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Egg size and density estimates for three gadoids in Icelandic waters and their implications for the vertical distribution of eggs along a stratified water column

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ABSTRACT

The vertical distribution of fish eggs can have important consequences for recruitment through its influence on dispersal trajectories and thus connectivity between spawning and nursery locations. Egg density and size are key parameters for the modelling of vertical egg distributions, both of which show variation at the species level, as well as between and within individuals (i.e., through ontogeny). We conducted laboratory experiments on the eggs of wild-spawning cod, haddock and saithe from Icelandic waters to estimate these parameters throughout ontogeny. Subsequently, this information was used in a 1-dimensional model to generate vertical distributions for each species along a stratified water column. Saithe eggs were significantly smaller and less dense than cod and haddock eggs. Cod eggs were slightly denser than haddock eggs in the first ontogenetic stage but statistically similar in the later stages. No significant differences were found between the egg diameters of cod and haddock. For each species, both parameters changed significantly through ontogeny. Yet despite these significant results, the 1-d model suggests that neither the interspecific nor ontogenetic differences would have a significant impact on the vertical egg distributions. Only under highly stratified conditions, when buoyancy is minimised due to the freshwater layer, do distributional differences become evident. In such situations, incorporating intraspecific variation in egg density into the model substantially reduced the distributional differences and this is highlighted as an important consideration for the modelling of pelagic vertical egg distributions.

1. Introduction

Owing to variation in the direction and amplitude of currents throughout the water column, plankton separated by small vertical distances can take vastly different drift trajectories. For pelagic fish eggs, this can lead to variation in the quality of habitat during the first feeding "critical period" (Hjort, 1914) and in the transport success to suitable nursery grounds (Parada et al., 2003; Huret et al., 2007; Kuroda et al., 2014; Santos et al., 2018). Knowledge of the vertical distributions of eggs and how they change along environmental gradients is therefore an important precursor to understanding the viability of early life-stages and subsequently populations. This entails consideration of how an egg's physical properties (or traits) interact with the prevailing abiotic conditions (Sundby, 1983, 1991). Biophysical models—which couple individual-based models (IBMs) to hydrodynamic models—are a widely used method to examine the dispersal of early life-stages (Fiksen et al., 2007; Staaterman and Paris, 2014). Flow fields from the hydrodynamic model advect individuals through heterogeneous, dynamic environments, whilst IBMs provide a platform to simulate how individuals respond to the prevailing environment. The key strength of IBMs is that they simulate populations of unique individuals, and through the interactions of these individuals with each other and the environment, populations properties emerge (Huston et al., 1988; Grimm and Railsback, 2005). For pelagic fish eggs, variation in traits that affect vertical positioning can ultimately lead to variation in key emergent properties including growth and mortality rates, and the spatiotemporal location at hatching (e.g., Hinrichsen et al., 2016).

Egg density (or specific gravity) and, to a lesser degree, size are important physical properties for the modelling of vertical egg distributions (Sundby, 1983; Ådlandsvik, 2000; Petitgas et al., 2006) and individual dispersal trajectories (Thygesen and Ådlandsvik, 2007). Naturally, these properties show great variation between species (e.g. Pauly and Pullin, 1988; Petereit et al., 2014; Sundby and Kristiansen,

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2015). Considerable variation can also exist between stocks of the same species (e.g. Thorsen et al., 1996) with important consequences for the survival of progeny. For example, the large size and low density of Baltic cod eggs ensure they remain above the stressful anoxic layer (Nissling and Westin, 1991; Vallin and Nissling, 2000). This is an adaptation to avoid low oxygen environments, one also seen in flatfish species (Nissling et al., 2017) and the spawning strategies of Cape hake females (Sundby et al., 2001). In contrast, the closely related Norwegian coastal cod produce smaller eggs of greater density that generate a pelagic rather than bathypelagic vertical distribution (Jung et al., 2012) which can lead to retention of offspring in local fjords, and thus a degree of segregation between spawning sub-populations (Ciannelli et al., 2010; Myksvoll et al., 2011, 2014). Furthermore, several studies have highlighted how ontogenetic variation in egg density (e.g., Jung et al., 2012) can have pronounced effects on vertical distributions (Ådlandsvik et al., 2001; Ospina-Álvarez et al., 2012; Petereit et al., 2014), possibly controlling the development and maintenance of mesopelagic egg distributions (Sundby and Kristiansen, 2015).

In Icelandic waters, the main spawning grounds for Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*) are in the southwest. Despite spatial and temporal overlap in spawning activity, there are distinct differences between the three species. The most notable of these differences is the sequential nature of spawning activity in time, with saithe spawning from late January to mid-March (Jónsson and Pálsson, 2013), cod from mid-March to mid-May (Marteinsdóttir and Björnsson, 1999), and haddock from early April to late May (Jónsson and Pálsson, 2013). From a spatial perspective, a sequential pattern is also seen with the distance-to-shore from the main spawning grounds increasing from cod and haddock (Marteinsdottir et al., 2000) to saithe (Armannsson et al., 2007). These interspecific differences in spawning activity will generate environmental exposures for eggs/larvae that vary between the three species. In particular, distance-to-shore may have a large influence on early life stage survival due to the influence of freshwater runoff which is hypothesized to be tightly linked to recruitment success in two ways. Firstly, the presence of coastal water stabilises the water column, providing conditions to initiate the early phytoplankton bloom in coastal waters (Thórdardóttir, 1986) which has been correlated with key prey items for gadoid larvae (e.g., Gislason et al., 1994). Secondly, through its influence on the Icelandic Coastal Current which is primarily driven by entrained runoff (Logemann et al., 2013) and thought to play a crucial role in the transportation of gadoid larvae to the preferred nursery habitats in the north (Olafsson, 1985; Begg and Marteinsdottir, 2002; Brickman et al., 2007; Jonasson et al., 2009).

In this study, we conducted laboratory experiments to measure the density and diameter of wild-spawning cod, haddock and saithe eggs. Subsequently, we used a one-dimensional advection-diffusion model to examine how these properties affect the vertical positioning of eggs in environmental gradients that encompass the range of realistic abiotic conditions for each species. The overall objectives of the laboratory experiments are to: (1) assess whether there are differences in the physical properties of eggs between the three species, and (2) assess whether these physical properties change through ontogeny for each species. Subsequently, the vertical distribution model is used to evaluate what impacts these differences and changes have on the vertical distribution of eggs along a stratified water column, and to examine how these impacts vary when accounting for intraspecific natural variation in the physical egg properties.

2. Materials and methods

2.1. Sampling procedure

Samples were collected aboard commercial fishing vessels at known spawning grounds in southwest Iceland (Fig. 1 and Table 1). Haddock and saithe were sampled in 2012 and combined with archived cod data from 2010 (Guðmundsdóttir, 2013). The procedure for collecting, fertilising and storing eggs followed those applied in previous studies in Icelandic waters (Marteinsdottir and Begg, 2002; Guðmundsdóttir, 2013). Eggs were stripped from freely running females and stored in separate 1 l plastic beakers, hereafter referred to as batches. Each batch was fertilised in vitro by applying fresh milt to the eggs, stirring, and adding fresh seawater. Although effort was made to cross-fertilise individual males and females, this was not always possible due to a scarcity of running males. In such cases, prompt fertilisation was prioritised and the milt from an individual male was used to fertilise up to three females (from the same haul). After fertilisation, organic debris was removed to avoid contamination, and to ensure batches were adequately oxygenated, water changes were conducted at 30 min post-fertilisation and subsequently at regular intervals never exceeding 3 h. The temperature of each batch was continuously monitored to ensure congruence with the ambient seawater (6–7 °C) by applying/removing ice surrounding each batch. All sampled fish were tagged and stored until morphological measurements could be taken. Total length (L) and total weight (W) were measured to the nearest centimetre and gram respectively. Weight measurements could not be taken for haddock.

Upon landing, samples were immediately transferred to the mariculture laboratory at Staður, Grindavík. Each batch was transferred to a 25-l hatching silo with running water pumped from the neighbouring sea. If hatching silos were not available, batches were stored in a temperature-regulated room using 6-l plastic cylinders filled with fresh seawater and aeration stones. In these cases, water changes were conducted daily until 3 days post-fertilisation (DPF), and at every measurement day thereafter. Temperature was kept at 7 ± 0.2 °C which, based on oceanographic monitoring at stations SB1 and SB2 (www.hafro.is/Sjora), adequately reflected the surface temperatures the eggs would likely experience in the wild (see Huret et al., 2016).

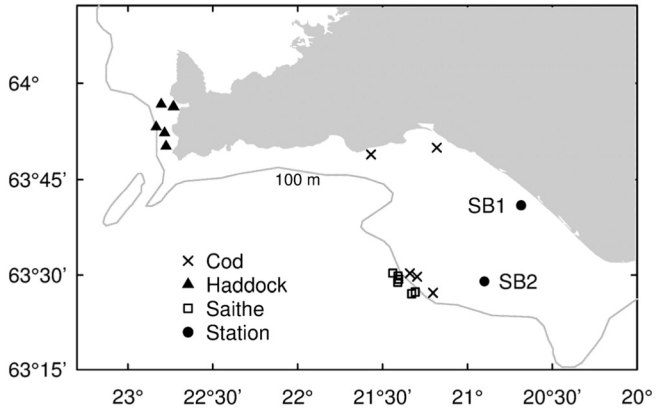

Fig. 1. Sampling locations for each species. Environmental profiles for modelling were extracted from a 3-dimensional hydrodynamic model at stations SB1 and SB2.

Table 1
Table showing the sampling dates, gear types and the number of spawning females sampled (n) whose eggs survived the duration of the experiments. The overall mean, standard deviation and range of female lengths (L) are shown for each species at each sampling date.

Species	Gear type	Date	n	$\bar{L}$ ± SD (cm)	Range (cm)
Cod	Gillnet	07/04/2010	4	97 ± 3.2	93–100
		13/04/2010	6	83 ± 6.1	74–90
Haddock	Danish seine	30/04/2012	9	50 ± 4.2	43–56
Saithe	Gillnet	10/04/2012	6	88.5 ± 5.1	81–94
		13/04/2012	8	97 ± 11.3	87–115

2.2. Egg density and diameter measurements

Egg density (ρ_{egg}) was measured using density gradient columns, following the protocol set out by Coombs (1981). Low and high saline solutions, corresponding to salinities of approximately 24.3‰ and 47.3‰ respectively, were prepared using de-ionised water and NaCl, and subsequently mixed to create a linear density gradient. The end-points were determined in a pilot study using eggs from captive cod and were chosen to encompass the range of neutral buoyancies displayed by the eggs and two sets of calibration beads (Martin Instrument, Inc). For beads not calibrated at 7 °C, a temperature adjustment was provided by Martin Instrument to account for the discrepancy. Density gradients were calibrated at the beginning of each measurement day and whenever new columns were created. The latter instance occurred every second measurement day unless calibrations suggested the density gradient was not linear ($r < 0.99$), the columns were physically disturbed, or eggs/larvae were not captured by the ascending basket.

Measurement days were synchronised between haddock and saithe but unsynchronised with cod. This was due to the sampling regime where opportunities to sample were dependent on the schedule of commercial fishing vessels. On each measurement day, random samples of eggs from each batch were gently placed into the top of the column. Eggs were given a minimum of 30 min (determined in the pilot study) to reach neutral buoyancy, but if visual inspection deemed them to still be adjusting their depth, they were re-checked at 15-min intervals until neutral buoyancy was achieved. By and large, 30 min was adequate for saithe, whilst 45–60 min was appropriate for haddock eggs. Measurements ceased when 50% of the surviving eggs in a batch had hatched. This was estimated by assessing random samples from the hatching silos under the microscope.

A subsample of the archived cod data was measured at 6 °C and 8 °C, therefore we employed a temperature correction using the UNESCO equation of state for seawater (Millero and Poisson, 1981) to standardise all density measurements at 7 °C. Subsequently, the same equation was used to calculate each egg's corresponding salinity of neutral buoyancy (S_{egg}) for use in the advection diffusion model.

Random samples of ten eggs per batch per measurement day were used to estimate egg diameters (D) and assess their quality and development. This was carried out independently of the density experiments. To obtain high resolution photographs, we deployed a Pixxelink PL-A662 camera attached to a Leica MZ95 stereomicroscope. Camera settings were individually calibrated to the eggs to obtain the maximal picture quality at a resolution of 1280 × 1024 pixels. For each batch at each measurement day, the camera was calibrated with a microscale allowing measurements of egg diameter to the nearest micrometre using the free domain image processing and analysing software ImageJ 1.45 (Schneider et al., 2012). The samples were staged according to the classification scheme developed by Thompson and Riley (1981) with the minor adjustment that stages IA and IB were pooled together (IAB). For each DPF, the data was pooled over batches and the dominant ontogenetic stage identified. This resulted in a unique ontogenetic stage for each measurement day per species (Table 2).

2.3. Statistical analyses

Mixed effects models were used to model egg density as a response to egg stage *ES* (ordered factor, see Table 2), female length *L* (covariate), batch *B* (factor), species *Sp* (factor), and mean diameter per batch $\overline{D}_B$ (covariate). Egg diameter was modelled as a response to the same explanatory variables excluding $\overline{D}_B$. Because the statistical procedures were identical for both responses, we solely focus on ρ_{egg} here. Batches were unique to each species, therefore a mixed effects modelling approach was used with *B* treated as a random effect. This allowed for correlations between individuals of the same species (see Zuur et al., 2009) and facilitated general conclusions about females within species rather than conclusions about the specific females sampled. A suite of linear mixed-effects models were fit using the nlme R package (Pinheiro et al., 2019). Species-specific models were fit with *ES*, *L* and $\overline{D}_B$ as additive explanatory variables (i.e., $ES + L + \overline{D}_B$). The species factor was introduced to test for significant interactions between species and each explanatory variable (i.e., $Sp{\bullet}ES + Sp{\bullet}L + Sp{\bullet}\overline{D}_B$). Differences between the inshore and offshore sampling sites (Fig. 1) for cod were tested by expanding the *Sp* factor to four levels (cod_{In}, cod_{Off}, haddock and saithe). Intraclass correlation coefficients (ICCs) were calculated to understand the proportion of random-effect variance explained by *B*; high values indicated strong correlations between individual eggs from the same batch, and vice versa (Zuur et al., 2009; Nakagawa and Schielzeth, 2010).

Prior to fitting the models, the protocol for data exploration set out by Zuur et al. (2010) was followed to visualise relationships between variables, identify outliers, heteroscedasticity and non-normality. Subsequently, the stepwise model selection procedure recommended by Zuur et al. (2009) was followed to obtain the optimal model structure and test the significance of explanatory variables/interactions. This involved using the Akaike- and Bayesian Information Criteria (AIC and BIC) and the log-likelihood ratio to test the goodness of fit between models. Starting with the full model, the optimal random structure was identified by comparing models fit by restricted maximum likelihood estimation (REML). This step included testing whether a mixed effects model performed better than an ordinary linear regression (fit using the "gls" function). The optimal fixed structure was then identified by comparing models fit by Maximum Likelihood. The final optimal model was presented using REML fits. At each step, normalised residuals were plotted against fitted values and all explanatory variables to check whether model assumptions were violated at each stage of the process. Heteroscedasticity was present for both response variables, so variance structures were employed to achieve homoscedasticity (using the "varIdent" function), these allowed the spread of residuals to vary between levels of a grouping factor (see Zuur et al., 2009). This method was more effective at stabilising the variances than transformations. The optimal structure for ρ_{egg} and *D* allowed for different variances at each level of the $Sp \cdot ES$ interaction. Post hoc analyses were carried out using the emmeans R package (Lenth, 2019). Contrasts between species at each specific *ES* were generated to examine interspecific differences. Contrasts were also generated for each successive *ES* comparison (i.e., IAB-II, II-III etc) to examine changes through ontogeny within each species.

Table 2
The dominant ontogenetic stage for each measurement day (DPF).

	Ontogenetic stage				
	IAB	II	III	IV	V
Cod	2	5	7	10	13
Haddock	1	3	6	9	12
Saithe	1	3	6	–	9

2.4. Vertical egg distribution model

The MATLAB VertEgg toolbox (Ådlandsvik, 2000) was used to model the vertical distribution of gadoid eggs. The toolbox contains analytical and numerical solutions to Sundby's (1983) one-dimensional vertical distribution model. The model is based on a transport equation, with the vertical flux determined by the egg's terminal velocity—the velocity an egg ascends/descends when the buoyant forces balance the frictional drag—and diffusion modelled by Fick's law using the vertical eddy diffusivity coefficient. The toolbox was converted to the R programming language and additional functionality added where required. The theory behind the model and its solutions is detailed in Sundby (1983), Westgård (1989), and Ådlandsvik, (2000).

2.5. Environmental gradients

Vertical profiles of the water column were extracted from the three-dimensional hydrodynamic model CODE (Cartesian coordinates Ocean model with three-Dimensional adaptive mesh refinement and primitive Equations [Logemann et al., 2013]). In Icelandic waters, CODE has a maximum horizontal and vertical resolution of 1 km and 2.5 m respectively. Freshwater runoff from 46 Icelandic watersheds, estimated by the hydrological model WaSiM (Schulla and Jasper, 2007), are assimilated together with 16,802 CTD profiles to provide a detailed simulation of the regional hydrography of Icelandic waters (Logemann et al., 2013). The model is fully documented in Logemann et al. (2012) and results from recent simulations covering the period between 1992 and 2006 are detailed in Logemann et al. (2013). Output from CODE is stored at 3 hourly intervals and at irregular depth intervals (due to the adaptive mesh refinement, see Logemann et al., 2012), therefore all variables of interest were linearly interpolated along depth to obtain values at 2.5 m intervals. These included temperature T (°C), potential temperature θ (°C), salinity S (psu), in situ density ρ (kg m^{-3}), potential density ρ_θ (kg m^{-3}), and vertical eddy diffusivity K (m^2 s^{-1}).

Vertical profiles were extracted at two locations (Fig. 1) at 00:00 UTC each day in 2006 for a period encompassing the spawning activities of all three species plus an additional 12 days (hatching time for haddock, Table 2) to account for unhatched eggs when spawning has ceased. These locations are part of the Marine Research Institute's annual monitoring programme for hydrography and biological productivity. Situated approximately 5 km offshore, SB1 is 40 m deep and in the path of the freshwater-driven Icelandic Coastal Current. Station SB2 is approximately 25 km offshore, 80 m deep and in the path of incoming Atlantic water. The spawning season of 2006 provided a suitable array of vertical density gradients (from well-mixed to highly stratified) to examine how stratification affects the vertical distribution of eggs.

To estimate the stratification for each vertical profile, we calculated an approximation of the Brunt-Väisälä frequency N^2 (s^{-1}) over the upper 40 m of the water column (see Li et al., 2015; Fig. S1). An exceptionally strong correlation (r_s = 0.98) between N^2 calculated over 40 m and 80 m at station SB2 suggests that constraining N^2 to the upper 40 m adequately captures the water column's stratification.

2.6. Model simulations

For each daily vertical profile, we found the steady-state solution (φ) to the advection diffusion equation using the "sstate" function from the VertEgg toolbox (equation 2.45 in Ådlandsvik, 2000). The "eggvelst" function was used to calculate the terminal velocities. Due to the variable temperature gradients, these were calculated using the S_{egg} values derived from the empirical dataset (see Section 2.2). To account for natural variation in the physical egg properties, we carried out Monte Carlo Markov Chain (MCMC) simulations. This involved generating 75,000 random samples of S_{egg} and/or D, calculating φ for each sample, summing all distributions by depth interval, and normalising the aggregated distribution to obtain the relative abundance of eggs per grid cell, φ^*. Random samples were generated by assuming Gaussian distributions characterised by the species-specific means and standard deviations from the laboratory measurements (Fig. 3), a reasonable assumption based on evidence from the observed dataset. Random samples were generated for S_{egg} and D independently (i.e., one variable was randomly generated whilst the other was fixed at its mean). To test the sensitivity of this assumption, simulations were also carried out by assuming a linear relationship between both variables based on a linear model. The MCMC simulations were carried out using summary statistics for each species pooled over stage (Fig. 3b), and for each individual stage within species to assess variation through ontogeny (Fig. 3a). Convergence between the normalised distribution and key descriptors of the vertical egg distribution (see below) at i and i-1 was used to gauge the number of simulations required to adequately account for natural variation in S_{egg} and D.

2.7. Model analyses

The output comprised the number of eggs per grid cell (grid cell thickness = 2.5 m) with a total of 100 eggs in the water column. Subsequently, we calculated the median depth $\tilde{z}$ (m) of the distribution and several percentiles to describe its spread. The median was preferred as a measure of central tendency as the distribution of eggs was often highly skewed. To compare distributions, the root-mean-square deviation RMSD (eggs m^{-3}) was calculated. This showed how two distributions differed in number of eggs per grid cell. To quantify interspecific differences in vertical egg distributions, the RMSD between φ_C^* and φ_H^* ($RMSD_{C^*H^*}$), φ_C^* and φ_S^* ($RMSD_{C^*S^*}$), and φ_H^* and φ_S^* ($RMSD_{H^*S^*}$) was computed for each daily profile. To quantify ontogenetic differences in vertical egg distributions, the RMSD was computed between the species-specific distributions (φ_C^*, φ_H^* and φ_S^*) and the stage-specific distributions for the corresponding species (e.g., for cod, $RMSD_{C^*C_{IAB}^*} = \varphi_C^*$ *vs* $\varphi_{C_{IAB}}^*$). For both the interspecific and ontogenetic comparisons, equivalent RMSD's were calculated for the analytical solutions without the MCMC procedure, these are denoted in a similar manner but without the asterisk superscript (e.g., $RMSD_{CC_{IAB}} = \varphi_C$ *vs* $\varphi_{C_{IAB}}$). To assess how the magnitude of interspecific or ontogenetic differences in vertical egg distribution changed when accounting for the natural variation in physical egg properties, RMSD's were computed between the egg distributions generated with and without the MCMC procedure (e.g., $RMSD_{C^*C} = \varphi_C^*$ *vs* φ_C).

3. Results

3.1. Empirical analyses

3.1.1. Egg density

The *Sp*: *ES* interaction was highly significant (L = 515, df = 1, p < .001). Saithe eggs were significantly less dense than haddock and cod eggs at each stage (Fig. 3a; p < .001). Cod eggs were significantly denser than haddock eggs at stage IAB (p < .01); however, both species had statistically similar densities from stages II–V (Fig. 3a; p > .05). Within species, cod egg density had a significant decrease between stages II and III (p < .001) which was followed by a significant increase between stages III and IV (p < .001), a trend seen at both sampling sites (Table 3). Conversely for haddock, there was a significant increase in egg density at stage III (Fig. 3a; p < .001) which was followed by a significant decline in density at stage IV (p < .001). Saithe egg density decreased prior to hatching (stage V, Fig. 3a) and this stage was significantly less dense than all other stages (p < .001). Stage IAB was also significantly less dense than stages II (p < .05); however, this was likely due to the model underestimating egg density at stage IAB for saithe as both stages had similar means and spreads (Fig. 3a; Table 3). For each species, all other between-stage comparisons were not significant (p > .05).

The cod eggs sampled offshore had a higher density than the coastal cod at each stage (Table 3). However, none of these differences were statistically significant (p > .05) so it was concluded that cod had similar densities at each sampling site. The *Sp*: $\overline{D}_B$ interaction was significant (L = 148, df = 1, p < .001) suggesting that egg diameter is an important predictor of egg density. For each species comparison, the density-diameter gradients were significantly different (p < .001). A negative slope was found for cod and positive slopes for haddock and saithe (Fig. 4). Neither the *Sp*: L interaction nor the length main effect were significant (L = 5, df = 1, p = .077; L = 0.7, df = 1, p = .4) highlighting that no relationship was found between egg density and L for any species.

Incorporating batch as a random intercept substantially improved the model (L = 2027, df = 1, p < .001). The optimal random structure

Table 3
Egg density (g cm^{-3}; at 7 °C) and diameter (mm) summary statistics for each species, including for the cod sampled inshore (Cod_{In}) and offshore (Cod_{Off}). The mean, standard error (SE [$\times 10^4$]), number of individual egg measurements (n), and intraclass correlation coefficients derived from the optimal statistical model are presented. ICCs were not computed for the inshore/offshore cod components because no significant differences in either egg density or diameter were found between these components.

		Density				Diameter			
Species	ES	Mean	SE	n	ICC	Mean	SE	n	ICC
Cod	IAB	1.0260	0.522	316	0.51	1.4112	49.16	100	0.82
	II	1.0259	0.426	340	0.53	1.4235	48.04	100	0.82
	III	1.0249	0.361	337	0.51	1.4196	46.64	100	0.83
	IV	1.0257	0.557	474	0.25	1.4255	54.89	100	0.72
	V	1.0258	0.801	238	0.32	1.4191	58.34	80	0.86
Cod_{In}	IAB	1.0256	0.178	133	–	1.4001	88.43	40	–
	II	1.0258	0.413	97	–	1.4052	84.97	40	–
	III	1.0249	0.607	114	–	1.4079	90.17	40	–
	IV	1.0253	1.501	131	–	1.4121	106.0	40	–
	V	1.0255	0.876	62	–	1.3813	143.9	20	–
Cod_{Off}	IAB	1.0264	0.798	183	–	1.4185	55.52	60	–
	II	1.0260	0.568	243	–	1.4356	51.42	60	–
	III	1.0249	0.449	223	–	1.4273	47.38	60	–
	IV	1.0259	0.491	343	–	1.4345	56.02	60	–
	V	1.0259	1.030	176	–	1.4317	52.71	60	–
Haddock	IAB	1.0248	0.559	421	0.26	1.4193	52.99	89	0.52
	II	1.0248	0.428	320	0.66	1.4232	52.31	90	0.62
	III	1.0256	0.497	442	0.65	1.4428	62.41	89	0.61
	IV	1.0251	0.844	258	0.16	1.4425	45.38	88	0.77
	V	1.0253	0.621	282	0.19	1.4326	47.33	87	0.78
Saithe	IAB	1.0231	0.344	683	0.45	1.2153	39.17	133	0.67
	II	1.0231	0.277	840	0.70	1.2000	44.96	137	0.58
	III	1.0231	0.352	601	0.46	1.2237	31.57	140	0.74
	V	1.0217	1.070	115	0.22	1.1703	89.39	20	0.65

included a random intercept (variance = 4.29×10^{-7} g cm^{-3}), incorporating a random slope per species did not improve the model ($L = 1.14$, $df = 1$, $p = .95$). The ICCs highlight that between-batch variation was greater than within-batch variation at stages IAB–III for cod, stages II–III for haddock, and stage II for saithe (Table 3). Notably, correlations between individual egg densities were lowest later in ontogeny for each species (Table 3).

3.1.2. Egg diameter

The mean egg diameter per stage for saithe was consistently lower than cod and haddock (Fig. 3a). This was highlighted by a highly significant *Sp*: *ES* interaction ($L = 80$, $df = 1$, $p < .001$). Saithe eggs were significantly smaller than haddock and cod eggs at each stage ($p < .001$) whilst no significant differences ($p > .05$) were found between haddock and cod eggs. Within cod, the only significant change in diameter through ontogeny was an increase between stages IAB and II ($p < .001$). For haddock, diameter increased significantly between stages II and III ($p < .001$) and to a less extent between stages IV and V ($p < .05$; Table 3). In contrast, the diameter of saithe eggs fluctuated significantly between each ontogenetic stage (Fig. 3a; $p < .005$ for IAB-II, $p < .001$ for the other contrasts).

The cod sampled at the coastal site had consistently smaller diameters than the cod sampled further offshore (Table 3). However, none of the stage-specific differences between sampling sites were significant ($p > .05$). The *Sp*: *L* was significant ($L = 6$, $df = 1$, $p = .041$) but the haddock: length effect was the only one that differed from zero ($p = .027$) with smaller females producing larger eggs. None of the interspecific contrasts were significant ($p > .05$) suggesting that the diameter-length trends were similar between species. Although removing the cod female which had the smallest diameter across stages (Fig. 2) led to a significant contrast in the diameter-length trend between cod and haddock with smaller cod producing smaller eggs.

Incorporating batch as a random intercept substantially improved the model ($L = 1466$, $df = 1, p < .001$). The optimal random structure included a random intercept (variance = 0.0017 mm), including a random slope per species did not improve the model ($L = 1.046$, $df = 1$, $p = .96$). The ICCs indicate substantial correlations within batches for each level of the *Sp*: *ES* interaction (Table 3) with the between-batch variation always exceeding the within-batch variation.

3.2. Vertical distribution model

3.2.1. Terminal velocities

Pooling the data over *ES*, saithe had the highest terminal velocity (Fig. 5). Taken alone, the smaller diameter of saithe eggs would suggest a lower terminal velocity. However, this effect was overridden by their lower densities (Fig. 3b), which always ensured higher ascent speeds. The greater importance of density in determining terminal velocities was exemplified by comparing the distributions of terminal velocities between the two parameters. For all species, the range of diameters led to a much smaller range of terminal velocities than the range of densities (Fig. 5).

3.2.2. Interspecific differences in vertical egg distribution

At each station, the interspecific differences in egg distributions were maximised under stratified conditions (Table 4a) with minimal vertical mixing (Fig. 6). However, it was only under strongly stratified conditions at SB1 that distinctive interspecific differences were visible (Fig. 6, HS). These differences were driven by the distribution of saithe eggs (i.e., cod and haddock had similar distributions), demonstrated by the substantially higher RMSD values for the saithe comparisons (Table 4a). In low mixing scenarios, the egg's buoyancy (the density difference between the egg and the ambient water [$\Delta\rho = \rho_{egg} - \rho$]) became the predominant factor determining the vertical egg distribution. At SB1, the surface density (1.023 g cm^{-3}) is sufficiently low to drive down the cod (84% of eggs between 0 m and 10 m with 50% at 6 m) and haddock (92% of eggs between 0 m and 10 m with 50% at 4.5 m) eggs but not the saithe eggs which agglomerated in the surface grid cell (87% of eggs with 50% at 1.25 m) due to their lower density (Fig. 3). At SB2, surface density under stratified conditions was 1.027 g cm^{-3} which is substantially greater than all egg densities (Fig. 3) leading to 71%, 81% and 95% of eggs residing in the surface grid cell for cod, haddock and saithe respectively (Fig. 6), hence the lower interspecific differences (Table 4a).

At SB2, all interspecific comparisons were substantially less than the LS–HS comparisons demonstrating that the environment (particularly *K*) was the most important factor in determining the vertical egg distributions at this location (Table 4b). At SB1, changing species from either cod or haddock to saithe had a larger impact on the vertical egg distribution than changing the environment, but this is only under HS conditions (Table 4b). The HS-LS RSMD values were all greater than interspecific comparisons in the well-mixed scenarios (LS, Table 4b), which emphasised the homogenising effect of turbulence in these scenarios.

At SB1, interspecific differences increased linearly, and then decreased slightly before plateauing (Fig. 7). The HS environment presented in Fig. 6 is located at or close to the peaks for all the comparisons in Fig. 7. As stratification increased beyond this point, a higher proportion of saithe eggs are driven down from the surface grid cell due to the lower ambient density, thus leading to the dip in RMSD values for the saithe comparisons. At SB2, although a positive linear relationship was seen between all interspecific differences and stratification, the RMSD values were negligible when compared to SB1 (Fig. 7).

3.2.3. Ontogenetic differences in vertical egg distribution

Whilst the *Sp*: *ES* interaction was a significant predictor of egg density, incorporating the ontogenetic changes into the vertical distribution model revealed little impact of ontogeny on the vertical distribution of eggs (Fig. 8). For cod, the decrease in density at stage III

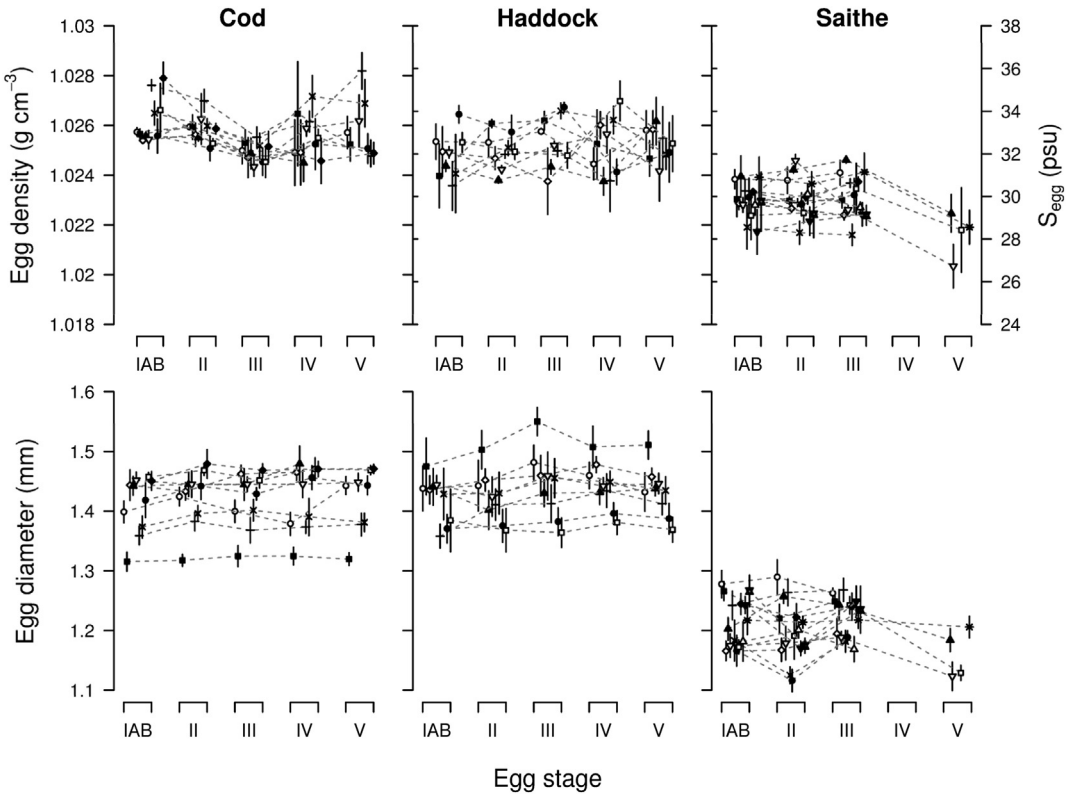

Fig. 2. The top row shows the mean (± 1 standard deviation) egg density and the corresponding salinity of neutral buoyancy (right axis) at 7 °C. The bottom row shows the mean (± 1 standard deviation) diameter at each ontogenetic stage for each batch. Each batch is represented by a unique symbol across stages.

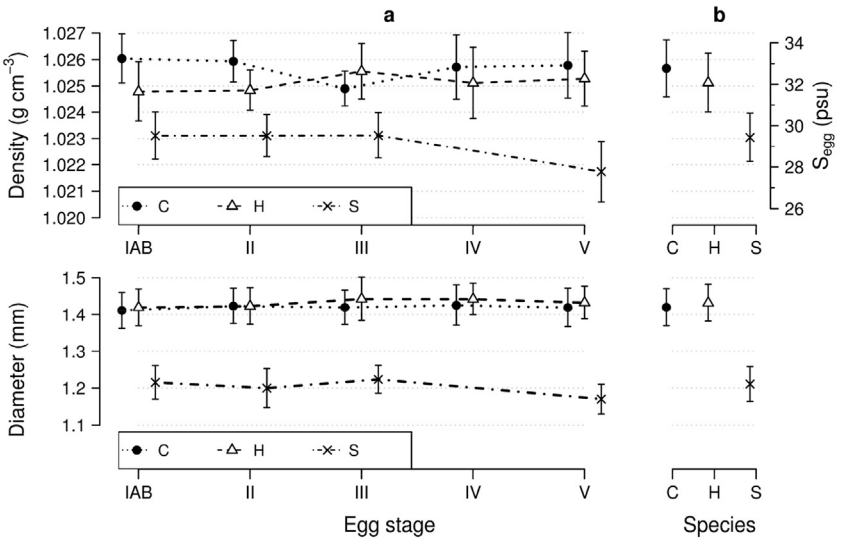

Fig. 3. The top row shows the mean (± 1 standard deviation) egg density and the corresponding salinity of neutral buoyancy (right axis) at 7 °C. The bottom row shows the mean (± 1 standard deviation) egg diameter. Stage-specific results are presented in panel a. Overall results (pooled over stage) are presented in panel b. For clarity, the points at each stage are staggered from left to right for cod (C), haddock (H) and saithe (S) respectively.

(Fig. 3a) led to an $RMSD_{C^*C_{III}^*}$ of 3.98 eggs m^{-3} and a decrease in $\tilde{z}$ from 4.00 to 1.25 m. This was substantially greater than any other stage and driven by a greater accumulation of eggs in the surface layer (Fig. 8). A similar pattern is seen for saithe where the decrease in density at stage V (Fig. 3a) leads to a greater abundance of eggs in the surface grid cell as opposed to the 2.5–5 m grid cell in the baseline ($RMSD_{S^*S_V^*}$ = 4.53 eggs m^{-3}; $\tilde{z}$ decreased from 2.98 to 1.25 m). Conversely, the increase in density at stage III for haddock leads to a reduced abundance in the surface grid cell ($\tilde{z}$ increased from 1.25 to 3.49 m); however, the magnitude of change from the baseline ($RMSD_{H^*H_{III}^*}$ = 1.73 eggs m^{-3}) is smaller than the changes seen within cod and saithe. For haddock and saithe, all the ontogenetic comparisons were smaller than the LS-HS comparison, whilst for the cod, the RMSD at stage III was slightly larger (Fig. 8 and Table 4a).

Out of the 396 simulations (132 days multiplied by 3 species) run at SB1, the grid cell containing the egg maxima changed depth through ontogeny on 62 occasions (38 cod, 22 haddock and 2 saithe comparison). Of these 62, on only two occurrences did the depth change by greater than one grid cell. This, together with the RMSD's (Fig. 8) highlights the minimal impact that ontogenetic variation has on φ.

At station SB2, the range of RMSDs found through ontogeny were 0.12–1.42 eggs m^{-3} for cod, 0.00–0.61 eggs m^{-3} for haddock, and 0.00–0.52 eggs m^{-3} for saithe (Fig. S2). These values are comparable to the interspecific RMSD's which are all < 2 eggs m^{-3} (Fig. 7) and are considerably lower than the LS–HS comparisons (Table 4b), further highlighting that at station SB2 the environment had a greater impact

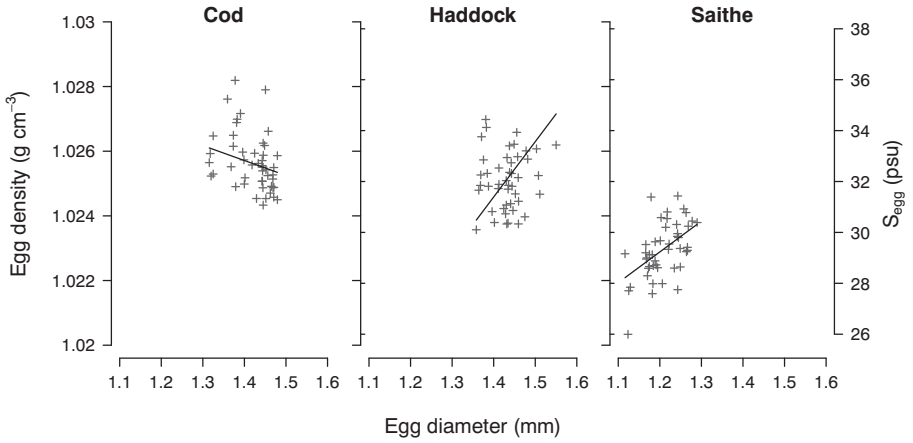

Fig. 4. The relationship between egg density and diameter for each species. The corresponding salinity of neutral buoyancy at 7 °C is shown on the right axis. The data points (+) represent the mean densities and diameters per batch per egg stage. The solid lines are model predictions across the range of diameters for each species.

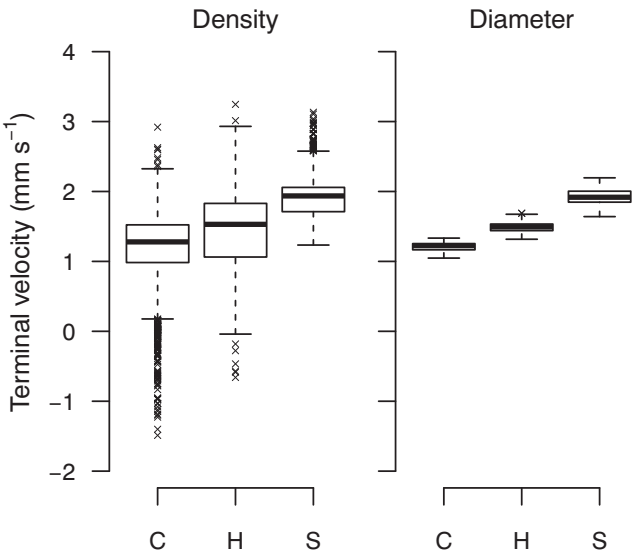

Fig. 5. Boxplots showing the distribution of terminal velocities calculated from the empirical egg density and diameter datasets (both pooled over *ES*) for cod (C), haddock (H) and saithe (S). When considering density, diameter was held constant at the species-specific mean, and vice versa. The median (central solid line), interquartile range (box limits) and 5th–95th percentiles (whisker limits) are shown. The points outlying the whiskers reflect the tails of the distribution. The environment's ambient density, temperature and molecular viscosity are assumed constant throughout the water column and equal to the means across time and both hydrological stations, 1027.6 kg m^{-3}, 7 °C and 1.5×10^{-3} kg m^{-1} s^{-1} respectively.

on egg distributions than either the species or the *ES* parameters. The grid cell containing the egg maxima did not change through ontogeny for any of the species in any environment at SB2.

3.2.4. Natural variation in egg density

For each interspecific comparison (Fig. 9, top row), accounting for natural variation in egg density reduced the spread of RMSD's by cutting down the right-hand tail of the distribution (i.e., the higher RMSD values). This was most noticeable for the C–H comparison where the range of RMSD's was reduced from 0.00–13.08 eggs m^3 to 0.53–2.13 eggs m^3 by incorporating distributional information on S_{egg}. This highlights the similarities in the distributions of S_{egg} between the two species (Fig. 3b). The saithe comparisons remained larger than the C–H comparison owing to the larger differences in the distributions of S_{egg} (Fig. 3b). The ranges were reduced from 0.00–14.09 eggs m^3 to 0.95–8.61 eggs m^3 for the C–S comparison, and 0.00–14.11 eggs m^3 to 0.41–7.53 eggs m^3 for the H–S comparison. On average, the differences between the two approaches were 1.70, 1.11 and 0.05 eggs m^3 for C–H, C–S and H–S respectively. This highlights the impact of stratification. In HS environments, using mean-only values will generate substantial interspecific differences in φ; however, these are substantially reduced when considering distributions of S_{egg} (Table 4). Under LS conditions (the majority of environments, Fig. 7), the MCMC procedure had little impact on φ because of the homogenising effect of turbulence (Table 4).

Accounting for natural variation in egg density substantially reduced the RMSDs characterising the ontogenetic comparisons for cod and haddock (Fig. 9). These reductions highlight that the differences between stage-specific φ and overall species-specific φ are minimised when accounting for natural variation in S_{egg} at each stage (also shown in Fig. 8). For saithe, the RMSD values did not change substantially when the MCMC procedure was used. Only at stage V were differences between stage-specific values and overall mean values seen (Fig. 9), and the MCMC procedure had minimal impact here suggesting that buoyancy ($\Delta\rho$) is high whether or not natural variation in S_{egg} is included.

At station SB2, the MCMC procedure had minimal impact on either the interspecific or ontogenetic differences. Whilst the RMSD's are typically higher when accounting for natural variation (Table 4; Fig. S3), the differences between the two approaches were sufficiently small to be considered negligible. For example, testing across the stratification gradient, the maximum absolute difference between the RMSD's was 0.52, 1.04 and 0.61 eggs m^{-3} for the C–H, C–S and H–S respectively and the mean differences were 0.08, 0.25 and 0.16 eggs m^{-3} respectively.

3.2.5. Sensitivity analyses

Sensitivity analyses showed that variation in neither egg diameter nor vertical molecular viscosity are important in determining the vertical distribution of eggs. Comparing with the baseline distribution for each species at each station, all RMSDs were below 0.07 eggs m^{-3} when assuming a linear relationship between egg density and diameter, and below 0.11 eggs m^{-3} when vertical gradients in molecular viscosity were incorporated. The model was also run with measured cod egg density parameters from 1996 (Marteinsdottir and Begg, 2002). Distributional differences were larger at SB1 (max RMSD = 3.89 eggs m^{-3}; mean RMSD = 2.54 eggs m^{-3}) than SB2 (max RMSD = 1.35 eggs m^{-3}; mean RMSD = 0.80 eggs m^{-3}). At SB1, $\tilde{z}$ was on average 1.25 m deeper in the baseline simulations whilst its interquartile range was 2.39 m larger, reflecting the heavier eggs found in the current study. However, in both simulations the egg maximum was located within 0–10 m and on only 27/132 occasions did it differ between the simulations (only by one grid cell in each instance). At SB2, the surface grid cell always contained the egg maximum in both simulations.

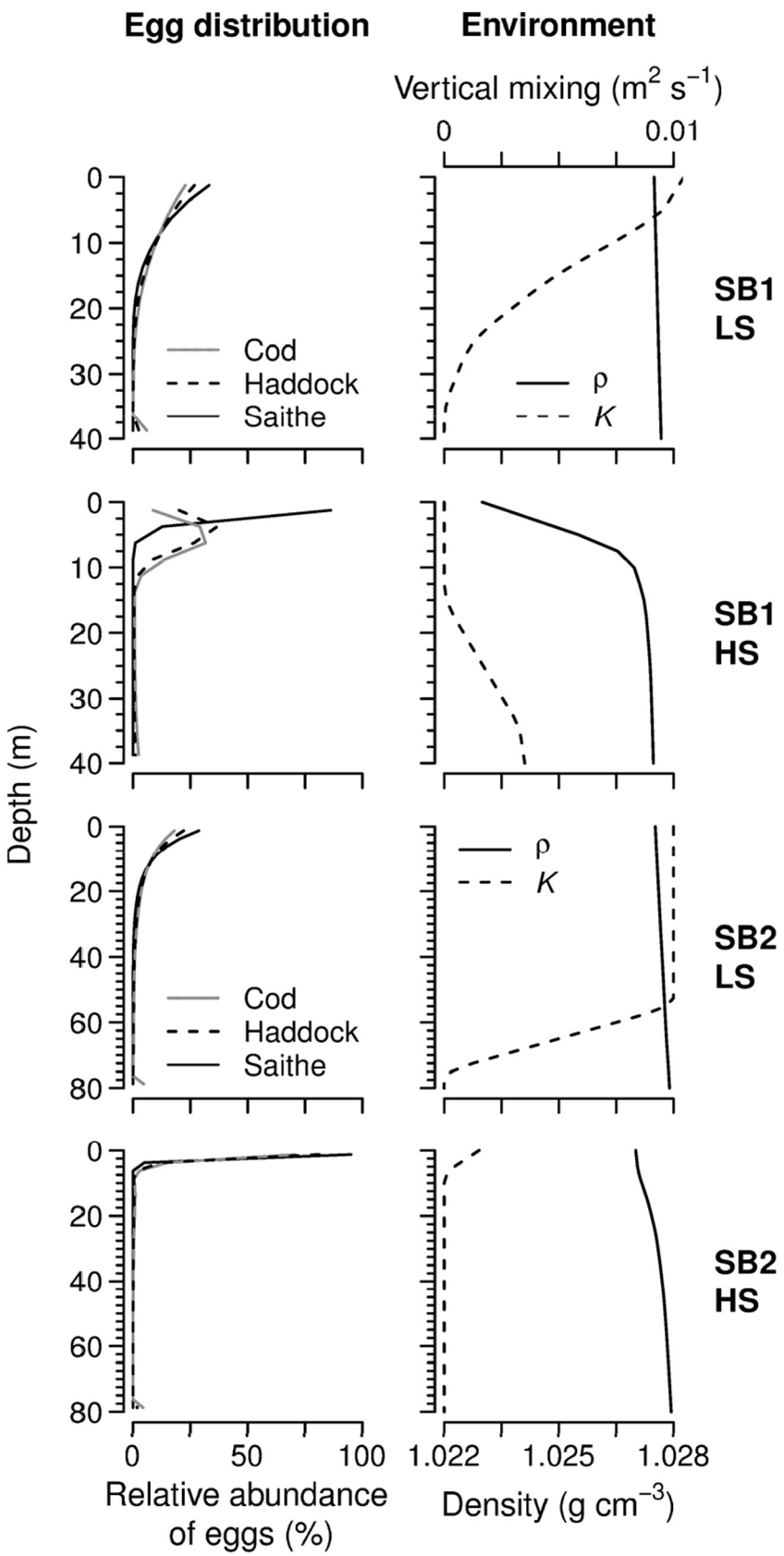

Fig. 6. Modelled vertical egg distributions (left-hand column) in highly stratified (HS) and well-mixed (i.e., low stratification, LS) conditions at both stations. The corresponding environmental gradients are shown in the right-hand column, K = vertical eddy diffusivity, ρ = ambient density.

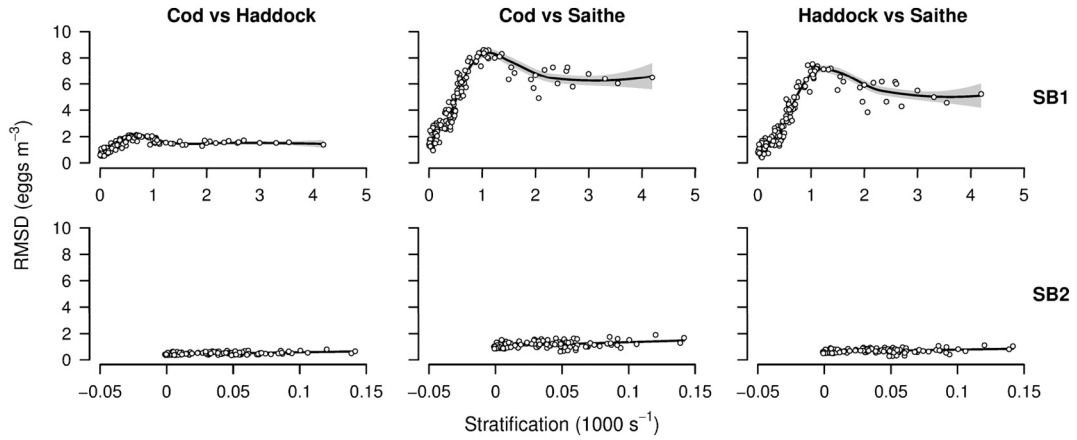

Fig. 7. RMSD values for each species comparison against total stratification N^2 ($\times 1000$) for the coastal (SB1) and offshore (SB2) stations. Loess model fits (solid line) and 95% confidence intervals (grey shaded area) are presented for each comparison.

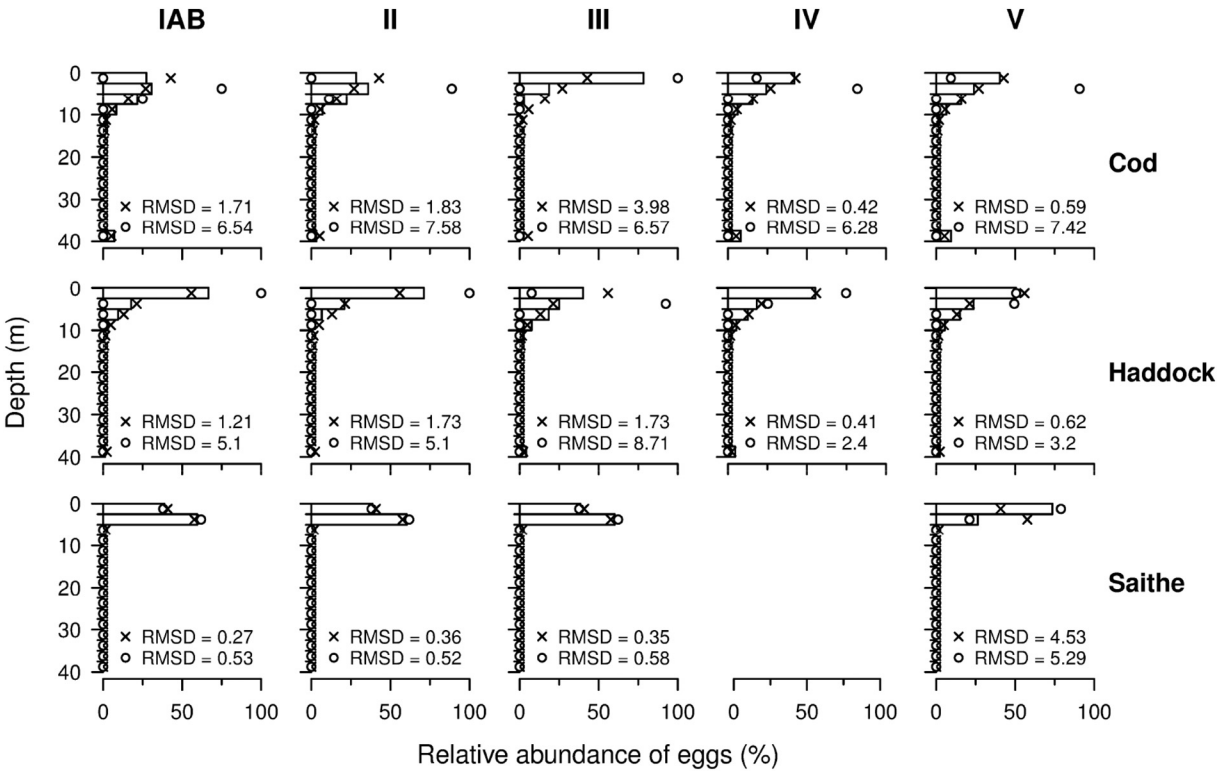

Fig. 8. Modelled relative abundance of eggs per grid cell at station SB1 for each species (different rows) at each ontogenetic stage (different columns). The bars indicate the relative abundance of eggs calculated using the stage-specific data for S_{egg} and D, i.e., $\varphi_{C_{IAB}}{}^{*}$ in the top left panel. The circles show the equivalent distribution calculated without the MCMC procedure, i.e., $\varphi_{C_{IAB}}$ in the top left panel. The crosses denote the baseline distribution, calculated from species-specific data pooled over *ES* ($\varphi_C{}^{*}$, $\varphi_H{}^{*}$ and $\varphi_S{}^{*}$), these distributions do not change per stage. The RMSD values at the bottom of each panel show the difference in eggs per m^3 between stage-specific distributions (the bars) and both the other distributions. Results are presented for the environments that maximised the intraspecific differences for each species (4th June for cod, 30th and 16th of May for haddock and saithe respectively).

4. Discussion

4.1. Interspecific differences

Distinctive differences were found between the three species in egg density and diameter. Whilst cod and haddock had similar values for both properties, saithe eggs were significantly smaller and less dense. Considering diameters, similar interspecific trends are shown in Breder and Rosen (1966) and Markle and Frost (1985) and have also been found in Icelandic waters (Fridgeirsson, 1978; Gislason et al., 1994). Furthermore, the size intervals observed in this study are largely comparable with the literature. For cod, the overall mean and standard deviation (1.42 ± 0.05 mm) is similar to the values obtained by Marteinsdottir and Steinarsson (1998) for freely running females sampled from southwest Iceland, though stage IV spawners had smaller eggs (1.34 ± 0.05 mm). For haddock, the range of diameters (1.31–1.57 mm) encompassed and extended upon the range (1.37–1.53 mm) found by Trippel and Neil (2004) for the northwest Atlantic haddock. Whilst for saithe, the mean (1.21 mm) and range (1.08–1.34 mm) were similar to the values (1.17 mm, 1.04–1.31 mm) found by Skjæraasen et al. (2017) for the North Sea stock.

Regarding egg densities, there is little egg density data available for haddock and saithe, although unpublished data from the Marine Research Institute in Norway suggests that cod and haddock have

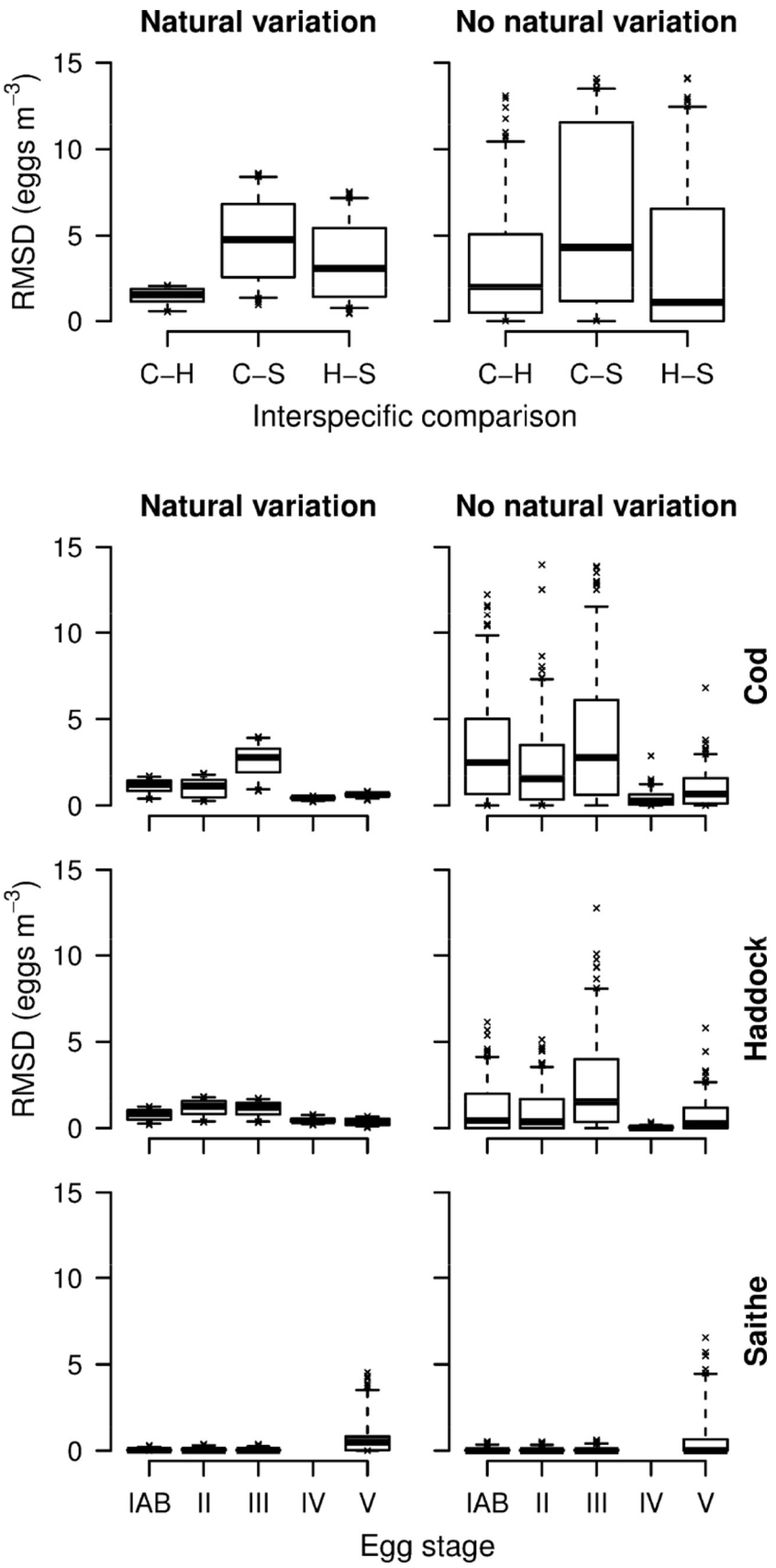

Fig. 9. Interspecific and ontogenetic differences at station SB1 are contrasted between the MCMC simulations that account for natural variation in S_{egg} (left column) and the analytical solution that assumes a single stage-specific density (right column). The top row shows the interspecific differences in egg distributions. The lower three rows show the ontogenetic comparisons between the baseline (pooled over *ES*) and the stage-specific vertical distributions for each species, i.e., for stage IAB cod eggs, the left panel shows $RMSD_{C\cdot C_{IAB}\cdot}$, whilst the right panel shows $RMSD_{CC_{IAB}}$.

Table 4
RMSD values (eggs m^{-3}) for the egg distributions in Fig. 6. The left-hand table (A) shows the interspecific comparisons. The right-hand table (B) shows comparisons for each species between the low- and high-stratification environments. The values in brackets show the equivalent RMSD's when vertical distributions are generated from the analytical solution without the MCMC procedure.

(a)	SB1		SB2		(b)	SB1	SB2
	LS	HS	LS	HS		LS – HS	LS – HS
C-H	0.60 (0.48)	1.57 (6.75)	0.41 (0.37)	0.80 (0.65)	C	2.67 (7.19)	3.90 (4.79)
C-S	1.41 (1.15)	8.62 (13.02)	1.00 (0.89)	1.90 (1.24)	H	2.29 (5.78)	4.39 (5.01)
H-S	0.82 (0.68)	7.53 (12.47)	0.60 (0.52)	1.11 (0.59)	S	5.81 (7.41)	5.03 (5.09)

similar densities (Castaño-Primo et al., 2014), a trend also found in this study. The data obtained in this study should therefore serve as useful baselines for future research on these two species.

For cod, a comparison with the results obtained by Marteinsdottir and Begg (2002) shows that the eggs of spawners in southwest Iceland at 5 DPF were less dense in 1996 (mean = 1.0247 g cm^{-3}; range = 1.0226–1.0266 g cm^{-3}) than 2010 (mean = 1.0259 g cm^{-3}; range = 1.0247–1.0278 g cm^{-3}). However, the results are not directly comparable due to the sampling regimes; Marteinsdottir and Begg (2002) sampled a far greater number of females that encompassed the complete spawning season and multiple spawning stages, whilst the current results are based on point estimates using far smaller sample sizes. Given that the size-structure of the spawning cod varies with proximity-to-shore (Marteinsdottir et al., 2000) and throughout the spawning season (Marteinsdóttir and Björnsson, 1999), the spot-sampling conducted in this study will be subject to biases with regards to the life-history traits of the spawning females. Furthermore, discrepancies between the two studies may be due to interannual variation (e.g., Petitgas et al., 2006; Petereit et al., 2009) which has been observed in relationships between maternal traits and egg properties of Icelandic cod (Marteinsdottir and Begg, 2002), or due to the complex sub-stock structure of Icelandic cod where multiple spawning components have been distinguished within the main spawning grounds (e.g., Marteinsdottir et al., 2000; Jónsdóttir et al., 2006; Petursdottir et al., 2006; Grabowski et al., 2011). This is discussed further in Guðmundsdóttir (2013) and requires research to test whether egg density is an appropriate discriminator of spawning components.

A limitation of the study was that the females were not staged, so it was not possible to standardise the datasets by batch number. All the species examined are batch spawners (Murua and Saborido-Rey, 2003), and with each successive batch, egg diameters have been shown to decrease for each the study species (e.g., Vallin and Nissling, 2000; Trippel and Neil, 2004; Skjæraasen et al., 2017) including the Icelandic cod stock (Marteinsdottir and Steinarsson, 1998; Marteinsdottir and Begg, 2002). Although relationships have been established (e.g., Kjesbu et al., 1992; Nissling et al., 1994), Marteinsdottir and Begg (2002) found no significant differences in egg density between batches. However, the lack of stage-data (and whether fish are recruit or repeat spawners, see Kjesbu et al., 1992, 1996) may be a confounding factor in the analyses. Ultimately, to understand the proximate mechanisms driving the interspecific and ontogenetic differences seen in this study, the relative contributions of each of the egg constituents (see Jung et al., 2014) across batches needs to be quantified for gadoids in Iceland.

4.2. Ontogenetic variation

Egg stage was a significant predictor of both egg density and diameter. Given that egg diameters are expected to remain constant throughout ontogeny (Jung et al., 2014), this was a surprising result. Linear models with "batch" as a fixed explanatory factor revealed that 5/10, 5/9 and 11/14 batches had at least one significant difference in diameter between stages for cod, haddock and saithe respectively ($p < .05$; Fig. 2), although the changes were small relative to the interspecific comparisons (particularly those involving saithe). The significant differences were most prominent in saithe with 18/32 of the comparisons tested significant, whereas 5/38 and 8/36 significant comparisons were found in cod and haddock respectively. These results may reflect the small sample size ($n = 10$) which was used to ensure adequate numbers of eggs remained for the density experiments. Furthermore, high within-batch correlations (Table 3) for each species highlight that more robust population estimates could be attained by sampling more females.

Ontogenetic changes in egg density have been observed for several species (e.g., Sundby et al., 2001; Coombs et al., 2004; Ospina-Álvarez et al., 2012; Nissling et al., 2017) including both Atlantic and Baltic cod stocks (Nissling and Westin, 1991; Jung et al., 2012, 2014). Based on developmental trends in egg specific gravity across three local populations of Atlantic cod, Jung et al. (2012, 2014) suggested a generic pattern for the ontogenetic development of egg specific gravity in pelagic fish eggs, the main characteristic of which was a gradual decline in ρ_{egg} from 4 to 11 DPF. Whilst the experimental setup was not appropriate for the direct evaluation of this hypothesis because individual eggs were not continuously monitored as they were in Jung et al. (2012, 2014), a significant decline through ontogeny was seen in all cod batches. The lowest density was recorded at stage III for 7/10 cod batches and stage IV for 3/10 batches, and the rate of decline from maximum ρ_{egg} (stage IAB or II) to minimum ρ_{egg} (stage III or IV) ranged from 0.0001–0.001 g cm^{-3} day^{-1} with a mean of 0.00038 g cm^{-3} day^{-1} which is ~90% faster than the rate described by Jung et al. (2014).

Excluding one batch, saithe eggs were relatively stable from stage IAB to stage III (Fig. 2; Table 3), whilst the decrease in ρ_{egg} at stage V was seen (and significant) for all batches that remained unhatched ($n = 4$; Fig. 2). This decline does not fit the general picture of increasing density prior to hatching found for Atlantic and Baltic cod (Nissling and Westin, 1991; Jung et al., 2012; Jung et al., 2014), and blue whiting (Ådlandsvik et al., 2001), and is further complicated by all four batches also showing a decrease in diameter (3/4 significant; Fig. 2). Conservation of egg mass implies that as egg volume increases, its density will decrease (see Kjesbu et al., 1992 for details), so a decrease in both volume and density implies a loss of material. Hall et al. (2004) describe the weakening of the chorion due to a hatching enzyme just prior to hatching, and the enzymatic dissolution of material was suggested as a potential cause of the chorion thinning observed for Norwegian Coastal cod at this stage (Jung et al., 2014), though this was considered to be of little significance in determining the chorion mass and thus ρ_{egg} (Jung et al., 2014). The saithe batches measured at stage V were all on the cusp of hatching, so this is a potential explanation for the observed density decrease in saithe eggs. It should also be noted that the three batches that displayed significant declines in diameter at stage V all had small sample sizes ($n = 2$, 4 and 6; $n = 8$ for the non-significant batch) so the confidence in these estimates is low (Table 3). Furthermore, at the species level, the standard error of ρ_{egg} at stage V was approximately three times greater than the other stages highlighting greater uncertainty in the mean (Table 3). Further work is required to determine whether the observed trend is a general pattern for saithe eggs and to examine the relative contributions of egg constituents prior to hatching. In general, the commonalities outlined above for cod and saithe suggest that a unifying mechanism exists; however, the results for haddock were more ambiguous with a variety of ontogenetic patterns found (Fig. 2).

4.3. Implications for the vertical distribution of eggs

The mean densities corresponded to salinities of neutral buoyancy

(S_{egg}) of approximately 32.8, 32.1 and 29.4 PSU at 7 °C for cod, haddock and saithe respectively. Thus, the majority of eggs for all three species were positively buoyant suggesting that the ultimate function of the egg traits is to maintain a high position in the water column. Exceptions occurred at the right tails of the haddock and cod distributions where S_{egg} exceeded 35.2 PSU. The model suggested that differences between φ_C and φ_H will be minimal (Fig. 9), irrespective of the strength of stratification (Fig. 7). Fridgeirsson (1984) observed surface agglomerations of cod and haddock eggs under calm conditions in southwest Iceland using a hydraulic pump in May 1981. Eggs of both species were found at all sampled depths (0–35 m) with the vertical distributions appearing more similar to the distributions under well-mixed conditions presented in Fig. 6. This suggests that the model may be underestimating the spread of eggs; however, without detailed information on the prevailing environmental gradients (particularly K) at the time of Fridgeirsson's study, it is not possible to test the model with these observed distributions. Interspecific differences were also noted by Fridgeirsson (1984) with late-stage haddock eggs having a deeper distribution than the cod equivalents, with an RMSD of 5.55 eggs m^{-3}. Whilst our study suggests a converse pattern as the cod eggs are slightly denser, the densities at stage V were statistically similar between the two species, so it is entirely plausible that owing to various sources of natural variation in egg density (discussed above), sampling that is restricted in time and space (i.e., a snapshot of the system) may capture haddock eggs that are slightly denser than cod eggs.

For each species, the observed ontogenetic changes in egg density had little to no impact on the vertical egg distribution when compared to using the overall mean. With only minor shifts in the concentration of eggs within the upper layer (0–10 m) when mixing was minimal, it is highly unlikely that ontogenetic changes in ρ_{egg}/S_{egg} will have a large impact on dispersal trajectories. Whilst Fridgeirsson (1984) observed a gradual increase in the depth of φ_C through development, the egg maximum concentration was always found at the surface, which is largely in agreement with the model output (100% in the surface at SB2; 67%, 20% and 11% at 0.0–2.5 m, 2.5–5.0 m and 5.0–7.5 m at SB1 respectively). As noted above, monitoring individual eggs continuously would provide a more "complete" picture of ρ_{egg}/S_{egg} development and how φ changes accordingly. This was done for Norwegian coastal cod subpopulations by Myksvoll et al. (2014) who developed an ontogenetic function for S_{egg} (which incorporated intraspecific variation) based on the continuous measurements from Jung et al. (2012). It was concluded that the ontogenetic function was not an important factor for the horizontal dispersion of eggs (Myksvoll et al., 2014).

Stratification over the entire spawning period was dominated by haline controls at both stations and was on average 22–23 times stronger at SB1 (Fig. S1). In general, the thermocline develops mid-late May in southern Icelandic waters (Thórdardóttir, 1986; SB2 in Fig. S1). Therefore, stratification throughout the spawning periods for each species will be predominantly determined by the interaction between freshwater runoff and wind stress. This varies considerably on an interannual basis (Thórdardóttir, 1986; Gislason et al., 1994), as does the horizontal extent of stratification (Gislason et al., 2016). For saithe, which spawn earlier in the season (Gislason et al., 1994; Jónsson and Pálsson, 2013) and further offshore than cod and haddock, the eggs will ascend quickly and agglomerate in the surface layer. And the model suggests similar patterns for cod and haddock that spawn further offshore in deeper waters (e.g., Marteinsdottir et al., 2000). For coastal spawners, sub-surface distributions may become evident when the freshwater layer promotes stability. Although, in these cases, the egg distributions remain pelagic with the majority of eggs found just below the surface and well within the vertical range of the Icelandic Coastal Current which extends from the surface to 10–30 m deep (Logemann et al., 2013).

4.4. Model assumptions

Solely focusing on the steady-state distribution does not allow inference regarding the temporal development of the vertical egg distributions. Whether or not the steady-state is achieved will depend on the 'characteristic time' of the system. If this exceeds the egg duration, the steady-state will not be achieved, and vice versa. If the steady-state is not achieved then the vertical distribution of eggs will be largely influenced by the initialisation depth (Sundby, 1991; Petitgas et al., 2006). Simulations using the numerical schemes in the VertEgg toolbox (Ådlandsvik, 2000) suggested that the "characteristic time" will be less that the egg duration under the HS and LS conditions presented in Fig. 6. However, whether this is the case for the early developmental stages requires further simulations, especially for individuals spawning at great depths as reported for particular spawning components of each study species (e.g., Grabowski et al., 2011; Jónsson and Pálsson, 2013).

The vertical distribution model assumed that an egg's buoyancy is unaffected by the surrounding environment. In reality, chorion permeability means an egg's perivitelline space maintains neutral buoyancy in relation to the ambient seawater (Sundby and Kristiansen, 2015), the effect of which can adjust an egg's density towards that of the surrounding fluid (e.g., Coombs et al., 1985; Nissling and Vallin, 1996). However, this effect is likely to be more pronounced for species with a large perivitelline volume (e.g., sardine, > 80% egg volume) and a primary consideration when utilising density gradient columns to measure egg densities for such species (Coombs et al., 1985, 2004; Boyra et al., 2003; Huret et al., 2016). Jung et al. (2014) obtained a range of 9% to 18% for Norwegian Atlantic cod perivitelline volume and showed that the influence of this range on overall ρ_{egg} was small compared to chorion volume fractions and the specific gravity of the yolk + embryo. The model also assumed that the thermal expansion of fish eggs is equal to that of the ambient seawater. Sundby and Kristiansen (2015) showed that whilst this is not strictly true, the discrepancy between the two is sufficiently small to be considered negligible for a variety of species (including Atlantic cod).

4.5. Implications for coupled biophysical models

Our results emphasise that accounting for intraspecific variation in ρ_{egg}/S_{egg} is an important consideration when modelling the vertical distribution of pelagic fish eggs, particularly in situations where buoyancy is marginal. This conclusion is in line with other studies that have examined how intraspecific variation in ρ_{egg}/S_{egg} affects φ, for example, Boyra et al. (2003) found that including distributions of ρ_{egg} substantially improved the model's fit to observed distributions of anchovy and sardine eggs. By comparing mean-only with distributional approaches, our results have highlighted specific instances where mean-only approaches may fail to truly represent the population. For instance, distribution differences in φ across ontogeny are substantially reduced when intraspecific variation is accounted for (Fig. 9). Whether or not ontogenetic variation will have an impact on the vertical distributions of eggs will depend upon the degree of overlap between variances throughout development, and how this compares to the ambient salinity. When there is considerable overlap between stages and all stages are positively buoyant (as in the study species), it is unlikely that the ontogenetic changes will impact φ if intraspecific variation is considered. More crucially, simulations based on mean-only values may lead to exaggerations in the magnitude and extent of changes in φ due to ontogenetic changes in ρ_{egg}/S_{egg}. When coupled to a spatially explicit hydrodynamic model, this could lead to misleading estimates of dispersal trajectories and magnitudes (assuming there is vertical variation in flow vectors), and thus connectivity. In Icelandic waters, this situation is likely to arise at coastal spawning grounds within proximity of the Icelandic Coastal Current. However, the implications extend to any system where buoyancy is small. For example, the aforementioned studies that consider mesopelagic egg distributions, where fine-scale

changes in buoyancy arise from ontogenetic changes in ρ_{egg}/S_{egg} (Ådlandsvik et al., 2001; Sundby et al., 2001; Ospina-Álvarez et al., 2012).

Carrying out such "virtual" experiments can be a useful tool for designing biophysical models by identifying the degree of complexity required in egg movement modules. Implementing distributional inputs requires a priori knowledge of the variable(s) probability distribution. From a coding perspective this is simple enough, however, owing to spatial-temporal variation in the physical properties of eggs, the parameters describing the distributions ought to reflect the egg properties at the simulation's time and space (see Petitgas et al., 2006), a concern that is also relevant when using mean-only values. Assuming a Gaussian distribution appears to be a reasonable assumption for D and S_{egg} based on visual inspection of histograms and qqplots, as was found by Goarant et al. (2007) for the neutral buoyancies of anchovy. That φ is far less sensitive to D than S_{egg} is well established in the literature (e.g., Sundby, 1983; Petitgas et al., 2006) and the results of the sensitivity analysis confirm this for each of the study species. Therefore, holding D at its mean level whilst allowing for variation in S_{egg} is a reasonable assumption to make. Although if strong, robust relationships exist between both variables, natural variation in both traits could be accounted for when initialising individuals in biophysical models.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2019.103290.

Data availability

The raw egg density and diameter data are available at Mendeley data (https://doi.org/10.17632/mz6vvzxdt5.1). The complete VertEgg toolbox (Ådlandsvik, 2000) translated into the R programming language is freely available at https://github.com/willbutler42/VertEgg-R.

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Author contributions

WB and GM jointly conceived the study idea. GM supervised the project. WB and TL carried out the sampling and laboratory experiments for haddock and saithe. LG carried out the sampling and laboratory experiments for cod. WB programmed the VertEgg model in R. WB performed all analyses. KL wrote a Fortran program for the extraction of environmental profiles from the 3-D hydrodynamic model CODE. WB prepared the initial manuscript. All authors contributed to revisions.

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