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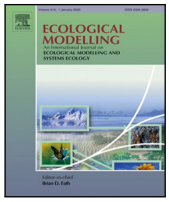

Testing a simple energy-budget model for yolk-feeding stages of cleaner fish

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ABSTRACT

The use of cleaner fish is an environmentally-friendly approach to combat the salmon louse, threatening commercial salmon farming. Dynamic Energy Budget (DEB) modelling helps understand the bioenergetics of early life stages of the cleaner fish, and can thereby aid optimisation of their culturing. Here, we report on our attempts to parametrise DEBkiss models for the yolk-feeding stages of two cleaner fish species, ballan wrasse (*Labrus bergylta*) and lumpfish (*Cyclopterus lumpus*). A range of measurements was taken over early development, including biometry (using imaging), weight and composition, as well as measurements of respiration rate. Despite the previous success of applying the DEBkiss model to early life stages of Atlantic cod, the model failed to capture the patterns of yolk depletion for ballan wrasse. The main issues were related to substantial changes in the water content of both yolk and structure over development, and a stop of growth before disappearance of the yolk sac. These issues require further experimental work to address, especially more efficient proxies for the dry mass of yolk and structure, such that these compartments can be efficiently separated. Nevertheless, apart from the pattern of yolk depletion, the model provides a reasonable explanation of all traits simultaneously. This indicates that model modifications may only need to be minor. For lumpfish, the data set was quite limited for testing of the DEBkiss model, due to the opacity of the egg and the fact that there was only one time point with measurements post hatch. Nevertheless, the data are consistent with the model. The modelling results indicate that both cleaner-fish species may have very similar bioenergetic parameters (and quite similar to Atlantic cod as well); the conspicuous difference in early life history may be mainly caused by the larger yolk provisioning in the egg, and late hatching, in lumpfish. The DEBkiss model is a simple and promising tool for bioenergetics of fish early-life stages. However, its application and in-depth testing is currently limited by the difficulties of obtaining detailed measurements on these life stages.

1. Introduction

The salmon louse (*Lepeophtheirus salmonis*) threatens commercial salmon farming in Norwegian waters. As an environmentally-friendly treatment strategy, the use of cleaner fish such as ballan wrasse (*Labrus bergylta*, Ascanius, 1767) and lumpfish (*Cyclopterus lumpus*, Linnaeus, 1758) has been proposed. However, to be safe and sustainable, the cleaner fish would have to be cultured rather than caught in the wild. Efficient production of fish requires a thorough knowledge of the life history of the species, and how environmental factors such as food and temperature affect it. This is especially true for the early-life stages, which form a bottleneck for fish culturing.

Dynamic Energy Budget (DEB) theory (Kooijman, 2001; Jusup et al., 2017) can help to quantitatively understand a species' life history in a integrated framework for metabolic organisation. The theory is generic, covering all life forms on the planet, and has found extensive application in aquaculture (e.g., Føre et al., 2016; Stavrakidis-Zachou et al., 2019). The theory is structured around the laws for mass and energy conservation. Resources are taken up from the environment, and are subsequently used for the energy-demanding processes such as growth, development and maintenance. DEB theory provides a set of simple rules for the intake and allocation of resources across the various processes. These rules vary only little between species; species mainly differ in the magnitudes of the various fluxes. For practical models derived from the theory, this implies that the same model structure can be used for many taxonomically-related species. For example, ray-finned fish seem to be well represented by a common model structure, but differences in their model parameters lead to very different life cycles (see e.g., Lika et al., 2014; Marques et al., 2018).

Once a DEB model is reliably calibrated for a species, the model can be used to predict life-history traits as a function of environmental

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variables (such as time-varying temperature and food availability), or even to reconstruct feeding history from measurements on field-collected or cultured fish (Pecquerie et al., 2012; Stavrakidis-Zachou et al., 2019). Furthermore, it is more meaningful to compare treatments (e.g., feeding strategies) or species (or strains within species) on the basis of DEB model parameters than on the basis of some arbitrary trait at some arbitrary point in the life cycle (Lika et al., 2014; Marques et al., 2018). DEB models thereby offer many possibilities to optimise fish culturing. However, parametrising such a model for a species is not a trivial task, especially for the so-called standard DEB model (see Jusup et al., 2017). Even though this task is supported by a parameter library, rules for filling data gaps, and dedicated software (Marques et al., 2018), it is often difficult to establish a unique parametrisation for a species (Potter et al., 2021). In this study, we decided to use a simplified DEB framework (DEBkiss, Jager et al., 2013; Jager, 2018), which has a tighter link to measurable properties and is therefore easier to apply. For feeding life stages, the DEBkiss framework provides a simple set of equations that works well for many species (see list of publications at http://www.debtox.info/debkiss_appl.html). For yolk-feeding stages, the model is less well tested, though it performed excellently on literature data for early-life stages of Atlantic cod (Jager et al., 2018) as well as eggs of pond snails (Jager et al., 2013).

In this study, we report on our attempts to parametrise DEBkiss models for the yolk-feeding stages of two cleaner fish species, ballan wrasse (*L. bergylta*) and lumpfish (*C. lumpus*). A range of biometrical size, weight and composition measurements were taken over early development, as well as measurements of respiration rate. Essential for modelling of yolk-feeding stages is a precise and accurate estimation of the biomass of yolk and structural tissue over development. In practice, this is complicated by the difficulty of separating the contributions of yolk and structure, changes in shape over ontogeny, the possibility for variations in water content, and the often substantial variation between individuals (even from the same batch of eggs). Length and body area measurement are, for example, relatively easy to obtain by imaging but have a rather uncertain relationship to biomass, especially when the species changes in shape (for a copepod example, see Jager et al., 2021). This study should therefore be seen as preliminary, to explore the usefulness of DEBkiss models for early life stages of these two species, and to investigate to what extent imaging can be used to parametrise such models.

2. Methods

2.1. DEBkiss model

The DEBkiss framework is described in detail elsewhere (Jager, 2018; Jager et al., 2013). The special case for yolk-feeding stages was presented and tested for Atlantic cod by Jager et al. (2018). Here, we use those model equations without further modification (given in supporting information), which were implemented in the BYOM platform under Matlab (http://debtox.info/byom.html). The mass flows in the model are shown in Fig. 1, and the model parameters are summarised in Table 1. This table also provides the parameter estimates for Atlantic cod as established by Jager et al. (2018), which will be used as reference.

Our initial idea was to fit the DEBkiss model to the data obtained for cleaner fish. However, due to limitations in the data set and unexpected behaviour of these species, we decided to stick to model simulations. The parameter setting for the cleaner fish species (Table 1) is discussed in Section 2.5. As shown in Table 1, the model contains a number of primary parameters (parameters directly related to the mass fluxes in the model) as well as a range of auxiliary parameters (e.g., conversions to make measured properties comparable to the model's state variables). The primary parameters cannot be directly determined, only indirectly from fitting the model to data. Auxiliary parameters and initial states may be directly estimated from observations, and can sometimes be fitted to the data.

Table 1
Model parameters for wrasse (BG1 and VAR) and lumpfish (NR and RK2), relative to the values established for cod (Jager et al., 2018). N.a. is 'not applicable', an equal sign implies the same value was assumed as used for cod, and an asterisk indicates values that were manually adapted to achieve an approximate correspondence to the data (see main text). All rate constants are given here at a reference temperature of 6 °C. All translations across temperatures are performed using the Arrhenius relationship. The values for the yield factors y_{AV} and y_{VA} are general defaults (Jager et al., 2013).

Sym.	Explanation	cod	wrasse BG1/VAR	lumpfish NR/RK2
Primary parameters				
f	Scaled functional response egg/larva (–)	1/0	=	=
J^a_{Am}	Specific assimilation rate (mg/mm^2/d)	0.0160	0.027*	0.027*
J^v_M	Specific maintenance rate (mg/mm^3/d)	0.00437	=	=
y_{AV}	Yield factor for shrinking (mg/mg)	0.8	=	=
y_{VA}	Yield factor for growth (mg/mg)	0.8	=	=
κ	Allocation fraction to soma (–)	1.0	=	=
Auxiliary parameters				
d_B	Dry-weight density yolk (mg/mm^3)	0.0745	0.25	0.28
d_C	Carbon content structure/yolk (mg/mg)	0.40	0.46	0.49
d_V	Dry-weight density structure (mg/mm^3)	0.15	0.25	0.28
F_{RQ}	Respiratory quotient (–)	0.8	=	=
T_h	Hatching time (d)	16	6–7/7–8	27–29
T_A	Arrhenius temperature (K)	n.a.	9900	8000
W_c	Weight of chorion (mg)	0.020	0.025*	0.31/0.44
δ_M	Shape-correction coefficient (–)	0.157	0.144/0.151	0.195
Test conditions and initial state variables				
T	Temperature in the test (°C)	6	8.6/9.3	9.4
W_{B0}	Initial yolk dry weight (mg)	0.10	0.065*	1.3/1.5
W_{V0}	Initial structural dry weight (mg)	0.00235	=	=

2.2. Experimental work ballan wrasse

Full details of the experiments are provided in the supporting information; below a short overview is provided. Two series of experiments were performed: an extensive experiment (with 4 replicates) for one batch of eggs (BG1), and a more limited experiment (no replication) with eggs from five different sources (VAR). Since there are no obvious differences between the VAR egg sources, and no replication, we decided to lump them for this analysis.

For each set of experiments, there were two separate samplings for different destructive measurements. The first series comprised measurements on 1–8 individuals combined, covering eggs and yolk-sac larvae. Measured variables, as used for the analysis in this paper, were total dry weight, carbon content, nitrogen content, and respiration rate (oxygen use). The second series comprised imaging of individual larvae (post hatch only), determining yolk biometry (area and length), total body area, standard length, and length along the myotome. At various time points, 12–50 individuals were imaged. Only for the BG1 experiment, there were also biometrical measurements on images from eggs (total egg diameter and yolk diameter). At various time points, 6–15 individual eggs were measured.

2.3. Experimental work lumpfish

Full details are again provided in the supporting information. A single experiment was conducted with eggs from five different sources. Here, the results from only two egg batches are used (eggs from wild caught animals); the differences between the egg batches were small, and the two selected batches provide representative results for the current analysis.

There were two separate samplings for different destructive measurements. The first series comprised measurements in triplicate for each batch, on 1–6 individuals combined, covering eggs and larvae. Measured variables, as used for the analysis in this paper, were total dry weight, carbon content, nitrogen content, and respiration rate (oxygen use). The second series comprised imaging of individual larvae (post hatch only) of yolk biometry (ventral and side area), body area (ventral area without tail), standard length, ventral length without tail, and lipid

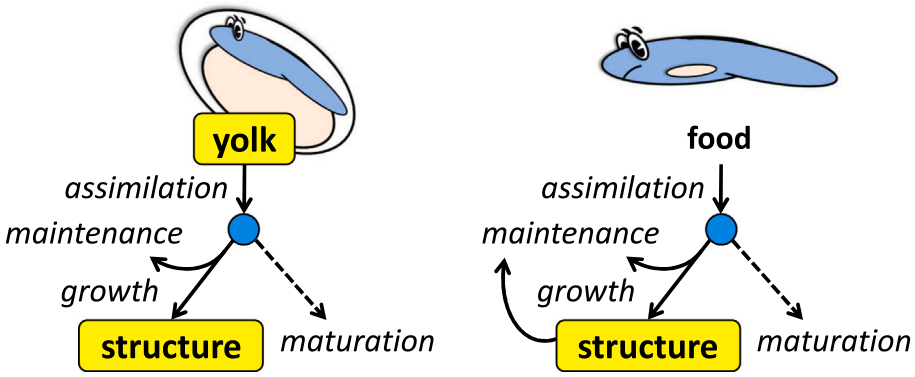

Fig. 1. Schematic representation of the DEBkiss model for yolk-feeding stages and larvae. For larvae, if no food is provided, structure will be used to fuel maintenance costs and the animal will shrink. Maturation (the investment into maturity status) is a source term, but the maturity level itself is not followed as a state variable in the DEBkiss model.

droplet area. At only one time point, 66–72 individuals were measured per egg batch. There were also biometrical measurements on images of eggs at the start of the experiment (total egg diameter); 36 individual eggs were measured per egg batch.

2.4. Translation of biometry data

The measurements made on the cleaner fish cannot be used directly for modelling: the model's state variables are body dry mass and yolk dry mass, which have not been (separately) measured. Therefore, auxiliary hypotheses are needed to compare model output to observations (see also Jager et al., 2021). Full details are provided in the supporting information.

For wrasse, the total volume of the egg was determined from the diameter of the egg, excluding the gum layer, assuming the egg is a sphere. The yolk volume inside the egg was estimated using the relationships for a prolate spheroid, from the two length measurements (longest and shortest diameter). For the larvae (post hatch), yolk sac volume was again calculated assuming a prolate spheroid, but using length and projected yolk-sac area. The structural area of the larva was calculated as the total area minus the yolk-sac area. The structural area is combined with body length into a structural volume, assuming the relationship for a cylinder.

For lumpfish, different biometrical measurements were taken, so the approach to derive volumes differs somewhat from that for wrasse. The egg is again treated as a sphere, and its volume calculated from the diameter. For the larvae, the yolk sac is rather oddly-shaped. We approach the shape by a general ellipsoid, and estimated volume from the yolk sac's side area, ventral area, and length. The yolk sac length was not measured in the images but estimated from side area by assuming that the projected area from the side is circular. From the images, it seems that the lipid droplet will be included in the volume calculated from the yolk-sac area. Therefore, lipid volume was estimated from its area (assuming a sphere), and subtracted from the yolk volume. For the total body, volume estimation is somewhat complex. The larvae are rather tadpole-like in shape, with a large body and a narrow tail. We estimate volume excluding the tail, approximated by a cylinder. Volume is calculated from ventral length (which excludes the tail) and ventral area (also excluding tail). Structural volume is calculated as total body volume minus lipid and yolk volumes. This will underestimate true volume somewhat as the tail section is ignored.

For both species, the measurements for dry weight, carbon content and nitrogen content are for the total egg or larva, and thus comprise contributions from yolk and structural body mass. Carbon and nitrogen content remains rather constant over early development, which implies that yolk and structure have a similar composition, in terms of these elements. The dry weight measurement is used as is, and can be compared to the sum of the two state variables in the model. For the egg stages, the chorion weight is added to the value of these two modelled states. Respiration is used as is, and can be compared to sum of several dissipating mass fluxes in the model: maintenance, maturation and the overheads of growth (full details in Jager et al., 2018).

2.5. Auxiliary model parameters and initial states

2.5.1. Wrasse

The carbon content of yolk and structure (d_C) is needed to link oxygen use to the dissipated mass flux in the model. Carbon content was measured in both experiments, and was rather constant at 0.46 mg/mg. Since there was no clear change in carbon content over development, the content in yolk and structure must be similar. For the estimation of oxygen use, an additional parameter is the respiratory quotient (F_{RQ}): the moles of CO_2 eliminated per mole of O_2 taken up. Following Jager et al. (2018), we take 0.8 as a reasonable value. Hatching time could be directly observed in the experiments, and is only used in the model in the calculation of the total dry weight: the chorion (and other egg materials such as the gum layer) will contribute to weight for the egg stage only.

The actual temperatures in the two sets of experiments (BG1 and VAR) turned out to be slightly different, and slightly different from the temperature at which the respiration rates where measured (10 °C). Furthermore, we want to relate our parameters to those for Atlantic cod, which were performed at 6 °C. Therefore, we need to apply temperature corrections. We use the Arrhenius relationship, and derived the Arrhenius temperature (T_A) from literature data on hatching time at different temperatures (D'Arcy et al., 2012, see supporting information).

The shape-correction factor (δ_M) relates the standard length to the volumetric length (the cubic root of structural body volume). This factor could be established from the biometrical measurements on the larvae only, and remained rather constant over time. The value in the VAR experiment is slightly larger, which likely relates to uncertainty in the volume estimation rather than to true differences in shape. Nevertheless, we decided to use separate values for the current analysis. Both values are close to that for cod, which indicates that the larvae of these two species have a similar shape.

We furthermore need initial values for the state variables, weights of yolk and structure in the egg, as well as weight of the chorion (and additional egg materials that are not part of yolk or body structure). As starting point, we assume the same initial structural weight for wrasse as established for cod. The initial yolk weight and chorion weight were manually tuned to provide an approximate match for the observations

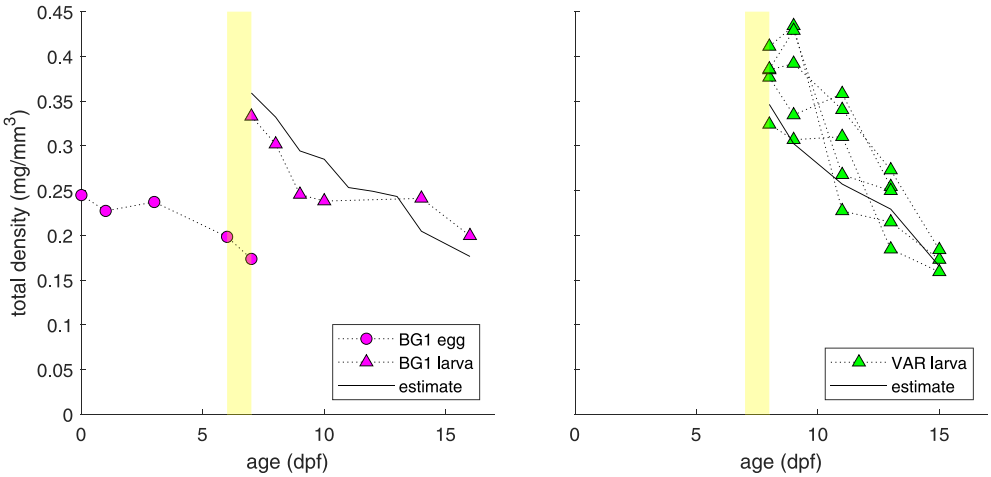

Fig. 2. Total density of egg and larva for both experiments with ballan wrasse. For VAR, each point represents a different egg source. The plotted estimate assumes a density of 0.15 mg/mm^3 for structure and 0.8 mg/mm^3 for yolk. Yellow bar show the approximate time of hatching.

on initial yolk volume and total egg weight, as well as for the drop in total dry weight at hatch.

Relating biovolumes to mass requires estimates for the dry-weight density of yolk and structure (d_B and d_V). We do not have measurements of volume and dry weight on the same animals, and not always at the same time point. However, from the time points on which both measures are available, we can use the means (all measurements from the same test container) to provide estimates for the density. We cannot separate the dry weights for yolk and structure, and therefore look at the development of the total density over time. Initially, density will be dominated by yolk, and at the end of the test by structure. For eggs, total density is the total measured dry weight divided by the egg volume. Egg volume is calculated from egg diameter, excluding the gum layer, but including chorion and perivitelline space. Therefore, the total density can only provide approximate information about the densities of yolk and structure. For the larvae, total density is the total dry weight divided by the sum of the estimated volumes of yolk and structure. The total density changes over time, but we start by setting both yolk density and structural density to 0.25 mg/mm^3, which provides a reasonable match to the initial total density of the egg, and for the late yolk-sac larvae.

2.5.2. Lumpfish

The initial egg weight for lumpfish is much larger than for wrasse, so we can safely assume that yolk and chorion represent the total mass. There was a substantial difference in egg size between the two egg batches (NR and RK2), so separate values will be used. We calculated chorion weight from the average weight difference before ($t > 21$ days post fertilisation, dpf) and after hatch. The initial yolk dry weight then follows from the total egg weight minus the chorion weight. The shape-correction coefficient was calculated from the standard length and the cubic root of estimated volume, the latter excluding the tail.

The total density of the eggs is estimated at 0.28 mg/mm^3 (using only the data for $t \leq 7$ dpf). The total density of larvae, shortly post hatch, is also 0.28 mg/mm^3 (although we calculated the volume without tail). We therefore start from the assumption that the density of both yolk and structure has this value. Carbon content remained rather constant at 0.49 mg/mg.

Incubation temperature was slightly lower than the temperature at which respiration was measured (10 °C), and we again want to use the reference temperature of 6 °C to compare the results for lumpfish to wrasse and cod. We used a default Arrhenius temperature of 8000 K (Lika et al., 2011), as no specific information for lumpfish could be found.

3. Results and discussion

3.1. Initial model parametrisation

The initial parametrisation for the auxiliary parameters and initial states is shown in Table 1. These values were used to provide the model predictions in Figs. 3 and 4. The performance of the model will be discussed in Sections 3.2 and 3.3; below, we start with a discussion of the parametrisation.

3.1.1. Wrasse

The initial yolk dry weight is somewhat smaller for wrasse than for cod, which is to be expected as the eggs are also somewhat smaller. The chorion of marine fish eggs makes up 10%–33% of the egg dry weight (Lønning et al., 1988). The tuned value here (0.025 mg, on a total egg dry weight of approximately 0.09 mg) would be at the upper end of that range. The model predicts a sudden decrease in dry weight at hatch, as the chorion is shed. The data, however, indicate a more smooth decrease, already before hatching (Fig. 3). This may relate to degradation of the chorion, and the gum layer surrounding the egg, during incubation, as a preparation to hatching. Thinning of the chorion before hatch was for example observed in halibut (Finn et al., 1991).

The results for the estimated total dry-weight density are plotted in Fig. 2. For the egg stage, density decreases somewhat over time, which likely relates to burning of yolk (as the transformation into structure is less than 100% efficient) while the total egg diameter remains constant. The yolk density of 0.25 mg/mm^3 is much higher than the value established for cod. This reflects a typical difference in yolk hydration between pelagic and demersal eggs (Craik and Harvey, 1986). It is good to realise that the density of the fresh egg does not necessarily equal the density of yolk. The estimated volume of the total egg (excluding the gum layers) is approximately 0.4 mm^3, while the yolk makes up some 0.25 mm^3. The rest is structure, chorion and perivitelline space. However, since the largest part of the egg is yolk, the initial dry-weight density of yolk should not be radically different from 0.25 mg/mm^3. The value is also well in line with the observations of Finn et al. (2002) who report an initial egg water content of 76%, implying a density of 0.24 mg/mm^3.

At hatching, density jumps up and decreases over the remainder of the experiment. This is rather surprising, as we assumed equal densities for yolk and structure of 0.25 mg/mm^3 (Table 1). Both observations are clearly inconsistent with equal and constant densities. The jump at hatching indicates that yolk has a much higher density, close to hatch, than initially in the egg. If yolk decreases in density, the remaining

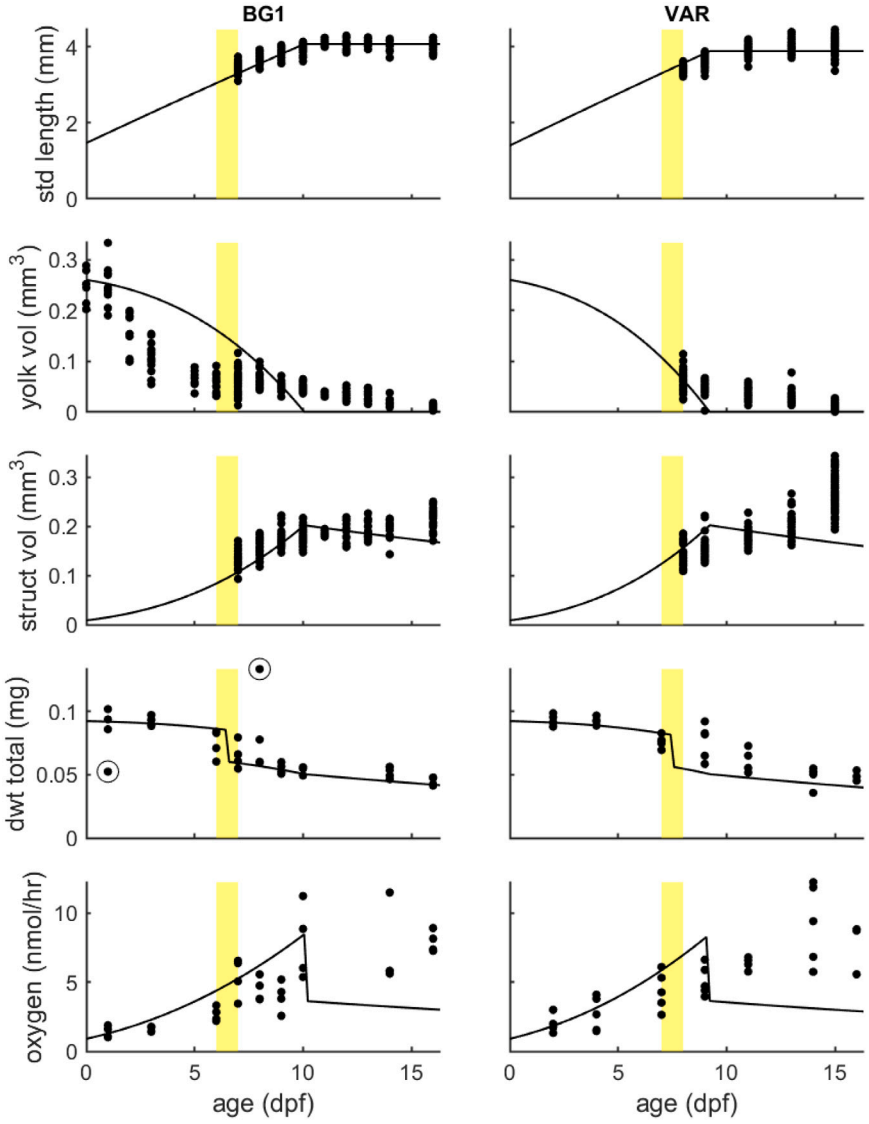

Fig. 3. Comparison of model and observations for ballan wrasse. Model curves result from the parameter values of Table 1. Yellow bar indicates the approximate time of hatching. Circles around two dry weight observations indicate values considered to be outliers. Measurements of the respiration rate were performed at 10 °C, so slightly higher than the incubation temperature in the experiments (Table 1).

space inside the egg will be filled with water (since total egg volume remains constant), which is lost at hatching. After hatching, there is a decline in density, which is especially prominent in VAR. Such a decline in total density could relate to the decreasing contribution of high-density yolk in the larva over development. To explain the observed changes in total density, we would require substantially different values than those in Table 1, with a large difference between d_V and d_B. To provide an approximate match (Fig. 2), we would need to set $d_V = 0.15$ (the value established for cod) and $d_B = 0.80$ mg/mm^3. This value for yolk implies a water content of just 20%, which seems unrealistic. However, it is possible that the density of structural tissues changes as well. From feeding experiments with wrasse larvae (unpublished results), the estimated density rapidly decreased from some 0.17–0.18 mg/mm^3, after disappearance of the yolk sac, to a rather constant 0.12 mg/mm^3 for later stages. Changes in water content, shortly post hatch, have been documented for other species. For example, Escaffre and Bergot (1984) report a steady increase in water content of trout, both in terms of structural tissues and yolk, after hatching. More direct measurements would be needed to address this issue, and to quantify the hypothesised changes in water content over early development.

3.1.2. Lumpfish

For the lumpfish, the opacity of the egg precluded biometrical measurements during the egg stage. On larvae, furthermore, measurements were only performed at one time point (immediately post hatch). Therefore, this data set is rather limited for the purpose of bioenergetic modelling. The initial parametrisation is mostly based on direct observations. The densities of structure and yolk, both estimated at 0.28 mg/mm^3, as well as the carbon content, are similar to those established for wrasse. For the lumpfish, the structural density is also considerably larger than for cod (lumpfish eggs are also demersal, just like the wrasse eggs). The data set does not allow identifying changes in water content over development. However, feeding experiments with lumpfish larvae after yolk-sac disappearance (unpublished results) yielded an estimated density decreasing from some 0.20 to 0.13 mg/mm^3. Therefore, it is likely that also for this species, there are changes in water content over early development.

Hatching time is much larger than for wrasse as well as cod, and the larva hatches in a more developed state. This difference in early development is permitted by the much larger eggs of the lumpfish, containing more yolk. The shape-correction coefficient was larger than

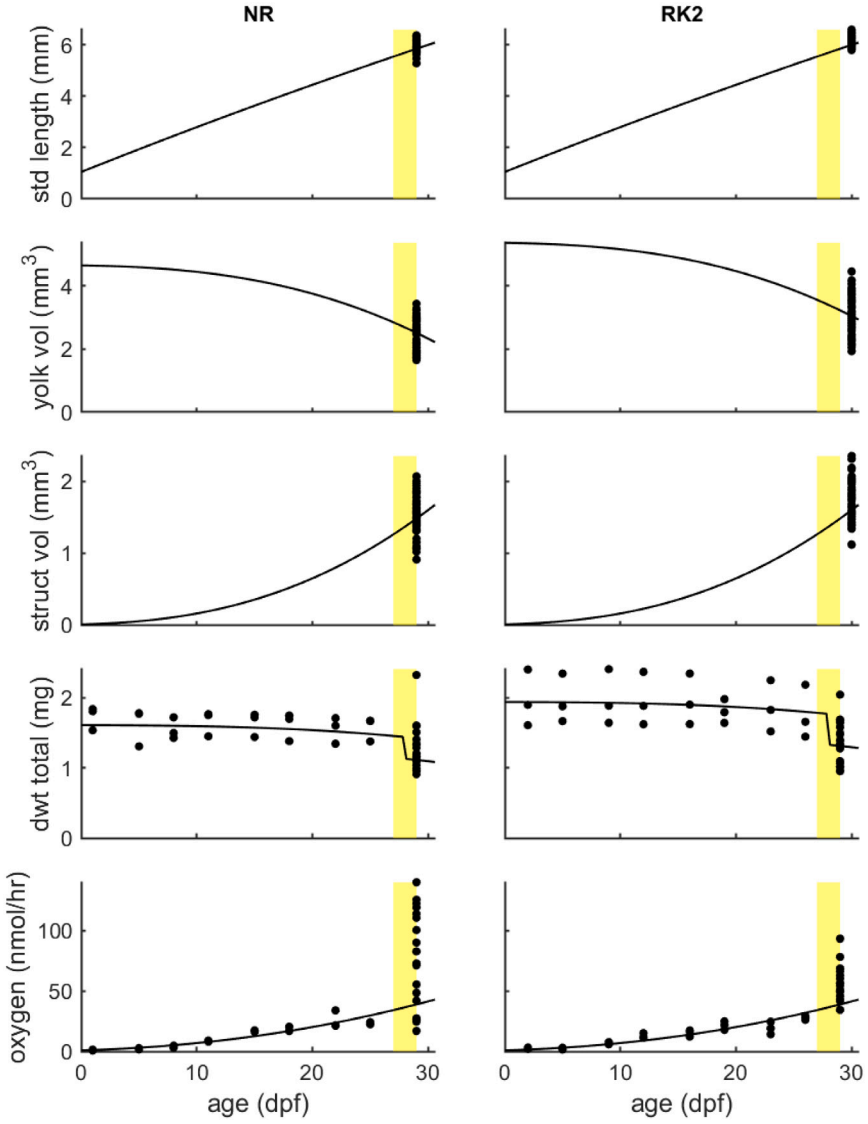

Fig. 4. Comparison of model and observations for lumpfish. Model curves result from the parameter values of Table 1. Yellow bar indicates the approximate time of hatching. Measurements of the respiration rate were performed at 10 °C, so slightly higher than the incubation temperature in the experiments (Table 1).

for wrasse, which indicates a more rounded animal, which is consistent with the visual appearance of the larvae.

3.2. General pattern in yolk depletion

First, we can compare the general patterns in the data set to the model expectations (Fig. 3). Most strikingly, the pattern of yolk depletion is completely different from the model expectation. The model predicts an increasing absolute rate of yolk use over development, as the assimilation of yolk only depends on the structural size of the embryo or larva. The data for wrasse, however, show a rapid initial yolk depletion over the first three days, followed by an extended period of very slow utilisation. The rapid initial phase makes little sense: only the structural part of the embryo utilises yolk, and this part is initially too small to use yolk at the rate indicated by the decrease in yolk volume. Furthermore, rapid metabolic usage of yolk should have led to a substantial peak in oxygen use, which was not observed. The only logical explanation is that the water content of yolk does not remain constant, but rapidly decreases over the first week of the experiment. This is consistent with the observed jump in density at hatching in Fig. 2.

The extended period of very slow yolk utilisation, roughly in the second week of the experiment, also requires further scrutiny. Yolk is not even completely depleted by the end of the experiment (16 dpf), while length growth stops around 11 dpf already. Note that body length likely provides a better indicator for structural growth than body volume, especially given the strong signs of changes in water content. This prolonged yolk utilisation is not in line with the assumptions of the DEBkiss model: yolk is assumed to be assimilated at the maximum rate that the embryo is capable of, given its current structural mass. The rate of yolk depletion will thus increase as the embryonic structure grows, and stop suddenly when the yolk is fully depleted. This prediction was consistent with the data for cod embryos (Jager et al., 2018), but clearly not with our wrasse data.

Also for other fish species, structural size was observed to reach a maximum before yolk would completely run out, and final yolk resorption was relatively slow, for example in trout (Escaffre and Bergot, 1984) and three tropical marine fish species (Bagarinao, 1986). Several authors have speculated that the rate of yolk use depends on the size or surface area of the yolk sac, rather than the embryos structural size (e.g., Beer and Anderson, 1997, for salmonids). This

pattern may also reflect a strategy whereby the larva prioritises survival under uncertain food conditions at the expense of growth. On the other hand, it is possible that the yolk sac is still present but that there is no yolk left inside. In fact, we are assuming that the estimated volume of the yolk sac, from side-view images, represents the volume of yolk present in the larva. Unfortunately, we have no way to test these competing hypotheses from the current data set; this would likely require dissection of the egg and extraction of the yolk-sac content.

Clearly the pattern in yolk depletion cannot be matched by the model. The initial rapid decrease in yolk volume, the slow rate of yolk use in larvae, and the stop of length growth before yolk runs out, cannot be captured. These observed patterns in wrasse are very different from those of Atlantic cod, for which the model was successfully tested (Jager et al., 2018). If this pattern of yolk depletion is real, and not an artefact due to the use of imaging, it would require structural model modifications.

It is good to realise that the DEBkiss model is simplified relative to the standard DEB models. In DEBkiss, the yolk sac represent a buffer of food that is assimilated by the embryo, while in standard DEB it is part of the reserve that is mobilised. In standard DEB models, the embryo's reserve compartment is thus partitioned in two fractions: the yolk sac and an internalised reserve. This complicates interpretation of yolk volume in relation to growth. If there is no internalised reserve, and yolk would represent the entire reserve, growth would indeed decrease and stop before the yolk sac is completely depleted. However, this situation seems unlikely for two reasons. Firstly, the maternal effects rule of standard DEB (Lika et al., 2011) states that reserve density at birth (start of exogenous feeding) equals that of the mother at egg production. Assuming that the eggs came from a well-fed culture, and assuming that birth coincides with the complete depletion of the yolk sac, we would expect the internal reserve of the larva at birth to be sufficient to support growth for a while (thus exaggerating the mismatch between model and data). Secondly, the reserve in DEB theory should not be seen as 'storage for later use'; reserve compounds can play active metabolic roles (Kooijman, 2001). For example, ribosomal RNA should, at least partly, be considered as a reserve compound. Reserve is thus closely integrated with structure. Therefore, it seems unlikely that reserve can be restricted to the yolk sac for fish larvae. A stop of structural growth before the yolk sac runs out is thus also not a straightforward result from standard DEB models.

The observations on wrasse early-life stages force us to reconsider our modelling efforts. The data strongly suggest that DEB models require some modification to the auxiliary hypotheses (e.g., allowing changes in water content of yolk and structure over early ontogeny). Furthermore, it is likely that modifications to the model structure are needed as well (e.g., allowing the rate of yolk usage to be affected by the size of the yolk sac). Unfortunately, the current data set is not strong enough to test alternative modelling options.

3.3. Comparison of data and model

3.3.1. Wrasse

The model is compared to the observations in Fig. 3. The observations on standard length, total dry weight and oxygen use are shown as is. Individual measurements are shown, which reveals that the variation is quite reasonable. Since the overall pattern of the data cannot be matched by the model (as explained in Section 3.2), it makes no sense to try to fit model parameters. Instead, we base the auxiliary parameters on the observations in the experiments with wrasse, as explained in Section 2.5. For the primary parameters, we remain as close as possible to the values for cod. Only the assimilation rate was increased by hand to provide an approximate fit to the data for standard length. This parameter turned out to be the only single parameter where a modification was sufficient to provide a reasonable correspondence (together with the changes in initial yolk and chorion weight, see Section 2.5). It is good to stress that the value for the assimilation rate, needed to provide correspondence to the data, is strongly dependent on the value for the dry-weight density of structure (d_V), which is quite uncertain (see Section 3.1.1). All parameters used are shown in Table 1.

The length growth over time is well captured by the model. However, as already discussed, this is possibly for the wrong reason: length growth in the model stops when yolk runs out, but in the data it stops well before yolk is depleted. It is good to realise that no external food is supplied in these experiments. Therefore, after yolk runs out in the model, maintenance costs will need to be paid from burning structure and the larvae shrink. Even though the animal will shrink in terms of structural biomass, there will be no shrinking in length, since length is determined by the notochord that resists shrinking. On structural volume basis, however, we expect to see shrinking. Surprisingly, the data do not show this. Total body weight indeed shows a decrease, but structural volume shows a tendency to increase, most strikingly for VAR. An increase in volume, without corresponding increases in dry weight or length, indicates an increase in the water content of the structural tissues (as also indicated for total density in Fig. 2).

The stop of growth also implies a drop in oxygen use in the model, since the overhead costs for growth are an important contribution to respiration. However, the data do not show such a rapid reduction, but rather a plateau in respiration. The initial part of the respiration curve, up to point where yolk is expected to run out (around 10 dpf), is consistent with the model predictions. However, the rapid decrease after that is not shown in the data. It is possible that the growth costs are lower than assumed in the model, or that the animals increase their swimming activity at this point (e.g., attempting to find prey, or due to stress in the respiration chamber). The importance of swimming activity was also indicated for larvae of cod. Finn et al. (1995) showed a markedly higher respiration rate for cod larvae, after the yolk sac ran out, when kept in light conditions compared to dark conditions. The DEBkiss model provided a good match to the respiration rates under dark conditions (Jager et al., 2018). In this study, measurements were done in the light, which may explain the observed discrepancy.

3.3.2. Lumpfish

Fig. 4 compares the model predictions to the observations. The data are extremely limited, but the model is able to provide a very good explanation for these data, with the same primary parameters as for wrasse. This is somewhat surprising, since the early life history of the two species is quite different. Lumpfish has a much larger egg, and the larva hatches at a more developed stage, and with a very different shape from the wrasse larvae. Nevertheless, the model analysis shows that this difference may be mainly caused by additional yolk provisioning in the egg, and a delayed hatching.

4. Conclusions

Despite the previous success of applying the DEBkiss model to early life stages of Atlantic cod, the model fails to capture the patterns for ballan wrasse. The main issues are related to substantial changes in the water content of both yolk and structure over development, and the stop of growth before the yolk sac disappears. These issues require model modifications and further experimental work to address, especially direct measurements, or more efficient proxies, for the dry mass of yolk and structure separately. Imaging provides an excellent approach to estimate volumes of (parts of) eggs and larvae, but when water content changes over development, this information does not suffice.

With more detailed observations, there is a basis for testing various hypotheses regarding these deviating patterns. Nevertheless, apart from the pattern of yolk depletion, the model provides a reasonable explanation of all traits simultaneously. This indicates that model modification

may only need to be minor. The auxiliary parameters were set to best estimates for wrasse, whereas the primary parameters were mostly kept at the values established for cod. Only the specific assimilation rate needed to be substantially larger for wrasse (a factor of 1.7). However, it is good to note that this parameter is particularly sensitive to the value for the density of structure, which is quite uncertain and likely changing over early ontogeny.

For lumpfish, the data set is quite limited for testing of the DEBkiss model. Nevertheless, the data are consistent with the model, using species-specific auxiliary parameters and initial yolk weight, but the same primary parameters as for wrasse. This indicates that primary parameter values may not differ too much between fish species, at least not for the early development stages. In fact, the conspicuous difference in early life history between wrasse and lumpfish seems to be explainable from the substantial difference in yolk provisioning of the egg.

The DEBkiss model is a simple and promising model for the bioenergetics of fish early-life stages. However, its application and in-depth testing is hampered by the difficulties of obtaining detailed measurements on these life stages. This is especially true for lumpfish where the opacity of the egg precludes biometrical analysis of yolk and structural biomass. For both species, there is a need for more direct estimation of yolk and structural dry weight. It is good to realise that even rather substantial data sets may still leave open questions, which require literature data, 'educated guesses', or specific experimental work. Nevertheless, bioenergetic modelling will help to identify those data gaps, and to test the consequences of various assumptions.

CRediT authorship contribution statement

Tjalling Jager: Methodology, Software, Formal analysis, Writing – original draft, Writing – review & editing. **Arne M. Malzahn:** Investigation, Writing – review & editing. **Andreas Hagemann:** Funding acquisition, Resources, Project administration, Writing – review & editing. **Bjørn Henrik Hansen:** Conceptualization, Methodology, Investigation, Writing – review & editing.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecolmodel.2022.110005.

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