Population Demographics of *Tridacna noae* (Röding, 1798) in New Ireland, Papua New Guinea

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**POPULATION DEMOGRAPHICS OF TRIDACNA NOAE (RÖDING, 1798) IN NEW IRELAND, PAPUA NEW GUINEA**

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**ABSTRACT** The recent resurrection of a *Tridacna maxima* sensu Rosewater (1965) ecotype as a distinct species, *Tridacna noae* (Rödinger, 1798), has raised concerns that inadvertent confusion of the two species in the past may have led to overestimates of *T. maxima* densities and errors in determining demographic parameters. To assess the potential impacts of such a scenario, this study examined the population demographics of *T. noae* within the center of its geographic distribution in the Kavieng lagoonal system of New Ireland Province, Papua New Guinea. The study found that 42% of the *T. maxima* sensu Rosewater population could be delineated as *T. noae*, with *T. noae* being the most abundant giant clam species at 7 of the 20 study sites. Past confusion of the two species is likely to be of the greatest concern on reef sites with high or medium levels of exposure to oceanic influences where *T. maxima* (2.08 ± 0.41 per 400 m², 1.86 ± 0.59 per 400 m², respectively) and *T. noae* (2.06 ± 0.36 per 400 m², 1.25 ± 0.28 per 400 m², respectively) densities were similar (P > 0.05). In analyzing size (shell length) frequency distributions, it was determined that the *T. noae* population had a larger mean size (206 ± 6 mm) than that of *T. maxima* (161 ± 6 mm, P < 0.001). Thus, in areas where the two species have overlapping distributions and fisheries regulations are based on size, reassessment of *T. maxima* stocks should be considered a priority given the high frequency at which the larger *T. noae* may comprise historical populations of *T. maxima* sensu Rosewater.

**KEY WORDS:** giant clam, *Tridacna noae*, *Tridacna maxima*, demographics, density, distribution, management, Papua New Guinea

**INTRODUCTION**


Initially, *Tridacna noae* was distinguished from *Tridacna maxima* on the basis of shell morphology by Rödinger (1798). The high plasticity in shell morphology shown by *T. maxima*, however, led Rosewater (1965) to consider *T. noae* and several other *Tridacna* species showing morphological similarities (*Tridacna elongata* (Lamarck, 1819), *Tridacna fossor* (Hedley, 1921), *Tridacna imbricata* (Rödinger, 1798), and *Tridacna lanceolata* (Sowerby, 1884)) as ecotypes of *T. maxima*. Recent evidence from mitochondrial DNA sequences and differences in mantle morphology of one such ecotype within *T. maxima* sensu Rosewater from Taiwan and the Ryukyu Islands provided a basis for resurrection of *T. noae* as a valid species (Su et al. 2014). Originally only reported from Taiwan and the Ryukyu archipelagos (Kubo & Iwai 2007, Su et al. 2014), the geographic range of *T. noae* is now considered to cover much of the Indo-Pacific, from its western boundary of the northern South China Sea to Sawu Sea, extending to New Caledonia and Kiriritimati in the east (Borsa et al. 2014). Thus, this delineation of *T. noae* from *T. maxima* may pose serious ramifications for the conservation of both species across much of the Indo-Pacific due to past research and management activities inadvertently consolidating *T. noae* and *T. maxima* as a single entity.

To enhance our knowledge and management for effective conservation and sustainable exploitation of both *Tridacna noae* and *Tridacna maxima*, studies distinguishing differences in population demographics of the two species are of primary importance. Using giant clam populations in the Kavieng lagoonal system of New Ireland Province, Papua New Guinea (PNG), this study derives demographic parameters from estimates of density and size-frequency distributions to provide clarity to the relative contribution of both *T. maxima* and *T. noae* to local giant clam populations. From such knowledge, baseline values for *T. noae* population demographics can be established and the potential impact(s) of past inadvertent confusion of *T. maxima* and *T. noae* can be considered.

**MATERIALS AND METHODS**

**Study Sites**

This study was conducted from the Nago Island Mariculture and Research Facility located within the Kavieng lagoonal system of northern New Ireland Province, PNG (2° 36′ S, 150° 46′ E).
The Kavieng lagoonal system is comprised of a large lagoon (ca. 18 km long and 12 km wide) with three distinct island chains that traverse the lagoon parallel to its seaward edge. Within the lagoon, depth rarely exceeds 20 m between islands with the maximum depth inside the lagoon approximately 30 m. Outside the lagoon, the seafloor gradually slopes into the Pacific Ocean reaching a depth of 200 m approximately 7 km from the outer island chain. Most of the shoreline within the lagoonal system is fringed by extensive coral reef development. North-easterly winds produce large swells which leave the outer island chain (O, Fig. 1) reefs highly exposed to these oceanic influences. Wave action on the northern edge of islands in the middle chain (M, Fig. 1) can also be substantial because of the lack of barrier reef development between islands of the outer chain allowing significant swells to pass through. The inshore island chain (I, Fig. 1) reefs are relatively sheltered in comparison.

Water quality increases and fluctuations in salinity decrease at more offshore sites within the Kavieng lagoonal system. Freshwater runoff from the main land mass can lower the salinity and increase the turbidity of near-shore waters after substantial rainfall. Similarly, the community compositions of reef associated organisms vary between inner and outer island reefs, with species diversity increasing with seaward progression through the lagoon (Hamilton et al. 2009).

Population Surveys

Population surveys of giant clams were conducted at 20 sites in the Kavieng lagoonal system during April 2015. Each site was categorically assigned to both an island chain (O, M, I) and relative exposure level (High, Medium, and Low). Within each site, six replicate 8 × 50 m long transects were conducted. Three transects were oriented along the reef flat/crest interface at a 0–2 m depth contour, and three transects were oriented along the reef slope at the 2–5 m depth contour. Both reef topographies sampled correspond to previous habitat records where Tridacna noae have been identified (Kubo & Iwai 2007, Borsa et al. 2014, Su et al. 2014). A benthos habitat of 20%–50% live coral coverage (assessed in situ) was a precondition for all transects to minimize habitat bias between sites. All transects were swum twice by two personnel using snorkel with a maximum sampling depth of 5 m. Along each transect, all live giant clams were counted, measured (antero-posterior shell length), and photographed with their mantles exposed.

Data Analysis

Given the low numbers of Tridacna gigas, Tridacna squamosa, and Hippopus hippopus encountered during the survey, these species were categorized as “Other spp.” for analysis. Differences in giant clam densities between island chains and relative exposure levels were independently analyzed using permutation multivariate analysis of variance (PERMANOVA) based on Euclidean distances with PRIMER 6 (Version 6.1.13) and PERMANOVA+ (Version 1.0.3) statistical package. Pairwise comparisons among sites nested within island chains or exposure level and comparisons between species were run where significant differences in the main effects term were realized. Monte Carlo P values (P_{MC}) were accepted for pairwise comparisons where the number of unique permutations was less
than 100 as recommended by Anderson et al. (2008). For all analyses using PERMANOVA computation, 9,999 permutations were run to produce the distance-based pseudo-\( F (F_{\text{pseudo}}) \) or pseudo-\( t (t_{\text{pseudo}}) \) statistics. Preliminary analysis revealed that there was no significant difference in *Tridacna noae* density between reef crest/flat and reef slope transects (\( F_{\text{pseudo}} = 2.75, P = 0.10 \)) so all six transects within a given site were pooled for the above analyses.

Differences in the shell lengths of *Tridacna noae* and *Tridacna maxima* as well as differences across island chains and relative exposure levels were independently analyzed in the same fashion as density, using a PERMANOVA with pairwise comparisons approach. Density and shell length values reported in the text are expressed as the arithmetic mean ± SE.

The photographs taken of all recorded *Tridacna noae* (\( n = 131 \)) were reviewed to identify apparent and distinguishing differences in phenotypes of this species. The frequencies of particular phenotypes within the population were analyzed with a Chi-square goodness-of-fit test to determine if they were equally represented in the population. For all tests, statistical differences were accepted at \( P < 0.05 \).

**RESULTS**

**Population Density**

Within the Kavieng lagoonal system *Tridacna noae* was present at 15 of the 20 study sites, and was the most abundant giant clam species at seven of those sites (Fig. 1). There was a clear trend of increasing *T. noae* density with a seaward progression from the inner island chain, where no specimens were recorded, to the middle island chain (\( 0.87 \pm 0.17 \) per 400 m\(^2 \)) and the outer island chain (\( 2.00 \pm 0.34 \) per 400 m\(^2 \)) (\( F_{\text{pseudo}} = 15.20, P < 0.001 \); Fig. 2). The absence of *T. noae* from inner island chain sites was determined not to be an artefact of site selection or transect length as an additional 4 km\(^2 \) of reef slope and crest/flat habitat stratified among the study islands (I\(_1\), I\(_2\), and I\(_3\)) were swum and found to be devoid of the species. For all tests, statistical differences were accepted at \( P < 0.05 \).

Differences in *Tridacna noae* density between sites were also assessed with respect to exposure level. Mean density among sites with low exposure (\( 0.25 \pm 0.10 \) per 400 m\(^2 \)) was roughly five and eight times lower than the density among sites with medium (\( 1.25 \pm 0.28 \) per 400 m\(^2 \)) and high exposures (\( 2.06 \pm 0.36 \) per 400 m\(^2 \)) respectively (\( F_{\text{pseudo}} = 14.10, P < 0.001 \); Figs. 1 and 2). When comparing sites within exposure level groupings, only a single comparison among the high exposure sites demonstrated a significant difference in density (\( F_{\text{pseudo}} = 1.88, P = 0.03 \); Fig. 1). Site differences, however, were minimal with only two of the 35 site comparisons for the middle island chain and four of the 21 site comparisons for the outer island chain showing significant differences in density (Table 1).

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In comparing the density of *Tridacna noae* and *Tridacna maxima* within the Kavieng lagoonal system, the densities of the two species were similar across the outer (\( t_{\text{pseudo}} = 1.27, P_{\text{MC}} = 0.21 \)) and middle island chains (\( t_{\text{pseudo}} = 0.15, P_{\text{MC}} = 0.87 \); Fig. 2). Unlike *T. noae*, *T. maxima* was found to inhabit the fringing reefs of the inner island chain with the mean density of 0.71 ± 0.34 per 400 m\(^2 \) being statistically different from zero (i.e., *T. noae* density; \( t_{\text{pseudo}} = 2.10, P_{\text{MC}} = 0.04 \); Fig. 2). Similarly, when comparing densities of the two species across exposure levels, densities were similar at high (\( t_{\text{pseudo}} = 0.05, P_{\text{MC}} = 0.97 \)) and medium (\( t_{\text{pseudo}} = 0.94, P_{\text{MC}} = 0.35 \)) exposure levels with a higher density of *T. maxima* (\( 0.81 \pm 0.21 \) per 400 m\(^2 \)) to *T. noae* (\( 0.25 \pm 0.10 \) per 400 m\(^2 \)) at low exposure sites (\( t_{\text{pseudo}} = 2.40, P_{\text{MC}} = 0.02 \); Fig. 2).

**Size Frequency Distribution**

Within the Kavieng lagoonal system the mean shell length of *Tridacna noae* (\( 206 \pm 6 \) mm) proved to be significantly larger than that of *Tridacna maxima* (\( 161 \pm 6 \) mm; \( F_{\text{pseudo}} = 27.54, P < 0.001 \); Fig. 3). Mean shell lengths of *T. noae* and *T. maxima* did not differ between the island chains (\( F_{\text{pseudo}} = 0.65, P = 0.41; F_{\text{pseudo}} = 2.46, P = 0.09 \); respectively) nor did the shell length of either
TABLE 1.
Permutational multivariate analysis of variance.

<table>
<thead>
<tr>
<th>Factor: Sites</th>
<th>t-Value</th>
<th>PNC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island chain</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1 west × M3 north</td>
<td>3.87</td>
<td>0.003</td>
</tr>
<tr>
<td>M1 west × M3 west</td>
<td>2.74</td>
<td>0.022</td>
</tr>
<tr>
<td>Outer</td>
<td></td>
<td></td>
</tr>
<tr>
<td>O1 west × O1 east</td>
<td>2.70</td>
<td>0.023</td>
</tr>
<tr>
<td>O1 west × O2 west</td>
<td>2.63</td>
<td>0.027</td>
</tr>
<tr>
<td>O1 east × O2 south</td>
<td>2.25</td>
<td>0.047</td>
</tr>
<tr>
<td>O2 west × O2 south</td>
<td>2.30</td>
<td>0.045</td>
</tr>
<tr>
<td>Exposure level</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td></td>
<td></td>
</tr>
<tr>
<td>O1 west × O2 west</td>
<td>2.63</td>
<td>0.027</td>
</tr>
</tbody>
</table>

Pairwise comparison results for *Tridacna noae* density where statistically significant differences between sites nested within island chains and between sites nested within exposure level occurred. Site labels correspond to the site location around the specified island designated (M1, M3, O1, and O2) in Figure 1.

species differ across exposure levels ($F_{\text{pseudo}} = 0.88$, $P = 0.42$; $F_{\text{pseudo}} = 0.77$, $P = 0.47$; respectfully). The maximum shell lengths recorded for *T. maxima* and *T. noae* were 370 and 350 mm, respectively.

Mantle Phenotypes of *Tridacna noae*

Mantle coloration of *Tridacna noae* varied considerably from brown, yellow, orange, green, blackish blue, and all hues in between with uniform or patchy distribution of colors. Only two phenotypes were, however, observed for coloration of the diagnostic oval patches bounded by white margins in *T. noae*: (1) brown (and brown hues); and (2) blue/green (Fig. 4). Furthermore, of the 131 *T. noae* specimens examined, the coloration of these oval patches was uniform and consistent for a given specimen despite background mantle coloration varying considerably. These phenotypes were not equally distributed within the *T. noae* population, with 90.1% of the population bearing the brown phenotype and 9.9% of the population bearing the blue/green phenotype ($\chi^2 = 84.16$, $P < 0.001$). In addition to mantle coloration, the presence of mantle papillae were identified in several specimens (Fig. 5), however, quantitative assessment of this attribute was not undertaken.

DISCUSSION

Approximately 42% of the *Tridacna maxima* sensu Rosewater (1965) population within the Kavieng lagoonal system can now be delineated as *Tridacna noae*. The high proportion of *T. noae* within the giant clam assemblage in the Kavieng lagoonal system highlights the importance of stock reassessments for *T. maxima*/*T. noae* throughout the distribution of *T. noae*. This is particularly important because commercial exploitation of *T. maxima* sensu Rosewater (1965) has occurred historically over much of the range of *T. noae* (Lucas 1994, Kinch 2002, 2008, Borsa et al. 2014).

Information on the contribution of *Tridacna noae* to giant clam populations is lacking with only qualitative data having been collected from locations at the edge of the species' geographical range such as New Caledonia (Borsa et al. 2014) and the Taiwan/Ryukyu archipelagos (Kubo & Iwai 2007). Assessments of population demographics at the periphery of a species' distribution may produce results that are influenced by “edge effects” with limited relevance to populations within the center of the range (Brown 1984, Guo et al. 2005, Bahn et al. 2006). The fisheries catch data of Kubo and Iwai (2007) suggest that *T. noae* comprises only a small component of the Taiwan/Ryukyu archipelago giant clam assemblages with only 1.9% of *Tridacna maxima* sensu Rosewater (1965) proving to be *T. noae*. In New Caledonia, *T. noae* was reported to be less abundant than *T. maxima* at sites where both species occur (Borsa et al. 2014). In contrast, this study has demonstrated, for the first time, that for a locale in the center of their distributions, densities of *T. noae* and *T. maxima* are statistically equivalent on fringing reefs with a high or medium exposure level.

The densities of *Tridacna noae* and *Tridacna maxima* recorded within the Kavieng lagoonal system in this study can be reasonably assumed to represent close to natural population levels. Unlike elsewhere in the Pacific and PNG (Lucas 1994, Kinch 2002, 2008, Kinch & Teitelbaum 2010), New Ireland has no history of commercial exploitation of giant clams for the marine aquarium trade, curios, or meat (international or domestic markets), though some giant clams are harvested for

![Figure 3. Size frequency distribution for maximum shell length of *Tridacna maxima* (n = 181) and *T. noae* (n = 131) throughout the Kavieng lagoonal system.](image-url)
subsistence (Wright et al. 1983). The lack of fishing pressure experienced by T. maxima and T. noae in the Kavieng lagoonal system is evident from the high proportion of large individuals within these populations. Roughly 15% of the lagoon’s T. maxima population exceeded the maximum size of T. maxima reported from presumed natural populations in Samoa (25 cm; Green & Craig 1999) and 12% exceeded the maximum size of T. maxima reported in French Polynesia where an active fishery occurs (26 cm; Gilbert et al. 2006).

In contrast to the Kavieng lagoon population, many Tridacna maxima populations face continual exploitation. Several counties within the geographical range of Tridacna noae actively exploit T. maxima sensu Rosewater (1965) with fishing regulations based on size (Kinch & Teitelbaum 2010). Six Pacific island countries have historically used maximum size limits in shell length for T. maxima ranging from 12 to 18 cm which, given the difference in size frequency distribution between T. maxima and T. noae observed in this study, could put T. maxima disproportionately at risk of exploitation. Using the giant clam population of the Kavieng lagoonal system as an example, the most commonly enforced size restriction of 18 cm would put 69% of the T. maxima population at risk of exploitation but only 34% of the T. noae population at risk. This highlights the need for thorough reassessments of current T. maxima fisheries management practices to distinguish T. maxima from T. noae.

Examination of the population structure of Tridacna noae within the Kavieng lagoonal system indicated that environmental variables associated with low exposure sites and/or inner island chain reefs are unfavorable for establishment or maintenance of T. noae populations. Active habitat selection by Tridacna maxima larvae and juveniles utilizes chemosensory abilities that allow individuals to distinguish from favorable and unfavorable reefs (Dumas et al. 2014). Similar processes of active habitat selection favoring reefs of the middle and outer island chains within the Kavieng lagoonal system are likely to help explain the distribution of T. noae reported in this study. Future research aimed at determining environmental variables affecting the distribution of T. noae could be extrapolated to elucidate preferential culture conditions for mariculture efforts with T. noae.

Figure 4. (A–I) Within the Kavieng lagoonal system two distinct mantle phenotypes of Tridacna noae were observed for the diagnostic oval patches bordered by white margins: brown (A–F) and blue/green (G–I). Images are of specimens representing the full scope of hues observed for each phenotype. Note that in all specimens the oval patches are uniform and consistent in color despite variations over the rest of the mantle.
The role of giant clam mariculture in conserving biological diversity in spite of exploitative human activity (Lucas 1994, Gomez & Mingoa-Licuanan 2006) is likely to be of high importance for *Tridacna noae*. This study identified two distinct mantle pattern phenotypes for the diagnostic oval patches bounded by white margins within the local *T. noae* population: (1) brown; and (2) blue/green. Of these, the latter is highly conspicuous in its natural environment and would be particularly valued by the marine aquarium trade for its aesthetic appeal. Where wild harvest of marine organisms for meat, curios, or the aquarium trade occurs, conspicuous and aesthetically attractive phenotypes would be at an increased risk of exploitation (Wabnitz et al. 2003, Dulvy & Polunin 2004, Rhyne et al. 2009, 2013). This concept coupled with the rarity of the blue/green phenotype in the Kavieng lagoon population of *T. noae* (<10%) highlights the importance of giant clam mariculture as a conservation effort in lieu of wild harvest for supplying such commodities.

This study also proposes that the diagnostic oval patches bounded by white margins on the mantle of *Tridacna noae* (Su et al. 2014) can be further defined as uniform and consistent in color. In examining published photos of *T. noae* from the northern South China Sea, Sulawesi Sea, Bismarck Sea, Coral Sea, Vanuatu (Borsa et al. 2014), and the Taiwan/Ryukyu archipelago (Kubo & Iwai 2007), this trend appears to be consistent across the species’ range and may help in identifying this taxon. Furthermore, the observation of mantle papillae has not been previously documented for *T. noae*.

This study has generated baseline knowledge of population demographics for *Tridacna noae* within the center of its geographic distribution. It is clear that past inadvertent confusion between *T. noae* and *Tridacna maxima* will have resulted in substantial over estimation of *T. maxima* population densities (see bin Othman et al. 2010), particularly on reefs with high or medium exposure. Many other possible ramifications from past research efforts with *T. maxima* were postulated by Borsa et al. (2014) and are likely to be realized if *T. noae* comprises a similar proportion of giant clam populations elsewhere within its distribution. Subsequently, a reassessment of *T. maxima* stocks, distinguishing *T. maxima* from *T. noae*, should be viewed as a management priority in view of the results of this study.

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LITERATURE CITED


Population Demographics of Tridacna noae


