Growth and survival of the giant clams, *Tridacna derasa*, *T. maxima* and *T. crocea*, at village farms in the Solomon Islands

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Abstract

A series of large-scale grow-out trials for giant clams (*Tridacna derasa*, *T. maxima*, *T. crocea*) were undertaken at 11 village farms in Solomon Islands. Eight hundred juveniles of each species, measuring 20–30 mm shell length (SL), were distributed equally between four replicate cages at each site. Growth and survival of the clams were then monitored for up to 24 months. Environmental and husbandry variables were measured throughout these experiments. *T. derasa* had the best growth and survival, attaining a mean SL of 150 mm $\pm$ 19.8 s.d., and mean weight of 710 g $\pm$ 26 s.d., after 24 months grow-out. Mean survival of *T. derasa* over this period was 92.2% $\pm$ 9.1 s.d. *T. maxima* grew to a mean size of 78.4 mm $\pm$ 14.9 s.d. in 19 months, and *T. crocea* reached 50.2 mm $\pm$ 8.1 s.d. in 22 months. After 19 months grow-out, survival of *T. maxima* was 38.9% $\pm$ 16.6 s.d., and survival of *T. crocea* after 17 months was 39% $\pm$ 22.6 s.d. Factors influencing growth of all species included water temperature, exposure to wave action, water clarity and water flow. Together, these factors explained between 66% and 79% of variation in growth, depending on the species. Regressions of environmental factors against survival were a poorer fit, they explained 15% (*T. derasa*), 53% (*T. maxima*), and 52% (*T. crocea*) of variability among sites. Estimated net revenue for village farmers growing giant clams for the aquarium market was greatest for *T. derasa*, due to high survival. Although *T. crocea* is in great demand by the aquarium trade, it was the least suitable species for village farming because it has slow growth and low survival. Unless survival rates at village farms can be enhanced considerably, *T. crocea*

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can probably be reared more successfully in a land-based system. © 1998 Elsevier Science B.V. All rights reserved.

1. Introduction

Since the taxonomy of the Tridacnidae was completed by Rosewater (1965, 1982), giant clams have become one of the most comprehensively studied groups of tropical marine organisms. Their biology, exploitation, and mariculture has been reviewed by Munro (1993) and Lucas (1994), and manuals exist for all aspects of their culture (Heslinga et al., 1990; Braley, 1992; Calumpong, 1992). Considerable effort has been made to transfer the technology to developing countries. However, commercial farming of giant clams is still in its infancy because: (a) economic and marketing analyses have focused on the production of adductor muscle from one species, *Tridacna gigas* (Tisdell, 1992), and (b) the economic viability of this type of farming hinges on a minimum of 7 years grow-out to reach market size (Hambrey and Gervis, 1993; Tisdell et al., 1993).

Not surprisingly, the production of *T. gigas* for its adductor muscle has not proved to be attractive. Instead, the emerging industry for farming giant clams (Tridacnidae) in the Indo-Pacific has concentrated on developing markets for small (50–100 mm shell length (SL)) individuals for the aquarium trade (Tisdell, 1992; Bell et al., 1997a; Foyle et al., 1997). This market is based on five species, *T. crocea*, *T. derasa*, *T. gigas*, *T. maxima* and *T. squamosa*, and is particularly attractive to small-scale producers in remote areas because grow-out times promise to be short, prices are relatively high and the small size of specimens reduces the problems and costs of air freight (Chew, 1996; Bell et al., 1997b). The smallest of these species, *T. crocea* and *T. maxima*, are of particular interest to the aquarium trade because of the iridescent colours of their mantles.

The only disadvantage with the aquarium market is its limited size. Expansion of giant clam farming will depend on finding larger markets in the seafood trade (Bell et al., 1997b,c). The two larger species (*T. gigas* and *T. derasa*) are best suited for this market, although previous studies disagree about which of the two species is likely to be most appropriate (Munro, 1988; Heslinga et al., 1988).

Hambrey and Gervis (1993) have demonstrated that it is possible to produce seed of giant clams at reasonable cost, and so the most pressing needs for research on giant clam farming in developing countries of the Indo-Pacific involve: (a) determining the average rates of growth and survival at small-scale (village) grow-out farms, and (b) assessing whether village farms are profitable. This has already been demonstrated for *T. gigas* (Bell et al., 1997a) and *T. squamosa* (Foyle et al., 1997). Their studies showed that although mean survival was 41% after 10 months grow-out for *T. gigas*, and 66% after eight months for *T. squamosa*, both species can be grown profitably for the aquarium trade. Bell et al. (1997a) also demonstrated that the simple husbandry procedure of removing and cleaning clams had a significant positive effect on survival, while Foyle et al. (1997) found that water flow, water clarity and exposure to wave action had a significant effect on growth of *T. squamosa*. Another issue arising out of the studies by

Bell et al. (1997a) and Foyle et al. (1997) was the need to monitor growth and survival for longer periods to determine whether greater profits could be made from the aquarium trade by holding clams until they reached a larger size.

In this study, we report the results of large-scale grow-out trials for *T. crocea*, *T. maxima* and *T. derasa* at 11 sites in the Solomon Islands over 2 years. During these experiments, we evaluated the influence of environmental variables and husbandry on growth and survival, and used this information to identify optimum growing sites for these giant clams. We also used the biological data in a simple economic analysis of growing each species to two different sizes.

2. Materials and methods

2.1. Spawning and culture of juveniles

Clams used in this study were cultured at ICLARM's Coastal Aquaculture Centre using the protocol of Gervis et al. (1996). Adults were spawned on the 28th of February 1994 (*T. derasa*), 21st of July 1994 (*T. crocea*), and 6th of October 1994 (*T. maxima*). Offspring were reared in outdoor nursery tanks for 8–9 months, then harvested and distributed to small-scale demonstration farms established at coastal villages by ICLARM.

2.2. Design of grow-out experiments

Initially, clams were distributed to 14 (*T. derasa*) and 12 (*T. crocea* and *T. maxima*) village farm sites spread across 500 km of Solomon Islands (Fig. 1). These sites (except
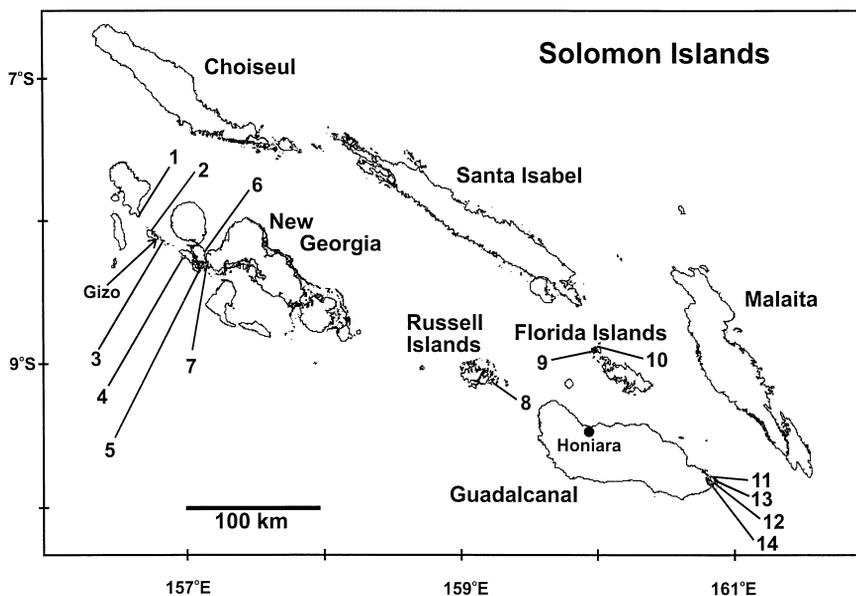
Fig. 1. Location of study sites within the Solomon Islands.

sites 9, 10, 11 and 12) were also used by Foyle et al. (1997) for assessing growth and survival of *T. squamosa*. Prior to distribution, all clams were graded through a 19 mm mesh to reduce the variability in size at distribution. Mean sizes of clams distributed to each site are given in Table 1. The coefficient of variation (CV) for size at distribution varied from 18% for *T. derasa* to 13% for *T. crocea*.

For each species, 200 clams were placed in each of four cages (see Foyle et al., 1997 for details of cage design). A mesh insert (5 mm size) was placed in each cage to prevent escape of clams during the first two months of grow-out for *T. derasa*, and for the first four months of grow-out for *T. crocea* and *T. maxima*.

To prevent retardation of growth, the numbers of clams in a cage were 'thinned' according to strict protocols. For *T. derasa*, cages were thinned at 4, 8, and 12 months: half the individuals were kept in the cages and the other half were given to clam farmers for commercial production. For *T. maxima* and *T. crocea*, cages were thinned on one occasion to 50 individuals per cage. This was done after 17 months grow-out for *T. crocea* and 12 months grow-out for *T. maxima*.

2.3. Collection of data

During the first year, survival was estimated every month by counting the number of live clams in each cage. The frequency of these counts was reduced when survival

Table 1
Summary of sites, and mean size-at-distribution ($n = 200$) for grow-out experiments involving three species of giant clams from the Solomon Islands

Site	Shell length (SL) of clams at distribution (mm)					
	T. derasa		*T. maxima*		*T. crocea*	
	$\bar{x}$	CV (%)	$\bar{x}$	CV (%)	$\bar{x}$	CV (%)
1	29.8	17	23.8	14	19.9	13
2	30.0	21	23.3	14	20.1	13
3	29.4	16	22.8	16	20.2	15
4	29.6	18	23.8	14	20.3	12
5[a]	30.0	19	23.6	15	19.7	12
6	30.3	14	23.2	16	20.3	13
7	30.6	19	23.8	15	20.4	12
8	30.1	19	23.3	14	20.0	13
9[b]	29.9	19	23.0	14	20.0	13
10	29.0	19	24.0	14	20.4	13
11[c]	28.9	20	23.5	15	20.3	12
12	31.2	19	23.5	16	19.9	11
13[d]	29.4	21				
14	28.5	19				
Overall mean and CV	29.8	18	23.5	15	20.1	13

[a] *T. derasa* cages lost, omitted from analysis.
[b] *T. crocea* suffered 98% mortality, and 2 cages of *T. derasa* and *T. maxima* lost; suspected poor husbandry, omitted from analyses.
[c] *T. maxima* had 100% mortality 6 weeks after distribution, suspected cause was unusually high freshwater input; 2 cages of *T. derasa* lost, suspected inadequate husbandry.
[d] Two cages of *T. derasa* lost from this site, omitted from analyses.

stabilized. Shell length measurements from 30–50 individuals per cage were taken at regular intervals (3–5 monthly) to monitor growth rate. After 24 months grow-out, the wet weights of 20 *T. derasa* were measured (to the nearest 10 g) at each site.

Data on water clarity (i.e., secchi disc reading), salinity, water temperature, total abundance of *Cymatium* spp. predators in all cages (see Govan, 1995), and cage husbandry (rated from 1 = non-existent to 5 = excellent on the basis of removal of epiphytic algae and sediment) were collected from each site on up to 22 occasions during the grow-out period. Other variables measured were exposure (fetch area measured from navigation charts), water flow (by the 'clod card' technique of Doty, 1971; Thompson and Glenn, 1994) and geographic location, i.e., eastern or western region of Solomon Islands (Fig. 1). Flow was measured over a 24 h period at each site on four occasions between January and April 1995. For details on measurement of these last two parameters, see Foyle et al. (1997).

2.4. Analysis of data

Variation in mean growth (mm month^{-1}) and survival (%) were compared across 11 sites for all three species; it was necessary to omit three sites from the analysis of *T. derasa*, and one site from the analysis of *T. crocea* and *T. maxima* (see Table 1). Variation in growth and survival was analysed by separate one-way ANOVAs, with site as the factor. Tukey's post-hoc test was used to differentiate among means where significant effects occurred (Zar, 1984). Assumptions of heteroscedascity were tested by Cochran's test. Because survival data for *T. crocea* exhibited heterogeneous variances, even after transformation to $\log_{10}(x)$, the α significance level was set at 0.01 for both the ANOVA and Tukey's tests (Underwood, 1981).

The importance of environmental variables and husbandry in explaining growth and survival were analysed by multiple regression. Mean values of secchi disc reading, salinity, temperature, husbandry, and total abundance of predators at each site were used in the regression analyses. For geographic location, a 'dummy' variable was coded according to Cohen (1968) and Mair and Pauly (1993). Values of the dummy variable were 1 (western region) and 0 (eastern region). Because geographic location and temperature were highly correlated, they were not included together in the same regression model. Exposure (fetch area) exhibited a log normal distribution and was transformed to $\log_{10}(x)$ prior to analysis.

For the regression analyses, relative contributions of each independent variable to total variability in growth and survival were summarised by the magnitudes of their Beta values (standardised partial regression coefficients), and partial correlation coefficients. Colinearity was tested using the tolerance statistic (Kleinbaum et al., 1988). Where tolerance was greater than 0.1 for each independent variable, the regression model was considered to have robust parameter values (Kleinbaum et al., 1988). A summary of the values of the environmental and husbandry variables used in the multiple regressions is given in Table 2.

2.5. Economic analysis

Data on mean growth and survival were used to calculate potential revenue from farming all three species. Estimates were derived for two size-classes. For *T. derasa*,

Table 2
Mean and standard deviations of environmental and husbandry data collected at each site and used in the multiple regression analyses

Site	Exposure	Predators[a]	Water flow[b]	Temperature (°C)	Salinity (ppt)	Secchi distance[c] (m)[c]	Husbandry
n =		22	16	22	22	22	22
1	0.72	3	5.6±3.2	31.3±1.0	34.2±0.5	13.7±4.0	3.8±0.4
2	2.27	49	6.4±1.3	30.5±1.0	34.2±0.6	17.3±1.8	3.0±1.7
3	2.11	16	3.7±1.1	30.3±0.8	34.0±0.8	20.1±5.1	4.0±0.0
4	1.58	40	4.3±1.7	30.9±1.2	33.6±0.5	10.4±2.3	3.5±0.5
5	1.45	27	3.3±1.0	31.2±1.1	32.5±1.0	8.6±2.1	1.9±0.8
6	0.31	9	4.3±1.9	30.6±0.8	32.9±0.7	14.6±3.4	3.7±0.5
7	0.23	38	2.2±1.0	31.0±0.8	32.6±1.3	6.0±3.1	3.1±0.6
8	0.47	11	2.7±0.6	29.9±1.1	33.1±0.6	13.3±4.2	3.4±1.1
9	0.24	13	4.5±1.6	29.3±0.8	33.4±0.6	20.7±4.7	2.6±0.7
10	0.44	9	5.3±1.0	30.2±0.7	33.6±0.7	13.3±4.5	2.8±0.8
11	1.25	6	4.3±1.1	29.1±1.0	33.3±0.7	14.7±3.6	3.1±0.9
12	1.22	10	2.5±0.8	29.0±1.1	33.7±0.6	19.3±4.0	4.0±0.5
13	0.75	1	3.2±0.6	29.0±1.0	33.4±0.7	14.1±3.7	3.4±0.5
14	0.61	6	4.6±1.7	29.5±1.0	33.4±0.6	14.9±3.1	3.8±0.4
Overall mean	0.87±0.82	17±15.2	4.4±1.8	30.0±0.9	33.5±0.7	14.8±3.9	3.4±0.8

Values for exposure are from the $\log_{10}$ transformed data.
[a] Represents total number observed in all cages throughout the study.
[b] This is a dimensionless index (see Doty, 1971).
[c] Measured horizontally.

estimates were made for clams of 75 mm SL, the most popular size for the aquarium market, and for clams of 150 mm SL. For *T. maxima* and *T. crocea*, we used data for clams of 35 mm SL and 50 mm SL, as these are the sizes in most demand from the aquarium trade. Revenues were based on farm gate prices obtained by village growers in Solomon Islands in 1997. Estimates of seed costs from a hatchery producing 500,000 seed per annum range from US$0.27 per clam (Hambrey and Gervis, 1993) to US$0.40 per clam (Tisdell et al., 1993). To allow for a profit margin of a hatchery producing smaller numbers, our seed costs were conservatively estimated at US$0.50 per clam. The costs of grow-out cages and internal freight and handling have also been included in the analysis. Costs of international airfreight and packaging were not included because they are met by the exporter.

3. Results

3.1. Growth

Growth rates for *T. derasa*, *T. maxima*, and *T. crocea* differed significantly among sites (Table 3). For each species, the highest mean growth rate was observed at Site 1

Table 3
Results of ANOVA and Tukey's post-hoc test for comparison of growth of *T. derasa* (24 months grow-out), *T. maxima* (19 months grow-out), and *T. crocea* (22 months grow-out) among sites

Source of variation	Tridacna derasa				Tridacna maxima				Tridacna crocea			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Site	10	1.26	20.32	<0.001	10	0.32	22.3	<0.001	10	0.32	22.3	<0.001
Residual	32	0.06			32	0.014			32	0.014		

Tukey's post-hoc test

Tridacna derasa

Site	1	9	6	2	14	7	3	4	12	10	8
$\bar{x}$ growth rate	6.18	5.66	5.65	5.36	5.25	5.07	5.00	4.81	4.72	4.34	4.08

Tridacna maxima

Site	1	7	6	9	10	12	2	3	8	4	5
$\bar{x}$ growth rate	4.22	3.58	3.40	3.19	2.88	2.86	2.80	2.52	2.47	2.43	2.19

Tridacna crocea

Site	1	7	6	3	5	8	4	10	11	12	2
$\bar{x}$ growth rate	2.02	1.73	1.61	1.44	1.36	1.35	1.31	1.19	1.15	1.13	1.08

Tridacna squamosa

Site	Site 1	7	4	2	6	13	5	11	8	3
$\bar{x}$ growth rate	7.11	6.02	5.74	5.72	5.54	4.93	4.58	4.19	4.15	3.61

For Tukey's tests, mean growth rate (mm month^{-1}) at each site is given. For comparative purposes, means of *T. squamosa* (8 months grow-out) from Foyle et al. (1997) are also given. Lines joining means indicate no significant difference at $\alpha = 0.05$ for *T. derasa* and *T. maxima*, and $\alpha = 0.01$ for *T. crocea*.
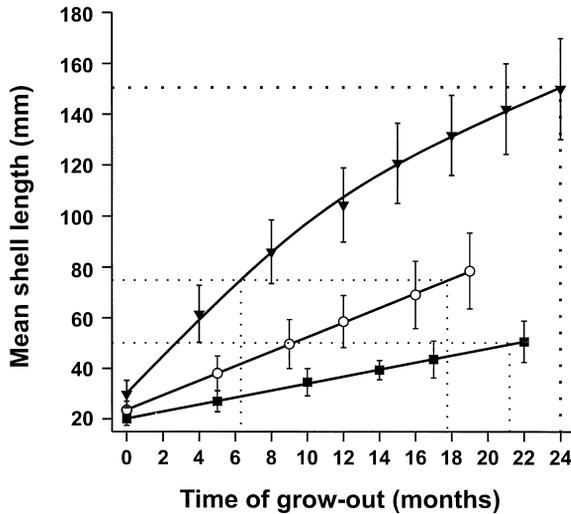
Fig. 2. Mean growth in shell length ($\pm$ s.d.) for *T. derasa* (—▼—), *T. maxima* (—○—), and *T. crocea* (—■—) at village sites. Growth curves are fitted with linear and 2nd order polynomial regressions. Fine dotted lines indicate the time taken for each species to reach aquarium market size. Heavy dotted lines show the time taken for *T. derasa* to reach 150 mm SL for the live seafood trade.

(Table 3). The second and third fastest rates of growth occurred at Sites 7 and 6 for both *T. maxima* and *T. crocea*. Conversely, sites 8, 10, and 11 were consistently among the sites where growth was slowest (Table 3).

T. derasa had a mean growth rate of 6.0 ± 0.6 s.d. mm month^{-1} over the first 16 months grow-out. This was twice as fast as *T. maxima* (2.9 ± 0.6 s.d. mm month^{-1}), and four times faster than *T. crocea* (1.4 ± 0.3 s.d. mm month^{-1}) over the same period (Fig. 2). Time of grow-out needed for clams to reach optimum size for the aquarium market was 7 months for *T. derasa*, 18 months for *T. maxima*, and 21 months for *T. crocea* (Fig. 2). Growth of both *T. maxima* and *T. crocea* was linear over their respective grow-out periods (19 and 22 months). After 2 years grow-out, *T. derasa* had a mean SL of 150 mm $\pm$ 19.8 s.d. (Fig. 2), and a mean wet weight of 710 g $\pm$ 26 s.d. Wet weight ranged from 500 g $\pm$ 14 s.d. where growth was slowest (Site 12), to 1110 g $\pm$ 19 s.d. where growth of clams was greatest (Site 1).

3.2. Environmental influences on growth

Exposure and geographic location were the most important variables influencing growth rates of *T. derasa* and *T. maxima* (Table 4). For *T. crocea*, the most important

Table 4
Multiple regression models for the influence of environmental variables on growth of giant clams

Variable	B	Beta	Partial correlation	Tolerance	t-value	P-value
T. derasa						
Intercept	3.52					
Geographic location	0.75	0.63	0.69	0.80	6.25	< 0.001
Exposure	−0.42	−0.57	−0.65	0.78	−5.60	< 0.001
Secchi disc reading	0.07	0.40	0.50	0.73	3.80	< 0.001
Water flow	0.13	0.25	0.37	0.87	2.64	0.01
T. maxima						
Intercept	−6.55					
Exposure	0.55	−0.83	−0.82	0.73	−8.49	< 0.001
Geographic location	0.60	0.49	0.63	0.71	4.93	< 0.001
Secchi disc reading	0.04	0.28	0.33	0.42	2.14	0.04
Salinity	0.27	0.24	0.33	0.55	2.11	0.04
T. crocea						
Intercept	−7.37					
Temperature	0.28	0.69	0.76	0.62	7.11	< 0.001
Exposure	−0.19	−0.57	−0.73	0.77	−6.54	< 0.001
Water flow	−0.05	−0.22	−0.35	0.64	−2.31	0.03
Husbandry	0.11	0.22	0.35	0.61	2.26	0.03
Secchi disc reading	0.02	0.20	0.27	0.39	1.69	ns

Variables are arranged in descending order of importance. B = partial regression co-efficient, Beta = standardised partial regression coefficient. Tolerance is a measure of the co-linearity (see Section 2). Significance of model and proportion of variance explained for each species are: *T. derasa*: $F(4,43) = 20.5$, $P < 0.001$, $R^2 = 0.66$; *T. maxima*: $F(4,37) = 26.3$, $P < 0.001$, $R^2 = 0.74$; *T. crocea*: $F(5,37) = 27.1$, $P < 0.001$, $R^2 = 0.79$.

Table 5
Correlation matrix for environmental and husbandry variables, and giant clam growth and survival data

	Exposure	Geographic location	Number of predators	Water flow	Temperature	Salinity	Secchi distance	Husbandry	Grow Td	Survival Td	Grow Tm	Surv Tm	Grow Tc
Geographic location	0.15												
Number of predators	0.55*	0.58*											
Water flow	0.06	0.29	0.18										
Temperature	−0.14	0.81*	0.49*	0.39*									
Salinity	0.34*	0.26	0.14	0.57*	0.08								
Secchi distance	0.40*	−0.14	−0.25	0.15	−0.48*	0.60*							
Husbandry	0.04	0.20	−0.30*	0.31*	−0.02	0.22	0.26						
Grow Td	−0.30*	0.60*	0.02	0.46*	0.43*	0.32*	0.02	0.15					
Survival Td	0.08	0.28	0.39*	−0.03	0.39*	−0.07	−0.06	0.03	−0.16				
Grow Tm	−0.72*	0.17	−0.41*	0.22	−0.17	0.33*	0.08	0.28	0.75*	−0.06			
Survival Tm	−0.11	0.23	−0.18	0.19	−0.23	0.44*	−0.03	0.35*	0.44*	−0.16	0.27		
Grow Tc	−0.67*	0.49*	−0.01	−0.01	0.59*	−0.10	−0.23	0.42*	0.55*	0.14	0.54*	0.44*	
Survival Tc	0.13	0.49*	0.31*	0.22	0.47*	−0.32*	−0.12	0.00	0.03	0.49*	−0.05	−0.41*	0.04

*Indicates a significant correlation ($P < 0.05$).

Td—T. derasa; Tm—T. maxima; Tc—T. crocea.
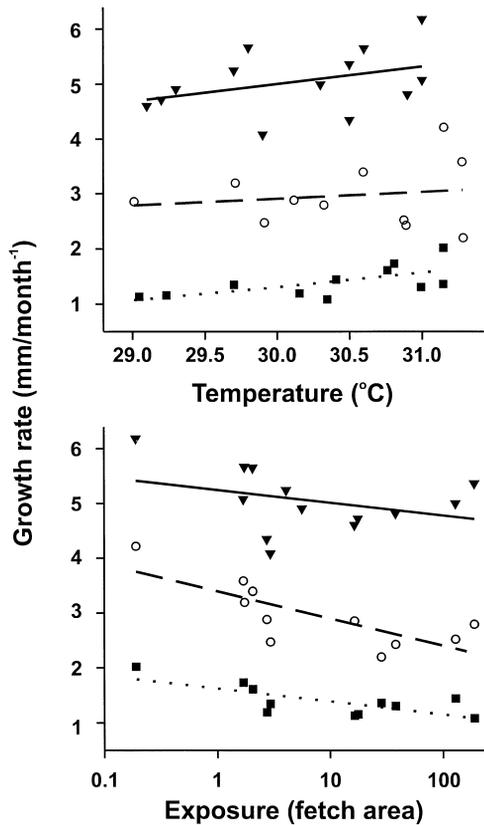
Fig. 3. Relationships between growth rate and water temperature, and growth rate and site exposure, for *T. derasa* (— ▼ —), *T. maxima* (—○—), and *T. crocea* (· · · · · · ■ · · · · · ·).

variables were temperature and exposure (Table 4), although temperature was highly correlated with geographic location ($r = 0.81$; Table 5). Growth rate was faster at higher temperatures, while exposure to wave action had a negative influence on growth (Fig. 3). Other characteristics of the environment that explained significant variation in growth were water clarity (i.e., secchi disc visibility) and, in the case of *T. derasa* and *T. crocea*, water flow (Table 3). Husbandry and salinity also had a significant positive influence on the growth of *T. crocea* and *T. maxima*, respectively. Together, environmental and husbandry variables explained a large proportion of the total variation in growth among sites (Table 4).

3.3. Survival

There was a significant difference in survival among sites for *T. maxima* and *T. crocea*, but not for *T. derasa* (Table 6). Mean survival of *T. derasa* after 24 months was 92.2% ± 9.1 s.d., and ranged between 99.1 and 80.1% (Table 6). Mean survival of *T.*

maxima (19 months grow-out) and *T. crocea* (17 months grow-out) was 38.9% ± 16.6 s.d. and 39% ± 22.6 s.d., respectively. Survival for the latter two species was quite variable across sites, ranging from 12% to 80% (Table 6). No obvious pattern in survival among sites was evident across species, although survival at Site 4 was consistently within the upper range (Table 6).

The temporal pattern of mortality of *T. maxima* and *T. crocea* was similar: it declined markedly after 6 months, but did not stop completely (Fig. 4). At 17 months, however, mortality rate of *T. crocea* increased, and survival dropped from 39% to 28% at the termination of the experiment (Fig. 4). This decline coincided with the thinning of *T. crocea* at 17 months. In contrast, *T. derasa* had a very low rate of mortality rate ($\sim 0.4\%$ month^{-1}) throughout the 2 years of grow-out (Fig. 4).

3.4. Environmental influences on survival

In general, regression models of survival were a poorer fit of the data than those for growth, explaining 15% (*T. derasa*), 53% (*T. maxima*), and 52% (*T. crocea*) of the variability in survival among sites (Table 7). Two important variables affecting survival were salinity and secchi disc visibility (Table 7); however, the nature of the effect differed among species. For example, salinity was negatively correlated with survival of *T. crocea*, but positively correlated with survival of *T. maxima*. In a similar manner,

Table 6
Results of ANOVA and Tukey's post-hoc test for comparison of survival of *T. derasa* (24 months grow-out), *T. maxima* (19 months grow-out), and *T. crocea* (17 months grow-out) among sites

Source of variation	Tridacna derasa				Tridacna maxima				Tridacna crocea			
	df	MS	F	P	df	MS	F	P	d.f	MS	F	P
Site	10	130.7	1.92	ns	10	895.9	10.2	<0.001	10	1847	19.9	<0.001
Residual	32	68.1			32	85.2			32	92.6		

Tukey's post-hoc test
Tridacna derasa (no significant differences among sites were detected)

Site	7	9	4	6	14	10	2	3	12	8	1
$\bar{x}$ survival	99.1	97	96.2	95.5	94.1	93.4	92.9	91.6	88.0	84.5	80.1

Tridacna maxima

Site	1	4	8	12	5	2	3	6	9	7	10
$\bar{x}$ survival	72.7	49.0	48.0	44.9	40.0	39.0	36.8	36.1	33.5	20.5	16.0

Tridacna crocea

Site	6	4	10	7	3	2	5	11	8	1	12
$\bar{x}$ survival	81.9	57.8	50.3	48.2	46.6	46.5	35.5	20.9	16.6	15.8	11.8

Tridacna squamosa

Site	13	5	4	1	3	6	2	8	11	7
$\bar{x}$ survival	83.1	80.7	76.7	76.2	75.1	64.7	62.7	52.8	51.6	42.2

For Tukey's tests, mean percent survival at each site is given. For comparative purposes, means of *T. squamosa* (8 months grow-out) from Foyle et al. (1997) are also given. Lines joining means indicate no significant difference at $\alpha = 0.05$ for *T. maxima* and *T. squamosa*, and $\alpha = 0.01$ for *T. crocea*.
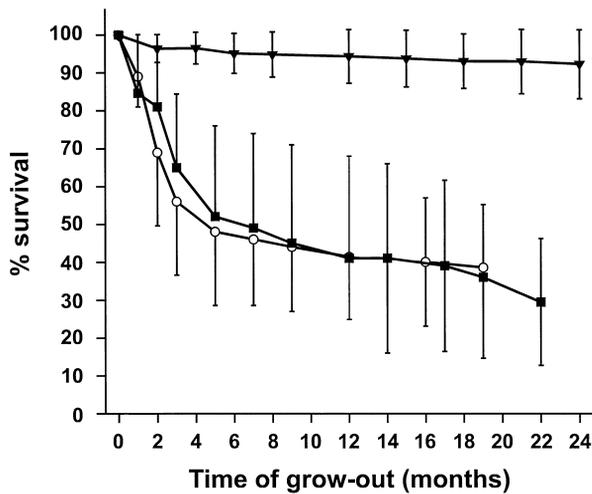
Fig. 4. Mean percent survival ($\pm$s.d.) over time of *T. derasa* (—▼—), *T. maxima* (—○—), and *T. crocea* (—■—) at village sites during the grow-out experiments.

Table 7
Multiple regression models for the influence of environmental variables on survival of giant clams

Variable	B	Beta	Partial correlation	Tolerance	*t*-value	*P*-value
T. derasa						
Intercept	415.8					
Salinity	-10.0	-0.53	-0.38	0.45	-2.42	0.02
Exposure	2.77	0.26	0.19	0.43	1.16	ns
Predator abundance	0.12	0.22	0.19	0.58	1.13	ns
Water flow	1.55	0.20	0.17	0.55	1.0	ns
T. maxima						
Intercept	-1370					
Salinity	445.5	0.71	0.58	0.54	4.28	< 0.001
Secchi disc reading	-4.87	-0.67	-0.43	0.27	-2.88	0.007
Geographic location	24.3	0.35	0.37	0.68	2.36	0.02
Predator abundance	-1.05	-0.54	-0.33	0.22	2.11	0.04
Exposure	14.1	0.38	0.27	0.29	1.66	ns
T. crocea						
Intercept	2680					
Salinity	-88.0	-2.15	-0.81	0.11	-8.35	< 0.001
Water flow	28.0	1.61	0.84	0.26	9.38	< 0.001
Husbandry	44.4	1.19	0.78	0.29	7.47	< 0.001
Exposure	11.4	0.53	0.66	0.74	5.36	< 0.001
Secchi disc reading	2.75	0.33	0.33	0.32	2.16	0.01

Variables are arranged in descending order of importance. Beta = standardised partial regression coefficient. Significance of model and proportion of variance explained for each species are: *T. derasa*: $F(4,35) = 2.75$, $P = 0.04$, $R^2 = 0.15$; *T. maxima*: $F(5,36) = 6.58$, $P < 0.001$, $R^2 = 0.53$; *T. crocea*: $F(5,37) = 7.9$, $P < 0.001$, $R^2 = 0.52$.

Table 8
Summary of revenues and costs to the village farmer of growing *T. derasa*, *T. maxima*, and *T. crocea* for aquarium markets, based on a cage of 200 'seed' clams of 25 mm shell length

Shell length of clams at harvest	*T. derasa*		*T. maxima*		*T. crocea*	
	75 mm	150 mm	35 mm	50 mm	35 mm	50 mm
Income						
Survival (%)	95	92	50	44	42	30
No. clams surviving in cage	190	184	100	88	84	60
Price per clam (US$)	1.24	2.31	1.65	2.23	2.27	3.18
Total revenue from clams (US$)	235.60	364.32	165.00	196.24	190.68	190.80
Costs						
200 seed clams at US$0.50	100.00	100.00	100.00	100.00	100.00	100.00
No. cages needed to grow-out clams	2	6	1	1	1	1
Total cost of cages at US$11.00 per cage	22.00	66.00	11.00	11.00	11.00	11.00
Mean weight (g) of clams	40	710	15	20	25	32
Air freight costs for delivery to exporter at US$0.95 per kg	7.60	124.10	1.50	1.67	1.92	1.82
Handling charge at US$0.12 per clam	22.80	22.08	12.00	10.56	10.08	7.20
Total costs (US$)	152.40	312.18	124.50	123.23	123.00	120.02
Net income (US$) (per 200 seed clams)	**83.20**	**112.86**	**39.50**	**73.01**	**67.68**	**70.78**

secchi disc visibility was positively correlated with survival of *T. crocea*, but negatively correlated with survival of *T. maxima*. Exposure and husbandry had a significant, positive influence on survival of *T. crocea*. Abundance of predators (which was significantly negatively correlated with husbandry; Table 5) had a negative influence on survival of *T. maxima*.

3.5. Economic analysis

Although farmgate prices were lowest for *T. derasa*, net revenue was greatest for this species due to its very high survival (Table 8). It amounted to US$83 (per 200 seed clams) after 7 months grow-out to 75 mm SL, and US$113 after 2 years grow-out to 150 mm SL (Table 8). Net revenue was similar for *T. maxima* and *T. crocea* of 50 mm SL and *T. crocea* of 35 mm SL, i.e., approximately US$70 per 200 seed clams (Table 8). Note, however, that it took 11 months to grow *T. crocea* to 35 mm SL, compared to 22 months to reach 50 mm SL. In contrast, grow-out time for *T. maxima* to reach 50 mm SL was 9 months. Revenue for *T. maxima* of 50 mm SL was considerably greater than for individuals of 35 mm SL (Table 8).

4. Discussion

Growth rates of juvenile *T. derasa*, *T. maxima*, and *T. crocea* at village farms in the Solomon Islands were faster than reported elsewhere in the literature. During the 24

months grow-out, *T. derasa* grew at a mean rate of 5.0 mm month^{-1}, and at a mean rate of 7.5 mm month^{-1} over the initial 8 months. In contrast, cultured *T. derasa* from the Philippines grew at 3.4–4.2 mm month^{-1} over 8 months (Gomez and Mingoa, 1993). The maximum length reported by Munro (1993) for 2-year-old *T. derasa* from cultured and natural stocks was 117 mm SL. At this age (i.e., after 15 months grow-out), overall mean size of *T. derasa* from village farms in Solomon Islands was 120 mm SL, with mean size at the fast growing sites being 132 mm SL.

Published estimates of growth for *T. maxima* and *T. crocea* also indicate that the growth we recorded is faster than elsewhere. At 2 years of age, *T. maxima* ranges from 21–51 mm SL (McKoy, 1980; Richard, 1981; Munro, 1993), while *T. crocea* attains 30 mm SL at Okinawa (Murakoshi, 1986), and 35 mm SL on the central Great Barrier Reef (Hamner and Jones, 1976). In our study, 2-year-old *T. maxima* and *T. crocea* (i.e., after 16 months grow-out), had mean sizes of 69 mm SL $\pm$ 13 s.d., and 42 mm SL $\pm$ 7 s.d., respectively. We also found that growth of *T. maxima* and *T. crocea*, in terms of increase in shell length, was linear over the entire grow-out period, a phenomenon not previously reported for these species.

The environmental parameters that influenced growth of *T. derasa*, *T. maxima*, and *T. crocea* were the same factors affecting growth of *T. squamosa* identified by Foyle et al. (1997). These were geographic location/temperature, exposure, water clarity, and water flow. For all four species, the fastest growth occurred at Site 1 (Table 3). This site was situated in the Western Province, and had the highest mean water temperature and salinity, second highest flow rate and husbandry rating, and the lowest exposure (Table 2).

Mean water temperature at farms in the western region (30.9°C $\pm$ 1.0 s.d.) was significantly higher than those in the eastern region (29.4°C $\pm$ 1.0 s.d.) ($n = 276$; $t = -10.9$; $P < 0.001$). The effect of temperature on growth of cultured molluscs has been well documented. For example, Lucas et al. (1989) found a strong seasonal effect of temperature on growth of *T. gigas*, and Hall (1984) developed a predictive model of oyster growth (*Crassostrea* and *Ostrea* spp.) based entirely on seawater temperature and oyster size.

Exposure was also a crucial factor affecting growth of the giant clam species in this study (Table 4), and *T. squamosa* (Foyle et al., 1997). Although all sites are protected from oceanic swell, they differ in their exposure to wind-generated waves. Because of the shallow depths of the cages (< 2 m), even minor wave action affected the ability of the clams to attach to the substrate, especially in the period immediately after distribution. Sites without turbulence provided better growing conditions; clams settled quickly, and presumably did not expend energy on maintaining stability or re-establishing byssal threads. Although they only examined two sites, Lucas et al. (1989) also found that growth of *T. gigas* was significantly lower at the more exposed site.

The significant positive influence of water flow on growth of *T. derasa* and *T. crocea* (Table 4) highlights the potential importance of flux in Particulate Organic Matter (POM) resulting from high volumes of water exchange. Klumpp and Griffiths (1994) showed that nutrition from POM is as important to juvenile *T. gigas* as that derived from photosynthesis. The importance of flow in determining growth suggests that substantial variability in growth can be expected at the micro-scale. Indeed, some farmers in the

Solomon Islands have found that growth improves if they move their grow-out cages relatively short distances to areas of faster currents.

Water clarity has been hypothesised as a determinant of growth and survival in giant clams, although the nature of the influence is thought to depend on the light/depth profile (Lucas et al., 1989) and the cause of turbidity. Foyle et al. (1997) found that secchi disc visibility had a negative influence on growth of *T. squamosa*. In contrast, we found that secchi disc visibility had a positive influence on growth of *T. derasa* and *T. maxima* (Table 4). The most parsimonious explanation for differences in the effect of water clarity among studies is that reduced water clarity may have been caused by different factors. For example, low visibility caused by sediment run-off would be detrimental to growth and survival, whereas low visibility due to high levels of POM would be beneficial. Studies on nutrient availability over an appropriate period at sites with different growth rates and water clarity would shed light on the nature of the relationship of this variable to growth of giant clams.

Environmental variables had little effect on survival of *T. derasa*: there was low variation in survival among sites (Table 6). Salinity had a significant positive influence on survival of *T. maxima*, but negative influence on survival of *T. crocea* (Table 7). This result is consistent with the natural distribution of the species, *T. maxima* is generally more abundant in open, clear waters, while *T. crocea* tends to be more abundant in lagoonal areas subject to runoff from islands. The opposite trend occurred for secchi disc visibility, which had a negative influence on survival of *T. maxima*, and a positive influence on survival of *T. crocea* (Table 7). This result does not match the natural distribution of these species, and is difficult to explain. Both species attach and burrow into coralline rock in shallow intertidal areas and should have some tolerance to periods of turbid water. However, as *T. maxima* is most abundant in clear water habitats in Solomon Islands, we would not expect clear water growing conditions to have a negative effect on survival.

Husbandry had a positive effect on survival of *T. crocea*, while abundance of predators had a negative influence on survival of *T. maxima* (Table 7). These results underline the importance of adequate husbandry practices, particularly the removal of predators such as *Cymatium* spp. (see Govan, 1995). Abundance of predators also had a negative influence on survival of *T. squamosa* (Foyle et al., 1997). The extent to which these predators are a problem depends on their settlement rates, which vary significantly among years and sites. Data collected in the early 1990s from Solomon Islands show that average numbers of *Cymatium* spp. settling each month into giant clam grow-out cages ranged from 0.8 to 19.5 snails m^{-2} within a year (Govan, 1995). In times of high abundance of *Cymatium* spp., mortality of giant clams is likely to increase, particularly at sites where husbandry is neglected. Govan (1995) concluded that, at a good grow-out site, most mortality of giant clams will be due to predators/parasites, and success of the grow-out phase will depend on their control.

Another major source of mortality for *T. crocea* and *T. maxima* was predation by small wrasses (*Thalassoma* spp.). These fish attacked the clams at distribution and after thinning. The wrasses dislodged unattached clams and attacked them through the byssal orifice. Prior to thinning, survival of *T. crocea* had stabilised around 40%, but then dropped sharply to 28% (Fig. 4). Clearly, thinning should be kept to a minimum for

these species. This is in contrast to husbandry protocols for other species of giant clams. For example, survival of *T. derasa* was not affected by thinning, and Bell et al. (1997a) showed that harvest and removal of *T. gigas* for cleaning significantly improved their survival.

Overall, our results provide strong evidence for the existence of optimum grow-out sites for giant clams. In general, growth was enhanced by high water temperature, minimal exposure, and good water flow. On the other hand, survival was dependent largely on husbandry practices because most of the mortality was due to predators.

The economic analysis showed that the greatest profits can be made by growing *T. derasa* (Table 8). Revenue from growing this species to 150 mm SL could be increased further if growers transport their clams to an exporter by sea, rather than by air. This is a real possibility for many of the farmers in Solomon Islands because Bell et al. (1997c) have shown that 100% of *T. derasa* of 150 mm SL survive for 16 h when packed 'moist' and kept in the shade. The high rates of growth and survival of *T. derasa* after 2 years grow-out also indicate that this species can be farmed for the seafood trade. Efforts are now being made to market *T. derasa* of 150 mm SL in the live seafood trade in Asia (Bell et al., 1997c).

For the other species, the most encouraging result was for *T. crocea* of 35 mm SL (US$68 per 200 seed clams). This species is brightly coloured and in much demand by the aquarium trade. However, it is vulnerable to predation and unless methods can be devised to improve survival during ocean culture, the potential of this species will not be realised. As this species can be sold as small as 25 mm, village farmers may also find it difficult to compete with growers using land-based facilities.

The excellent performance of *T. derasa* in grow-out trials over 2 years may also provide a solution to the problems encountered with the initial attempts to grow-out the larger species of giant clams to supply the market for adductor muscle. A critical factor affecting the viability of village farming of *T. gigas* for meat and adductor muscle markets was the predicted low survival over the long-term (Hambrey and Gervis, 1993). This was recently confirmed by Bell et al. (1997a), who found that mean survival of *T. gigas* at 30 coastal villages was 41.3% after only 10 months.

Munro (1988) compared theoretical production levels for *T. gigas* and *T. derasa* based on stocking 10,000 clams, and concluded that survival of *T. derasa* would have to be at least four times greater than *T. gigas* to obtain a similar biomass production after 6–10 years. Our data are based on an actual stocking of 11,200 clams. Survival of 92% of *T. derasa* at village farms after 2 years is more than double that obtained for *T. gigas* (41.3%) after less than a year of grow-out. Thus, over longer grow-out periods, it is probable that survival of *T. derasa* at village farms would be 3–4 times greater than for *T. gigas*. In addition, growth of *T. derasa* at 2–3 years of age in the Solomon Islands was considerably greater than the figures used by Munro (1988), who assumed that a 3-year-old clam had a mean weight of 360 g. Watson and Heslinga (1988) estimate mean weight at 3 years to be 500 g. Our data show that *T. derasa* produced at village farms in Solomon Islands attain a mean weight of 710 g within 3 years.

If the pattern of growth and survival we recorded for *T. derasa* continues, the long-term biomass production of this species after 7 years grow-out should be considerably greater than estimated previously. To confirm the potential of this species to supply

an adductor muscle market, we intend to monitor the morphometrics, growth and survival of *T. derasa* for a total of 7 years. The other important area of research is the development of methods to improve growth, survival and mantle colour of *T. maxima* and *T. crocea* reared for the aquarium trade.

Acknowledgements

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