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EDITED BY

Torstein Pedersen,
UiT The Arctic University of Norway,
Norway

REVIEWED BY

Zachary Siders,
University of Florida, United States
Francisco Arreguin-Sanchez,
Centro Interdisciplinario de Ciencias
Marinas (IPN), Mexico

*CORRESPONDENCE

Berthe M. J. Vastenhou
[✉ bmjv@aqu.dtu.dk](mailto:bmjv@aqu.dtu.dk)

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Growth and natural mortality of *Maurolicus muelleri* and *Benthoosema glaciale* in the Northeast Atlantic Ocean

Berthe M. J. Vastenhou^{1*}, Tobias K. Mildenerger¹,
Alexandros Kokkalis¹, Silvia Paoletti¹, Paula Alvarez²,
Dorleta Garcia², Alina M. Wieczorek³, Thor Klevjer⁴,
Webjørn Melle⁴, Sigurður T. Jonsson⁵ and J. Rasmus Nielsen¹

¹National Institute of Aquatic Resources, Technical University of Denmark, Lyngby, Denmark,

²Arrantza eta Erikaigintzarako Institutu Teknologikoa (AZTI) Marine Research, Basque Research and Technology Alliance (BRTA), Gipuzkoa, Spain, ³Marine Institute (MI), Galway, Ireland, ⁴Research Group Plankton, Institute of Marine Research, Bergen, Norway, ⁵Pelagic Division, Marine and Freshwater Research Institute, Reykjavik, Iceland

Mesopelagic fish are considered a possible future fisheries resource, but the biological sustainability of their potential exploitation has not yet been assessed. Sustainability should be evaluated at the population level, for which accurate stock-specific life-history parameters are required. Here, we use a length-based model to estimate life-history parameters related to growth and natural mortality, and their uncertainty, for the assessment of Northeast Atlantic populations of *Maurolicus muelleri* (Gmelin, 1789, Mueller's Pearlside) and *Benthoosema glaciale* (Reinhardt, 1837, glacier lantern fish). We compare three different approaches to estimate natural mortality rates and provide recommendations for future data collection and monitoring programs. For *M. muelleri*, we estimated an asymptotic length of 57.98 mm and a von Bertalanffy growth constant of 1.28 year⁻¹, while for *B. glaciale*, we estimated an asymptotic length of 78.93 mm and a von Bertalanffy growth constant of 0.41 year⁻¹. Estimates of natural mortality rates for *M. muelleri* were around 1.29 year⁻¹ and 1.80 year⁻¹ based on empirical formulae with the estimated growth parameters and maximum age, respectively, and around 1.51 year⁻¹ with the length-converted catch curve method for *B. glaciale* estimates ranged between 0.5, 0.68, and 0.75 year⁻¹, with the three respective methods. Due to limited data availability, the estimated uncertainty of the provided life-history parameters is large and should be considered in the evaluation of the sustainability of potential mesopelagic exploitation following the precautionary approach.

KEYWORDS

Maurolicus muelleri, *Benthoosema glaciale*, TropFishR, length-based assessment, mesopelagic zone, data-limited stock assessment methods, Von Bertalanffy growth function, natural mortality

Introduction

The mesopelagic zone of the ocean is located between 200 and 1,000 m deep, enclosed by the epipelagic zone, where light is available, and the bathypelagic zone, where no light penetrates. Global estimates of the mesopelagic fish biomass are large but remain variable, with estimates ranging between 1 and 15 Gt (Gjøsæter and Kawaguchi, 1980; Irigoien et al., 2014; Anderson et al., 2019; Proud et al., 2019; Hill Cruz et al., 2023). These high biomass estimates have revived interest in the potential exploitation of mesopelagic species, mainly for the production of fish meal, fish oil, and nutraceuticals (Valinassab et al., 2007; FAO, 2011; FAO, 2016; St. John et al., 2016; Prellezo, 2019; Alvheim et al., 2020; Grimaldo et al., 2020; Olsen et al., 2020; Paoletti et al., 2021). While the potential for exploitation and the economic viability are already being investigated, the ecological sustainability of a potential mesopelagic fishery remains uncertain (Hidalgo and Browman, 2019; Prellezo, 2019; Paoletti et al., 2021; Dowd et al., 2022; Elsler et al., 2022; Kourantidou and Jin, 2022; van der Meer et al., 2023). Nonetheless, potential management strategies should aim for exploitation according to the stock-specific maximum sustainable yield following a precautionary and ecosystem-based approach (UN, 1982; FAO, 1995; UN, 1995; UN, 2002).

In the Northeast Atlantic Ocean, the main potential target fish species are *Maurollicus muelleri* (Gmelin, 1789, Mueller's pearlside) and *Benthoosema glaciale* (Reinhardt, 1837, glacier lantern fish) (Grimaldo et al., 2020; Olsen et al., 2020; Albrektsen et al., 2023). The distribution of both *M. muelleri* and *B. glaciale* spans the North Atlantic and the Mediterranean Sea (Halliday, 1970; Gjøsæter and Kawaguchi, 1980; Rees et al., 2020). Both species perform diel vertical migrations, which vary seasonally and according to life stage—a characteristic of many mesopelagic species (Staby and Aksnes, 2011; Dypvik et al., 2012; Staby et al., 2013; Prihartato et al., 2015). The longevity of *M. muelleri* can reach up to a maximum of 5 years but varies regionally: Grimaldo et al. (2020) and Kawaguchi and Mauchline (1982) mainly observed 0- and 1-year-old fish, while individuals up to 3 years were found in Norwegian waters (Gjøsæter, 1981b; Goodson et al., 1995). *M. muelleri* usually reaches a length of 40–50 mm, but individuals up to 70 mm have been observed (Gjøsæter, 1981b). *B. glaciale* grows to a maximum length of about 100 mm over 7–8 years (Gjøsæter, 1973). Both species have an extended spawning period, ranging from approximately March to October in the Northeast Atlantic Ocean (do Carmo Lopes, 1979; Gjøsæter, 1981b; Rasmussen and Giske, 1994; Goodson et al., 1995; Alvarez et al., 2023) and show high natural mortality rates (Kristoffersen and Salvanes, 1998a; Kristoffersen and Salvanes, 2009). *M. muelleri* and *B. glaciale* feed on copepods and euphausiids and are an important resource for higher trophic levels, including commercially important species such as blue whiting (*Micromesistius potassium*), saithe (*Pollachius virens*), and juvenile albacore tuna (*Thunnus alalunga*) (Gjøsæter and Kawaguchi, 1980; Gjøsæter, 1981b; Kawaguchi and Mauchline, 1982; Bergstad, 1991; Pusineri et al., 2005; Dypvik et al., 2012).

For many stock assessment and ecosystem models used to evaluate the sustainability of potential mesopelagic exploitation, life-history characteristics related to growth and mortality are an

essential input (St. John et al., 2016). The current estimates of growth and mortality for *M. muelleri* and *B. glaciale* are ontogenetically, seasonally, and regionally variable and often based on limited time series of aging data and/or from geographically confined areas such as fjords (Halliday, 1970; Gjøsæter, 1973; Gjøsæter, 1981b, Gjøsæter, 1981a; Kristoffersen, 2007; Kristoffersen and Salvanes, 2009). For example, both *M. muelleri* and *B. glaciale* showed larger asymptotic lengths and higher mortality rates in offshore areas in Norway compared to fjords, and rates between fjords varied (Halliday, 1970; Gjøsæter, 1973; Gjøsæter, 1981a; Gjøsæter, 1981b; Kawaguchi and Mauchline, 1987; Gartner, 1993; Salvanes and Stockley, 1996; Kristoffersen and Salvanes, 1998a). On the other hand, reduced growth rates were reported for adult *M. muelleri* during autumn and winter, due to reduced feeding, while adult *B. glaciale* showed lower growth rates during spring and summer, potentially related to spawning (Gjøsæter, 1973; Kawaguchi and Mauchline, 1982; Sameoto, 1988; Prihartato et al., 2015).

It is vital to base future stock assessments and the evaluation of the sustainability of a potential mesopelagic fishery on robust growth and mortality information that takes spatial and temporal variability and observation uncertainty into account. There are, however, challenges related to the input data for growth and mortality estimations and common stock assessment methods for those mesopelagic species: the lack of aging and catch data hampers the use of age-based stock assessment and surplus production models [e.g., SPiCT, Pedersen and Berg (2017)], gear avoidance might lead to an underestimation of species-specific abundances of trawl surveys (Kaartvedt et al., 2012), and the use of hydro-acoustic surveys in the mesopelagic zone is challenged by the distinction between trophic levels, species, stocks, and life stages (Proud et al., 2019; Grimaldo et al., 2020; Khodabandeloo et al., 2021; Gjeitsund Thorvaldsen et al., 2023). Length data are a valuable data source that is relatively easy to collect and are often routinely collected during ecosystem surveys and used in length-based methods for data-limited stock assessments (Kokkalis et al., 2015; Kokkalis et al., 2017; Schwamborn et al., 2019; Andersen, 2020). Also for both *M. muelleri* and *B. glaciale*, length data provide currently better coverage in space and time compared to age data.

In this study, we used a length-based method developed for data-limited situations (Mildenberger et al., 2017) to estimate robust growth parameters and mortality rates and their uncertainties for *B. glaciale* and *M. muelleri* in the Northeast Atlantic that account for the biological variability in growth and mortality and observation uncertainty. We compared those to existing parameter estimates in the region for the two species and evaluated the future perspectives and management implications for their exploitation. We addressed the following aims:

- (i) To estimate robust von Bertalanffy growth parameters, and their uncertainties, for *M. muelleri* and *B. glaciale* in the Northeast Atlantic region based on available length information.
- (ii) To estimate robust natural mortality rates, and their associated uncertainties, for *M. muelleri* and *B. glaciale* in

the Northeast Atlantic region with empirical formulae and the length-converted catch curve, and to evaluate if the methods result in similar natural mortality estimates for an unexploited population.

Materials and methods

Available data

We used length frequencies collected during the field campaigns of the H2020 MEESO project (www.meeso.org) and other scientific surveys. The data covers the Norwegian Sea and the North Atlantic region, from the north of the North Sea (58°N) up to 73°N and between 16°W and 12°E (Figure 1).

The data cover the period from 2009 to 2020, with sampling conducted between March and October (Table 1). A detailed description of the data collection and processing can be found in Supplementary Material (SM) Section S1. The data were aggregated by species and month, and we only included samples in the analysis where more than 100 individuals were measured. The measured length-frequency distribution in each haul was raised to the total catch of that haul if a subsample was measured to account for differences in sample sizes between hauls within months. The length-frequency distributions used in our analyses are by species, as shown in Supplementary Material Figures 1, 2.

Estimation of growth parameters

We applied the Electronic Length Frequency Analysis (ELEFAN) compiled in the TropFishR package (Mildenberger et al., 2017). This method is used globally for the estimation of growth parameters required by fish stock assessment and is robust in even very data-poor circumstances (Chen et al., 2019; Karim

et al., 2019; Osei et al., 2021; Asiedu et al., 2022). ELEFAN uses length-frequency (LFQ) data to estimate the parameters of the von Bertalanffy Growth Function (VBGF, von Bertalanffy, 1938):

$$L(t) = L_{\infty}(1 - e^{-K(t-t_0)})$$

Here is the length at age $L(t)$ (mm) depending on the asymptotic length L_{∞} (mm), the von Bertalanffy growth constant K (year^{-1}), and the theoretical age where length is zero (t_0). Using ELEFAN, the parameter t indicates “time” rather than “age”: t_a is therefore the equivalent of t_0 in the year-length coordinate system and can be interpreted as the fraction of the year where the length is equal to zero or the estimated time just before spawning (Pauly, 1980).

Growth parameters are estimated in three steps: (i) the length-frequency data is restructured by scoring the length bins relative to a moving average (MA) calculated from neighboring bins; (ii) a set of VBGF parameters is scored based on the number of peaks that are crossed by the growth curves; and (iii) the set of VBGF parameters is selected, which results in the maximum score value (Taylor and Mildenberger, 2017). The search space of L_{∞} corresponds to the maximum length in the dataset ($L_{\text{max}} \pm 50\%$). The search space of K was limited between 0.1 and 2 year^{-1} , and the search space of t_0 ranges between 0 and 1. The selected search space limits are based on available data, consider literature values, and are large enough in order not to restrict parameter estimates while ensuring meaningful estimates within the biological limits of the species. We selected a maximum age of 3 and 8 years for *M. muelleri* and *B. glaciale*, respectively, which corresponds to the maximum age reported in the region (Gjøsæter, 1973; Gjøsæter, 1981b). We performed a sensitivity study to determine the optimal bin size and MA, where the best model fits were selected visually according to the number of peaks that were crossed by the growth curves. To estimate the uncertainty of the parameters, we used a nonparametric bootstrapping approach (Schwamborn et al., 2019). It is important to note that the estimated growth parameters represent average values across the sampled years, allowing for the possibility of interannual variability.

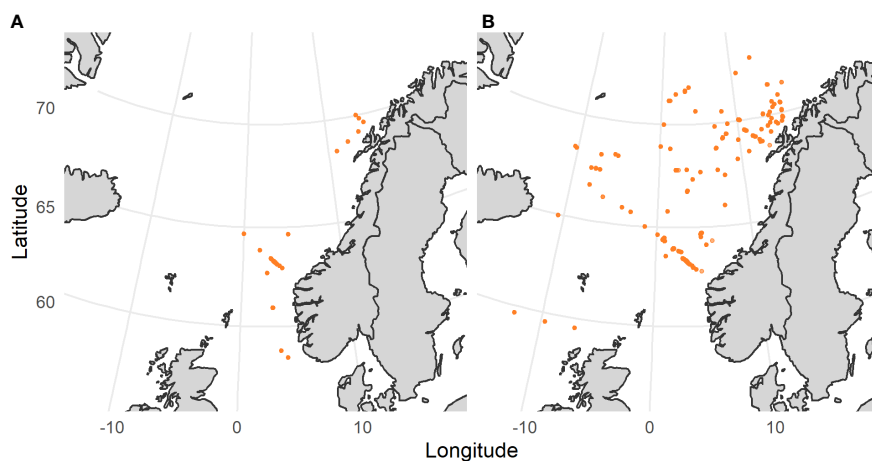


FIGURE 1

(A) Sampling locations of *Maurolicus muelleri*. (B) Sampling locations of *Benthosema glaciale*. Orange dots indicate single-trawl haul samples.

TABLE 1 Data overview of *Maurolicus muelleri* and *Benthoosema glaciale*, with an overview of the total number of fish measured in each year and month as well as the minimum and maximum observed length [standard length (SL)].

Year	Month	No. of fish measured and the raised No. of fish in between brackets	Min. length (SL, mm)	Max. length (SL, mm)
Maurolicus muelleri				
2009	5	110 (122)	27	50
2010	7	133 (1,320)	40	60
2011	5	193 (673)	25	52
2011	8	321 (18,604)	10	53
2016	10	682 (43,700)	11	51
2020	3	585 (5,235)	18	66
Benthoosema glaciale				
2008	6	185 (223)	20	67
2009	4	530 (2,275)	15	73
2009	5	535 (1,456)	16	73
2009	7	470 (925)	22	70
2010	5	590 (2,560)	20	70
2010	7	504 (1,539)	20	73
2011	6	125 (264)	20	70
2012	5	152 (275)	18	72
2013	5	360 (638)	18	73
2013	6	441 (1,989)	21	70
2014	5	185 (1,182)	17	66
2015	5	352 (858)	15	73
2016	10	1573 (35,899)	13	73
2017	5	797 (930)	15	73
2018	5	128 (685)	20	72
2018	6	129 (1,095)	21	71

Estimation of the natural mortality rate

We used three independent approaches to estimate the natural mortality rate M (year^{-1}) and associated uncertainty for the two species. The first approach estimates the natural mortality rate based on its relationship with estimated VBGF growth parameters according to the empirical formula by [Then et al. \(2015\)](#). The second approach is a modified version of [Hoenig \(1983\)](#) natural mortality estimator, relying on the correlation between the total mortality rate Z (year^{-1}) and the inverse of the maximum observed age t_{\max} (year). The Hoenig estimator based on t_{\max} is widely used and more robust than other estimators ([Kenchington, 2014](#)). In this study, we utilized an updated version of this estimator ([Hamel and Cope, 2022](#)), drawing on a comprehensive dataset proposed by [Then et al. \(2015\)](#) and incorporating a more appropriate transformation of the input data. For *M. muelleri*, we assumed a maximum age of 3 years, while for *B. glaciale*, the maximum age was

set at 8 years, in accordance with the observed maximum ages in the region ([Gjøsæter, 1973](#); [Gjøsæter, 1981b](#)).

As the third approach, we used the length-converted catch-curve method to estimate the total mortality rate Z (year^{-1}) and parameters related to gear selectivity (L_{50} (mm) and L_{75} (mm), the lengths at which the fish have a 50% and 75% probability of being caught, respectively). For unexploited stocks where fishing mortality F (year^{-1}) is zero, the estimated total mortality Z is equal to the natural mortality M (year^{-1}). In this method, Z is estimated according to:

$$\log(N_i/dt_i) = a - Zt$$

with N_i the number of individuals in length class i , dt_i the time necessary to grow through the length of class. The relative age (age – t_0) is indicated by t , and a is the intercept. We assume a logistic selection ogive, characteristic for trawl selectivity, parameterized using length at 50% and 70% retainment (L_{50} and L_{75}). The length-

converted catch-curve method requires a sample of the catch representative of the full year. While combining all samples from all years could result in a more complete length distribution representative of a complete year, it does not account for interannual variability in natural mortality and recruitment success and combines data from different surveys with different sampling regimes. Therefore, we only apply the catch curve to specific years with better data coverage and discuss potential problems caused by incomplete sampling. For *M. muelleri*, we present the $M_{\text{Catch curve, 2020}}$ for the year 2020. This is the most representative year as it originates from the only trial survey specifically targeting *M. muelleri*. This is also the only year where the entire length range from around 18 mm to 66 mm was measured, while the other years often show one strong cohort. For *B. glaciale*, we present the $M_{\text{Catch curve, 2018}}$, which is the most recent sampling year and shows the entire length range of the species (21–73 mm). For exploration purposes, we also estimated the mortality rates for the other years for each species as an indication of the interannual variability (Supplementary Material Section S6).

Sensitivity study

The length measurements were aggregated into length bins of 4 mm for both species. Alternative lower and higher bin sizes between 2 and 10 mm led to noisy or overly aggregated length frequency distributions, respectively (Supplementary Material Section S2). For demonstration purposes, we performed a sensitivity study of the aggregation of the length frequencies to 5 mm, which generated similar growth parameters (Supplementary Material Section S3). The data for *M. muelleri* mainly showed one or two peaks in the length distribution over a range between 10 and 66 mm, while the data of *B. glaciale* covered a larger size range (13–73 mm) and mostly showed three length peaks. We performed a sensitivity analysis for MA values between 3 and 7 given the data and length bin sizes. While an MA of 5 or 7 resulted in similar growth parameters (Supplementary Material Section S3), an MA of 3 resulted in low K estimates for both species (Supplementary Material Section S3). A sensitivity study varying the maximum age for both species (*M. muelleri*: 2 and 4 years and *B. glaciale*: 6 and 10 years) indicated that the results were consistent (Supplementary Material Section S3). We also performed a sensitivity study on the ELEFAN model settings, which showed that the model fits were robust to the ELEFAN growth model settings (Supplementary Material Section S4).

Results

Maurolicus muelleri

For *M. muelleri*, the final growth model estimated maximum density parameter values of $L_{\infty} = 57.98$ mm, $K = 1.28$ year⁻¹ and $t_a = 0.33$. The growth curves of this model cross most length peaks (Figure 2).

Using the empirical formula from (Then et al., 2015) and considering the estimated growth parameters along with

their uncertainties, we calculated a natural mortality rate of $M_{\text{Then (growth)}} = 1.29$ year⁻¹ for *M. muelleri*, while the estimate derived from the maximum age was higher, corresponding to $M_{\text{CopeHamel (Max. age)}} = 1.80$ year⁻¹ (Table 2). The estimates obtained with the length-converted catch curve fell within this range with an estimate of $M_{\text{Catch curve, 2020}} = 1.51$ year⁻¹. Inter-annual variability among catch curve estimates ranged between $M_{\text{Catch curve, 2020}} = 1.51$ year⁻¹ and $M_{\text{Catch curve, 2016}} = 9.1$ year⁻¹ (Supplementary Material Section S6.1).

The distributions of the parameter estimates show a distinct peak for L_{∞} , t_a and the selectivity parameters and a wider range of plausible values for K and the natural mortality estimates (Figure 3). A distinct second peak can be seen in the distribution of t_a . Correlation plots between the estimates of L_{∞} and K showed a primary aggregation of combinations of L_{∞} and K around $L_{\infty} = 57$ mm and $K = 1.3$ year⁻¹, and a secondary aggregation with lower estimates of $K = 0.7$ – 1.0 year⁻¹ (Supplementary Material Section S5.2).

Benthoosema glaciale

The maximum density estimates for growth parameters of *B. glaciale* are $L_{\infty} = 78.93$ mm, $K = 0.41$ year⁻¹ and $t_a = 0.39$. Figure 4 shows the fit of the growth curves to the length data.

For *B. glaciale*, we estimated $M_{\text{CopeHamel (Max. age)}} = 0.68$ year⁻¹ based on the relationship with maximum age, and $M_{\text{Then (Growth)}} = 0.5$ year⁻¹ with the empirical formula based on relationships with the estimated growth parameters (Table 3). The $M_{\text{Catch curve}}$ was 0.75 year⁻¹ for 2018, and the estimates ranged between 0.5 and 1.44 year⁻¹ between years (Supplementary Material Section S6.2).

The bootstrapping distributions show distinct peaks for all parameters (Figure 5). Correlation plots between the estimates of L_{∞} and K showed one main aggregation of L_{∞} – K combinations (Supplementary Material Section S5.2).

Discussion

In this study, we have used an integrated modeling approach specifically designed for data-poor situations (Mildenberger et al., 2017; Taylor and Mildenberger, 2017; Schwamborn et al., 2019) to estimate growth parameters, mortality rates, gear selectivity parameters, and their uncertainties for *M. muelleri* and *B. glaciale* in the Northeast Atlantic. The analyzed dataset is one of the longest existing time series covering a large area in the Northeast Atlantic region and therefore an essential complement to the existing life-history estimates of the two species, especially since parameter uncertainties are also considered here. Providing accurate estimates of population vital rates related to growth and mortality is an essential step in ensuring sustainable potential harvesting of mesopelagic resources as a basis for tropho-dynamic or population-dynamic modeling.

For *M. muelleri*, we estimated an asymptotic length of 57.98 mm and a von Bertalanffy growth constant of 1.28 year⁻¹. *M. muelleri* is a fast-growing species that often reaches maturity

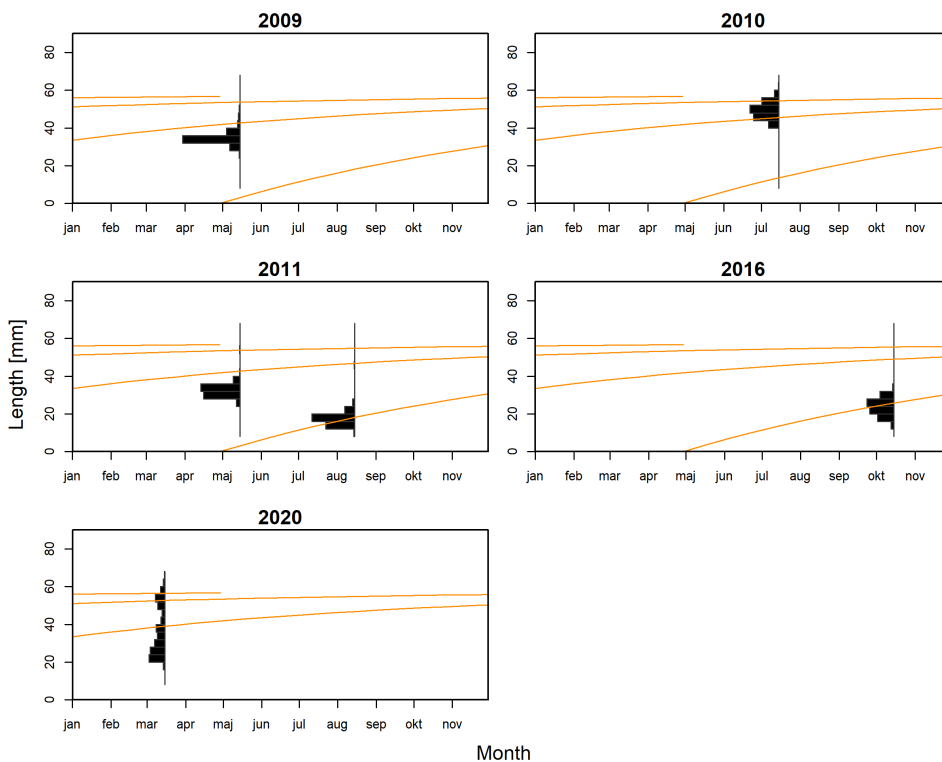


FIGURE 2 The von Bertalanffy growth curves of *Maurolicus muelleri* fitted to the length-frequency data.

after the first year (Gjøsæter, 1981b; Rasmussen and Giske, 1994; Alvarez et al., 2023). Previously reported L_{∞} estimates for *M. muelleri* in the Norwegian Sea ranged between 43.8 and 61.2 mm, and K estimates ranged between 0.88 and 2.0 year⁻¹ (Supplementary Material Table S6). The estimates in this study fall within those previously reported ranges, and the high estimates of K and few length peaks in the data correspond to the observation of mainly 0- and 1-year-old fish (Gjøsæter, 1981b; Goodson et al., 1995; Grimaldo et al., 2020). The L_{∞} is slightly lower than the maximum observed length of the species [70 mm,

(Gjøsæter, 1981b)], which is not uncommon. Small-scale differences in growth have been observed for the species in the Norwegian Sea: individuals in the open sea show a lower growth rate and larger asymptotic size ($K = 0.88 \text{ year}^{-1}$, $L_{\infty} = 59.4 \text{ mm}$) compared to populations from individual fjords ($K = 1.05 \text{ year}^{-1}$, $L_{\infty} = 48.8 \text{ mm}$) (Gjøsæter, 1981b), but also populations between fjords showed differences in growth (Kristoffersen, 2007). Furthermore, female *M. muelleri* can reach a larger asymptotic size (Kristoffersen, 2007; Alvarez et al., 2023), but the analyzed dataset contained insufficient information to include this factor in the analyses. The parameter t_a indicates the fraction of the year where the length is equal to zero (see Estimation of growth parameters), and is for *M. muelleri* estimated at 0.33. This estimate indicates a spawning time of April–May which falls within the reported spawning season in the region ranging from March to October (Gjøsæter, 1981b; Rasmussen and Giske, 1994). Although this is the best fit for the growth curve for *M. muelleri*, not all length peaks are crossed, and the growth curves do not pass through the first length peaks in May 2009, May 2011, and March 2020. Changes in parameter settings related to bin size, moving average, or maximum age did not improve the model fit (Supplementary Material Section S3.1). However, increasing the model fit from one to two spawning events in a year improved the model fit (Supplementary Material Section S3.1). It is possible that multiple spawning events occur for the species: Gjøsæter (1981b) found ripening and ripe fish in the region in March–May and October–November and reported two size groups of oocytes. In the Bay of Biscay, there was an indication of spawning of *M. muelleri* in

TABLE 2 Overview of the growth, mortality, and selectivity estimates of *Maurolicus muelleri*.

Parameter	Estimate
L_{∞} (mm)	57.98 (50.99–83.48)
K (year ⁻¹)	1.28 (0.26–1.80)
t_a	0.33 (0.04–1.00)
$M_{\text{CopeHamel}}$ (Max. age) (year ⁻¹)	1.80
M_{Then} (Growth) (year ⁻¹)	1.29 (0.41–1.45)
$M_{\text{Catch curve, 2020}}$ (year ⁻¹)	1.51 (0.68–2.82)
L_{50} (mm)	19.69 (19.53–20.10)
L_{75} (mm)	20.30 (19.90–20.78)

The table shows for each parameter the maximum density estimate (MDE), indicating the maximum of the parameter distributions resulting from the bootstrapping, and the lower and upper bound of the 95% confidence intervals in between parenthesis.

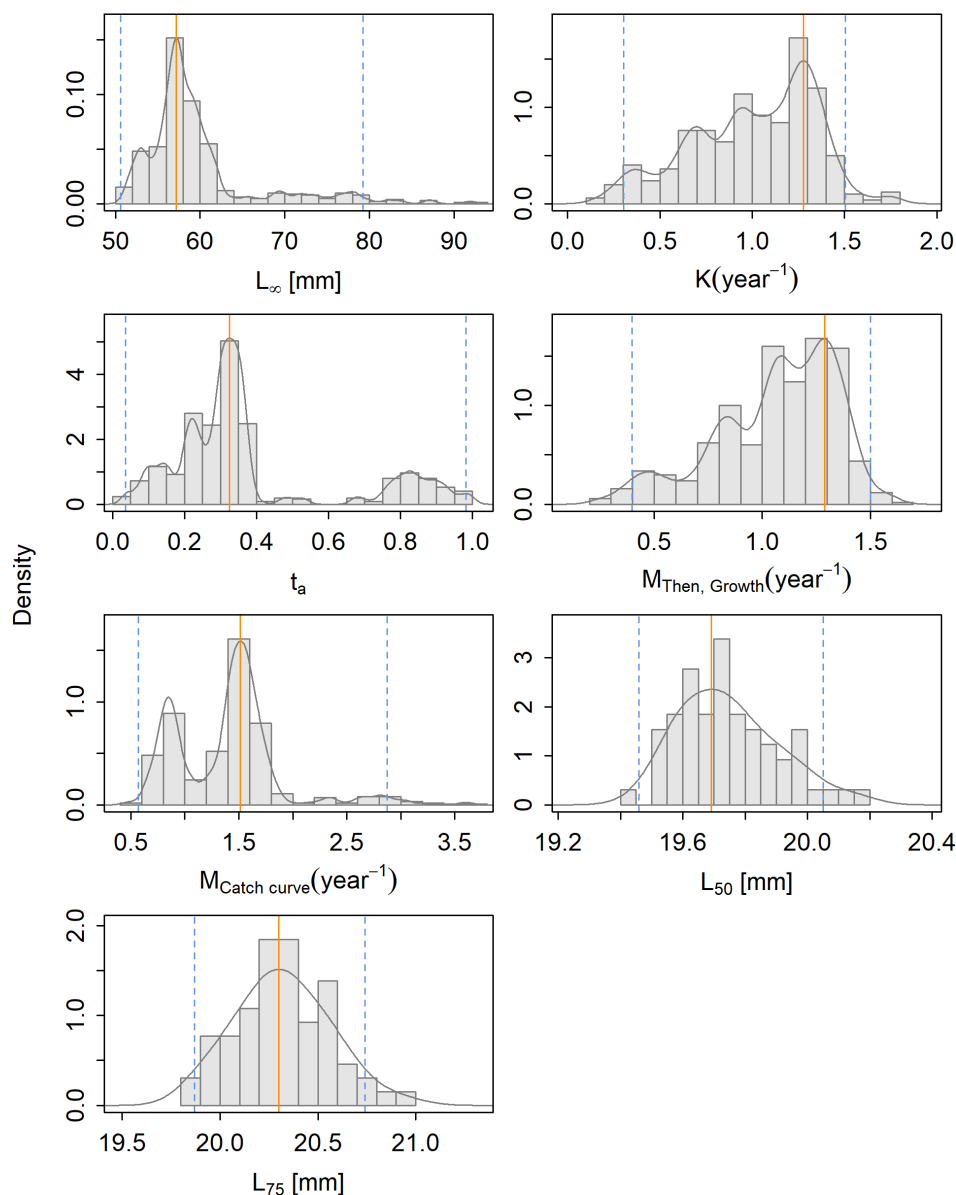


FIGURE 3

The density of the parameter estimates resulting from the bootstrapping of the selected model for *Maurolicus muelleri* with the maximum density estimate (solid orange line) and the 95% confidence interval (striped blue line).

March–May and in September (Alvarez et al., 2023). A prolonged spawning season has also been reported in the Rockall Through (Kawaguchi and Mauchline, 1987). However, the improved model fit might also result from the sparsity of the data or from other variability, including interannual variation in spawning time or the presence of multiple populations. As the current study does not allow us to identify the driver of the improved model fit allowing for two spawning events, we do not present this model in the main results.

For *B. glaciale*, we estimated an asymptotic length of 78.93 mm and a von Bertalanffy growth constant of 0.41 year⁻¹. Comparative estimates in the Norwegian Sea (L_{∞} = 64.8–106.2 mm and K = 0.18–0.60 year⁻¹, see also Supplementary Material Table S6) indicated

lower asymptotic length and higher K estimates in fjords compared to open waters, potentially resulting in differences in visibility or food availability (Gjøsæter, 1973; Gjøsæter, 1981a; Kristoffersen and Salvanes, 2009). The L_{∞} estimated in this study is smaller than another estimate from the Norwegian Sea but larger than the fjord estimates from that same study (Kristoffersen and Salvanes, 2009) and corresponds to the range reported by Gjøsæter (1981a). Our K estimates fall within the range of estimates combining fjord and open water samples (Gjøsæter, 1973; Gjøsæter, 1981a) but are larger than a sample from open water alone reported by Kristoffersen and Salvanes (2009) and Gjøsæter (1973; Gjøsæter, (1981a). The lower von Bertalanffy growth coefficient (K) and larger L_{∞} for *B. glaciale* reflect its higher longevity compared to *M. muelleri*, where maturity

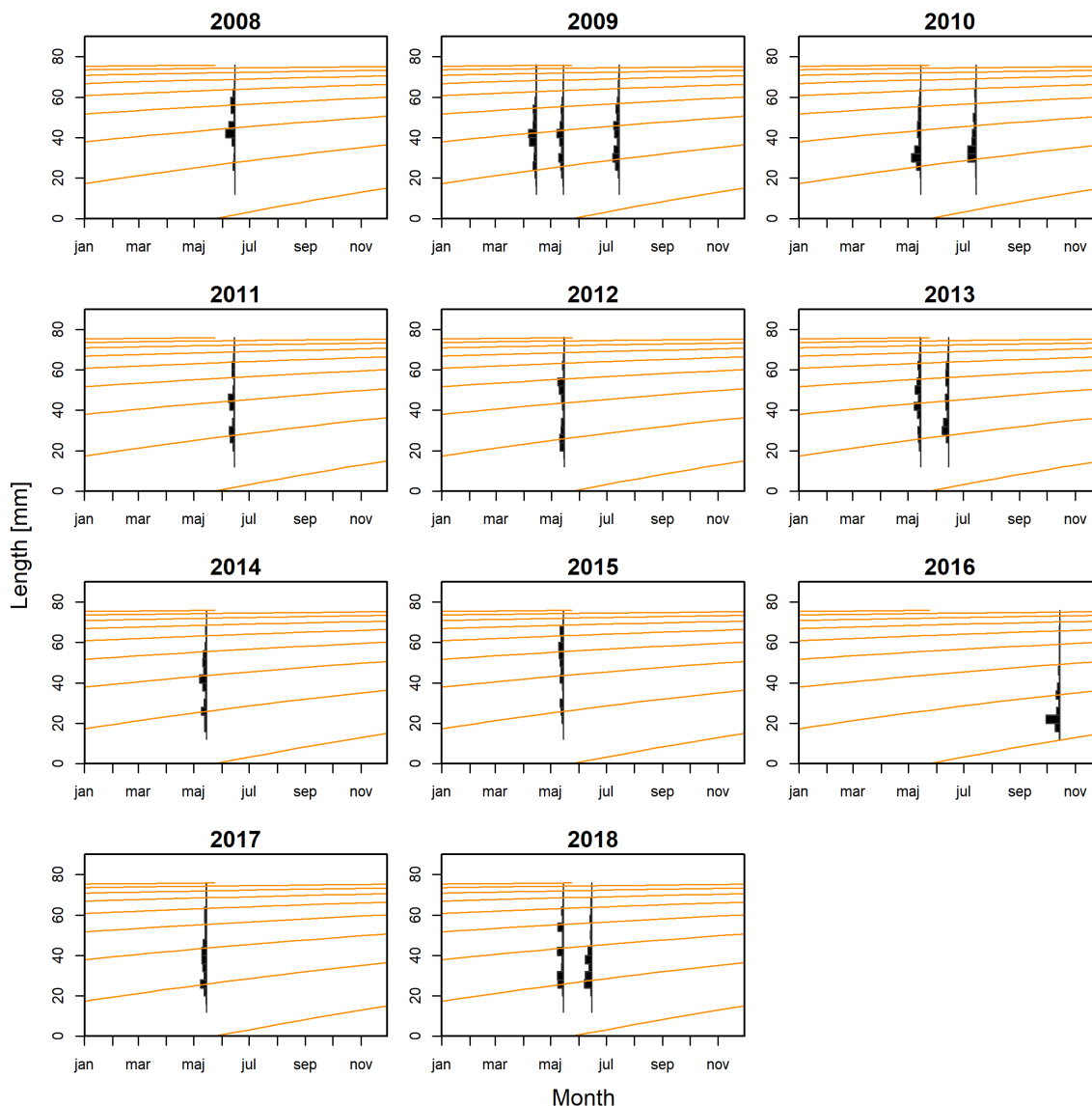


FIGURE 4 The von Bertalanffy growth curves of *Benthosema glaciale* fitted to the length-frequency data.

TABLE 3 Overview of the growth, mortality and selectivity estimates of *Benthosema glaciale*.

Parameter	Estimate
L_{inf} (mm)	78.93 (60.61–108.71)
K (year ⁻¹)	0.41 (0.19–0.8)
t_a	0.39 (0.01–1)
$M_{CopeHamel}$ (Max. age) (year ⁻¹)	0.68
M_{Then} (Growth) (year ⁻¹)	0.5 (0.28–0.76)
M_{Catch} curve, 2018 (year ⁻¹)	0.75 (0.28–1.76)
L_{50} (mm)	23.67 (22.82–24.14)
L_{75} (mm)	24.5 (23.43–25.62)

The table shows for each parameter the maximum density estimate (MDE), indicating the maximum of the parameter distributions resulting from the bootstrapping, and the lower and upper bound of the 95% confidence intervals in between parenthesis.

is only reached after 2–3 years and the maximum lifespan is 8 years. The t_a estimate of 0.39 indicates a spawning time in late May, slightly preceding the June–July peak reported for *B. glaciale* in the region (Gjøsæter, 1981a).

In this study, we used the classic ELEFAN method, improved with more powerful optimization methods and nonparametric bootstrapping, for the estimation of uncertainty in the growth estimations (Pauly, 1980; Efron and Tibshirani, 1993; Mildenerger et al., 2017; Schwamborn et al., 2019). The use of a length-based method following length cohorts is appropriate for the species, though especially *M. muelleri* grows fast; differences in mean length could be found between different age groups for both species (Gjøsæter, 1981a; Alvarez et al., 2023). ELEFAN is an established method that continues to be used to date for different data-limited instances (see, e.g., Osei et al., 2021; Asiedu et al., 2022) and has been further developed since the early versions (Pauly and David, 1981). The ELEFAN_GA approach used in this

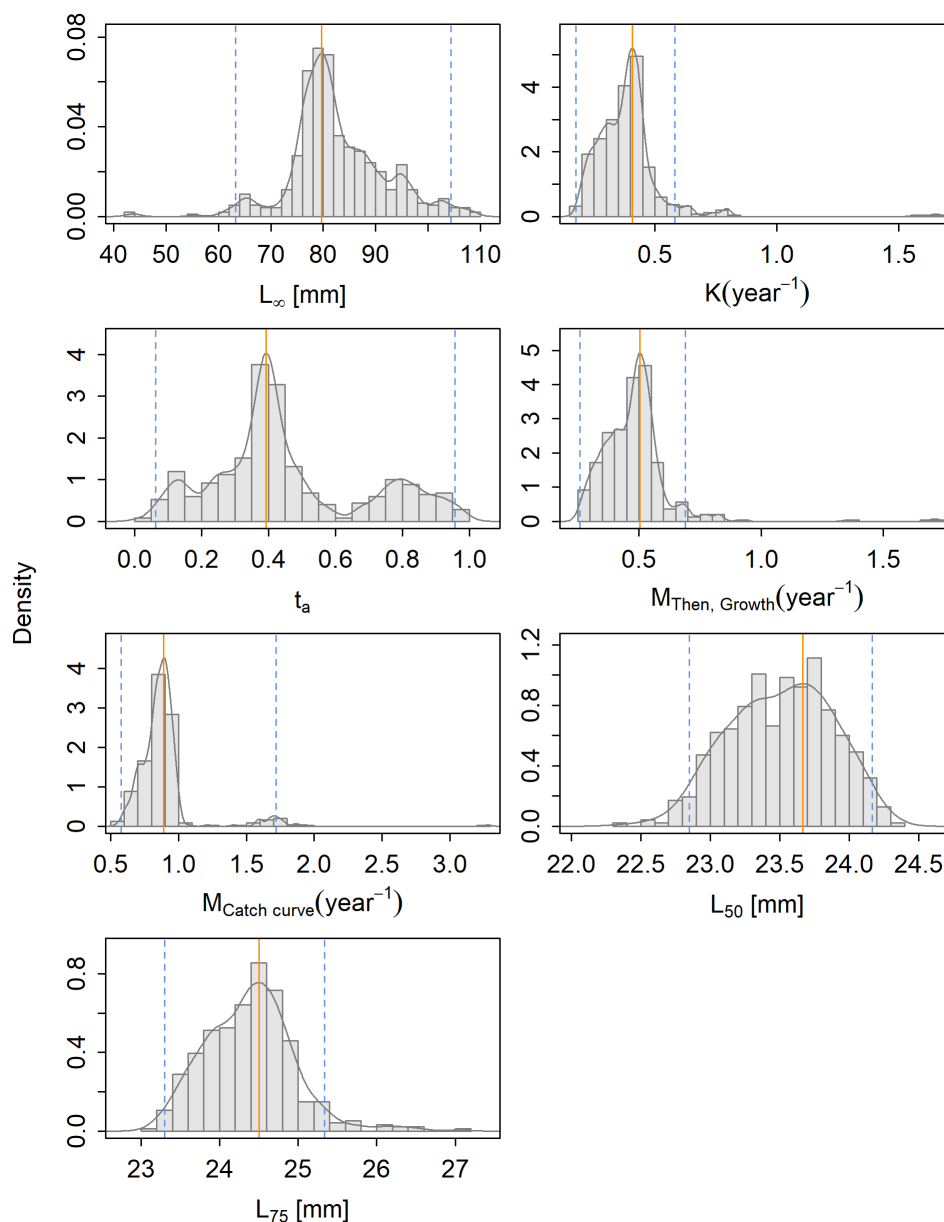


FIGURE 5

The density of the parameter estimates resulting from the bootstrapping of the selected models for *Benthosema glaciale*.

study has a curve-fitting algorithm that allows for unconstrained search within a multidimensional parameter space and is more flexible compared to the original (Mildenberger et al., 2017). Furthermore, the nonparametric bootstrapping approach addresses the variability in goodness of fit within the data and provides 95% confidence intervals for all estimates (Schwamborn et al., 2019). However, the ELEFAN method remains sensitive to the model settings and configuration that must be provided by the user, such as the moving average in the restructuring or the lower and upper limits of the search space for the genetic algorithm (Taylor and Mildenberger, 2017; Wang et al., 2020; Zhou et al., 2022). To take this sensitivity into account, we did extensive sensitivity studies selecting robust model settings (see Results and Discussion).

The estimates of the natural mortality rate for *M. muelleri* using an empirical formula and the catch curve method, with $M_{\text{Then, Growth}} = 1.29 \text{ year}^{-1}$, $M_{\text{CopeHamel (Max. age)}} = 1.80 \text{ year}^{-1}$ and $M_{\text{catch curve, 2020}} = 1.51 \text{ year}^{-1}$, were slightly lower than other estimates in the Norwegian Sea, which range between 1.8 and 2.25 year^{-1} as estimated with different methods (Gjøsæter, 1981b; Rasmussen and Giske, 1994; Kristoffersen and Salvanes, 1998a). Higher natural mortality rates were observed in open waters compared to fjords (Gjøsæter, 1981b; Kristoffersen and Salvanes, 1998b). An overview of previously estimated natural mortality rates can be found for both species in Supplementary Material Table S7. Potential factors influencing natural mortality include light intensity and turbidity. A reduction in predation rates of an order of magnitude has been observed with a 50-m depth increase, potentially due to those

factors (Rasmussen and Giske, 1994; Kristoffersen, 2007). Increased mortality of 2- and 3-year-old fish was observed during the summer, potentially due to spawning (Gjøsæter, 1981b). The estimates of natural mortality for *B. glaciale* ($M_{\text{Then (Growth)}} = 0.5 \text{ year}^{-1}$, $M_{\text{CopeHamel (Max. age)}} = 0.68 \text{ year}^{-1}$, $M_{\text{Catch curve}} = 0.75 \text{ year}^{-1}$) correspond to previously reported estimates in the region between 0.52 and 1.75 year^{-1} , without clear patterns between fjords and open water samples (Gjøsæter, 1973; Gjøsæter, 1981a; Kristoffersen and Salvanes, 2009).

Natural mortality M is an important parameter in productivity estimates of populations and stock assessments but is also notoriously difficult to estimate (Kenchington, 2014; Punt et al., 2021). The parameter varies with sex, length, age, and other ecological and physiological factors, including food availability, predator abundance, disease, and environmental effects, and complex interactions between those factors, resulting in potential bias and variance when these factors are little understood, as in the current case. Overestimation of M can result in a positive bias in biomass estimates in stock assessments and vice versa, as well as biased fisheries management reference points and ineffective management advice that can be directly related to the error in the M estimates (Punt et al., 2021). This error can result from the use of biased estimates, incorrect estimates of precision, or an increased likelihood that incorrect models are selected (Punt et al., 2021). In the case of data-limited stocks, where it is not possible to estimate M directly within stock assessments, M can be estimated indirectly from empirical relationships between M and life-history parameters such as longevity (t_{max}) and growth (Pauly, 1980; Hoenig, 1983; Gislason et al., 2010; Kenchington, 2014; Then et al., 2015), life-history theory, or directly by the use of catch-at-age data, allowing for the application of the catch curve method, or mark-recapture data.

The different methods have advantages and disadvantages when applied to the current data and species, and when estimating M outside stock assessment models, the use of multiple estimating methods with robust sensitivity exploration is required (Kenchington, 2014; Punt et al., 2021; Maunder et al., 2023). Different methods show different relationships with M , and they are only as good as the quality of their input parameters (Kenchington, 2014). A general consideration when applying an empirical formula exploiting the correlation with maximum age and life-history parameters is that the underlying meta-studies used to derive the relationships hardly include any mesopelagic species or information from species below 10 cm (e.g., Gislason et al., 2010). The Hoenig estimator based on t_{max} is widely used and performs relatively well (Kenchington, 2014; Hamel and Cope, 2022). Though widely used, estimators based on maximum age are challenged by the quality of the data used in the meta-analysis and the representation of species with similar life histories, but also by the determination of maximum age, which is often difficult to do accurately, requires a validated aging protocol, and varies for the species under investigation according to region. In terms of selectivity and gear avoidance behavior, it is important to note that the estimate is based on the maximum age observed rather than the maximum age in the population (Maunder et al., 2023). The use of only the old fish might cause instability and extreme sampling

error when using only age-based estimators, as there might be significant interannual variability in year-class strength, especially for short-lived species such as *M. muelleri*. The estimator based on relationships with growth parameters requires accurate estimates of the associated life-history parameters, and bias or error in those estimates will impact the predictions of M (Kenchington, 2014; Punt et al., 2021; Maunder et al., 2023). It can also be assumed that the error already exists in the data used to obtain the relationships, and therefore the relationships should be considered the correlation between estimated rather than true values of M and life-history covariates (Maunder et al., 2023). Furthermore, K and L_{∞} estimates are often confounded, resulting in significant uncertainty in the K estimates. We hence applied the method to the estimated growth parameters, including their estimated uncertainty from the non-parametric bootstrapping. However, the prediction error of M from empirical methods remains complicated due to the multiple and often unknown sources of uncertainty (Hoenig et al., 2016). The length-converted catch curve method provides information on the total mortality, from which natural mortality can be derived when fishing mortality is known to be negligible (Maunder et al., 2023). However, M estimates from this method might be confounded by changes in selectivity and catchability, and the model might be sensitive to nonequilibrium conditions such as recruitment strength, length-at-age, or predator and prey abundance, which are highly variable in the case of short-lived species (Hordyk et al., 2019). Therefore, this method might be especially sensitive to the gear avoidance behavior of the species as discussed below, potentially leading to an overestimation of M (Punt et al., 2021). The length-converted catch curve method is also more sensitive to sparse data as it assumes the availability of data throughout an entire year.

The length-based methods used to estimate growth and natural mortality rates assume the length-frequency distributions to be representative of the population over the sampled period. However, size distribution sampling is affected by many confounding factors, including (i) environmental conditions, (ii) the selectivity of the gear, and (iii) the spatial and temporal coverage of the sampling and under-sampling, which we discuss in the following paragraphs (Fock et al., 2019). Environmental conditions affect size-distribution sampling and subsequent parameter estimations, and seasonal and ontogenetic differences in vertical distributions have been observed for both *M. muelleri* and *B. glaciale* (Dypvik et al., 2012; Prihartato et al., 2015). This underlines the importance of sampling time and depth to cover representative parts of the population. For example, *M. muelleri* forms two distinct sound scattering layers (SSL) during winter, where the upper layer consists of juveniles and the lower layer consists of adults (Gjøsæter, 1981a; Kawaguchi and Mauchline, 1982; Giske et al., 1990; Gjeitsund Thorvaldsen et al., 2023). The adults remain in the lower water layers while juveniles continue their vertical migrations from the upper SSL to shallow waters during dusk. The migrating behavior of juveniles and adults synchronizes again in spring. In the mesopelagic zone, light is an important factor driving the vertical migrations of species since visual foragers require light to find their prey (McFarland, 1986; De Robertis, 2002). The vertical distribution patterns and migrating behavior of many mesopelagic species are determined by their “light comfort zone”,

which is also associated with foraging, prey density, and predator avoidance (Kaartvedt et al., 2009; Staby and Aksnes, 2011; Prihartato et al., 2015; Røstad et al., 2016; Langbehn et al., 2019; Gjeitsund Thorvaldsen et al., 2023).

To take into account the selectivity of the gear, we estimated gear selectivity parameters according to a trawl-type logistic curve (Grimaldo et al., 2020; Grimaldo et al., 2022) and found for *M. muelleri* a value of $L_{50} = 19.69$ mm and for *B. glaciale*, the estimate of $L_{50} = 23.67$ mm. Selectivity is affected by the gear and mesh size used and other factors including the trawling operation, trawling speed, net opening, geometry, retention, and morphology of the fish, as well as the species-specific behavior in relation to those factors (Pearcy, 1983; Heino et al., 2011; Fock et al., 2019). Escaping and avoidance behavior of mesopelagic fish to trawls have been reported (Gjøsæter and Kawaguchi, 1980; Pakhomov and Yamamura, 2010; Kartvedt et al., 2012), which could be affected by bio-luminescence, environmental conditions related to visibility, such as turbidity or light availability, or by the light and noise emitted by research vessels (Pearcy, 1983; Koslow et al., 1995; Jamieson et al., 2006; Benoit-Bird et al., 2010; Penã and Ratilal, 2019). Such behavior can result in under-sampling, especially of larger individuals. A misspecified asymptotic selectivity curve might result in positively biased estimates of natural mortality (Maunder et al., 2023). However, knowledge gaps remain regarding the behavioral patterns and catchability of the species, and potential size-specific differences herein are necessary to correct for the escaping behavior (Grimaldo et al., 2020; Grimaldo et al., 2022).

The spatial and temporal coverage of the data used in this study is limited, increasing the uncertainty of the parameter estimates. To reduce the parameter uncertainty and ensure appropriate evaluation of the sustainability of a potential mesopelagic fishery, it is vital that future sampling strategies and data collection methods are expanded and aligned between sea regions. In this study, we included months with a minimum sample size of 100 length measurements per month, which is lower than the general recommendation of 200 samples for the analysis of length frequency distributions (Hoenig et al., 1987; Gulland and Rosenberg, 1992). The two species in this study are fast-growing and have a small maximum length, leading to more distinct cohorts and fewer length bins across the length range. For these two mesopelagic species, a minimum sample size between 100 and 200 samples per month might be sufficient. For slow-growing species with a large maximum length, more than 200 samples might be required, similar to other length-based models [e.g., LIME (Rudd and Thorson, 2018)]. The size range of samples with fewer than 200 length measurements is comparable to samples with more than 200 measurements (Table 1). Nevertheless, for more reliable and less uncertain growth parameters for both species, future sampling efforts should aim at large sample sizes with a good representation of large fish over a long and regular time period. Sampling should take place each month for at least a year and in 6–12 months during the second year, allowing to estimate reliable growth and natural mortality parameters and interannual differences in life-history parameters. These samples should optimally be taken throughout the entire geographical area of the potential fishery and distribution areas of the populations, with enough replication within strata to establish an accurate idea of within-strata variance. A measurement accuracy of 1 mm would be recommended for both species, considering their

maximum length of 70 mm (*M. muelleri*) and 103 mm (*B. glaciale*) and a minimum gear selection size of 10 mm, to obtain the recommended 20–40 length classes required for length-based methods (Gulland and Rosenberg, 1992).

Although the usage of length-based methods is challenging in the case of short-lived species (ICES, 2019), they provide more robust and useful estimations in the absence of longer time series of age data, as is the case with the species under investigation. To ensure the sustainability of potential future mesopelagic exploitation, simultaneous efforts are necessary to collect age data required for age-based stock assessment methods, as well as genetic studies required to identify potential subpopulations and stock structure. In the Bay of Biscay, a population connectivity study suggested the possibility of population differentiation within the area (Rodríguez-Ezpeleta et al., 2017), and studies comparing populations from individual fjords and offshore areas in Norway also showed genetic differentiation between populations of both *M. muelleri* and *B. glaciale* (Suneetha and Nævdal, 2001; Suneetha and Salvanes, 2001). Whether population differentiation occurs on a larger scale in the Northeast Atlantic remains uncertain, and partial isolation, suggested as the main driver for population differentiation in Norway, may also occur on larger basin scales. A preliminary estimation of growth and natural mortality parameters in Iceland and the Bay of Biscay suggests there might be differences in life-history parameters between the regions (Supplementary Material Section S8). For a thorough evaluation of such patterns, more data is required.

The high mesopelagic biomass estimates (e.g., Irigoien et al., 2014) and potentially large catches make *M. muelleri* and *B. glaciale* attractive target species for a commercial fishery; however, high costs and technological challenges have prevented the commencement of a fishery to date (Prellezo, 2019; Grimaldo et al., 2020; Standal and Grimaldo, 2020; Paoletti et al., 2021; Kourantidou and Jin, 2022; Albrektsen et al., 2023). Additionally, gaps in our knowledge remain regarding the global biomass, distribution patterns, and composition of mesopelagic diversity, as well as the function of the mesopelagic community in the marine ecosystem and its importance for ecosystem services (St. John et al., 2016; Hidalgo and Browman, 2019; Wright et al., 2020; van der Meer et al., 2023). The mesopelagic community has a significant role in the sequestration of atmospheric carbon into the deep ocean (Anderson et al., 2019; Buesseler et al., 2022), and exploitation could alter the capture and cycling of carbon (Cavan and Hill, 2022). Many mesopelagic species also act as a key resource for higher trophic levels, such as marine mammals (the elephant seal, *Mirounga angustirostris*, and the common dolphin *Delphinus delphis*), yellowfin tuna (*Thunnus albacares*), saithe, and blue whiting (Bergstad, 1991; Potier et al., 2007; Brophy et al., 2009; Naito et al., 2013). To ensure the sustainability of potential mesopelagic exploitation, it is necessary to understand and quantify the population dynamics and resilience of mesopelagic target species such as *M. muelleri* and *B. glaciale*, as well as potential subpopulation structures, their trophic links, ecosystem function, and links to biological, physical, and chemical processes and interactions (St. John et al., 2016; Wright et al., 2020; Caiger et al., 2021; van der Meer et al., 2023). An essential step in this process is the estimation of appropriate life-history parameters related to growth and mortality, and their associated uncertainty, for the potential target species.

Conclusion

We have estimated life-history parameters related to growth and natural mortality for *M. muelleri* and *B. glaciale* in the Northeast Atlantic Ocean, which are the main species of interest for a potential targeted mesopelagic fishery in the region. *M. muelleri* showed an asymptotic length of 57.98 mm and a von Bertalanffy growth constant of 1.28 year⁻¹, while for *B. glaciale* we estimated an asymptotic length of 78.93 mm and a von Bertalanffy growth constant of 0.41 year⁻¹. Estimates of natural mortality rates for *M. muelleri* ranged between 1.29 year⁻¹ based on an empirical formula using a relationship with the estimated growth parameters, 1.79 year⁻¹ based on an empirical relationship with maximum age, and 1.51 year⁻¹ with the length-converted catch curve method. Natural mortality estimated for *B. glaciale* ranged between 0.5, 0.73, and 0.75 year⁻¹, with the three respective methods. The parameters were estimated based on the longest currently available time series of length data for both species in the region using a length-based method, providing robust estimates of the life-history parameters, including their uncertainty. The integrated method is flexible and valuable in highly data-limited situations, as in the current case.

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: The data underlying this article will be shared on reasonable request to the corresponding author. Requests to access these datasets should be directed to Berthe M. J. Vastenhoud, bmjv@aqu.dtu.dk.

Author contributions

BV: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. TM: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. AK: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. SP: Conceptualization, Writing – original draft. PA: Data curation, Writing – review & editing. DG:

Data curation, Writing – review & editing. AW: Data curation, Writing – review & editing. TK: Data curation, Writing – review & editing. WM: Data curation, Writing – review & editing. SJ: Data curation, Writing – review & editing. JN: Conceptualization, Funding acquisition, Resources, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1278778/full#supplementary-material>

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