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Physiological individual-based modelling of larval Atlantic herring (*Clupea harengus*) foraging and growth: insights on climate-driven life-history scheduling

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A physiological individual-based model for the foraging and growth of Atlantic herring (*Clupea harengus*) larvae was constructed, validated using laboratory and field data, tested for parameter sensitivity, and used to examine climate-driven constraints on life-history scheduling. Model scenarios examined how natural (phenological and magnitude) changes in key environmental factors (temperature, prey, and photoperiod/daylength) affected the estimates of survival and growth of spring- and autumn-spawned larvae. The most suitable hatching seasons agreed well with the periods of larval abundance in Northeast Atlantic waters. Modelled survival is unlikely in June, July, and November. Mean annual temperature, prey concentration, and composition significantly influenced larval growth of both autumn and spring spawners. The model suggested that climate-driven changes in bottom-up factors will affect spring- and autumn-spawned larvae in different ways. It is unlikely that autumn-spawning herring will be able to avoid unfavourable conditions by delaying their spawning time or by utilizing more northern spawning grounds because of limitations in daylength to larval growth and survival. Conversely, earlier spawning in spring, or later, midsummer spawning will be tightly constrained by match–mismatch dynamics between larvae and zooplankton production.

Keywords: bioenergetics, climate, foraging, growth, herring, larvae, marine fish, modelling, physiology.

Introduction

Climate-driven changes in the productivity of fish stocks will depend (to some extent) on the degree of specialization of life stages to specific habitats; species tightly coupled with specific habitats (i.e. spawning, nursery, or feeding grounds) will potentially experience the largest changes in productivity (Rijnsdorp *et al.*, 2009). Temperature is a particularly important factor, because it controls the rates of metabolic processes that govern growth energetics directly by altering the rates of digestion, gut evacuation, enzyme activity, swimming activity, and general catabolism (Blaxter, 1965; Overnell and Batty, 1999; Gillooly *et al.*, 2001; Peck *et al.*, 2006). Other key physical (light, salinity, pH, and O_2) and biotic factors (prey availability and size/quality) interact with temperature to influence the spatial and temporal extent of environmental windows supporting growth and survival (Pörtner and Peck, 2010). Because of the complexity of interactions among environmental factors, the large areas inhabited by some marine fish populations and the importance of early survival to year-class strength, biophysical individual-based models (IBMs) have become increasingly used to understand the effects of climate variability and change on marine fish early life stages (Gallego *et al.*, 2007; Miller, 2007). A challenge facing many current efforts to build biophysical IBMs for marine fish larvae is to parametrize correctly the physiological components, because advancements in modelling physics have greatly outpaced those in ecophysiology in the past two decades (Buckley *et al.*, 2000; Peck and Daewel, 2007).

Herring in the Atlantic (*Clupea harengus*) and Pacific (*Clupea pallasii*) are among the most thoroughly investigated fish in the world's oceans (Geffen, 2009; Simmonds, 2009), making them excellent candidates for the development of detailed, physiologically based models of foraging and growth of different life stages (Fiksen and Folkvord, 1999; Megrey *et al.*, 2007). In the Northeast Atlantic, the productivity of *C. harengus* is apparently strongly coupled with climate variability. For example, Gröger *et al.* (2009) reported a strong correlation between the North Atlantic Oscillation and Atlantic Multidecadal Oscillation and recruitment strength in Atlantic herring. More detailed life cycle analyses of autumn- and winter-spawned herring in the North Sea revealed that processes affecting larvae 12–20 mm in length during their overwinter period, when larvae drift passively from western spawning grounds to eastern nursery areas, are apparently driving fluctuations in recruitment strength (Payne *et al.*, 2009). Similarly, for Norwegian spring spawners, warm winter temperatures and early hatch dates of larvae were highly correlated with strong year classes (Husebø *et al.*, 2009). However, during larval ontogeny, spring- and autumn-spawned herring experience markedly different (contrasting) changes in environmental factors (e.g.

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Table 1. Summary of all equations, parameter settings for an IBM simulating the foraging, and growth of larval herring (*C. harengus*).

Description	Parameter/value/equation	Unit	Equation number
Length at exogenous feeding	$L_{EF} = 11 - 0.09\,T$	mm	(1)
Temperature	T	°C	
Dry weight growth	$G = -R + \beta(1 - \mathrm{SDA})(3\,600\,C)$	μg dw h^{-1}	(2)
Standard respiration	$R = (1.392\,\mathrm{dw}^{0.7722}\,e^{0.05369T})\gamma\zeta$	μg dw h^{-1}	(3)
Oxycalorimetric equivalent	$\zeta = 0.00463$	cal μl O_2^{-1}	
Conversion factor calorie to dw	$\gamma = 227$	μg dw al^{-1}	
Activity multiplier k	$k = 1.22\,\mathrm{pc}^{-0.1922}\left[-2\left(\frac{GC}{GC_{max}}\right)^2 + 2\frac{GC}{GC_{max}} + 0.5\right]$	dimensionless	(4)
Assimilation efficiency	$\beta = 0.6(1 - 0.3\,e^{-0.003\mathrm{dw} - \mathrm{dw}_{min}})$	dimensionless	(5)
Dry weight ($CI = 1$)	$\mathrm{dw}_{(1)} = 0.018521L^{3.6028e^{0.006267T}}$	μg	(6)
Dry weight at L_{EF}	dw_{min}	μg dw	
Specific dynamic action	$\mathrm{SDA} = 0.10$	dimensionless	
Consumption	$C = \frac{\sum \mathrm{pdw}_i \mathrm{ER}_i \mathrm{CS}_i}{1 + \sum \mathrm{ER}_i \mathrm{HT}_i}$	μg dw s^{-1}	(7)
Prey dry weight	$\log(\mathrm{pdw}_i) = (5.544\log(\mathrm{pL}_i) - 7.476)\times 2$	μg dw	(8)
Catch success	$\mathrm{CS} = 1.1 - 1.1 \times (\mathrm{pL}_i/\mathrm{pL}_{max})$	# s^{-1}	(9)
Maximum prey length	$\mathrm{pL}_{max} = 2\,200/(1 + (L/14)^{-2})$	mm	(10)
Handling time	$\mathrm{HT}_i = \exp\left(0.264 \times 10^{20(\mathrm{pL}_i/L)}\right)$	s	(11)
Encounter rate	$\mathrm{ER}_i = \left(\frac{2}{3}\pi\,\mathrm{RD}_i^3\frac{\mathrm{pc}_i}{1000}\mathrm{PF}\right) + \left(\pi\,\mathrm{RD}_i^2\frac{\mathrm{pc}_i}{1000}\mathrm{PF}\,\mathrm{PD}\,V_i\right)$	# s^{-1}	(12)
Velocity component of contact rate	$V_i = (\nu_{pi}^2 + \nu_L^2 + \omega^2)$	mm s^{-1}	(13)
Swimming speed	$\nu_L = \frac{127.21}{1 + e^{(L - 30.57/3.67)}} + 6.7$	mm s^{-1}	(14)
Prey speed	$\nu_{p_i} = 3\mathrm{p}L$	mm s^{-1}	(15)
Turbulent velocity	$\omega = 1.3$	mm s^{-1}	
Pause frequency	$\mathrm{PF} = 0.35$	s^{-1}	
Pause duration	$\mathrm{PD} = 1.3$	s	
Reactive distance	$\mathrm{RD}_i = \mathrm{pL}_i/(2\times\tan(\alpha/2))$	mm	(16)
Angle of visual acuity	$\alpha = 0.0167\,e^{9.14 - 2.4\,\ln(L) + 0.229(\ln(L))^2}$	degree	(17)
Maximum gut content	$\mathrm{GC}_{max} = 10^{1.72 + 1.02\log(\mathrm{dw}_1)}$	μg	(18)
Gut evacuation rate	$\mathrm{GER} = 1.792\,L^{-0.828}2.52^{(T - 12)/10}$	% h^{-1}	(19)
Constant feeding factor	$\mathrm{cff} = 2 + (2/(1 + e^{2 - 5\mathrm{pc}}))$	dimensionless	(20)
Condition	$\mathrm{CI} = \mathrm{dw}/\mathrm{dw}_1$	dimensionless	(21)
Proportion allocated to length growth	$\mathrm{plg} = 0.5 + 0.36\,\mathrm{atan}\left(0.25\left(\frac{CI \times 360 - 360}{2\pi}\right)\right)$	fraction	(22)
Random daily temperature	$T_i = \chi T_1 + 6\,\sin(2\pi/365(cd - \chi T_2))$	°C	(23)
Random daylength via latitude	$\mathrm{dl} = \arccos\left(1 - \left(1 - \tan\left(\frac{\chi\mathrm{lat}\,\pi}{180}\right) \times \tan\left(\frac{23.439\pi}{180}\cos\left(\frac{\pi}{182.625}\mathrm{cd}\right)\right)\right)\right)\frac{24}{\pi}$	h	(24)
Random total prey concentration	$\mathrm{pc} = \chi C_1 + 160\left(\frac{1}{\chi C_2(2\pi)^{0.5}}\right)^2 e^{-((cd - \chi C_3)^2/2\chi C_2^2)}$	# ml^{-1}	(25)
Relative length frequency distribution of prey	$\mathrm{pc}_{irel} = \frac{\mathrm{pL}_i^{-b}}{\sum_{i=1}^{i=\max}\mathrm{pL}_i^{-b}}$	fraction	(26)
Random slope of prey length frequency distribution	$b = -1.85 - \chi b_2\cos(-2\pi/365(cd - \chi b_2))$	ln(#) mm^{-1}	(27)
Random seasonal mortality multiplier	$sZ = 1 + \chi\mathrm{s}Z\,\sin\left(\frac{2\pi}{365}\mathrm{cd} - 125\right)$	fraction	(28)

The top section refers to model equations and the bottom section to environmental forcing used in the simulations.

temperature × prey). Therefore, understanding the mechanisms causing changes in survival (e.g. bottom-up vs. top-down) in these different spawning populations/stocks depends on our ability to disentangle the relative roles of various abiotic and biotic factors.

In the current study, a physiological-based IBM depicting the effects of key abiotic and biotic factors on the foraging and growth of larval herring was developed, validated, and used. Earlier field and laboratory studies were thoroughly reviewed, so that parametrizations were (to the greatest extent possible) herring-specific. Model predictions and observations were compared and a sensitivity analysis was done to assess model performance. Finally, the growth and survival of larvae experiencing different realistic climatologies of key environmental factors (e.g.

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seasonality in temperature, photoperiod, and prey) were estimated. Simulations also included different (constant, length-based, seasonally varying) mortality. These simulations allowed us to examine how bottom-up and top-down processes might constrain the ability of Atlantic herring to shift spawning times in response to climate-driven changes in key environmental factors.

Material and methods

Basic equations and model structure

The model includes the effects of abiotic and biotic factors on the growth physiology of yolk-sac and exogenously feeding larval Atlantic herring. The current study focused on exogenously feeding larvae, so only a few relevant aspects of modelled yolk-sac larvae are provided. Larval foraging is influenced by prey concentration and size spectrum, whereas growth is based on the balance between assimilated energy gained from foraging and that lost via routine and active metabolism. Using a size-based prey field was considered best for a generic herring model (one that can be applied across stocks), although some authors have reported that herring prefer specific copepod species/genera (Arrhenius, 1996), and prey selection might not only be energy-driven (Marcotte and Browman, 1986). The model structure is comparable with that employed for larval Atlantic cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) presented by Daewel *et al.* (2008a, 2011). Because Atlantic herring larvae can tolerate (at least over short time-spans) temperatures between −0.75 and 23°C (Blaxter, 1960) and can experience North Sea winter temperatures close to 0°C (Townsend *et al.*, 1989), we included a number of temperature-dependent processes and did simulations across a wide range of temperatures (e.g. 2–20°C).

Yolk-sac larvae

On hatching from demersal eggs, larval herring display temperature-dependent growth and development during the endogenous feeding (yolk-sac) phase. The duration of the yolk-sac phase in the current model [60 degree-days (°d; °C days)] was based on the timing of rapid decline in biochemical condition (RNA–DNA ratio; MAP, unpublished data) and the results of several other authors (see the "Discussion" section). Larvae were assumed to start active foraging at a maximum standard length (L, mm) of 11 mm (von Westernhagen and Rosenthal, 1981; Geffen, 2002), but length at first-exogenous-feeding (L_{EF}, mm) declined with increasing temperature (T, °C) at a rate of 0.09 mm °C^{-1}, in agreement with temperature-dependent changes in length-at-hatching [Table 1, Equation (1)] derived from work on Baltic herring larvae by von Westernhagen and Rosenthal (1979).

Exogenously feeding larvae

For exogenously feeding larvae, a bioenergetics model was used to calculate the growth rate (G, μg) in dry weight (dw) per model time-step (1 h) from the balance between the rates of energy gained from food consumption (C, μg dw s^{-1} 3600 s h^{-1}) and that lost via various components of metabolism [Table 1, Equation (2)]. During each model time-step, G was calculated with the difference between food consumption (C, μg dw time-step^{-1}) and the assimilation efficiency (β, %) and metabolic losses from specific dynamic action (SDA, %) and respiration (R, μg dw time-step^{-1}) at different levels of activity. All parameters and equations contributing to this basic budget are described in the following sections.

Assimilation efficiency and respiration rate

The rate of respiration (R) in larval herring increases with increasing larval dry weight (dw, μg) and temperature [T, °C; Table 1, Equation (3); Almatar, 1984; Kiørboe *et al.*, 1987; MAP, unpublished data]. Two terms (γ and ζ) converted O_2 (μl) into μg dw of larval herring tissue (Brett and Groves, 1979; Theilacker and Kimball, 1984). During daylight, modelled larvae were more active and had higher rates of energy loss ($R_{forage} = kR$) than at night. The activity multiplier (k) was a function of prey concentration (pc, prey ml^{-1}), based on observations of (i) increasing swimming activity at low prey concentrations, and (ii) lower levels of activity at extremely low and high prey concentrations (Munk and Kiørboe, 1985; MacKenzie and Kiørboe, 1995). Swimming activity (k) was modulated by the degree of gut fullness, the difference between gut content (GC, μg dw), and maximum gut capacity (GC_{max}, μg dw). Larvae with a completely filled ($GC = GC_{max}$) or empty ($GC = 0$) gut had the same (low) activity. When food was evacuated from the gut and not replaced (prey unavailable or not caught), k increased [Table 1, Equation (4)] in proportion to the decrease in gut fullness (Figure 1) to simulate more active food searching. A final source of metabolic loss was SDA, a term representing the proportion of consumed food energy used for digestive processes (e.g. protein deamination, absorption of macromolecules, gut evacuation, and/or egestion; Beamish, 1974; Jobling, 1981). In the current model, SDA was set to a value of 0.1 (10%).

The maximum value of assimilation efficiency was based on laboratory measurements made by Kiørboe *et al.* (1987) on larval herring. The value of β was assumed to change with increasing larval size in a manner similar to that reported for summer flounder (*Paralichthys dentatus*) larvae by Buckley and Dillman (1982) [Table 1, Equation (5)]. The function for β was based on

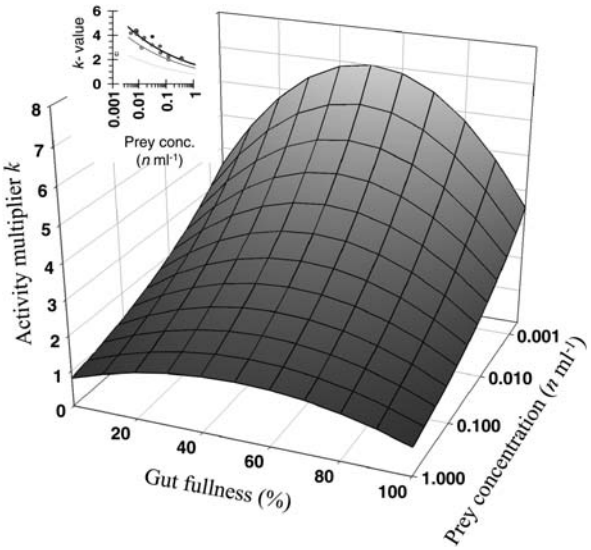

Figure 1. Values of the activity multiplier (k) used to modify metabolic losses by larval herring vs. the concentration of prey organisms (number l^{-1}), and for larvae with different amounts of prey within guts (represented using a percentage of gut fullness, %). Gut fullness was calculated as the quotient of gut content and maximum gut volume. Insert graph: relative changes in the foraging/swimming activity of herring larvae at different prey concentrations (including zero) reported by Kiørboe and Munk (1986).

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that used by Daewel *et al.* (2008a) and other IBMs created for temperate marine fish larvae.

Larval dw-at-L was parametrized based on morphometric data collected from 8.5 to 20 mm L herring reared at 7, 10, and 13°C (Hauss, 2008; MAP, unpublished data). Larvae growing at warmer (colder) temperatures exhibit higher (lower) dw-at-L [Equation (6)].

Optimal foraging

Larval herring have a low light threshold required for successful foraging (Batty, 1987) and, in the current model, foraging was only possible during daylight (the duration of the photoperiod). In the foraging routine, capture success (CS, prey s^{-1}) and handling time (HT, s) of specific prey sizes were functions of larval size. An optimal foraging approach was used (Letcher *et al.*, 1996; Kühn *et al.*, 2008), where different prey size classes (pL_i) were ranked [Table 1, Equation (7)] according to prey weight [pdw, μg; Table 1, Equation (8)] and CS [Table 1, Equation (9)], which depended on maximum ingestible prey size [Table 1, Equation (10)], handling time [HT; Table 1, Equation (11)], and encounter rate [ER, prey s^{-1}; Table 1, Equation (12)]. The functional response of HT was adopted from Walton *et al.* (1992), reparametrized using the measurements of Rosenthal (1969) on the amounts of time required for larval herring to (i) form the characteristic S-shape feeding strike posture and either (ii) successfully or (iii) unsuccessfully catch brine shrimp (*Artemia* sp. 500 μm) nauplii. The function for CS was adapted from that reported by Munk (1992), but a maximum ingestible prey length (pL_{max}) was included as suggested by Daewel *et al.* (2008a). Several studies have examined prey size selectivity and measured prey sizes found in the guts of larval herring. These data were summarized (Figure 2) and used to parametrize a function describing pL_{max} as a function of larval length [Table 1, Equation (10)].

Larval swimming and prey encounter

The prey encounter rate (number prey s^{-1}) was calculated based on the concentration of prey within a specific prey size class (pc_i, prey ml^{-1}) and larval foraging characteristics, such as pause frequency (PF, s^{-1}), pause duration (PD, s), reactive distance (RD_i, mm), and the velocity component V_i [mm s^{-1}; Table 1, Equation (13)]. All parameters, except PF and PD, were functions of prey size, with the subscript i representing the midpoint of a prey size class (Letcher *et al.*, 1996). The velocity component $V_i = (v_{p_i}^2 + v_L^2 + \omega^2)$ includes the turbulence velocity (ω = 1.3 mm s^{-1}; MacKenzie and Kiørboe, 1995), larval swimming speed (v_L), and prey velocity (v_{p_i}). Note that ω was set to zero in model runs simulating laboratory rearing.

The swimming speed (v_L) of herring larvae and post-larvae was examined in several earlier studies (Rosenthal, 1968; von Westernhagen and Rosenthal, 1979; Munk, 1992). The data reported in those studies were digitized and used to create a function describing v_L vs. fish length [L, mm; Table 1, Equation (14)]. The swimming speed of each prey size class i (v_{p_i}) was assumed to be 3 body lengths s^{-1} [Table 1, Equation (15)], an average value determined for different copepod species (Buskey, 1994; Mauchline, 1998) and also employed in other larval fish IBMs (Daewel *et al.*, 2008a). The values for PD and PF were set to 1.3 and 0.35, respectively, based on measurements made on herring larvae by Hauss (2008). The reactive distance [RD_i; Table 1, Equation (16)] was calculated for different prey length classes (pL_i, mm) using an angle of visual acuity [α; Table 1, Equation (17)] according to Breck and Gitter (1983).

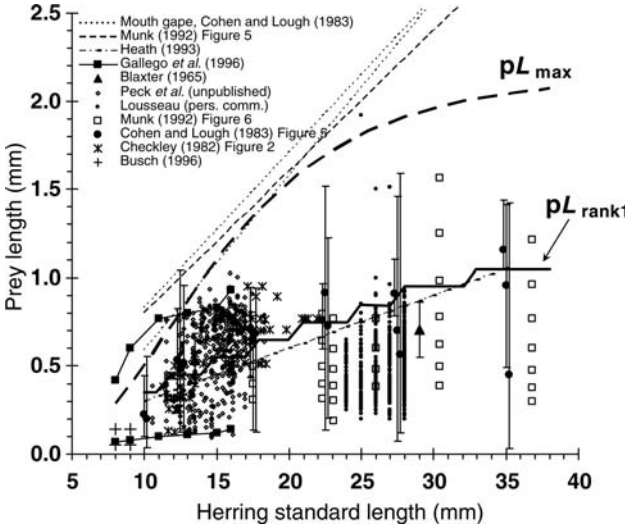

Figure 2. Size of prey observed in gut contents of larval herring as reported by different authors (see text for a detailed description). The dashed, thick line represents the estimates of maximum ingestible prey size (pL_{max}) calculated in the IBM. The solid thick line indicates the best prey category according to the ranking procedure, including catch success and handling time [Equation (7)]. Note that Checkley's (1982) prey width data were converted to length according to the relationships reported by Cohen and Lough (1983). Moreover, the mouth gape function of Cohen and Lough (1983) for 1975 was excluded because of the statement of the authors that two different measurement methods were used in that year.

Mechanistic limits to feeding rate

In each model time-step, the consumption of prey was limited by GC_{max} (μg), the gut evacuation rate (GER, h^{-1}), and the dry weight (μg) of earlier consumed prey. The GC_{max} [Table 1, Equation (18)] was estimated based on *in situ* gut contents of larval herring (Cohen and Lough, 1983; Pepin and Penney, 2000) indicating an upper limit of 5–6% of larval dw. The length-based GER [Table 1, Equation (19)] reported by Peck and Daewel (2007) was used. Furthermore, a sigmoid function was fitted to the GER data collected by Werner and Blaxter (1980) to account for higher evacuation rates observed during constant feeding conditions. The value for GER was multiplied by a constant feeding factor [cff; Table 1, Equation (20)] that was a function of prey concentration.

Larval morphometrics, condition, and growth partitioning

A dynamic growth allocation was included that accounted for the momentary larval condition based on its temperature and feeding history [Table 1, Equation (21)]. The quotient of the actual (current) dw and a reference dry weight (dw_1, μg; calculated with the temperature history, compare Table 1 Equation (6)] was considered a condition index (CI). If the CI was <0.65, the larva was assumed to die of starvation and was removed from the simulation. Excess assimilated food energy (above metabolic costs) was allocated to length growth [plg = proportion of dry weight available for length growth; Table 1, Equation (22)], and the remaining portion was allocated to larval dw. For example,

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larvae with a CI of 0.65 (poor condition, low dw) and 1.35 (highest observed in the laboratory) allocated all excess food energy to increase dw and length, respectively. Length was increased without changing the current CI of the larvae, whereas weight allocation allowed condition to increase or decrease. It was impossible for a larva to lose length. The CI decreased when assimilated food energy did not cover metabolic costs. This allocation scheme represented a biologically reasonable allocation and was needed to match inter-individual variability in dw-at-L observed during larval rearing.

Model sensitivity and validation

Sensitivity analysis

A sensitivity analysis was done using methods comparable with those employed by Megrey and Hinckley (2001). Parameter values were perturbed ($\pm$30, 50, and 100%) and the growth rate (mm d^{-1}) to 20 mm L was determined for larvae feeding at an intermediate prey concentration (pc, 0.1 prey ml^{-1}). The percentage deviation between modelled and observed (*in situ*, Oeberst *et al.*, 2009) growth rates was calculated and compared with the (randomized) input parameters using Spearman's rank correlation.

Parametrizations of validation scenarios

In all, eight different validation scenarios were examined. First, comparisons were made between modelled and observed/measured values (e.g. duration of survival for unfed larvae, rates of feeding by larvae, gross growth efficiency). Second, modelled and observed growth rates for larvae in controlled laboratory conditions were compared. In this case, model larvae experienced conditions (e.g. temperature, daylength, and prey size) that matched those reported for larvae reared by Kiørboe and Munk (1986, scenario 1), Kiørboe *et al.* (1987, scenario 2), Werner and Blaxter (1980, scenario 3), Pederson (1993, scenario 4), and Geffen (1996, scenario 5; Table 2). In a third type of validation, prey concentrations required in the model to re-create *in situ* larval growth rates (e.g. based on otolith analyses) were compared with *in situ* prey concentrations. Model prey field requirements were estimated based on *in situ* larval growth rates reported by Bolz and Burns (1996, scenario 6), Henderson *et al.* (1984, scenario 7), and Oeberst *et al.* (2009, scenario 8). For the validation of scenarios 6–8, turbulent velocity (ω) was set to 1.3 mm s^{-1} and the model used *in situ* temperature and photoperiod and a prey size spectrum (PSS) according to Daewel *et al.* (2008a).

Model application: predicting suitable spawning seasons

Environmental variability: temperature, prey, and daylength

The model was applied to estimate the effect of different environmental factors on larval growth and survival. Latitude, temperature cycle, prey abundance, and prey length frequency distributions were varied randomly within realistic seasonal ranges to simulate different magnitudes of annual variability. In all, 45 000 different simulations were done, each using 365 different starting calendar days. For each calendar day, the time required for larvae to achieve 20 mm L and a survival index was calculated. The latter was based on both mortality and growth rates. In the following section, we discuss how various input parameters were varied and how the survival index was calculated.

Temperature was simulated as a sine function that could vary in the timing of the peak (χT_1) and in the annual mean value [χT_2; Table 1, Equation (23)], where $5 \leq \chi T_1 \leq 15$ and $100 \leq \chi T_2 \leq 150$ were drawn from uniform and random distribution, respectively, and cd = calendar day. The seasonal temperature cycle (Figure 3a) was modelled as a sine function that was adjusted to match water temperatures in the North Sea ($\leq$50 m depth, 51–63°N) predicted from the three-dimensional hydrodynamic HAMburg Shelf-Ocean-Model (HAMSOM; Pohlmann, 2006) and the minimum and maximum sea surface temperatures reported by ICES (2008). Seasonal differences in daylength were varied indirectly via the latitude [Equation (24), where $50 \leq \chi\text{lat} \leq 61$ and $\chi\text{lat} \in \mathbb{N}$, uniform, random distribution].

A Gaussian distribution in prey concentration was assumed (Figure 3b) that had a randomly varying offset, mean, and standard deviation [Equation (25), where $0 \leq \chi\text{pc}_1 \leq 0.01$, $70 \leq \chi\text{pc}_2 \leq 130$, and $133 \leq \chi\text{pc}_3 \leq 247$, uniform, random distribution]. The Gaussian distribution was adjusted to encompass

Table 2. IBM settings used for eight different validation scenarios comparing model and observed larval herring growth rates or prey requirements.

Validation scenario	Reference	Temperature (°C)	Daylength (h)	Prey type (dry weight)	Prey size (µm)	Prey concentration
(i)	Kiørboe and Munk (1986; KM86)	8	14	*Acartia tonsa* nauplii	250 $\pm$ 30	$<$0.4 *n* ml^{-1}
(ii)	Kiørboe *et al.* (1987)	8	14	*Acartia tonsa* copepodites	400 $\pm$ 25	0.12 *n* ml^{-1}
(iii)	Werner and Blaxter (1980; WB80)	9	14	*Artemia* nauplii	440 $\pm$ 30	0.03, 0.1, 0.3, 1, 3 *n* ml^{-1}
(iv)	Pederson (1993)	11	15	*Acartia tonsa* nauplii	250 $\pm$ 30	78–359 *n* ml^{-1} (varied daily accord. to ref.)
(v)	Geffen (1996; G96)	10	16	Rotifers *Artemia* + rotifers	280 $\pm$ 30 440 $\pm$ 30	10 *n* ml^{-1}, 3 + 5 *n* ml^{-1}
(vi)	Bolz and Burns (1996; BB96)	5 to 17	9	PSS	PSS	Estimated with model
(vii)	Henderson *et al.* (1984; H84)	11 to 14	15	PSS	PSS	Estimated with model
(viii)	Oeberst *et al.* (2009; O09)	2 to 20	9–15	PSS	PSS	0.064–1.024 *n* ml^{-1}

In scenarios 6–8, a prey size spectrum (PSS) was employed [see Table 1, Equations (8) and (27)].

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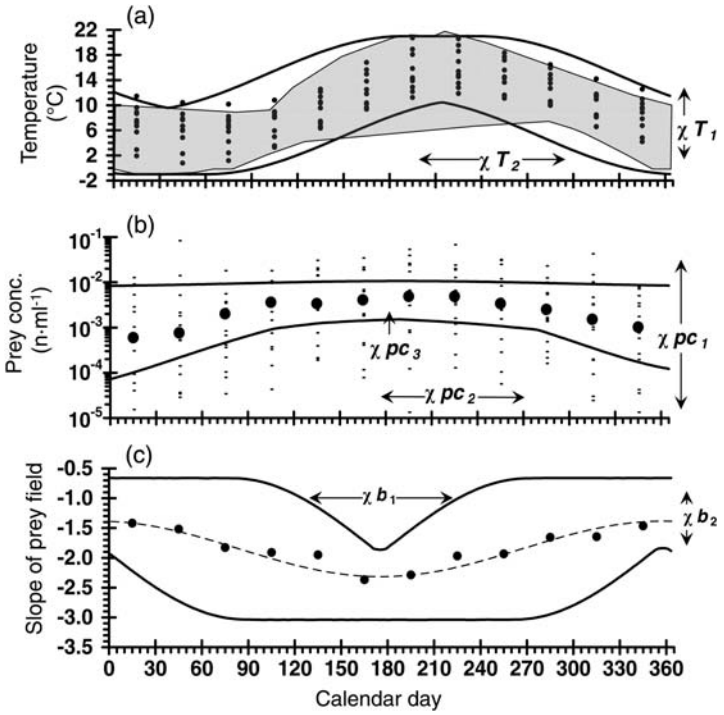

Figure 3. Seasonality in key environmental factors utilized in IBM scenarios performed on larval herring. Dots refer to observations, solid lines to maximum and minimum values of all simulations. (a) Water temperature. Grey shaded areas indicate the variability (minimum and maximum values) from 1970 to 2005 of North Sea-wide sea surface temperatures (<50 m) obtained from the hydrodynamic model "HAMSOM" (Pohlmann, 2006). Datapoints are "Reynolds surface temperatures" as reported in ICES (2008). (b) Daily total prey concentration. Black lines indicate minimum and maximum values of the scenarios, whereas large and small datapoints are *in situ* data and mean North Sea zooplankton concentrations reported in ICES (2008). (c) Slope of the prey size spectrum. Dashed and solid lines represent the mean and minimum and maximum simulated values, respectively. Datapoints are values from the Stonehaven long-term zooplankton dataseries (supplied by M. Heath, University of Strathclyde).

long-term zooplankton concentrations compiled by ICES (2008) at four North Sea locations (Arendal, Helgoland, Plymouth, and Stonehaven). The total prey concentration (pc, prey ml^{-1}) was allocated within 14 prey length classes of 100 μm (pc_i = 100–200, 201–300, …, 1401–1500 μm) based on a relative prey length frequency distribution [Table 1, Equation (26)], and the slope (b) of the logarithmic relationship between prey length and prey size was varied seasonally [Table 1, Equation (27) with $87.5 \leq \chi b_1 \leq 262.5$ and $0.21 \leq \chi b_2 \leq 1.19$, uniform, random distribution] based on monthly slope values from the Stonehaven zooplankton time-series (M. Heath, University of Strathclyde, pers. comm.; Figure 3c). Additionally, the prey dry weight-at-length [pdw; Table 1, Equation (8)] for each prey size class was varied ±30% using a uniform, random distribution.

Mortality

Herring cohorts experienced different exponential daily mortality rates. Two mortality rates were constant (Z_{const}, d^{-1}) at 0.02 or 0.06 d^{-1} and two others were size- (weight-) based formulations reported by Peterson and Wroblewski (1984) [PW mortality = $5.26 \times 10^{-3}(0.001\ dw)^{-0.25}$] or McGurk (1986) [McG mortality = $2.20 \times 10^{-4}(0.001\ dw)^{-0.85}$]. At 10°C, values of PW ranged between 0.07 and 0.03 d^{-1} for 7 and 20 mm L larvae, respectively. Under similar conditions values of McG ranged between 1.41 and 0.05 d^{-1}. Finally, a seasonally varying mortality rate was applied where the highest and lowest rates were assumed to occur during summer and winter, respectively. A sine function [Table 1, Equation (28)] modulated mortality rate based on mean temperature [Table 1, Equation (23)] with $0 \leq \chi sZ \leq 0.4$ in a uniform, random distribution. When $\chi sZ = 0$, mortality was not seasonal and when $\chi sZ = 0.4$, the mortality rate increased and decreased by 40% during the warmest and coldest periods, respectively.

Analysis of the simulations and modelled survival index

In all, 45 000 simulations were done, which allowed for a coverage of sufficient combinations of the nine randomly varying environmental factors [χ; to achieve at least three states (low, medium, and high) a minimum of 3^9 (19 683) simulations were required]. On each hatch date (calendar day) of a simulation, the time required for the larvae to reach 20 mm L was determined. The development time was correlated with each of the randomly varied parameters on each start date to identify which parameters were most influential. Only significant correlations (F-tests, significance level $p < 0.05$) are displayed and discussed.

A "successful" run was defined as one where larvae could grow to 20 mm L. The number of successful runs was tallied for each calendar day and divided by the total number of simulations; then this fraction was used as a measure of "suitability". Low values reflect days when spawning would not be favourable for offspring survival in a long-term (evolutionary) sense. Next, the percentage of remaining (20 mm L) individuals within each cohort was determined (based on the two constant, PW, and McG mortality simulations). Finally, for each day, a normalized

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"suitability/survival index" was calculated with the fraction of successful runs multiplied by the remaining fraction of starting individuals. Moreover, the survival index was normalized to the annual maximum number of successful individuals obtained for each of the different (constant, PW, or McG) mortality settings to normalize for the large differences in annual survival. This relative survival index has a range of values between 0 and 100. High values represent a high suitability and high probability of larvae survival.

To reveal factors that constrain potential hatch periods for spring and autumn spawners, the total number of successful (suitable) hatch days was summed between day 40 (10 February) and day 183 (3 July), and 183 and 325 (22 November), respectively. The number of potential hatch days and/or the duration of the successful hatch period was related and correlated with the randomized parameter values to determine the main environmental drivers acting during both periods on growth and suitability of the hatch day.

Results

Sensitivity

After a 30, 50, or 100% perturbation, ten model parameters significantly influenced modelled temperature-dependent growth rates (Table 3, only 100% presented, because other results were comparable). Growth rates were most sensitive to changes in assimilation efficiency. Gut volume and gut evacuation rate, maximum ingestible prey size, and respiration rate also significantly ($p < 0.01$) influenced growth. Angle of visual acuity (α), which determines reactive distance and therefore encounter rate, was also a sensitive parameter.

Table 3. Results of a sensitivity analysis (100% parameter perturbation) for an IBM simulating the foraging and growth of larval herring.

Parameter	r^2
Assimilation efficiency (β)	0.396
Gut content (GC_{max})	0.333
Maximum prey size (pL_{max})	0.322
Gut evacuation rate (GER)	0.236
Respiration rate (R)	−0.214
Angle of visual acuity (α)	−0.213
Pause frequency (PF)	0.097
Activity multiplier (k)	−0.087
Catch success (CS)	0.078
Specific dynamic action (SDA)	−0.070

Only those model parameters that significantly ($p < 0.01$, Spearman's rank correlation) influenced temperature-dependent larval growth rates in length are listed.

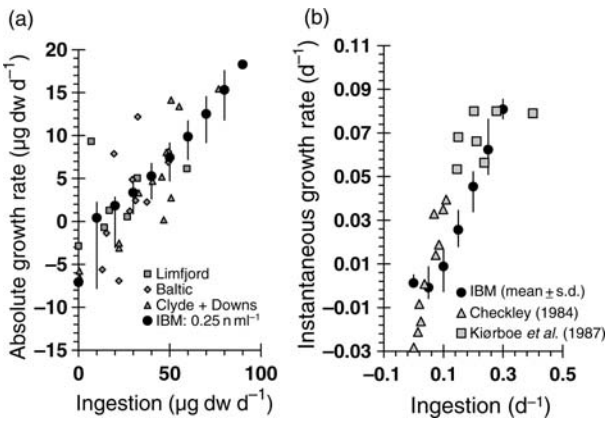

Figure 4. Comparison of IBM and field estimates of larval herring growth rate at the same temperatures and within comparable prey fields. (a) Validation scenario (i): absolute growth rate of Limfjord, Clyde, and Baltic herring reported by Kiørboe and Munk (1986) compared with model results at the same water temperature (8°C) and prey conditions (250 particles l^{-1}). (b) Validation scenario (ii): instantaneous growth rate (d^{-1}) vs. instantaneous ingestion (d^{-1}) reported by Checkley (1984) and Kiørboe *et al.* (1987) compared with model estimates.

Validation scenarios

A number of basic model outputs of larval growth physiology was compared with measured values (see Discussion). For example, assuming a start condition of CI = 1.0 (start dry weight = reference dry weight) or CI = 1.3 (start dry weight 30% higher than reference dry weight), first-feeding larvae survived for 130 and 170°d, respectively, without food. Starved larvae at 7, 13, and 17°C survived 61, 52, 42 (low start condition: CI = 0.8, start dry weight 20% lower than reference dry weight), 120, 102, 86 (intermediate start condition: 1.0), and 194, 168, 140 h (CI = 1.3), respectively.

Validation of larval physiology

When fed at *ad libitum* (total prey concentration of 2 ind. l^{-1}), weight-specific food consumption rates (% dw d^{-1}) were 20–30 and 40–50% at 4 and 16°C, respectively, and these rates decreased with increasing larval L and dw. Under these feeding conditions, between 10 and 30 individual prey items (of the preferred prey size class) were present in larval guts and the number of prey consumed each day varied between 50 (4°C) and 250 (16°C) prey items, respectively. Growth efficiency [GGE (%) = 100 G C^{-1}] of 11 mm L larvae was 20–25% at cold water temperatures (2°C), and asymptotically increased at 4, 8, 12, and 16°C to 35, 40, 45, and 50%, respectively.

Validation scenarios (i)–(viii)

(i) Modelled (absolute) growth rates increased from 0 to 15 µg dw d^{-1} at prey consumption rates of 0–80 µg dw d^{-1}. Growth rates observed by Kiørboe and Munk (1986, Figure 4a) ranged between −5 and 15 µg dw d^{-1} at comparable prey concentrations. Modelled (weight-specific) growth rate (% d^{-1}) increased from −6 to 5% d^{-1} at prey concentrations between 0.2 and 38.6 µg l^{-1}. At similar prey concentrations, Kiørboe and Munk (1986, Figure 5a) reported growth rates within the same range.

(ii) Modelled (instantaneous) growth rate increased from 0 to 0.09 d^{-1} at prey consumption rates between 0 and 0.3 d^{-1}. Modelled rates slightly underestimated growth measurements made by Kiørboe *et al.* (1987) and those based on nitrogen uptake determined by Checkley (1984, Figure 4b).

(iii) Modelled (weight-specific) growth was 5.9, 6.3, 8.0, 12.2, and 12.6% d^{-1}, at prey concentrations of 39, 129, 387, 1288, and 3866 µg l^{-1}, respectively. At similar concentrations, Werner and Blaxter (1980, Figure 5a and c) reported mean growth rates of 4.3, 8.4, 9.3, 8.0, and 8.22% d^{-1}, but their highest

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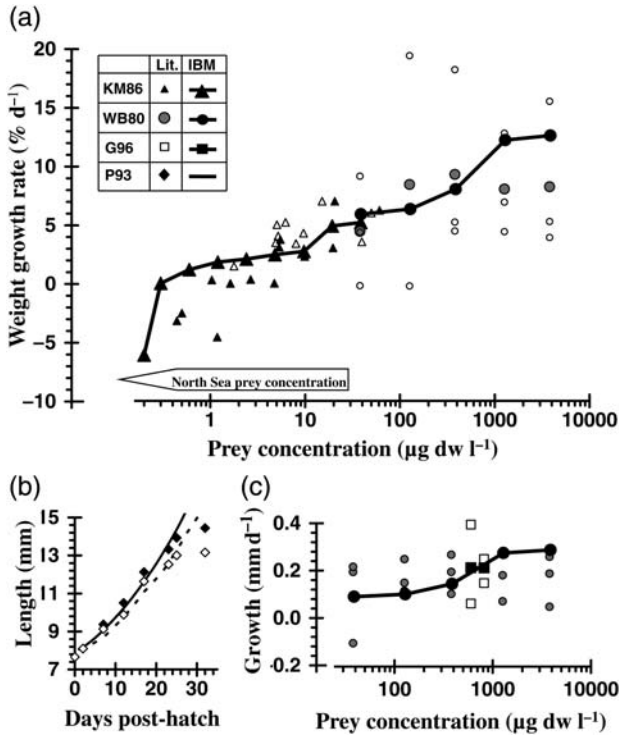

Figure 5. Comparison of modelled and observed larval herring growth rates in weight and length vs. prey concentrations. (a) Validation scenarios (i) and (iii): specific growth rate (% d^{-1}) vs. prey concentration reported by Kiørboe and Munk (1986; KM86) and Werner and Blaxter (1980; WB80). Unfilled and filled triangles represent data compiled from other studies and those measured by KM86, respectively. Small and large grey circles represent the observations and mean values of WB80. Comparison of length- and/or weight-at-age reported for laboratory-reared herring larvae and predicted by the IBM using laboratory temperatures and prey (8°C, 0.25 prey ml^{-1} copepod nauplii). (b) Validation scenario (iv): length (mm) at age (dph) reported by Pedersen (1993) for herring larvae fed at high (filled diamonds: observations, solid line: model) and varying (open diamonds observations, dotted line: model) food rations. (c) Length growth of herring larvae reported by Geffen (1996; G96) and Werner and Blaxter (1980; WB80) compared with model results [validation scenarios (iii) and (v)] utilizing the same prey size spectra (or rotifers). For settings, see Table 2.

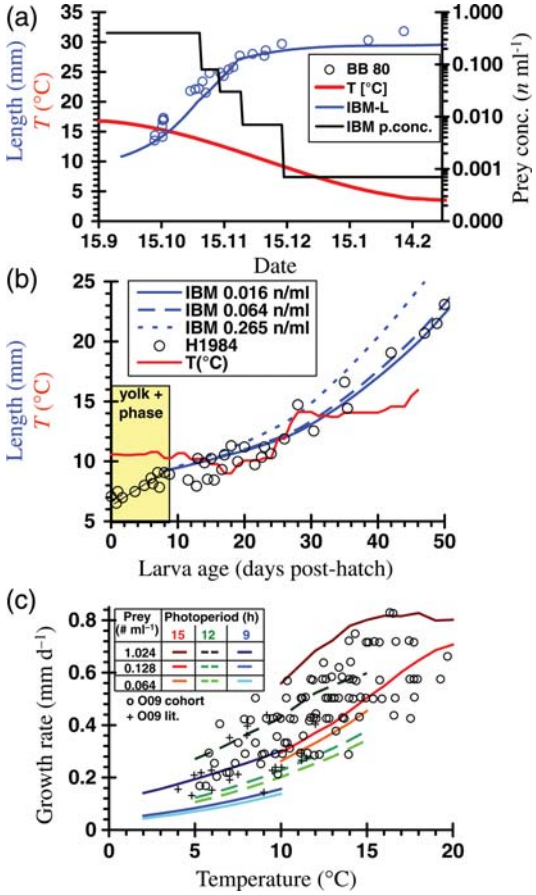

Figure 6. (a) Validation scenario (vi): length-at-age data (open circles) determined by Bolz and Burns (1996; BB80) plus modelled length (blue) and required prey concentrations (black) at given temperature (red). (b) Validation scenario (vii): length-at-age (open circles) and temperature (red) data observed by Henderson *et al.* (1984; H84) and modelled length assuming three different prey concentrations (blue). (c) Validation scenario (viii): modelled larval herring growth rates (solid and dashed lines) at different temperatures, prey concentrations, and photoperiods (feeding daylengths) compared with growth rates reported by Oeberst *et al.* (2009; O09) for Baltic herring. Crosses indicate data from the literature search done by them, and circles are based on cohort studies observed in their study.

and lowest values ranged between −0.22 and 19.4% d^{-1} (Figure 5a).

(iv) Modelled length-at-age data were close to those observed in laboratory trials done by Pedersen (1993, Figure 5b, $r^2 = 0.92$). On day 32, observed growth rates declined and modelled estimates were higher.

(v) Modelled (L) growth rates were 0.22 mm d^{-1} in relation to mean growth rates of 0.20 and 0.23 mm d^{-1} (range 0.06–0.25 mm d^{-1}) observed by Geffen (1996, Figure 5c).

(vi) A winter prey concentration of 0.0007 particles ml^{-1} was needed for overwintering herring larvae at the assumed temperature (~5°C) and length (25–30 mm). Prey concentrations during the first-feeding phase were 0.08–0.4 prey ml^{-1} (Figure 6a).

(vii) Constant prey concentrations of 0.016 to 0.265 prey ml^{-1} were needed at the observed temperatures (11–15°C) to match reported L-at-age and growth rates (Figure 6b).

(viii) At various prey concentrations, modelled growth rates overlapped with observed (field) growth rates reported by Oeberst *et al.* (2009). Growth rates ranged between 0.13 and 0.85 mm d^{-1}, depending on temperature (2–20°C), prey concentration (0.064–1.024 prey ml^{-1}), and feeding daylength (9–15 h; Figure 6c).

Application of the model: predicting suitable spawning seasons

Only 20% of simulations were successful between release days 149 (28 May) and 251 (3 September), with only 10% successful between days 169 (13 June) and 229 (31 July; Figure 7b). Mean

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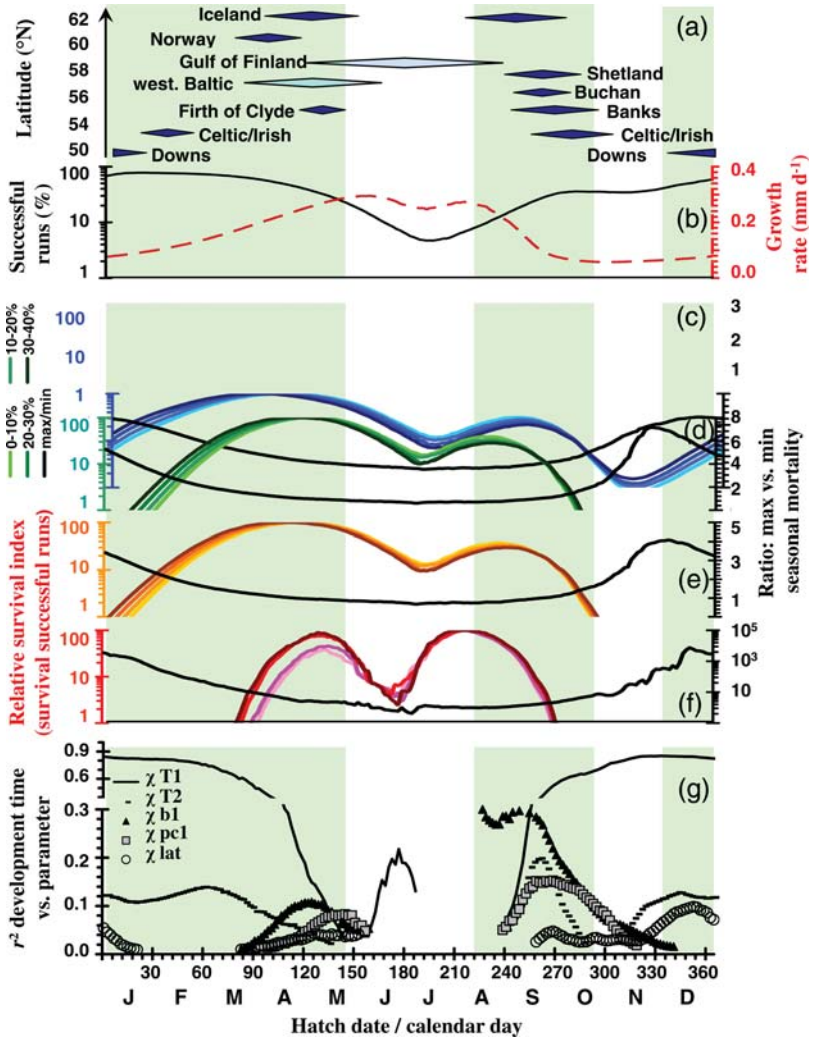

Figure 7. (a) Summary of the seasonal timing of larval hatch for various herring populations in the Northeast Atlantic compared with various model outputs including (b) the percentage of simulation runs where herring larvae reached a size of 20 mm *L* and mean herring growth rate of 20 mm Ld^{-1}, (c) values of a model "survival index" calculated using three different mortality scenarios: constant mortality $Z = 0.02\ d^{-1}$, (d) $Z = 0.06\ d^{-1}$, (e) length-based according to Peterson and Wroblewski (1984), and (f) to McGurk (1986). Darkest colours always represent the mean of runs where seasonal *Z* was between 30 and 40%. The lightest colours represent runs where sZ = 0 to 10%. (g) Daily values of the coefficient of determination (r^2, $p < 0.05$) for linear regressions of development time vs. each of five randomly varied environmental parameters.

development time was longest (173 d) in autumn for releases made on day 299 (27 October) and shortest (34 d) during summer where growth rates reached 0.29 mm d^{-1} for larvae released on day 151 (1 June; Figure 7b).

For the three mortality scenarios, the relative survival indices peaked in spring and displayed a second, smaller peak in late summer or autumn (Figure 7c–f). Maximum survival for the constant mortality ($Z = 0.06$) and PW weight-based mortality happened on days 121 (2 May) and 231 (20 August), and days 115 (26 April) and 239 (21 October), respectively. Assuming a higher length-based mortality rate (McG), the peak in the survival index was shifted towards warmer (summer) temperatures and happened on days 127 (8 May) and 211 (31 July).

Mean temperature (χT_1) had the greatest influence ($r^2 = 0.8$) on development time (growth rate), with larvae at higher temperatures growing more rapidly to 20 mm (Figure 7g). The timing of the minimum slope of the prey size spectrum was correlated negatively with development time during late spring and early autumn and explained 30% of growth variability. Growth rates declined as the timing of the minimum value [Table 1, Equation (27)] was shifted earlier in the year (Figure 3c). Latitude explained 10% of growth variability during autumn and winter, and growth rates declined with increasing latitude. The parameter representing minimum prey concentration (χpc_1) was negatively correlated with larval development time between October and March (Figure 7g), and it explained 15% of growth variability.

For spring-hatched larvae, successful development to 20 mm *L* was generally associated with low annual mean and delayed (later) maximum temperatures (Figure 8a and b). Additionally, a late, large zooplankton bloom increased the survival of spring-hatched larvae (Figure 8d and f). Autumn-hatched larvae depended more on low temperatures than spring-hatched larvae (Figure 8a). Larger prey during winter favoured the survival of autumn-

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hatched larvae and more successful simulations happened at day-lengths characteristic of lower latitudes (Figure 8c).

The length of the possible spring and autumn hatch periods was mainly influenced by mean annual temperature, minimum prey concentration, and minimum of the slope of the prey size spectrum (Table 4, Figures 7g and 8). The duration of potentially successful hatching days increased with decreasing temperature and increasing prey concentration. Additionally, the timing of the peak zooplankton abundance (χb_1) increased the length of the successful hatch period when it happened later (earlier) in spring (autumn), respectively.

The effect of seasonally varying mortality depended on whether constant or weight-based schemes were applied. Applying seasonal varying constant mortality shifted the maximum survival probability towards summer; winter survival doubled when a 30–40% decrease in seasonal mortality was included. These effects increased if a weight-based mortality scheme was assumed, but the shift in successful runs towards summer was less pronounced (Figure 7c–f).

Discussion

The IBM presented in this study is similar in many facets to earlier models built to understand aspects of the foraging and growth of marine fish larvae, including prey capture (Drost *et al.*, 1988; Heath, 1993; Caparroy *et al.*, 2000), and the roles of turbulence (Dower *et al.*, 1997; Fiksen and Folkvord, 1999; MacKenzie and Kiørboe, 2000; Franks, 2001) or patchy prey distributions (Pitchford *et al.*, 2003). Our model also complements other, bioenergetics-based models developed to explore seasonal growth dynamics in juvenile and adult herring (Arrhenius and Hansson, 1993; Arrhenius, 1998; Maes *et al.*, 2005), predator–prey match–mismatch (Letcher and Rice, 1997), or larval growth in relation to food intake (MacKenzie *et al.*, 1990). Some models have attempted to represent all herring life stages (Rudstam, 1988), with the most recent efforts focused on coupling lower- and upper-trophic level models (Megrey *et al.*, 2007; Rose *et al.*, 2008). Naturally, all these models were designed to answer different questions, and their different structures make direct comparisons difficult, if not impossible. The current model was also designed to answer a specific question: how does variability in a suite of bottom-up (climate-driven) factors influence the survival and growth of young (premetamorphic) herring larvae? Below, we discuss the model structure and its sensitivity, as well as the results of scenarios that suggest constraints on the timing of profitable spawning by herring in light of continuing changes in climate-driven factors.

Parameters and sensitivity

Model estimates were quite sensitive to parameters, such as β, R, or SDA, directly included in the backbone equation [Equation (2)] of the model, but also to GC_{max}, pL_{max}, GER, α, PF, k, and CS (Table 4). In the following sections, we discuss our basis for formulating these parameters.

Yolk-sac larvae

The growth and development of the earliest larval stage (yolk-sac and first-feeding larvae) were depicted by a relatively simple, temperature-dependent function indicating survival (on yolk only) for 59°d. Similar yolk-sac stage durations have already been reported. For example, yolk-sac stage durations have been reported as between 60°d (12°C, 5 d; Bang *et al.*, 2007) and 67°d (8°C, range 4.5–14.0 d among Atlantic stocks; Blaxter and Hempel, 1963). The yolk-sac duration of Pacific herring (*C. pallasi*) was reported to be somewhat shorter. McGurk (1984) reported a slightly shorter duration (40°d, 6°C, 6 d; 8°C, 5 d; 10°C, 4 d) for unfed larvae and observed signs of starvation of feeding larvae between 72 and 90°d (6°C, 12 d; 8°C, 11 d; 10°C,

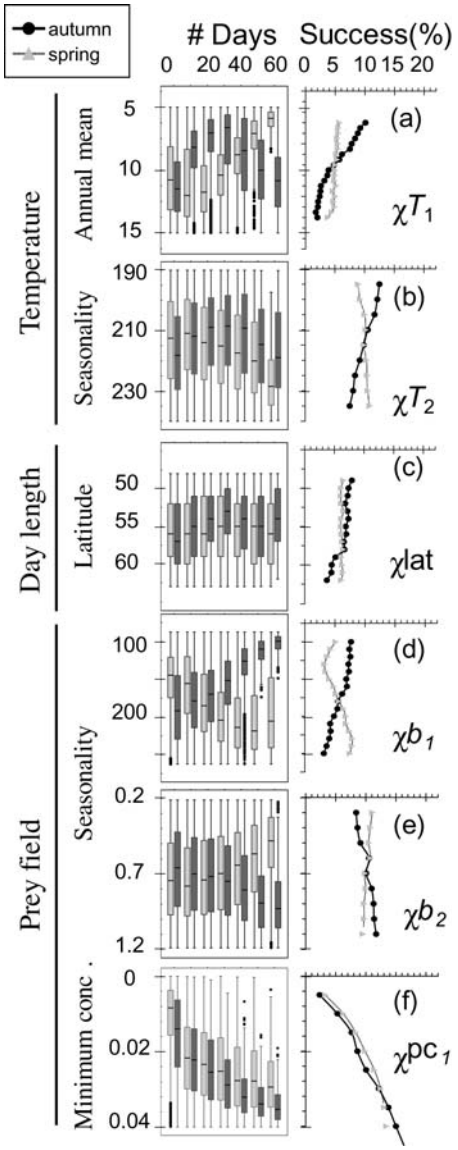

Figure 8. Influence of modelled environmental parameters on the maximum possible time window of successful spawning (time window of larval survival). Parameters from top to bottom are: (a) χT_1, mean annual temperature; (b) χT_2, time of maximum temperature; (c) χlat, latitude; (d) χb_1, annual difference (amplitude) of the value for the slope of the zooplankton size spectrum; (e) χb_2, timing of the minimum of the slope function; and (f) χpc_1, minimum annual prey concentration. The right column is the relative fraction of successful runs (in relation to all successful runs) for autumn (black) and spring (grey) periods. The left column displays the parameter values used in the simulations vs. the length of the possible spawning period plotted. Lines indicate the median, boxes the 25 and 75% confidence intervals. Whiskers represent all values within two times the box length, dots are outliers (values more than two times the box length).

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Table 4. Best-fit model (linear, squared, cubed, or exponential) and corresponding correlation coefficients (r^2) for the duration of the possible spawning period (days, dependent variable) vs. changes in each parameter (independent variable) for either spring (days 40–183) or autumn (183–225).

	Spring				Autumn			
	All runs		Successful runs		All runs		Successful runs	
Variable	Model	r^2	Model	r^2	Model	r^2	Model	r^2
χT_1	Linear	−0.160	Linear	−0.232	Squared	−0.105	Squared	0.076
χT_2	Linear	+0.035	Linear	+0.046	Linear	−0.014	Exponential	−0.002
χb_1	Cubed	+0.185	Exponential	+0.133	Squared	−0.147	Squared	−0.226
χb_2	Linear	−0.030	Cubed	−0.046	Linear	+0.026	Linear	+0.032
χpc_1	Squared	+0.267	Linear	+0.061	Squared	+0.230	Squared	+0.160
χpc_2	Linear	−0.007	Linear	−0.002	Linear	−0.003	Linear	−0.005
χpc_3	Linear	−0.004	Linear	−0.001	Linear	+0.006	Linear	+0.004
χlat_3	–	–	Linear	–	Linear	−0.026	Exponential	−0.012
χdw_{prey}	–	–	Linear	–	Linear	+0.001	Linear	–

Values are included for all runs and only for successful runs (those that do not include zero values). Negative and positive signs in front of each r^2 value refer to negative and positive correlations, respectively.

9 d). Additionally, the yolk duration was comparable with the function used by Fey (2001): yolk phase duration = 13.82 − 0.614 *T*.

First-feeding larvae

A key parameter for early feeding success is the size of larvae at first-feeding, because this affects prey-field utilization and other developmental attributes (e.g. assimilation efficiency, gut evacuation rate). Although herring larvae can feed during the latter portion of the yolk-sac phase, prey size appears to be limited by yolk volume (Busch, 1996). The length at first-feeding depends on the herring stock, but appears to be >8 mm *L*, based on gut content analyses, field samples, and laboratory experiments (Checkley, 1982; Cohen and Lough, 1983; McGurk, 1984). Field-caught larvae >12 mm *L* do not have a yolk sac (Lebour, 1921; Fox *et al.*, 1999) and exhibit different swimming activities in the laboratory than smaller larvae (Batty, 1987).

Assimilation efficiency

The results of the sensitivity analysis done here (and those done for other larval fish IBMs) suggested that assimilation efficiency (β) was a key parameter influencing larval growth rates (Table 3). Unfortunately, β is a difficult physiological parameter to measure in young fish larvae, because excreted nitrogenous products of catabolism are mixed with soluble faecal material. Estimates for different species ranged between 67 and 99% (Govoni *et al.*, 1986; Peck and Daewel, 2007). Fortunately, previous studies have estimated β in larval herring, finding nitrogen absorption coefficients between 48 and 83% (Klumpp and von Westernhagen, 1986) and carbon assimilation of 90% (Pedersen and Hjelmeland, 1988). Lower values of the former (38.5–68.2%, depending on prey concentration) were measured for Pacific herring larvae by Boehlert and Yoklavich (1984). An ontogenetic increase in β has been assumed in various studies (e.g. Blaxter and Hunter, 1982; Govoni *et al.*, 1986; Peck and Daewel, 2007) and was also assumed here, based on increasing efficiency of digestion related to differentiation of the digestive tract during early ontogeny.

Maximum gut volume

Maximum gut volume was slightly higher in the model than that reported for field-caught larvae (Pepin and Penney, 1997), because of two potential caveats. First, *in situ* prey conditions might not allow *ad libitum* feeding and therefore result in an underestimation of absolute GC_{max}. For example, Cohen and Lough (1983) reported only 30% feeding incidence; Rosenthal and Hempel (1971) observed that herring larvae usually egested portions of their gut contents during catch, which might result in underestimates of GC_{max}. Busch *et al.* (1996) indicated that gut content of anaesthetized larvae could be lost within 5 min. In a literature search for maximum prey biomass (in the gut), Peck and Daewel (2007) determined a general ratio of 6.4% larval fish dry weight.

Maximum prey size

Model-derived estimates of growth were also sensitive to changes in the maximum prey size; therefore, a thorough review of the literature is warranted to corroborate our pL_{max} parameter and how this changes with larval size. Busch (1996) reported that the size of the oesophagus limits the size of prey ingested at first-feeding; a statement that contrasts with earlier studies assuming that mouth gape was the only factor limiting prey size. At this early stage, ingested prey sizes have been reported to be 50–80 μm (Blaxter and Hunter, 1982; Spittler *et al.*, 1990). Fossum and Moksness (1993) reported that larvae switch from consuming copepod eggs to nauplii after 1 week, and Checkley (1982) reported a switch from nauplii to copepodites at 17 mm *L*. Fox *et al.* (1999) reported that herring larvae positively select prey >150 μm (7–15 mm *L*). Munk (1992) and Cohen and Lough (1983) determined linear relationships between mouth gape and larval *L*, which agree well with other reports of maximum observed prey sizes in the guts of first-feeding to 25 mm *L* herring (Checkley, 1982; Cohen and Lough, 1983; Gallego *et al.*, 1996; Hauss and Peck, 2009; Figure 2). For herring >25 mm *L*, the mouth gape functions overestimate maximum observed prey sizes (Figure 2), which apparently are limited to 1600 μm (Cohen and Lough, 1983; Munk, 1992). Within a large dataset on the gut contents of 24–28 mm *L* herring (S. Lusseau, Marine

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Laboratory, Aberdeen, unpublished data), only a single, 1900-μm prey item was observed. It appears that, for larvae >25 mm *L* (larger than the larvae modelled here), mouth gape is not the factor limiting prey size, but that some other factor(s), e.g. oesophagus width, is (are) operating.

Gut evacuation rates

Gut evacuation rate estimates used in this study agree well with those reported in various studies (e.g. for reviews, see Govoni *et al.*, 1986). The temperature term (Q_{10} of 2.52) was derived from the increase in larval herring GER from 7.8, 9.1 to 15.0°C reported by Blaxter (1965) and Werner and Blaxter (1980) and was comparable with that (2.4) reported for herring larvae by Blaxter (1962). Estimates of herring GER include 4–10 h in 10–15 mm *L* larvae (Rosenthal and Hempel, 1971), 0.66–3 h in 22–52 d post-hatch (dph) larvae at 9.5°C (Pedersen, 1984), and 4–8 h at different body sizes and temperatures (Blaxter, 1965).

One key factor is the potential increase in GER at high prey concentrations. Rosenthal and Hempel (1971) reported that GER in 10–15 mm *L* was more rapid in completely filled guts than in guts that were one-third full. Werner and Blaxter (1980) reported that GER increased by a factor of 7–9 as prey concentration increased from 0.03 to 30 *Artemia* nauplii ml^{-1}. Boehlert and Yoklavich (1984) reported decreases in assimilation efficiency with increasing prey concentration, but calculated that larval Pacific herring still would have an exponential increase in the growth rate with increasing prey concentration, which is most likely not the case in the field. A more physiologically reasonable expectation would be a sigmoid function, because, at very high GER, prey passes through the guts too rapidly for adequate digestion (Werner and Blaxter, 1980). Furthermore, at very high GER, energy could be lost via defaecation of enzymes as observed for stressed herring larvae (Pedersen and Hjelmeland, 1988). Assimilation efficiency could possibly decrease at very high prey concentrations, which might explain why our model slightly overestimates the growth of laboratory fish feeding at high prey concentrations. It must be emphasized that our literature review on "average" prey concentrations in the field suggests that herring are unlikely to find such high *in situ* prey concentrations during winter.

Respiration

The level of energy lost via metabolism is a key model component for feeding larvae, because it sets basal (maintenance) requirements that must be met before larvae apportion energy into positive somatic growth. Measurements of the rate of respiration (*R*, μl O_2 $larva^{-1}$ h^{-1}) have been made for inactive, quiescent (anaesthetized) herring larvae (R_s = standard respiration; Kiørboe *et al.*, 1987) and during routine foraging activity (R_r = routine respiration) by Almatar (1984) and MAP (unpublished data). The non-foraging respiration rate (*R*) applied in the current model (at night) was higher than that measured in anaesthetized larvae, which agrees with observations of activity of herring larvae at night (Blaxter, 1968; Batty, 1987). Our model was constructed so that herring larvae constantly increased their rate of swimming activity during initial food deprivation (1–7 h), but, similar to the results of earlier studies (Munk and Kiørboe, 1985; Figure 1, insert), larvae decreased their swimming activity when experiencing environments with extremely low (or zero) prey concentration for >24 h.

Angle of visual acuity

Although the function used here to describe α has also been used in many mechanistic IBMs built for larval marine fish, it was originally based on studies done on juveniles of a freshwater fish (bluegill sunfish, *Lepomis macrochirus*). Nevertheless, the predicted α agrees with foraging observations made on herring larvae by Rosenthal (1969). Moreover, for prey <500 μm, the reactive distance is comparable with values reported by other researchers examining herring (e.g. Rosenthal and Hempel, 1970; Munk and Kiørboe, 1985; MacKenzie and Kiørboe, 1995).

Pause frequency and pause duration

The values for PD and PF were set at 1.3 and 0.35, respectively, based on observations by Hauss and Peck (2009). These values are comparable with observations made by MacKenzie and Kiørboe (1995) of PD (1.8–2.4) and PF (0.22–0.30) for herring larvae.

Catch success

Catch success was parametrized as a function of prey length (and pL_{max}), and modelled values agree well with observations of Munk (1992) and Rosenthal (1969). The latter study reported that CS of herring larvae feeding on *Artemia* nauplii increased during 35 d of growth from 1 to 10% to values between 60 and 70%. Checkley (1982) reported that gut fullness at the end of the day increased with increasing larval length, which also suggests that CS (and general foraging ability) increases with increasing larval length in agreement with the findings of Drost *et al.* (1988). Therefore, the length-based approach used in the current study appears to be valid.

Specific dynamic action

In adult fish, SDA varied between 10 and 29% (Beamish and Trippel, 1990). Our value is lower than earlier assumed values of 15% (Arrhenius, 1998) and 17.5% (Rudstam, 1988), but comparable with the value determined for larval herring by Kiørboe *et al.* (1987) of ~10% (of assimilated ration). To date, robust measurements of SDA for larval marine fish are largely unavailable because of methodological constraints.

Larval swimming speed

Larval swimming speed was included, because well-developed herring larvae are cruise predators (Rosenthal, 1969; Rosenthal and Hempel, 1971; Munk and Kiørboe, 1985; MacKenzie and Kiørboe, 1995), but also exhibit pause–travel behaviour during the early larval period (MacKenzie and Kiørboe, 1995; Hauss and Peck, 2009; MAP, unpublished data). For larvae <12 mm *L*, the current model predicts that between 150 and 200 l d^{-1} will be searched, which agrees with earlier estimates of 52–222 l d^{-1} (Munk and Kiørboe, 1985), 20–100 l d^{-1} (Rosenthal and Hempel, 1971), and 1–240 l h^{-1} (Munk, 1992).

Temperature-based length–weight relationship

The morphometric (length and weight) data used to parametrize the model indicated a clear temperature dependence of weight-at-length for this size range of larvae. The 95% confidence intervals for slope parameter (*b*) of the allometric relationship $dw = aL^b$ increased significantly between 7 and 13°C (MAP, unpublished data), likely in response to temperature-dependent differences in herring larval muscle fibre development and growth (Johnston *et al.*, 1998; Johnston and Hall, 2004). The

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modelled dw of a 12-mm *L* larva at 6 and 15°C (201 and 345 μg, respectively) compared well with that (209 and 353 μg) reported by Fossum (1996) for field-caught larvae. The 0.65 lower CI threshold for death is similar to the value in the model by Fiksen and Folkvord (1999) and it agrees with dry weights measured for starved larvae (Checkley, 1984).

Validation

For yolk-sac larvae, starvation times estimated with the model were comparable with laboratory observations. For example, Blaxter and Hempel (1963) reported that larvae survived between 14 and 17 d at 8°C (112–136°d), whereas Bang *et al.* (2007) reported survival for 12–25 d at 8–12°C (144–209°d). Model-based estimates of starvation times of newly hatched and unfed larvae, and hence the rate of metabolic losses, agree well with laboratory observations.

In the model, feeding larvae contained a maximum of 10–30 prey items of optimal prey size in their guts. A synthesis of the literature on field-caught herring larvae, 5–35 mm *L*, indicated a range of 0–150 prey, but typically, values were <30 (Blaxter, 1962; Cohen and Lough, 1983; Pedersen and Hjelmeland, 1988; Purcell and Grover, 1990). Based on search volumes and clearance rates, a maximum food consumption rate of 400 prey d^{-1} was estimated (Rosenthal, 1969; Bang *et al.*, 2007). Our estimates for 14 mm *L* larvae consuming optimally sized prey (50–250 prey d^{-1} between 2 and 20°C) were of the same order of magnitude. It is unknown whether field estimates were based on larvae feeding on optimally sized prey. In our model, smaller prey would be consumed at higher rates. Moreover, modelled weight-specific growth rates (16–26 and 30–50% d^{-1} at 2–20°C for 12 and 20 mm larvae, respectively) and GGE were also within the range of literature values. For example, Øiestad (1983, cited in Kiørboe and Munk, 1986) reported an increase of GGE from 5 to 40% with increasing larval size, but higher estimates of GGE (e.g. 71%) have been reported (reviewed by Blaxter and Hunter, 1982).

Our validation scenarios (Figures 4–6) suggested that the IBM provided robust estimates of the effects of various environmental factors on growth and survival of young herring larvae within the ranges of prey concentrations reported for the North Sea. Under *ad libitum* (laboratory) feeding conditions, our model slightly overestimated growth rates. However, to compare modelled and observed growth rates, some notion of the prey field experienced by field-caught larvae was required. For this purpose, a prey length frequency distribution as described by Daewel *et al.* (2008b) was chosen. Based on the increase in prey concentration with decreasing prey size, prey sizes in the two smallest size classes (100–200 and 201–300 μm) formed 49% of the available prey for our first-feeding herring. A comparison with field data is therefore only possible if *in situ* prey concentrations are corrected for the potential deficiency of these two groups, because of inadequate sampling and gear issues. For example, if a field concentration of 58 prey l^{-1} was determined using a 333-μm mesh net, this translates to a total concentration of 128 prey l^{-1} if size classes not caught by that net were included.

Depth-integrated prey concentrations (100 m, 0.165 mm mesh) measured during winter on Georges Bank/Nantucket Shoals were <0.004 prey ml^{-1} (Cohen and Lough, 1983). To obtain *in situ* growth rates, the model required <0.001 prey ml^{-1} (validation scenario 6), which is well within the range of the observations allowing survival of herring larvae (Figure 6a).

The range of observed prey concentrations allow growth at observed rates (Figure 6b and c). Purcell and Grover (1990) observed 40.8 ± 21.5 prey l^{-1} (333 μm, 1 m, and 5-m depth) comparable with a total concentration of 0.074 prey ml^{-1} that would be applied in the model. Gallego *et al.* (1996) determined prey biomasses between 4 and 18 g l^{-1} during September (200 μm, 30-m depth) west of the Orkney Islands, an important spawning location of autumn spawners, which is comparable with a total prey concentration (including everything smaller than 200 μm) of 0.41 prey ml^{-1}. Maes *et al.* (2005) report copepod concentrations between 1 and 595 prey l^{-1} with highest values observed close to the coast. Including the smallest size classes of 100 and 200 μm, the highest concentration would translate to 1214 prey l^{-1}.

In summary, our attempts to validate the model can be summarized as follows. (i) All sensitive parameters (except α) were based on measurements made in at least one (and often more) study on herring. (ii) Consumption rates (particles in the gut, encountered per day), metabolic losses (starvation time) and gross growth efficiency were all comparable with observations. (iii) Modelled and observed growth rates at known prey concentrations were comparable (validation scenarios 1–5). (iv) Predicted prey concentrations required for modelled larvae to grow at observed (*in situ*) rates were comparable with field prey concentrations (validation scenarios 6 and 7). (v) Observed and modelled growth rates overlapped at suitable environmental conditions (daylengths, prey concentrations, temperature; validation scenarios 6 and 8). The model presented here could overcome the often-described mismatch between laboratory and field growth at similar prey concentrations by including prey size-specific foraging. Small larvae cannot prey effectively on large zooplankton and, more importantly, large larvae cannot support positive growth when foraging on prey that are too small (Hauss and Peck, 2009). Sensitivity of modelled growth estimates to respiration parameters indicates that measurements of larval metabolic rates at different activity levels, particularly for larvae that have been food-deprived or adapted to low prey concentrations and low temperatures (mimicking winter conditions in the North Sea and elsewhere), would be particularly useful.

Suitable spawning times for herring

Our simulations used environments (seasonality in temperature, light, and prey characteristics) based on annual mean and inter-annual variability in North Sea conditions. Using those environmental factors as drivers, our results suggest that there are two periods most suitable for the survival of herring progeny: (1) from early January to end of May and, (2) from early August to late October. Larvae that hatched in June, July, and November had a very low probability (<20%) of survival. Development durations to attain 20 mm *L* were ~40 d in spring and four times longer (~160 d) in autumn. Because of the daily mortality rate applied in our simulations, spring larvae had the highest "survival index". Generally, periods of spawning and early larval abundance for newly hatched spring-, autumn-, and winter-spawned herring in the North Sea and other regions of the North Atlantic matched the most suitable times based on modelled larval survival up to 20 mm *L* (Figure 7a). For example, young larvae from Downs, Orkney–Shetland, Buchan, and Banks spawning components are abundant between mid-December and mid-January, late August and early October, early September, and late October, respectively (ICES, 2010). The larvae of Norwegian spring-spawning herring

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are abundant from mid-March to the end of April (Moksness and Fossum, 1992; Fossum, 1996; Husebø *et al.*, 2009), whereas larvae of Firth of Clyde spring-spawning herring occur between mid-April and mid-May (Rankine *et al.*, 1990). Celtic and Irish Sea herring larvae are found from mid-September to late October and mid-January to mid-March, respectively (Brophy and Danielowicz, 2002), and Icelandic herring larvae from early April to the end of May (Fridriksson and Timmermann, 1951). Various studies indicate spawning by Baltic herring in May/June (Oulasvirta, 1987; Rajasilta, 1992; Arrhenius and Hansson, 1996). In short, documented periods of larval herring abundance in the field that do not match the predicted periods of high larval survival in the model are areas outside the North Sea, where seasonal dynamics of prey production and/or temperature are likely different from those used in our simulations.

The model simulations predicted that water temperature, prey concentration and latitude (a proxy for seasonally changes in daylength) all influenced the survival and growth potential of larval herring and contributed to the window of successful spawning times in the Northeast Atlantic. Water temperature was the main driver with the survival of (early) autumn-spawned larvae increasing with decreasing water temperature: a total of $<10\%$ successful simulations happened at mean annual temperatures $\geq 11^{\circ}$C. Prey concentration was also linked to the survival of spring- and autumn-hatched larvae. The effects of prey concentration were size-specific, because smaller larvae can only ingest relatively small prey, have lower catch success and conversion efficiency, and have higher prey-handling times than larger larvae. The results of earlier studies suggest that patches of zooplankton favour the survival and growth of marine fish larvae (e.g. Fortier and Leggett, 1984; Letcher and Rice, 1997), and our model results support that assertion. In agreement with optimal foraging theory, increasing the dry weight-at-length of prey also benefited larval survival, but at no point in the year did that factor affect development time significantly. Finally, latitude was also an important factor affecting the suitability of spawning times from October to early January; it is, therefore, important to the dynamics of autumn-spawned larvae. Herring larvae are visual feeders (Blaxter, 1968; MacKenzie and Kiørboe, 1995), and their potential daily feeding period declines with decreasing daylength. As autumn-spawned larvae develop, their daylength decreases, as does their potential energy gained from foraging. The influence of changes in seasonal daylength might explain, to some extent, the two-month delay in spawning time of the low latitude Downs spawning ground (winter spawners) compared with the higher latitude, Orkney–Shetland, and Banks spawning grounds (late summer/early autumn).

Physiological benefits of larger larval body size help explain seasonal suitability patterns predicted by the model. First, larger larvae grow more efficiently and can utilize prey-size spectra that have decreased (less negative) slopes (more large prey items). Therefore, autumn-spawned larvae grow through critical (small) sizes before overwintering at very low prey concentrations (Figure 6a). Larger larvae also have lower weight-specific metabolic rates and can tolerate shorter (winter) daylengths, because of the lower activity rates (and energy loss) at night. However, these relatively large larvae also have relatively slow growth rates during winter, which increases predation risk and, hence, decreases the relative survival index. Conversely, small (first-feeding) larvae required longer photoperiods for survival because of increased handling times and lower catch success of prey. These small larvae cannot ingest the relatively large and high-energy prey available to them in our simulations.

The brief review of observed spawning times (and periods of early larval herring abundance) suggests that herring utilize the entire range of what the model projected to be suitable hatching periods. However, compared with spring-spawners, our model suggests that climate-driven changes in environmental factors would have a greater effect on the larvae of autumn-spawners. With climate-driven warming, a shift toward more northern spawning grounds might be an option for spring-, but not for autumn-spawners, because of limitations imposed by shorter daylengths during winter at higher latitudes. Increasing temperatures could result in earlier spawning in spring, but, similar to spatial shifts, any delay in spawning would negatively affect larval survival, because of a shorter daylength for autumn-spawners. Any autumn shift would have to match with the availability of zooplankton in edible size fractions. During recent winters, warmer water temperatures coincided with recruitment failures in autumn-spawning herring and low larval (overwinter) survival (Nash and Dickey-Collas, 2005; Payne *et al.*, 2009). In contrast, recruitment of Downs (Schmidt *et al.*, 2009) and Norwegian spring-spawning herring (ICES, 2009) has increased, and Husebø *et al.* (2009) reported that earlier spawning of Norwegian spring-spawning herring was correlated with stronger year classes. Such observations agree with our findings indicating that survival declines as summer approaches and that spring-spawners can compensate for increasing water temperature better than autumn-spawners.

Our model results are not expected to reflect the spawning times for herring in all regions, because they used environmental forcing based on the mean North Sea climatology. For example, summer spawning was unsuitable in our simulations, because of relatively high temperatures and low prey availability. The fact that yolk-sac herring larvae are observed routinely during summer in northern areas of the Baltic Sea and Icelandic waters reflects ecosystem-specific differences in key environmental factors. For example, summer zooplankton concentrations in the Gulf of Finland (10^3–10^6 ind. m^{-2}) apparently are up to two orders of magnitude greater than those in some coastal areas of the North Sea (e.g. 10–10^5 ind. m^{-2} at Arendal station; ICES, 2008), where surface water temperatures are also slightly higher. Peak zooplankton abundance is shifted to later months and it happens in one pronounced summer peak at higher latitudes compared with lower (temperate) latitudes, where there are bimodal or broader, less-pronounced peaks (Colebrook, 1979; Lenz *et al.*, 1993). Therefore, latitudinal differences in zooplankton production would likely allow herring to survive in more northern areas, but as earlier discussed, larval survival after autumn spawning might be constrained by short daylengths.

Including the role of predation

Although the focus of the current study was mainly on climate-driven bottom-up factors, daily mortality rates were included to gain a more holistic understanding of climate-driven constraints on larval survival. The approach was preliminary and included only four different simulations: length-based mortality rates that were at either (1) high or (2) moderate levels, and (3, 4) constant daily mortality at two different levels. Intermediate mortality simulations included the length-based PW scenario (1984,

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$<0.06\ d^{-1}$ for larvae >8 mm) and the constant simulation ($Z = 0.06,\ 0.02\ d^{-1}$). In those scenarios, larval survival was possible during late autumn and winter, which suggested that the effects of bottom-up factors are apparently more important than predation during spring than during autumn. A similar conclusion can be drawn from the analysis of seasonal varying mortality levels, a scenario that appears likely because of lower appetites and reduced gut-evacuation rates of predators at lower temperatures (Temming *et al.*, 2000) and the increase in some predator populations (e.g. gelatinous zooplankton) during summer. Assuming an increase in mortality during summer and a decrease in winter expanded the period of favourable survival into winter.

Determining robust *in situ* mortality rates of marine fish and partitioning between losses caused by top-down vs. bottom-up processes is, arguably, impossible when working only with field data. Hence, models will play a key role in helping us understand the causes and consequences of mortality in marine fish early life stages. All the simulations done in the current study were based on observed and published mortality rates and resulted in highly variable survival indices. For instance, applying the weight-based function reported by McGurk (1986) caused slower-growing cohorts to experience larger losses, which constrained suitable hatching periods to relatively warm periods (having negative implications for larvae spawned by Downs and Celtic herring). However, Downs recruitment has constantly increased since the 1980s (Schmidt *et al.*, 2009), suggesting that predation mortality has likely been relatively low during winter. Field surveys characterizing seasonal changes in predator fields and predator–prey overlap could help to distinguish the roles of top-down and bottom-up processes and should be a future research priority.

Although we employed different simulations of predatory effect (e.g. length-based or seasonal changes in mean daily mortality rates of larvae) these were "hard wired" and not mechanistic. Capturing climate-driven changes in the spectrum of possible predators will require more sophisticated approaches. There are a number of potential predators, some of which are new members of the North and Baltic Sea ecosystems. For example, mass blooms of ctenophores observed in the Baltic Sea (Möller, 1984; Javidpour *et al.*, 2009) might prey directly on herring larvae or could increase mortality indirectly by competing for (limiting) prey resources. Therefore, a more holistic, ecosystem-based approach, including key trophodynamic interactions will ultimately be required to capture all relevant processes affecting mortality rates of target species. Our modelling approach can only be viewed as one required "link in the chain".

Summary and future directions

Recently, studies utilizing physiology to understand climate effects on the productivity and distribution of marine organisms, such as fish, have been pursued with renewed vigour (Pörtner and Farrell, 2008; Pörtner and Peck, 2010). In this regard, modelling tools that incorporate physiology represent one of the best approaches to exploring future climate effects on marine fish species. However, as with any model, trade-offs exist between the need to increase biological realism and the ability to parametrize relevant processes adequately. The current study describes a detailed, physiology-based model of the foraging and growth of Atlantic herring larvae, and it includes a thorough analysis of model sensitivity and performance. Our simulations suggest that a complex array of factors contribute to the survival of herring larvae. Periods allowing growth and survival in model simulations agreed with observed spawning times in the North Sea, and any potential changes in profitable spawning times in spring and autumn were predicted to be constrained by different environmental factors. When combined with three-dimensional drift modelling (e.g. Heath *et al.*, 1991, 1997; Gallego *et al.*, 1996; Dickey-Collas *et al.*, 2009), our physiological-based estimates of prey requirements and/or growth rates can be examined with respect to key transport dynamics (e.g. retention vs. dispersion), which appear to affect different stock and/or spawning components in different ways (Sætre *et al.*, 2002; Husebø *et al.*, 2009; Dickey-Collas *et al.*, 2010). Although the changes in larval survival during the overwintering phase appear to govern historical changes in recruitment strength of herring in the North Sea (Payne *et al.*, 2009), physiology-based models that close the life cycle (e.g. adding juvenile and adult stages) might ultimately be required to obtain better projections of the effects of climate change on stocks of Atlantic herring and other marine fish. Herring are distributed over the entire northern hemisphere, and it would be interesting to apply this model using environmental forcing data from other regions. One could then compare different habitats and reveal whether bottom-up processes limit Pacific herring to only spring-spawning (with the possible exception of San Francisco Bay, December–January) or Baltic, Iceland, or Gulf of St Lawrence herring to spawning during summer.

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