

## **BUILDING SIMULATION MODELS OF COMPLEX ECOLOGICAL SYSTEMS BY SUCCESSIVE COMPOSITION AND REUSING SIMULATION EXPERIMENTS**

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### **ABSTRACT**

With an increasing demand to manage biological resources even when the supporting systems undergo significant changes there is great need for ecological models which take into account all system levels relevant to the resource. However, the large ecological models rising to this challenge require expertise from, at times, quite distinct branches of science. Therefore, rather than tasking a single individual or working group to expand models beyond their area of expertise, fusing smaller submodels into large complex ones appears as a natural way forward. We propose to ensure the semantic validity of the fused models by carefully interlinking composition and validation steps exploiting earlier simulation experiments. A simulation model of the cod in the Baltic sea will elucidate the approach as the different aspects of respiration, energy budgets and behaviour are fused and validated as a whole after being modeled and validated individually.

### **1 INTRODUCTION**

Building large ecological models requires expertise from a wide array of distinct branches of biology, e.g., physiology, ethology and expertise in abiotic conditions. Each of these fields is almost a scientific domain in its own right and only few, if any, individual scientists could handle formalizing them all. Developing and validating smaller submodels for the different phenomena is practical and in many areas such models are already in use or under development. These models, concerned with a manageable amount of complexity, can be handled by a single or a few scientists. Constructing a larger, more complex, model from such existing models is the next step, but there is the risk of “breaking” the model i.e., it losing its semantic validity in the process (Szabo and Teo 2009). For the purpose of this paper (semantic) model validation shall be defined as: “substantiating that the model, within its domain of applicability, behaves with satisfactory accuracy consistent with modeling and simulation objectives” (Balci 1997). In the validation of simulation models, the execution of simulation experiments are vital. Current trends emphasize the role of making these experiments explicit, thereby facilitating their genesis, reuse, and reproduction (Ewald and Uhrmacher 2014; Teran et al. 2015; Schmidt et al. 2016). In particular, a systematic reuse of validation experiments can ensure semantic validity of larger models, as has been shown in (Peng et al. 2016; Peng et al. 2017). In this approach hypotheses about the behavior of the model over time defined in terms of temporal logic and tested by statistical model checking played a central role. However, this idea can be adopted for validation experiments in general.

## 2 SUCCESSIVE COMPOSITION BY REUSING SIMULATION EXPERIMENTS

Our approach carefully interlinks composition and validation steps. Thereby, earlier validation experiments are reused to support the development of a simulation model.

### 2.1 The Composition Step

There are several different manners in which two or more models can be used to build a single model. Generally, although more detailed characterizations exist (Shaffer et al. 2006), black-box and white-box composition can be distinguished. In biology white-box composition prevails as it avoids the “inaccessible variable problem” associated with hiding the internals of black-box composition (Neal et al. 2014). Fusion, a white-box composition, combines models into a single unified model without redundancies, and as such is an irreversible process. Fusion appears most suitable to developing ecological models by composition, since there is no advantage in keeping the models separate. Additionally, we argue that the fusion process itself can increase scientific understanding. The simulation model is defined in the domain-specific modeling language for simulation ML-Rules.

**ML-Rules:** The smaller and larger models used in this paper are formalized in ML-Rules. This is a rule-based language developed for supporting the modeling of cell biological systems (Maus et al. 2011; Helms et al. 2014) but has since been applied to modeling ecological systems (Pierce et al. 2017). An ML-Rules manual can be found at (Helms et al. 2014).

### 2.2 The Validation Step

The validation step is based on different artifacts. Those need to be accessible, i.e., the simulation model, the validation experiment, the data used for validation, and the post-processing of the data. The simulation model is defined in the domain-specific modeling language for simulation ML-Rules, the validation experiments are specified in the embedded domain specific language SESSL, the data are defined as csv files, and for post-processing scripts in R are used.

**SESSL:** The execution and documentation of the validation experiments is undertaken via the embedded domain-specific language SESSL (Simulation Experiment Specification via a Scala Layer) (Ewald and Uhrmacher 2014). SESSL is open source (Apache 2.0 license). Its source repository is freely accessible at <http://sessl.org>.

**R:** A major difference between the field of cell biology, where similar approaches have been applied, and fisheries science is the likely academic background of modelers and supporting scientists. Little to no programming experience is the norm and new tools are hard to sell. Therefore, we have chosen to use the statistical language R (R Core Team 2018) to evaluate simulation results, since this is the most widespread tool for data analysis in the fisheries science community.

### 2.3 Interlinking Composition and Validation Steps

The process of successive composition we want to present, is schematically depicted in Figure 1. Separately  $\mathbf{m}_1$  and  $\mathbf{m}_2$  are validated using the experiment specifications  $\mathbf{Ex}_1$  and  $\mathbf{Ex}_2$  respectively by comparing the simulation outputs to wet lab results in the form of face validation. Then  $\mathbf{m}_1$  and  $\mathbf{m}_2$  are fused into model  $\mathbf{m}_{1,2}$  and, if need be, calibrated or otherwise refined. Next the original validation experiments are adjusted for the new model. This entails adapting formal changes such as denotation, the amount of attributes of entities or the position of the observed attributes. Now the adjusted validation experiments  $\mathbf{Ex}_{a1}$  and  $\mathbf{Ex}_{a2}$  can be applied to  $\mathbf{m}_{1,2}$  and again the simulation outputs are compared to the respective wet lab results. If the fusion is deemed successful model  $\mathbf{m}_3$ , already having been validated, is fused with  $\mathbf{m}_{1,2}$  and all three experiments are adapted. Finally the new model  $\mathbf{m}_{1,2,3}$  is now validated using  $\mathbf{Ex}_{b1}$ ,  $\mathbf{Ex}_{b2}$  and  $\mathbf{Ex}_{b3}$ . Our approach will be elucidated by a cod model which comprises different sub-models, dedicated to the processes of respiration, growth and behavior. The main part of the model, our method is applied to, has

already been published (Pierce et al. 2017) and is equivalent to the model  $m_{1,2,3}$  in this paper. Our focus here is on replaying essential development steps based on the new approach.

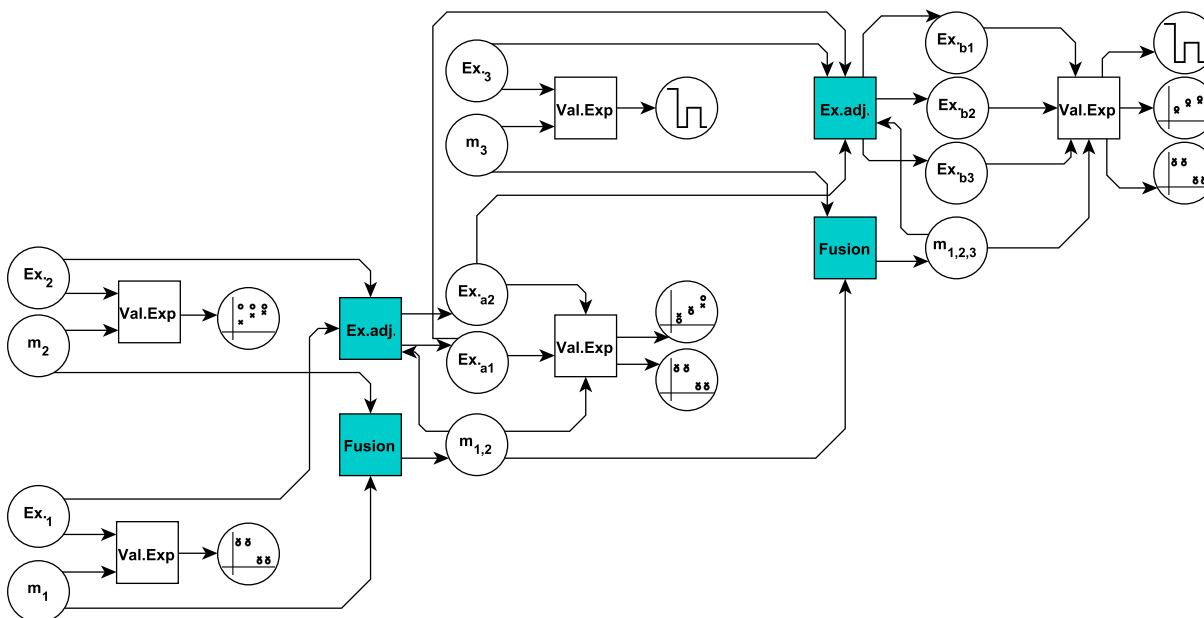


Figure 1: Schematic representation of successive composition. Circles stand for artefacts and squares represent activities. Three steps of model development including are shown: **m**: models; **Ex**: simulation experiments; **plots**: results from validation experiments; **Val.Exp.**: conduct respective validation experiments; **Fusion**: fuse respective models; **Ex. adj.**: adjustment of validation experiment.

### 3 APPLICATION - THE EASTERN BALTIC COD

The application of the methods presented here is Baltic fisheries science, in particular the ecology of the Eastern Baltic Cod (EBC). The EBC stock is a population unit of the species *Gadus morhua* in the Baltic Sea and is of great ecological importance and economical value (ICES 2017). But despite a large amount of available data and the means to implement fishing restriction, the stock has undergone great fluctuations both in terms of biomass and in terms of condition of individuals over the last decades (Eero et al. 2015). Currently there is an ongoing scientific debate on the understanding of the mechanisms and their interactions and how they are causal to these fluctuations.

Hypotheses include factors as diverse as fishing pressure, the decrease of sufficiently oxygenated areas and an increase in infestation levels of liver parasites. Arguably all of these and more factors influence the condition of individual EBC and in turn of the entirety of the stock, but quantifying their impact and accounting for cumulative effects can not always be handled by conventional population models used in fisheries science such SAM or XSA. Especially multicausality renders a strong inference methodology infeasible as the traditional hypothetico-deductive can not account for interactions between causes (Quinn and Dunham 1983) .

#### 3.1 Submodel 1: Respiration

Aquatic environments are generally oxygen limited (Pauly 2010) and the Baltic is particularly vulnerable to the formation of hypoxic and even anoxic areas due to strong stratification in the deeper basins, their dependence on inflow events and increasing eutrophication during the past decades (Conley et al. 2009). Therefore a sound representation of respiration is needed as a baseline.

For cod the fundamental biological functions either use oxygen or result in a physiological 'oxygen debt'. The wet lab experiments conducted by Claireaux et al. (2000) determined the influence of water temperature and oxygenation on the metabolic scope of cod. This relation was formalized into an ML-Rules model. In addition, the maximum amount of oxygen a cod can contain was based on Burke (1966). The result is a straightforward model of the oxygen budget of cod under different oxygen saturations and temperatures. Model definition must include its limitations or, inversely, its scope of applicability. For this respiration model no limitations for environmental variables are included, meaning that unrealistic oxygen saturation and temperatures are not excluded. Although peak performance of the metabolism can not yet be validated since it has no functionality beyond respiration, mortality due to asphyxiation can be validated.

To validate realistic mortality due to asphyxiation the behavior of the modeled cod was tested against wet lab results by Plante et al. (1998). In their experiments cod of different weight classes were kept at two temperatures and six different oxygen saturations for 96 hours to determine cumulative mortality. This experiment was reproduced with the ML-Rules respiration model using SESSL. The SESSL experiment (Figure 2) scans through the temperature and oxygen combinations with the different weight classes of cod. The number of cod not perished at the end of the simulation are observed and results are written in systematically organized csv files.

<i>Import SESSL core</i>	<code>import sessl._</code>
<i>Import ML-Rules binding</i>	<code>import sessl.mlrules._</code>
<i>Execute the following experiment</i>	<code>execute {</code>
<i>Include observation and parallelization</i>	<code>  new Experiment with</code>
	<code>  Observation with ParalleExecution CSVOutput{</code>
<i>Location and name of model file</i>	<code>  model = "./ml.mlrxj"</code>
<i>Choice of simulator</i>	<code>  simulator = StandardSimulator()</code>
<i>Use 1 thread</i>	<code>  parallelThreads = -1</code>
<i>20 replication of each configuration</i>	<code>  replications = 20</code>
<i>Simulation stops at time 9600</i>	<code>  stopTime = 9600</code>
<i>Observe at 9600</i>	<code>  observeAt(range(0, 9600, 9600))</code>
<i>Vary between 4 different initial states</i>	<code>  scan("init" &lt;~ ("GM(570)", "GM(1740)",</code>
	<code>    "GM(890)", "GM(1790)"))</code>
<i>Vary parameter t between 2 and 6</i>	<code>  scan("t" &lt;~ (2, 6))</code>
<i>Vary parameter o for the given values</i>	<code>  scan("o" &lt;~</code>
	<code>    (13.8, 17.8, 23.7, 29.5, 36.5, 42.5))</code>
<i>Observe attribute 0 of GM</i>	<code>  observeAttribute("GM", 0)</code>
<i>Set output directory</i>	<code>  csvOutputDirectory( =&gt; "result_asph_ml")</code>
<i>Write observed attribute values to file</i>	<code>  withExperimentResult(writeCSV</code>
	<code>    })</code>
	<code>  }</code>
	<code>}</code>

Figure 2: A SESSL experiment using ML-Rules (Scala keywords are shown in blue). This simulation experiment runs the metabolism submodel (with the suitable initial solution for this specific simulation) for variations of the parameter t (temperature), o (oxygen saturation) and init (initial state) with 20 replications per combination. It reproduces the wet lab experiment by Plante et al. (1998) on hypoxia tolerance.

Since the output of SESSL is systematically organized it can be imported into any data analysis software in a systematic manner. As reasoned before our choice of data analyzing software is based on the habits and customs within the community of fisheries scientist. All of the R scripts used to generate the results presented in this paper will be made available with the complementary software package. For the

asphyxiation experiment, the results from the original wet lab experiment were extracted and the results of the simulation experiment prepared in the same manner.

The results (Figure 3) reveal a general consistency with the wet lab results. An obvious difference between the wet lab and simulation results is that the simulation results are comparatively regular. There are several facts which explain the resulting difference. Firstly, there is no experimental variability for the abiotic conditions in the simulation experiment e.g., pockets of water with higher oxygen content near the surface of experimental tanks or fluctuations in temperature. Secondly, although ML-Rules includes stochasticity this is not the only factor in variability of the individuals tested. Differences in efficiency of metabolism, developmental stage and even personality and grouping of animals tested are not present in the modeled cod but are in the experimental animals.

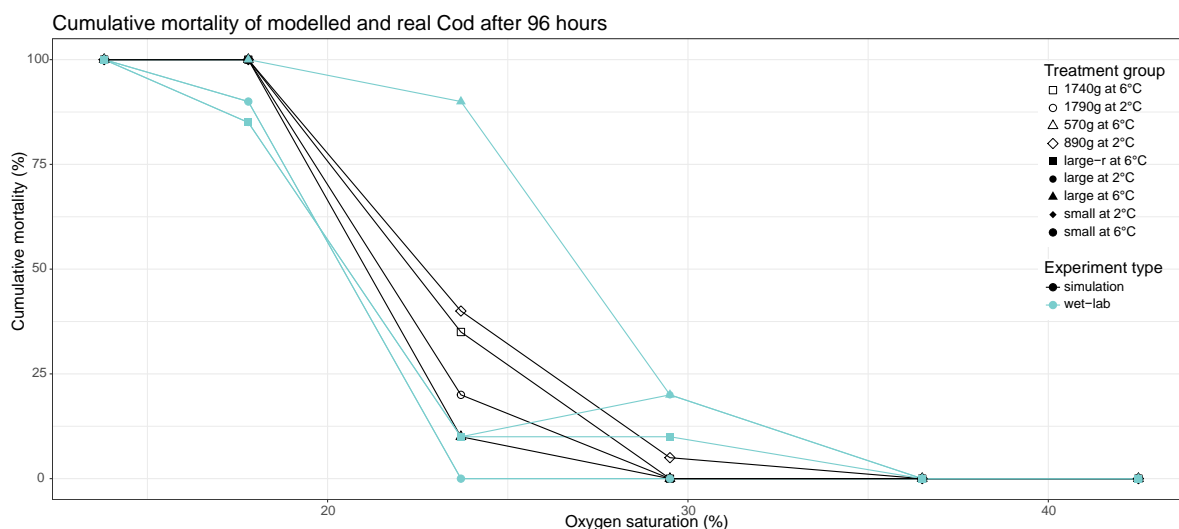


Figure 3: Comparing wet lab and simulation results for identical asphyxiation experiment (Plante et al. 1998); cod are held at different oxygen saturation for 96 hours. Wet lab results in blue and simulation results in black.

### 3.2 Submodel 2: Energy Budget

Fish stock in ICES (International Council for the Exploration of the Sea) waters are generally managed according to the principle of MSY (maximum sustainable yield (Russell 1931)). This is the practice of keeping a stock in a state of continuous maximum productivity. Therefore the goal of management is to understand and influence stock dynamics in such a way that it produces the highest possible yield per recruit (cod which have survived to become part of the population) resulting in a large amount of individuals in good condition i.e., healthy and fat. Typically the energy budget of individual fish is treated like a balance sheet. **Consumption** (food intake) is on one side of the equation and the other side represents the sum of **maintenance** (basal metabolic rate), **production** (somatic growth and maturation) and **loss** (digestive, fecal and urinary loss) (Kleiber 1961). However, this is only sufficient when total biomass is of interest. Since information about condition (how plump an individual is) is also required the model needs to be more advanced. Additionally points to address are the speed of digestion and the different percentages of loss for particular types of food. Regardless of the complexity of any model having a modeled rather than a living organism allows to track processes easily which otherwise would be hard or impossible to track.

Taking advantage of this fact the prey ingested by the modeled cod is tracked using the additional attribute 'prey count'. This submodel is more complex than the respiration model. As a footing it formalizes basal metabolic rate, both in regular and in starvation mode, and growth, both in length and in body mass. Building on this, death from starvation, the process of ingestion and stomach evacuation are formalized,

which allows to model appetite and different gut transit times for particular types of food or prey. Wherever these processes are understood to be regulated by temperature this has been formalized accordingly.

For this submodel several aspects of model behavior can be validated but for the purpose of this paper we will focus on the validation of growth including condition. We compare the growth of the modeled cod with the wet lab results by Chabot and Dutil (1999) who tested the growth of juvenile cod at different non-lethal oxygen saturations. In this experiment cod were held for 12 weeks being fed three times a week for one hour. This experimental design was formalized and included in the ML-Rules model.

The SESSL experiment for this model calls the ML-Rules model  $m_2$  and lets it complete the twelve weeks of simulation time and reproduces the experiment twenty times, equivalent to the number of cod in the wet lab experiment.

The results of the simulation experiment (Figure 4) match the wet lab results only for the higher oxygen concentrations. Still the model can be considered valid within the limitation of not including respiration and only including the stochasticity of ML-Rules of variability.

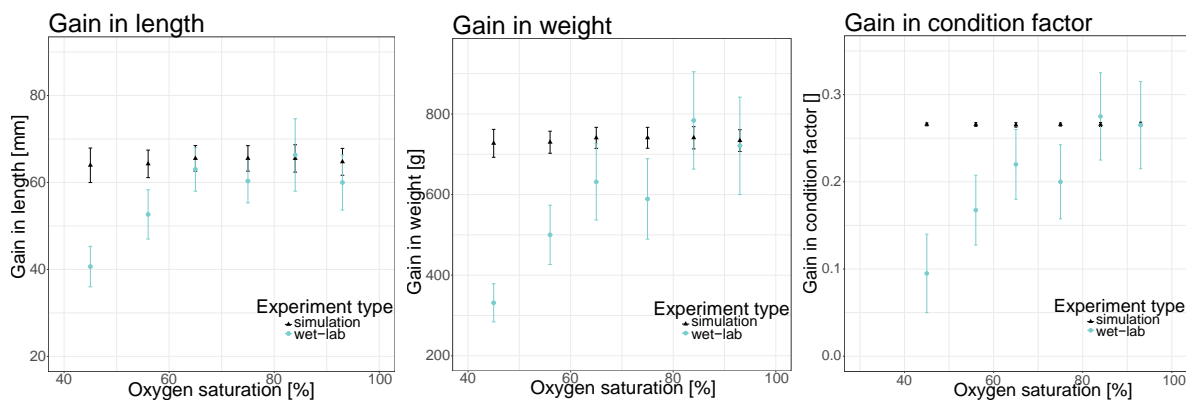


Figure 4: Comparing wet lab by (Chabot and Dutil 1999) and simulation results of the energy budget model for a growth experiment. Wet lab results in blue and simulation results in black.

### 3.3 Fused Model I: Metabolism

The fusion of two physiology models is a process which in itself increases, or at least refines, scientific understanding of the system in question, since the exercises increases the amount of “...common language between modelers and experimentalists...” (Cooper et al. 2015). By this we mean that the fusion process, as well as the fused model itself can serve as the basis of scientific debate. Here we expect them to reduce misunderstandings as the formalized models allow for more rigor in aligning understanding than verbalized conceptual models do. In this particular example the fusion of the two submodels reaffirmed the understanding that the aquatic environment and by extension the physiology of EBC is capped by the availability of oxygen. Bringing together the balance-sheet approach of the energy budget and the wet lab result based mechanistic approach of the respiration did not require alterations of the semantics of either model and calibrating factors used in the original model were no longer needed. The SESSL experiment on asphyxiation was adjusted by changing the executed model to the fused one and extending the attributes of the cod to those it now holds in the model ( $m_1$ : weight;  $m_2$ : length, weight  $\rightarrow$   $m_{1,2}$ : length, weight and prey count).

This first check of continuing semantic validity was successful as the results of the asphyxiation experiment on the  $m_{1,2}$  model are as satisfactory as the results of the  $m_1$  model (Figure 5). But the results are still very regular which can be interpreted as showing the need to further refine the model. This situation is an example of a fused model serving as the bases for scientific debate in fisheries science. If the difference between reality (wet lab results) and the modeled entity are lacking which phenomena are missing from the (formalized) conceptual model?

The SESSL experiment to validated growth (EX<sub>2</sub>) was adjusted in the same manner as EX<sub>1</sub> adjusting the attributes of the modeled cod to the ones it was assigned in the fused model (m<sub>1,2</sub>).

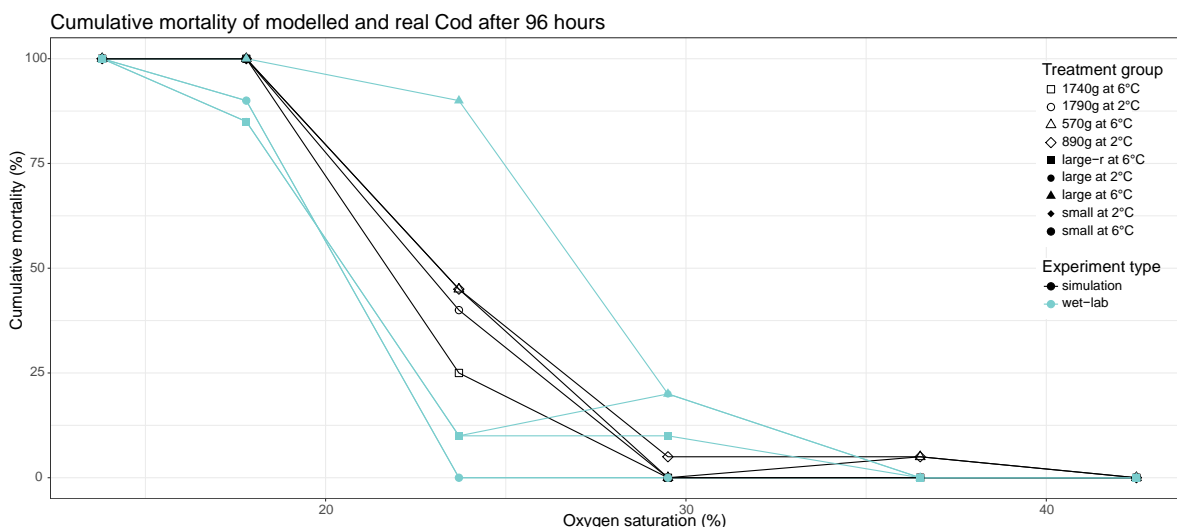


Figure 5: Comparing wet lab and simulation results for identical asphyxiation experiment (Plante et al. 1998); cod are held at different oxygen saturation for 96 hours. Wet lab results in blue and simulation results in black.

The results of the growth experiment (Figure 6) with the fused model show how the fusion process has increased the scope of applicability of the modeled cod. Now the simulation results are in line with the results from the original wet lab experiment across all oxygen saturations. But as with the asphyxiation experiment the simulated results are unrealistically regular and show the need for further refinement of the model.

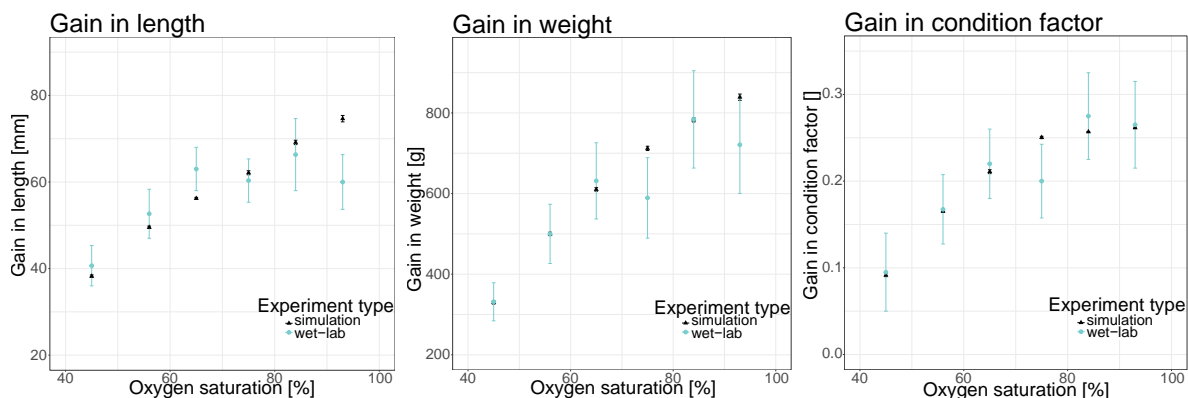


Figure 6: Comparing wet lab and simulation results for growth experiment by (Chabot and Dutil 1999). Wet lab results in blue and simulation results in black.

### 3.4 Submodel 3: Behavior

Ethology, the study of animal behavior, to date, is rarely included into both the conceptual and the formalized models in fisheries science. But current hypotheses more and more find the need to include behavior to fit observations. One example for the EBC is that this demersal (sea floor dwelling) fish used to be caught with ground fishing gear but in recent years pelagic gear (gear used in the water column) has become the rule. To fully understand all changes therefore behavior needs to be included in a comprehensive model.



The behavior submodel governs the vertical movement of the EBC between volumes of water with different abiotic (oxygen saturation and temperature) and biotic (food availability) conditions. Currently it is based on expert knowledge of field scientists familiar with the Baltic Sea. It governs behavior thus that the cod dwells as near the sea floor as possible without asphyxiating or starving while additionally undertaking exploratory upward and downward dives for prey. A complementary development of abiotic conditions is included in the ML-Rules model to test for appropriate reactions. The abiotic structure, which is modeled as four stacked volumes, changes over time: primarily the abiotic conditions of the demersal volume shift from inhabitable to hypoxic back to inhabitable. This should prompt the modeled cod to dwell at the sea floor while remaining above the lowest volume during the hypoxic period and undertaking random vertical dives. These take place when cod investigate an environment for its suitability (oxygen, temperature, proximity to sea floor) or its prey abundance. The SESSL experiment replicates this 23 day run for three individuals ten times. The results (Figure 7) show the expected behavior both in terms of avoiding dangerous conditions as well as undertaking vertical dives for feeding.

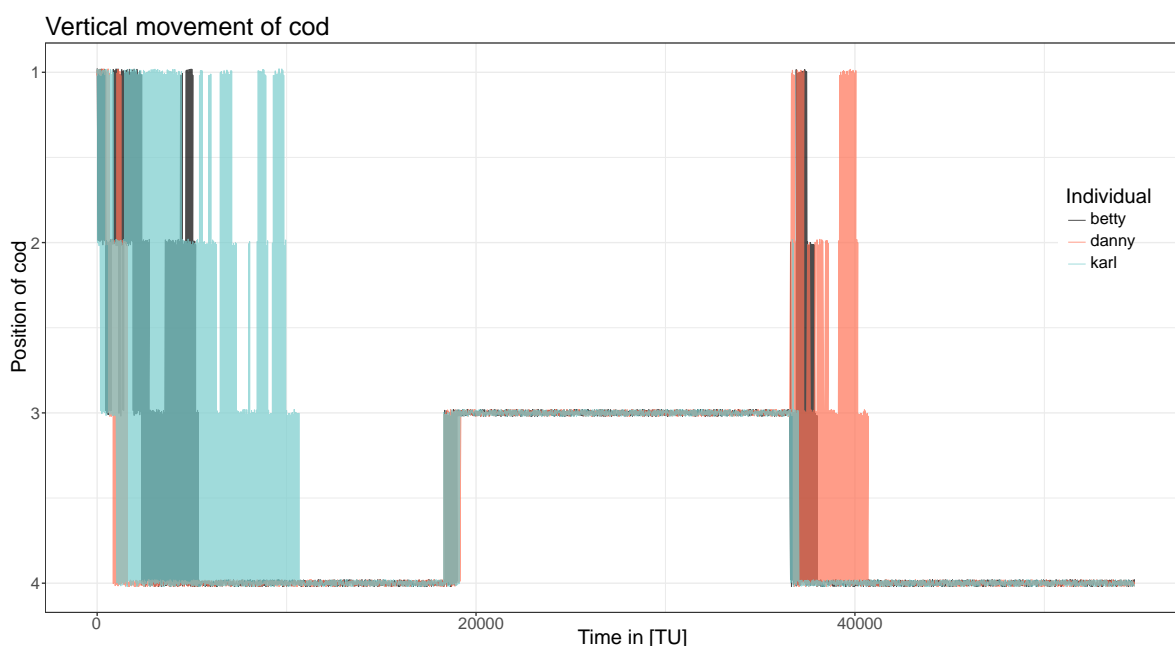


Figure 7: Behavior in terms of vertical movement of modeled cod for three individuals with ten replications. The simulation represents 23 days of simulation time with model  $m_3$ .

### 3.5 Fused Model II: Juvenile Cod

Fusing the metabolism model ( $m_{1,2}$ ) with complex behavior (more than is now contained in model  $m_3$ ) will ultimately result in the model of a juvenile cod (a model of an adult cod in contrast would require a reproductive cycle). With our example, fusing model  $m_{1,2}$  with model  $m_3$  raised a number of interesting issues concerning behavior, for example how behavioral priorities are connected to the condition of the individual. As long as behavior is seen largely independent of the individual and based mostly on environmental conditions, known phenomena such as collective memory (De Luca et al. 2014) or knowledgeable mature individuals can not be included in a comprehensive model. Another issue raised is the intricate and regulatory interdependence of energy available to the organism and energy expenditure necessary for movement i.e., behavior and both issues raised are valuable input to the further development of the model.

The SESSL experiment for asphyxiation  $Ex_{b1}$  was further adjusted to account for the increase in attributes of the cod ( $m_{1,2}$ : length, weight and prey count  $\rightarrow$   $m_{1,2,3}$ : length, weight, prey count, name, cube



of residence) both for the initial state and the observations. The results of the experiment (Figure 8) remain satisfactory with the same shortcomings as with model  $m_1$  and  $m_{1,2}$ .

Adjustments of the growth experiment (Ex.b2) and the behavior experiment (Ex.3) were parallel to the adjustment of the asphyxiation experiment. The results of the growth experiment (Figure 9) are not further improved from the results of the same growth experiment with model  $m_{1,2}$  however, there is also no loss of semantic validity. When the model is further refined to meet the issue raised during fusion of  $m_{1,2}$  and  $m_3$  and behavior is linked with energy expenditure a loss of regularity and therefore a more realistic modeled cod can be expected. Results of the behavior experiment (Figure 10) also show no decrease in semantic validity compared to the results of Ex.3.

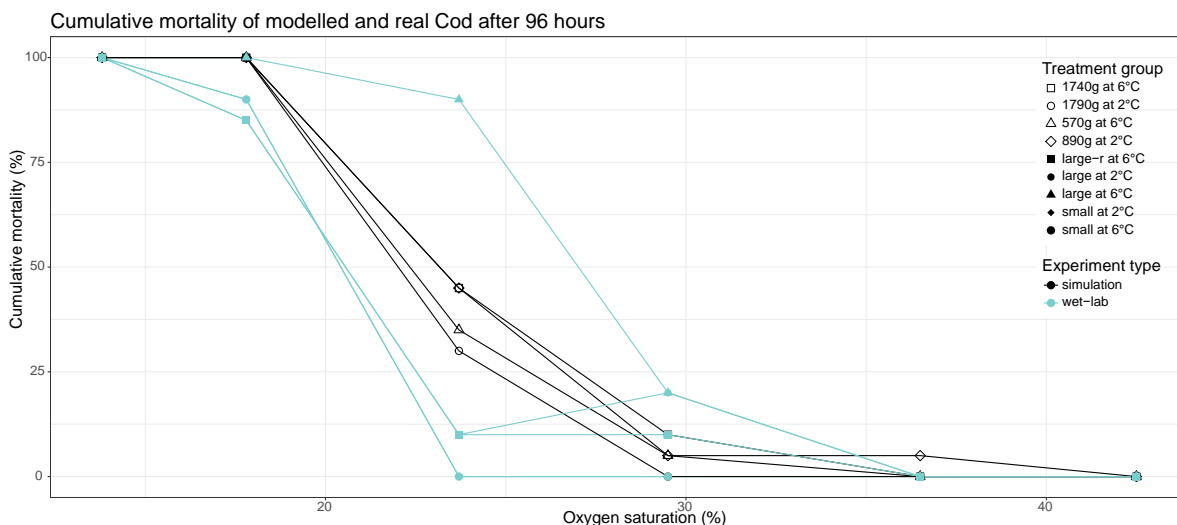


Figure 8: Comparing wet lab and simulation results for identical asphyxiation experiment (Plante et al. 1998); cod are held at different oxygen saturation for 96 hours. Wet lab results in blue and simulation results in black.

#### 4 DISCUSSION AND CONCLUSION

In developing the cod model expertise in abiotic conditions, physiology and ethology is required, and reflected in the sub-models on respiration, growth, and behavior. Each of the submodels involved different validation experiments (Pierce et al. 2017), one of which was used to elucidate the benefits of our approach. Carefully interlinking composition and validation steps and the reuse of earlier experiments revealed how by successive composition, the range of validity increased. It also demonstrated the benefit of making small steps in extending and composing a model, as the first fused model is able to realistically depict that the growth of cod is capped by the availability of oxygen, making superfluous the calibration factors introduced in the original model. Although the fusion of metabolism and behavior did not further refine or broaden the scope of the model the mindfulness of the process raised important and clear issues in our understanding of the link between physical condition and behavior of cod.

More generally, the approach facilitates the discourse between experts of different sub-fields by the realized “divide and conquer” strategy of our approach and the discourse between modelers and experimentalists by associating simulation sub-models with validation experiments that reflect wet-lab experiments and expert knowledge.

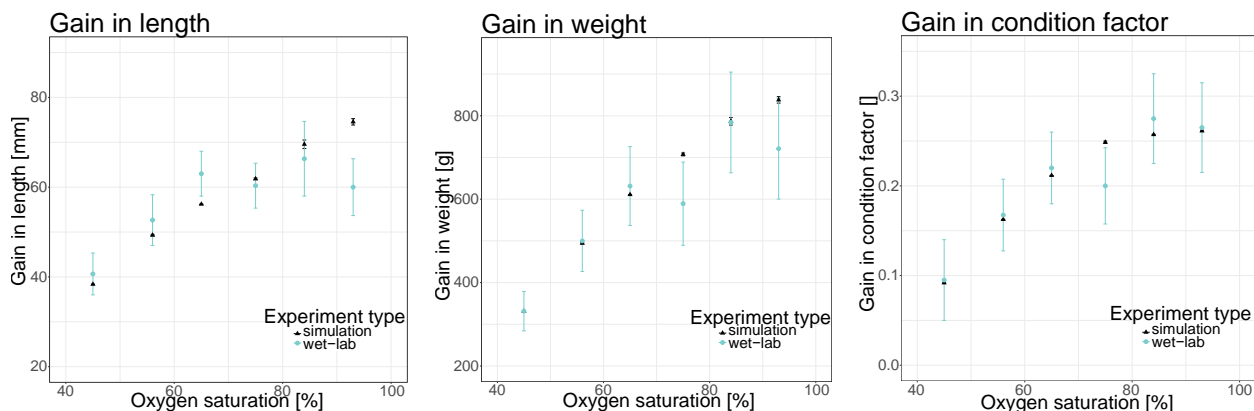


Figure 9: Comparing wet lab and simulation results for growth experiment by (Chabot and Dutil 1999). Wet lab results in blue and simulation results in black.

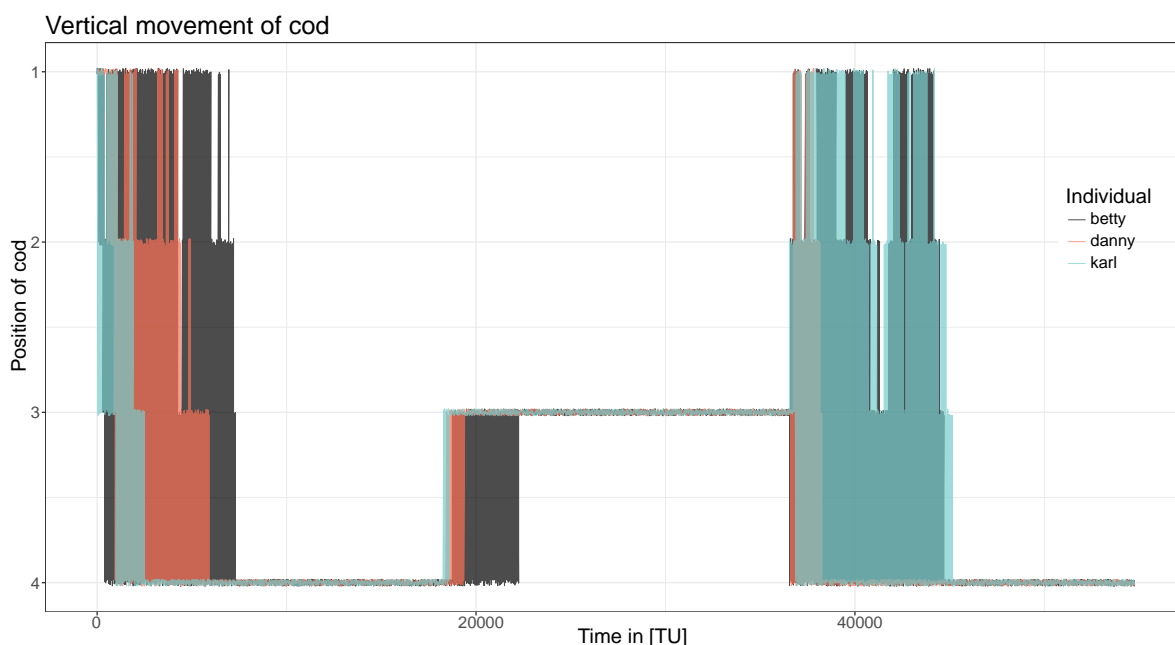


Figure 10: Behavior in terms of vertical movement of modeled cod for three individuals with ten replications. The simulation represents 23 days of simulation time with model  $m_{1,2,3}$ .

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