Prospects for the Commercial Cultivation of Giant Clams (Bivalvia: Tridacnidae)

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ABSTRACT

The status of tridacnid clam resources in the Indo-Pacific region and studies of their basic biology and ecology, including life histories, growth rates and phototrophic capabilities, spawning induction and larval and juvenile rearing are reviewed. They are the only phototrophic potential farm animals known to mankind.

It is concluded that large-scale extensive mariculture operations are now technically feasible and could make a major contribution to the economies of Indo-Pacific countries, particularly the island states. The possibility of introducing tridacnid clams to parts of the Indo-Pacific outside their present ranges and to the Caribbean Sea should be seriously considered. *Tridacna gigas* is currently being re-introduced to Guam where the species has undergone recent extinction.

Priority topics for future research are identified.

Clams of the family Tridacnidae (Cardiacea: Bivalvia) are reef-dwellers of the tropical Indo-Pacific and include the largest bivalve molluscs ever to have existed. In addition to their large size, their principal feature is the brightly-colored siphonal tissue (the mantle) which harbours enormous numbers of symbiotic dinoflagellates, termed zooxanthellae. The zooxanthellae contribute substantially to the nutrition of the clams and possibly also to the process of calcification; the successful evolution of the symbiosis probably is responsible for the large sizes attained. The largest recorded specimen of the largest species, *Tridacna gigas*, measures 137 cm in shell length (Rosewater, 1965) and had a live weight of at least 300 kg (our estimate). They are the only phototrophic potential farm animals known to mankind.

Yonge (1980) has recently comprehensively reviewed the basic biological features of the tridacnids, their evolution, and the anatomical changes which occurred in the adoption of the symbiotic relationship. All species exhibit the same basic features in their life histories. Namely, fertilized eggs develop rapidly through typical planktonic trochophore and veliger stages before settlement on suitable reef substata (La Barbera, 1975; Jameson, 1976). The juvenile clams are extremely cryptic, have a well-developed foot and are motile. Later stages have a byssal attachment but adults of the larger species lose their attachment. They are protandrous hermaphrodites but soon transform into simultaneous hermaphrodites (Wada, 1954).

Fertilization of eggs is external and spawning is induced in nature by the presence in the water of one or more chemicals which are associated with the eggs. Under normal circumstances, the spawning cycle involves the initial release of sperm and subsequent release of eggs. This mechanism results in a chain spawning reaction over a reef but renders the species liable to the non-fertilization of eggs in depleted populations. Fecundity is prodigious.

Species of Tridacnid clams are found throughout most of the tropical Indo-West Pacific region, from the Red Sea to the Tuamotu Archipelago and Pitcairn Island

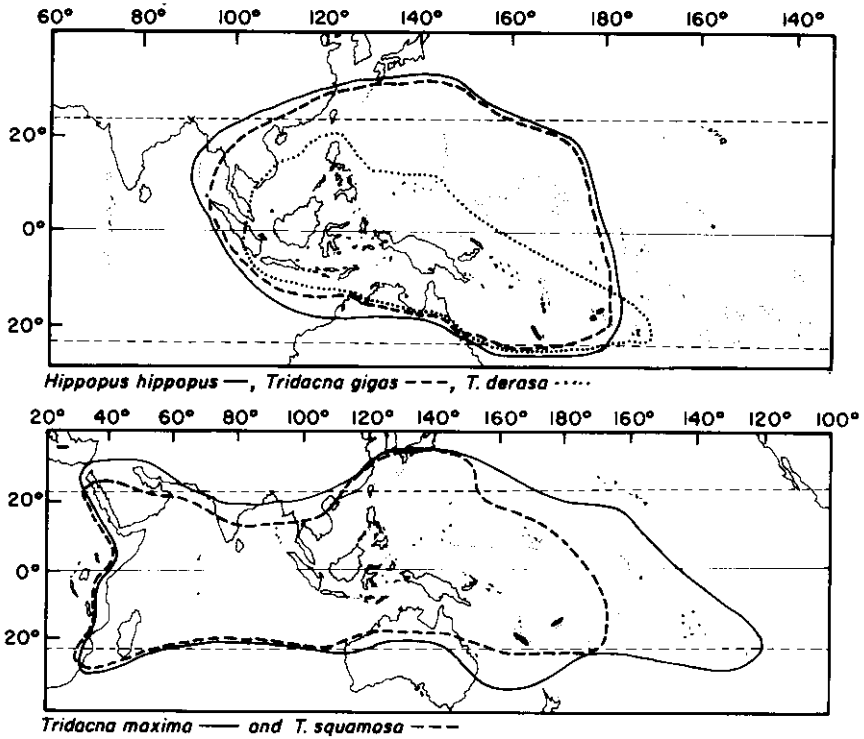

Figure 1. Present known limits of distribution of tridacnid clams (modified from Rosewater, 1965).

(Rosewater, 1965). *Tridacna maxima* has the widest distribution and distributions of the other species are more restricted (Fig. 1). All species appear to have basically similar ecological requirements, including clear, high-salinity water and a secure foundation for attachment, at least during the early life history.

Hippopus hippopus normally lives on a sandy substratum. *T. gigas* and *T. derasa* are unattached and usually embedded in the reef or in coral rubble by virtue of their own weights. *T. maxima* and *T. squamosa* are firmly attached to the reef by byssal threads. *T. crocea* burrows deep into the reef. All species appear to thrive best in shallow (1-2 m) back-reef areas but all appear to be capable of surviving in a wide range of habitats. In clear water, they are found to a maximum of 20 m (McKoy, 1980) but most are concentrated in much shallower depths. *T. maxima* and *T. squamosa* by virtue of their strong byssal attachments can colonize shallow fore-reef zones, as can *T. crocea*. It appears that *T. derasa* is restricted to oceanic environments and it is not found on fringing reefs adjacent to large land masses. Possibly, the larvae are unable to survive relatively low salinities. *T. squamosa* is uncommon in atoll environments.

Tridacnid clams have formed a part of the diets of the indigenous people of the Pacific for many centuries and the huge numbers of shells in middens, for example in Papua New Guinea, suggest that they might have been major items in the diets of some people. We are not aware of any part of the Pacific where they are not esteemed as food. Normally, all parts of the clam are consumed with the exception of the kidney which is of unpleasant taste.

The adductor muscle in its dried form is much sought-after in Southeast Asia and in the last decade, many reef areas have been systematically scoured for clams (par-

ticularly the large species, *T. gigas* and *T. derasa*) by distant-water vessels, mostly from Taiwan (Yamaguchi, 1977). The demise of the once extensive stocks at Helen Reef has been documented by Hester and Jones (1974), Bryan and McConnell (1976) and Hirschberger (1980) and the battle to keep poachers off the Great Barrier Reef recounted by Pearson (1977). Numerous poachers have been apprehended in Papua New Guinea (Maclean, 1978).

Increasing human populations in many island areas have reduced the most accessible stocks of tridacnids very severely, to the extent that they are now reserved for special occasions in some areas. In Tonga and American Samoa, *H. hippopus* appears to be recently extinct or extremely rare (McKoy 1980; Wass, pers. comm.), possibly as a result of over-exploitation, although the possibility of a recent ecological change cannot be discounted as both areas are on the fringe of the range of the species. Also, according to resident scientific and fisheries personnel in Micronesia, *T. gigas* has undergone recent extinctions in Guam and in the Eastern Caroline Islands of Truk, Ponape and Kosrae (Heslinga et al. MS). Again it is not possible to single out human predation as the causative agent, but the persistence of remnant *T. gigas* populations in some Marshall Islands, for example Eniwetak and Kwajalein, argues against the probability of climate-induced extinctions in the Carolines. An attempt to re-introduce *T. gigas* to Guam began this year with a successful shipment of 500 juvenile clams maricultured in Palau.

The International Union for the Conservation of Nature has recently listed the larger species of tridacnid clams as threatened species (S. Wells, pers. comm.)

Table 1. Summary of successful methods of induction of spawning of eggs in tridacnid clams. Methods which resulted only in the spawning of sperm are excluded.

	Tridacna gigas	*T. derasa*	*T. squamosa*	*T. maxima*	*T. crocea*	*Hippopus hippopus*
Macerated or blended gonad			1, 3, 4, 5 6, 8	1, 2, 6, 8	2	1, 2
Biopsy			6			6
Freeze-dried gonad				6		
Temperature shock				9		
Hydrogen peroxide		5				
Spontaneous spawning	5, 6, 10		5, 7, 8, 10			10

Key to investigators: (1) Wada, 1954; (2) Jameson, 1976; (3) Rosewater, 1965; (4) Hardy and Hardy, 1969; (5) Beckvar, 1981; (6) Gwyther and Munro, 1981; (7) Fitt and Trench, 1981; (8) La Barbera, 1975; (9) Michel, A., pers. comm.; (10) Heslinga et al (MS).

CULTIVATION OF TRIDACNID CLAMS

Spawning

Wada (1954) used macerated clam gonads to induce spawning in tridacnids. A variety of methods of inducing spawning have been used by subsequent investigators (Gwyther and Munro, 1981; Munro et al., 1983). Table 1 shows which methods have been successfully used in inducing egg production in at least one species. A high proportion of attempts at spawning induction have failed to produce eggs and only sperm has been produced (Gwyther and Munro, 1981; Fitt and Trench, 1981). *T. gigas* has not yet been induced to spawn eggs but fairly often spawns spontaneously.

The spawning process in clams has been described by Wada (1954) and this description elaborated on by subsequent investigators (La Barbera, 1975; Jameson, 1976; Gwyther and Munro, 1981; and Beckvar, 1981). Basically, the spawning process starts with ejaculation of large quantities of sperm at intervals of between 30 sec. and 3 min. for up to several hours. After a quiescent period of several minutes to 0.5 h, the same individual might then spawn eggs, and this can also continue intermittently for several hours.

The eggs have a substance associated with them which can be detected in minute quantities by other clams of the same species and which initiates a spawning reaction by the receiving clam. This ensures that eggs drifting down-current will be fertilized. Investigations of the chemical properties and steps towards identifying this substance have been made by Munro et al. (1983).

Tridacnids are protandrous hermaphrodites, but the simultaneously hermaphroditic stage is soon attained. Also, it appears that most clams are capable of producing sperm in response to the presence of eggs for most of the time whereas the ability to ovulate might be related to lunar or seasonal cycles. These cycles are not yet well understood.

Additionally, the efficacy of a particular gonad in inducing egg production appears to relate to the presence of a specific chemical associated with mature eggs. Gwyther and Munro (1981) found that freeze-dried powdered gonad remained effective for inducing egg production for over a year. It now appears that it is very important that a gonad be tested for efficacy in inducing egg production before it is freeze-dried as not all ripe, egg-laden gonads are effective in inducing spawning.

Temperature shocks have also been used for *T. maxima* (A. Michel, pers. comm.) and progressive elevation of temperatures was used to induce mass spawning of *T. squamosa* in Palau (unpublished data). Beckvar (1981) and Heslinga et al. (MS) found that spontaneous spawning of *T. gigas* occurred on a fairly regular basis in Palau but this occurred only rarely in Papua New Guinea (Gwyther and Munro, 1981).

Overall, the best method of inducing spawning reliably appears to be by obtaining a "good" gonad and freeze-drying it. The substance involved in spawning induction appears to be species specific (Wada, 1954; Jameson, 1976).

Jameson (1976) described fecundity (F) of *T. maxima* as a function of length and derived the relationship

$$F = 0.00743\ L^{4.03}$$ where L is

the shell length in mm. He also found that a *H. hippopus* of 249 mm shell length spawned approximately 25×10^6 eggs in a single day.

Larval Culture

La Barbera (1974; 1975) described the larval stages of *T. squamosa* and *T. maxima* and raised larvae to settlement. Jameson (1976) raised *T. crocea*, *T. maxima* and *H. hippopus*. Gwyther and Munro (1981), Beckvar (1981) and Fitt and Trench (1981)

elaborated upon larval culture methods and described the growth of larvae, feeding and acquisition of zooxanthellae. Jameson (1976) succeeded in taking small numbers of *T. maxima* and *H. hippopus* through metamorphosis. Beckvar (1981) achieved the same for *T. gigas, T. derasa* and *T. squamosa* and raised them to modest sizes in the laboratory.

More recently, staff at the Micronesian Mariculture Development Center have succeeded in raising *T. gigas, T. squamosa* and *H. hippopus* in mass culture. The technique has consisted basically of permitting clams to spawn spontaneously in outdoor tanks, draining the tanks after the sperm production cycle has been completed, refilling with fresh unfiltered sea water and permitting egg production to continue undisturbed. Sufficient sperm will be retained in the mantle cavities and in the tank to ensure fertilization of the eggs and avoid the problem of polyspermy and subsequent failures in embryogenesis (Jameson, 1976). Thereafter, the larvae are siphoned into adjacent tanks and left undisturbed. Within 7 days they have settled on the walls of the tank and after 90 days can be scraped off and placed in raceways. This method has yielded 5,000-10,000 5-mm seed clams per 8 x 2 x 1 m tank per 90-day rearing cycle.

Gwyther and Munro (1981) and Fitt and Trench (1981) have discussed the nutrition of and acquisition of zooxanthellae by larval clams. Gwyther and Munro (1981) concluded that the larvae could survive in filtered sea water but were then unable to metamorphose whereas 15% of fed larvae metamorphosed successfully. They also observed what appeared to be zooxanthellae in the gut and within the velum of a 4-day old veliger. Fitt and Trench (1981) found that veligers ingested zooxanthellae (particularly motile stages) into their stomachs and that 2-9 days after metamorphosis, the zooxanthellae moved by an unknown mechanism into the siphonal tissues. The implication of these observations is that ingested zooxanthellae are not digested, remain viable, photosynthesize, contribute nutrients to their host and after metamorphosis migrate to the siphonal tissues of the juvenile clam. It is not yet established whether the veligers actually digest any foods or how zooxanthellae are able to resist digestion.

Beckvar (1981) and Jameson (1976) both found extremely slow growth rates in juveniles but it appears that these were kept indoors and in restrospect, it is clear that the juveniles will survive and grow best in full sunlight. Munro and Gwyther (1981) and Gwyther and Munro (MS) have shown that it is likely that juvenile clams would have some difficulty in attaining autotrophy if not exposed to the greatest possible amount of sunlight, whereas adult clams are capable of autotrophy even in low light intensities.

Juvenile Rearing

Beyond the hatchery phase, at the end of which the stock might have attained a length of about 5 mm it is necessary to identify optimal strategies for growing the clams until they reach a size at which they can be placed on relatively unprotected natural reefs and stand a reasonable chance of survival to a larger size. This is an area which is largely unknown and will undoubtedly form the main focus of future research programs.

At the MMDC in Palau, where mass culture has been achieved, the best growth of juveniles has to date been in troughs with good exposure to sunlight and a moderately strong water flow of 30 ℓ $min.^{-1}$ Present techniques involve harvesting the infant clams from settlement tanks at a size of about 5 mm and stocking them at a density of up to 1,000 m^{-2} in plastic "Nestier" shellfish trays filled with 1 cm-diameter basalt chips. The basalt chips, which are used for road construction in Palau, form an excellent substratum for byssal attachment of the juvenile clams and make handling

Table 2. Summary of available data on the growth of juvenile tridacnid clams. Figures in brackets have not been used in estimating means as they are based on large samples. Other data are individual measurements or small samples.

	Initial size (mm)	Increment (mm)	Time (days)	Rate of increase (mm/d)	Reef or laboratory	Source
T. gigas	0	0.43	25	(0.017)	L	Heslinga et al. (MS)
	0	5.2	70	(0.074)	L	Heslinga et al. (MS)
	0	22.7	195	(0.116)	L	Heslinga et al. (MS)
	0	26	300	0.087	L	Beckvar 1981
	0	83	520	0.160	L	Beckvar 1981
	0	187	1280	0.146	L	Heslinga et al. (MS)
			Mean	0.131	L	
	113	45	125	0.360	R	Munro and Gwyther (MS)
	118	34	92	0.370	R	Munro and Gwyther (MS)
	118	44	114	0.386	R	Munro and Gwyther (MS)
			Mean	0.372	R	
T. derasa	130	24	180	(0.133)	R	Heslinga et al. (MS)
	134	22	180	(0.122)	L	Heslinga et al. (MS)
	0	156	1095	0.142	L	Heslinga et al. (MS)
	0	17	150	0.113	L	Beckvar 1981
			Mean	0.128	L	
H. hippopus	0	39	270	(0.144)	L	Heslinga et al. (MS)
	0	56.7	330	(0.172)	L	Heslinga et al. (MS)
	0	19.3	150	(0.129)	L	Heslinga et al. (MS)
	72	21	100	0.210	R	Munro and Gwyther (MS)
	79	13	177	0.073	R	Munro and Gwyther (MS)
	81	24	182	0.132	R	Munro and Gwyther (MS)
			Mean	0.138		excluding Heslinga et al. data
T. squamosa	0	19.5	270	(0.072)	L	Heslinga et al. (MS)
	0	29.6	330	(0.090)	L	Heslinga et al. (MS)
	0	12.6	150	(0.084)	L	Heslinga et al. (MS)
	86	47	782	0.060	R	Munro and Gwyther (MS)
	81	132	993	0.133	R	Munro and Gwyther (MS)
	75	37	217	0.171	R	Munro and Gwyther (MS)
	29	31	142	0.148	R	Munro and Gwyther (MS)
	50	26	200	0.130	R	Munro and Gwyther (MS)
	67	3.1	60	(0.052)	L	Beckvar 1981
	67	8.5	60	0.142	R	Beckvar 1981
			Mean	0.130	R	
T. maxima	86	2	125	0.016	R	Munro and Gwyther (MS)
	64	77	1395	0.055	R	Munro and Gwyther (MS)
	64	112	1487	0.075	R	Munro and Gwyther (MS)
	52	22	240	0.092	R	Munro and Gwyther (MS)
	74	8	125	0.064	R	Munro and Gwyther (MS)
	82	5	108	0.046	R	Munro and Gwyther (MS)
	46	37	640	0.058	R	McMichael 1975
	73	30.5	640	0.048	R	McMichael 1975
	93.5	27	640	0.042	R	McMichael 1975
	37.5	38	426	0.089	R	McMichael 1975
	68	24	426	0.056	R	McMichael 1975
	93	17.5	426	0.041	R	McMichael 1975
	42-99	var	134-267	(0.058)	R	McKoy 1980
			Mean	0.057		(excluding McKoy data)

of the juveniles very easy. The clams are thinned every few months to prevent overcrowding.

Little is presently known about growth rates of juvenile tridacnids. Early estimates of growth rates by Jameson (1976) and Beckvar (1981) pertained to laboratory-reared individuals and their requirements for strong light intensities were not yet recognized. More recent experimentation at Palau (Heslinga et al., MS) have shown that mean sizes of 1.53 cm, 1.26 cm and 1.93 cm shell length can be attained by *T. gigas*, *T. squamosa* and *H. hippopus*, respectively, in 5 months post-fertilization.

Factual data on the maximum rates of growth achievable by juvenile tridacnid

clams remains the critical determinant of whether maricultural operations will be feasible. However, there are extremely few data available on the early growth of tridacnids under natural or laboratory conditions. These data are summarized in Table 2 and appear to show some consistency. These data suggest that for all species, except *T. maxima*, a size of about 50 mm might normally be attained in the first year under average conditions. It appears that *T. gigas* might reach 100 mm within 18 months. *T. maxima* appears to be much slower growing in the early stages than all other species and there is a remarkable constancy in the average rates observed in PNG, Tonga and on the Great Barrier Reef. The data suggest that 2 to 3 years might be required to attain a length of 50 mm.

Trials conducted by Heslinga et al. (MS) in Palau show that cultured clams in the 1-2 cm size range suffered total mortality from predation within a few days of being placed in unprotected conditions on the reef. Clams in the 3-4 cm range survived well in nature when placed in predator exclusion cages made from Nestier shellfish trays and 2.5 cm mesh Vexar screen. Cultured *T. derasa* released without protection at 13 cm showed 89% survival after 1 year, while 17 cm *T. deresa* had no mortality during a 3-month period of unprotected release. These preliminary findings suggest that unless some form of protection is provided, clams smaller than 10-15 cm may suffer unacceptably high losses from predators in nature.

Alternatives for raising juveniles to a size at which they could be stocked on reefs appear at present to be raceway cultivation, bottom cultivation in cages (Heslinga et al. MS) or off-bottom cultivation in floating trays or rafts (Munro and Gwyther, 1981). It seems likely that the length of the juvenile phase, which will require significant operating costs, will ultimately determine the economic viability of tridacnid cultivation. The possibilities of enhancing growth by assisting the phototrophic process by application of fertilizer or other means must be studied.

Production of Adult Clams

Bonham (1965) studied two specimens of *T. gigas* at Bikini Atoll and on the basis of radioautography and annular marks revealed by sectioning the shells, concluded that his 52-cm and 55-cm specimens were 9 years and 6 years old, respectively. Additionally, McMichael (1975), McKoy (1980) and Beckvar (1981) have estimated growth rates, but almost all of such data have been subjected to different analytical techniques.

Munro and Gwyther (1981) presented preliminary estimates of growth rates based upon the periodic measurement of 206 clams over periods of up to 4.5 years. A more definitive paper incorporating additional data and refined analytical techniques (Munro 1982) is in preparation (Munro and Gwyther, MS) but the final estimates of growth rates in terms of the von Bertalanffy growth function are now available and are given in Table 3, together with estimates derived from the literature. A synthesis of available information is shown in Figure 2. It is apparent from Table 3 and Figure 2 that *T. gigas* is the prime candidate for maricultural research and that insufficient is known about *T. derasa*. The smaller species, *T. squamosa*, *T. maxima* and *H. hippopus* achieve lower maximum sizes.

Present adult growth estimates mostly are derived from clams placed in shallow reef environments. The latitudinal differences of the various study sites must be borne in mind, and it appears from the data for *T. maxima* that decreased growth rates occur towards the edges of the distributions of the clams (Table 3). The small maximum sizes attained by *T. maxima* in French Polynesia (Richard, 1978) and to a lesser degree in American Samoa (Wass, n.d.) are rather puzzling.

Clams of 20 cm and 30 cm shell length will weigh 1.5-1.9 kg and 5.7-6.7 kg, respectively, according to species. Flesh weights range from 16% to 23% and the

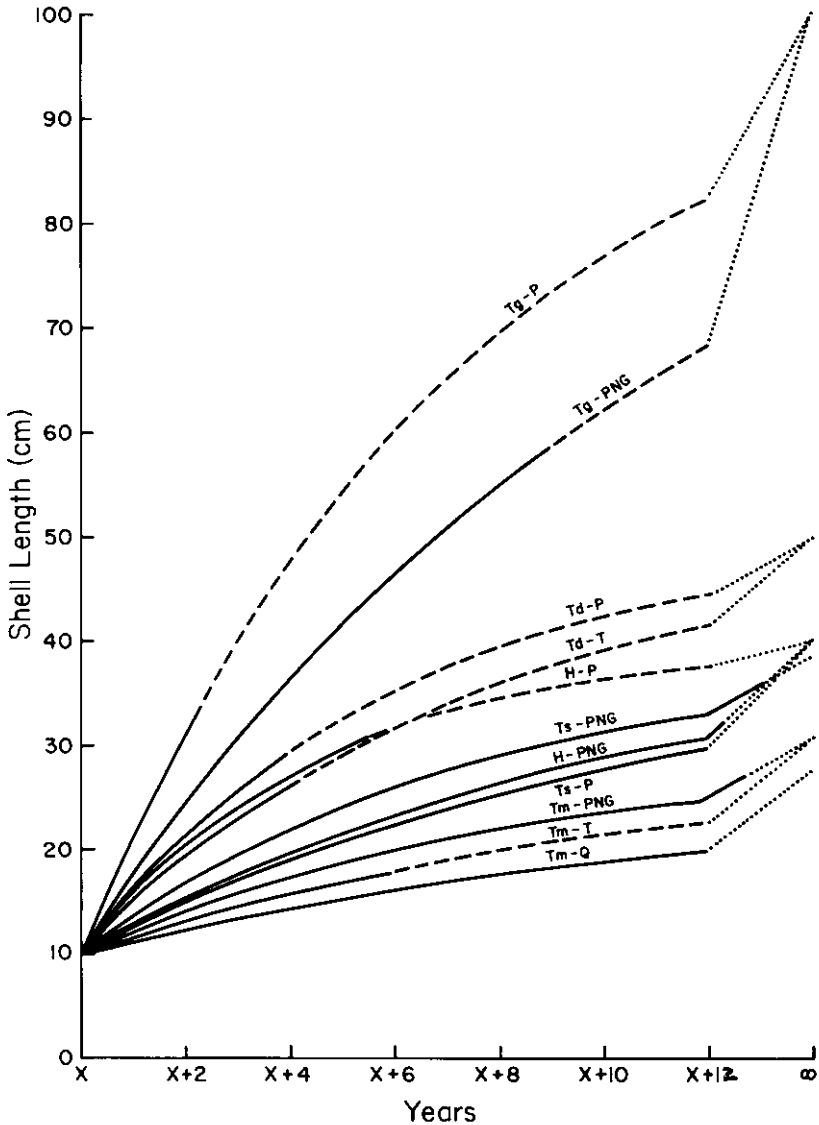

Figure 2. Calculated growth curves, from a length of 10 cm at unknown age x, of *Tridacna gigas* Tg), *T. derasa* (Td) *T. squamosa* (Ts), *T. maxima* (Tm) and *Hippopus hippopus*) (H) in Papua New Guinea (PNG). Palau (P), Tonga (T) and Queensland (Q). Based on data of Munro and Gwyther (MS), Beckvar (1981), McKoy (1980) and McMichael (1975). Broken and dotted lines are extrapolations.

adductor muscle is 1.8-3.0% of the total weights. A 50-cm *T. gigas* would weigh about 30 kg of which 0.6 kg would be adductor muscle, 6.3 kg other flesh and 23.1 kg of shell. Further details of morphometrics are given by Munro and Gwyther (MS).

A final point noted by several observers (Beckvar, 1981; McKoy, 1980 and by ourselves), is that there is great variation in growth rates of individual clams growing under identical circumstances. Munro and Gwyther (MS) will show that there are enormous differences in individual growth rates, even between clams which appear

Table 3. Summary of published growth estimates for adult tridacnid clams, including largest sizes, L_{max} (cm shell length), recorded in various areas and estimates of the parameters of the von Bertalanffy growth function. $L_{(\infty)}$ is an estimate of asymptotic size, L_{∞}, based upon maximum size data.

Tridacna gigas			
L_{max} =	137 cm	Sumatra	Rosewater (1965)
=	101-110 cm	Helen Reef	Motoda (1938)
=	111-120 cm	Palau	Motoda (1938)
=	94 cm	Papua New Guinea	Munro and Gwyther (MS)
$L_{(\infty)}$ =	100 cm K = 0.087 ± 0.007	Papua New Guinea	Munro and Gwyther (MS)
$L_{(\infty)}$ =	100 cm K = 0.136	Palau	recalculated from Beckvar 1981
Tridacna derasa			
L_{max} =	51.4 cm	?	Rosewater (1965)
=	52.5 cm	Tonga	McKoy (1980)
$L_{(\infty)}$ =	50 cm K = 0.167	Palau	recalculated from Beckvar (1981)
$L_{(\infty)}$ =	50 cm K = 0.132	Tonga	recalculated from McKoy (1980) (based on 4 measurements only)
Tridacna squamosa			
L_{max} =	40.8 cm	Thailand	Rosewater (1965)
=	38.5 cm	Papua New Guinea	Munro and Gwyther (MS)
=	37.2 cm	Tonga	McKoy (1980)
$L_{(\infty)}$ =	40 cm K = 0.091	Palau	recalculated from Beckvar (1981)
$L_{(\infty)}$ =	40 cm K = 0.187	Tonga	recalculated from McKoy (1980) (based on 2 specimens only)
$L_{(\infty)}$ =	38.5 cm K = 0.140 ± 0.021	Papua New Guinea	Munro and Gwyther (MS)
Tridacna maxima			
L_{max} =	35.3 cm	Philippines	Rosewater (1965)
=	25.0 cm	Queensland	McMichael (1975)
=	30.5 cm	Papua New Guinea	Munro and Gwyther (MS)
=	30.1 cm	Tonga	McKoy (1980)
=	23.5 cm	American Samoa	Wass (n.d.)
=	17.0 cm	French Polynesia	Richard (1978)
$L_{(\infty)}$ =	30.5 cm K = 0.082	Tonga	recalculated from McKoy (1980)
$L_{(\infty)}$ =	30.5 cm K = 0.112 ± 0.032	Papua New Guinea	Munro and Gwyther (MS)
$L_{(\infty)}$ =	27.5 cm K = 0.074	Queensland	recalculated from McMichael (1975)
L_{∞} =	12.4 cm K = 0.26	French Polynesia	Richard (1978)
Hippopus hippopus			
L_{max} =	33.7 cm	Philippines	Rosewater (1965)
=	39.7 cm	Queensland	Rosewater (1965)
=	33.0 cm	Queensland	Stephenson (1934)
=	40.0 cm	Milne Bay, PNG	Munro and Gwyther (MS)
=	33.0 cm	Motupore Is., PNG	Munro and Gwyther (MS)
=	47.9 cm	Tonga	McKoy (1980)
$L_{(\infty)}$ =	40.0 cm K = 0.213	Motupore Is., PNG	Munro and Gwyther (MS)
$L_{(\infty)}$ =	40.0 cm K = 0.100 ± 0.013	Palau	recalculated from Beckvar (1981)

to be of the same cohort. Trench et al. (1981) have suggested that species-specific strains of zooxanthellae might, at least in part, be responsible for differences in growth rates.

For any grow-out phase of tridacnid clams stocked on an unprotected reef environment, productivity will relate to predation and mortality rates of the clam. Available data are inadequate to evaluate this problem. McKoy (1980) estimated total mortality rates in exploited populations of *T. maxima* in Tonga at Z (the coefficient of mortality) = 0.25 to 0.29, corresponding to annual survival rates of 75-78%. The natural mortality rates under unexploited conditions could not be established.

The length-frequency distribution of the sample of *T. maxima* measured in 1968 by McMichael (1975) at One Tree Island on the great Barrier Reef has been analyzed using the ELEFAN II program devised by Pauly (1982). The program converts length-frequency distributions to catch curves, given inputs of the growth coefficient, K, and the asymptotic length, L_∞. Using the growth parameters given in Table 3, the natural mortality coefficient, M, of this protected population is estimated at 0.21, equivalent to an annual survival rate of 81% from an age of 15 years and virtual extinction at an age of 40 years. This is close to that estimated by McKoy for the exploited *T. maxima* population in Tonga.

The only data available for other species of adult tridacnids are those obtained in Papua New Guinea, by Munro and Gwyther (unpublished data) who found that in an enclosure on a fringing reef adjacent to Motupore Island Research Centre in Papua New Guinea, 3% of *T. maxima* and 6% of *T. squamosa* died each year. Under the same circumstances, only two *H. hippopus* died during a 5-year period (out of an average stock of 35 clams) and no *T. gigas* died in the enclosure during the same period, when the stock averaged about 25 individuals. The enclosure served to exclude large predators but had no effect upon small predators. Pearson (1982), on the other hand, mentions high mortality rates on the Great Barrier Reef, but details of a major tagging study there are not yet available.

The final and most important point concerning the growout phase is the fact that adult clams in shallow water are almost certainly totally phototrophic under most circumstances (Jaubert, 1977; Trench et al., 1981; Munro and Gwyther, 1981; Gwyther and Munro, MS). This means that they appear to require no nutrient inputs other than those provided by their symbiotic zooxanthellae. Furthermore, they appear to necessarily export dissolved organic matter to the reef environment by virtue of their inability to fully utilize or store the primary production of their symbionts.

MARICULTURAL PROSPECTS AND FUTURE RESEARCH REQUIREMENTS

The principal purpose of the paper is to draw to the attention of the scientific community the maricultural potential of tridacnid clams. By available data, *Tridacna gigas* would appear to be the species meriting the most attention, but *all* species are worthy of further investigation. The principal known features can be summarized as follows: (a) All species can be induced to spawn or will spontaneously spawn under controlled conditions, they are enormously fecund and the larvae are amenable to mass-culture techniques. (b) The juvenile clams are hardy, free-living and amenable to handling *en masse*. (c) The growth rates attained by the larger species are comparable with those attained by many commercially important aquatic organisms, but are generated in shallow-tropical waters by sedentary organisms which require no supplementary feeding or special handling. (d) They are readily marketable and highly acceptable traditional foods throughout their range. Additionally, the adductor muscle which comprises about 10% of the total flesh weight is marketable at very high prices in Southeast Asia. (e) The nutritional requirements of all species appear to be fully met by their symbiotic zooxanthellae and at least a high degree of phototrophy is attained early in the juvenile life. They are the only phototrophic potential farm animals known to mankind.

Although the basic features of the biology and ecology of tridacnid clams are now known, most studies have only been made under a single set of conditions and many details are unknown. For example, details of the reproductive cycle are lacking, as is an understanding of the factors involved in inducing spawning. The basic features of larval development are known but details, particularly pertaining to *T. gigas* and *T. derasa* are lacking. The role of zooxanthellae, particularly in relation to nutrition of

early juveniles is not clearly defined and the intricacies of the symbiosis are unknown and of fundamental importance. The growth rates of all species have only been estimated in a few locations and under a restricted set of conditions and we know little of the effects of environmental variables.

Finally, we know nothing of the economic and sociological complexities which would emerge if tridacnid clams become an abundant commercial commodity. The options range from small-scale hatcheries intended to supplement and conserve locally consumed stocks, through large-scale extensive maricultural enterprises employing many people on production and processing, to intensive high technology cultivation systems operating at the near side of science fiction. We require some visionary projections on the options which are likely to emerge.

Whether or not mariculture of tridacnids becomes a commercial reality, the possibility that the larger species will be introduced to coral reef areas outside of their known range in the Indo-Pacific and to the Caribbean Sea must be recognized and the possible consequences very carefully considered at an early stage.

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