

Impact of hatch date on early life growth and survival of Mueller's pearlside (*Maurolicus muelleri*) larvae and life-history consequences¹

Arild Folkvord, Geir Gundersen, Jon Albretsen, Lars Asplin, Stein Kaartvedt, and Jarl Giske

Abstract: Growth and survival of *Maurolicus muelleri* larvae in Herdlefjorden, Norway, were investigated by daily otolith increment analysis. While high egg densities were generally observed throughout the spawning season, three cohorts each with a narrow window of hatching dates were identified. The first of these cohorts was characterized by low growth and poor morphometric condition and disappeared from the fjord during autumn. High-resolution drift modeling indicated that Herdlefjorden had a net export of larvae and negligible import in the period cohort 1 disappeared. Yet, the advective loss rate of larvae was not considered high enough to explain the near complete disappearance of the first cohort. An otolith-based growth chronology indicated that growth conditions in Herdlefjorden improved noticeably around mid-September and remained favorable the following month. The analysis of daily otolith increments could thus be used to document within-season variability in larval growth and survival. The low and variable survival due to short-term fluctuations in environmental conditions indicate that multiple batch spawning is an adequately evolved life-history strategy for marine planktivorous fish such as *M. muelleri*.

Résumé : La croissance et la survie des larves de *Maurolicus muelleri* dans le Herdlefjorden (Norvège) ont été étudiées par l'analyse des incréments quotidiens d'otolithes. Si de fortes densités d'œufs ont été généralement observées durant toute la saison de frai, trois cohortes ont néanmoins été identifiées, chacune présentant sa propre fourchette restreinte de dates d'éclosion. La première cohorte était caractérisée par une faible croissance et un faible embonpoint morphométrique et a disparu du fjord durant l'automne. La modélisation à haute résolution de la dérive indique que le Herdlefjorden présentait une exportation nette de larves et une importation négligeable dans la période durant laquelle la première cohorte a disparu. Le taux de perte de larves par advection n'est toutefois pas jugé assez élevé pour expliquer la disparition presque complète de la première cohorte. Une chronologie de la croissance reposant sur les otolithes indique que les conditions de croissance dans le Herdlefjorden se sont améliorées de manière marquée vers la mi-septembre et sont demeurées favorables le mois suivant. L'analyse des incréments quotidiens d'otolithes pourrait donc être utilisée pour documenter la variabilité au cours d'une même saison de la croissance et de la survie des larves. Une survie faible et variable causée par des fluctuations de courte durée des conditions ambiantes indique que frayer en plusieurs épisodes constitue une bonne stratégie d'évolution du cycle biologique pour les poissons marins planctonivores comme *M. muelleri*. [Traduit par la Rédaction]

Introduction

A hundred years ago, Johan Hjort initiated a paradigm shift in fisheries ecology by documenting year class variation in boreal fish species by means of scale increment analysis (Hjort 1914). Since then, analyses of annual biochronological data in scales and otoliths have been routinely used in age-based fisheries assessments. Although the pattern of annual structures in scales and otoliths was convincing in documenting annual variations in recruitment, no firm conclusion could be drawn as to **what** were the underlying mechanisms behind this variation. Two main hypotheses were put forward that would explain variations in mortality and recruitment, one based on food shortage during the transi-

tion from endogenous to exogenous feeding, the other relating to transport of young offspring to unfavorable areas (Hjort 1914). The discovery of daily otolith increments by Pannella (1971) opened up the possibility of documenting within-season variation in growth and survival of larval fish. Otolith microstructure analysis thus provided a new method for documenting **how** and **why** recruitment varied between years. Several authors have subsequently used this methodology to infer regional, seasonal, and size-related differences in growth and survival (e.g., Methot 1983; Meekan and Fortier 1996; Baumann et al. 2003; Sponaugle 2010).

Here we present a case study from a highly abundant, albeit not commercially exploited, fish species, the Mueller's pearlside

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(*Maurolicus muelleri*), which is part of the mesopelagic fish community that comprises a huge biomass in the world's oceans (Irigoien et al. 2014). Mueller's pearlside is a small (4–5 cm), short-lived (maximum 5 years), mesopelagic fish reported from most of the world's continental slope areas (Grey 1964), yet more recent studies suggest the separation into several regional species (Parin and Kobylansky 1996; Kim et al. 2008). *Maurolicus muelleri* is an important planktivore in Norwegian fjords (Gjøsæter 1981; Kaartvedt et al. 1988; Rasmussen and Giske 1994), as *Maurolicus* spp. are in many coastal ecosystems (e.g., Okiyama 1971; Robertson 1976; Armstrong and Prosch 1991). *Maurolicus muelleri* is also an important prey for many piscivores (e.g., Giske et al. 1990; Bergstad 1991; Falautano et al. 2007). The spawning season lasts from March to September in Norwegian waters (Lopes 1979; Gjøsæter 1981; Goodson et al. 1995), and a wide geographic distribution and long spawning period indicate a greater tolerance to variations in hydrographic conditions (Gamulin and Hure 1985; Zenteno et al. 2014). While each fish spawns through a series of batches during the spawning season, the total population displays unsynchronized spawning (Goodson et al. 1995). Eggs and larvae have geographical distributions similar to the adults (Okiyama 1971), indicating no major spawning migrations (Gjøsæter 1981).

Offspring survival is reported to be influenced by four main sources in the early life history of fish: mainly starvation and predation, but also disease and physical environmental conditions (Houde 1987; Leggett and DeBlois 1994). Hjort's "critical period" hypothesis (Hjort 1914) links larval survival and subsequent recruitment to initial larval feeding and drift conditions, while Cushing's match–mismatch hypothesis (Cushing 1990) covers a longer period in the early life history of fish and focuses on the match between larval production and plankton production during the entire larval period. Predation is reported to be the major source of mortality during the egg and yolk sac stages (Bailey and Houde 1989), and disease and parasitism can be locally important in later stages (e.g., Hershberger et al. 2007). Predation mortality can indirectly be exasperated during poor larval feeding conditions, which will prolong the period of high size-dependent predation (Houde 1987; Takasuka et al. 2003; Fiksen and Jørgensen 2011). Physical environmental variations can influence larval survival in habitats where hydrographical conditions change rapidly over small spatial and temporal scales (e.g., Maillet and Checkley 1991; Lough et al. 2006; Hinrichsen et al. 2012). In addition, the oceanographic and meteorological conditions determine to a large extent the water current directions and thereby drift routes of planktonic stages of fish (Bolle et al. 2009; Churchill et al. 2011). Several factors influence the advection of water masses in the Norwegian fjords and coastal areas: most important are local winds and the variable water mass densities of the Norwegian coastal water (Sætre et al. 1988; Aksnes et al. 1989; Asplin et al. 1999, 2014). This may cause larval drift to unsuitable habitats and unfavorable growth conditions for the larvae.

This study aims to investigate the impact of hatch date on early life growth and survival of *M. muelleri* larvae. By repeated sampling of larvae of a population, one can estimate within-season early life growth and survival of different hatch date cohorts from otolith microstructure analysis. The present study is based on field samples collected in 1995 and extends the work of Salvanes and Stockley (1996). Sampling was carried out during late summer and autumn months to potentially include all larvae hatched during the entire spawning season. The larval characteristics were combined with an updated high-resolution oceanographic and particle tracking model, which enabled us to estimate the relative importance of the two major mechanisms behind the initial loss of larvae put forward by Hjort (1914): unfavorable food conditions and aberrant drift. Based on these estimates, a wider understanding of early life-history recruitment dynamics and reproductive strategies of *M. muelleri* may be attained (Houde 2008).

Table 1. Distribution and catch rate of *M. muelleri* larvae during three cruises in Herdlefjorden in 1995.

| Depth (m) | 11 September | | 12 October | | 13 November | |
|-----------|---------------|--------------------------|---------------|--------------------------|---------------|--------------------------|
| | No. of larvae | caught-min ⁻¹ | No. of larvae | caught-min ⁻¹ | No. of larvae | caught-min ⁻¹ |
| 0–29 | 23 | 2.30 (1) | 15 | 1.50 (1) | 0 | 0.00 (1) |
| 30–49 | 31 | 1.55 (2) | 131 | 3.30 (4) | 6 | 0.60 (1) |
| 50–69 | 57 | 1.90 (3) | 37 | 1.85 (2) | 20 | 1.00 (2) |
| 70–99 | 12 | 0.60 (2) | 4 | 0.40 (1) | 138 | 4.60 (3) |
| 175 | — | — | — | — | 7 | 0.70 (1) |
| Total | 123 | — | 187 | — | 171 | — |
| Mean | — | 1.54 (8) | — | 2.34 (8) | — | 2.13 (8) |

Note: A dash indicates no haul was taken at a given depth for a respective cruise. Numbers in parentheses represent number of 10 min hauls at each depth interval and cruise.

Materials and methods

Sampling of larvae

The study area was Herdlefjorden (60°32'N, 5°8'E) northwest of Bergen (Fig. 1). The fjord is 17.2 km long, has a maximum width of 2.3 km, and has a maximum depth of 476 m. It is open, with no sill into Byfjorden in the southeast and a very shallow outlet (<10 m) to Hjeltefjorden in the northwest. Larvae were collected during three cruises: 11 September (Cruise I), 12 October (Cruise II), and 13 November 1995 (Cruise III) with R/V *Hans Brattström*. A similar cruise was carried out 12 June, but no *M. muelleri* larvae were captured. However, large concentrations of *M. muelleri* eggs were found on this cruise. High egg densities were also found on the September and October cruises, but no eggs were found in November.

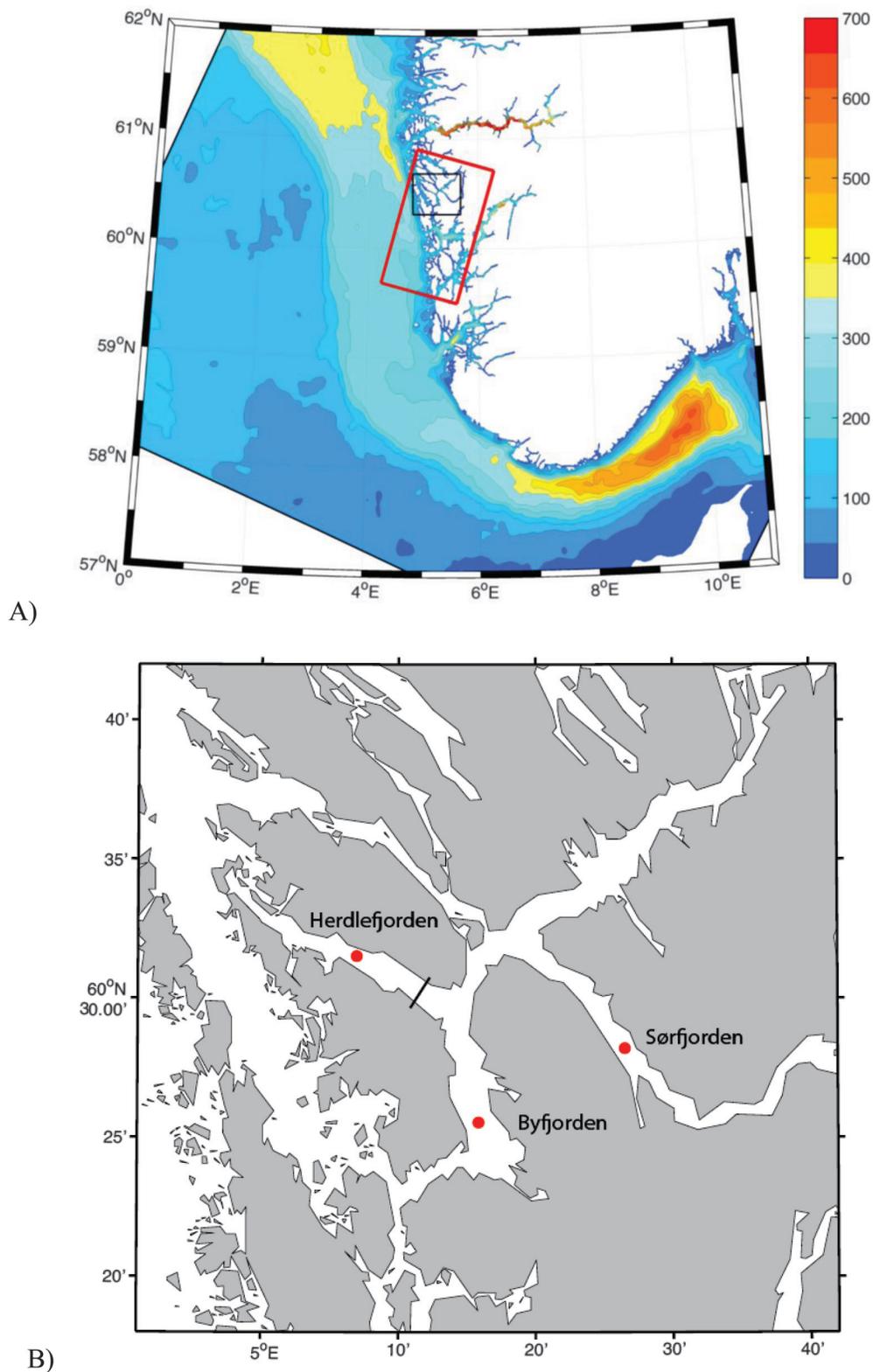
Sampling of fish larvae was performed with a bongo net of 360 µm mesh size and mouth openings with a circular radius of 60 cm. This net was towed at constant speed of about 2 knots (1 knot = 1.853 km·h⁻¹) for 10 min. Eight hauls were taken from the same station in the fjord on each cruise during daytime between 1000 and 1500 h. A total of 481 *M. muelleri* larvae were caught. The depth range varied between 15 and 100 m, with one additional haul at 175 m in November (Table 1). The trawling depth was controlled by a Simrad trawl eye, and a possible sound scattering layer (SSL) of fish larvae was obtained by printouts from a 38 KHz Simrad EK 500 echo sounder. Larvae from the September and October cruises were mainly distributed in the upper 70 m, while most of the fish in November were caught in the depth range 70–100 m (Table 1). The latter larvae comprised a separate SSL, which could be monitored on the echo sounder. No such SSL was observed during the three previous cruises.

The larvae were immediately identified (Robertson 1976), counted on board, and fixed in 96% ethanol in individual tubes. All larvae were dead before transfer to ethanol, and shrinking effects caused by death are assumed to be the same for all larvae. Standard length (SL, from the snout tip to the distal end of the caudal peduncle) of all larvae was recorded in the laboratory and rounded to the nearest 0.1 mm below. The SL of the larvae from Cruise II was also measured on board before fixation in alcohol, and mean shrinkage was estimated to be approximately 1%. The otoliths (sagittae) were dissected out, and the dry masses (DM) of the remaining larvae were measured to nearest 0.001 mg after 24 h in 60 °C using a Sartorius M3P microbalance. As in many other mesopelagic fish species, *M. muelleri* develops pairs of light organs on the ventral side of the body (Cavallaro et al. 2004), and the numbers of visible light organs on the sampled larvae were counted under a stereomicroscope with 25× magnification.

Otolith extraction and measurement

The sagittal otoliths were dissected out using fine needles and mounted on glass slides. This was done under polarized light at

Fig. 1. (A) Bathymetric map (colors indicate depth in m) of the coastal NorKyst800 model showing the extension of the 200 m fjord model (red rectangle) and study area (small black square). (B) Study area showing the modelled release positions for the particles and the line marking the border between Herdlefjorden and the surrounding fjords.



50× magnification with a stereomicroscope. The otoliths were covered with a small drop of transparent nail polish, without polishing, and were then ready for examination (Moksness and Wespestad 1989). Some larvae and otoliths were lost or destroyed

during preparation, yielding a total of 425 larvae and 819 otoliths for otolith microstructure analysis.

Otolith increments (zones) were counted and measured one by one across the postrostral axis, starting at the hatch check (Campana

1992), by using the data program OTO 2.0 (Andersen and Moksness 1988) with a light microscope at 1000× magnification. The sum of all increments and the hatch check constituted the otolith radius (OR). Left and right otoliths were read once by the same reader. If one otolith was missing, the other was read twice. Some of the inner zones (0–5 µm outside the hatch check) could be difficult to measure and were set to 0.8 µm, since the narrower visible increments in the same area were measured to be of this width. The increments are supposed to be deposited daily (Gjøsaeter 1981; Boehlert et al. 1994), and back-calculation of hatch dates was estimated by subtracting the number of increments from date of catch. Comparison of left and right OR and increment counts revealed no significant differences (pairwise tests, $p > 0.1$, $n = 394$), and one otolith was chosen for increment analysis per fish based on overall read quality of transect. In total, 15 634 daily increment measurements were used for the 425 larvae in the analysis.

Otolith growth chronology and standardized increment widths

A seasonal growth chronology was established based on average incremental otolith growth-at-age using data from July to November. The purpose was to establish an index of relative larval otolith growth based on daily otolith increments within a year of a given population, similar to annual chronologies based on annual tree rings or annual fish otolith increments between years (e.g., Black et al. 2005). Particle drift simulations were carried out to substantiate that offspring originated from Herdlefjorden (see below). The data was restricted to fish younger than 61 days to include more than 30 growth measurements at all ages. The estimated fit closely matched the mean increment widths, with deviations less than 0.14 µm at any given age (polynomial regression, $R^2 = 0.997$, $n = 60$, $p \ll 0.001$). Individual detrended and standardized increment widths-at-age were constructed by taking the difference of observed increment width-at-age and estimated increment width-at-age, divided by estimated age-specific standard deviation (SD) of age-specific increment width (polynomial regression, $R^2 = 0.968$, $n = 60$, $p \ll 0.001$). The resulting 15 475 individual standardized increment widths had a mean \pm SD of 0.01 ± 1.09 µm. Of these, 15 310 originated from dates with more than 20 cases in the period from 3 August to 13 November.

The oceanographic model

A set of models was used with historical meteorological data to estimate the potential wind-induced transport loss of larvae from Herdlefjorden. The numerical ocean model applied for provision of ocean currents and hydrography to the drift model was the ROMS (The Regional Ocean Modeling System, <http://www.myroms.org>; see Shchepetkin and McWilliams 2005; Haidvogel et al. 2008 and references therein). ROMS is a state-of-the-art, three-dimensional, free-surface, primitive equation numerical model using a generalized terrain-following s -coordinate in the vertical. The fjord model covering Herdlefjorden and adjacent fjords has a horizontal grid resolution of 200 m and receives open boundary values from a coastal model with grid resolution of 800 m (NorKyst800; see Albretsen et al. 2011) in a one-way nesting on hourly intervals (see maps in Fig. 1). The configuration of the fjord model is similar to the NorKyst800 as explained in Albretsen et al. (2011).

A data-driven hydrological model developed by the Norwegian Water Resources and Energy Directorate was used in the fjord model (Beldring et al. 2003). Atmospheric forcing of surface winds, air temperature, specific humidity, mean sea level pressure, cloud cover, and precipitation were retrieved from NORA10 (Norwegian ReAnalysis 10 km), which is a high-resolution hindcast archive covering the Nordic Seas, developed by the Norwegian Meteorological Institute (Reistad et al. 2011).

Particle tracking model

The particle tracking model is a modified version of a Lagrangian Advection and Diffusion Model (LADIM; Ådlandsvik and Sundby 1994). The particle tracking model applies hourly values of simulated currents from the ROMS current model that are interpolated linearly to a subgrid position. The temporal resolution will be typically a few minutes to make a valid interpolation based on the current model's resolution and velocities. A small stochastic velocity to represent subgrid-scale mixing based on a random walk formulation is added to the total current for each time step. The particles were assumed to remain neutrally buoyant at respective release depths. This model has been used successfully for investigations on dispersion of cod eggs and larvae in fjords (Mykssvoll et al. 2011) and the open sea (e.g., Vikebø et al. 2007, 2011; Opdal et al. 2011).

The experimental setup consisted of three series of drift simulations. First, we used a single release position inside Herdlefjorden with batches of 1800 particles released and allowed to drift by the current at fixed intermediate depths of 40 and 60 m for 70 days (Fig. 1). The release date was 11 September 1995, corresponding to the date of the first cruise where larvae were collected. Second, we released a similar number of particles at 40 m depth from two of the sites outside Herdlefjorden to evaluate any reciprocal return of particles. Finally, we released batches of 1800 particles at the position in Herdlefjorden and allowed them to drift at additional fixed depths of 10, 20, and 80 m to obtain a finer vertical resolution of particle drift. Results are presented as hourly values of all particles during the simulations, and we calculated the relative number of particles inside Herdlefjorden (the defined border marked by the black line in Fig. 1).

Statistical analysis

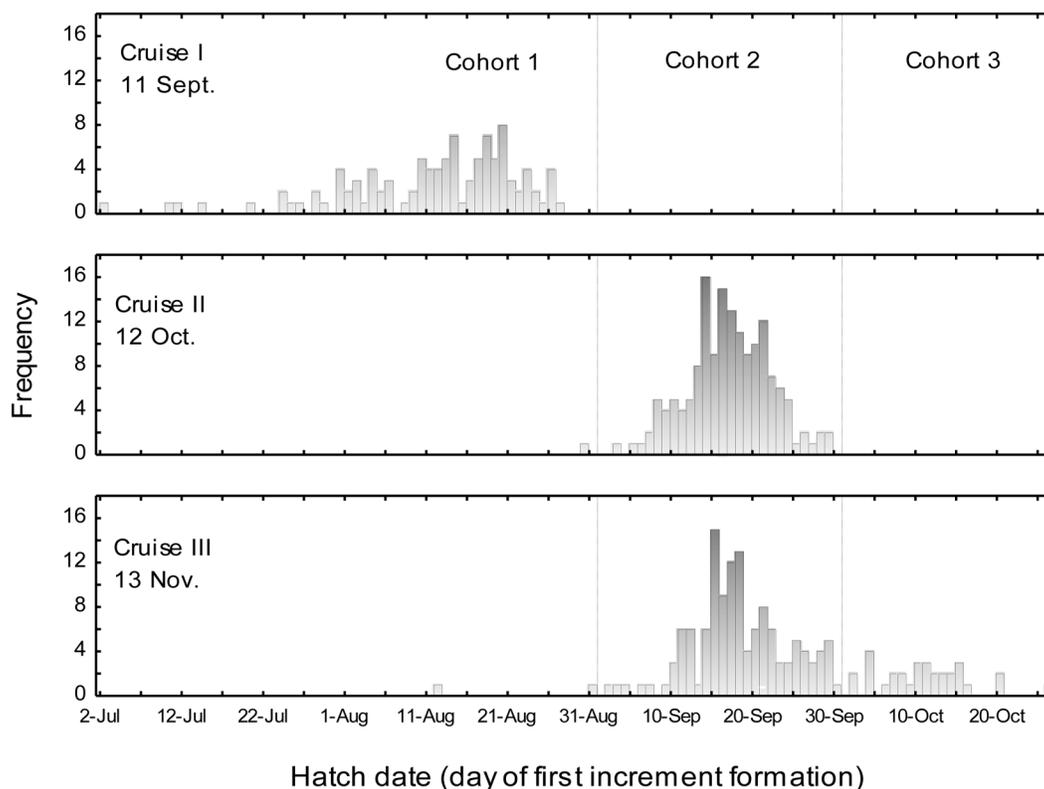
Larvae from the three cruises were categorized into three cohorts based on their hatch dates (see below). Test of morphometric relationships among the three cohorts were carried out in one of two ways. Preferably, the relationship was linearized by transformation (e.g., DM versus SL and DM versus age); otherwise, a common second-order polynomial was fit to the transformed data, and the residuals were used as inputs in GLM (ANOVA) analysis to test for cohort differences (e.g., DM versus OR, and number of light organs versus DM). In the figures, either Lowess smoothing or negative weighted least squares fits were added for visual clarification of trends. For DM versus age and DM versus SL comparisons, the data range was restricted to larvae younger than 80 and 45 days, respectively, to avoid nonlinearity and reduce non-overlapping data ranges between cohorts. GLM (ANCOVA) was employed using log DM as response variable, age or SL as covariate, and cohort as independent variable. Nonsignificant interaction terms were removed, and models were refit using main effects only. Comparisons of increment widths and otolith radii among larvae from different cohorts were carried out separately on 10-day intervals from day 10 until day 40 using one otolith measurement per fish at each analysis. Larvae of cohort 2 obtained from Cruise II or Cruise III were also compared at the same ages. Differences in back-calculated increment widths between the larvae from the three cohorts (and cruises) were tested using GLM (ANOVA). All data were checked for homogeneity of variances (Bartlett's test and F_{\max}), and Tukey honestly significant difference post hoc tests were used following the ANOVA (Zar 1999). All statistical analyses were carried out with Statistica for Windows (StatSoft, Inc. 2012).

Results

Back-calculation of hatch date and cohort assignment

Back-calculation of hatch date indicates that larvae originated in batches, representing at least three separate larval cohorts (Fig. 2). Half of all larvae caught at the last sampling had hatched

Fig. 2. Back-calculated hatch dates of *M. muelleri* larvae from three cruises in Herdlefjorden, western Norway. Three cohorts representing larvae hatched before, during, and after September are separated by vertical lines.



within a window of 10 days, and 75% had hatched within 20 days. Larvae hatched during the five first months of the spawning season do not seem to have contributed to the 1995 year class of *M. muelleri* in the fjord (Fig. 2).

The first cohort hatched in July–August, and larvae caught in the September cruise consisted almost entirely of this cohort. Larvae from this cohort were not caught in subsequent cruises. Larvae hatched in September belonged to cohort 2, and these larvae were caught on both the October and November cruises. The third cohort was only caught on the November cruise. Mean age of the larvae from cohort 2 was 31 days older in November than in October, corresponding to the 31-day time lag between the cruises. Thus, these larvae seem to represent the same cohort, consistent with a daily increment deposition rate. Age, size, and other developmental characteristics had increased markedly in November (Table 2), an indication of a declining larval production in the fjord towards the end of the season. The mean number of larvae caught per 10 min haul was highest for the October cruise (2.34), approximately 50% higher than observed in September (Table 1).

Size distribution, population growth, and morphometric condition

The length distribution of all the sampled larvae was bimodal, with a peak at about 8 mm SL and another at about 13 mm SL. The peak of small larvae consisted mainly of cohort 2 larvae from the October cruise, while the other was mostly cohort 2 larvae from the November cruise (Fig. 3). The daily growth between the modes of the two cruises, representing an estimated mean daily population growth rate, was approximately 0.2 mm·day⁻¹.

The initial mass-at-age differed between the three cohorts, with larvae from cohort 2 being approximately 18% and 39% heavier at age than cohorts 1 and 3, respectively, for ages less than 45 days (Fig. 4a; GLM, $F_{[2,280]} = 25.58$, $p < 0.001$). The average mass increase was similar among cohorts, however, and averaged 6.8%·day⁻¹.

Table 2. Mean values (\pm SD) of age (number of increments), otolith radius (OR), standard length (SL), and dry mass (DM) of *M. muelleri* larvae from the three cruises, categorized in three cohorts.

| Cohort | Cruise | <i>n</i> | Age (days) | OR (μ m) | SL (mm) | DM (mg) |
|--------|--------------|----------|-----------------|------------------|----------------|-----------------|
| 1 | 11 September | 105 | 31.7 \pm 10.9 | 56.7 \pm 34.1 | 9.2 \pm 1.9 | 0.44 \pm 0.45 |
| | 12 October | 1 | 44.0 | 132.5 | 12.3 | 1.06 |
| | 13 November | 2 | 84.5 | 258.9 | 14.6 | 4.07 |
| 2 | 12 October | 157 | 26.2 \pm 5.0 | 53.4 \pm 20.1 | 8.6 \pm 1.2 | 0.31 \pm 0.15 |
| | 13 November | 129 | 56.9 \pm 5.8 | 170.1 \pm 27.5 | 12.4 \pm 0.8 | 1.77 \pm 0.61 |
| 3 | 13 November | 31 | 34.3 \pm 5.6 | 66.6 \pm 19.1 | 9.6 \pm 1.1 | 0.38 \pm 0.18 |

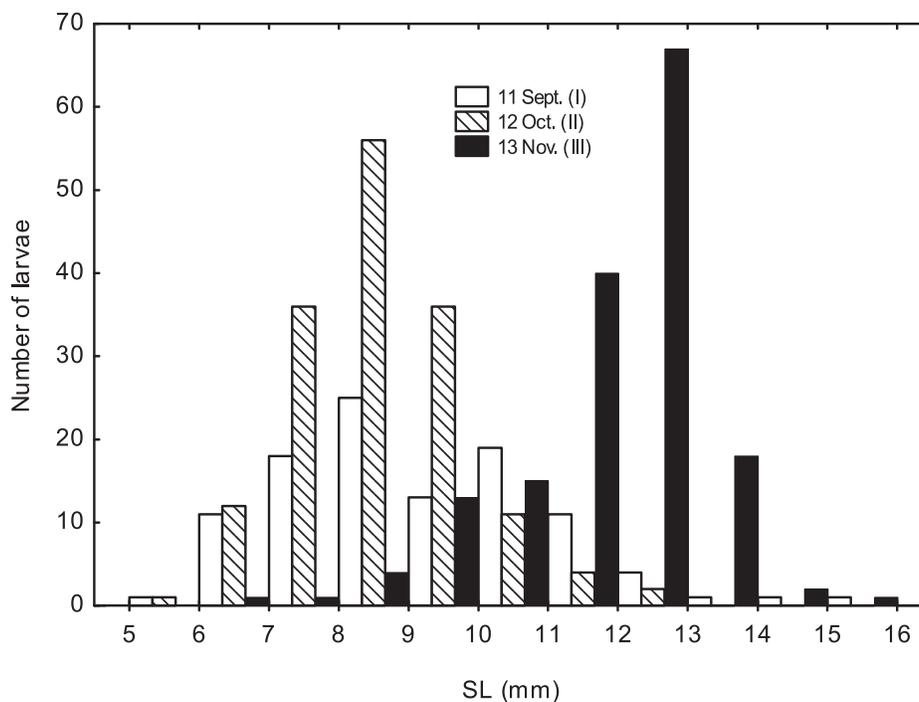
Note: Cohort 1 consists of larvae born in July and August, while cohorts 2 and 3 consist of larvae born in September and October, respectively. “*n*” = number of larvae; SD not calculated for $n \leq 2$.

Larvae from cohort 2 were also on average 6% and 12% heavier at length than larvae from cohorts 1 and 3, respectively (Fig. 4b; GLM, $F_{[2,280]} = 3.61$, $p = 0.028$), implying that cohort 2 larvae also had a better morphometric condition.

Otolith increment growth

The otolith growth was higher among cohort 2 larvae than cohorts 1 and 3 larvae, and the estimated radius-at-age diverged notably after day 10 (Fig. 5a). By day 20, this difference was significant (Table 3; GLM, $p < 0.001$) and remained so until day 40. From the individual increment widths, the faster otolith growth of cohort 2 larvae was also apparent by day 10 (Table 3; GLM, $p < 0.001$), and the daily otolith growth rate (increment width) was higher until day 40. Typically, the increment widths increased for all cohorts, levelling off at around 4 μ m, before they eventually decreased (data not shown). Wider increment widths were also found at a given otolith size for cohort 2 larvae (Fig. 5c), providing added support for the otolith growth interpretation irrespective of imprecisions in increment counts.

Fig. 3. Length distributions (standard length (SL), mm) for *M. muelleri* larvae from three cruises in Herdlefjorden.



No marked differences were apparent between growth patterns of cohort 2 larvae from cruises II or III with increment width-at-age differing generally by less than $0.2 \mu\text{m}$ (GLM, $p > 0.1$ for ages >10), further strengthening the otolith increment analysis and cohort assignment. This also indicated that there had been insignificant levels of size-selective mortality on cohort 2 larvae. No assessment of size-selective mortality was possible for cohorts 1 and 3 owing to lack of repeated samples of larvae.

Development

Light organs started appearing on the ventral side of the fish at around 7 to 8 mm length. The number of light organs increased notably (in pairs) during the size range studied, and 70-day-old larvae had about 70 light organs. Cohort 1 had fewer light organs at a given size (mass) than larvae of the two other cohorts (Fig. 6; GLM, $F_{[2,278]} = 22.9$, $p \ll 0.001$), indicating a slower size-dependent development.

Simulated particle drifts

The two initial simulations of 70 days revealed a spreading of particles originating from 40 and 60 m in Herdlefjorden into adjacent fjord systems (Fig. 7). The extent of particle spreading was more pronounced at 40 m than at 60 m. For the subsequent simulations with particles originating at 40 m depth from two of the sites outside Herdlefjorden receiving particles, Sørfjorden and Byfjorden (Fig. 7), both gave negligible reciprocal import of particles back into Herdlefjorden (Fig. 8). The final simulations of particle releases at depths between 10 and 80 m revealed a higher loss of particles out of Herdlefjorden in the upper part of the water column due to southerly currents (Fig. 8). Among the particles released at 60 and 80 m depth, about 50% were retained in the fjord 70 days later. At 10 and 20 m depth, nearly 80% of the particles were flushed out within 2 weeks after release, and by 70 days after release only 6%–7% of the particles were still inside Herdlefjorden. The particles released at 40 m displayed an intermediate pattern compared with those at shallower and deeper layers, with the proportion of retained particles in the fjord decreasing from about 30% after 30 days to slightly more than 10% after 70 days.

Seasonal otolith growth chronology

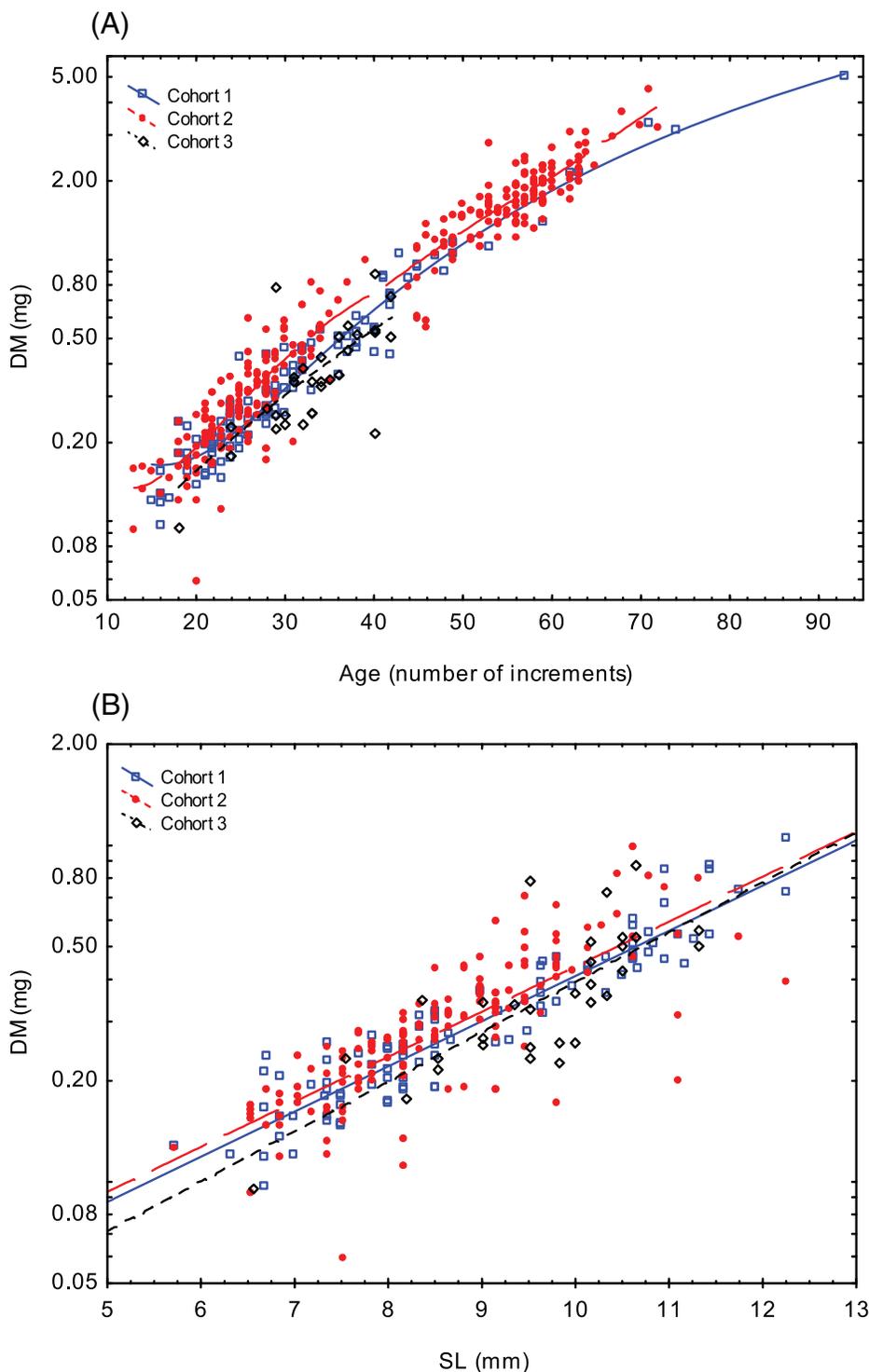
The drift simulations indicate that the larvae were mainly recruited from within Herdlefjorden, and an assumption was made that the *M. muelleri* in Herdlefjorden this year either constituted a source population or a closed population for the construction of a seasonal otolith growth chronology. The standardized seasonal otolith growth revealed a lower than average growth until mid-September when the growth rapidly increased (Fig. 9). This was apparent for both younger and older larvae with a short time offset, indicating better than average feeding conditions during a restricted time period for both younger and older larvae. The otolith growth was above average for about a month, before it declined markedly during the end of October and November.

Discussion

Within-year variability in survival and recruitment

The coupling of larval drift simulations and otolith-based individual larval growth trajectories has successfully been employed in a wide range of species and ecosystems, increasing our understanding of seasonal larval growth and survival dynamics (e.g., Itoh et al. 2011; La Mesa et al. 2015; Mountain et al. 2008). However, this study represents one of the few studies in northeastern Atlantic waters where larval growth trajectories are coupled with high-resolution simulated drift patterns to partition major sources of mortality (but see Gallego et al. 1996; Allain et al. 2003; Hinrichsen et al. 2010). The recruitment of species inhabiting high-latitude North Atlantic ecosystems are expected to be particularly influenced by within-season variations in environmental conditions because of the marked seasonal changes in key physical forcing factors such as ambient temperature and light conditions (Kristiansen et al. 2011). The most striking feature in this study was the negligible contribution of the first cohort as well as all earlier spawning noted by Salvanes and Stockley (1996) to the subsequent survival and, ultimately, recruitment of the 1995 year class of *M. muelleri* in Herdlefjorden. Apart from possible methodological explanations that will be discussed below, at least two main possible explanations emerge in line with Hjort's postulations

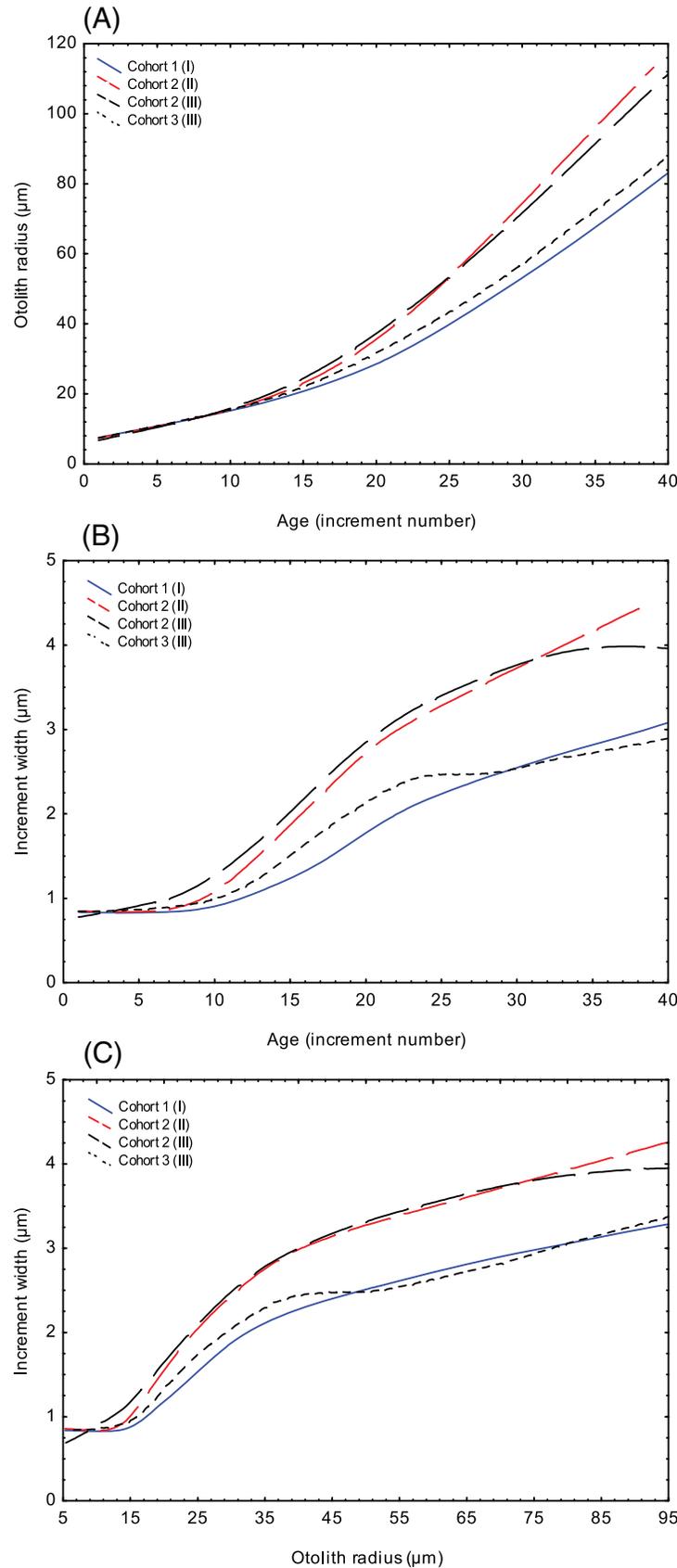
Fig. 4. Dry mass (DM, mg) of *M. muelleri* larvae from three cruises versus (A) age (number of increments). Separate negative exponential weighted least squares fitted lines and symbols are provided for the three cohorts. (B) Standard length (SL, mm) of larvae younger than 45 days. Note logarithmic y axes. Separate exponential fitted regression lines for the three cohorts are given: Cohort 1: $DM = 0.0186 e^{(0.309 \times SL)}$, $n = 95$, $r^2 = 0.874$, $p < 0.001$, SE (estimated) = 0.186; Cohort 2: $DM = 0.0200 e^{(0.308 \times SL)}$, $n = 158$, $r^2 = 0.626$, $p < 0.001$, SE (estimated) = 0.284; Cohort 3: $DM = 0.0130 e^{(0.351 \times SL)}$, $n = 31$, $r^2 = 0.584$, $p < 0.001$, SE (estimated) = 0.309.



from 1914; (a) increased mortality due to poor feeding conditions early in life or (b) increased mortality or advective loss to areas outside the fjord. Later studies have focused on predation as an important potential contributor to early fish stage mortality (Bailey and Houde 1989), either directly or indirectly during peri-

ods of reduced growth and prolonged stage duration. Any inferred growth effects on the larvae could result in altered starvation and predation risk (Skajaa et al. 2003; Fiksen and Jørgensen 2011). In this study, we are not able to separate direct or indirect predation effects from growth and starvation effects and will treat these

Fig. 5. (A) Otolith radius (μm) and (B) increment width (μm) versus age (number of increments) and (C) increment width (μm) versus otolith radius (μm) for three cohorts of *M. muelleri* larvae. Cohort data from individual cruises are shown separately when more than three larvae were available from each cohort and cruise. Lines are based on Lowess smoothing.



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Fig. 6. Number of light organs versus DM (mg) in three cohorts of *M. muelleri* larvae. Smaller larvae with no light organs are excluded from the graph. Separate negative exponential weighted least squares fitted lines and symbols are provided for the three cohorts.

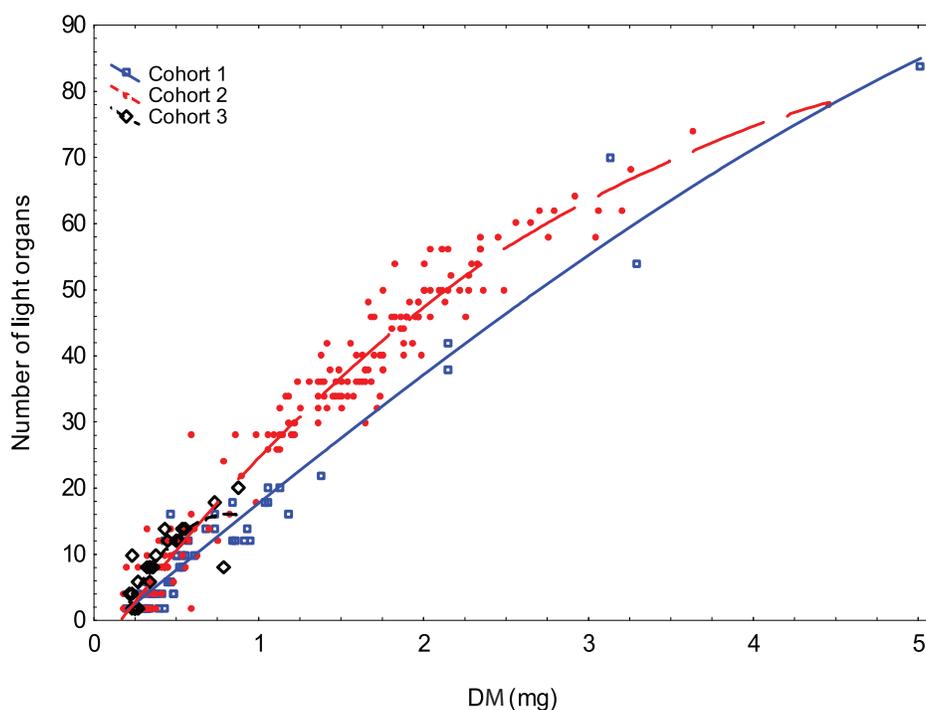


Table 3. Mean otolith radii (μm) and increment widths (μm) for the three cohorts of *M. muelleri* larvae at ages 10 to 40.

| Day | Cohort 1 | | | Cohort 2 | | | Cohort 3 | | |
|------------------------|----------|-----|------|----------|-----|-----|----------|----|------|
| | Mean | n | SD | Mean | n | SD | Mean | n | SD |
| Otolith radius | | | | | | | | | |
| 10 | 15.1 | 108 | 0.8 | 15.4 | 286 | 1.0 | 15.5 | 31 | 0.7 |
| 20 | 28.7c | 96 | 3.1 | 36.2a | 267 | 4.8 | 32.1b | 30 | 3.1 |
| 30 | 52.8b | 50 | 6.8 | 71.9a | 157 | 7.4 | 57.5b | 24 | 6.6 |
| 40 | 85.0b | 24 | 12.6 | 111.0a | 129 | 9.4 | 90.1b | 6 | 11.7 |
| Increment width | | | | | | | | | |
| 10 | 0.9b | 108 | 0.2 | 1.1a | 286 | 0.3 | 1.0ab | 31 | 0.2 |
| 20 | 1.9c | 96 | 0.5 | 2.9a | 267 | 0.6 | 2.3b | 30 | 0.6 |
| 30 | 2.6b | 50 | 0.4 | 3.8a | 157 | 0.6 | 2.7b | 24 | 0.5 |
| 40 | 3.2b | 24 | 0.8 | 4.0a | 129 | 0.5 | 2.9b | 6 | 0.6 |

Note: Number of observations (n) and standard deviations (SD) are indicated. Different letters after mean cohort values at a given age represent significantly different mean values (GLM, $p < 0.05$).

jointly as a “biological” explanation as opposed to the “physical”-based transport explanation for the observed reduction in offspring numbers. Having documented a within-year variability in survival and recruitment, we will then proceed to evaluate which factors could be underlying this variability and finally discuss how the life history of *M. muelleri* is adapted to coping with this variability.

Variations in cohort mortality and recruitment

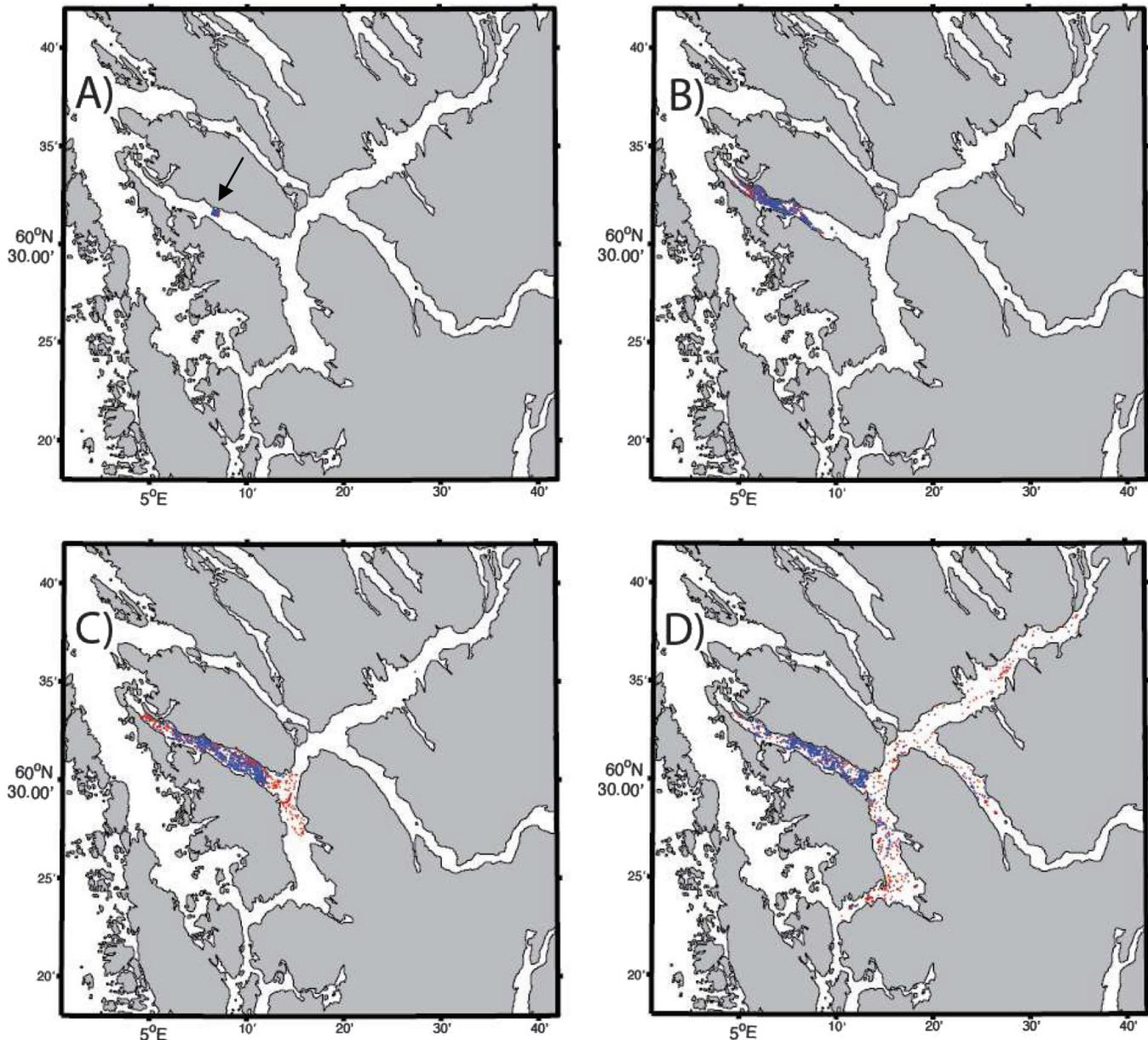
Physical explanations for differential cohort mortality

For the nearby Masfjorden, it has been demonstrated from field and modelling studies that zooplankton advection may have a strong impact on zooplankton and fish recruitment and production (Aksnes et al. 1989; Kaartvedt 1991). Northerly winds dominated from August to September in 1995 (Norwegian Meteorological Institute, www.met.no, weather station Bergen) and have been reported to cause outflow of upper layers in Norwegian fjords, giving poor growth conditions for planktivores. Southerly winds have the oppo-

site effect, giving inflow of plankton-rich water with higher temperature and better growth conditions for planktivores (Giske et al. 1991). Correspondingly, observations along the west coast of Norway indicated that prevailing southerly winds distributed Atlantic herring (*Clupea harengus*) larvae nearshore, whereas after only 2 days of northerly winds ($\leq 14 \text{ m}\cdot\text{s}^{-1}$) larvae were distributed up to 30 km offshore (Johannessen et al. 1995). Similarly, studies on larval fish inside Beaufort Inlet, North Carolina, indicated a rapid and distinct shift in larval populations, which coincided with a 3-day shift to southwesterly winds and full moon spring tides, including distinct temperature shifts during the same period (Hettler et al. 1997). Thus, physical environmental variations due to wind and advection potentially have large impacts on early life growth, distribution, and survival of fish larvae.

The simulations indicate that Herdlefjorden had a much higher outflux from 10 to 40 m than from 60 to 80 m. Based on the number of larvae caught at each depth interval during the three cruises, it can be concluded that a major proportion of the larval population in September and October resided in the part of the water column with most pronounced southward transport (out of the fjord), at least during daytime. Further, the influx of particles at 40 m depth, which constitutes a typical depth range for the main occurrence of *M. muelleri* larvae, seems to have been negligible from neighboring fjords. This was also partly corroborated by the observation that no major cohorts of older larvae with distinct birth dates and growth patterns occurred late in the season, without having been present in Herdlefjorden as younger larvae in previous samples. The population of *M. muelleri* in Herdlefjorden cannot be assumed to be a closed population, however, even though the expected exchange of older individuals residing in deeper layers in adjacent fjords is expected to be low because of reduced water exchange at these depths and limited horizontal fish movement of fish of this size (Kristoffersen and Salvanes 1998; Nøttestad et al. 1999). The main potential for population connectivity would therefore be during the early life stages, and the *M. muelleri* population in Herdlefjorden at least this year poten-

Fig. 7. Particle drift model output after a simulation period corresponding to 0 days (A), 16 days (B), 20 days (C), and 70 days (D) after release. Arrow in panel A indicates point of particle release. Red dots represent particles released at 40 m, and blue dots are particles released at 60 m depth inside Herdlefjorden.



tially constituted a source population of a more widely distributed metapopulation (Suneetha and Nævdal 2001; James et al. 2002).

Biological explanations for differential cohort mortality

We documented a difference in size-at-age but not somatic growth rate between cohorts for larvae younger than 45 days, in contrast with larvae older than 44 days for which growth differences were significant between cohorts 1 and 2. Region-specific larger size-at-age has been linked to increased foraging success in a closely related species, *Maurollicus parvipinnis*, in Chilean waters (Landaeta et al. 2015). In our case, this can indicate that prey availability was similar for the younger larvae, but a possible decrease in food supply may have occurred for the first cohort as they grew older and switched to other larger prey items (Landaeta et al. 2011). Starvation as a direct source of mortality is typically only documented within the first few weeks after the onset of

feeding (Hewitt et al. 1985), and Leggett and DeBlois (1994) concluded that neither Hjort's critical period hypothesis nor Cushing's match-mismatch hypothesis generally were main explanations of recruitment variations in marine fish. However, suboptimal feeding conditions may manifest itself not through reduced growth rate, but rather as reduced survival partly caused by trade-offs between foraging and survival (Fiksen and Jørgensen 2011), as also seen in a model of *M. muelleri* in the nearby and ecologically similar Masfjorden (Rosland and Giske 1997). Still, it seems unreasonable to assume that starvation was the sole direct cause of mortality in cohort 1 since the sampled larvae already had survived the most critical age or stage in terms of starvation risk. The seasonal otolith growth chronology indicated a month of deteriorating growth conditions from mid-August to mid-September, which corresponded to the period of high observed mortality of

Fig. 8. Fraction of particles released at depth inside Herdlefjorden and remaining in the fjord during the five 70-day drift experiments. Only a negligible amount of particles drifting at 40 m from the two sources outside Herdlefjorden (SF, Sørfjorden; BY, Byfjorden) enter the fjord.

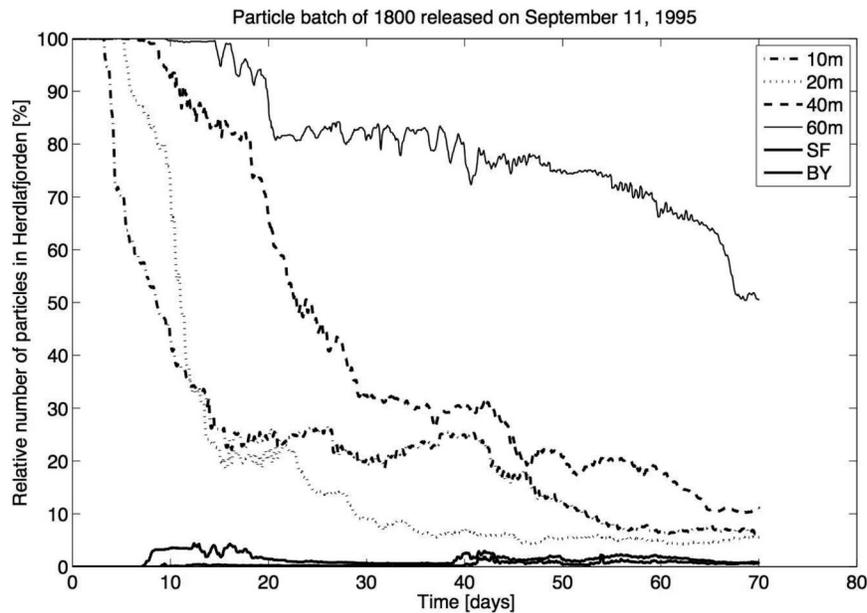
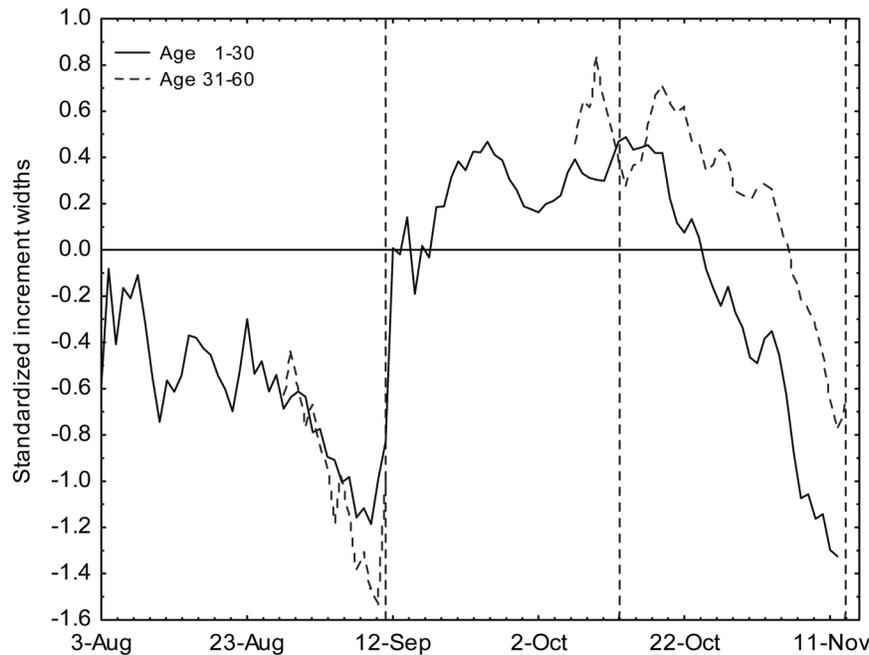


Fig. 9. Mean standardized otolith increment widths of *M. muelleri* larvae over time (age groups 1–30 in solid line and 31–60 in dashed line). Vertical dashed lines indicate date of cruises. Line for older larvae is not shown at dates when it is based on fewer than five cases.



cohort 1. In addition to starvation-induced mortality, the reduced growth rate may have rendered the larvae more susceptible to predation mortality, either due to reduced predator avoidance or prolonged size-dependent mortality rates (Meekan and Fortier 1996; Takasuka et al. 2003).

Predation

Predation is considered to be the major cause of mortality during the egg and yolk sac stages in marine fishes (Rice et al. 1987; Bailey and Houde 1989). Older larvae sampled in this study had survived these early life stages and were probably less susceptible to predation. However, an optimal predator should selectively pursue prey that maximizes the predator's energy cost-benefit

ratio (Takasuka et al. 2007). This suggests that larger larvae may be preferred even though their probability of escape is higher. Preference for larger members of cohorts due to predation is reported in many other studies (Fuiman 1989; Litvak and Leggett 1992; Pepin et al. 1992). Larger fish are also more exposed to visual predators (Giske et al. 1994; Rosland and Giske 1997; Aksnes and Utne 1997). Thus, seasonally variable abundances of other fish predators, such as herring, pollack (*Pollachius pollachius*), and saithe (*Pollachius virens*), may have caused a distinct decline in larval and zooplankton populations, including *M. muelleri* larvae (Husebø et al. 2009). No predator data were available for the actual period, however, and a total extinction in Herdlefjorden of co-

hort 1, and not cohort 2, due to predation seems unlikely, since this would suggest a very sporadic and intense predation period before cohort 2 hatched.

Cohort 1 had fewer light organs at a given length than larvae of the two other cohorts. Counter-illumination by ventrally located photophores is the rule among mesopelagic fishes, and this efficiently disguises their silhouette (Warrant and Lockett 2004). Species in the genus *Maurolicus* have almost the same number of photophores (Parin and Kobylansky 1996), indicating it is an important attribute of the fish. The photogenic apparatus represents about 10% of the biomass in *M. muelleri* (Cavallaro et al. 2004), but the costs of producing light organs are not known. Our results suggest some phenotypic flexibility related to nutritional state, and the slowest-growing cohort apparently had to sacrifice the optimal number. We interpret this reduction in antipredation defenses as a consequence of physiological stress ultimately caused by low feeding, demonstrating the close connection between risks of starvation and predation. In summary, cohort 1 larvae were subject to higher transport loss, poorer feeding conditions, and potentially higher predation risk than cohort 2 and 3 larvae.

Age and hatch date

The mean age difference between larvae from the October and November cruises of cohort 2 was the same as the time lag between these cruises. This is a good indicator of daily increment formation for *M. muelleri* larvae, confirming the assumption of Gjørseter (1981) and Boehlert et al. (1994). However, the age and hatch dates of the larvae may be underestimated, as expected for many fishes. This is generally explained by variable time of hatch check formation due to start of exogenous feeding or methodological problems such as limited resolution of the light microscope (Geffen 1982; Morales-Nin 1992). The otolith increments widths were generally above 1 μm after the first 10 increments, which have been shown to be associated with daily increment deposition in herring, a co-occurring species (Folkvord et al. 2000; Fox et al. 2003). The potential bias is thus not believed to be of major importance in the present study because underestimations will be similar for all larvae and would only apply for a short limited period the first days after hatching.

Vertical distribution

Maurolicus muelleri larvae stayed in the upper 70 m until they reached a specific age or stage, which seemed to be 40–50 days and 10–12 mm SL, respectively. This coincides with observations by Okiyama (1971) in the Japan Sea. He found diel changes of vertical distribution and size composition. The biggest larvae were caught at night, and these larvae were distributed deeper (75 m) than the smaller ones (50 m). Staby et al. (2011) noted diel vertical migration of *M. muelleri* 8–15 mm postlarvae in the nearby Masfjorden from depths around 50 and 80 m to the upper 10 m during September and October, respectively, with relatively longer duration of the near-surface night distributions in October. Although the duration of the near surface distribution (<30 m depth) of ascended larvae was even shorter in August (less than 8 h), larvae in Herdlefjorden with the same distribution would also be substantially affected by the directional advection in the upper 20 m during nighttime.

Impact of hatch date and survival on spawning strategy

High egg densities in early June and high hatching frequency from July to October indicate that spawning took place from at least May to October in Herdlefjorden in 1995. Salvanes and Stockley (1996) reported maturing oocytes already in April in the same year. Other studies in the same area have reported that spawning lasts from March to September (Gjørseter 1981; Rasmussen and Giske 1994; Goodson et al. 1995), with highest spawning activity in May and June (Lopes 1979).

High egg densities in June should have resulted in high larval densities 60–90 days later (in September), but no larvae in this age group were found during the September cruise, and no SSL could be monitored with the echo sounder. This is in accordance with additional observations from Herdlefjorden in 1995 by Salvanes and Stockley (1996). They found no smaller individuals in late June, probably due to extremely low recruitment in 1994 or a net outward transport of individuals from the fjord due to wind-driven currents (Salvanes and Stockley 1996; Kristoffersen and Salvanes 1998). Thus, larvae from cohort 2 had a match in hatching time, which resulted in favorable growth conditions in the fjord during most of the larval period (Cushing 1990). Larvae of cohorts 1 and 3 surviving the critical first feeding period probably mismatched later in the larval stage, while larvae born early in the season (March–August) seemingly never survived the egg or larval stages or, for other reasons (i.e., advection), disappeared from the fjord. Salvanes and Stockley (1996) found that a whole year class was missing in an oceanic population off the west coast of Norway, and Kristoffersen and Salvanes (1998) noted much higher recruitment of the 1995 year class than the 1994 year class in Herdlefjorden. Significant interannual differences in *M. muelleri* larval abundance were also observed off the west coast of Ireland (O'Brien and Fives 1995), and the short life-span (3–5 years) makes the fish susceptible to interannual environmental variation (Armstrong and Prosch 1991).

The early life growth and survival of *M. muelleri* have consequences for its life history and adult behavior. Diet of first feeding *Maurolicus* larvae has elsewhere been shown to be dominated by copepod eggs and nauplii (Landaeta et al. 2011, 2015). In the fjords of western Norway, advective processes may be more important than local population dynamics in determining available zooplankton (mainly copepod) biomass (Aksnes et al. 1989), and in the nearby Masfjorden the biomass has varied both interannually and on shorter time scales by more than a factor of 10 (Giske et al. 1991). Models of the life history of *M. muelleri* have shown that both multiple batch spawning and iteroparous life cycle depend on seasonal (Rosland 1997) and stochastic (Strand et al. 2002) larval survival, which suggests that the life cycle is driven by reproductive bet hedging (Gillespie 1974; Slatkin 1974).

There are very few species of marine pelagic planktivores in the North Atlantic with a single reproductive event (i.e., a strict semelparous life cycle). Exceptions are beach spawning populations of capelin (*Mallotus villosus*) (e.g., Frank and Leggett 1982; Christiansen et al. 2008), for whom adult predation risk during spawning may override the effects of recruitment variation (Fiksen et al. 1995). The occurrence of batch spawning mesopelagic fish species such as *M. muelleri* found in deep sound scattering layers worldwide (Melo and Armstrong 1991; Irigoien et al. 2014) suggests general ecological forcing on the life history extending beyond the realm of western Norwegian fjords. It is a stretch to generalize the findings of Rosland (1997) and Strand et al. (2002) that multiple batch spawning in *M. muelleri* is driven by environmental unpredictability to all pelagic planktivores, but we hypothesize that the global dominance of repeat spawning in planktivores, either by frequent batch spawning in resident populations or by multiple spawning migrations in migratory species, is a signal of variable early life growth and survival opportunities in the pelagic zone.

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