A Growth model for *Alexandrium fundyense*

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This document gives a detailed description of the *Alexandrium fundyense* growth model that was developed as part of the ECOHAB-Gulf of Maine program. The model described is that used in Stock et al. (2005) with several minor corrections to the temperature and salinity dependence. Detailed descriptions of the corrections, as well as a timeline of model development can be found at:

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

The growth parameterization described here is in version 3.1 of the *A. fundyense* biological model.

The growth parameterization takes the form suggested by Platt and Jassby (1976) for photosynthesis, irradiance relationships and used by Langdon (1987, 1988) in studies of phytoplankton growth:

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

Where μ_{max} is the maximum growth rate (days^{-1}) for a given temperature (T) and salinity (S), μ_o^r is the maintenance respiration rate (days^{-1}), E is the daylight-averaged irradiance (6 AM – 8 PM, watts/m^2), and α_g is the growth efficiency (m^2 watt^{-1} day^{-1}). Best estimates, ranges, and references are given in Table 1. Table 2 summarizes the origins of the different *A. fundyense* isolates used in the studies that contributed to function construction.

The dependence of $\mu_{\max}$ on temperature and salinity is formulated as follows:

$$\mu_{\max}(T,S) = \mu(T_{opt}, S_{opt}) \times f(T) \times f(S)$$

Where T_{opt} and S_{opt} are the optimal temperature and salinity for growth. *f(T)* and *f(S)* are scaling factors with a maximum value of 1. The temperature relationship was formulated using data from isolates GTCA29, GTCA28, GT6, GTMP, BOF, and MI that measured growth as a function of temperature. The data points from each isolate are plotted as fractions of the maximum growth rate attained for that isolate. A cubic polynomial was fit to this data. Growth rates below 5^{o}C were approximated with a linear extrapolation of the slope at 5^{o} C (i.e. the first term in the Taylor expansion of the polynomial about T = 5^{o}C) to prevent anomalous extrapolation. The resulting relationship achieves an R^2 of 0.80. Lastly, the fit polynomial is again normalized to ensure that a value of 1 is reached under optimal growth conditions (figure 1). This yields:

$$\begin{aligned} &f(T \geq 5) = -0.000536T^3 + 0.0169T^2 - 0.0961T + 0.379 \\ &f(T < 5) = f(T = 5) - 0.0327(5 - T) \end{aligned}$$

The salinity dependence *f(S*) was constructed in similar fashion using data from Prakash (1967) and Etheridge and Roesler (isolates MI and BOF, figure 2). The resulting polynomial is:

$$f(S) = 0.0000577S^3 - 0.00622S^2 + 0.186S - 0.693$$

The salinity dependence is secondary to temperature over the normal range of salinities encountered in the western Gulf of Maine (25-33 PSU), and the relationship is rather noisy (R^2 = 0.50 before normalization). However, retaining the relationship despite this uncertainty allows assessment of the hypothesis that elevated cell concentrations in river plume waters can be explained by increased growth rates in waters of depressed salinity. The final relationship with both the T and S functionality is shown in figure 3.

The range of μ_{max} at optimal temperature and salinity is estimated based on adjustment of measured rates using the polynomial relationships described above. Most experiments used in this study measured the light saturated growth rate at only a limited number of T, S values (often only one). For example, in the case that the growth rate for an isolate was measured only at 15C and ~30 ppt salinity, the relationships above suggest that measured rates here are about 93% optimal with respect to temperature, and 83% optimal with respect to salinity. The adjustment was thus done as follows:

$$\mu_{\max}(T_{opt},S_{opt}) = \frac{\mu_{\max}(T,S)}{f(T)\times f(S)} = \frac{\mu_{\max}(T,S)}{0.93\times 0.83}$$

Note that there is an assumption here that the two factors act independently, and no attempt to account for variable uncertainty in growth estimates from the various studies.

The estimates of the growth efficiency (α) and the maintenance respiration (μ_o^r) relied solely on the Cullen data, which was exceptionally well resolved at low light conditions. This added resolution greatly improved confidence in the estimates of these two parameters relative to previous iterations of this model.

When nutrient dependence is added, it is assumed that only one factor apart from T and S can limit growth. For example, a dependence on dissolved inorganic nitrogen (DIN) is added as follows:

$$\mu(T,S,DIN) = \mu_{\max}(T,S)\times f(DIN)$$

f(DIN) is specified with a Monod relationship:

$$f(DIN) = \frac{[DIN]}{[DIN] + K_{DIN}}$$

[DIN] is the concentration of dissolved inorganic nitrogen in μM and K_{DIN} is an approximate half saturation constant for DIN (also in μM). *μ(T,S,DIN)* is then compared to *μ(T,S,E)* and the minimum of the two is taken:

$$\mu(T,S,E,DIN) = \min(\mu(T,S,E), \mu(T,S,DIN))$$

Interpretive limitations are imposed by the assumptions used in the model formulation. The model can only be used to test hypotheses concerning systems where temperature, salinity, light, and nutrients are thought to be the primary factors controlling growth. Several other potentially important factors, such as the role of turbulence (Thomas and Gibson 1990; Sullivan et al. 2003) and bacterial abundance (Yentsch et al. 1975) have been neglected. The neglect of these factors must be considered an implicit part of each hypothesis tested with the above model.

Table 1: Growth function Parameters. Central value followed by standard deviation (in parentheses).

Symbol	Description	Value	Sources
$\mu_{max}(T_{opt},S_{opt})$	The maximum growth rate (day^{-1}) at optimal temperature and salinity.	0.59 (0.48-0.69)	Cullen et al. (in preparation); Langdon (1988); Watras et al. (1982); Keafer (unpublished data); Kulis (unpublished data); Etheridge and Roesler (2005)
α_g	The growth efficiency (m^2 $watts^{-1}$ day^{-1})	0.036 (0.024-0.048)	Cullen et al. (in preparation)
μ_o^r	The maintenance growth rate (day^{-1})	0.20 (0.15-0.25)	Cullen et al. (in preparation)

Table 2: Summary of different isolates used in growth function construction

Designation	**Origin**	**Source**
ccmp1978	Bay of Fundy	Cullen et al. (in preparation)
ccmp1979	Bay of Fundy	Cullen et al. (in preparation)
ccmp1980	Bay of Fundy	Cullen et al. (in preparation)
cb301	Casco Bay	Cullen et al. (in preparation)
cb307	Casco Bay	Cullen et al. (in preparation)
cb501	Casco Bay	Cullen et al. (in preparation)
GTMP	Mill Pond (Cape Cod)	Watras et al. (1982)
GTCA29	Near Cape Ann	Keafer (unpublished)
GTCA28	Near Cape Ann	Kulis (unpublished)
BOF	Bay of Fundy	Etheridge and Roesler (2005)
MI	Monhegan Island	Etheridge and Roesler (2005)
gt6	Near Cape Ann	Langdon (1987; 1988)
none	Head Harbour, Bay of Fundy	Prakash (1967)

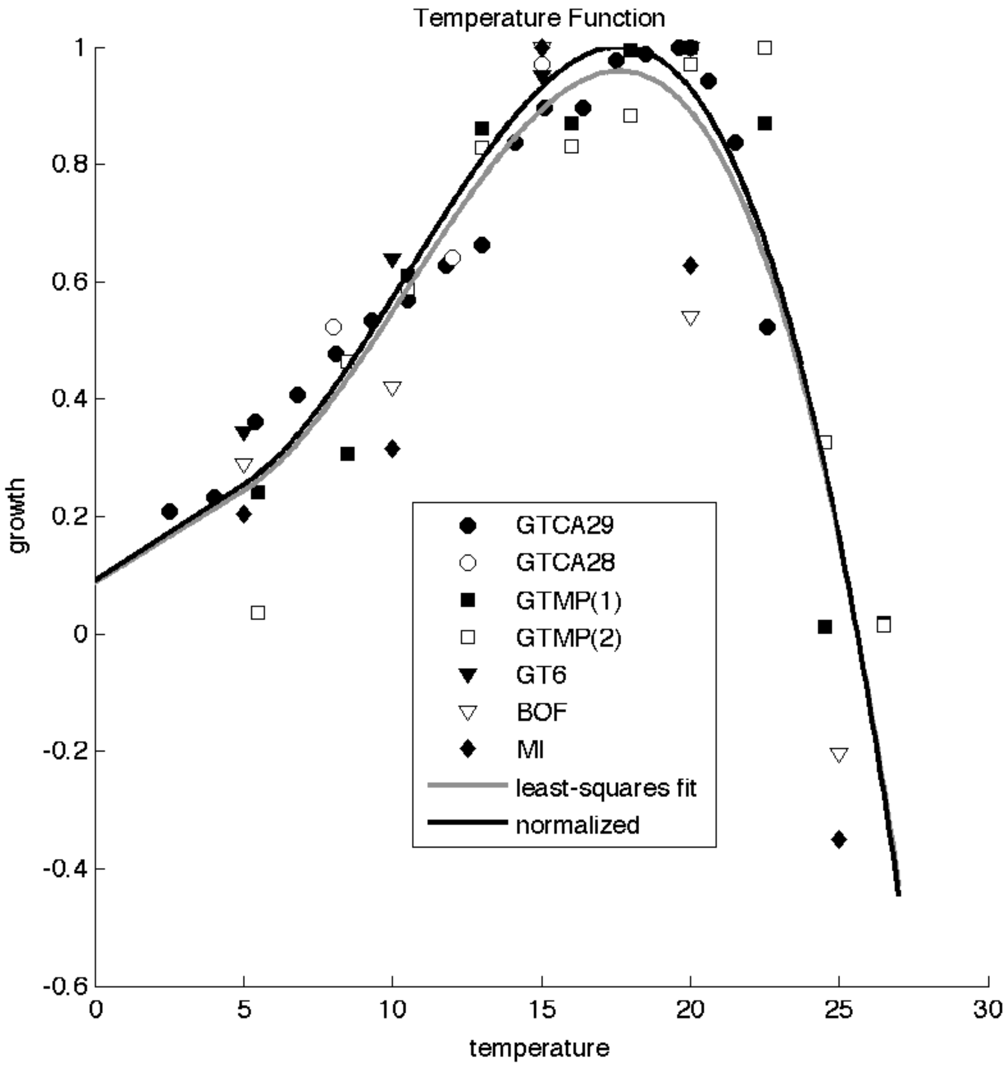

Figure 1: Temperature Scaling factor for application to the growth function. The gray line is the relationship before final normalization to ensure a maximum value of 1 (black line).

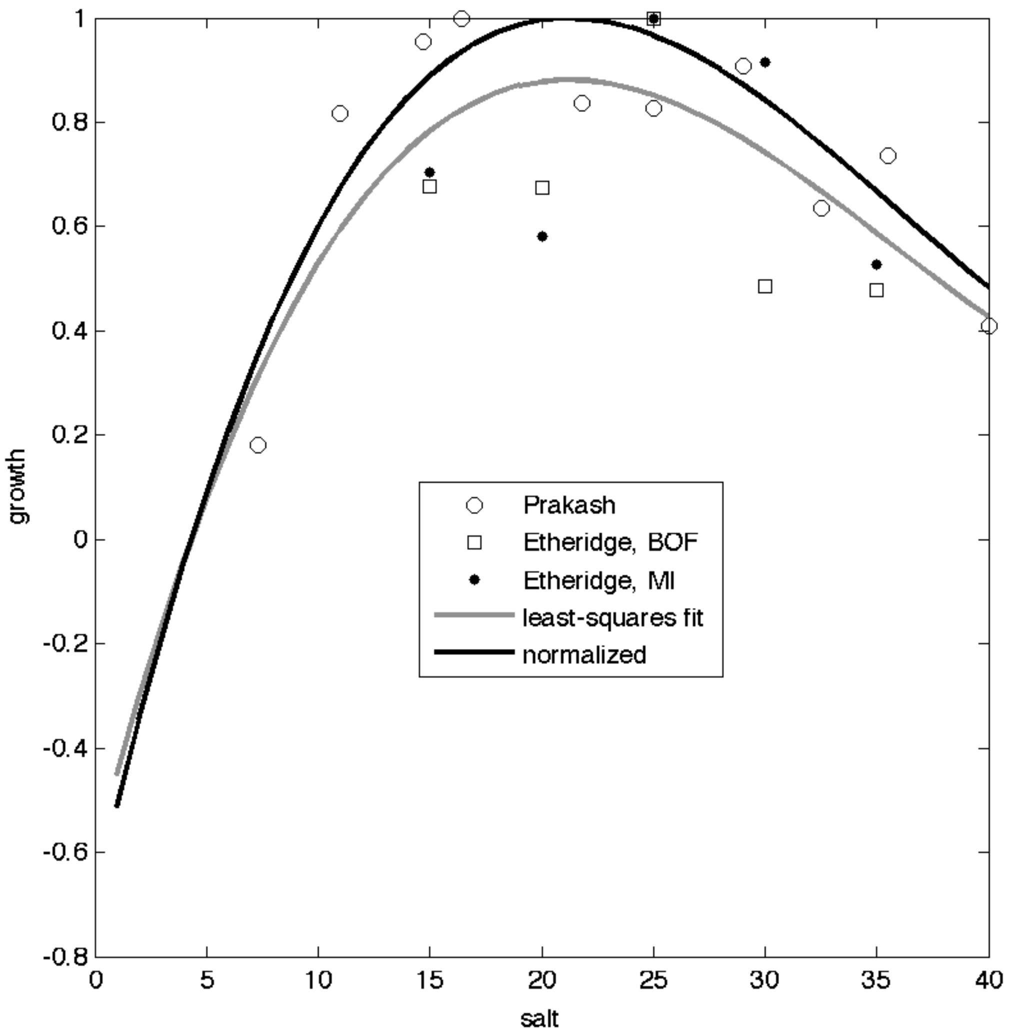

Figure 2: Salinity scaling factor for application to the growth function. The gray line is the relationship before final normalization to ensure a maximum value of 1 (black line).

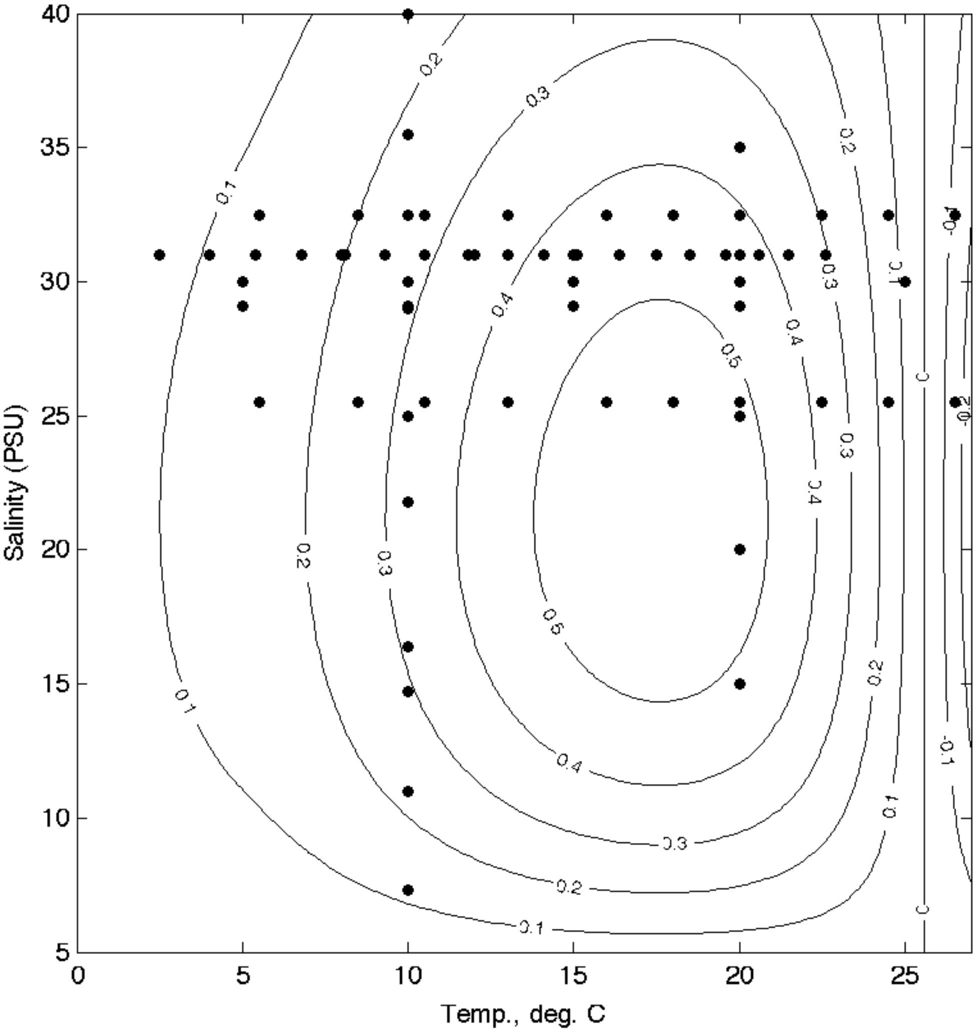

Figure 3: Maximum Growth Rate as a Function of T, S. Points indicate data coverage.

This plot is with $\mu_{max}(T_{opt}, S_{opt}) = 0.58$ day^{-1}.

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