CHAPTER 13

Giant Clams[1]

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I. INTRODUCTION

In the past decade there has been an enormous upsurge in interest in the giant clams (Family Tridacnidae), resulting largely from the realization that their artificial propagation is technically feasible (La Barbera, 1975; Jameson, 1976; Beckvar, 1981; Gwyther and Munro, 1981), that growth rates of the larger species are relatively rapid (Munro and Gwyther, 1981) and that, by virtue of their symbiotic relationship with a species or species group of dinoflagellate algae, they are the world's only self-feeding farm animals (Munro, 1983). These factors combined with the realization that stocks of the larger species had been dramatically depleted in most parts of the South Pacific, both by poachers intent on supplying the lucrative Taiwanese market for giant clam adductor muscle and by continuing local harvests by expanding populations of South Pacific Islanders, led to a number of research projects being launched at various institutions in the region; notably at the University of Papua New Guinea and the Micronesian Mariculture Demonstration Center in Palau (both in 1976), by the International Center for Living Aquatic Resources Management (ICLARM) in 1983 and by the Australian Center for International Agricultural Research (ACIAR) in 1984.

As a result of these collective efforts, there is a substantial body of information available on many aspects of the biology and ecology of giant clams and a reasonable understanding of the factors which constrain the intensive harvesting of giant clam stocks for commercial or subsistence purposes. It is now technically feasible to spawn routinely mature giant clams and raise the larvae through their juvenile stages to maturity (Heslinga and Fitt, 1987). Furthermore, there is a good understanding of the various cultivation technologies and of the economic feasibility of giant clam farming (*e.g.* Copland and Lucas, 1988). It should be added however that there are many aspects of the cultivation process which have not yet been optimized or tested under a variety of conditions and that information on giant clam predators, pathogens and parasites is minimal.

The possibility of restocking depleted reefs with hatchery-reared spat has been examined. Munro (1989) concluded that there would need to be substantial advances in cultivation technology and corresponding reductions in unit costs before it became feasible to restock reefs by simply broadcasting clam spat

onto reef systems. The reason for this lies in the very high mortality rates experienced by unprotected clam spat and juveniles on coral reefs.

II. LIFE HISTORY AND POPULATION BIOLOGY

TAXONOMY

Within the bivalve molluscs the giant clams are classified in the Order Cardiacea and the Family Tridacnidae. Their nearest relatives are the cockles. Within the group there are nine recognized living species, comprised of seven species of the genus *Tridacna* and two of the genus *Hippopus*. Additionally, there are a number of extinct species which are conspicuous in the fossil record (Rosewater, 1965).

They are unique in the bivalve molluscs in having established a symbiosis with one or more species of dinoflagellate algae, termed zooxanthellae, which enables them to survive almost exclusively on the products of photosynthesis.

Lucas (1988) gives a comprehensive guide to the taxonomic features and distribution of seven of the living species. Two additional species, *T. tevoroa* (Lucas *et al.*, 1991) and *T. rosewateri* (Sirenko and Scarlato, 1991) have recently been described.

DISTRIBUTION

The recent fossil record, together with historical accounts shows that the range of *T. gigas* has been dramatically attenuated by over-exploitation or climatic change. Relic stocks occur in Indonesian, Malaysian and Philippines waters and possibly on the west coast of Thailand and in southern Burma, but in most cases it appears that these stocks are for all practical purposes extinct because of the wide dispersal of the survivors - which renders successful fertilization unlikely (Munro, 1989). In the tropical and subtropical Pacific *T. gigas* have been eliminated from most of the Federated States of Micronesia (FSM) and from Taiwanese and Japanese waters, from Vanuatu and probably from New Caledonia. There is no record of them having occurred in Tuvalu (Braley, 1988) and, although reported from Fiji by Rosewater (1965), there are some indications that the shells which are commonly used as garden ornaments are not of local origin. A casual trade in large clam shells by crews of boats plying between Suva and Kiribati has been reported to exist and no fossil or subfossil shells have been reported. Cultivated stocks of *T. gigas*, originating in Australia, have recently been established in Fiji, Tonga, Western Samoa and the Cook Islands but wild stocks have not yet become established.

T. derasa, the second largest species has a more restricted range than *T. gigas* and its natural range does not extend east of Palau in the northern

tropical Pacific. In southern waters, *T. derasa* extends as far east as Tonga and Munro (1989) has suggested that this eastward extension might be anthropogenic in origin as a result of early voyagers having carried live *T. derasa* eastwards in the bilges of ocean-going canoes. However, Benzie (*in press*) has pointed out that the eastward limit of *T. derasa* follows the edge of the western Pacific plate. The range of this species has been extended by introductions of Palau stock for aquacultural purposes throughout Micronesia, and to Western and American Samoa, Tuvalu and the Cook Islands.

The range of the small species, *T. maxima,* extends from eastern Polynesia to the Red Sea and to East African shores, while that of *T. squamosa* is somewhat more restricted. The small, rock-boring, *T. crocea* has a distribution from Southern Japan to Australia but does not extend eastward into Oceania beyond Palau and Solomon Islands.

The genus *Hippopus* is represented by the widely distributed *H. hippopus* ranging from Burma to the Marshall Islands and from the northern Philippines to New Caledonia and by *H. porcellanus,* which has a very restricted distribution, being found only in northern Indonesia, southern Philippines and Palau. Like *T. gigas, H. hippopus* appears to have been greatly reduced in abundance and eliminated from Fiji, the Samoas and Tonga.

Even more restricted ranges are exhibited by the newly discovered *T. tevoroa,* which has been found in relatively deep waters (to 40 m) in eastern Fijian waters (Lucas *et al.*, 1990), and in northern Tonga (Lucas *et al.*, 1991) and by *T. rosewateri* which is known only from the Saya de Malha Bank in the Indian Ocean (Sirenko and Scarlato, 1991).

HABITAT

Giant clams typically inhabit coral reefs but it this does not appear to be an obligate relationship. It would seem that giant clams have evolved in a coral reef environment, have adopted as commensals or symbionts the same or similar dinoflagellate algae which are symbiotic with corals and that the larvae will settle readily wherever there is a suitable substratum.

Surveys made in many areas (Salvat, 1971; Pearson, 1980; Alcala, 1986; Braley, 1987a;1988a; Munro, 1988; Gomez and Alcala, 1988) suggest that adults of most species of giant clams can live in most of the habitats offered in coralline tropical seas but that a degree of selective exclusion occurs in the early life history stages. *T. derasa* appears to prefer inhabiting clear offshore or oceanic waters away from high islands with significant run-off of freshwater. For example, it is not recorded from the Papuan Barrier Reef running along the south coast of Papua New Guinea (PNG) nor from the fringing reefs of the north coast of PNG but makes its appearance within a few miles of the south-east point of mainland PNG. Lewis *et al.* (1988) report a similar situation in Fiji where

T. derasa is only found on barrier reefs far from shore. How does a giant clam larvae detect the presence of a high island?

T. squamosa appears to favour fairly sheltered lagoon environments adjacent to high islands but in the closed atoll lagoons of Polynesia appears to be excluded by *T. maxima*. *T. gigas* is perhaps the most versatile of species, being found in all habitats, whether high- or low-islands, lagoon or fringing reefs and in this respect is matched by *H. hippopus* which has a similar geographical distribution but a wider range of habitats, apparently being equally at home on sandy atoll lagoon floors or exposed intertidal habitats. Of course, the relative growth or survival rates achieved in these different habitats are unknown.

All species appear to be depth-limited by their symbiotic algae, with the little-known *T. tevoroa* of Fiji and Tonga inhabiting the deepest (40 m) waters (Lucas *et al.*, 1991).

NUTRITION

It is clearly established that giant clams are facultative planktotrophs. That is, they are essentially planktotrophic but can derive all of the maintenance requirements from their symbiotic algae and even grow in shell length in filtered sea water (Munro and Gwyther, 1981). However, it is likely that they attain their optimal growth when their nutrition is supplemented by phytoplankton or dissolved organic matter extracted from the sea water (Klumpp *et al.*, 1992).

The symbiotic algae are ingested at an early stage in the life history, selectively not digested and are propagated in an extensive diverticulum of the gut which ramifies throughout the body. Photosynthetic products are released into the tubules of the diverticulum and migrate across the membranes of the tubules to the blood stream (Mansour, 1946; Norton *et al.*, *in press*).

REPRODUCTION, SEASONALITY, SIZE AT MATURITY AND FECUNDITY

All giant clams are protandrous hermaphrodites, becoming simultaneous hermaphrodites in later years (Wada, 1952;1954; La Barbera, 1974;1975; Jameson, 1976; Beckvar, 1981; Gwyther and Munro, 1981). The gonad is a single organ which envelops the intestine and collectively is referred to as the visceral mass.

Ripe gonads are greatly enlarged and can represent over 13 per cent of the total flesh weight. In the case of *T. gigas* the degree of ripeness can be judged visually by the degree to which the ripe gonad projects into the gill chamber.

The normal spawning sequence is for sperm to be produced first, followed by egg production after a short interval. However, this pattern seems to be more

often followed in the smaller species, and in *T. gigas* it is often the case that clams will enter into egg production without having produced significant amounts of sperm on the same day. Release of sperm is triggered in nature by the presence of a spawning inducer associated with ripe eggs (Wada, 1952; La Barbera, 1974; Gwyther and Munro, 1981; Munro *et al.*, 1982).

In the central tropics there is no evidence of any seasonality in reproduction (Munro and Gwyther, 1981; Beckvar, 1981; Heslinga *et al.*, 1984) but it appears that gonads ripen on a seasonal basis at the northern and southern limits of distribution because spawning of *T. gigas*, *T. crocea* and *H. hippopus* is restricted to a short summer season in the central region of the Great Barrier Reef (Braley, 1984; Nash *et al.*, 1988; Shelley and Southgate, 1988). Detailed data are lacking for other areas.

Heslinga *et al.* (1984) and Beckvar (1981) reported a degree of lunar periodicity in spawning of *T. derasa*. Records at the Coastal Aquaculture Centre in Solomon Islands support the suggestion of a tendency to spawn between the first lunar quarter and the full moon (around a moon age of about 10 days) but this appears to be heavily overlaid by other environmental factors, particularly sunshine. Periods of continuous bright sunshine and calm weather appear conducive to spawning, and it is possible that additional nutrients released to the clam by their zooxanthellae trigger final maturation of the gonads.

Jameson (1974) estimated fecundity (F) of *T. maxima* as $F = 0.00743\ L^3$, and a ripe gonad of a 20 cm specimen would therefore contain about 20 million eggs. Individual *T. gigas* in the 70-80 cm size range have produced up to 240 million eggs at the Coastal Aquaculture Centre. It is not known how many times in a season or a year any individual can spawn.

There is very little information on the size of giant clams at maturity. Nash *et al.* (1988) reported that *T. gigas* on the Great Barrier Reef reached male maturity at 25-35 cm. The smallest egg producers appear to be around 50 cm (Heslinga *et al.*, 1984). This is confirmed by spawning records at the Coastal Aquaculture Centre in Solomon Islands (Munro, *in press*).

McKoy (1980) found that *T. maxima* reached male phase maturity at 5 cm and started producing eggs by 6-8 cm. *T. squamosa* were also mature at 5 cm, but no females were found until 15 cm. Older clams (>35 cm appeared to be exclusively female).

LARVAL BIOLOGY AND ECOLOGY

Fertilized eggs of tridacnid clams have a slight negative buoyancy and usually develop into swimming trochophores within 12 hours and into shelled veligers within 36 hours (La Barbera, 1975; Munro and Gwyther, 1981; Beckvar, 1981; Alcazar 1988, Heslinga *et al.*, 1990), but with much variability according to temperature and species. Eggs of *H. hippopus* are less buoyant. The

Table I. Compilation of growth parameters and growth estimates for tridacnid clams.

Genus/ species	Ref.	Locality	L_∞ (cm)	K	t_o(yr)	age in years: 1	2	3	4	5	6	8	10	15	20
						shell length in cm									
Tridacna gigas															
	2	Various				4.78									
	1	PNG	80	.13	0.52	4.80	13.97	22.02	29.09	35.29	40.74	49.73	56.66	67.82	73.64
	2	PNG	100	.087	0.43	4.80	12.73	20.00	26.67	32.78	38.38	48.22	56.49	71.84	81.77
	3	Palau	100	.136	0.64	4.80	16.91	27.47	36.69	44.74	51.77	63.26	72.01	85.82	92.82
	7a	Michaelmas Reef	88.7	.07	0.03		11.4	16.63	21.50	26.04	30.28	37.91	44.55	57.58	66.77
	7b	Michaelmas Reef	80	.105	.145		14.16	20.72	26.63	31.95	36.74	44.93	51.58	63.19	70.05
	7c	Michaelmas Reef	80	.083	.145		11.35	16.82	21.85	26.48	30.74	38.32	44.69	56.69	64.60
	7d	Michaelmas Reef	80	.150	.145		19.43	27.87	35.13	41.38	46.76	55.37	61.76	71.38	75.93
	9	Orpheus Is., GBR				5	14								
	13	Bolinao, Phils.					9.8								
	14&15	Orpheus Is., GBR				3-4	9-13	16-22							
	14	Lizard Is. GBR						15							
T. derasa	2	Various				4.67									
	3	Palau	50	.167	0.41	4.7	11.67	17.56	22.55	26.77	30.35	35.93	39.92	45.63	48.10
	4	Tonga	50	.132	0.25	4.7	10.30	15.21	19.51	23.28	26.59	32.02	36.19	42.86	46.31
	7	Michaelmas Reef	46.9	.108	-0.20		9.87	13.66	17.06	20.12	22.86	27.55	31.31	37.81	41.60
	18	Fiji	47.3	.134	0.22	4.7	10.04	14.71	18.80	22.38	25.50	30.63	34.55	40.77	43.96
	10	Philippines				5	8.5	12.5							
	13	Bolinao, Phils.							15-16						
	14	Orpheus Is., GBR				1.82									
	14	Lizard Is. GBR						8.0							
	16	Dumaguete, Phils.				4.3									
	18	Palau				5.0	10.0	15.0	20.0	25.0	27.5				

Genus/ species	Ref.	Locality	L (cm)	K	to(yr)	age in years 1	2	3	4	5	6	8	10	15	20
						shell length in cm									
T. squamosa	2	Various				4.75									
	11	Philippines				4.75									
	3	Palau	40	.091		4.75	7.82	10.62	13.17	15.51	17.64				
	4	Tonga	40	.187		4.75	10.76	15.75	19.89	23.32	26.16				
	2	PNG	38.5	.14		4.75	9.16	12.99	16.32	19.22	21.74				
	13	Philippines					3.8								
	16	Dumaguete, Phils.				3.5									
T. maxima	2	Various				2.08									
	12	Philippines				(4.9)									
	4	Tonga	30.5	.082		2.08	4.32	6.38	8.28	10.03	11.64				
	2	PNG	30.5	.112		2.08	5.09	7.78	10.19	12.34	14.27				
	5	Queensland	27.5	.074			2.08	3.89	5.58	7.14	8.59	9.94			
	6	French Polynesia	12.4	.26											
	13	Philippines				1.9									
	16	Dumaguete, Phils.				3.8		6.3							
T. crocea	8	Okinawa				1.88			6.61						
	12	Orpheus Is., GBR				2	3.5	5					9		
Hippopus	2	Various				5.04									
hippopus	2	PNG	40	.213		5.04	11.75	17.17	21.55	25.09	27.95				
	3	Palau	40	.1		5.04	8.37	11.38	14.10	16.57	18.80				
	13	Philippines					8.0								
	14	Lizard Is. GBR						11.0							
	16	Dumaguete, Phils.				6.7	8.1								
	17a	Orpheus Is., GBR	34.7	.205		5.04	10.54	15.02	18.66	21.64	24.06				
	17b	Orpheus Is., GBR	41.5	.155		5.04	10.28	14.76	18.60	21.89	24.70				
T. porcellanus	16	Dumaguete, Phils.				6.1									

References:

1. Munro and Gwyther (1981), 2. Munro and Heslinga (1983), 3. Beckvar (1981), 4. McKoy (1980), 5. McMichael (1975), 6. Richard (1978), 7. Pearson and Munro (1991) [a. empirical curve, b. average growth, c. poor growth (1 SD below mean), d. good growth (1 SD above mean), 8. Murakoshi (1986), 9. Lucas, *et al.*, (1989), 10. Belda *et al.*, (1989), 11. Alcazar and Solis (1986), 12. Hamner and Jones (1976), 13. Gomez and Belda (1988), 14. Crawford *et al.*, (1988), 15. Barker *et al.*, (1988), 16. Solis *et al.*, (1988), 17. Shelley (1988) [a. Iris Point, b. Pioneer Bay], 18. Watson and Heslinga (1988), 19. Adams *et al.*, (1988).

veligers are highly motile and feed on microalgae of up to 10μ in diameter. Although some larvae are capable of developing and metamorphosing using only their maternally-derived reserves (Fitt *et al.*, 1984), larvae which have actively fed have greater survival rates after settlement (Southgate, 1988). The duration of the larval life is variable, presumably depending upon feeding, but most investigators cite a larval life of around 8 days with ranges of between 5 days and 15 days, presumably depending on the lipid reserves of the egg and the availability of feed and temperature.

Towards the end of the larval life the larva develops a foot; then it is termed a pediveliger and settles onto the substratum. Soon afterwards it metamorphoses into a juvenile clam or spat. Failure to locate a suitable substratum will result in death and it is the fate of most larvae to be swept into water which is too deep to permit survival of the spat.

The spat are highly motile and actively search for a suitable substratum and attach themselves with a byssal thread. This can be broken at will and the spat are capable of quite extensive movement up to a size of several cm.

GROWTH

Information on growth rates of giant clams is derived from mark and remeasure studies, age estimation from daily and or annual rings and from the rearing of cultivated clams. The latter aspect has been of particular importance in filling the blank area between settlement of spat and the smallest clams marked and measured.

Bonham (1965) provided the first estimates of growth of *T. gigas* based on radioautography of two shells from Bikini Atoll which had been exposed to atomic radiation. These placed the ages of the 52 cm and 55 cm shells at nine and six years respectively. Numerous studies have been made since that time. Table I shows a compilation of published data and parameter estimates.

An important feature which has not yet been studied in sufficient detail is the enormous individual variability in growth rates in both wild and cultivated stocks (Pearson and Munro, 1991). It also appears likely, but unproven at this stage, that wild stocks have more rapid average growth rates than unculled hatchery reared stocks, owing to the intense natural selection against slow growers in unprotected wild spat and juveniles.

MORTALITY

Pearson and Munro (1991) and Munro (1988) discuss the mortality rates of *T. gigas* and *T. derasa* at Michaelmas Reef, on the Great Barrier Reef, based on mark and remeasure data. Mortality rates, entirely attributable to natural causes, are size-specific, being greatest in the youngest clams, declining to

negligible levels in the middle years then increasing again as the clams become senile and die of old age. The data also indicated a catastrophic change in mortality rates during the study, thought to be attributable to a large portion of the stock of *T. gigas* having been recruited within a short time frame and subsequently reaching senility at about the same time (possibly around 30 years of age). Michaelmas Reef was selected for this study because of the large stock of mature clams.

Information on mortality rates in the early juvenile stages is very sparse and is derived almost exclusively from cultivated stocks owing to the extreme difficulty in finding specimens of wild juveniles. Heslinga *et al.* (1984) showed that juvenile *T. derasa* in the 1-2 cm size range suffered total mortality if placed on the reef without protection and this is presumably the fate of almost all naturally recruited juveniles.

The only other sources of information on mortality rates are length converted catch curves (Pauly, 1980) derived from the size compositions of exploited and unexploited stocks. Their accuracy is limited when they are applied to relatively slow growing stocks in which individual asymptotic sizes are highly variable (Isaac, 1990).

However, it would be instructive to examine the size distributions of tridacnids in the shell middens which are so plentiful in the South Pacific, as the oldest layers would give indications of the mortality rates in very lightly exploited stocks and a comparison with present day size distributions. The work of Swadling (1976) provides an indication of the sort of result which can be derived from such investigations.

RECRUITMENT

The term recruitment in the context of giant clams requires some definition. The juveniles of the largest species, *T. gigas*, *T. derasa*, *H. hippopus* and *H. porcellanus* are all highly cryptic and become progressively more "findable" with increasing size. The smaller species, *(T. squamosa*, *T. maxima* and *T. crocea*) are more conspicuous because of their brightly coloured mantles and therefore can be located at a smaller size.

The analyses of Pearson and Munro (1991) indicate that even when experienced divers enumerate the contents of quadrats, relatively large juvenile *T. gigas* and *T. derasa* will be overlooked and only reach full "findability" at about 20 cm SL.

Braley (1988b) concluded that recruitment to clam stocks on the Great Barrier Reef was episodic. Likewise, routine field surveys conducted by Adams *et al.* (1988) in Fiji did not find significant numbers of *T. derasa* smaller than 25 cm SL, although intensive searches produced small numbers of juveniles. They concluded that the observed recruitment was insufficient to maintain observed

stocks and that recruitment must therefore be very erratic. At Michaelmas Reef, on the Great Barrier Reef, the rate at which the stock was replenished was around 1.5 per cent per year for *T. gigas* and 4 percent per year for *T. derasa* (Pearson and Munro, 1991).

Unfortunately, it is a feature of giant clam biology that stocks will become non-sustaining when densities fall below certain undefined levels. This is because of the mode of spawning of hermaphroditic giant clams. Giant clam eggs contain, or are associated with, a chemical which will induce spawning in a conspecific clam which detects the spawning inducer. Sperm is released by the second clam; the eggs are thus fertilized. The second clam might also release eggs after an interval and the entire process progresses downstream. However, if there is no conspecific clam downstream, the eggs are unfertilized and the chain of events does not eventuate. Thus the clams are highly vulnerable to local stock depletion which will result in a collapse in the fertilization rates and consequent reduction in recruitment rates. In other words, if stocks are reduced below some unknown point, recruitment will collapse and stocks will subsequently collapse. If a reef is entirely stripped of clams, repopulation will depend entirely on planktonic larvae brought in from other reefs by prevailing currents. If the reef is isolated or the current direction is unfavourable, the re-establishment of a stock could take hundreds of years.

STOCK DENSITIES

Average stock densities in the Pacific vary enormously and reflect the combined effects of exploitation and of episodic recruitment, combined with largely unknown factors affecting habitat preferences.

On the Great Barrier Reef an average of around five *T. gigas* and five *T. derasa* can be expected per hectare of shallow reef, with occasional reefs having much higher densities of several hundred clams per hectare. Similar densities have been recorded by Tarnawski (1980) in Milne Bay, Papua New Guinea. Hester and Jones (1974) recorded densities of 50 *T. gigas* and 33 *T. derasa* per hectare at Helen Reef before these stocks were totally decimated by distant-water fishing vessels. In lightly exploited areas, densities of *H. hippopus* of 30-90.ha^{-1} appear to be normal (Hardy and Hardy, 1969; Tarnawsky, 1980) but can rapidly be reduced to very low values by intensive exploitation (Gomez and Alcala, 1988).

The smaller species can reach very high stock densities. Hardy and Hardy (1969) recorded 1390 *T. crocea*.ha^{-1} in Palau and Richard (1981) reported similar stock densities of *T. maxima* in Takapoto Lagoon, French Polynesia. Densities of over 3000 *T. crocea*.ha^{-1} have been recorded at several sites in the Philippines, but such occurrences were exceptional (Gomez and Alcala, 1988).

II. PACIFIC REGION FISHERY INFORMATION

EXPLOITATION AND DISTRIBUTION OF PACIFIC STOCKS

The shell middens which are found throughout the tropical Pacific leave no doubt that tridacnids were an important component of the diets of Pacific Islanders in past centuries. The middens at Motupore Island, on the South Coast of Papua New Guinea, contain large quantities of shells, particularly of *H. hippopus*. Their relative importance in the total diet is difficult to gauge but there is little doubt that they were frequently used as food. This has continued throughout the Pacific to the present, and there are few parts of the tropical Pacific where tridacnids are not gathered on a daily basis and found in the local markets.

Fishing methods for giant clams are exceedingly simple. In remote areas where the shells have no significant value and have strong byssal attachments to the reef, the flesh is simply excised from the shells by slipping a sharp knife along the inner surface of the shell to cut one end of the adductor muscle. This also applies to the larger species in which the shell is too heavy to be readily lifted from the water.

Where the shell is of value or is of manageable size the clams are retained in their shells until landed. They can survive many hours out of water if kept in shaded or moderately moist conditions (Govan, 1988). In Fiji it is reported that *T. derasa* are harvested from deep waters by dropping an iron weight on the end of a line onto the mantle. The clam closes its valves on the weight and is hauled to the surface (Lewis *et al.*, 1988).

There are very few reliable statistics on the total harvest of giant clams in the South Pacific region. The small scale and subsistence harvests are undoubtedly small. Rough estimates, based on estimates of mortality rates and stock densities suggest that the total annual harvest of all species would not exceed 200 tons of flesh.

Commercial fisheries appear to have been confined to long-range Taiwanese fishing vessels, targeting the adductor muscles of the larger species. This activity reached its peak in the mid-1970s then subsided in the face of depleted stocks, strong international pressures and improved surveillance of reef areas (Dawson and Philipson, 1989). Overall, it would appear that the depletion of the stocks had more to do with the diminution of the fishery than any enforcement measures.

Commercial fisheries developed in Papua New Guinea, Fiji, and the Maldives in the wake of the reduction of Taiwanese activities and in response to the sustained demand (Lewis *et al.*, 1988; Barker, 1991). These fisheries rapidly depleted local stocks and the authorities closed the fisheries. Clams continue to appear on local markets on a regular basis.

The short-lived local commercial fisheries amounted to a few hundred tons of flesh per year, most of the adductor muscle being exported and the remainder disposed of locally. The Fiji fishery, exclusively for *T. derasa*, landed a total over 218 tons over a nine-year period, with the largest annual harvest totalling 49.5 tons and is thought to have removed most of the available stock (Lewis *et al.*, 1988). The PNG fishery was closed after removal of at least 85 tons of adductor muscle over a five-year period, equivalent to over 750 tons total flesh weight.

Dawson and Philipson (1989) estimated the Taiwanese harvest to have totalled not more than 100 tons of adductor muscle per year during the height of the fishery. Munro (1989) regarded this as likely to be an underestimate. Most of the harvest would have been of *T. gigas* and *T. derasa*. Based on the size distributions of unexploited stocks on the Great Barrier Reef (Pearson and Munro, 1991), this tonnage would have been derived from an annual harvest of about 50,000 individual *T. gigas* and a similar number of *T. derasa*.

III. REVIEW OF RESEARCH METHODOLOGY

Like other sedentary invertebrates, tridacnids lend themselves to visual surveys, with the important qualification of that small specimens are likely to be overlooked. Pearson (1982) has described survey methods developed for use on the Great Barrier Reef in Australia, mainly involving the use of manta boards for rapidly surveying wide areas. Munro (1988) developed a parallel-track survey technique in which pairs of divers are towed alongside a survey vessel covering a predetermined track. The statistics of the method are based on the analogous aerial survey techniques developed in East Africa for aerial surveys of large mammals. Braley (1988a) adopted this survey technique in Tuvalu.

Lewis *et al.* (1988) made extensive surveys in Fiji using a non-quantitative towed-diver technique and using timed searches (number of clams.hr^{-1} searched) for more precise estimates. Pearson and Munro (1991) and McMichael (1975) used quadrats to survey and monitor stocks on tridacnids the Great Barrier Reef. Surveys of Helen Reef, near Palau, used line transect methods to document the decimation of the giant clam stocks by distant-water fishing vessels (Hester and Jones, 1974; Hirschberger, 1980, Bryan and McConnell, 1976). Similar methods have also been used in the Philippines (Gomez and Alcala, 1988). Mark and remeasure methods were used by Munro and Gwyther (1981), Shelley (1988) and Pearson and Munro (1991) to estimate growth, mortality and recruitment rates in giant clams in Papua New Guinea and Australia. The methods for analyzing the data are quite complex (Pearson and Munro, 1991), but when done on a sufficiently large scale give unparalleled results, including information on individual variability in growth, mortality and recruitment rates.

Possible avenues for future research include the examination of size distri-

butions and species compositions of tridacnid shells in middens in various parts of the Pacific. If shells are recoverable in sufficient quantities in the various strata, their size frequency distribution can give valuable information on the survival rates under condition of light exploitation, particularly in comparison with that of present day surviving stocks. The use of permanently-fixed quadrats such as those developed for use by Pearson at Michaelmas Reef, Great Barrier Reef, is highly recommended for long-term monitoring of growth and recruitment, particularly if done in conjunction with broader studies of the community ecology of the reef.

More detailed studies of the growth and mortality rates of all species are needed before the potential harvests can be fully assessed and management measures recommended.

IV. CONSIDERATIONS FOR FISHERY DEVELOPMENT AND MANAGEMENT

STOCK ASSESSMENTS

Potential harvests of tridacnids can be assessed using conventional yield per recruit methods, once estimates of growth and mortality parameters are available (McKoy, 1980). The most important factors are that asymptotic sizes are relatively large, growth coefficients are relatively high (probably because of the endogenous food source provided by the symbionts) and the survival curve follows a pattern similar to that exhibited by other large organisms, including mammals - namely, high mortality in the larval and juvenile states, as is common in most marine invertebrates, followed by a phase of decreasing mortality rates until or beyond the size at maturity, then a progressive decrease in life expectancies with increasing age.

Yield per recruit curves based on the data given in Table I show that for all species the maximum sustainable harvest is taken by restricting harvests until a relatively large size. This is because, beyond recruitment at a findable size, mortality rates progressively decrease to negligible levels, only increasing with the onset of senility. For example, McKoy (1980) calculated that *T. maxima* stocks in Tonga would have optimum minimum harvestable sizes of 10.5-14 cm, when L_∞=25 cm and Z=0.30. Much higher rates of exploitation occur in many areas and it is likely that minimum sizes of 70-80 per cent of L_∞ would be appropriate.

Munro (1989) showed that at Michaelmas Reef, Great Barrier Reef, biomasses of cohorts of *T. gigas* would still be increasing after 10 years and after sizes in excess of 57 cm (=71 per cent of L_∞) had been attained.

However, as tridacnids are normally recruitment limited, there being almost

unlimited habit on a reef relative to normal population densities, it is clear that the all-important parameter in the equation is recruitment and this will determine overall harvests. It can also be added that the same parameters will pertain to cultivated stocks which can actually be stocked at some currently unknown optimum density.

MANAGEMENT

Owing to the low natural mortality rates of giant clams, the largest yields will be obtained by taking giant clams at relatively large sizes. Thus it would be possible to stipulate minimum sizes of adductor muscles and corresponding shell lengths and body weights for each species. The value of adductor muscle increases with increasing size (Dawson and Philipson, 1989) and such a move would be beneficial to the fishery. However, if a giant clam mariculture industry comes into being, these large clams would be of vital importance as broodstock and it would be essential to conserve a major part of the stocks of large adult giant clams.

Imposition of a single minimum size would eliminate the smaller species from the catches because adults of these species have body dimensions similar to those of immature *T. gigas*. This difficulty could be overcome by stipulating that all clams be landed with the adductor muscle not separated from the body. Alternatively, examination of the muscles might reveal some feature which would readily distinguish the adductor muscles of different species.

The imposition of strict annual quotas, to be harvested in a single short season, coupled with the size restrictions discussed above, would appear to offer the best prospects for management. Quotas could be determined for individual areas on the basis of stock appraisals done by fisheries scientists. Such a system might also encourage individuals or communities to develop further the traditional "clam garden" concept, in which undersized clams could be accumulated in individually owned "gardens" until they attain the minimum harvestable size.

The possibility of enhancing or rehabilitating depleted stocks of tridacnids by distributing hatchery-reared spat has been advocated in many quarters. However, experience in giant clam cultivation and the results obtained by Pearson and Munro (1991) all suggest that mortality rates of unprotected juveniles might be prohibitively high relative to the cost of the spat. Stocking strategies are examined by Munro (*in press*).

The establishment of protected areas or refuges for giant clams and other threatened or endangered species is an obvious course of action which can be advocated for all areas where stocks have been depleted - if only to conserve the remaining genetic resources (Braley, *in press*). However, natural recruitment rates to wholly protected stocks on the Great Barrier Reef appear to be very low, despite their prodigious fecundity and the apparently unlimited substrata offered

for settlement on a coral reef. It cannot be shown at this stage that refuges will markedly increase recruitment rates in surrounding areas. This is perhaps indicative of the lack of sufficient information on the recruitment process in sedentary invertebrates.

NOTE

[1] ICLARM Contribution No. 787

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