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LARVAL COD IN PONDS AND MODELS

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1 Introduction

Growth of larval cod is largely determined by body size and environmental conditions such as temperature, prey availability, light and turbulence. In order to investigate the effect of these processes on larval and juvenile cod, an Individual-Based Model (IBM) has been developed. Using data from a macrocosm study on the growth of Atlantic cod (*Gadus morhua*), we are able to evaluate model predictions with observations. Temporal variations in prey abundance, prey size and temperature from the experiment are used as forcing of the IBM and a variety of variables from the simulations are compared with experiment data, i.e. growth rate of larvae in the experiment. It appears that the larvae is unable to sustain the potential (size- and temperature-limited) growth, then growth must be a function of food ingestion.

2 Macrocosm data

The macrocosm experiment ([Folkvord et al., 1994]), studied a number of cod larva in an enclosed pond with no predators. Zooplankton densities and temperature were measured weekly, together with samples of 4354 larvae used in growth analysis.

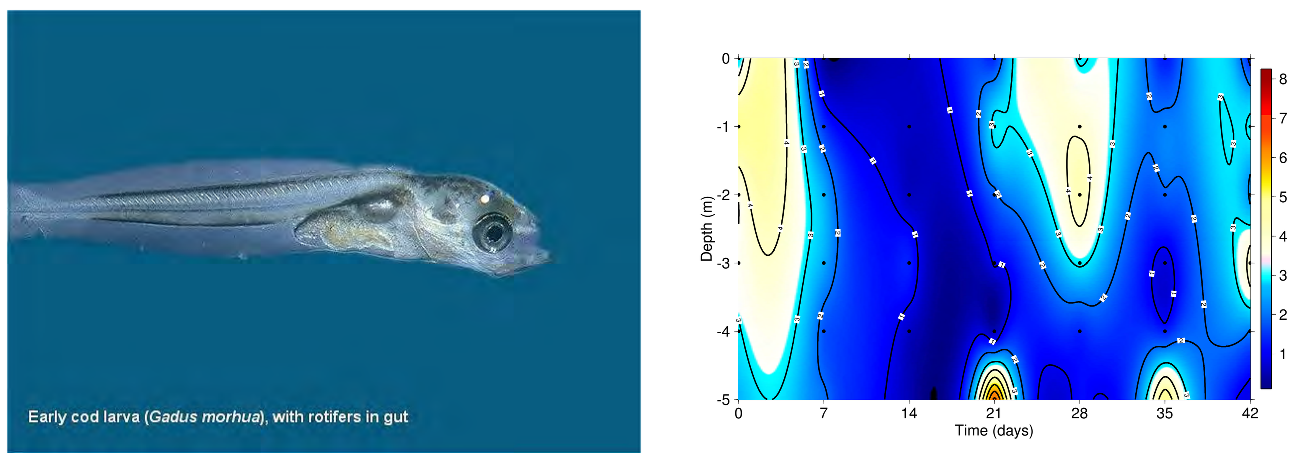

Figure 1: Our hero is shown to the left. The temporal and vertical distribution of nauplii (number per litre) is captured in the figure. The time period extends from mid March to mid April 1983.

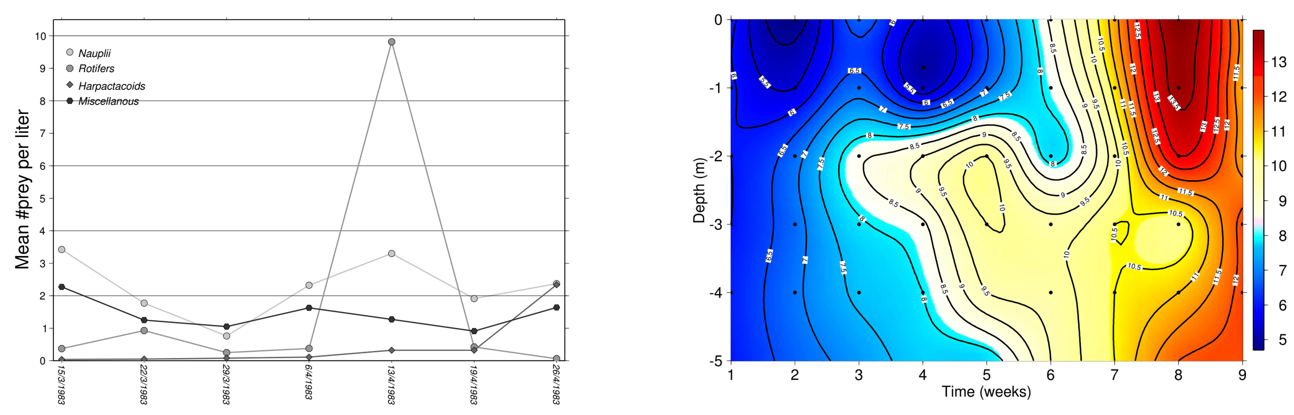

Figure 2: The mean prey values (number per litre) for rotifers, nauplii and copepodes (left). The temperature (^{o}C) (right) distribution for the macrocosm experiment.

3 The model

The model is run for 100 individuals for 35 days. Each individual experiences the same temperature and prey density, but the turbulence varies randomly between 0-10 mms^{-1}. The encounter rate is a function of the prey- and larva-size, the light at the given date, hour and depth, and the turbulence. The larva is subject to encounters with 8 different prey sizes (1 rotifer, 3 nauplii, 2 copepodits, 1 harpactacoids, misc), each with a different handling time. The capture success for a given prey is a function of the relative prey-predtor ratio. Every 24 hours the total ingested material for each prey type is summed up and the metabolistic cost and growth is calculated. The prey density and temperature distribution from the pond measurements are used as input to the model.

$$G_{max} = a \exp^{-0.5(\frac{ln(w/x_0)}{b})^2}$$

$$e = \frac{2}{3}\pi r^3 N f + \pi r^2 N \sqrt{u^2 + 2\omega^2} f \lambda$$

$$r \approx \sqrt{E' C A_p \frac{E_b}{K_e + E_b}}$$

$$M(W,T) = 0.93 P_a Q_{10}^{\frac{T-5}{10}} min(1.827(0.001W)^{1.107}, 1.983(0.001W)^{0.831})$$

$$G = (G_{max}(W,T) + M(W,T))(1 - \exp^{-\beta i}) - M(W,T)$$

Encounter rate	e	(prey/s)	([MacKenzie and Kiørboe, 1995])
Visual range	r	(m)	([Aksnes and Giske, 1993])
Max growth	G_{max}	(%)	([Otterlei et al., 1999])
Metabolism	$M(W,T)$	(g/gday)	([Blom et al., 1991])
Growth-Metabolism	G	(g/gday)	([Fiksen and Folkvord, 1999])

4 Results

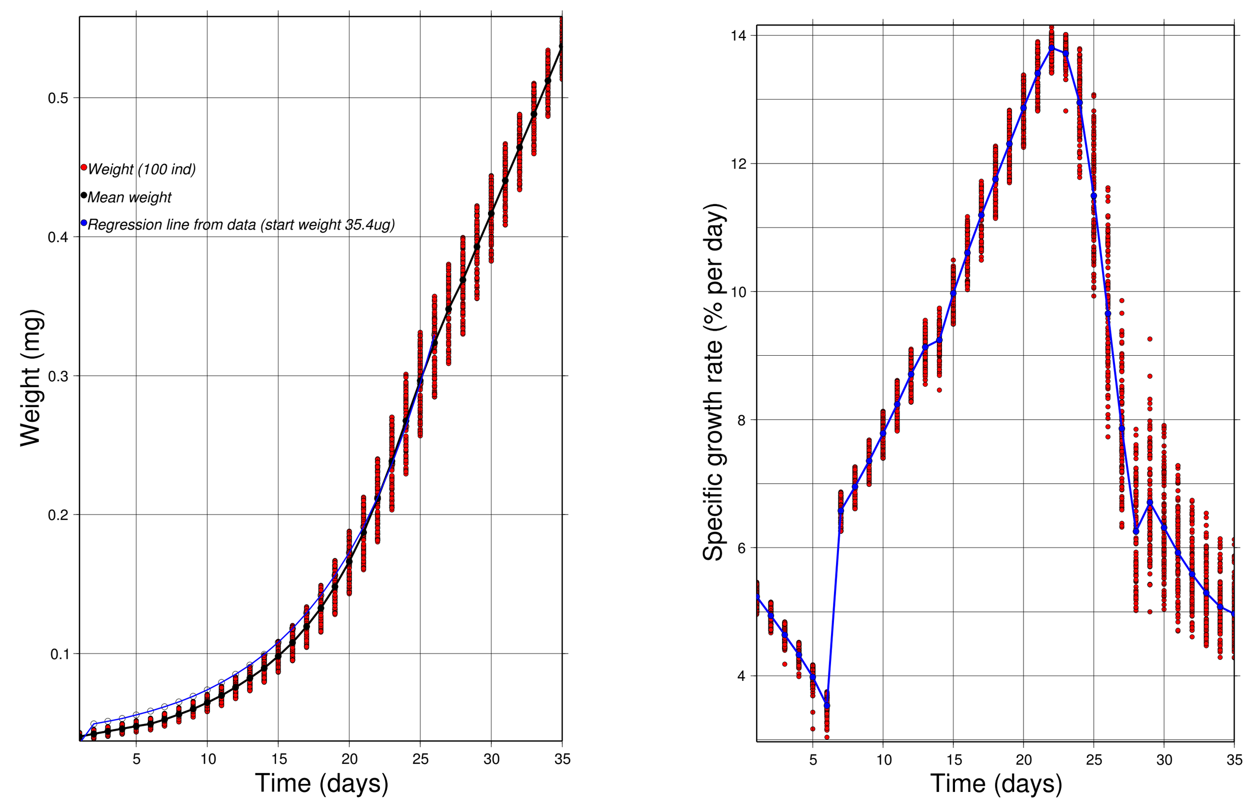

Figure 3: Weight (left) and specific growth rate (right), as a function of time, of a 100 individuals with a random initial weight between $35 \pm 5.6\mu g$ are shown as red dots. The larva stays at a chosen depth of 3 meters. The black line indicates the mean weight. The blue line is the regression line from the experiment measurements.

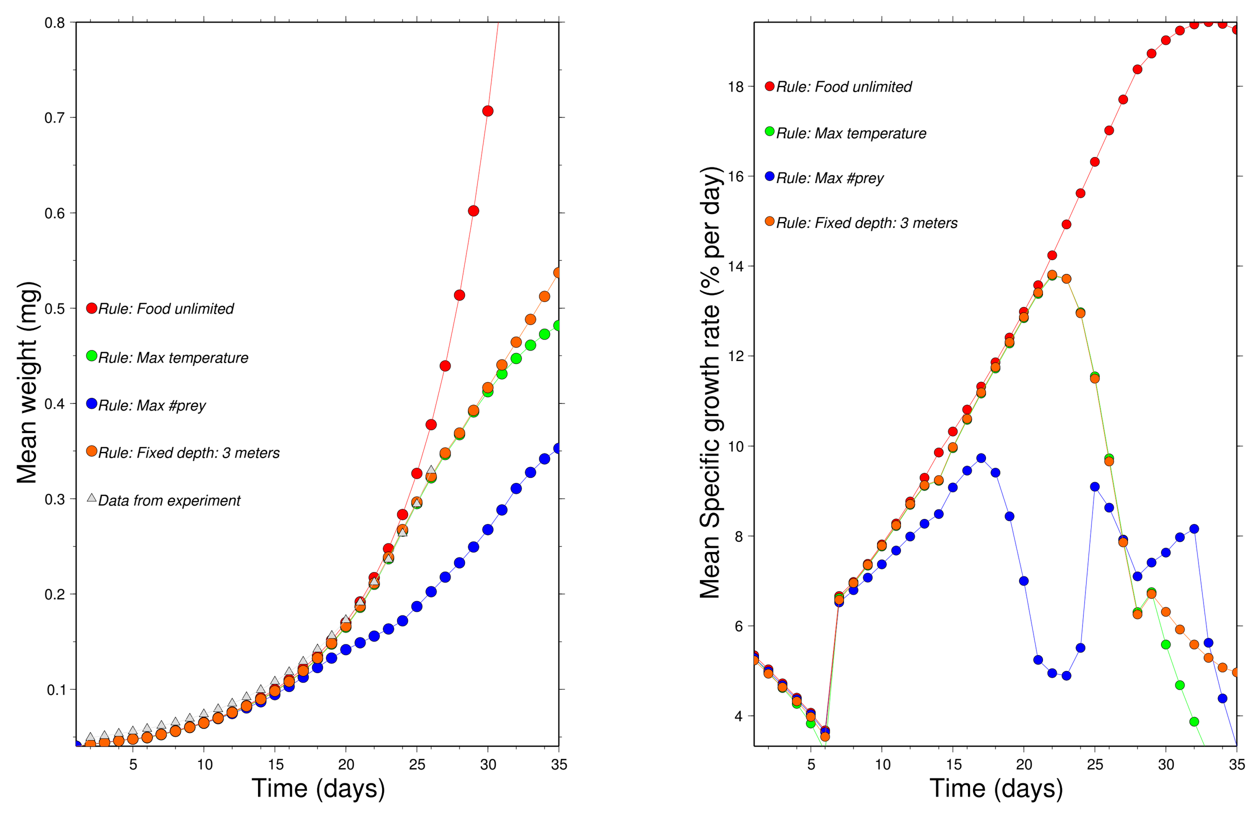

Figure 4: Various rules yield varying results in the weight (left) and specific growth rate (right). Blue dots indicate that larva chooses the depth of max prey, green dots the depth of max temperature, orange dots a fixed depth of 3 meters, and red dots growth with unlimited food supply at max temp.

5 Conclusions

- The ingested material is not able to sustain the potential (size- and temperature-limited) growth, hence the growth must be food limited.
- The model is able to predict growth rates which are in good agreement with the measurements from the experiment.

6 Acknowledgements

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Larvae cod in ponds and models

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Introduction

Among the classical hypotheses regarding the annual variability of year class strength are 'the critical period' concept of Hjort (1914) and the 'match-mismatch' hypothesis of Cushing (1990, 1996). Both of these consider food intake, growth and the impact of growth on survival, and are not mutually exclusive. Individual based models (IBM's, e.g. Hinckley et al. (1996), Werner et al. (1996)) provide a method for specifying physiological and developmental features of larvae, the specific differences in history of individual larvae and therefore the recognition of critical or sensitive periods in the life cycle.

In this work, we develop an individual based model (IBM) that inhibits the most important factors of biological and physical properties that influence growth of cod (*Gadus morhua*) larva. This includes both temperature- and food-limited growth. In addition, we validate the model by explicit simulations of a macrocosm experiment (Folkvord et al. 1994) and compare the observed growth and diet of larvae in the rearing experiment with the predictions from the IBM. In particular, we emphasize the effects of habitat selection by the larvae and the effect this has on realized growth rates. To what extent is larval cod able to sustain high growth rates by switching habitat?

Model description

Model forcing

During spring 1983, a macrocosm experiment was conducted by Folkvord et al. (1994) at Austevoll biological station in Norway. Three cohorts of 1200000, 400000, and 250000 cod larvae were released with ten days interval into an enclosed pond of size 63000 m^3 water. Weight, length, and gut filling were measured once a week from a representative number of larvae in addition to measurements of the density of zooplankton (mainly rotifers, nauplii and copepods) and hydrography (temperature, salinity, and oxygen) from surface to bottom (5 meters). The resulting observations of hydrography, prey density and prey distribution are used as input, or forcing, to this IBM. The measurements of cod larvae from the experiment are used to evaluate the model.

Temperature- and food-dependent growth rate

If the larvae are able to find more food than they can process and assimilate, then size- and temperature-dependent physiological processes will limit their growth. Otterlei et al. (1999) provided data on growth rates of larval cod under high food concentrations and

temperatures ranging from 4-14ºC. From these experiments we derive an equation for the optimal growth rate as a function of temperature and body weight.
Kiørboe et al. (1987) suggested an expression for food-limited specific growth in herring larvae. This was further modified by Fiksen & Folkvord (1999) to include temperature-dependence. When we combine the temperature- and food-dependent growth model with the metabolic rate from Blom et al. (1991), the daily growth rate as a function of temperature, time, ingested material and body-size can be estimated for cod larvae, including both body size and temperature.

Prey densities from the macrocosm experiment are used as input to the larva's search for food. Light, prey density, turbulence, and visual range determine the larva's prey encounter rate which is calculated according to MacKenzie & Kiørboe (1995) and Fiksen & Folkvord (1999). The capture success is determined by the larva's ability to pursuit the prey without noticing the prey of its presence. Zooplankton detects the presence of predators by small changes in the surrounding water pressure. Successful pursuit is achieved if the larva moves toward the prey without creating deformation rates above the detection-threshold of the prey. When the larva is within strike distance of the prey, successful capture is a function of the prey-predator ratio, strike distance, prey escape angle and the variability of this escape angle, and the relative prey-predator ratio (Fiksen & Folkvord 1999, Caparroy et al. 2000).

The model was setup for 100 individuals with an initial weight of $35.4 \pm 5.6 \ \mu gdwgt$, which corresponds to the mean weight of cohort 1. Release date was 20th of March 1983 and the simulation was run for 35 days. The time-step of the model is 1 hour for the foraging functions, and 24 hours for growth and metabolism.

Results

From model runs it is evident that the growth rates are strongly determined by the level of depth the larva chooses (see Figure 1 and Figure 2). We applied three vertical behavioral rules that the larva could adapt: 1) Stay at a fixed depth of 3 meters (middle of the water column), 2) always find the depth of maximum prey biomass, and 3) always stay at the depth with maximum temperature. The simulated growth rates for the three rules are compared to the growth rate when assuming unlimited food supply at the depth of maximum temperature. This tells us whether the growth rates are only temperature-limited (optimal prey density) or food- and temperature-limited (not enough food for optimal growth.

Discussion

The growth rates for the three different vertical behavioral rules are lower than the growth rate for unlimited food. This indicates that the larvae grow at a rate below their optimal rate (Figure 1), and the growth is food-limited. The model is able to predict growth rates which are in agreement with the measurements from the experiment.

Being able to stay in the middle of the water column seems ideal for the given prey-density and temperature distribution. If the larva chooses depth of maximum prey, it experiences a cold ambient temperature, which reduces the growth rate. The depth of max temperature yields a slightly higher growth rate, but the prey density is too small to obtain optimal growth rates.

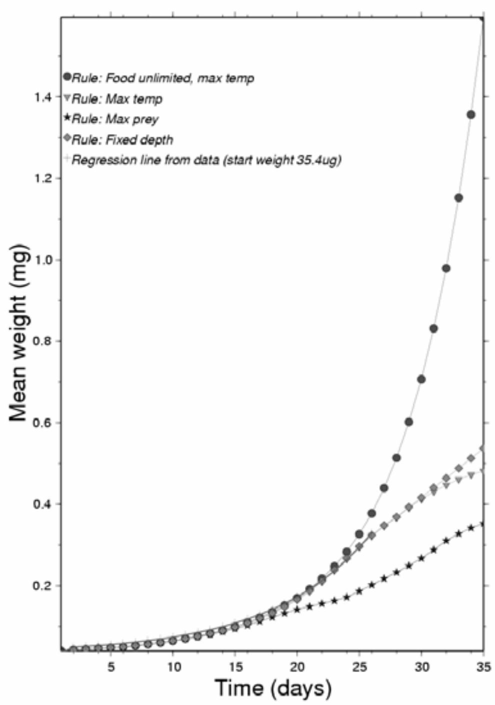

Figure 1: Weight as a function of time

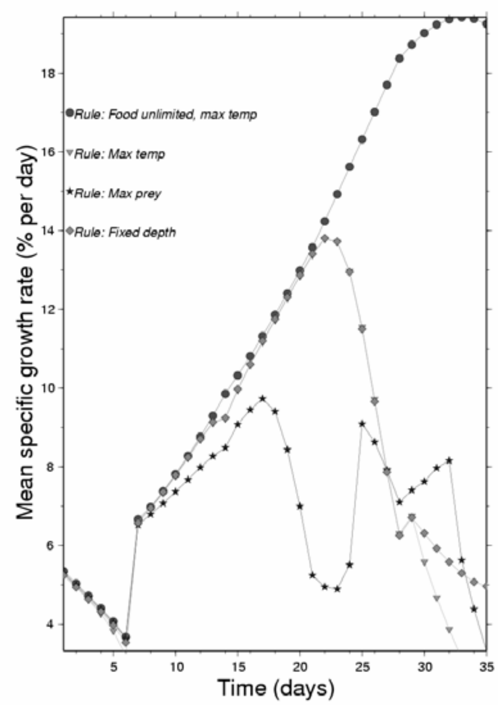

Figure 2: Mean specific growth rate

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