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A Comparison of Models Used in the ECOHAB Gulf of Maine Project

This document compares the versions of the *A. fundyense* biological model (germination and growth) used during the ECOHAB-Gulf of Maine program. Familiarity with the basic elements of the model is assumed, and those not familiar with these are directed to the detailed descriptions at:

http://www.whoi.edu/science/cohh/alexbiomodels.htm

Descriptions can also be found within the published literature referenced herein. Each model version represents a different stage of model development. New data was incorporated as it became available, and corrections and adjustments were made as necessary. The model versions are designated as model 1.0 through model 3.1. Model 3.1 is the latest, and this is recommended. Differences between the models are summarized in Table 1. While there are changes, the basic properties of the formulation have remained throughout its development. The pages that follow will discuss the evolution of each of the three basic components of the biological model: 1) the germination response to temperature and light, 2) the endogenous clock, and 3) the growth function.

The Germination Rate as a Function of Temperature and Light

The only change in the germination response to temperature and light came between model versions 2.0 and 3.0. A second set of germination time series experiments carried out during the ECOHAB-Gulf of Maine program replaced data collected in 1985 (Keafer, unpublished). Refinements to experimental techniques suggested that the more recent data replace the older data, rather than being combined with it (Keafer, Anderson, personal communication). There were also small adjustments to the fitting procedure, and the functional form of the temperature dependence was changed from a piece-wise linear representation to a hyperbolic tangent. However, these changes did not alter the

Table 1: Summary of models used during the ECOHAB Gulf of Maine program

Version	Germination Rates	Endogenous Clock	Growth Rate[1]	References
1.0	Western Gulf of Maine isolate (Anderson et al. 2005). Unpublished data from Keafer (1985)	Station 38 data (first 14 points) collected by Bronzino, Anderson lab.	**Temp:** Watras **Salt:** Prakash	Franks and Signell (1997)
2.0	As above	As above	**Temp:** Watras, Langdon, Keafer **Salt:** Prakash, Watras **Light:** Langdon	McGillicuddy et al. (2003a,b) McGillicuddy et al. (2005) McGillicuddy et al. (In Press)
3.0	Replaced data from Keafer (1985) with data from eastern Gulf of Maine isolates from ECOHAB-GOM (Anderson et al. 2005)	Added completed Station 38 series, data from Matrai et al. (2005), and earlier data from Anderson and Keafer (1987)	**Temp:** Watras, Langdon, Keafer, Kulis, Etheridge (MI and BOF strains). **Salt:** Prakash, Etheridge (MI and BOF strains) **Light:** Cullen	Anderson et al. (2005), (germ. only), Stock et al. (2005); Stock et al. (Under Review)
3.1	As above	As above	As above, but with minor correction to temperature and salinity dependence	

[1]Prakash: Prakash (1967), Watras: Watras et al. (1982), Langdon: Langdon (1987; 1988), Keafer: unpublished (contact bkeafer@whoi.edu), Kulis: unpublished (contact: bkeafer@whoi.edu), Etheridge: Etheridge and Roesler (2005), Cullen: Cullen et al. (in preparation).

basic germination response (Fig. 1). The largest change is in warm (~15^{O}C) and dark conditions (4.24 %/day for the new function versus 1.79 %/day for the old). Such conditions are rare in the Gulf of Maine but may be important in other regions.

The Endogenous Clock

Additional data was added to constrain the endogenous clock function between model 2.0 and model 3.0. These included the data of Matrai et al. (2005), the completed data set from station 38, and older data from Anderson and Keafer (1987). Patterns in this additional data suggested a shift from a piece-wise linear function with 4 segments (Fig. 2, left panel), to a piece-wise linear function constructed from the monthly medians of the data points. However, the essential properties of the endogenous clock were robust to these changes, particularly during the spring/early summer season of primary interest.

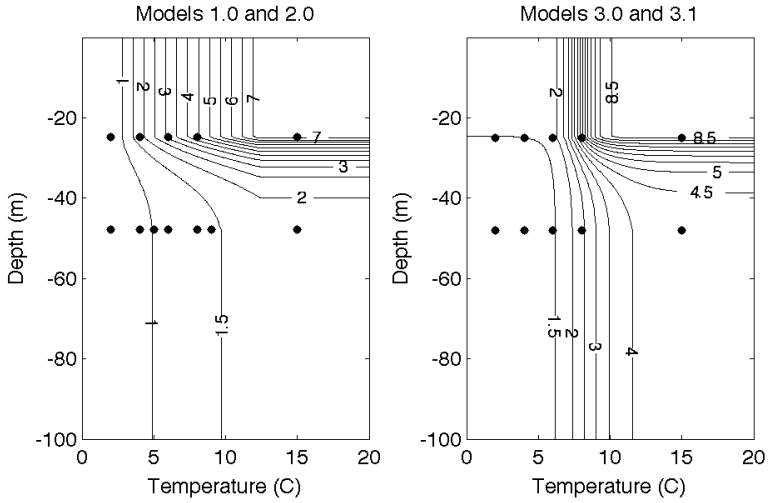

Figure 1: Comparison of the germination rate (%/day) estimated by the model at the sediment surface for the two germination rate parameterizations used during the ECOHAB-Gulf of Maine project. Light conditions have been translated to an equivalent depth using a typical solar radiation (~350 watts/m^2) and light attenuation (~0.2 m^{-1}) values for the Gulf of Maine. The contour interval for both plots is 0.5 %/day. **Note:** the germination rate figure for Model 2.0 in McGillicuddy et al. (2003) and McGillicuddy et al. (In Press) contained an erroneous contour a 2 %/day stretching into dark conditions. The correct figure is shown in the left panel.

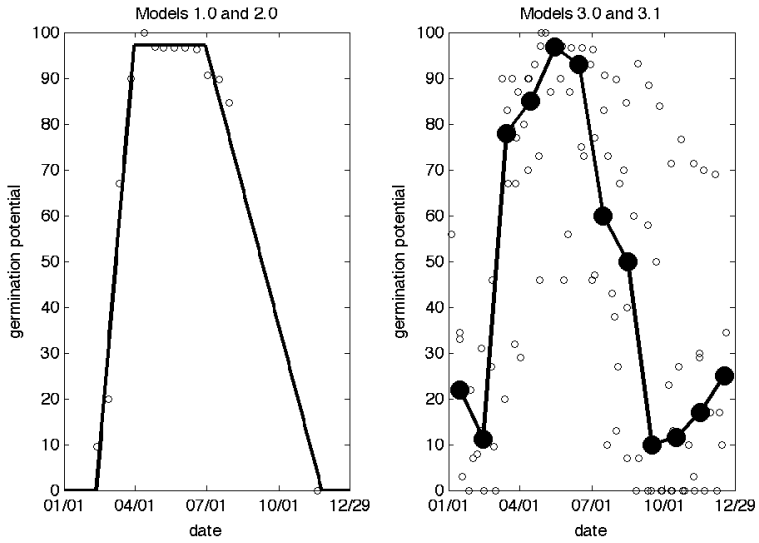

Figure 2: Comparison of the two endogenous clock functions used in the ECOHAB-Gulf of Maine project. The germination potential is the percentage of cysts that are able to germinate. In the germination model, the values above are normalized by the maximum value attained by each fitted curve to produce a factor between 0 and 1 that modifies the germination rates in Fig. 1.

The Growth Function

The growth function has gone through the most changes since the initial model formulation. Model 1.0 was from Franks and Signell (1997). It was based on data from Watras et al. (1982) and Prakash (1967), but details of the function construction were not available. Additional constraints were added to the temperature, salinity, and light dependences in Model 2.0. Model 3.0 added data collected during the ECOHAB-Gulf of Maine program, and model 3.1 implemented some minor corrections to the 3.0 formulations.

The maximum growth rates (as a function of temperature and salinity) for all of the growth functions are shown in Fig. 3. All functions show an optimal growth rate at temperatures between 15-20 Celsius and at fairly low salinities (15-25 ppt). The overall maximum growth rate for the first function is less than the others, but there is considerable uncertainty in this parameter (e.g. Stock et al. (2005), Table 2). Growth functions 3.0 and 3.1 exhibit negative growth at very high temperatures as suggested by the Etheridge and Roesler (2005) data. Model structure 3.1 has a somewhat lower growth rate at very high salinities (> 35 ppt) than model structure 3.0. This is because the 40 ppt growth point from Prakash was assigned a value that was too high during the construction of Model 3.0 (these points were picked manually from the plots of Prakash). The influence of this change is very small for salinities of 35 ppt and below.

The functional form used by Platt and Jassby (1976) for photosynthesis-irradiance relationships and later adopted by Langdon (1987, 1988) for growth was used for models 2.0-3.1:

$$\mu(E,T,S) = \left(\mu_{\max}(T,S) + \mu_o^r\right)\tanh\left(\frac{\alpha_g E}{(\mu_{\max}(T,S) + \mu_o^r)}\right) - \mu_o^r$$

Parameter definitions and values for each of the models 2.0-3.1 are summarized in Table 2. The primary changes in the model are refinements in the maintenance growth rate and growth efficiency parameters based on the data of Cullen, and a slight upward shift in the estimates of maximum growth. The uncertainty ranges are approximate, and the

smallness of the bounds in model 2.0 partly reflects the relative scarcity of data upon which to make estimates.

The uncertainty range for α_g was chosen liberally in published versions of model 3.0 (Stock et al. 2005). This was done to include past estimates of the growth efficiency and encompass an entire plausible range. The revised estimate for model 3.1 in Table 2 is simply the standard deviation around the Cullen estimates.

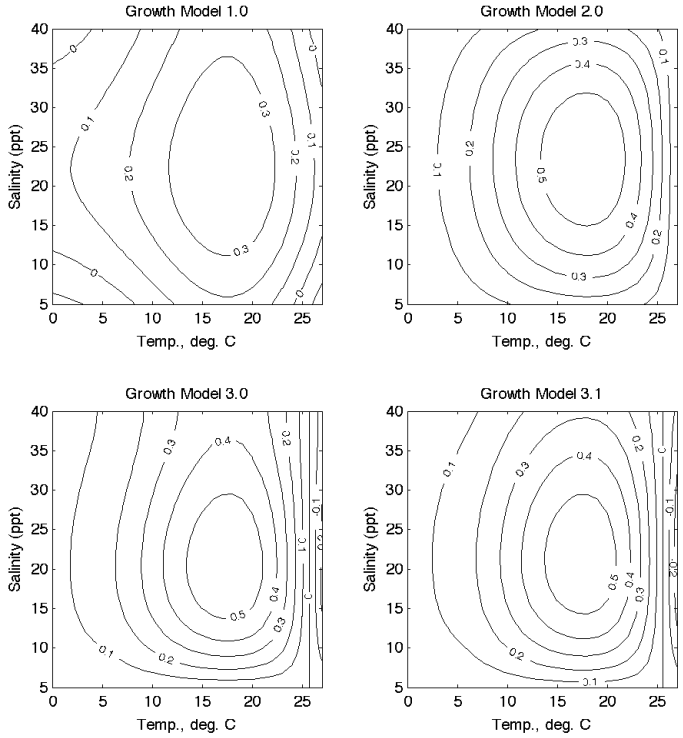

Figure 3: Comparison of the maximum growth rate as a function of temperature and salinity for each model formulation. Plots for model 2.0 and 3.1 are constructed using $\mu_{max}(T_{opt},S_{opt}) = 0.58$ day^{-1}.

Table 1: Growth function Parameters. Central value followed by standard deviation.

Symbol	Description	Model 2.0	Model 3.0	Model 3.1
$\mu_{max}(T_{opt},S_{opt})$	The maximum growth rate (day^{-1}) at optimal temperature and salinity.	0.46 (0.35-0.65)	0.58 (0.46-0.70)	0.59 (0.48-0.69)
α_g	The growth efficiency (m^2 watts^{-1} day^{-1})	0.017 (0.013-0.021)	0.036 (0.017-0.056)	0.036 (0.024-0.048)
μ_o^r	The maintenance growth rate (day^{-1})	0.05 (0.005-0.1)	0.20 (0.15-0.25)	0.20 (0.15-0.25)

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