A Model of Giant Clam Growth

Robyn Hean and Oscar Cacho
Department of Agricultural & Resource Economics
University of New England, Armidale, NSW 2351

Abstract In this paper, a biological model of individual giant clam growth is presented. The model describes the metabolic processes associated with growth of the giant clam, and incorporates the effects of environmental conditions such as turbidity and temperature. The model can be used to gain insight into efficient management of giant clam mariculture production systems in different localities.

1. INTRODUCTION

Giant clams are marine bivalve molluscs of the family Tridaciidae, found only in tropical and subtropical waters of the Indo-Pacific region, largely contiguous with the distribution of reef-building corals. They are unique by virtue of a symbiotic relationship with dinoflagellate algae called zooxanthellae, which convert sunlight through photosynthesis into nutrients for the giant clam. Giant clams are essentially autotrophic, potentially capable of satisfying all their respiratory carbon requirements through photosynthesis, although they may supplement their nutrition through filter feeding (Klumpp et al 1992).

Since the early 1980s intensive field and laboratory research, funded by organisations such as the Australian Centre for International Agricultural Research, International Center for Living Aquatic Resources Management, and Micronesia Mariculture Demonstration Centre, has been directed into developing methods for the mariculture of giant clams. The intent of this research has been to develop mariculture techniques to replenish wild stocks, and satisfy subsistence and commercial demand for giant clams, for food, shells and aquarium specimens (Tisdell and Menz 1992).

The success of giant clam mariculture development necessitates an understanding of the performance of the biological production system under different environmental conditions. This may be achieved through a biological model, such as the one presented in this paper, for individual giant clam growth. Giant clam survival is also a critical indicator of the performance of the biological production system, but is not considered here.

2. MODEL

The growth of a giant clam may be described by Figure 1.

\[ \text{Photosynthesis} \]
\[ \text{Filter feeding} \]
\[ \text{Irradiance} \]
\[ \text{Translocated photosynthate} \]
\[ \text{Particulate organic carbon} \]
\[ \text{Absorbed ration} \]
\[ \text{Metabolisable energy} \]
\[ \text{Routine respiration} \]
\[ \text{Surplus energy} \]
\[ \text{Growth} \]

**Figure 1: Energy flow diagram for a giant clam**

Metabolisable energy represents the energy intake of the giant clam. This is in the form of translocated photosynthate, which is derived by the clam from the zooxanthellae with which it has a symbiotic relationship, and absorbed ration from filter feeding of water containing particulate organic matter flowing through its gills. Metabolisable energy is used by the giant clam to satisfy its energy needs for routine respiration (maintenance metabolism), and surplus energy demand for metabolic processes such as reproduction (Klumpp and Griffiths 1994; Munro 1997, pers. comm). Remaining energy is allocated to growth which, of these energy uses, has the lowest metabolic priority.

2.1 Growth

In terms of an energy budget, growth is the difference between energy intake and expenditure:
\( G = TP + AR - RH - SE \)

where \( G \) is growth, \( TP \) is translocated photosynthetic energy, \( AR \) is absorbed ration, \( RH \) is routine respiration, and \( SE \) is surplus energy. All variables are measured in mg carbon (C/hr).

Growth is partitioned between growth of tissue, \( G_T \), and growth of shell, \( G_S \), such that:

\[ G = G_T + G_S \]

Partitioning is described by a carbon-partitioning function, \( C_T \), which gives the proportion of carbon going to tissue growth, as a power function of tissue dry weight (TDW, g dry weight):

\[ C_T = \alpha_T TDW^{\beta_T} \]

Hence, \( G_T \) and \( G_S \) are given by the products:

\[ G_T = C_T \cdot G \]

and:

\[ G_S = (1 - C_T) \cdot G \]

which, when multiplied by constants \( k_T \) and \( k_S \), respectively, convert growth to grams of tissue dry weight/hr (dTDW) and grams of shell dry weight/hr (dSDW) as follows:

\[ dTDW = G_T \cdot k_T \]

and:

\[ dSDW = G_S \cdot k_S \]

Initial tissue dry weight and shell dry weight are given by \( TDW_0 \) and:

\[ SDW_0 = \alpha_S TDW_0^{\beta_S} \]

while shell length (SL, mm) is calculated as follows:

\[ SL = \alpha_L SDW^{\beta_L} \]

2.2 Photosynthesis

The amount of photosynthetic energy translocated by the algal symbionts to the clam host (\( TP \), mg C/hr) is given by:

\[ TP = [(P, PQ) - (R, RQ, k_A)] \cdot TR \]

where \( P \) is gross algal photosynthesis (mg C/hr), \( PQ \) is the photosynthetic quotient, \( R \) is respiration of the entire clam (host plus algae, mg C/hr), \( RQ \) is the respiratory quotient, \( k_A \) is the proportion of entire clam respiration attributable to the algae, and \( TR \) is the proportion of the excess algal photosynthetic energy that is translocated to the host.

Gross algal photosynthesis is described by a hyperbolic tangent function, or photosynthesis-irradiance function:

\[ P = P_{max} \tanh \left( \frac{I_D}{I_K} \right) \]

in which:

\[ P_{max} = \Psi_T \alpha_T \cdot TDW^{\beta_T} \]

\[ I_D = I_0 e^{-X \cdot D} \]

and:

\[ X = 1.7 \frac{V_{SD}}{\psi} \]

\( P_{max} \) is the asymptote of the photosynthesis-irradiance function (i.e., photosynthesis at saturating irradiance, mg C/hr), \( I_D \) is the irradiance (\( \mu \text{E} \cdot \text{m}^2 \cdot \text{sec} \)) penetrating to depth \( D \) (m), and \( I_K \) is the irradiance at which the initial slope of the photosynthesis-irradiance function intersects \( P_{max} \). \( I_D \) is calculated using Lambert's Law (13) in which \( I_0 \) is surface irradiance, and \( X \) is the light extinction coefficient (Boyd 1979). \( X \) is inversely related to Secchi disk visibility (\( V_{SD} \), m), and captures the effect of water turbidity on photosynthesis.

\( \Psi_T \) describes the rate of temperature-dependent photosynthetic response, and is described by the O'Neall equation:

\[ \Psi_T = \Psi_{max} \left( \frac{T_{max} - T}{T_{max} - T_{opt}} \right) e^{\frac{n(T - T_{opt})}{T_{max} - T_{opt}}} \]

in which:

2 The respiratory quotient is the ratio of the volume of carbon dioxide produced to oxygen consumed during respiration.

3 A Secchi disk is a weighted disk, 20 cm in diameter and painted with alternative black and white quadrants. The distance (horizontal or vertical) for which a Secchi disk is visible underwater provides a measure of transparency. The greater the turbidity of water, the smaller the Secchi disk visibility (Boyd 1979).
\[
\eta = \frac{\tau^2}{400} \left( 1 + \frac{1 + \frac{1}{\tau}}{1 + \frac{1}{40}} \right)^2
\]

and:

\[(17) \qquad \tau = (Q_{10} - 1)h(T_{\text{max}} - T_{\text{opt}})\]

\(\Psi_T\) captures the effect of temperature \((T, ^\circ C)\) on \(P_{\text{max}}\), which increases with increasing temperature, up to a maximum at the optimum temperature, \(T_{\text{opt}}\), and then rapidly decreases as the lethal temperature, \(T_{\text{max}}\), is approached (Spain 1982). \(\eta\) and \(\tau\) are constants defined by the temperature coefficient\(^4\), \(Q_{10}\), \(T_{\text{max}}\) and \(T_{\text{opt}}\).

2.3 Filter Feeding

Absorbed ration, \(AR\), from filter feeding is expressed as:

\[(18) \qquad AR = IR \cdot AE\]

where \(IR\) is the ingested ration (mg C/hr) and \(AE\) is the efficiency with which the ingested ration is absorbed. \(IR\) is given by:

\[(19) \qquad IR = CR \cdot POC\]

in which:

\[(20) \qquad CR = \alpha_F \cdot TDW^{\beta_F}\]

\(CR\) is the rate at which water is cleared for filter feeding (l/hour), and \(POC\) is the particulate organic carbon content of the filtered water (mg C/l).

2.4 Respiration

Routine respiratory carbon demand of the clam host, \(RH\), is expressed as:

\[(21) \qquad RH = R \cdot RQ \left( 1 - k_A \right)\]

in which \(R\) is given by:

\[(22) \qquad R = \Omega_T \cdot \alpha_R \cdot TDW^{\beta_R}\]

\(\Omega_T\) is a temperature-response function described by a modified Eyring and Urry (1975) equation:

\[(23) \qquad \Omega_T = \frac{\phi_1 T e^{-\phi_2/T}}{1 + \phi_3 e^{-\phi_4/T}}\]

and captures the effect of temperature on respiration rate. Respiration increases with increasing temperature, up to a maximum, and then rapidly decreases as the lethal temperature is approached.

2.5 Surplus energy

Surplus metabolisable energy, \(SE\), is expressed as a power function of energy intake:

\[(24) \qquad SE = \alpha_E \cdot (TP + AR)^{\beta_E}\]

It represents energy expended on unaccounted metabolic processes such as reproduction (Klumpp and Griffiths 1994; Munro 1997, pers. comm.).

3. MODEL CALIBRATION

The model was calibrated to simulate giant clam growth under levels of irradiance and particulate organic carbon typical of inshore reef flat environments on the Great Barrier Reef, for the species *Tridacna gigas*.

Irradiance data are reported in Figure 2. These data were estimated from a graph presented by Klumpp and McKinnon (1989), for Davies Reef, on cloudless days in December 1986. Although Davies Reef is approximatively 50km offshore, irradiance would have been similar at inshore reefs. Data for particulate organic carbon was taken from Klumpp and Griffiths (1994), who reported that the mean particulate organic carbon concentration in waters from reef flats in the Orpheus Island region, monitored over a 2 year period, was 0.2 mg C/l.

![Figure 2: Irradiance](image)

Most parameter values were taken from the literature (see Table 1). Parameters for (3), (23) and (24) were estimated statistically (using a Marquardt algorithm) based on data reported in various sources (see Table 1 for details).

---

\(4\) The temperature coefficient gives the increase in photosynthetic rate (expressed as a multiple of the initial rate) produced by raising the temperature by 10\(^\circ\)C.
Table 1: Model Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Unit</th>
<th>Value</th>
<th>Sources(^{\text{a}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\alpha_T)</td>
<td>-</td>
<td>0.745</td>
<td>A, E</td>
</tr>
<tr>
<td>(\beta_T)</td>
<td>-</td>
<td>0.018</td>
<td>A, E</td>
</tr>
<tr>
<td>(k_T)</td>
<td>g dry wt/mg C</td>
<td>0.003</td>
<td>E</td>
</tr>
<tr>
<td>(k_S)</td>
<td>g dry wt/mg C</td>
<td>0.333</td>
<td>E</td>
</tr>
<tr>
<td>(\alpha_S)</td>
<td>g dry wt</td>
<td>46.221</td>
<td>E</td>
</tr>
<tr>
<td>(\beta_S)</td>
<td>-</td>
<td>0.926</td>
<td>E</td>
</tr>
<tr>
<td>(\alpha_L)</td>
<td>mm</td>
<td>24.538</td>
<td>E</td>
</tr>
<tr>
<td>(\beta_L)</td>
<td>-</td>
<td>0.322</td>
<td>E</td>
</tr>
<tr>
<td>(P_Q)</td>
<td>-</td>
<td>1.0</td>
<td>B, E</td>
</tr>
<tr>
<td>(R_Q)</td>
<td>-</td>
<td>0.8</td>
<td>D, E</td>
</tr>
<tr>
<td>(k_A)</td>
<td>-</td>
<td>0.05</td>
<td>B, D, E, G</td>
</tr>
<tr>
<td>(TR)</td>
<td>-</td>
<td>0.95</td>
<td>C, E</td>
</tr>
<tr>
<td>(I_K)</td>
<td>(\mu E/m^2/sec)</td>
<td>488</td>
<td>E</td>
</tr>
<tr>
<td>(\alpha_F)</td>
<td>mg C/hr</td>
<td>3.673</td>
<td>A, E</td>
</tr>
<tr>
<td>(\beta_P)</td>
<td>-</td>
<td>0.693</td>
<td>E</td>
</tr>
<tr>
<td>(\psi_{\text{max}})</td>
<td>-</td>
<td>1</td>
<td>A</td>
</tr>
<tr>
<td>(T_{\text{max}})</td>
<td>°C</td>
<td>33.0</td>
<td>F</td>
</tr>
<tr>
<td>(T_{\text{opt}})</td>
<td>°C</td>
<td>28.0</td>
<td>A</td>
</tr>
<tr>
<td>(Q_{\text{opt}})</td>
<td>-</td>
<td>1.67</td>
<td>F</td>
</tr>
<tr>
<td>(\alpha_E)</td>
<td>(\ell/hr)</td>
<td>3.380</td>
<td>E</td>
</tr>
<tr>
<td>(\beta_E)</td>
<td>-</td>
<td>0.397</td>
<td>E</td>
</tr>
<tr>
<td>(\alpha_R)</td>
<td>mg C/hr</td>
<td>0.791</td>
<td>A, E</td>
</tr>
<tr>
<td>(\beta_R)</td>
<td>-</td>
<td>0.654</td>
<td>E</td>
</tr>
<tr>
<td>(\phi_1)</td>
<td>-</td>
<td>30.591e(^{\text{c}})</td>
<td>A, F</td>
</tr>
<tr>
<td>(\phi_2)</td>
<td>-</td>
<td>-301.74</td>
<td>A, F</td>
</tr>
<tr>
<td>(\phi_3)</td>
<td>-</td>
<td>71.459e(^{\text{c}})</td>
<td>A, F</td>
</tr>
<tr>
<td>(\phi_4)</td>
<td>-</td>
<td>-312.26</td>
<td>A, F</td>
</tr>
<tr>
<td>(\alpha_C)</td>
<td>mg C/hr</td>
<td>0.687</td>
<td>A, E</td>
</tr>
<tr>
<td>(\beta_C)</td>
<td>-</td>
<td>0.983</td>
<td>A, E</td>
</tr>
</tbody>
</table>

\(^{\text{a}}\) Sources: A, this study; B, Fisher et al. (1985); C, Fitt (1993); D, Klumpp et al. (1992); E, Klumpp and Griffiths (1994); F, Mingoa (1990); G, Trench et al. (1981).

\(^{\text{c}}\) Parameters estimated in this study used data reported in the source following.

4. MODEL IMPLEMENTATION

The model was implemented using SIMULINK\(^{\circ}\) and MATLAB\(^{\circ}\) (MATLAB 1992). Model equations were numerically integrated by the Runge-Kutta method (Nakamura 1996) at 1-hour intervals for 35000 hours (or 4 years), assuming controlled environmental conditions with a constant diel pattern in irradiance typical of summer, and constant level of particulate organic carbon.

The model was used to explore the effects of environmental conditions on growth of *T. gigas*, by defining a base case with the following values:

\(TDW_0 = 0.1\) grams

\(D = 0.5\) m

\(V_{\text{SD}} = 16.5\) m

\(T = 25.5\) °C

The model was run for the base case, and the growth of tissue dry weight, shell dry weight and shell length determined. The influence of turbidity and temperature on growth were then investigated, by altering Secchi disk visibility and temperature.

5. RESULTS AND DISCUSSION

Results for growth in terms of tissue dry weight, shell dry weight and shell length for the base run of the model are presented in Figure 3a.

```

Figure 3a: Growth in tissue and shell dry weights
```

These results agree both qualitatively and quantitatively with growth rates for *T. gigas* reported in the literature for clams prior to the onset of sexual maturity growing under similar environmental conditions (Klumpp and Griffiths 1994). Growth is initially slow, after which it is rapid and nearly linear.

```

Figure 3b: Growth in shell length
```

These results agree both qualitatively and quantitatively with growth rates for *T. gigas* reported in the literature for clams prior to the onset of sexual maturity growing under similar environmental conditions (Klumpp and Griffiths 1994). Growth is initially slow, after which it is rapid and nearly linear.
With the onset of sexual maturity, there would be a significant slowing of growth, as the production of gametes involves a considerable energy demand (Munro 1997, pers. comm).

Results for final tissue dry weight, shell dry weight and shell length are presented in Table 2, for the base run, and experiments in which Secchi disk visibility was varied by 10 m, and temperature by 5 °C, above and below their base case values, while keeping all other variables at their base case values.

Table 2: Effect of turbidity and temperature on growth

<table>
<thead>
<tr>
<th>Temperature (T, °C)</th>
<th>State variable</th>
<th>Secchi disk visibility (V_{SP}, m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>20.5</td>
<td>TDW (g)</td>
<td>52.75 77.65 85.25</td>
</tr>
<tr>
<td></td>
<td>SDW (g)</td>
<td>1597.99 2275.37 2476.97</td>
</tr>
<tr>
<td></td>
<td>SL (mm)</td>
<td>263.87 295.67 303.87</td>
</tr>
<tr>
<td>25.5</td>
<td>TDW (g)</td>
<td>64.37 109.44 127.64</td>
</tr>
<tr>
<td></td>
<td>SDW (g)</td>
<td>1917.24 3111.61 3579.27</td>
</tr>
<tr>
<td></td>
<td>SL (mm)</td>
<td>279.81 327.02 342.11</td>
</tr>
<tr>
<td>30.5</td>
<td>TDW (g)</td>
<td>0.34 0.65 1.12</td>
</tr>
<tr>
<td></td>
<td>SDW (g)</td>
<td>15.52 27.92 46.02</td>
</tr>
<tr>
<td></td>
<td>SL (mm)</td>
<td>59.33 71.68 84.20</td>
</tr>
</tbody>
</table>

5.2 Temperature effects

For a given Secchi disk visibility, final growth increased with increasing temperature from 20.5-25.5 °C, and decreased thereafter. For example, at a Secchi disk visibility of 16.5 m, final tissue dry weight increased by 6.36 g/m² from 20.5-25.5 °C, and decreased by 21.76 g/m² from 25.5-30.5 °C. This was expected given the temperature dependence of photosynthesis and respiration. Between 20.5-25.5 °C, $\psi_T$ and $\Omega_T$, are both increasing, with $\psi_T$ being greater than, and increasing at a faster rate than, $\Omega_T$. Between 25.5-30.5 °C, $\psi_T$ still exceeds $\Omega_T$, but reaches a maximum at 28.0 °C and decreases thereafter, while $\Omega_T$ continues to increase throughout the range. ($\Omega_T$ does not reach a maximum until 34.5 °C.) Hence, as temperature increases from 20.5-25.5 °C, photosynthesis at saturating irradiance increases at a greater rate than the corresponding increase in respiration, and greater growth is achieved. Beyond 25.5 °C, growth is reduced, however, since photosynthesis is maximised at 28.0 °C and declines thereafter, while respiration continues to increase.

6. CONCLUSION

In this paper, the simulation of a model of individual giant clam growth has demonstrated the effects of turbidity and temperature on the biological production system. The model was calibrated to simulate the growth of the species T. gigas under levels of irradiance and particulate organic carbon typical of inshore reef-flat environments on the Great Barrier Reef during summer. Validation of the model for different localities and environmental conditions is the topic of future research. Development of the model will also extend to other giant clam species, and the inclusion of environmental factors such as emersion and the annual cycles of temperature and irradiance. The opportunity exists for the model to contribute significantly in its application to the management analysis of giant clam mariculture throughout the Indo-Pacific region.

7. ACKNOWLEDGEMENTS

The authors would like to thank the International Center for Living Aquatic Resources Management for useful discussions which have contributed to the content of this paper.

8. REFERENCES


