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Nutritional ecology of the giant clams *Tridacna tevoroa* and *T. derasa* from Tonga: influence of light on filter-feeding and photosynthesis

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ABSTRACT: This study compares the nutrition of 2 species of giant clam (Tridacnidae) from Tonga: the rare *Tridacna tevoroa*, which inhabits relatively deep waters (9 to 33 m), and *T. derasa*, a more common and widespread species usually found in shallower habitats (1 to 20 m). The principal aim of the comparison was to determine how *T. tevoroa* survives at greater depths than other tridacnid species. Rates of filter-feeding, respiration and the photosynthesis-irradiance response were measured in clams of a wide size range (ca 20 mm to ca 500 mm) which had been acclimated to 4 levels of shading, simulating depths of 1, 5, 15 and 28 m. Carbon utilisation by the tissues of the host, partitioned into growth and respiration components, were compared with the supply of carbon via filter-feeding and photosynthate from zooxanthellae. Rates of respiration, growth, filter-feeding and maximum photosynthesis did not vary between species or level of shading. Only *T. tevoroa* significantly increased its photosynthetic efficiency with increasing depth. Consequently, it was able to rely on phototrophy while at greater depth (ca 10 m deeper) than *T. derasa*. At their normal depths, phototrophy provides most (*T. tevoroa*: 70 % at 28 m, 105 % at 15 m), if not all (*T. derasa*), of the carbon required for growth plus maintenance, and filter-feeding is a relatively minor source (8 to 14 %). These 2 species contrast with the largest tridacnid species, *T. gigas*, in which filter-feeding is a major source of carbon, at least in small clams, and the relative allocation of carbon for growth compared to respiration is much higher.

KEY WORDS: Giant clam · *Tridacna derasa* · *Tridacna tevoroa* · Filter-feeding · Coral reef · Respiration · Photosynthesis · Photoadaptation · Carbon budget

INTRODUCTION

Rosewater (1965) effectively commenced the modern era of research on giant clams (Family Tridacnidae) by providing the first comprehensive study of their taxonomy. He recognised 6 extant species in 2 genera. Subsequently, 3 less-common species have been described: *Hippopus porcellanus* Rosewater, *Tridacna tevoroa*[1] Lucas et al., and *T. rosewateri* Sirenko and Scarlato. *T. tevoroa* occurs in the eastern Lau Islands of Fiji and in Tonga (Lucas et al. 1991, Ledua et al. 1993), and is notable for occurring at greater depths than other tridacnid species. Ledua et al. (1993) tabulated recent collections of *T. tevoroa*, with mean depths and ranges being 27 m and 20 to 33 m for specimens from Fiji and 26 m and 9 to 33 m for specimens from Tonga.

Giant clams obtain their nutrition mainly from translocated photosynthates from symbiotic zooxanthellae in their exposed mantle tissues (see recent reviews by Fitt 1993, Lucas in press). They are thus limited to relatively shallow areas by light attenuation and most occur at less than 10 m depth. Where they occur at greater depths, it is usually in very clear oceanic water. Thus, large *Tridacna derasa* (Röding) were commonly found at 10 to 20 m depth in the clear oceanic conditions of the windward islands and barrier reefs of eastern Fiji (Adams et al. 1988). In these regions, juveniles of *T. derasa* were usually found attached to the tops and sides of coral outcrops at shallow depths, from which they detached and fell when their byssus broke (Adams et al. 1988). *T. derasa* and *T. tevoroa* co-occur in oceanic barrier reef and island conditions of Fiji and

[1] Recently identified as *Tridacna mbalavuana* Ladd (unpubl.)

Tonga, but *T. tevoroa* occurrence extends to a greater depth and, judging from its size distribution, it recruits at these depths.

Giant clams also filter-feed, like most bivalve molluscs, but there was no quantification of the relative importance of phototrophic nutrition versus filter-feeding until a study of *Tridacna gigas* L. by Klumpp et al. (1992). They showed that this clam is an efficient filter-feeder and that carbon derived from filter-feeding in Great Barrier Reef (GBR) waters supplies substantial proportions of the total carbon needed for respiration and growth. This proportion is size-dependent, decreasing from 65% in 42.5 mm shell length clams to 34% at 167 mm shell length.

The importance of filter-feeding in small *Tridacna gigas* raises the question of its contribution to the nutrition of other giant clam species, particularly *T. tevoroa* which occurs in deeper waters where light intensity is attenuated. There are 2 obvious mechanisms whereby *T. tevoroa* could extend down to greater depths than other tridacnid species: (1) it uses the low irradiance levels at those depths more efficiently for photosynthesis; (2) it relies increasingly on filter-feeding to supplement the deficient phototrophic nutrition at depths.

The fact that *Tridacna derasa* and *T. tevoroa* are closely related (Lucas et al. 1991) and co-occur, with the latter extending to greater depths, suggested that a comparison of filter-feeding, respiration and the photosynthesis-irradiance response in these 2 species could provide the key to the depth distribution of *T. tevoroa.*

MATERIALS AND METHODS

Maintenance and treatment of clams. The study was conducted at the Tonga Fisheries facilities, Sopu, Tongatapu Island. The facilities included a seawater system consisting of a series of large outdoor tanks supplied with a constant flow of unfiltered seawater, pumped from the adjacent reef/seagrass flats. This seawater system was used for conditioning clams and during the experiments. The study was conducted over the period July to October 1992 when seawater temperature ranged from 20 to 23°C at 09:00 h and from 23 to 26°C at 14:00 h.

Tridacna tevoroa and *T. derasa* 300 to 500 mm in shell length (SL), hereafter termed 'large clams', were obtained from brood stock assembled by Tonga Fisheries. These brood stock originated from wild populations in Tonga, and were kept beyond the edge of the Sopu reef flat at ca 18 m depth. *T. derasa* 75 to 120 mm SL ('medium clams') were obtained from cultured stock kept on the Sopu reef flat at ca 3 m depth. Medium-sized *T. tevoroa* were not available. Small (15 to 25 mm SL) specimens of both species were obtained from cultured stocks growing in outdoor concrete tanks (2 × 10 × 3 m deep) at the Sopu laboratory. The tanks were covered with translucent roofing, effectively reducing ambient sunlight by 10%.

For experimental purposes, 1 outdoor tank was divided into 4 shading regimes using various grades of shade cloth. The percentages of surface irradiance, and their equivalent depth in coral reef waters, for the 4 shading regimes were: 83% = 1.0 m or reef flat conditions; 46% = 5 m; 22% = 15 m; 11% = 28 m (light extinction coefficients provided by B. E. Chalker, Australian Institute of Marine Science). In July 1992, clams from each of the size groups and species were distributed at random between these 4 light regimes and left for at least 2 wk to acclimate before being used in clearance rate or respirometry measurements. The clam shells were brushed clean of epibionts before being placed in the tank. The shade cloth was also regularly brushed to maintain constant shade conditions. Clams were supported on mesh trays suspended just beneath the water surface, and supplied with constant flowing seawater and strong aeration.

Shell length was used as a general measure of size, while wet wt of the soft tissues was used as a measure of metabolising tissue. Clams of both species over the size range studied were sacrificed; their soft tissues were removed and weighed soon after death. Logarithmic relationships were determined between wet tissue wt and standard length for each species, and these were used to calculate wet tissue wt for specimens which were not sacrificed.

Respirometry. Two data-logging respirometers, as described by Klumpp et al. (1987), were used, each being able to monitor irradiance, temperature and oxygen flux in 4 replicate chambers at 1 min intervals. The respirometers were used to measure variations in dark respiration rates (R) and net photosynthetic rate - irradiance (P-I) relationships for each clam species, size class and shading regime. Respirometers were immersed in a 1 m deep, 12 000 l capacity outdoor tank with running seawater. The usual monitoring protocol was to expose clams to natural variations of sunlight for ca 6 h, combined with several hours in natural darkness to obtain respiration rate. Water in each chamber was completely and automatically replaced at 5 to 15 min intervals, and chamber volume could be varied between 2 and 57 l depending on the size of clam. Shells of freshly-shucked clams were run as blanks.

P-I relationships for the 2 clam species under the 4 levels of shading were modelled using the hyperbolic tangent function (Jassby & Platt 1976, Chalker 1981), as described in Klumpp et al. (1987) and Klumpp & McKinnon (1989). This function gave the best fit to the

P-I data of this study ($r > 0.95$, $p < 0.001$). Parameters used to describe the *P-I* response curve are: the asymptotic P (P_{max}); the initial slope of the *P-I* plot ($\propto$); the irradiance at which $\propto$ intersects P_{max} (I_k); and the irradiance at which gross P and R are equal (I_c, the compensation point). Thus $\propto$ is a measure of the efficiency of the *P-I* response, and I_k is a standardised measure of the level of irradiance at which photosynthetic rate approaches the asymptote ($I_{95\%\ saturation} = 1.832\ I_k$ for the hyperbolic tangent function).

Daily gross oxygen production (P_g) by small and large clams of both species during winter and summer, and under the 4 simulated depths, was modelled by solving for P of the relevant *P-I* function over the 24 h cycle of irradiance expected at each depth. *P-I* functions were assumed not to vary between summer and winter. The 24 h irradiance cycle, which was divided into 15 min intervals, was derived from an extensive set of measurements by Klumpp & McKinnon (1989) taken on cloudless days in summer and winter at Davies Reef, GBR. Measurements taken in Tonga gave similar light results. Daily oxygen consumption ($R_{24\,h}$) was calculated from R, assuming this to remain constant over day and night (see Klumpp et al. 1992). Daily net oxygen production was then derived as the difference between P_g and $R_{24\,h}$.

Clearance rate measurements. Clearance rates (*CR*, $l\ h^{-1}$) of clams, defined as volume of water cleared of particulate material per hour, were determined using a flow-through system in which water containing natural particulates at ambient concentrations was pumped continuously through 4 perspex chambers each containing a clam. From the flow rate (F, $l\ h^{-1}$) and particle concentrations in the water entering (C_i) and leaving (C_o) each chamber, *CR* is given as: $F(C_i - C_o)/C_o$. C_o was used as the best approximation to the concentration immediately surrounding the clam (Hildreth & Crisp 1976; for technical details see also Bayne et al. 1985, Klumpp et al. 1992).

In this study, C_i was the particle concentration in the outlet water of a fifth chamber without a clam. A flow rate equivalent to at least 5 times the clearance rate of specimens was maintained to minimise recirculation of water by clams, and yet give detectable concentration differences (10 to 20%) between control and test chambers. Tests with higher flows than this did not influence *CR* (see Klumpp et al. 1992). Clams ranging in size from 15 to 515 mm were tested using chamber volumes of 120 ml to 120 l. Concentration of particles within the size range 3 to 54 µm was measured (mean of 4 counts) immediately after taking a sample, by means of a Coulter Counter (Model ZM) with a 140 µm orifice tube.

After acclimation to shade conditions, clams were introduced to the chambers, which were supplied with a constant flow of seawater, and left undisturbed for a minimum of 4 h before commencing at least 5 replicate *CR* measurements on each specimen at ca 30 min intervals.

Ingestion rates of clams were calculated as the product of *CR* and concentration of particles in the water. It is assumed that all particles cleared from the water are ingested based on observations that clams do not produce pseudofaeces at particle concentrations occurring on coral reefs (Klumpp & Hawkins unpubl. data). Food concentration was monitored in 20 separate 1 l water samples collected from both the reef/seagrass flat and adjacent reef crest over the period of the study. Total particle concentrations within the size range 3 to 54 µm were analysed using the Coulter Counter, and particulate organic carbon (POC) and particulate nitrogen (PN) of the acid-treated residues collected on pre-ashed GFF filters were analysed using an ANTEK C & N analyser.

Growth rate of juveniles. Shell lengths of 50 juveniles of each species were measured and the clams were then placed in cavities on concrete slabs: the *Tridacna tevoroa* on one slab and *T. derasa* on another. Cavities were in rows of 10 so that the juvenile clams were identifiable by their position on the slab, except for some that initially moved about before attaching with their byssus. This experiment commenced in August 1992 and, thereafter, the juveniles were measured at monthly intervals.

Data analysis. Because regression analysis showed that *CR*, P_{max} and R varied markedly with clam size, variations in these parameters in relation to species and light level were examined using ANCOVA with clam size as the covariate. I_k and I_c were independent of clam size (regression analysis), thus the effect of species and light regime on these parameters was tested using 2-way ANOVA. Where differences were significant, means were compared using the Ryan-Einot-Gabriel-Welsh test. All statistical analyses were performed using programs from SAS (1985).

RESULTS

Photosynthesis and respiration

Acclimation of a wide size range of clams to 4 light intensities ranging from 83 to 11% of surface irradiance had no significant effect on either maximum rate of net oxygen production (P_{max}) or dark oxygen consumption (R) (ANCOVA, Table 1). Both P_{max} and R were strongly correlated with clam size (Table 1, Figs. 1 & 2). Relationships between P_{max} and R (µmol $O_2\ min^{-1}$) and size of clam (wet tissue wt, W, in g) are described by the functions:

Table 1. *Tridacna* spp. Summary of ANCOVA testing for similarity in clearance rate (*CR*), maximum photosynthetic rate (P_{max}) and respiration rate (*R*) across species of clam (*T. derasa*, *T. tevoroa*) and level of shading (equivalent to 83, 46, 22, 11% of surface irradiance) with wet tissue wt (*W*) as the covariate. NS: not significant at $p < 0.05$; $^{\bullet}p < 0.05$; $^{\bullet\bullet}p < 0.01$; $^{\bullet\bullet\bullet}p < 0.0001$

Source of variation	Variate *CR*	P_{max}	*R*
Weight (*W*)	•	•••	•••
Species (Sp)	NS	NS	NS
Shading (Sh)	•	NS	NS
Sp × Sh	•	NS	NS
Sp × *W*	NS	NS	NS
Sh × *W*	NS	NS	NS
Sp × Sh × *W*	NS	NS	NS

Tridacna derasa

$\ln P_{max} = -0.707 + 0.744 \ln W \quad (r^2 = 0.98, n = 145);$

$\ln R = -2.101 + 0.736 \ln W \quad (r^2 = 0.98, n = 145);$

T. tevoroa

$\ln P_{max} = -0.853 + 0.710 \ln W \quad (r^2 = 0.98, n = 71);$

$\ln R = -2.188 + 0.726 \ln W \quad (r^2 = 0.98, n = 71).$

There was no significant difference between the size relationships of the 2 species (ANCOVA, Table 1). The exponents of the above relationships show a close approximation to the theoretical exponent of 0.67 expected for surface area (i.e. P_{max} or *R*) to volume (body mass) relationships. This is similar to the *R* exponent of 0.755 for *Tridacna gigas* (Klumpp et al. 1992). Indeed, the average *R*:*W* exponent value for bivalve molluscs is 0.7 (Bayne & Newell 1983).

Another parameter which describes the *P-I* relationship is I_k, the irradiance at which *P* approaches saturation. This did not vary significantly with size in either species (regression analysis, Table 2). However, I_k did vary significantly (2-way ANOVA) between species ($p = 0.044$) and with irradiance level ($p = 0.026$). In *Tridacna tevoroa*, decreased levels of irradiance were accompanied by a progressive reduction in I_k from 270 to 160 µE m^{-2} s^{-1} (Table 2), but irradiance had no significant influence on I_k in *T. derasa*. Compensation irradiance, I_c, did not differ between species (ANOVA, $p = 0.16$), but declined significantly with light intensity (ANOVA, $p = 0.0001$), from 80 µE m^{-2} s^{-1} at 83% to 50 µE m^{-2} s^{-1} at 11% surface irradiance.

Daily gross oxygen production (P_g) of *Tridacna tevoroa* and *T. derasa* at the 4 light levels, or simulated depths, was estimated using the expected diel variation in irradiance at each depth on a typical coral reef and the known relevant *P-I* parameters (calculation of P_g is explained in 'Methods'). R_{24h} was constant between species and across light levels (Table 1) and averaged

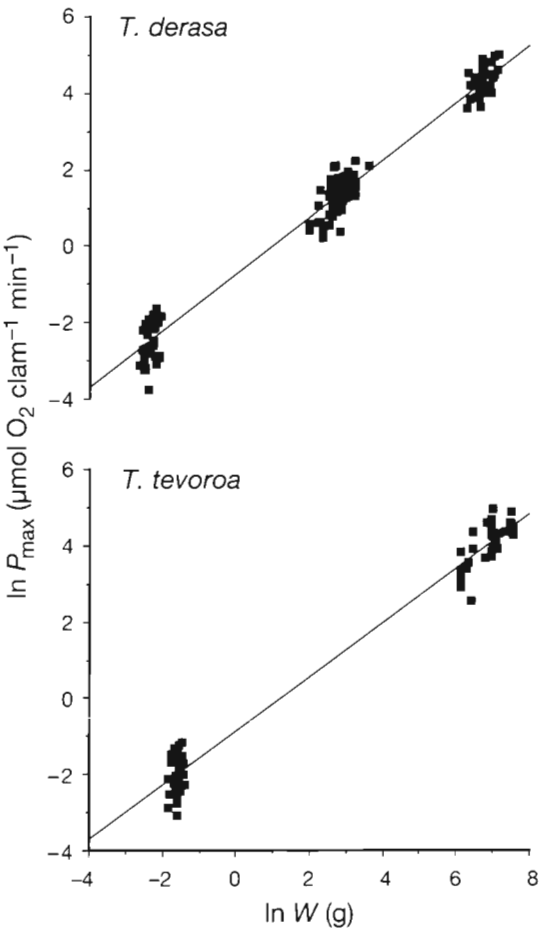

Fig. 1. *Tridacna derasa*, *T. tevoroa*. Relationship between maximum rate of net photosynthesis (P_{max}) and wet tissue wt (*W*) for giant clams. Each data point is the rate for a single clam. Regression equations in text

51.8 µmol O_2 d^{-1} for small clams and 28.8 mmol O_2 d^{-1} for large clams. The ratio P_g:R_{24h} for both clam species on the reef flat in winter ranged from 1.4 in small clams to 1.5 in large clams, but these ratios declined to 0.5 and 0.8, respectively, at a simulated depth of 28 m (Table 3). Reduction in P_g:R_{24h} with depth was much less marked for *T. tevoroa* than for *T. derasa*.

The relationship of daily net oxygen production ($P_n = P_g - R_{24h}$) with transmitted irradiance, expressed as a proportion of surface irradiance, is illustrated for large clams (*W* = 850 g or 400 mm SL) in Fig. 3. This shows that in shallow reef flat conditions, P_n of the 2 species are equivalent, but that net productivity of *Tridacna tevoroa* declines less rapidly than that of *T. derasa* as irradiance levels decrease with depth (Fig. 3). Thus in winter, *T. tevoroa* remains a net producer of oxygen ($P_g > R_{24h}$) at irradiances exceeding 16% of surface levels, equivalent to 21 m depth on cloudless days. By comparison, *T. derasa* requires at least 27% of surface irradiance to maintain net productivity. This irradiance

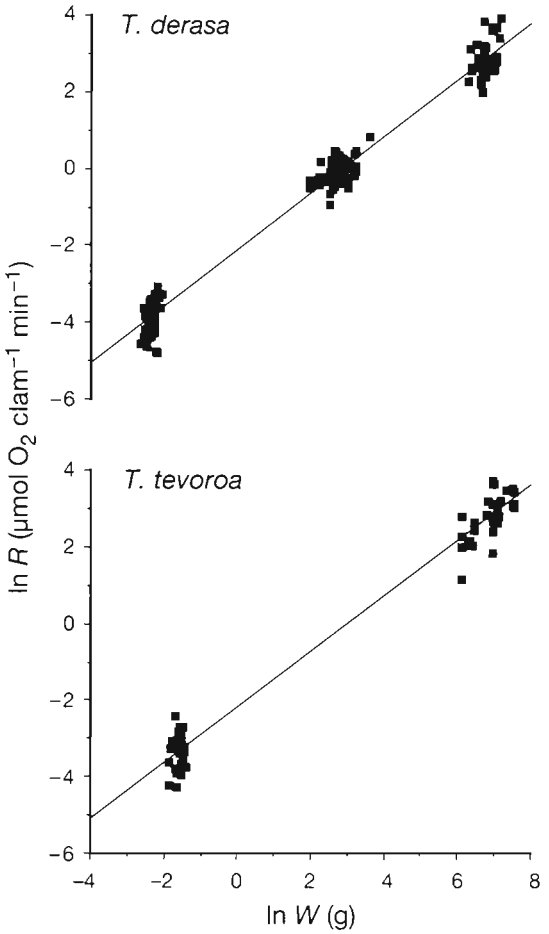

Fig. 2. *Tridacna derasa*, *T. tevoroa*. Relationships between respiration rate (R) and wet tissue wt (W) for giant clams. Each data point is the rate for a single clam. Regression equations in text

level is only achieved at less than 12 m depth. The equivalent compensation depths for large clams on cloudless summer days are 26 m or 12% of surface light for *T. tevoroa*, and 16 m or 21% of surface light for *T. derasa* (Fig. 3). Although not shown, the pattern is similar for small specimens (W = 0.2 g), except that the compensation depths are consistently ca 2 m shallower than those of large clams.

Contribution of photosynthates to host respiratory requirements

Measurement of a positive net 24 h production of oxygen for clams at a particular depth does not mean that they can survive, let alone grow, at that depth. For this to occur we need at least to account for the utilisation of photosynthate by the symbiont and the efficiency of translocation to the host (T). This is accounted for by calculating the percentage contribution of algal (zooxanthellae) carbon to the host's daily requirements for routine respiration (called by convention CZAR) using the formula:

$$\text{CZAR} = \frac{[(P_{n,\,day} \times PQ^{-1} \times 0.375) + (R_{day} \times RQ \times 0.375)(0.95)] \times (\%T) \times 100}{R_{24\,h} \times RQ \times 0.375 \times 0.95}$$

as derived from Trench et al. (1981), where $P_{n,\,day}$ = measured production during daylight; R_{day} = respiration during daylight. It was assumed that 1 mg O_2 = 0.375 mg C, RQ = 0.8, PQ = 1.0, host R = 95% of the measured entire clam R (see Klumpp et al. 1992), and $\%T$ = 95% of photosynthate produced by algae is translocated to the host (see Muscatine 1990, Fitt 1993). From $R_{24\,h}$ data, the daily routine respiratory requirements of the host tissues of *Tridacna tevoroa* and *T. derasa* in winter were estimated to be 472 µg C for small clams and 262 mg C for large clams (Table 3). Converting P_g to the gross amount of carbon translocated daily to host tissues shows that in the shallow reef flat habitat 840 µg C is available to small clams, compared with 491 mg C in large clams (Table 3). This is equivalent to 1.78 and 1.87 times the host's respiratory requirement, respectively. Clearly these results represent the maximum potential phototrophic contribution to nutrition, since P_g declines with depth, shading or cloudiness, while $R_{24\,h}$ remains constant (Table 3). For example at 28 m depth (11% surface irradiance; Table 3), *T. tevoroa* could satisfy 91 to 96% of its maintenance requirements from symbiont photosynthesis, depending on size, but *T. derasa* would receive only 59 to 62% of respiratory needs from this source.

Table 2. *Tridacna* spp. Relationships between I_k and clam species, clam wet tissue wt (W) and irradiance. Mean I_k values are given for the 2 species of clam acclimated to 4 light regimes; significant differences between means are denoted by different letters after I_k values (ANOVA, Ryan-Einot-Gabriel-Welsh test, $p < 0.05$). Results of regressions of I_k on W are presented as the slopes of lines and their r^2 values

% Surface irradiance	I_k	n	Slope	r^2
Tridacna derasa				
83	262 a	43	−0.09	0.03
46	254 a	33	−0.19	0.16
22	244 a	29	−0.04	0.07
11	238 a	40	−0.09	0.03
Tridacna tevoroa				
83	269 a	16	−0.03	0.03
46	209 b	13	−0.05	0.23
22	176 c	23	−0.08	0.32
11	160 c	19	0.00	0.00

Table 3. *Tridacna* spp. Daily gross oxygen production (P_g in µmol O_2 for small clams and mmol O_2 for large clams), ratio of daily oxygen production to respiration (P/R), daily translocated carbon production (TP in µg C for small clams and mg C for large clams), and TP as a percentage of daily routine respiratory requirements (CZAR). Results are presented for small (0.2 g) and large (850 g) specimens of clams at 4 simulated depths in winter. Daily respiration (R) was 51.8 µmol O_2 in small clams and 28.8 mmol O_2 in large clams for all species and depths. Conversion of oxygen to carbon is explained in 'Results'

% Surface irradiance	Depth (m)	Large clams P_g	P/R	TP	CZAR	Small clams P_g	P/R	TP	CZAR
Tridacna derasa									
83	1	43.1	1.50	491	187	73.7	1.42	840	178
46	5	37.1	1.29	423	161	63.6	1.23	725	154
22	15	25.3	0.88	288	110	43.2	0.83	492	104
11	28	14.4	0.50	164	63	24.6	0.47	280	59
Tridacna tevoroa									
83	1	43.1	1.50	491	187	73.7	1.42	840	178
46	5	39.9	1.39	455	174	68.3	1.32	778	168
22	15	32.3	1.12	368	140	55.3	1.07	630	133
11	28	22.0	0.76	251	96	37.6	0.73	428	91

Comparative growth rates in juveniles

Growth rates measured from shell lengths (SL) of juvenile *Tridacna derasa* and *T. tevoroa* were essentially linear over the 8 mo measurement period (Fig. 4; regression slopes = 4.7 mm mo^{-1}, $r^2 = 0.98$, n = 40 for *T. derasa*; 4.2 mm mo^{-1}, $r^2 = 0.98$, n = 38 for *T. tevoroa*). These growth rates apply approximately to clams in our small to medium size categories, but not to larger specimens in which growth normally slows with the onset of sexual maturity (see Lucas in press). There was no significant difference between the growth rates of juvenile *T. derasa* and *T. tevoroa* (Fig. 4), thus an average shell growth rate of 4.5 mm mo^{-1} (0.15 mm d^{-1}) was used in further calculations. This growth rate is close to reported values of ca 5 mm mo^{-1} for *T. derasa* in Fijian waters (Adams et al. 1988).

Daily weight increments were calculated from measured growth in SL and our regressions of wet tissue wt (W, g) on SL:

Tridacna derasa

$\ln W = 2.852 \ln SL - 10.361$
($r^2 = 0.99$, n = 24);

T. tevoroa

$\ln W = 2.811 \ln SL - 10.047$
($r^2 = 0.99$, n = 32).

These calculations showed that small clams with W = 0.2 g (equivalent to 21.51 mm SL for *T. derasa* and 20.12 mm SL for *T. tevoroa*) are growing at 4.0 mg d^{-1} and 4.3 mg d^{-1}, respectively. These growth rates are equivalent to 32–34 µg N d^{-1} and 124–133 µg C d^{-1} (dry wt = 10% of wet wt, from this study; clam dry tissues are 8% N and 31% C, from Klumpp et al. 1992).

Clearance rate and ingestion of particulate matter

The rates at which *Tridacna derasa* and *T. tevoroa* cleared ambient water of suspended particles depended very strongly on body size (Fig. 5, Table 4). Slopes of the regressions of CR on body size did not vary between species or with light level (Table 1; ANCOVA: Sp×W, Sh×W interactions), but light level and species appeared to have a significant effect on weight-specific CR (i.e. intercepts; see Table 1). Removal of the 11% surface irradiance *T. tevoroa* data set from the analysis showed that the effect was due to this treatment alone. Thus CR of *T. derasa* was not significantly affected by the 3 levels of irradiance, and was identical to that of *T. tevoroa* under all light levels except 11% surface irradiance, where the CR of small *T. tevoroa* was relatively low.

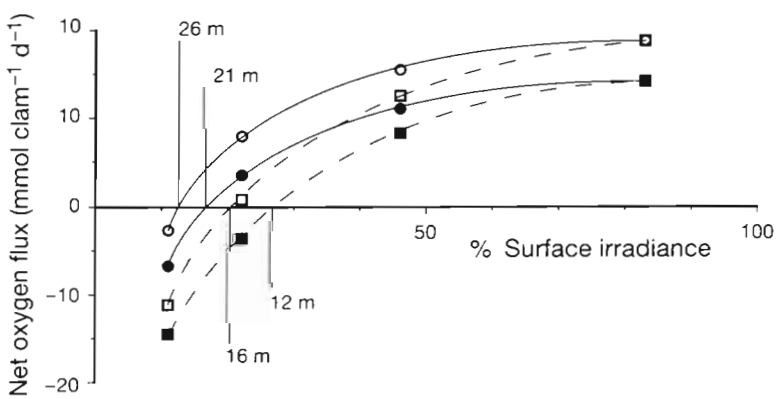

Fig. 3. *Tridacna* spp. Variation in daily net oxygen flux (net production or consumption) of large *T. derasa* (squares) and *T. tevoroa* (circles) with irradiance expressed as a percentage of surface irradiance on cloudless days in winter (solid symbols) and summer (open symbols). The equivalent depths (m) where net production is zero (compensation depths) are indicated

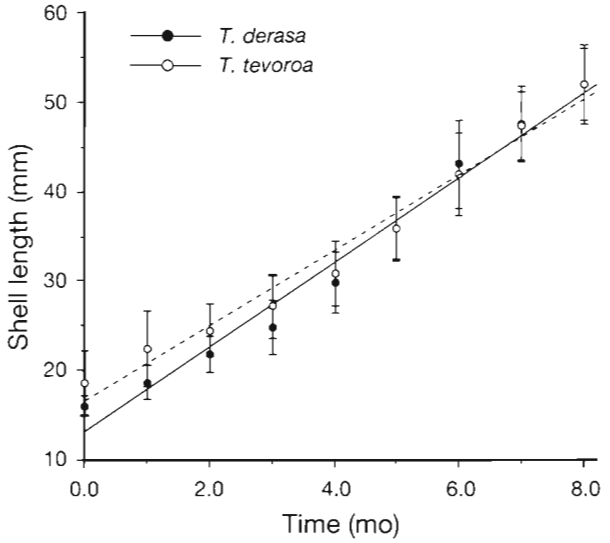

Fig. 4. *Tridacna* spp. Growth in shell length of juvenile giant clams held in the seawater system at Tonga Fisheries, Sopu, from August 1992 to April 1993

Ingestion rates of clams (in µg organic C or N h^{-1}) were calculated as the product of *CR* and concentration of suspended particles (µg organic C or N l^{-1}). Seawater supplied to the *CR* chambers from the reef/seagrass flat had an average suspended particle concentration of 6200 particles ml^{-1}, while POC and PN averaged 358 µg C l^{-1} and 51 µg N l^{-1}, respectively. Adjacent reef waters, where clam brood stocks were maintained, contained 65 µg C l^{-1} and 11 µg N l^{-1}. This level of POM is within the range reported in other non-oceanic reef waters (see Klumpp et al. 1992). In calculating ingestion rates of *Tridacna derasa* and *T. tevoroa*, we used the average of *CR*-size relationships for clams in shallow water (83% surface irradiance, Table 4: slope 0.69, intercept 0.78) and an average particulate concentration of 65 µg C l^{-1} and 11 µg N l^{-1}. Thus, small (W = 0.2 g) and large (W = 850 g wet tissue wt) clams on the reef around Sopu clearing water at rates of 1.03 l d^{-1} and 330 l d^{-1}, respectively, would ingest 67 µg C d^{-1} and 21.5 mg C d^{-1}. If all ingested material was absorbed, intake of carbon from this filter-feeding would satisfy 14% and 8% of the respiratory requirements of small and large clams respectively. Absorption efficiencies were not determined for *T. derasa* and *T. tevoroa*, but 3 other tridacnid species absorbed 50 to 60% of ingested reef particles (Klumpp et al. 1992, Klumpp & Griffiths unpubl. data). Daily intake of nitrogen from filter-feeding would range from 11 µg N d^{-1} in small clams to 3.63 mg N d^{-1} for large clams. The measured growth rates of small clams were equivalent to 32 to 34 µg N d^{-1} and, hence, a maximum 33% of the nitrogen deposited in tissues of small clams could be derived from ingestion of PON.

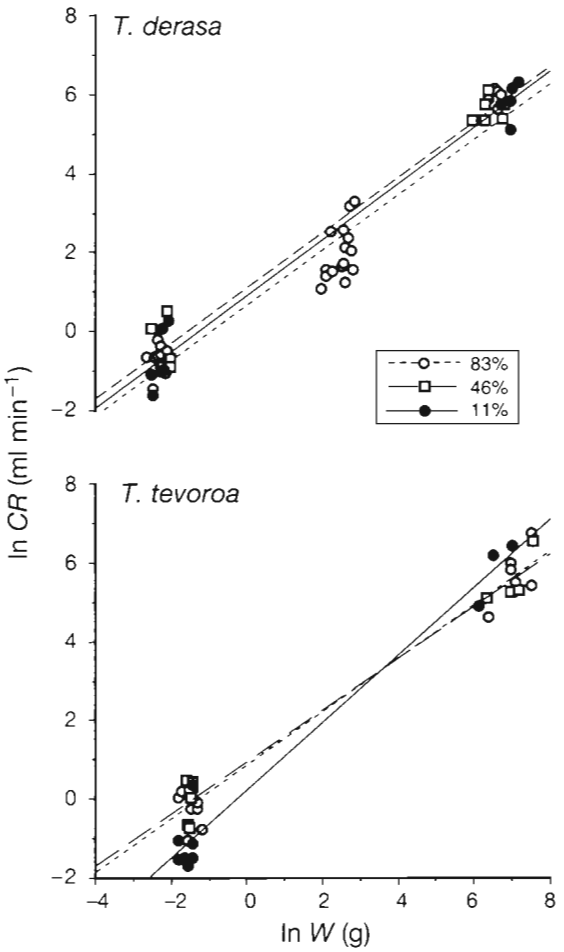

Fig. 5. *Tridacna* spp. Relationship between clearance rate (*CR*) and wet tissue wt (W) for *T. derasa* and *T. tevoroa* acclimated to 3 light regimes, equivalent to 83, 46 and 11% of surface irradiance. Each data point is the rate for a single clam. Regression equations given in Table 4

Table 4. *Tridacna* spp. Relationships between clearance rate (*CR*, ml $clam^{-1}$ min^{-1}) and wet tissue wt (W, g) of clams acclimated to 3 light regimes (83, 46 and 11% of surface irradiance). Data are presented as the slopes and intercepts from linear regressions of ln *CR* against ln W (see Fig. 5)

% Surface irradiance	Slope	Intercept	r^2	n
Tridacna derasa				
83	0.70	0.68	0.92	30
46	0.70	1.12	0.98	12
11	0.71	0.91	0.98	12
Tridacna tevoroa				
83	0.68	0.88	0.97	16
46	0.66	0.97	0.97	10
11	0.86	0.24	0.97	10

DISCUSSION

Comparative nutrition of *Tridacna tevoroa* and *T. derasa*

This study provides the first quantification of the nutrition of the little-known giant clam *Tridacna tevoroa* which was recently discovered inhabiting relatively deep (range 9 to 33 m, mean 26 to 27 m) and clear oceanic waters off Tonga and Fiji (see Lucas et al. 1991, Ledua et al. 1993). We have compared it with the closely related sympatric *T. derasa*, which occurs down to 20 m but is more common in shallower waters, especially in the juvenile stage (Adams et al. 1988). These comparisons show that the 2 clam species function identically in shallow waters (< 2 m) both in terms of filtration rate and the relationship between irradiance and net primary production. However, *T. tevoroa* is able to maintain its photosynthetic capabilities at lower light intensities than *T. derasa* and is hence able to maintain energy balance at approximately 10 m greater depth (see Fig. 3, Table 3). This corresponds well with the known depth distributions of the 2 species (Ledua et al. 1993). Under increasing simulated depths, *T. tevoroa* somehow increases the efficiency of its photosynthetic-irradiance response. With decreasing irradiance, the *P-I* parameters I_k and I_c decreased, $\propto$ increased, while R and P_{max} remained constant. At sub-saturating light intensities, this species thus photosynthesises at a significantly greater rate than *T. derasa*, which showed no evidence of photoadaptation under reduced light intensities.

Several unique morphological adaptations, likely to facilitate the utilisation of reduced light intensities in *Tridacna tevoroa*, were noted by Lucas et al. (1991). These are the rugose mantle, unusually wide gape of the valves, paucity of iridophores and shallow distribution of zooxanthellae in the mantle tissue. The first 2 features should increase available surface for zooxanthellae, while the last 2 features should maximise transmittance of light to these cells. Lucas et al. (1991) further proposed that photoadaptation by zooxanthellae may be important in *T. tevoroa* based on experimental evidence for such photoadaptation in *T. gigas* (Mingoa 1988). Work primarily on corals has shown that photoadaptation by zooxanthellae may be effected through alterations to the quantity and size of the light-capturing apparatus of chloroplasts or photosynthetic units, and thus the chlorophyll *a* concentration, as well as the rates of associated chemical reactions (see Dustan 1982, Chang et al. 1983). Of these, increase in photosynthetic unit size as a photoadaptive response has been identified in *T. maxima* (Chang et al. 1983). This is consistent with the recent observation of a doubling in chlorophyll *a* concentration per zooxanthellae in juvenile *T. gigas* kept under 90% shading (Mingoa 1988, 1990).

Nutritional roles of phototrophy and filter-feeding in clams

We have sufficient data to compare the contributions made by phototrophy and filter-feeding to the nutritional requirements (growth plus respiration) of the giant clam species tested. Small *Tridacna derasa* and *T. tevoroa* from Tonga respire carbon at a rate of 470 µg C d^{-1}, and phototrophy provides considerably more than this under cloudless, reef flat conditions (840 µg C d^{-1}). Furthermore, phototrophy matches respiratory needs at the respective depth limits of each species (20 m and 30 m; Table 3). The amount of carbon derived from phototrophy would, however, decline under cloudy conditions. Trench et al. (1981) measured a 50% reduction in irradiance under cloudy conditions on a coral reef, and this reduced the contribution of phototrophy to respiratory carbon demand by 20% in 2 specimens of *T. maxima*. Assuming that clouds cause a similar shading in Tongan reef waters, it is apparent from Table 3 (46% surface irradiance = 5 m depth) that *T. derasa* and *T. tevoroa* under cloudy conditions on the reef flat could still satisfy 155 to 175% of respiratory needs via phototrophy.

Other species of giant clam also appear to derive a high proportion of their respiratory carbon needs from zooxanthellae, even under cloudy conditions. Equivalent CZAR figures for *Tridacna gigas* vary from 73 to 126% (Fisher et al. 1985, Mingoa 1988, Klumpp et al. 1992) and for *T. maxima* from 63 to 84% (Trench et al. 1981). It must be emphasised that all of these estimates were based on the assumption that only 30 to 40% of carbon production was translocated to the host. However, recent reviews of symbiotic associations in reef corals and clams conclude that these are serious underestimates and that translocation efficiency is 78 to 98% for corals (Muscatine 1990) and 90 to 95% for clams (Fitt 1993). Given this, recalculated CZAR values for all giant clam species examined to date would be well in excess of 100%. This aside, comparison of daily oxygen flux in *T. gigas* (Klumpp et al. 1992) with those of *T. tevoroa* and *T. derasa*, using the same techniques and under similar environmental conditions (cloudless, winter, reef flat), reveals interesting differences in their metabolism. While gross oxygen production standardised to size is the same for all 3 species, rates of oxygen consumption are significantly higher in *T. derasa* and *T. tevoroa*. For example, 66 mm SL *T. gigas* produced 28.8 mg O_2 daily and consumed 8.2 mg O_2, i.e. a *P:R* ratio of 3.5 (Table III in Klumpp et al. 1992), compared with the production of 30 mg O_2 and consumption of 19.9 mg O_2 (*P:R* of 1.5) in the same sized *T. tevoroa* and *T. derasa* (Table 3).

The rapid growth of tridacnid clams compared with most other bivalve molluscs has been shown to be

based on their ability to access substantial food resources in the form of both POM and photosynthate and to allocate a high proportion of this energy to growth (Klumpp et al. 1992). These authors showed that *T. gigas*, the largest and fastest-growing giant clam species, deposited as much carbon in tissues as it respired. In contrast *T. tevoroa* and *T. derasa* expended more energy in respiration and utilised only 22% of carbon for growth (G: 130 µg C d^{-1}, R: 470 µg C d^{-1} in small clams). This is similar to typical non-symbiotic bivalves in which $G:R$ ratios average 1:3 or 25% (Bayne & Newell 1983).

Our experimental results indicate that under optimum light conditions (sunny, shallow waters), phototrophy more than satisfies (140%) the daily carbon requirements for both maintenance and growth (i.e. 600 µg C) in rapidly growing small *Tridacna tevoroa* and *T. derasa*. However, this needs to be assessed in the context of the natural distributions of these clams. In Fijian waters, juvenile *T. derasa* (up to 310 mm) are usually found loosely attached to coral on the tops and sides of shallow coral outcrops (Adams et al. 1988). They thus experience optimal phototrophic conditions and should be able to maintain their rapid growth solely on the carbon derived from symbiosis (Table 3). Large *T. derasa* are found down to 20 m in clear oceanic conditions; but it is thought that they have fallen there as adults following detachment of their byssus. These adults grow more slowly (Adams et al. 1988, Lucas in press), and the results of Table 3 suggest that they probably receive sufficient energy from phototrophy. Thus, the carbon budget for this species can be balanced from phototrophy alone.

Juvenile *Tridacna tevoroa* have never been found in nature, which is not surprising given the rarity of this clam. However, from what is known of the distribution of adults in Fiji and Tonga, it appears that juveniles settle on slopes of off-shore reefs in deep (down to 33 m) oceanic waters (Lewis & Ledua 1988, Ledua et al. 1993). Comparison of the balance between growth and maintenance requirements (600 µg C d^{-1} in small clams) and the potential contribution of photosynthate indicates that this species cannot rely entirely on phototrophy at the deeper limits of its distribution. For example, at 28 m depth, *T. tevoroa* acquires a maximum of 428 µg C d^{-1} (Table 3) or 70% of its total carbon needs from phototrophy, and thus must utilise alternative, heterotrophic sources of energy.

Apart from phototrophy, clams can obtain nutrition from filter-feeding (Morton 1978, Reid et al. 1984a, Fankboner & Reid 1990), possible digestion of zooxanthellae in the digestive tract (not in the kidney, e.g. as discussed by Reid et al. 1984b), and uptake of dissolved organic molecules (Fankboner 1971, Goreau et al. 1973, see review by Fitt 1993). While giant clams probably do take up dissolved organic matter (DOM) (Goreau et al. 1973), the nutritional value of this and the digestion of zooxanthellae have never been quantified. Filter-feeding, however, is now known to be a significant source of nutrition in *Tridacna gigas*, especially in juveniles (Klumpp et al. 1992). These authors calculated that filter-feeding in GBR waters can supply 65% of requirements for growth and respiration in a 42 mm *T. gigas*, decreasing to 34% at 167 mm. In contrast, filter-feeding provides relatively little carbon to both *T. tevoroa* and *T. derasa*, contributing at most 8% and 14% of respiratory carbon demands of large and small clams, respectively.

The apparent differences between the contributions of filter-feeding in *Tridacna gigas* relative to *T. tevoroa* and *T. derasa* are partly due to the higher levels of POM available in GBR waters compared to Sopu reef (97 µg C l^{-1} cf. 65 µg C l^{-1}), and the interspecific differences in respiration rates described above. However, the main difference is the much slower clearance rates of *T. tevoroa* and *T. derasa* (ca 1 l d^{-1} for small clams) compared with equivalent-sized *T. gigas* (ca 7 l d^{-1}) at similar temperature. This greater reliance on filter-feeding in *T gigas* may be reflected in various distinctive features of its gills, including it being the only tridacnid species with both dorsal and ventral demibranch food grooves (Norton & Jones 1992).

In conclusion, a range of nutritional strategies is apparent from these studies. *Tridacna derasa* is able to function as a complete autotroph in its natural habitat (down to 20 m), and *T. tevoroa* achieves this in the shallower parts of its distribution (10 to 20 m). *T. gigas* shows a different strategy, comfortably satisfying all apparent carbon requirements from the combined sources of filter-feeding and phototrophy (Klumpp et al. 1992). Despite the increased efficiency of its photosynthetic-irradiance response, at the deeper limits to its distribution (ca 30 m), *T. tevoroa* must access other sources of nutrition, such as DOM, in order to supplement particulate matter and photosynthate which can provide a maximum 83% of nutritional requirements.

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