture* **1999**, *177*, 171–190. [CrossRef]
62. Suuronen, P.; Erickson, D.L.; Orrensalo, A. Mortality of Herring Escaping from Pelagic Trawl Codends. *Fish. Res.* **1996**, *25*, 305–321. [CrossRef]
63. Suuronen, P.; Peres-Comas, J.; Lehtonen, E.; Tschernij, V. Size-Related Mortality of Herring (*Clupea harengus* L.) Escaping Through a Rigid Sorting Grid and Trawl Codend Meshes. *ICES J. Mar. Sci.* **1996**, *53*, 691–700. [CrossRef]
64. Berillis, P. Factors that can lead to the development of skeletal deformities in fishes: A review. *J. Fish. Sci.* **2015**, *9*, 17–23.
65. Cobcroft, J.M.; Battaglene, S. Jaw Malformation in Striped Trumpeter (*Latris lineata*) Larvae Linked to Walling Behavior and Tank Color. *Aquaculture* **2009**, *289*, 274–282. [CrossRef]
66. Noble, C.; Cañon Jones, H.A.; Damsgård, B.; Flood, M.J.; Midling, K.Ø.; Roque, A.; Sæther, B.-S.; Cottee, S.Y. Injuries and Deformities in Fish: Their Potential Impacts Upon Aquacultural Production and Welfare. *Fish Physiol. Biochem.* **2012**, *38*, 61–83. [CrossRef]
67. Huse, G. Sex-Specific Life History Strategies in Capelin (*Mallotus villosus*)? *Can. J. Fish. Aquat. Sci.* **1998**, *55*, 631–638. [CrossRef]
68. Ólafsdóttir, A.H.; Anderson, T. Growth and Survival of Icelandic Capelin *Mallotus villosus* Larvae. *Mar. Ecol. Prog. Ser.* **2010**, *403*, 231–241. [CrossRef]
69. Jacquaz, B.; Able, K.W.; Leggett, W.C. Seasonal Distribution, Abundance, and Growth of Larval Capelin (*Mallotus villosus*) in the St. Lawrence Estuary and Northwestern Gulf of St. Lawrence. *J. Fish. Res. Board Can.* **1977**, *34*, 2015–2029. [CrossRef]
70. Shikon, V.; Pepin, P.; Schneider, D.C.; Castonguay, M.; Robert, D. Spatiotemporal Variability in Newfoundland Capelin (*Mallotus villosus*) Larval Abundance and Growth: Implications for Recruitment. *Fish. Res.* **2019**, *218*, 237–245. [CrossRef]
71. Jakobsen, R.A.; Pedersen, T.; Moksness, E. Growth Rates and Age Distribution of Capelin (*Mallotus villosus*) Larvae in the Barents Sea Investigated by Otolith Increment Analysis. ICES CM 2004, DD:08, 1–17. Available online: https://www.ices.dk/sites/pub/CM%20Doccuments/2004/DD/DD0804.pdf (accessed on 10 February 2024).