A Model of Giant Clam Growth

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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 Tridacnidae, 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 Micronesian 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.

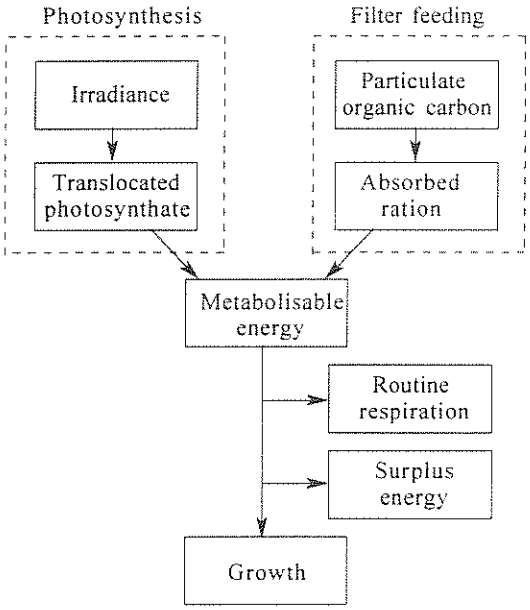

Figure 1: Energy flow diagram for a giant clam

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:

(1) $G = TP + AR - RH - SE$

where G is growth, TP is translocated photosynthate, 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:

(2) $G = G_T + G_S$

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):

(3) $C_T = \alpha_T TDW^{\beta_T}$

Hence, G_T and G_S are given by the products:

(4) $G_T = C_T . G$

and:

(5) $G_S = (1 - C_T) G$

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:

(6) $dTDW = G_T . k_T$

and:

(7) $dSDW = G_S . k_S$

Initial tissue dry weight and shell dry weight are given by TDW_0 and:

(8) $SDW_0 = \alpha_S TDW_0^{\beta_S}$

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

(9) $SL = \alpha_L SDW^{\beta_L}$

2.2 Photosynthesis

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

(10) $TP = \left[(P . PQ) - (R . RQ . k_A) \right] TR$

where P is gross algal photosynthesis (mg C/hr), PQ is the photosynthetic quotient[1], R is respiration of the entire clam (host plus algae, mg C/hr), RQ is the respiratory quotient[2], k_A is the proportion of entire clam respiration attributable to the algae, and TR is the proportion of the excess algal photosynthate that is translocated to the host.

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

(11) $P = P_{max} \tanh\left(\frac{I_D}{I_K} \right)$

in which:

(12) $P_{max} = \Psi_T \alpha_P TDW^{\beta_P}$

(13) $I_D = I_0 e^{-X.D}$

and:

(14) $X = \frac{1.7}{V_{SD}}$

P_{max} is the asymptote of the photosynthesis-irradiance function (ie. photosynthesis at saturating irradiance, mg C/hr), I_D is the irradiance ($\mu E/m^2/sec$) 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[3] (V_{SD}, m), and captures the effect of water turbidity on photosynthesis.

Ψ_T describes the rate of temperature-dependent photosynthetic response, and is described by the O'Neill equation:

(15) $\Psi_T = \Psi_{max} \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right)^{\eta} e^{\left(\frac{\eta (T - T_{opt})}{T_{max} - T_{opt}} \right)}$

in which:

[1] The photosynthetic quotient is the ratio of the volume of oxygen produced to carbon dioxide consumed during photosynthesis.

[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).

$$\eta = \frac{\tau^2\left(1+\sqrt{1+\frac{40}{\tau}}\right)^2}{400} \quad (16)$$

and:

$$\tau = (Q_{10}-1)(T_{max}-T_{opt}) \quad (17)$$

Ψ_T captures the effect of temperature (T, °C) on P_{max}, which increases with increasing temperature, up to a maximum at the optimum temperature, T_{opt}, and then rapidly decreases as the lethal temperature, T_{max}, is approached (Spain 1982). η and τ are constants, defined by the temperature coefficient[4], Q_{10}, T_{max} and T_{opt}.

2.3 Filter Feeding

Absorbed ration, AR, from filter feeding is expressed as:

$$AR = IR.AE \quad (18)$$

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:

$$IR = CR.POC \quad (19)$$

in which:

$$CR = \alpha_F TDW^{\beta_F} \quad (20)$$

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:

$$RH = R.RQ(1-k_A) \quad (21)$$

in which R is given by:

$$R = \Omega_T \alpha_R TDW^{\beta_R} \quad (22)$$

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

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

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:

$$SE = \alpha_E (TP + AR)^{\beta_E} \quad (24)$$

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 approximately 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.

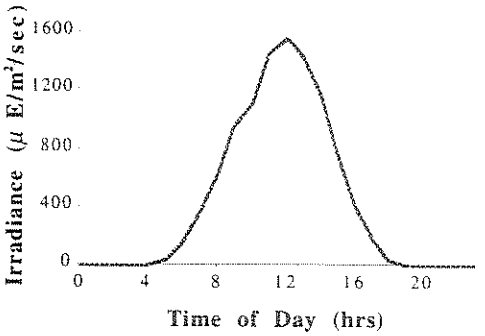

Figure 2: Irradiance

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 °C.

Table 1: Model Parameters

Parameter	Unit	Value	Sources[a]
α_T	-	0.745	A[b],E
β_T	-	0.018	A,E
k_T	g dry wt/mg C	0.003	E
k_S	g dry wt/mg C	0.333	E
α_S	g dry wt	46.221	E
β_S	-	0.926	E
α_L	mm	24.538	E
β_L	-	0.322	E
PQ	-	1.0	B,E
RQ	-	0.8	D,E
k_A	-	0.05	B,D,E,G
TR	-	0.95	C,E
I_K	μE/m^2/sec	488	E
α_P	mg C/hr	3.673	A,E
β_P	-	0.693	E
Ψ_{max}	–	1	A
T_{max}	°C	33.0	F
T_{opt}	°C	28.0	A
Q_{10}	–	1.67	F
AE	-	0.508	E
α_F	ℓ/hr	3.680	E
β_F	-	0.397	E
α_R	mg C/hr	0.791	A,E
β_R	-	0.654	E
ϕ_1	-	30.591e^{-6}	A,F
ϕ_2	-	-301.74	A,F
ϕ_3	-	71.459e^{-5}	A,F
ϕ_4	-	-312.26	A,F
α_E	mg C/hr	0.687	A,E
β_E	-	0.983	A,E

[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).

[b] Parameters estimated in this study used data reported in the source following.

4. MODEL IMPLEMENTATION

The model was implemented using SIMULINK© and MATLAB© (MATLAB 1992). Model equations were numerically integrated by the Runga-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_{SD}=16.5 m

T= 25.5 ^{0}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 3.

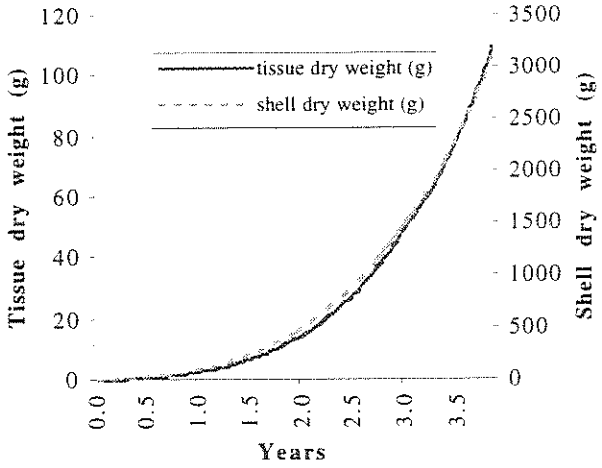

Figure 3a: Growth in tissue and shell dry weights

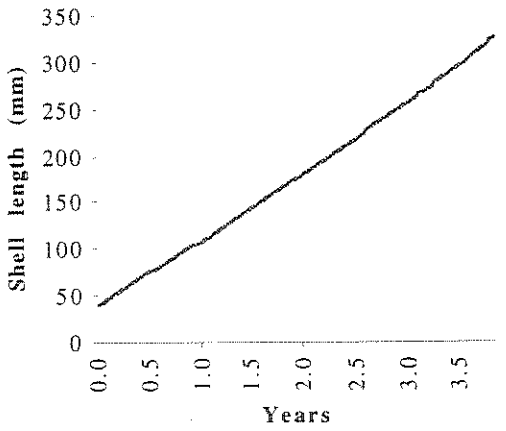

Figure 3b: Growth in shell length

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

Temperature (T, ^{0}C)	State variable	Secchi disk visibility (V_{SD}, m)		
		6.5	16.5	26.5
20.5	TDW (g)	52.75	77.65	85.25
	SDW (g)	1597.99	2275.37	2476.97
	SL (mm)	263.87	295.67	303.87
25.5	TDW (g)	64.37	109.44	127.64
	SDW (g)	1917.24	3111.61	3579.27
	SL (mm)	279.81	327.02	342.11
30.5	TDW (g)	0.34	0.65	1.12
	SDW (g)	15.52	27.92	46.02
	SL (mm)	59.33	71.68	84.20

5.1 Turbidity effects

For a given temperature, final growth increased with increasing Secchi disk visibility. For example, at a temperature of 25.5 °C, final tissue dry weight increased by 4.51 g/m of Secchi disk visibility, and 1.82 g/m, as visibility increased from 6.5-16.5 m and 16.5-26.5 m respectively. This was expected given the positive relationship between Secchi disk visibility and gross algal photosynthesis, since greater visibility (ie. less turbidity) allows for a higher proportion of surface irradiance to reach the clam. At the Secchi disk visibilities considered, the percentage surface irradiance reaching the clam was 88 per cent, 95 per cent, and 97 per cent respectively. Hence, a greater increase in final growth was expected for an increase in Secchi disk visibility from 6.5-16.5 m, than from 16.5-26.5 m. This is observed at temperatures of 20.5 °C and 25.5 °C, but the trend is reversed at 30.5 °C. For example, at 30.5 °C, final tissue dry weight increased by 0.03 g/m up to 16.5 m Secchi disk visibility, and by 0.05 g/m thereafter. Since growth was negligible at this temperature, this result was not further investigated.

5.2 Temperature effects

For a given Secchi disk visibility, final growth increased with increasing temperature from 20.5-25.5 °C, and decreased therafter. For example, at a Secchi disk visibility of 16.5 m, final tissue dry weight increased by 6.36 g/°C from 20.5-25.5 °C, and decreased by 21.76 g/°C from 25.5-30.5 °C. This was expected given the temperature dependence of photosynthesis and respiration. Between 20.5-25.5 °C, Ψ_T and Ω_T, are both increasing, with Ψ_T being greater than, and increasing at a faster rate than, Ω_T. Between 25.5-30.5 °C, Ψ_T still exceeds Ω_T, but reaches a maximum at 28.0 °C and decreases thereafter, while Ω_T continues to increase throughout the range. (Ω_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 conditons 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

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