For George my best regards, Gerard

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The Domestication of Reef-dwelling Clams

Farming, using land-based nurseries and natural coral reefs, may restore giant clams to importance in the Indo-Pacific diet

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Aquaculture is nowhere more evident than in the protein-poor coastal and archipelagic nations of Southeast Asia, which are responsible for about 80% of the world's cultivated aquatic food production. Most aquaculture in this part of the world is conducted in land-based fishponds or on soft, shallow ocean bottoms. A geographically extensive habitat, the coral reef, remains virtually untapped as a site for human food cultivation. To date only certain red seaweeds, valuable for their agar and carrageenan, have been farmed with commercial success in coral reef environments (Doty 1983). Recently, however, an unusual family of reef-dwelling molluscs, the Tridacnidae, has emerged as an eminently cultivable group. It offers increased sustainable production of edible protein from coral reefs (Heslinga 1986).

The giant clams (Figure 1) have long been an important component of the diet of Indo-Pacific peoples. In the shallow, transparent waters of coral reefs, the colorful tridacnids are among the most conspicuous members of the benthos. They are easily accessible to subsistence fishermen, who consume the entire flesh of the animal in raw, cooked, or dried form.

Like the surrounding reef corals, giant clams harbor enormous numbers of unicellular dinoflagellates, the zooxanthallae (*Symbiodinium microadriaticum*). These algal symbionts function as internal solar collectors, converting sunlight, carbon dioxide, and dissolved nutrients into carbon-based photosynthates, some of which are released directly into the bloodstream of the host. The clams thus benefit from a highly efficient, internal food source that minimizes energy loss between trophic levels. These clams are able to grow faster and larger than conventional filter-feeding bivalves, even in the plankton-poor waters of coral reefs. Although many marine invertebrates are known to house autotrophic symbionts, the tridacnids stand out as the most amenable to mass cultivation and human food production. This article examines the role of symbiosis in the physiology of tridacnids, and reviews recent technical advances that are making the domestication of these animals attractive from economic, social, and ecological perspectives.

Giant clams harbor algal symbionts that act as an efficient internal food source

Interest in cultivating giant clams began in the mid 1970s, when investigators working in Fiji and Palau independently demonstrated the feasibility of small-scale laboratory culture (Jameson 1976, LaBarbera 1975). At the same time the international conservation community started to recognize that natural tridacnid populations in many areas were threatened with extinction (Yamaguchi 1977). Centuries of subsistence harvesting by indigenous Pacific peoples, in conjunction with recent massive commercial exploitation by foreign poachers (Figure 2), has led to an alarming decline in overall giant clam population and to numerous local extinctions (Heslinga et al. 1984b, IUCN 1983). In Taiwan a flourishing, illicit trade in giant clam adductor muscle has arisen to meet the demand for 100 tons of product annually, worth $7.50–$21.25/kg (US dollars) at dockside (Dawson 1986). The destruction of coral reef habitats near some urban centers has also contributed to the decline of the tridacnids. It is now believed that *Tridacna gigas* and *Tridacna derasa*, the largest and most heavily harvested species in the family, have been essentially eliminated from vast areas of Indonesia, the Phillippines, Papua New Guinea, Micronesia, and southern Japan (IUCN 1983).

The giant clam life cycle

There are seven species in the tridacnid family, all of which are thought to live for decades. The largest, *T. gigas*, grows to more than a meter in length and may weigh 300 kg (Munro and Heslinga 1983). The clams are simultaneous hermaphrodites, reaching full sexual maturity at roughly five years of age (Heslinga 1986). They regular-

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ly broadcast enormous numbers of sperm and eggs into the surrounding seawater. Pheromonal communication among individuals, as well as diurnal, lunar, and annual environmental cues, ensure synchronized spawning (Braley 1984, Heslinga et al. 1984b). A large *T. gigas* is capable of releasing hundreds of millions of microscopic eggs in a single day—a distinction that ranks it among the most fecund of marine invertebrates. In the sea, however, high fecundity is always offset by high mortality, and tridacnid larvae suffer tremendous losses during their one-week planktonic period. Those that survive the swimming phase settle on a patch of hard reef substrate and quickly metamorphose into juveniles. The young clams anchor themselves to the reef with sticky byssal threads and orient their fleshy mantles toward the sun.

Postlarval growth in *T. gigas* and *T. derasa* is rapid by clam standards, averaging 5–10 cm/yr. But until the juveniles are 2.5 years old they are vulnerable to predation by numerous reef carnivores, including crabs, fishes, snails, and octopuses (Heslinga et al. 1984b, Heslinga and Watson 1985). Adult tridacnids seem for the most part immune to predation (except by man), but even under ideal conditions the larger species are rare in nature, with population densities higher than 100 per hectare seldom occurring. On most exploited reefs the number is much lower. Successful recruitment of baby clams to the reef appears to occur erratically (Yamaguchi 1977).

In sum, the life history features of giant clams include relatively great longevity, large body size, late maturity, and prodigious fecundity. Dispersal is achieved with energetically cheap offspring, and there is no parental care. In many respects tridacnids resemble trees in climax forests, with their sedentary habit, adult resistance to predation, and dependence on photosynthesis.

The clam-alga association

Although zooxanthellae play an integral part in the nutrition of giant clams, and no adult tridacnids have been found in nature without their symbionts, the algae are not inherited by the young clams. Tridacnid eggs appear to be free of zooxanthellae, making it necessary for the baby clams to acquire their complement of symbionts from the environment. Likely sources of zooxanthellae for this infection include other tridacnids and symbiotic reef coelenterates, such as corals or anemones.

The developmental stages of tridacnids are similar to those of most other bivalves. The fertilized egg divides rapidly, passing through the gastrula stage and becoming a trochophore in about 12 hours. The mobile trochophore is not capable of ingesting solid foods during its 12–24-hour life (Fitt et al. 1984). Veligers (the next larval stage) ingest small species of phytoplankton when digestive system development is complete, by the third day after fertilization (LaBarbera 1975). In the laboratory, veligers of giant clams fed the phytoplankton *Isochrysis galbana* have faster growth rates and higher survival rates through metamorphosis than veligers fed other species of flagellated phytoplankton (Fitt et al. 1984). Interestingly, veligers fed only yeast extract and vitamins also have high growth and survival rates (Figure 3a), suggesting that uptake of dissolved nutrients may be an important source of nutrition for the larvae.

Veligers will also ingest zooxanthellae (Figure 3b), although they do not establish a symbiosis until after meta-

Figure 1. An island fisherman examines a *Tridacna gigas* (foreground), the world's largest bivalve species, on a coral reef in the Republic of Palau. This once-important food clam is now threatened with extinction throughout most of its range.

Figure 2. A confiscated clam boat. During the past two decades, poaching by Taiwanese pirates has had a devastating impact on giant clam stocks of the Indo-Pacific.

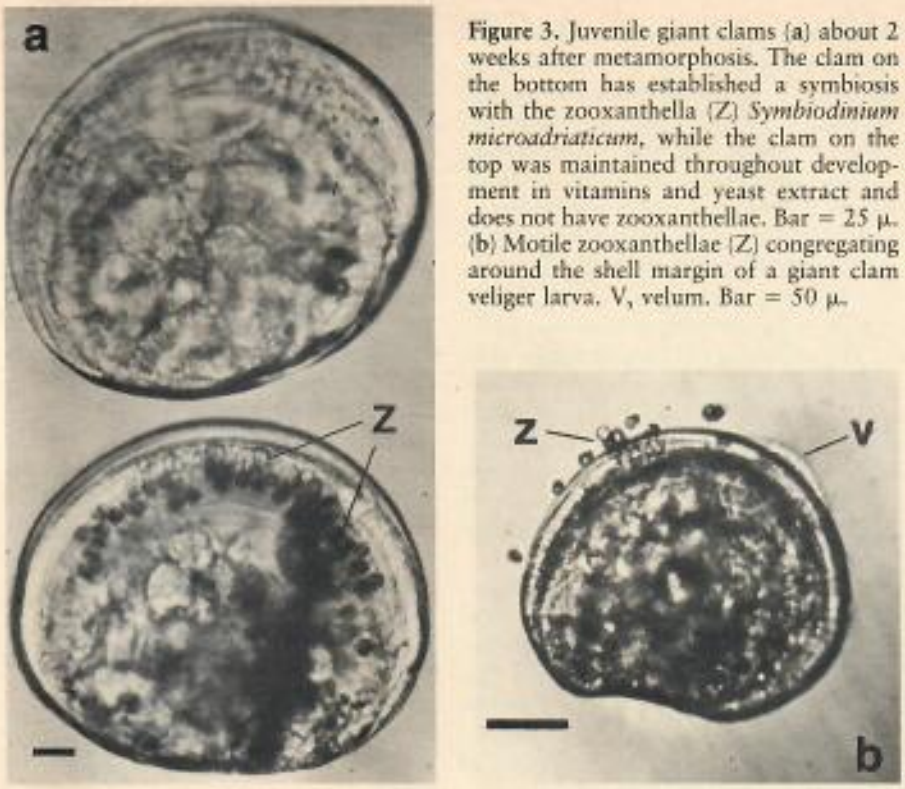

Figure 3. Juvenile giant clams (a) about 2 weeks after metamorphosis. The clam on the bottom has established a symbiosis with the zooxanthella (Z) *Symbiodinium microadriaticum*, while the clam on the top was maintained throughout development in vitamins and yeast extract and does not have zooxanthellae. Bar = 25 μ. (b) Motile zooxanthellae (Z) congregating around the shell margin of a giant clam veliger larva. V, velum. Bar = 50 μ.

morphosis when the algae pass from the stomach into the developing mantle. Veligers with freshly isolated zooxanthellae (from other clams) in their stomachs exhibit better growth and survival than unfed control clams, implying that the nutrients released from live or senescent symbionts are responsible (Fitt et al. 1986).

Metamorphosis of veliger larvae into juvenile clams typically occurs one to two weeks after fertilization, with larger tridacnid species having a shorter larval life in vitro than the smaller species (Fitt et al. 1986). The presence of zooxanthellae is not required for metamorphosis, and factors important in substrate selection and cueing metamorphosis are not presently known.

Establishment of symbiosis

Symbiodinium microadriacticum, the symbiont found in all adult tridacnid clams, is the same algal species found living symbiotically in most reef-building corals. The life cycle of this alga inside a molluscan or coelenterate host is simple: coccoid vegetative cells, which measure 6–12 μ in diameter, divide to produce daughter cells. When outside the host in culture media or seawater, however, these algae alternate between a dumbbell-shaped motile form and the round vegetative form. The motile cells are present only during the day, or light period of a light-dark cycle, and appear to be important in the reinfection of invertebrate hosts, such as tridacnid clams, that do not directly pass their symbionts to the next generation in the egg (Fitt 1984).

Laboratory observations have shown that motile zooxanthellae can swim up to 10 m/day (Fitt and Trench 1983) and are attracted to dissolved nitrogen, such as ammonium (Fitt 1985a), which is typically released as a by-product of protein catabolism by most nonsymbiotic marine organisms. When living in symbiosis, zooxanthellae take up ammonium so that little is released from their clam hosts, thereby inhibiting attraction of other motile zooxanthellae (Fitt 1984).

The coming together of zooxanthellae and a larval or juvenile clam by either the chemosensory abilities of the motile zooxanthellae or random dispersal of zooxanthellae with the ocean currents is only the first step in the establishment of a symbiosis. Motile and nonmotile zooxanthellae are taken into the stomach via the esophagus in the same manner as phytoplankton food. But unlike other phytoplankton species, which are typically digested soon after they are eaten, at least some of the *S. microadriaticum* are able to resist digestion by their herbivorous host (Fitt et al. 1986). Zooxanthellae may remain in the stomachs of larval or juvenile tridacnids for over a week. A few days after metamorphosis, intact zooxanthellae are seen in the tissues adjacent to the stomach and subsequently are found in rows extending up into the developing mantle (Figure 3) (Fitt and Trench 1981).

The mechanisms by which zooxanthellae evade digestion and pass through the basal membranes of the stomach, through the digestive gland region adjacent to the stomach, and into the haemal sinuses of the mantle are currently unknown. Nor is it known if the zooxanthellae reside in the host vacuoles or cells during this transition. However, zooxanthellae in adult tridacnids live extracellularly in the mantle haemal sinuses, unlike the zooxanthellae in most symbiotic corals and other coelenterates where they are found in host cells (Trench et al. 1981). The final step in establishing a symbiosis is the growth of the algal cell population in the host.

One of the characteristics of algal-invertebrate symbioses is that neither partner in the consortium outgrows the other. It is not clear whether the host clam plays an active or passive role in regulating its symbionts. The symbiotic algae may be regulated in the host by nutrient limitations. When zooxanthellae are introduced to nonsymbiotic juvenile tridacnid clams, the symbionts grow at rates similar to logarithmically growing zooxanthellae in culture media. As the population of algae increases, though, its growth rate declines to almost zero. These observations suggest that, as with phytoplankton blooms in other aquatic habitats, zooxanthellae in a clam may become nutrient limited (Fitt 1985b).

Tridacnid clams also may limit the zooxanthellae population by transporting the excess in the mantle through the digestive gland, into the stomach, and out the intestine—many in a morphologically and physiologically intact condition (Trench et al. 1981). A third possible method of regulating numbers of symbionts is by

digesting them, but there is no convincing evidence that giant clams do this.

Physiological interactions

Most zooxanthellae in juvenile and adult tridacnids are found in the mantle, but lower densities also inhabit the heart, stomach, and digestive gland. The zooxanthellae photosynthesize and translocate a portion of the photosynthetic products—glycerol and alanine—to their host (Muscatine 1967). The clams use the translocated photosynthate in "all major centers of metabolic activity" (Yonge 1980), including mucous production, byssus production, digestive activity, and shell growth (Goreau et al. 1973).

It is of considerable practical importance to know the extent to which photosynthetic products satisfy the metabolic needs of giant clams. Fisher et al. (1985) examined photosynthesis and respiration in *T. gigas* at Palau and confirmed that the zooxanthellae play a significant role in nourishing the host; under favorable conditions the algae appear capable of supplying over 100% of the host's respiratory carbon requirements. Symbiont contribution to clam nutrition is influenced by ambient light intensity—through its regulatory effect on photosynthesis—and by clam body size, which determines the percentage of ambient light actually reaching the zooxanthellae.

Large clams contain more zooxanthellae than small clams, but have lower densities per unit of tissue. For example, a 25-cm-long *T. gigas* contains about 9×10^9 zooxanthellae, but has only one-third the symbiont density of a 1-cm-long juvenile containing 2×10^5 algal cells. Still, the densities of zooxanthellae in *T. gigas* more than 4 cm long are high enough and the mantle tissue thick enough to reduce significantly the amount of light reaching the algae, thereby lowering their potential photosynthetic output and the contribution of carbon from algae to host.

Zooxanthellae in small (1–2-cm-long) juvenile *T. gigas*, for example, photosynthesize at near maximal rates even at ambient light intensities as low as 500 $\mu E/m^2/sec$, about one-fourth that of natural above-water, noontime intensity on a clear day (and equivalent to the intensity at noon in 5–10 m depths of clear reef water). Zooxanthellae in a 25-cm-long *T. gigas*, on the other hand, receive an average of only 25% of incident light and photosynthesize at only 14% of their potential at 1000 $\mu E/m^2/sec$ of incident light (equivalent to noon intensity in 1–2 m of reef water); this level drops to about 11% at 500 $\mu E/m^2/sec$. These findings indicate that small clams living on the reef or in culture systems can realize maximal growth rates even in shady conditions or deeper water, whereas larger clams need maximal light exposure to achieve maximal growth rates (Fisher et al. 1985).

Tridacnids have other means of acquiring the nutrients needed for growth, reproduction, and basic metabolism. As with most other bivalves, they are filter feeders, capable of ingesting and digesting phytoplankton. The convoluted mantle is efficient in absorbing dissolved nutrients from seawater (Fankboner 1971, Goreau et al. 1973). In addition, degenerate zooxanthellae are often seen in the digestive gland. Early investigators hypothesized a "farming" mechanism, by which the host selected some of the live algae from the mantle and digested them (Yonge 1936). However, observations of degenerate zooxanthellae in clams may also be explained by autodegradation of the algae, and there is no compelling evidence of host digestion of live zooxanthellae. In sum, the tridacnids may acquire nutrients through the uptake of dissolved nutrients; translocation of photosynthates from symbionts; and digestion of phytoplankton and senescent zooxanthellae.

One of the characteristics of an algal-invertebrate symbiosis is that both partners may benefit from nutrient recycling. This characteristic may be especially important in tridacnid symbiosis, because these clams normally inhabit nutrient-poor reef waters. Typically, marine molluscs excrete nitrogenous wastes, primarily as ammonia. In light, intact symbiotic tridacnids efficiently accumulate ammonium and nitrate. Isolated zooxanthellae also demonstrate net influx of these nitrogen compounds. Prolonged dark treatment of intact clams stops the influx of ammonium and nitrate, but the influx resumes upon exposure to light. This observation indicates that the influx of these compounds into clams is due primarily to the symbionts (Wilkerson and Trench 1986).

Symbiotic algae in tridacnids can use exogenous sources of nitrogen, including nitrogenous wastes of their hosts, to make amino acids, which may then become available to the animal. Zooxanthellae also appear to be responsible for the observed uptake of phosphate by symbiotic tridacnids (Deane and O'Brien 1981a, Yonge 1936), and *S. microadriaticum* isolated from *Tridacna maxima* have been shown to take up sulfate and sulfur-containing amino acids (Deane and O'Brien 1981b). Because the ambient reef waters are low in such nutrients, it is possible that providing clams with increased levels of dissolved inorganic nitrogen, phosphate, or sulfate under conditions of mariculture could increase their growth rates.

Advances in cultivation

In the Asia-Pacific region today there are more than 15 groups of scientists involved in experimental giant clam culture and related research. Research programs have been established throughout Micronesia (Palau, Yap, Saipan, Pohnpei, Truk, Kosrae, and Marshalls) as well as in Australia, the Philippines, Fiji, Papua New Guinea, the Solomon Islands, the Cook Islands, American Samoa, Hawaii, and Japan (Heslinga and Watson 1985). About half of the research teams that have been working on tridacnids have succeeded in spawning the adult clams and rearing the larvae beyond metamorphosis. In Australia, two commercial giant clam hatcheries have opened near Cairns on the Great Barrier Reef.

At the Micronesian Mariculture Demonstration Center (MMDC) in Palau (Figure 4a), a multiyear, research and development effort sponsored by the Pacific Fisheries Development Foundation (NMFS-NOAA) and the US Department of the Interior has led to the establishment of the region's first commercial-scale hatchery. Four of the seven tridacnid species (*Tridacna squamosa, T. gigas, T. derasa,* and *Hippopus hippopus*) have

Figure 4. Giant clams under cultivation. Small coastal hatcheries (a) can now produce hundreds of thousands of seed clams (b) each year. Land-based nurseries require only sunlight and flowing seawater to grow clams to reproductive maturity (c); no feeding is necessary because nutrition is provided by symbiotic zooxanthellae. Ocean-based clam farms (d) are currently being established in many Indo-Pacific island nations.

been mass cultured (Heslinga et al. 1984b).

T. derasa, the focus of present efforts, has been reared to maturity at five years postfertilization, and several second-generation cohorts have been produced. Cultured specimens planted on the reefs of Palau have attained an aggregate weight of more than 30 tons and in some areas have started to breed. Between 1979 and 1982, production from the Palau hatchery was low and sporadic. In 1983, however, about 30,000 seed clams (Figure 4b) were produced; output was increased to 100,000 seed in 1984 and to more than 250,000 in 1985 (Heslinga and Watson 1985). Two seed clam sizes are currently being marketed: 6-month-old specimens (15 mm long) at $0.25 each and 12-month-old specimens (50 mm long) at $1.00 each.

Most of these juvenile clams have been planted in the waters of Palau, but a portion has been air-shipped abroad as part of a regional transplanting program. Tens of thousands of young clams have been exported and planted on the reefs of Guam, Yap, Saipan, Truk, Ponpei, Kosrae, Majuro, American Samoa, the Philippines, and the Cook Islands. An experimental, land-based giant clam nursery has been established in Kona, Hawaii. Concomitant with the production and sale of seed clams at Palau's MMDC has been a tridacnid mariculture training program, which has been completed to date by more than 35 biologists representing 14 Pacific nations.

Early problems overcome

The most serious technical obstacles to giant clam mariculture had been considered to be the limited spawning season in wild populations, the unknown larval diet, the difficulty of handling bysally attached postlarvae, the rapid fouling of culture tanks by filamentous algae, and the vulnerability of juvenile clams to natural predators (Beckvar 1981, Heslinga et al. 1984b, Yamaguchi 1977). Today these problems have been largely overcome.

Spawning in giant clam hatcheries is now being induced year round with reasonable reliability. Like many broadcast-spawning invertebrates, gravid tridacnids respond to mildly stressful stimuli, such as handling,

warming, or rapid water movement. Excised gonadal material from conspecifics is effective in stimulating gamete release, and it retains its potency when frozen or freeze-dried (Munro and Heslinga 1983). In addition, workers in Australia have recently shown that the neurotransmitter serotonin, effective in inducing oysters, scallops, and mussels to spawn (Gibbons and Castagna 1984), works equally well with giant clams (Braley 1985).

Tridacnid larvae are now known to thrive on a diet of phytoplankton species such as *I. galbana* and its congeners, which are routinely cultured in laboratories around the world. In Australia, intensive larval rearing techniques like those used in the oyster hatchery industry have been applied successfully to giant clam culture. This high-tech approach is appealing because it relies on relatively small, space-saving culture vessels, high larval densities, and a carefully controlled larval feeding regime. Disadvantages include high labor and capital costs and a susceptibility to bacterial blooms in culture vessels.

The most dramatic results in giant clam seed production have been achieved with the Wells-Glancy method, a simple, low-cost approach that feeds larvae on multispecific blooms of local phytoplankton (Heslinga 1986). The larvae are cultured at low density in large, sunlit raceway tanks (Figure 4a). The Wells-Glancy procedure has proven successful in the culture of many bivalve species (Castagna and Kraeuter 1981), so it is not surprising that it works with tridacnids. Zooxanthellae in the postlarval phase are provided by the addition of cells freshly isolated from adult or juvenile conspecifics. This low-tech approach to giant clam larval rearing seems most appropriate for the developing nations of the Asia-Pacific region; it is similar in essence to the method now used successfully in China for mass production of the clam *Tapes philippinarum* (Zhong-Qing 1982).

The problem of handling byssally-attached tridacnids in the postlarval phase has been solved with an aggregated culture substrate, such as basalt chips or crushed coral. Young clams readily attach to these materials but may still be moved easily without traumatizing the byssus (Heslinga et al. 1984b). This technique parallels the use of sand grains as settlement surfaces in the commercial production of "cultchless" oyster seed.

Biofouling can cause potentially serious difficulties in any aquaculture system. Giant clam nursery tanks are conducive to the growth of filamentous algae, which are undesirable because they shade and smother the clams while stripping nutrients from the seawater. This problem has been overcome by the introduction of algal-grazing snails (*Trochus niloticus*). Trochus of the appropriate sizes for polyculture with juvenile clams can now be produced routinely in hatcheries (Heslinga 1981a,b, Heslinga and Hillman 1981). When the snails grow too large for polyculture, they can be released in sanctuaries to help augment natural stocks (Heslinga et al. 1984a).

The Palau giant clam hatchery now produces 10,000–20,000 seed clams per 20 m^2 tank per five to six month rearing cycle, and an average of two rearing cycles can be completed each year. With present ocean nursery methods, 20–30% of the seed clams survive to sexual maturity. Better survival rates can be attained in land-based nurseries (Figure 4c), but cultivation costs are generally higher. Judging by the pace of recent advances in production technology it is reasonable to project that within a few years giant clam hatcheries will be capable of producing millions of seed juveniles annually. Large hatcheries will be required to achieve this output, because physical constraints limit production of 10-mm seed to a maximum of about 2000/m^2 per rearing cycle.

Tridacnids require direct exposure to sunlight, so they must be grown in two-dimensional systems. In the sea, only the surface or the bottom, not the entire water column, may be used. Floating giant clam nurseries have been proposed, but bottom culture in trays is probably more practical and less likely to interfere with other uses of the coastal zone. Bottom-based tray nurseries have already been established at more than 20 sites in the tropical Pacific and are working well. These nurseries use lightweight, modular plastic trays that rest directly on the shallow bottom near leeward reefs (Figure 4d). The trays are deployed by divers, filled with basalt or coral aggregate and fitted with covers of 2.5-cm polyethylene mesh (Heslinga et al. 1986). Seed clams are planted in the trays and allowed to grow for about two years before being transferred directly onto the sandy bottom. After outplanting no further care is required and survival is high.

The lidded trays are effective against such predators as carnivorous fishes, crabs, and octopuses. When the lids are removed in experiments, these predators devour the baby clams with startling speed and efficiency. In Micronesia only one predator, the small snail *Cymatium muricinum*, is able to penetrate the mesh lids (Perron et al. 1985). Damage from this pest can be kept to acceptable levels by twice each week manual removal by divers. Biofouling of the mesh lids is controlled fortuitously by the grazing activities of parrotfish, surgeonfish, and rabbitfish.

Production potential

Under conditions of mass cultivation, tridacnid biomass production per unit of area is remarkably high, especially considering that no supplemental feeding is required beyond the larval phase. *T. derasa* juveniles raised in Palau produced edible meat at the rate of 1.6 kg/m^2/year (equivalent to 16 tons/ha/year) during ages 0–3 years (Heslinga et al. 1984b). Meat weight in maricultured *T. derasa* quadruples between ages three and five years, and shell weight increases by a factor of seven. Growth rate begins to decline with the onset of reproductive maturity at age five years. Tridacnid farmers harvesting five-year-old animals could, in theory, produce edible meat at the rate of 22 tons/ha/year, with about 140 tons of shell as a by-product (Heslinga and Watson 1985). By terrestrial or marine standards, these are exceptional production rates, and the achievement of even a fraction of these yields would be attractive to subsistence or commercial mariculturists (cf. Munro 1983).

Of the meat produced, about 85% is soft tissue (e.g., mantle, gonad, and viscera), esteemed by Pacific peoples and highly suitable for local consumption. The remaining 15% is adductor muscle, which can be eaten

locally or exported to Asian markets (Dawson 1986, Munro 1983). The tridacnid shell is also valuable as an export product in itself or as a raw material for local cottage industries (Heslinga 1986).

Giant clam farming is one example of an aquaculture activity that could help raise local nutritional standards and generate cash income simultaneously (Kent 1986); often these are conflicting goals. Our optimism, however, must be tempered by the recognition that in the traditional villages of Oceania, agriculture and fisheries activities are pursued primarily to satisfy nutritional needs, secondarily to fulfill social obligations, and only very rarely for cash profits. While it can be expected that private companies in such developed nations as Australia will pursue tridacnid mariculture as a business-for-profit, remote Pacific Island communities will more likely embrace the technology as a means of supplementing their subsistence farming and fishing activities, providing enhanced nutritional security, and reducing dependence on imported foods. An appreciation of these fundamentally divergent objectives will be central to the planning, implementation, and evaluation of future tridacnid mariculture programs.

Conclusions

Although the process of domesticating giant clams is still in its early stages, there is reason to be encouraged both by the technical progress to date and by the enthusiastic response to the concept, particularly in the developing countries of the Pacific Basin. A great deal has been learned about the biology and culture of tridacnids in the last decade, and it is not unrealistic to envision an array of beneficial spinoffs—some already being realized—ranging from local conservation and subsistence food production schemes to large-scale commercial enterprises generating employment opportunities and export revenue.

Much remains to be done to stimulate the development of the giant clam mariculture industry, however. There is an immediate need for the establishment of production-oriented hatcheries to meet the expanding regional demand for seedstock; at present insufficient seed supplies are the most serious constraint limiting the proliferation of tridacnid farms. There is also a need for hatcheries with research orientation to assist the industry by developing improved culture technology, conducting training courses, selecting genetically superior broodstock strains, disseminating information, and developing computer software to facilitate hatchery and nursery management.

Finally, there is a continuing need for basic research on tridacnid life processes, particularly physiology, pathology, and interaction with symbionts. Such work can be expected to yield valuable insights. A good example is the recent discovery of different strains of *S. microadriaticum*, distinguishable by biochemical, physiological, morphological, and genetic characteristics (Blank and Trench 1985, Trench 1979). It has been demonstrated in the laboratory that giant clams infected with fast-growing strains of zooxanthellae grow faster than those living in symbiosis with slow-growing strains (Fitt 1985b). It may now be possible to increase the productivity of giant clams under maricultural conditions by introducing optimal strains of zooxanthellae to the juveniles.

Acknowledgments

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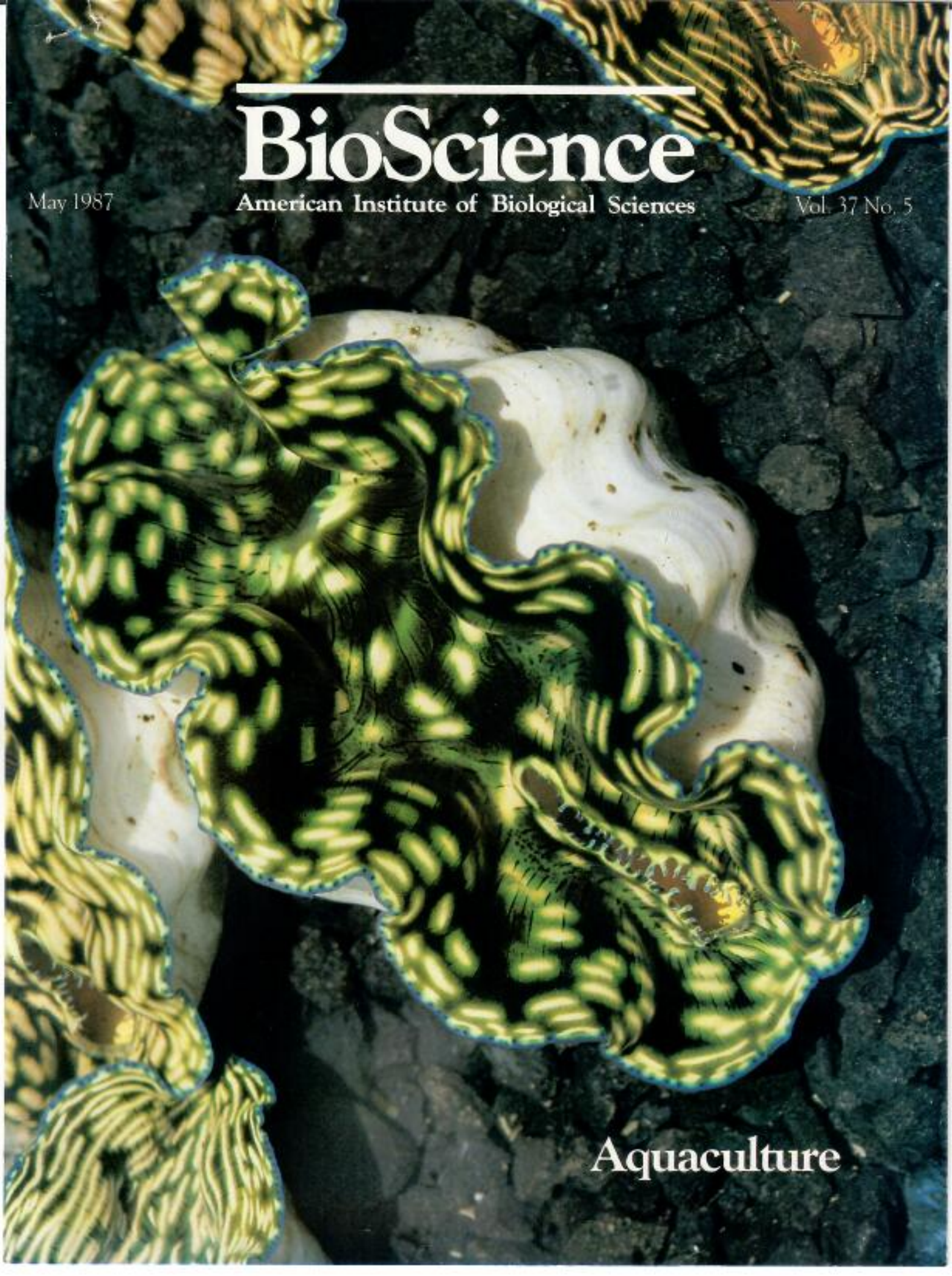

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