Comparing observed and modelled growth of larval herring (*Clupea harengus*): Testing individual-based model parameterisations

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**Summary:** Experiments that directly test larval fish individual-based model (IBM) growth predictions are uncommon since it is difficult to simultaneously measure all relevant metabolic and behavioural attributes. We compared observed and modelled somatic growth of larval herring (*Clupea harengus*) in short-term (50 degree-day) laboratory trials conducted at 7 and 13°C in which larvae were either unfed or fed *ad libitum* on different prey sizes (~100 to 550 μm copepods, *Acartia tonsa*). The larval specific growth rate (SGR, % DW d⁻¹) was generally overestimated by the model, especially for larvae foraging on large prey items. Model parameterisations were adjusted to explore the effect of 1) temporal variability in foraging of individuals, and 2) reduced assimilation efficiency due to rapid gut evacuation at high feeding rates. With these adjustments, the model described larval growth well across temperatures, prey sizes, and larval sizes. Although the experiments performed verified the growth model, variability in growth and foraging behaviour among larvae shows that it is necessary to measure both the physiology and feeding behaviour of the same individual. This is a challenge for experimentalists but will ultimately yield the most valuable data to adequately model environmental impacts on the survival and growth of marine fish early life stages.

**Keywords:** IBM, marine fish, larval growth, feeding, behaviour, bioenergetics.
INTRODUCTION

Biophysical individual-based models (IBMs) have been recognised as important tools for understanding how environmental conditions influence larval fish growth and survival (e.g. see reviews by Werner et al., 2001; Miller, 2007). Larval fish IBMs differ in the complexity of their biological components depending on the research questions asked. For example, some models ignore mechanistic depictions of feeding and/or growth and employ relatively simple temperature-growth functions, making the assumption that larval growth rates do not depend on variability in prey fields encountered along drift routes (Heath et al., 1997; Hinrichsen et al., 2003). However, some IBMs have been created to explore bottom-up regulation of survival and include highly detailed, mechanistic descriptions of growth physiology and foraging (Fiksen and MacKenzie, 2002; Lough et al., 2005; Ruzicka and Gallager, 2006). The reliability of physiologically-based growth estimates generated by these more complex IBMs depends on their ability to correctly depict how key abiotic and biotic factors influence the processes of foraging and growth.

In many larval fish IBMs, growth rates are calculated at each time step using a balanced energy budget (units of dry mass or energy per unit time):

\[ G = C\beta(1 - SDA) - R, \]

where growth \( (G) \) is a function of consumed prey \( (C) \), assimilation efficiency of food \( (\beta) \), costs due to digestion and protein synthesis (specific dynamic action, \( SDA \)) and total respiration \( (R) \). Respiratory costs are separated into inactive (standard metabolism, \( R_s \)) and active foraging \( (R_a) \) periods (Brett and Groves, 1979). The amount of food consumed at each time step is normally calculated using a separate foraging routine. An optimal foraging approach has been implemented in some larval fish IBMs (Walton et al., 1992) based on changes in the prey encounter rate, capture success and handling time at different predator and prey sizes (Fiksen and Folkvord, 1999; Peck and Daewel, 2007; Daewel et al., 2008). In theory, capturing relatively large prey items has a greater reward in energy gain \( (C \text{ increased}) \) but larvae may incur greater costs \( (R) \) in terms of time spent swimming and searching, especially if larger prey are relatively less abundant and are not captured as efficiently when encountered. However, the ability of larval IBMs to capture the costs and tradeoffs (in terms of growth) of larvae feeding on prey of different sizes has not, to our knowledge, been previously tested (for example, by comparison with observations). This is due to a general lack of adequate data collected in controlled laboratory experiments performed on modelled species.

Efforts are now underway to parameterise an individual-based model that includes optimal foraging and growth of Atlantic herring \( (Clupea harengus) \) larvae in the North Sea. Atlantic herring is a particularly well-studied species (e.g., Folkvord et al., 2009; Geffen, 2009). A number of experimental studies have provided detailed descriptions and quantitative estimates of the components of Equation 1 and of key aspects of foraging, including factors influencing swimming behaviour, the perception of prey, feeding ability and prey capture success (e.g., Blaxter, 1968; Rosenthal, 1969; Munk and Kiørboe, 1985; Kiørboe et al., 1987; Munk, 1992; Hauss, 2008). In the present study, we combined parameterisations for Equation 1 previously employed in larval clupeid IBMs (Peck and Daewel, 2007; Daewel et al., 2008) with new observations of larval herring foraging behaviour, food consumption and growth (Hauss, 2008; Peck, unpublished data) at different temperatures, larval ages and prey sizes. In the present study, we compared these new estimates of observed growth rates with those predicted by larval IBM foraging and growth subroutines. Particular emphasis was placed on assessing whether current IBM formulations correctly reflect the costs and benefits (in terms of larval growth) for larvae foraging within different prey environments.

MATERIALS AND METHODS

Observations of larval herring

The foraging behaviour, growth and nutritional condition of Atlantic herring larvae in different prey environments were investigated in short-term growth trials (Hauss, 2008). Four trials were conducted using two temperatures (7 and 13°C) and two fish sizes (~10 mm and 15 mm standard length, \( SL \)). In each case, trials were conducted within temperature-controlled rooms for approximately 50 degree-days \( (^{1 \circ}d) \), resulting in four days at 13°C and seven days at 7°C. Surface light intensities were ~5-10 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) during a 14 h photoperiod (14:10, L:D). In each
trial, a total of eleven, 16-L cylindrical (Ø 35 cm) plastic tanks was used: groups of larvae were either unfed (two tanks) or provided “small”, “medium” or “large” copepod (Acar...
used to calculate a daily, treatment- (prey size-) specific food consumption rate \( C \) in Eq. 1 that included a size-specific capture success \( (CS) \) function (Table 1, Eq. [1]) previously reported for Atlantic herring feeding on the same copepod species used as prey in the present trials (Munk, 1992). The number of copepods consumed was converted into µg dry mass (Berggreen et al., 1988) using the mean of the copepod prosome lengths measured at the beginning and end of the trial for each prey size treatment (Table 1, Eq. [2]). Parameters describing assimilation efficiency of food \( (\beta) \) and costs due to digestion and protein synthesis \( (SDA) \) were taken from the literature (Table 1, Eqs. [3] and [4]). We did not attempt to limit \( G \) by introducing a maximum growth term since we wished to investigate the performance of a model that included mechanistic growth constraints (see Peck and Daewel, 2007).

After an initial comparison of observed and predicted growth, the budget (Eq. 1) was adjusted using two different scenarios based on expected differences between laboratory and field conditions and potentially among individual larvae. First, temporal or inter-individual variability in feeding among larvae was explored. In this scenario, a single factor \( (\alpha) \) was applied to reduce feeding strike frequency observed in all treatments and trials. The value of \( \alpha \) was determined statistically by minimizing the sum of squared errors (SSE) between modelled and observed \( G \) where the latter was based on a mean value calculated for the three tanks at each prey size in a trial (total \( n = 12 \); three feeding treatments in each of the four trials). A second scenario investigated the possibility of decreased assimilation efficiency \( (\beta) \) due to intensive rates of feeding within prey patches (Peck and Daewel, 2007) or unrealistically high prey concentrations used in the laboratory. In this case, a theoretical weight of copepods that could be consumed each day \( (C_{\text{MAX}}) \) was calculated based on maximum weight-specific gut capacity \( \text{Gut}_{\text{CAP}} \) according to the prey found in field-caught herring larvae (Pepin and Penney, 2000, Table 1, Eq. [10]) and gut evacuation rate (Table 1, Eq. [11]). In cases in which estimated \( C \) exceeded \( C_{\text{MAX}} \), assimilation efficiency \( \beta \) was reduced by \( \beta C_{\text{MAX}} C^{-1} \), so that

\[
\beta' = \beta C_{\text{MAX}} C^{-1}, \text{ if } C > C_{\text{MAX}}
\]

To assess the “goodness of fit”, linear regression analyses were performed on modelled and observed values. Modelled growth rates include those in the original “base case” and within each of the two adjusted scenarios. Residuals \( (SGR_{\text{obs}} - SGR_{\text{pred}}) \) of these regressions were calculated to determine whether modelled growth rates were biased at specific temperatures, larval ages/sizes or prey sizes.

RESULTS AND DISCUSSION

Observed growth and foraging activity

Mean larval growth rates in the replicate tanks of the “feeding” treatments ranged between -12.2 and 21.2% \( \text{DW d}^{-1} \) for larvae at 13°C (Fig. 1, open symbols) and between -5.0 and 5.9% \( \text{DW d}^{-1} \) for larvae at 7°C (Fig. 1, filled symbols). To be able to compare growth across different larval sizes, prey size was expressed in relative length \( (100*PL_{\text{prey}}/SL_{\text{lateral}}) \). Compared to the group of larvae measured at the start of the trial, unfed larvae lost weight and mean \( SGR \) in these tanks ranged from -32.0 to -0.3% \( \text{d}^{-1} \). Negative \( SGR \) (weight loss) was also observed in larvae foraging on the smallest and largest prey items, while larvae foraging on intermediate-sized prey had the highest \( SGR \) (~3% SL). Compared to previous studies in which herring larvae were reared in the laboratory (Werner and Blaxter, 1980; McGurk, 1984; Folkvord et al., 2000), growth rates at optimum prey sizes in this study were quite high. In
In the unadjusted budget, modelled and observed growth agreed poorly (Fig. 3A, note scaling on y-axis and position of 1:1 line). The former being substantially higher, particularly in cases where larvae were provided medium and large prey sizes for which the mean (±SD) residual values were -45.3 (±30.5) and -48.5 (±16.7) respectively. For larvae experiencing poor feeding conditions, mean (±SD) residual values were 0.4 (±10.2) and -11.4 (±22.9) for “no prey” and “small prey” treatments respectively, indicating that parameterisations of metabolic losses in unfed larvae were robust. Furthermore, estimates at 7°C were better and less variable than at 13°C with mean (±SD) residuals of -13.1 (±15.8) and -39.9 (±34.2) respectively, and the size/age of larvae did not impact predictions.

A key parameter that is particularly challenging to estimate is the activity multiplier ($k$) that converts inactive rates ($R_s$) to rates used during daytime for-
Simultaneous measurements of larval swimming activity and respiration are scarce (Hunt von Herbing and Boutillier, 1996; Ruzicka and Gallager, 2006) and have not been made on Atlantic herring. Our modelled estimates of $R_a$ were obtained using a $k$-ratio of 2.0, which appears to be robust based on a) the observed rate of weight loss of starved herring and b) a similar magnitude of the difference in $R$ (2.0 to 2.5) measured at the same temperature for anaesthetised (Kiørboe et al., 1987) and active herring confined to small chambers (Peck unpublished data). However, as is the case in the vast majority of larval respirometry studies, the level of activity occurring during these latter measurements was unknown.

Since parameters representing metabolic losses appeared robust, model overestimates of growth in larvae feeding on more suitable prey could have stemmed from either food consumption rates or assimilation efficiencies that were too high. These two possibilities were explored in the following scenarios.

**Temporal variability in feeding**

Modelled estimates of $C$ based on observed feeding strike frequency ($FSF$) were, in some cases, unrealistically high (e.g. >4000 nauplii larva$^{-1}$ d$^{-1}$ in the 13°C, 13.7 mm SL trial). Direct estimates of the food consumed by larvae (based on the number of prey added to the tanks at the beginning of the trial and the number remaining at the end) were available. Unfortunately, it is not possible to estimate food consumption rates from counts of copepods since a) natural copepod mortality was not assessed (e.g. by including a tank that contained copepods but no fish larvae) and b) the feeding contribution of the small percentage of larvae that died in tanks was unknown. Interestingly, a reduction of observed $FSF$ by a single factor (0.11) for all feeding treatments and all trials led to good agreement between the predicted and observed values (Fig. 3B). Predicted and observed growth agreed well with an average residual (±SD) of 5.0 (±0.3) and had a linear relationship ($r^2 = 0.5; p<0.01$) with a slope of 0.7 (±0.2). After the adjustment (89% reduction) in $FSF$, modelled food consumption rates were between 1 and 12 prey items larva$^{-1}$ h$^{-1}$ except in one case (34 prey larva$^{-1}$ h$^{-1}$). All of these estimates are well within the range of food consumption rates calculated from larval herring gut content analyses (Hauss, 2008). One explanation for this could be that $FSF$ repre-
Table 2. Average residuals (% DW d⁻¹) for different temperatures (7 and 13°C; n = 8), prey sizes (no, small, medium and large prey; n = 4), and ontogenetic stages (larval SL ~10 and 14 to 15 mm, n = 8) in the three scenarios.

<table>
<thead>
<tr>
<th>Average residuals (±standard deviation)</th>
<th>No adjustment</th>
<th>FSF reduced</th>
<th>β reduced</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7°C</td>
<td>-13.1±15.8</td>
<td>-1.4±3.8</td>
<td>-0.9±1.9</td>
</tr>
<tr>
<td>13°C</td>
<td>-39.9±34.2</td>
<td>-0.8±8.4</td>
<td>0.5±7.4</td>
</tr>
<tr>
<td>Prey environment</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>no prey</td>
<td>0.4±10.2</td>
<td>0.4±10.2</td>
<td>0.4±10.2</td>
</tr>
<tr>
<td>small prey</td>
<td>-11.4±22.9</td>
<td>3.7±1.8</td>
<td>-0.4±1.4</td>
</tr>
<tr>
<td>medium prey</td>
<td>-45.5±30.5</td>
<td>-1.3±6.6</td>
<td>-1.3±3.1</td>
</tr>
<tr>
<td>large prey</td>
<td>-48.5±16.7</td>
<td>-1.6±5.5</td>
<td>0.4±4.8</td>
</tr>
<tr>
<td>Larval SL</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>~10 mm</td>
<td>-25.1±29.4</td>
<td>-2.2±7.3</td>
<td>-2.4±4.5</td>
</tr>
<tr>
<td>~15 mm</td>
<td>-27.3±30.7</td>
<td>2.8±4.5</td>
<td>-2.0±5.3</td>
</tr>
</tbody>
</table>

The observed foraging by all larvae at all times but capture success of prey was markedly lower than expected due to the high concentrations of prey (2 ml⁻¹) used in the present growth trials. Marcotte and Brownman (1986) suggested that capture success is not merely a function of relative prey size, but may decline at high prey concentrations (>0.4 ml⁻¹, 25 mm Salmo salar alevins) due to 'sensory overload' (i.e. perceptual confusion in extremely high prey concentrations that may hamper larvae from focusing on single prey items). In the present study, capture success was not measured, however, values of FSF were within the range of those (0.3 to 1.0 min⁻¹) observed by other researchers for herring at 10- to 100-fold lower (0.02 to 0.2 copepods ml⁻¹) prey concentrations (Munk and Kristboe, 1985).

Patch-feeding scenario

Intensive feeding by larval fish in areas of high prey concentration may increase gut evacuation rates and decrease assimilation efficiency of ingested prey items (Werner and Blaxter, 1980; Boehlert and Yoklavich, 1984; Theilacker, 1987; Peck and Daewel, 2007). In this scenario, we decreased assimilation efficiency by the degree of potential over-filling of the available gut volume. With a gut capacity of 3.06% larval DW (Pepin and Penney, 2000) and gut evacuation rate ranging between 0.37 and 0.81 h⁻¹, $C_{\text{MAX}}$ values were expected to range between 19 and 35% larval DW d⁻¹, while estimates of food consumption rate based on mean FSF were as high as 200 to 500% DW d⁻¹ in some cases.

Observed and modelled specific growth rates agreed more closely after this adjustment compared with the base case (see Fig. 3C) or scenario 1 (food consumption reduction). Also, modelled growth rate estimates were less variable, and no trend was observed in residuals with respect to the three prey sizes, two larval sizes or two water temperatures (Table 2), which indicates that the model performed well across different experimental conditions. In some cases, the adjustment led to values of assimilation efficiency that were extremely low compared to the base model (no adjustment) in which the assimilation efficiency was between 42 and 66% (calculated using Equation [3] in Table 1). At small prey sizes, $\beta$ was not reduced except in the 13°C, 13.7 mm SL larvae experiment. At medium prey sizes, $\beta$ values were 14 to 15% at 7°C and 4 to 6% at 13°C, while at large prey sizes, $\beta$ values ranged between 4 and 8% for both temperatures. However, there is a general lack of experimental data (or agreement in the presence of data) concerning the assimilation efficiency of larval clupeids in different feeding regimes and developmental stages. For example, a nitrogen absorption coefficient of 48 to 83% was determined (Klumpp and Westernhagen 1986) and carbon assimilation rates have been reported to be 90% (Pedersen and Hjelmeland 1988) and between 38.5 and 68.2% (Boehlert and Yoklavich 1984), these last estimates decreased as prey concentration increased.

Reconciling model estimates and observed data

What is the explanation of the discrepancy between observed foraging behaviour (feeding strike frequencies) and “biologically reasonable” rates of food consumption by larval herring? In our opinion, there are at least three possible explanations which are not mutually exclusive.

First, it is possible that there were large differences in the foraging activity among larvae in the same group, and that the observed FSF (Fig. 2) represented the behaviour of only a small percentage of the individuals in the group. This appears reasonable...
given that there were large differences in RNA-DNA ratios (and thus SGRs, Buckley et al., 2008) among larvae in the same tank in all fed treatments in each trial (Hauss, 2008). However, modelled growth rates in each treatment (base case, no adjustments) were still almost four to five times higher than the mean of the top quartile of larval SGRs in each tank (individual SGRs obtained from measurements of RNA-DNA ratios at the specific temperature). Therefore, the inter-individual variation alone does not explain the discrepancy.

A second explanation is that FSF observations were relevant for only a small percentage of the time for each larva. In every trial and each prey size treatment, larvae used the entire area of the tank but the FSF could only be measured for a larva when it was not in contact with the tank wall, the tank bottom or the water surface. We did not quantify the amount of time that larvae spent at these tank “edges”. Munk and Kiorboe (1985) estimated the proportion of time larval herring swam along the tank wall to be 15 to 40% in larger tanks (170 L) and corrected estimates of food consumption rates accordingly. Our tanks were smaller (16 L) and thus the correction factor required for our “tank effect” may be larger. However, even among free-swimming larvae, the variability in feeding behaviour (Fig. 2) was high, and 30% of all observed individual larvae (n = 313) did not attempt feeding strikes during the three-minute observation period. We therefore conclude that, in addition to artificial constraints on swimming behaviour, there is considerable temporal variability in foraging activity of herring larvae.

A third explanation is that, as the feeding rates were indeed extremely high for larvae in tanks, gut overfilling occurred and assimilation efficiency was markedly reduced. As previously mentioned, reduced assimilation efficiency (β) has been reported for larvae feeding within high prey concentrations. However, to fit the model to the experimental data, it was necessary to reduce β to extremely low values, and it is unknown whether this is realistic. It is therefore not possible to entirely disentangle the two mechanisms (temporal variability and reduced assimilation).

CONCLUSION

In the present study, we made a simple assessment of larval herring IBM physiological parameterisations by comparing observed and modelled growth rates of different sizes of larvae at different water temperatures that were provided different prey sizes. Model parameters representing metabolic energy losses in unfed larvae appeared to be robust, including k-ratios employed to convert between Rs (inactive, night) and Rf (active, daytime) rates of energy loss. In fed larvae, the model greatly overestimated SGR except for larvae feeding on suboptimal (small) prey. The introduction of correction factors to account for either temporal variability in foraging behaviour (scenario 1) or reduced assimilation efficiency at high feeding rates (scenario 2) resulted in good agreement between modelled and observed growth across larval ages, prey environments, and temperatures.

Future laboratory trials are needed to test larval fish IBM estimates of foraging and growth, and several recommendations can be made based on our results. First, growth trials that utilise groups of larvae are useful since they capture general (average) impacts of environmental factors (e.g., growth versus temperature and prey size). Second, the parameter rates of Equation 1 (e.g., C, G, R, β) should also be measured on individual larvae, as our results demonstrated that large variability can exist in food consumption and growth rates among larvae in the same environment. This challenges experimentalists by highlighting the importance of making physiological and behavioural measurements of the same individual. Moreover, it shows modellers that including individual variability in physiological and behavioural attributes may be necessary to adequately model the survival and growth of individuals within variable environments.

REFERENCES
