A Review of Tridacnid Ecology and Some Possible Implications for Archaeological Research

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BARBARA G. MOIR

INTRODUCTION

The manufacture and use of Tridacna adzes have long been associated with cultures inhabiting atolls and raised coral islands in the Pacific region. A survey of the archaeological and ethnographic literature reveals that Tridacna adze blades have been found on numerous volcanic islands as well, establishing a fairly broad range of island habitats for the distribution of these tools.

To date, the study of Tridacna adzes by archaeologists has focused almost exclusively on typological classification and culture-historical relationships (Kennedy 1931; Thompson 1932; Speohr 1957; Osborne 1966; Rosendahl 1969; Davidson 1971; Garanger 1972; Craib 1977; Ward 1979; Takayama and Intoh 1980; Kirch and Yen 1982; Sinoto 1984), with primary analytic emphasis given to the form and style of the blade. The materials (Tridacna spp. and, rarely, Hippopus hippopus) from which these tools were made have received minimal attention, except to consider their morphological properties and the relevance of these to tool form and efficiency. The Tridacnidae as components of reef ecosystems, together with their microenvironmental requirements for life, suggest a different focus for investigation that may have important implications for archaeological research.

This article surveys the ecology of two tridacnid species, Tridacna (Tridacna) gigas (Linne) and Tridacna (Chametraechea) maxima (Röding)—the species most often identified in Tridacna adze assemblages—and examines the recorded distribution of Tridacna adze blades throughout the Pacific from an ecological perspective. It offers five propositions that might be of use to archaeologists in the development of an ecologically based model of Tridacna adze distribution. Finally, it underscores the significance of a multidisciplinary approach to the study of material culture, and suggests that ecological as well as cultural variables will affect the form and geographical distribution of Tridacna tool assemblages.

Barbara G. Moir is affiliated with the Anthropology Department of the University of Hawaii—Manoa.
THE FAMILY TRIDACNIDAE GOLDFUSS:  
AN ECOLOGICAL SKETCH

Distribution

The seven extant species of the family Tridacnidae (Tridacna gigas, T. maxima, T. derasa, T. squamosa, T. crocea, Hippopus hippopus, and H. porcellanus) are found only in the Indo-Pacific region, where they inhabit the shallow waters of coral reefs to a depth of some 20 m (Rosewater 1965, 1982). Depending on the species, these sessile bivalves either rest unattached on the reef or lagoon bottom, or form weak to strong byssal attachments to the coral substrate. Some species bore into coral pockets, becoming embedded to varying degrees.

Of the two species with which this article is concerned (T. gigas and T. maxima), the latter is widespread in geographical distribution (Fig. 1), ranging from coastal East Africa (Indian Ocean) to the Tuamotus (eastern Pacific), and from the Mariana Islands (northern Pacific) to offshore eastern Australia (Coral Sea). *Tridacna gigas* has a far more limited range at present, extending from western Sumatra (Indian Ocean) to Tuvalu (central Pacific), and from the Philippines (northern Pacific) to Australia's Great Barrier Reef. It should be noted that populations of these species are not ubiquitous throughout their ranges. Moreover, there is evidence that *T. gigas* was once much more widely distributed than it is today: fossil specimens have been found on reefs as far west as eastern Africa (Taylor 1978) and as far north as Guam (Rosewater 1965). *Tridacna gigas* became extinct in Fijian waters as recently as the early 1970s, and today is only rarely found in the Philippines (Munro n.d.) and Indonesia (Usher 1984; Brown and Muskanofola 1985).

The present disparity in geographical extent between these two species is not readily accounted for on environmental grounds, as the two ranges share the same general mix of reef-habitat variables. Length of the larval stage may be a contributive factor. Under laboratory conditions, larvae of the widespread *T. maxima* were observed to have settled by day 11 and metamorphosed by day 12 postfertilization (Jameson 1976), while for larvae of *T. gigas*, the more narrowly distributed species, settlement and metamorphosis had occurred by days 6 and 8, respectively (Heslinga et al. 1984; cf. Crawford et al. 1986). Probably a number of factors affect species distribution. It is likely that the more restricted tridacnid ranges are due at least in part to differential retraction in “territories” during the Pleistocene (Taylor 1971, 1978), and in part to overexploitation by humans.

Reproduction and growth

All members of this family are sequential, simultaneous hermaphrodites; the gonads of mature individuals contain both sperm and eggs. Spawning behavior appears to correlate with water temperature and other environmental stimuli (Rosewater 1965; Yonge 1974; Jameson 1976; cf. Wada 1954 and LaBarbera 1975), notably a chemical signal emitted by the eggs that instigates the spawning sequence (Munro et al. 1983; Braley 1984; Munro n.d.). Lunar and perhaps seasonal spawning periodicities are indicated for the Tridacnidae on the basis of laboratory observations (Jameson 1976; Beckvar 1981; Fitt et al. 1984; cf. Gwyther and Munro 1981 and Crawford et al. 1986) and *in situ* reef studies (Braley 1984). Diel periodicity has been noted for spawning in *T. gigas* (Braley 1984; Heslinga et al. 1984). Tridacnid popula-
Fig. 1 Geographical distributions of *Tridacna (Chametraeia) maxima* (Röding) and *Tridacna (Tridacna) gigas* (Linne). Redrawn after Rosewater (1965) and Munro (n.d.).
tions are believed to maintain themselves through "recruitment" of juveniles that develop from the gametes of local adults (Yamaguchi 1977)—i.e., the majority of offspring tend to settle and metamorphose in the vicinity of their spawning.

Long- and short-term scientific data demonstrate considerable variability in the growth rates of *T. gigas*. Tagged specimens showed annual increases in shell length of 51 mm (Rosewater 1965), from 50–80 mm (Bonham 1965), from 80–120 mm (Beckvar 1981), and means of 55 mm (J. Munro, pers. comm.) and 142 mm (Hamner n.d.) during the respective periods of investigation. There is also evidence for marked variation in tridacnid growth rates relative to latitude (Munro and Gwyther 1981; Munro and Heslinga 1983; Pearson and Munro n.d.) and to habitat—e.g., between *T. gigas* specimens found on pristine reefs and in more turbid sites near areas of human activity (J. Munro, pers. comm.)—and even among members of the same apparent cohort under uniform environmental conditions (McKoy 1980; Beckvar 1981; Munro and Heslinga 1983).

McMichael (1974) measured the growth of different size classes of *T. maxima* under natural conditions; their annual mean increment ranged from 1.0 mm (for the largest clams) to 38 mm (smallest clams). For all tridacnids, growth increment appears to be a function of the size of the clam at first measurement; the rate of growth seems to be most rapid during the early years of life, slowing as the clam grows larger (McMichael 1974; Yamaguchi 1977; Beckvar 1981; Romanek et al. 1987; Pearson and Munro n.d.). Specimens of *T. maxima* have achieved shell lengths of 35 cm, while *T. gigas* has been known to reach more than 1 m in length (Rosewater 1965), but in extant populations of both species such individuals appear to be rare.

### Nourishment

The Tridacnidae, like most bivalves, are filter feeders of phytoplankton, and they absorb dissolved inorganic nutrients from seawater (Fankboner 1971; Goreau et al. 1973). Perhaps the greatest metabolic benefit, however, is obtained through a highly specialized method of nourishment that is nearly unique among bivalves (Rosewater 1965). In addition to extracting nutrients from phytoplankton and utilizing dissolved inorganic substances found in seawater, tridacnids also harbor and benefit from vast numbers of zooxanthellae—unicellular algae residing in the haemal sinuses of the clam's haemocoele (Yonge 1936; Muscatine 1967; Trench et al. 1981; Fisher et al. 1985) and to a lesser extent in the heart, stomach, and alimentary tract (Goreau et al. 1973; Trench et al. 1981). Zooxanthellae are also found in the hermatypic corals. The highly developed association of these algae and the Tridacnidae is reflected in the clams' morphology, habits, and the environmental conditions under which they occur (Rosewater 1965; Goreau et al. 1973; Yonge 1974).

The initial uptake of zooxanthellae from the environment apparently occurs in the veliger stage of clam development (Fitt and Trench 1981). Colonies of these symbionts infest the enlarged inner folds of the mantle. When covered by the tide, these folds extend laterally from the gaping valves and are maximally exposed to sunlight, permitting photosynthesis to take place within the zooxanthellae. Tridacnids may receive some food energy via digestion of the algae, but the primary metabolic gain is believed to derive from released photosynthates (Goreau et al. 1973; Yonge 1980; Trench et al. 1981), specifically glycerol and alanine (Muscatine 1967).
The relationship between tridacnid and zooxanthellae is that of a more or less mutualistic symbiosis (Barrington 1982): the algae are sheltered, nourished with nitrogenous wastes, and given access to sunlight by their host; the clam in turn has a ready source of nitrogen compounds (Wilkerson and Trench 1986), phosphate (Yonge 1936; Deane and O’Brien 1981), and other nutrients that occur only in low concentrations in reef waters. The efficiency of this relationship may be partially responsible for the ecological success and extremely large sizes attained by some of the tridacnid species. Moreover, the morphology of both the animal and its shell has apparently undergone significant modification through time in adaptive response to the specialized development of this feeding method (Yonge 1980). The specializations in morphology, habitat, and behavior of these species may be viewed as adaptations to this bivalve–algal symbiosis (Rosewater 1965).

Habitat

Hermatypic Coral Substrate

All species of tridacnid occur in association with hermatypic coral formations, including reefs (atoll, fringing, barrier, and patch) and massive coral structures (such as those formed by Porites and Acropora spp.).

*Tridacna maxima* is firmly attached to coral by means of strong byssal threads and is often found burrowed deeply into the substrate, but not to the extent of imprisonment. *Tridacna gigas*, by contrast, has no burrowing tendencies whatsoever and inhabits sandy lagoon bottoms as well as reefs and coral heads. Only in the pediveliger stage does *T. gigas* form a weak byssal attachment to a coral substrate; in maturity the bivalve maintains its upright position solely by the weight and mass of its shell. These stabilizing features may enhance the species’ ecological success on windward reefs, under surf conditions. Adult *T. gigas* observed on such reefs in Belau were much heavier and more massive than those found in nearby lagoon waters (Hardy and Hardy 1969).

The hermatypic corals may also be the source of the young clams’ first infestation with zooxanthellae (LaBarbera 1975; Yonge 1980; Fitt 1984). Hermatypic corals and various reef invertebrates are known to harbor populations of the same algal species (*Symbiodinium [= Gymnodinium] microadriaticum*) as that found in the Tridacnidae (Freudenthal 1962; Taylor 1973), and to expel numbers of these algae into the marine environment under certain conditions (Yonge and Nicholls 1931; Goreau 1964; Steele 1975, 1977; Jaap 1979; Gwyther and Munro 1981).

Seawater Temperature

The Tridacnidae apparently require a warm marine environment for spawning and for the growth and development of juveniles. Spawning has been induced in *T. maxima* at temperatures ranging from 24.9°C (LaBarbera 1975) to 28.5°C (Jameson 1976) and from 30–35°C (Fitt and Trench 1981), and in *T. gigas* at 22.5°C (Crawford et al. 1986), from 27–30°C (Heslinga et al. 1984), and from 27–33°C (Beckvar 1981). Other tridacnid species as well have successfully spawned under laboratory conditions at similar temperatures (Stephenson 1934; Wada 1954; Rosewater 1965; Hardy and Hardy 1969; Hirschberger 1976; Jameson 1976; Beckvar 1981; Fitt et al. 1984; Heslinga et al. 1984). Some fluctuation in temperature is evidently tolerated (under natural conditions this could be a seasonal factor), but the confinement of Tridacnidae distribution to consistently warm waters indicates that this family is effectively stenothermal.
For marine fauna in general, temperature ranges favorable to reproduction and juvenile development are far more narrow than those tolerated by adult individuals (Sverdrup et al. 1954). Beyond providing a necessary condition for spawning, however, water temperature plays an important role in determining the rate at which the developing tridacnid animal can precipitate calcium carbonate from seawater for the formation of its shell (Sverdrup et al. 1954; Romanek et al. 1987).

**Seawater Clarity**

The clear water habitat of tridacnids facilitates the transmission of light to their zooxanthellar symbionts. Hardy and Hardy (1969) found that the limiting depth (10–20 m) for the growth of tridacnids on Belau’s reefs was determined in large part by the water’s clarity, and by the insufficiency of light for photosynthesis at depths greater than this (see also Brown and Muskanofola 1985). Their study of *Tridacna* ecology in Belau revealed the following microhabitat distributions for *T. gigas* and *T. maxima*: both were very seldom found in the bays, occasionally in the lagoons, and most often in the clear waters of the fringing and barrier reefs. The primary hydrographic difference between these microhabitats is that of water clarity, with the reef areas providing the optimal condition (Motoda 1940).

On Fanning Atoll, Kay and Switzer (1974) found the lagoon basin effectively divided into a clear-water area near the deep reef pass (transparency to 10–15 m), and turbid-water sectors elsewhere (transparency less than 2 m). Distribution of *T. maxima* (the only tridacnid species present) was confined to the clear lagoon, where massive corals (*Porites* and *Acropora*) permitted settlement above the carbonate mud sediments. However, fossilized *Tridacna* valves were found embedded in exposed sections of fossil reefs. Their occurrence in areas presently devoid of living *Tridacna* suggests changes in lagoon character associated with the closure of former reef passes that would have affected water clarity, coral growth, and/or sea level.

Renaud-Mornant et al. (1971) demonstrated the confinement of *T. maxima* distribution on an atoll in the Tuamotus to the more shallow, transparent depths of that atoll’s lagoon. Their data underscore the importance of seawater clarity to tridacnid survival. Moreover, studies of the geomorphological effects of tropical storms on coral reefs suggest that increased turbidity of reef waters following erosion may delay recovery of hermatypic corals (and their faunal associations) for as many as 30 years (Stoddart 1971).

**Seawater Salinity**

Tridacnids are found in waters with salinity levels of near 35 ppt. The minimum salinity level tolerated by tridacnids is not known, but it may be related to that of the hermatypic corals with which they are associated; tropical corals have been reported to withstand a 20 percent reduction in the salinity of their environment (Sverdrup et al. 1954). *Tridacna gigas* has been successfully maintained in raceways at a level of 32 ppt (Beckvar 1981; Heslinga et al. 1984) and on reef sites, together with *T. maxima*, at about 30 ppt (Munro and Gwyther 1981).

At the opposite end of the spectrum, at least one species of *Tridacna* is known to tolerate higher saline levels than those normally found in the open ocean. *Tridacna maxima* occurs in enormous numbers in the closed lagoons of Rcaö, Maturei Vavao, and Takapoto atolls in the Tuamotus, which have salinity levels of 37.5, 37.5, and 43 ppt, respectively (Salvat 1970; Renaud-Mornant et al. 1971; J. Newhouse, pers.
Viable populations of *T. maxima* are maintained in the less saline waters of open atolls and barrier reefs as well, indicating this species apparently will withstand some fluctuation in this variable.

**Sunlight**

Light is essential to photosynthesis in zooxanthellae; in the tridacnid environment it warms the water to temperatures favorable for spawning and development. Laboratory experiments suggest that sunlight may be the single most influential factor in tridacnid growth (Beckvar 1981; see also Fisher et al. 1985 and Crawford et al. 1986). The ocean's photic zone, in which illumination is adequate for photosynthesis, extends to a depth of about 80 m; however, hermatypic corals do not grow much below 50 m, and the Tridacnidae are confined to depths of about 20 m or less. The highly specialized exploitation of zooxanthellae probably dictates the tridacnid habitat of relatively shallow, sunlit reef water. The availability of phytoplankton on which these bivalves also feed is limited, particularly during daylight hours (Gorcău et al. 1973); the Tridacnidae inhabit those environmental zones in which the greater nutritive benefits of zooxanthellal photosynthates may be realized.

**Limiting Factors and Habitat Variables**

The foregoing discussion illustrates the physical and biological requirements of the Tridacnidae, together with the general environmental conditions under which these needs may be met. Consideration of certain limiting factors, or variables that tend to limit the rate of metabolism or potential growth of a *Tridacna* population, may be especially relevant to Indo-Pacific archaeologists.

Within a reef ecosystem, three factors are of importance in limiting the viability of tridacnid populations. Two of these, seawater salinity and turbidity, are environmental variables, which are circumstantial in their operation and probably affect a wide range of organisms in addition to the Tridacnidae. The third factor, human exploitation, concerns the relationship between man and his environment, operates under cultural impetus, and may affect only the *Tridacna* population being exploited. The environmental conditions under which the Tridacnidae occur, together with the cultural factors that constrain their potential for viability, are seen to combine in ways that may have predictive value for the archaeologist. These combinations of variables may be characterized, in terms of the ecological success of tridacnids, as marginal, competitive, and exceptional habitats.

*Marginal habitats* offer the basic requirements for tridacnid growth and reproduction, but are highly subject to the operation of one or more limiting factors, which tend to adversely affect a population's chances for survival. Examples of marginal habitats include reef areas adjacent to volcanic islands where freshwater stream and silt runoff continually reduces seawater salinity and increases turbidity; atolls (particularly those with fairly shallow lagoons) that are frequently subject to tropical storms and the accompanying desedimentation of islets; heavily sedimented reefs or lagoon floors, usually the result of poor lagoon circulation and/or cultural activity; and reefs where *Tridacna* populations are intensely exploited by humans for food and/or material culture.

Human exploitative behavior can have a significant impact on the viability of
Tridacna populations. If one assumes the normal maintenance of population levels through local recruitment of juveniles by adults, it would be reasonable to predict that intensive exploitation of a population might well result in decimation or local extinction of a species (Wells et al. 1983). Should this happen, it would be unlikely to recover without reintroduction (Yamaguchi 1977; Hirschberger 1980; Hamner n.d.). Studies by Hardy and Hardy (1969) and by Bryan and McConnel (1976) indicate a substantial decline in population densities for larger tridacnid species on the reefs of Belau; this decline is viewed as the direct result of overfishing for the export of shell (see also Hester and Jones 1974). In recent years T. gigas has become extinct in the waters off Pohnpei, Truk, and Kosrae, presumably as a consequence of human exploitation (Heslinga et al. 1984). Taiwanese fishing vessels, in particular, are known to poach enormous quantities of the adductor muscle—abandoning the remaining flesh of the clam—from isolated and vulnerable reefs in the western Pacific (Pearson 1977; Wankowski 1979; Gwyther and Munro 1981; Hamner n.d.; Moir n.d.a). In the prehistoric period as well, the success of any Tridacna population would have been directly related to the density of local human settlement and to the extent and rate of exploitation. Where rates of tridacnid reproduction, recruitment, and growth do not keep pace with the demand for this resource, human behavior creates a marginal habitat for the Tridacnidae.

The conditions necessary for tridacnid life are also found to combine in ways that permit a high level of species richness, but where competition for resources may limit the number of individuals the habitat can support. These combinations may be termed competitive habitats. Open atolls (with three or more deep reef passes) in particular, and those fringing and barrier reef areas unaffected by freshwater runoff and siltation, are examples of competitive habitats, where the basic ecological requirements for tridacnid success are met and which are characterized by a higher species richness but lower numerical abundance for some species. The researches of Salvat and Richard (Salvat 1969, 1970, 1971a, 1971b, 1971c, 1972, 1973; Richard and Salvat 1971, 1972) have clearly demonstrated the contrast in molluscan species representation and individual numbers between open atolls/reefs and closed atolls. These reef systems differ primarily in the exchange of open seawater and lagoon water, with corresponding differences in circulation, salinity, and turbidity. Open reef systems apparently offer conditions favorable to a variety of tridacnid species, but competition for available resources may restrict the number of individuals of some species to comparatively low levels.

The findings of Richard and Salvat suggest a third combination of environmental variables that affect the ecological success of the Tridacnidae: the exceptional habitat. Here too are found all the basic requirements for tridacnid survival, but they combine with low faunal diversity and minimal competition for resources to comprise a habitat wherein the represented species may be exceptionally successful. The best example of this habitat where T. maxima is concerned may be the closed atoll (lacking deep reef passes), although semiclosed forms (with one or two such passes) appear to offer comparable opportunities. Radtke et al. (n.d.) found the semiclosed reef of Rose Atoll in American Samoa to support a single tridacnid species, T. maxima, at a density of nearly three specimens per m². Studies by Richard and Salvat of the benthic fauna of Reao, Tureia, Pukarua, Marutea, Puka Puka, Nukutavake, Maturei Vavao, Fangataufa, and Vahitahi atolls in the Tuamotus—all of them closed—revealed T. maxima (the only tridacnid present) to be dominant among all
bivalve species in absolute numbers, in biomass, or in both. On several of the atolls, the average density of *T. maxima* was recorded at 63 individuals per m² (Salvat 1969). Closed atolls, then, would appear to represent exceptional habitats for *T. maxima*, and particularly so in areas (such as the Tuamotus) beyond the current geographical distribution of other tridacnid species.

By contrast, closed atolls within the distributional extent of *T. gigas* may offer only marginal habitats for this species. It is suggested that closed-reef conditions of water flow, turbidity, salinity, and perhaps other variables, tolerated by *T. maxima*, may constitute limiting factors for *T. gigas*. It is further suggested that where the latter species is found on a closed atoll, it will be represented by individuals on the outer reef slope, under environmental conditions rather different from those provided in the closed lagoon—and within range of receiving viable larvae carried by ocean currents from populations on open reefs.

**ARCHAEOLOGICAL CONSIDERATIONS**

The issue of habitat specificity poses a set of problems for archaeologists that warrants further investigation. Do the limiting factors outlined above tend to confine the distribution of viable *T. gigas* populations to specific environments within this species’ range, i.e., open and semiclosed reef systems? Did the prehistoric human inhabitants of such environments have ready access to a wider range of tridacnid species (including *T. gigas*), from which to obtain tool material, than did inhabitants of closed atolls? If, on closed atolls within the distributional overlap of *T. maxima* and *T. gigas*, the latter species were found to inhabit only the outer slope of the reef while other tridacnids were present in more accessible biotopes, might the disparity in access to these resources be reflected in the evidence for their use?

Systematic studies might be conducted to determine the presence or absence and relative abundance of *T. maxima* and *T. gigas* on closed, semiclosed, and open atolls, within the distributional overlap of these two species. Exposed areas of older reefs could be surveyed for embedded valves of these species, which may or may not now be represented as live populations. If *T. gigas* populations were found to occur primarily on open and semiclosed reef systems, then the presence of significant numbers of *T. gigas* artifacts in the cultural deposits of a closed atoll should stimulate investigation into the possibility of external origins for such artifacts. (Certainly this would be the case for any atoll beyond the Recent distribution of *T. gigas*, as the shell of this species would constitute an exotic material in such a context.)

Similarly, if *T. maxima* is demonstrated to have inhabited a variety of reef–lagoon biotopes, one might account for the wider distribution, higher frequency, and greater abundance of *T. maxima* adze blades in the archaeological record from an ecological perspective. Perhaps blades of *T. maxima* predominate not for reasons of cultural/functional preference for this material, but in direct relation to the greater availability of *T. maxima* across habitats. Evidence for a habitat-specific natural distribution of these species, if it exists, would provide an ecological base for a predictive model of *Tridacna* adze distribution.

Open and semiclosed atolls, and the reefs surrounding volcanic and raised coral islands, may be found to support more species of tridacnid than will closed atolls, within the distributional overlap of any or all species. Available data suggest that the two species most often utilized for tool material—*T. maxima* and *T. gigas*—will be
found together on open reefs; on closed atolls, *T. maxima* will be abundant across reef biotopes while *T. gigas* may occur only rarely and only on the outer reef slope. These impressions underlie the following propositions that relate environmental variables (habitat) to ecological variables (success of Tridacnidae):

P1: Open and semiclosed atolls (with one or more deep reef passes) will be characterized by a greater diversity of Tridacnidae species than will closed atolls (lacking such passes), within the distributional overlap of any or all species.

P2: Within the distributional range of *T. gigas*, open and semiclosed atolls will be found to support viable populations of this species in both reef and lagoon biotopes. Populations of *T. gigas* will rarely occur on closed atolls within the range of this species. Where *T. gigas* is represented on a closed atoll within its range, it will be as individuals established on the outer reef and not in the closed lagoon.

*Some Possible Implications for Tridacna Technology*

A fundamental understanding of tridacnid ecology is essential to the study of tools made from this material, particularly for comparative analyses of assemblages between island groups and across habitats. Within the distributional overlap of *T. gigas* and *T. maxima*, prehistoric human populations on open and semiclosed atolls, or on islands with associated reefs, may have had ready access to more species of *Tridacna* for tool material than did communities living on closed atolls. If this were the case, one might anticipate the tool kits of the former to be representative of more *Tridacna* species than those of the latter. It might be argued that whereas open reef systems offered competitive habitats for both *T. gigas* and *T. maxima*, closed atolls constituted only marginal habitats for *T. gigas* but competitive or even exceptional habitats for *T. maxima*, and that differences in the availability of these resources might correspond with variation in the extent to which they were exploited for tool material.

These speculations may be stated in the form of the following propositions that relate environmental variables (habitat) to material culture variables (*Tridacna* adzes):

P3: Within the distributional overlap of *T. gigas* and *T. maxima*, *Tridacna* adze kits manufactured and used by the prehistoric inhabitants of open and semiclosed atolls, or of volcanic and raised coral islands with associated reefs, will in general include blades made from the valves of both species.

P4: Within the distributional overlap of *T. gigas* and *T. maxima*, *Tridacna* adze kits manufactured and used by the prehistoric inhabitants of closed atolls will in general be characterized only by blades made from the valves of *T. maxima*. The low frequency with which *T. gigas* populations occur in this environmental context suggests the possibility of external origins for locally recovered tools made from this material.

Artifactual and ethnoarchaeological data (Moir n.d.b, 1989; BPBM and other collections) indicate that more parts of the *T. gigas* valve were utilized for tool material than was the case for *T. maxima* or other tridacnid valves. Valve features identifiable from *T. gigas* adze blades include the hinge line, individual radial folds, the hinge line plus anterior valve end, and the umbonal region (Fig. 2). By contrast, *T. maxima* blades were fashioned primarily from the valve body between the dorsal margin (lip) and ventral/hinge lines (Fig. 3)—an area frequently misidentified by
Fig. 2. Exterior and interior views of valves of *Tridacna (Tridacna) gigas* (Linné). Valve sections most often identified from *T. gigas* are outlined.
archaeologists as the "ventral lip"—as were two H. hippocus adze preforms recovered from Takuu (Moir n.d.b) and another from Bikini (C. Streck, unpublished data). The same region of the T. squamosa valve may also have been used for blade material (Sinoto 1984), as well as the thicker umbonal section (Moir n.d.b). In general, owing to their proportionately greater mass, the umbonal and hinge line areas of a mature T. gigas valve would have yielded a more plastic tool material than the corresponding features of the valves of smaller species. Given this greater morphological plasticity, and the evidence that more parts of the T. gigas valve were used for tool material than of other tridacnid valves, it might be argued that the inhabitants of open and semiclosed atolls and islands with associated reefs possessed Tridacna adze kits characterized by a greater diversity of blade form than those produced on closed atolls.

This suggests a further environmental–material proposition:

P5: Within the distributional overlap of T. gigas and T. maxima, Tridacna adze kits manufactured and used by the prehistoric inhabitants of open and semiclosed atolls, or of volcanic and raised coral islands with associated reefs, will be characterized by a greater diversity of blade form than will those produced on closed atolls.

These last three propositions may easily be tested, initially through a careful examination of the available literature and collections, and more rigorously through archaeological investigation. The findings should be interpreted from the perspec-
tive of local environmental conditions, resource availability, and general tridacnid ecology.

"Armchair" investigation of these issues is fraught with a number of problems, including incomplete data, inaccurate identification of Tridacnidae species by anthropological fieldworkers and various writers, and inadequate familiarity (on the part of some archaeologists) with differential tridacnid morphology. Such limitations notwithstanding, an extensive survey of archaeological, ethnographic, and other reports of Tridacna adze blades was undertaken. The survey did not address the issue of typological variability (P5) but focused on the species identification (where possible) of tool material (P3 and P4).

The geographical and environmental distribution of specimens recorded in the literature and/or available to me in collections is presented in Tables 1–3. These tables reveal a fairly extensive diffusion throughout much of the Pacific region, a range that is not confined to atolls where lack of basaltic or other rock might dictate a reliance on shell for tool material. Tridacna blades are found on all three landforms surveyed—atolls, raised coral islands, and volcanic islands—including areas known to offer alternative tool substances. Whether this suggests in some cases a cultural or functional preference for Tridacna is not considered here. Rather, in examining the recorded occurrence of Tridacna adze blades throughout the Pacific region, relative to the ecological conditions under which the relevant species are known to occur, some possible implications of this ecological approach for archaeological inquiry are briefly explored.

Tables 1–3 illustrate the recorded distribution of Tridacna blades on volcanic islands, raised coral islands, and atolls, respectively. A special distinction was made between the categories of volcanic and raised coral islands. Many islands in the Pacific (e.g., Santa Cruz, Niuatoputapu, Palawan, Guam) possess both volcanic and emerged limestone features; for the purposes of this survey, such islands were included in the volcanic category. Islands designated in Table 2 as "raised coral" have no emerged volcanic characteristics.

Each table differentiates the data on the basis of material (T. gigas, T. maxima, and unidentified Tridacna sp.). In constructing these tables, tool material was categorized as "T. gigas" or "T. maxima" if reported as such and/or clearly identifiable as such from photographs, line drawings, descriptions, or inspection of collections. Where the reported species differed from that identifiable from accompanying photographs or drawings on the basis of known differences in shell morphology, the corrected categorization was used. Where species was not clearly recognizable on the basis of morphology, or where species identification was not given in reports, tool material was classified as "unidentified Tridacna sp."

Table 3 is further subdivided in the classification of atolls as "open" (having three or more deep reef passes), "semiclosed" (one or two deep passes), and "closed" (lacking such passes).

The data in Table 1 reflect the reported presence of Tridacna adze blades on volcanic islands with associated reefs. No Tridacna blades have been recorded for islands without adjacent reefs, with the exception of two anomalous specimens from New Zealand (Skinner 1920). It is clear from the biophysical evidence that the common denominator of Tridacnidae habitats is the presence of hermatypic corals; where such corals do not occur, the presence of Tridacna tools in cultural deposits may be viewed as the result of human importation.
TABLE 1. RECORDS OF *TRIDACNA* ADZES ON VOLCANIC ISLANDS

<table>
<thead>
<tr>
<th>Localities</th>
<th>Species</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beaulieu; France</td>
<td><em>T. gigas</em></td>
<td>Aneityum, Buka, Efate, Ishigaki, New Britain, New Ireland, Niuatoputapu, Pohnpei, Retoka, Sanga Sanga, Santa Cruz, Tikopia, To'io, Tongoa, Yap</td>
</tr>
<tr>
<td>Fefan; Guam</td>
<td><em>T. gigas</em></td>
<td>Garanger, Bath &amp; Shun, Hiro &amp; Clayshulte, Kosrae, Lelepa, Okinawa, Palawan, Pohnpei, Retoka, Sanga Sanga, Santa Cruz, Tikopia, Tol, Tongoa, Yap</td>
</tr>
<tr>
<td>Palau; Okinawa</td>
<td><em>T. gigas</em></td>
<td>Christian, Christian &amp; Shun, Garanger, Hiro &amp; Clayshulte, Okinawa, Palawan, Retoka, Sanga Sanga, Santa Cruz, Tikopia, Tongoa, Yap</td>
</tr>
</tbody>
</table>

*Localities in parentheses indicate island was unspecified.*


TABLE 2. RECORDS OF *TRIDACNA* ADZES ON RAISED CORAL ISLANDS

<table>
<thead>
<tr>
<th>Localities</th>
<th>Species</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Banaba</td>
<td><em>T. gigas</em></td>
<td>Annua, Bougainville, Buka, Efate, Ishigaki, New Britain, New Ireland, Niutoputapu, Pohnpei, Retoka, Sanga Sanga, Santa Cruz, Tikopia, To'io, Tongoa, Yap</td>
</tr>
<tr>
<td>Fais</td>
<td><em>T. gigas</em></td>
<td>Garanger, Bath &amp; Shun, Hiro &amp; Clayshulte, Kosrae, Lelepa, Okinawa, Palawan, Pohnpei, Retoka, Sanga Sanga, Santa Cruz, Tikopia, Tol, Tongoa, Yap</td>
</tr>
<tr>
<td>Pakea</td>
<td><em>T. gigas</em></td>
<td>Christian, Christian &amp; Shun, Garanger, Hiro &amp; Clayshulte, Okinawa, Palawan, Retoka, Sanga Sanga, Santa Cruz, Tikopia, Tongoa, Yap</td>
</tr>
</tbody>
</table>

TABLE 3. Records of *Tridacna* Adzes on Open, Semiclosed, and Closed Atolls

<table>
<thead>
<tr>
<th></th>
<th><em>T. gigas</em></th>
<th><em>T. maxima</em></th>
<th><strong>UNIDENTIFIED</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Open atoll</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Ailinglaplap</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†And</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Aur</td>
<td>X</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>†Bikini</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Eloa-a-Emananus</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>(Mussau Is.)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Faraulap</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Funafuti</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Jaluit</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>†Kwajalein</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>†Lamotrek</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Likiep</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Maloelap</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Ngulu</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Nukumanu</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Nukuria</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Ontong Java</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Sikaiana</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Tabiteua</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tongareva</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Ulithi</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Woleai</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Wotho</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>†Wotje</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><strong>Semiclosed atoll</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Arno</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Atafu</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Ebon</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Faluk</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>†Kapingamarangi</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Lae</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>†Majuro</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Ngarik</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Nonou</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Nukufetau</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Nukuoro</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>†Onotoa</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Puluwae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Satawan</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>†Takuu</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><strong>Closed atoll</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Christmas</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Eita</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fangatau</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Manihiki</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Mokil</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Nanumea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Napuka</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Niutao</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>†Pingelap</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pukapuka</td>
<td>X</td>
<td></td>
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</tr>
</tbody>
</table>
This notion may be carried a step further, as indicated by the data for atolls in Table 3—namely, that there may be a correlation between the kind and number of *Tridacna* species represented in an adze kit, and the relative “openness” of the atoll on which the blades were found.

Table 3 indicates that human populations on open and semiclosed atolls used both *T. gigas* and *T. maxima* for adze material, although on open atolls the former appears to have been predominant (among identifiable species and reported specimens). These data support P3 (that *Tridacna* kits associated with open and semiclosed atolls will tend to include blades of both *T. gigas* and *T. maxima*) and, inferentially, P1 (that such atolls are viable habitats for both species). The near absence of reliably reported *T. gigas* blades from closed atolls within the range of this species lends qualified support to P4 (that the closed-atoll *Tridacna* kit will in general comprise only blades of *T. maxima*) and, inferentially, to P2 (that populations of *T. gigas* will rarely occur on closed atolls within its range). While suggestive, these data are as yet inconclusive in light of inadequate sample size and the limited excavation conducted on atolls to date. Comprehensive investigations (both biological survey and archaeological excavation) are needed in order to further test these initial findings.

Some preliminary data that may contribute to a test of P1, P2, and P3 are provided in Fujimura and Alkire’s (1984) report of excavations on Lamotrek Atoll in the central Caroline Islands. Lamotrek is an open atoll, situated within the distributional overlap of *T. gigas* and *T. maxima*. The authors state that they did not find *T. gigas* populations on the reefs of Lamotrek or other nearby atolls, but that smaller tridacnids (e.g., *T. squamosa, T. maxima, H. hippopus*) were present. Adze blades manufactured from *T. maxima* valves were included in the artifact assemblage, as were several “larger, more massive” *Tridacna* (apparently *gigas*) adze blades—including a 27.60-cm specimen—recovered from the lower levels of the excavations.

Fujimura and Alkire suggest that valves of the larger tridacnid species and/or blades fashioned from such material may have been imported to Lamotrek, possibly as a trade commodity from Belau, in the absence of a local source of supply. Citing
early evidence that such a trade link existed between Belau and Yap (Müller 1917)—
*T. gigas* blades or valves were reportedly brought from Belau (where the species was
represented) to Yap (where it was not, except as ancient valves embedded in coral)—
the authors hypothesize that a similar situation obtained on prehistoric Lamotrek.

As Yap is a volcanic island with associated reefs, situated within the distributional
extent of *T. gigas*, this species may be expected to have inhabited those reefs in the
past. Subsequent local extinction of *T. gigas* may have been related to adverse en-
vironmental conditions (e.g., sedimentation of reefs following one of the typhoons
common to the area) or to overexploitation by humans. This may have been the case
on Lamotrek as well, except that an extant population of *T. gigas* may have been
drastically reduced rather than completely eliminated. While Fujimura and Alkire
found no live *T. gigas* specimens on Lamotrek during their research in 1976, a
“relict” population was reported there by marine biologists a decade later (Munro
n.d.), specimens that probably had been overlooked by the archaeologists. This
suggests that Lamotrek may well have been a viable habitat for *T. gigas* in the past;
that a local population of these bivalves could have supplied the raw material for the
adze blades recovered in excavation; and that later in the sequence (perhaps more
than once) environmental and/or cultural factors were instrumental in reducing the
*T. gigas* population to an extremely low level. It is also possible, of course, that the
large *Tridacna* adze blades recovered by Fujimura and Alkire—or the raw materials
themselves—were obtained from external sources.

A comprehensive survey of Lamotrek’s reef for embedded tridacnid valves could
serve as a initial test of P1 and P2 for prehistoric Lamotrek, by attempting to deter-
mine which *Tridacna* species were present on the atoll in earlier times. Evidence for a
prehistoric local population of *T. gigas* would simplify the archaeologist’s search for
the source of this tool material. The possibility of external origins for *T. gigas* tools
recovered from Lamotrek would not be discounted, but might be argued less con-
vincingly on environmental-ecological grounds in the face of a local supply of raw
material. The artifactual data from Fujimura and Alkire’s (1977, 1984) excavations
support P3: the adze assemblage includes blades made from more than one species of
*Tridacna*, apparently including *T. gigas*.

A closed atoll in the eastern Carolines would offer an equally interesting oppor-
tunity for tests of P1, P2, and P4. Some 150 km distant from the volcanic island of
Pohnpei, Mokil Atoll lacks deep reef passes that can be navigated by ship. Bryan
(1971) recorded four shallow “canoe passages” on the north and west reef sectors,
one of which has been expanded to accommodate small motorized craft. Mokil is
located within the distributional range of *T. gigas* but reportedly does not today
support a population of this species (A. Sepedi, pers. comm.). Rosendahl (1979)
conducted a reconnaissance survey of Mokil, focusing on a traditional chiefly resi-
dence site, and recovered a number of artifacts from the surface and from inform-
ants. Among these were two *Tridacna* adze blades (illustrated in Rosendahl 1987
and represented in Table 3) that appear to have been manufactured from quite mas-
sive valve hinges, and very likely from valves of *T. gigas*. The brief survey report
(1979) does not specify whether these two blades were obtained through surface
collection or from informants. In the latter case, information regarding the context
and history of the artifacts’ possession by informants would provide a more solid
basis for establishing their cultural provenience.

A systematic survey of Mokil’s reef and lagoon biotopes, both for live specimens
and for ancient and recent valves, could aid in determining the local presence or absence, habitat distribution, and relative abundance of tridacnid populations (P1 and P2) in modern and prehistoric contexts, and could address the question of variability in species representation over time. Informant interviews and islet surveys may assist in this regard as well. A local fisherman recalled seeing several large tridacnid valves used as pig troughs during his youth in the 1940s; he was told by his grandfather that the empty valves had been found on the outer edge of the reef (A. Sepedi, pers. comm.). If T. gigas could be shown to have inhabited Mokil’s reef in the prehistoric era, one could present the case for a local source of this adze material.

However, an equal and perhaps stronger case could be made for the possibility of external origins for T. gigas tools recovered on Mokil (P4). There is considerable linguistic and material culture evidence for early, extensive contact between Mokil and the atolls of the neighboring Marshall Islands (Rehg and Bender 1988), an area known to support T. gigas populations and to have produced T. gigas adzes. Further, Pohnpeian tradition holds that Mokil was part of an early trade network that also included Pohnpei, Kosrae, and Yap (M. Actouka, pers. comm.). Local oral histories also reflect the existence of an early social and perhaps political relationship linking Mokil with Pohnpei and Kosrae— islands where T. gigas adze blades have been recovered and which, until recently, supported populations of this species—and it has been suggested that such blades may have served as intranetwork, high-status items of exchange (C. Streck, pers. comm.). The recovery of what appear to be T. gigas blades from a traditional chiefly residence site on Mokil (Rosendahl 1979, 1987) lends preliminary weight to this conjecture. Even more provocative is the evidence of linguistic and material culture borrowing by Mokil from the Marshalls, but more comprehensive studies (including excavation) would be needed for a valid test of P4 for Mokil.

**CONCLUSION**

Archaeological research in island environments is often focused on the more accessible, visible, terrestrial biotopes. Certainly this makes sense when the problem or issue under study concerns settlement patterning, agricultural systems, structures, tool manufacture, terrestrial resource use, and the like. Yet the marine component of an island ecosystem may contribute as much or more to a culture, in food and other useful materials, as may be obtained from the land. Archaeologists concerned with the typology and possible external relationships of a shell tool assemblage should initially determine whether or not the local environment offers—and might have offered in the past—all of the materials represented in the kit.

A basic familiarity with tridacnid ecology should provide a solid and necessary foundation for any study of Tridacna technology. That such an awareness thus far has not sufficiently been incorporated into studies of Tridacna tools may be inferred from the literature and from discussions with researchers. Very few archaeological reports of sites where Tridacna adzes were recovered have even mentioned whether tridacnid species—to say nothing of which species—were present on associated reefs (notable exceptions are Ward 1979; Kirch and Yen 1982; Fujimura and Alkire 1984). In the archaeological investigation of such sites, care must be taken not to presume the presence of environmental conditions under which all species of Tridacnidae may be equally successful. Basalt and volcanic glass would not be considered mate-
rial indigenous to a true atoll environment; neither, perhaps, would it be justified to assume a local source for T. gigas tools recovered from cultural deposits associated with every type of reef system.

Procedures for tracing the sources of Tridacna materials to individual island groups, similar to those for sourcing volcanic glass and pottery tempers, have not been and may never be developed. Nonetheless, the formulation and testing of environmental–ecological correlates (such as P1 and P2) should contribute to our awareness of the ecology of these species. An improved understanding of the habits and habitats of the Tridacnidae would allow archaeologists to anticipate, within known geographical distributions, the presence or absence and relative abundance of these resources in given biotopes, relating the concepts of marginal, competitive, and exceptional habitats for each Tridacna species to the conditions present on any reef system.

Further, environmental–material correlates (such as P3, P4, and P5) would enable us to test and to build upon the ecological propositions through the survey of atoll and island ecosystems and through excavation. New evidence, including anomalies in the biological or archaeological records, should stimulate further investigation and help to modify this preliminary model in useful ways.

A multidisciplinary approach of this kind suggests that it is not enough to examine the tools of a culture apart from the ecosystemic contexts in which they occur; the materials from which tools are made are as much components of an ecosystem as are the human beings who make them. The complex associations of the Tridacnidae with their natural habitats are directly related to their ecological success, and thus to their availability for human exploitation.

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Yamaguchi, M.

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