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Significance of new records of *Tridacna squamosa* Lamarck, 1819, in the Tuamotu and Gambier Archipelagos (French Polynesia)

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The giant clam subfamily Tridacninae (family Cardiidae) is an important group of bivalve molluscs found throughout the Red Sea and Indo-Pacific, from East Africa to the Eastern Pacific biogeographic region. The *Tridacna* genus is currently revised with numerous cryptic species identified with molecular markers. New *Tridacna* records from the fringe of the known distribution areas are extremely useful to identify genetically unique species, geographic ranges, and to examine processes associated with species differentiation. While *Tridacna maxima* is abundant in French Polynesia (Central South Pacific Ocean) the larger fluted giant clam *Tridacna squamosa* was formerly reported only in the Austral Islands in the south. Following a recent survey that spanned 23 islands and atolls of the Society, Tuamotu and Gambier Archipelagos, the presence of *T. squamosa* between the Cook Islands and Pitcairn Islands is confirmed using both morphological and molecular information, suggesting a relic distribution across the Central Pacific Ocean. *Tridacna squamosa* is rare, but present throughout Tuamotu and Gambier. However, it remained undetected from the Society Islands, probably due to historical over-fishing. This species is valued by local inhabitants, and is sought after mainly as gifts and also for a limited local shell trade. The rarity of *T. squamosa* may call for conservation measures in the near future.

Keywords: Central Pacific; Fakarava UNESCO Biosphere Reserve; fishery management; giant clam; Society Islands; Tridacna

Introduction

The giant clam subfamily Tridacninae (family Cardiidae) is an important and conspicuous mollusc family found throughout the Red Sea and Indo-Pacific, from East Africa to the Eastern Pacific biogeographic region (Rosewater 1965; Othman *et al.* 2010). The Tridacninae includes two genera, *Tridacna* and *Hippopus*, with nine and two species, respectively. The genus *Tridacna* currently includes *Tridacna squamosa* Lamarck, 1819, *Tridacna maxima* (Röding, 1798), *Tridacna crocea*, Lamarck 1819, *Tridacna derasa* (Röding, 1798), *Tridacna gigas* (Linnaeus, 1758), *Tridacna mbalavuana* Ladd, 1934, *Tridacna rosewateri* Sirenko and Scarlato, 1991, *Tridacna squamosina* Sturany, 1899 and *Tridacna noae* (Röding, 1798). The taxonomy and phylogeography of *Tridacna* is currently experiencing substantial revisions: for example, a distinct clade of *T. maxima*, recently found from Taiwan south to the Solomon Islands (Huelsken *et al.* 2013; DeBoer *et al.* 2014a), is now the resurrected *T. noae* (Su *et al.* 2014). *Tridacna costata* (Roa-Quiaoit, Kochzius, Jantzen, Zibdah, Richter, 2008), described from the Red Sea, was synonymised with *Tridacna squamosina* by Huber and Eschner (2011). More changes may be expected, given the identification of cryptic species from the Coral Triangle using molecular techniques (Huelsken *et al.* 2013; DeBoer *et al.* 2008, 2014a, 2014b). This area comprises most of Malaysia and Indonesia, as well as Papua New Guinea, Philippines, Timor Leste and the Solomon Islands. It is characterised by a complex palaeo and present oceanography, coastline and climate. These configurations have created numerous physical barriers that have moved across time since the Pleistocene, resulting in species differentiation between isolated regions for a large number of marine taxa that often display concordant phylogeographic patterns (Carpenter *et al.* 2011), with some variations due to periods of recolonisation.

Taxonomic revisions of *Tridacna* in the Coral Triangle result from research aiming to define priority areas for conservation based on connectivity (DeBoer *et al.* 2014a; Beger *et al.* 2014). For this objective, it is necessary to elucidate which species are present, cryptic, genetically unique and how they are distributed, especially if they are endangered, such as giant clams. Indeed, all *Tridacna* species worldwide are protected by the Convention on International Trade in Endangered Species (CITES) and

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appear on the IUCN Red List of Threatened Species (Wijnstekers 2000). Giant clams are also a conservation priority outside the Coral Triangle (Gilbert *et al.* 2005; Van Wynsberge *et al.* 2013).

In the western and central Pacific Ocean, several of the known giant clam species are iconic and of cultural importance. Despite their endangered status, they still offer a significant food source for islanders, and a source of income when traded for their 'meat' or shells. This is especially the case in the eastern Tuamotu Archipelago of French Polynesia where semi-enclosed lagoons harbour stocks of several million individuals per lagoon (Andréfouët *et al.* 2005; Gilbert *et al.* 2006). However, this stock is comprised exclusively of *T. maxima* (Salvat 1972). In French Polynesia, *T. maxima* is commonly found in the Austral, Society, Tuamotu and Gambier archipelagos, but not in the Marquesas Islands (Salvat 1972; Andréfouët *et al.* 2005; Gilbert *et al.* 2006; Othman *et al.* 2010). This species has been the focus of a large number of recent studies performed on fishery, aquaculture, population dynamics (e.g., Addesi 2001; Gilbert *et al.* 2005; Andréfouët *et al.* 2009, 2013; Van Wynsberge *et al.* 2013) and genetics (Laurent *et al.* 2002) in French Polynesia.

Recently, Gilbert *et al.* (2007) reported occurrences of the fluted giant clam *T. squamosa* on forereefs of Tubuai Island, in the Austral Archipelago (south French Polynesia) based on both morphological and molecular evidence. Trondlé and Boutet (2009) subsequently added *T. squamosa* to their mollusc check list for French Polynesia. Gilbert *et al.* (2007) suggested that this discovery could indicate recent eastward colonisation from the Cook Islands. Newman and Gomez (2007) rejected this hypothesis by highlighting known archaeological records of *T. squamosa* shells in the southeast of French Polynesia, and modern records in the Cook Islands (Paulay 1987) and Pitcairn Islands (Paulay 1989). Indeed, Paulay (1987) reported *T. squamosa* on the forereefs of Aitutaki, Mauke and Rarotonga (Cook Islands), west of French Polynesia. Eastwards, Paulay (1989) also reported this species as fairly common between 15 and 20 m on the forereef of Ducie and Henderson atolls in the Pitcairn Islands. Paulay (1989) was unsure whether the apparent absence of *T. squamosa* in French Polynesia was real or due to the inaccessibility of habitats. With the exception of the observations by Gilbert *et al.* (2007) in Tubuai, *T. squamosa* remained formally unrecorded elsewhere in French Polynesia. Large shells (up to 40 cm) were known informally from the Tuamotu atolls, as gifts (e.g., to officials), and from sightings during recreational scuba dives along forereefs (e.g., in Tikehau atoll, J. Orempuller pers. comm. April 2013, Andréfouët pers. obs.). However, it remained unclear if these large shells were from unusually large *T. maxima* or from *T. squamosa*. *Tridacna maxima* reaching 20 cm are not rare, but *T. squamosa* can easily grow to 30 cm in length, and frequently more than 40 cm, which is unusual for *T. maxima*.

From September 2012 to February 2013, the Global Reef Expedition of the *Khaled bin Sultan Living Ocean Foundation* (KSLOF) visited 23 islands and atolls in the Society, Tuamotu and Gambier archipelagos. The surveys included 201 diving locations, both in lagoons and forereefs. This large sampling effort helped to fill gaps in knowledge of *T. squamosa* distribution in French Polynesia. Here, we report the evidence (or lack thereof) for the presence of *T. squamosa* in the different archipelagos, and update the distribution of this species for the French Polynesia and Central Pacific region. We discuss the current threats to what appears to be a rare species in the Tuamotu-Gambier region, and suggest possible conservation measures that could be established to protect these large bivalves. We also discuss the relevance of these findings for the on-going revision of the *Tridacna* genus.

Materials and methods

Surveys and in situ *morphological identification*

Twenty-three islands and atolls were sampled between September 2012 and February 2013 (Fig. 1). Two or three divers and snorkelers searched for large edible organisms, namely sea cucumbers (numerous species), trochus (*Tectus niloticus* (Linnaeus, 1767)), turbos (*Turbo marmoratus* (Linnaeus, 1958)) and giant clams. To identify giant clams, the following morphological criteria were used *in situ* during the dives, and photographs were taken of all individuals that could be *T. squamosa*. *Tridacna maxima* is distinguished by its close-set scutes or lack of scutes. The shell length reaches a maximum of about 35 cm but most animals are smaller than 20 cm. The mantle is often brightly coloured and is very variable in colour and pattern. It tends to bore into the reef, but is not usually deeply embedded (Lucas 1988). The byssal orifice is elongated and the shell is usually asymmetrical about the umbo (Lucas 1988). Conversely, *T. squamosa* is distinguished by its large, well-spaced scutes. The shell is semi-circular and can frequently reach about 25 cm and up to 40 cm (Norton and Jones 1992). The mantle tends to be mottled in various mixes of green, blue, brown, orange and yellow. Some mantles are orange-pink in colour. Large dots are a common mantle pattern. The byssal orifice is much larger in proportion to the shell length than in *T. maxima* and, unlike *T. maxima*, the inhalant aperture is fringed by tentacles (Lucas 1988).

Genetic identification

Morphological observations were sufficient in most instances to record the presence of *T. squamosa* in Tuamotu and Gambier atoll forereefs. However, genetic

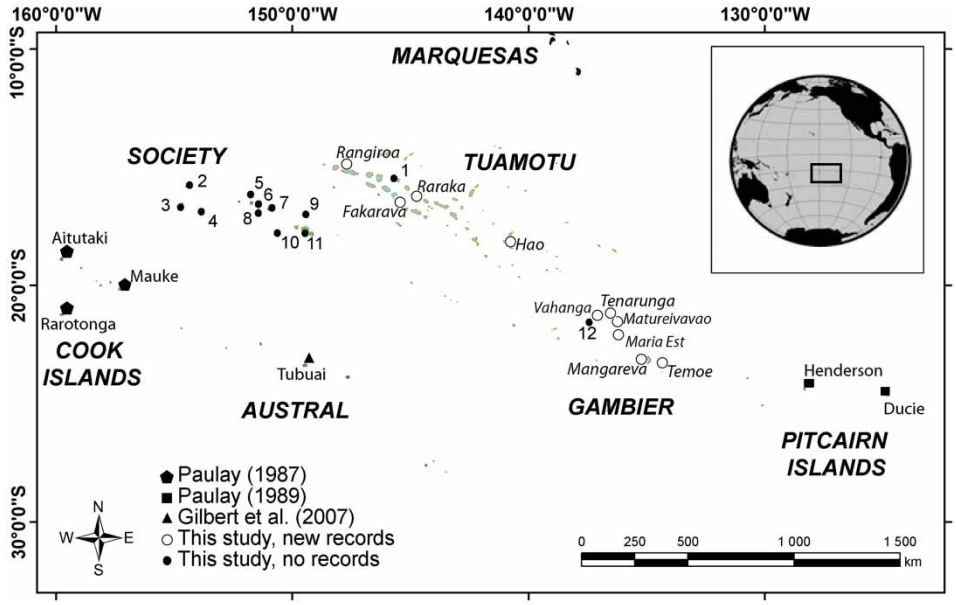

Figure 1. Location of past and new records of *Tridacna squamosa* in the Central Pacific. Islands and atolls sampled during the KSLOF expedition in 2012–2013 but without records are: in the Tuamotu: 1) Aratika. In the Society: 2) Bellinghausen; 3) Scilly; 4) Mopelia; 5) Tupai; 6) Tahaa; 7) Huahine; 8) Raiatea; 9) Tetiaroa; 10) Maiao; 11) Tahiti. In the Gambier: 12) Tenararo.

identification was performed for two samples to provide additional proof of identification. The two samples were collected in Vahanga and Temoe atolls (Fig. 1, Supplementary Material SM1). In the field, these had the same morphological attributes as many of the individuals seen from Rangiroa to Temoe (Fig. 2).

For genetic identification, between 10 and 30 µg of genomic DNA was isolated from the muscle (for sample #17) or the mantle (for sample #33) tissues preserved in 95% ethanol using the DNeasy Blood and Tissue Kit (Qiagen). A 450-base-pair fragment of the mitochondrial DNA Cytochrome Oxidase subunit I gene was amplified using the COI-Tricro-Frwd and COI-Tricro-Rev primers described in Kochzius and Nuryanto (2008). Polymerase chain reactions (PCR) were conducted in a final volume of 25 µl containing 1× GoTaq® Flexi DNA Polymerase Buffer, 2 mM of $MgCl_2$, 0.16 mM of each dNTP, 0.8 µM of each primer, 0.5 U of *Taq* polymerase (GoTaq® Flexi DNA Polymerase, Promega) and 1 µL of DNA template. The following temperature profile was used for the PCR: 94°C for 3 min, followed by 38 cycles of 1 min at 94°C, 1.5 min at 50°C, and 1 min at 72°C. Final extension was conducted at 72°C for 5 min. PCR were sent to Macrogen (Korea) where they were purified and sequenced in both directions using forward and reverse primers.

Sequences were aligned manually using BioEdit version 7.1.3.0 (Hall 1999), together with several sequences acquired from GenBank corresponding to COI fragments of *T. squamosa* from Indonesia (EU346361 to EU346364, DeBoer *et al.* 2008; HE995524, HE995494 and HE995498, Hui 2012), *Tridacna crocea* from Indonesia, as the species is absent from French Polynesia (FM253523 and FM253552, Kochzius and Nuryanto, 2008), and *T. maxima* from French Polynesia (HE995475 to HE995480, Hui *et al.*, unpublished). Unfortunately, but not surprisingly, no *T. squamosa* samples from the Central Pacific Ocean were available in GenBank. The partial sequences of the COI gene from the two samples used here have been deposited in GenBank (accession numbers KJ648612 and KJ648613 for samples 17 and 33, respectively). A neighbour-joining tree was constructed based on pairwise distance among sequences and tested using 1000 bootstrap replications in MEGA version 5.05 (Tamura *et al.* 2011).

Results

Supplemental material SM1 lists all the photographic records made during the expedition. In addition, Table 1 provides the information of the specimen and shells that are conserved in Papeete, French Polynesia, at the Direction des Ressources Marines et Minières (French Polynesia Fisheries).

Genetic analysis unambiguously confirmed the presence of *T. squamosa* in the Gambier Archipelago. Indeed, Fig. 3 shows that the *T. squamosa* published sequences and our sequences from French Polynesia form a highly supported (bootstrap 100) monophyletic clade. This clade is clearly differentiated from its sister species *T. crocea* and *T. maxima*. Since the two sequenced specimens also

Figure 2. Giant clams identified as *Tridacna squamosa* in Tuamotu and Gambier archipelagos. On the lower right panel: large shells visible in Raraka atoll village, with various degrees of scute erosion. The diameter of the black circle (a polarising filter) is 7.7 cm.

Table 1. List of shells conserved at the Direction des Resources Marines et Minières. Tahiti. French Polynesia. Curator: Georges Remoissenet.

Station	Record	Status when collected	ID DRM	Date	Origin	Size (cm)
GAVA23	17	live	1	24/01/2013	Vahanga	26
GAMG37		dead	2	30/01/2013	Mangareva	42
GATE64	33	live	3	09/02/2013	Temoe	24
GATE64		dead	4	09/02/2013	Temoe	39

had typical *T. squamosa* morphology, this indirectly confirms that identification using morphological traits was sufficient to confirm the species' presence from Rangiroa to Temoe.

Figure 1 maps the distribution of *T. squamosa* throughout French Polynesia according to the KSLOF expedition. Not a single *T. squamosa* was reported from the Society Islands. All individuals were seen in oceanic forereef locations, with no records from lagoon dives.

Keeping in mind that *T. squamosa* sampling efforts (number of dives on forereefs) varied between atolls (Fig. 4), the abundances were highest in the southeastern atolls, especially in Temoe Atoll with 28 records in four dives (Supplemental Material SM1). However, no observations were made on Tenararo atoll, in the Acteon Group. Overall, 87% of *T. squamosa* records for which depth was precisely recorded were seen in the 8–19 m depth range, but the species occurred down to 33 m (Fig. 5).

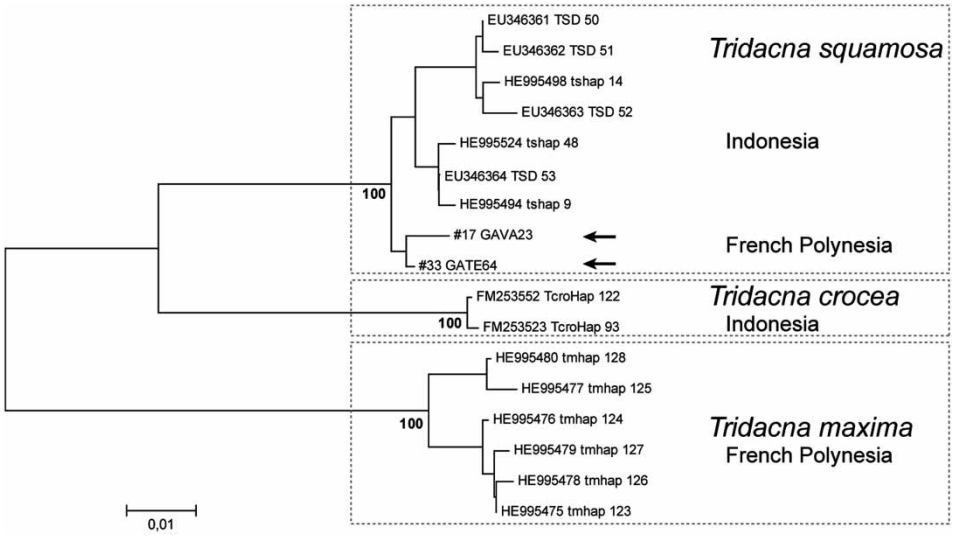

Figure 3. Neighbour-joining tree using partial mitochondrial DNA cytochrome oxidase I (COI) sequences from two collected *Tridacna squamosa* specimens (#17 and #33), indicated by two arrows, and sequences acquired in GenBank for *T. squamosa*, *T. crocea* and *T. maxima*: EU346361 to EU346364, DeBoer *et al*., 2008; HE995524, HE995494 and HE995498, Hui 2012; FM253523 and FM253552, Kochzius & Nuryanto, 2008; HE995475 to HE995480, Hui 2012).

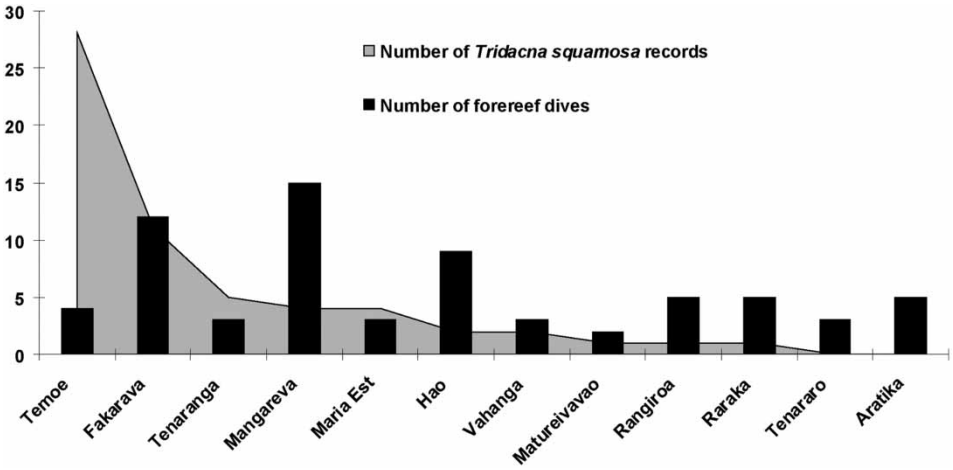

Figure 4. Number of *Tridacna squamosa* observed in Tuamotu and Gambier islands/atolls. Black bars indicate the number of dives completed in *T. squamosa* habitat (forereef).

Discussion

The observations reported here for Tuamotu and Gambier archipelagos fill a large distribution gap that was left after the reports by Paulay (1987, 1989) and Gilbert *et al*. (2007) for, respectively, the Cook Islands in the west, the Pitcairn Islands in the east, and the Austral Islands in the south. The only gap now left is for the Society Islands, even after the significant effort made during the KSLOF cruise during which 10 islands and atolls were visited (Scilly, Mopelia, Bellinghausen, Huahine, Raiatea, Tahaa, Tupai, Maiao, Tetiaroa and Tahiti). The online Biocode census data set (http://biocode.berkeley.edu/) for Moorea Island in the Society Islands also lacked reports of any records for *T. squamosa*. There are no clear environmental reasons that could readily explain the absence of *T. squamosa* in this archipelago. A possible explanation might be the historically high human pressure around the main populated islands of the group, as Richter *et al.* (2008) reported for *T. squamosina* in the Red Sea. Skilled free-diving fishermen could have depleted the deep resource after centuries of fishing, but this is not a convincing explanation for the remote Scilly, Bellinghausen and Mopelia atolls that are occupied by even fewer inhabitants than the Tuamotu atolls that we visited between Rangiroa and Hao. One could hypothesise that *T. squamosa* was present in these three remote atolls but we simply missed them. This is a reasonable hypothesis, but it is also worth noting that these three atolls are also lacking common echinoderms that are abundant in other Society lagoons, such as sea cucumbers (e.g., *Holothuria atra* (Jaeger,

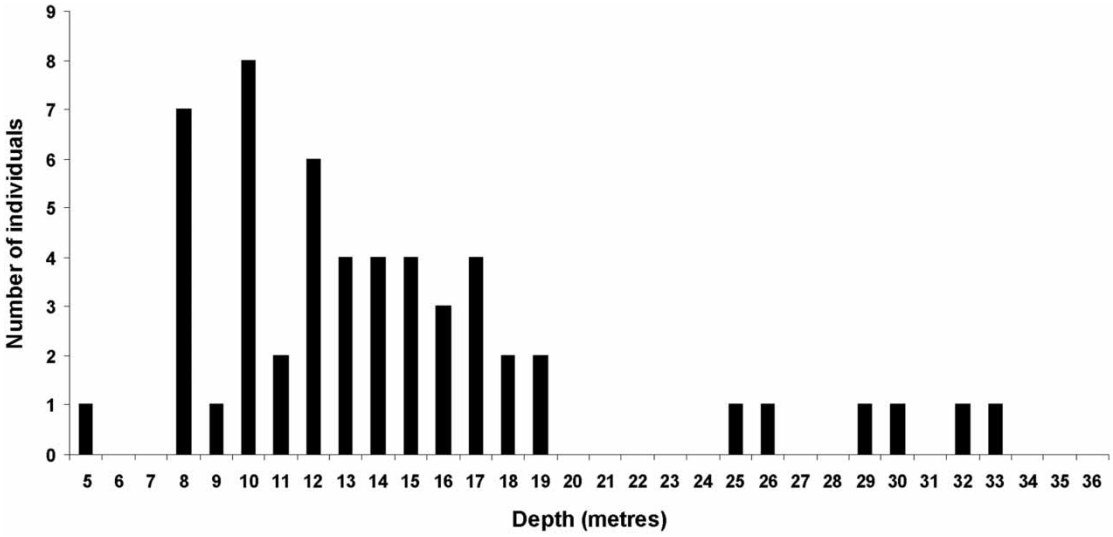

Figure 5. Recorded depth of observed *Tridacna squamosa* in Tuamotu and Gambier archipelagos.

1933)) (Salvat 1983, and S.A. pers. observation in 2013). Hence, a combination of human pressure and limited natural larval dispersal may explain the lack of records for the Society group from its eastern sector to its western sector.

In the Tuamotu and Gambier archipelagos, *T. squamosa* appears today as a fairly rare species. Its presence from the Cook Islands to the Pitcairn Islands suggests that this species has not recently settled in the Austral Islands area, as thought by Gilbert *et al*. (2007). The species in the Austral Islands is therefore probably a relic population that was missed in previous sampling (Newman and Gomez 2003, 2007). Whether or not the populations from the different archipelagos (Cook Islands, Pitcairn Islands, Tuamotu, Gambier and Australs) are connected, share the same origin, and arrived at the same period are interesting questions that warrant further investigation, using systematic sampling for genetic analysis. In any case, our observations suggest a widespread relic population for the Tridacninae (Newman and Gomez 2003).

Recent papers on *Tridacna* systematics have focused on *T. maxima* and *T. crocea*, especially around the Coral Triangle area (Huelsken *et al.* 2013; DeBoer *et al.* 2014b; Su *et al.* 2014). However, it is expected that these revisions will soon also consider the other *Tridacna* species such as *T. gigas*, *T. derasa* and *T. squamosa* that can be found in the Western Pacific Ocean and eastwards. With *T. maxima* and *T. crocea*, *T. squamosa* was included in the multi-species investigations by DeBoer *et al*. (2014a) while searching for common phylogeographic patterns in the Coral Triangle. Although the results were consistent between species, the lack of *T. squamosa* records for western Indonesia (on the Indian Ocean side) precluded a complete comparison of the spatial patterns of differentiation with the other two species. The expectation is that distributional fringes are more likely to exhibit the most pronounced differentiation, consistent with a peripatric speciation model. To test this hypothesis for giant clams, and complete the on-going revisions of giant clam taxonomy and phylogeny, samples from the easternmost extremes of the giant clam's range, the Central Pacific, will be critical.

The new records reported here add more knowledge about the conservation values of several atolls of the Tuamotu–Gambier archipelagos. In particular, the Fakarava UNESCO Biosphere Reserve, that includes the Fakarava, Aratika and Raraka atolls, gains additional value by the listing of this large, emblematic and endangered bivalve species. Our report therefore brings additional responsibilities for managers and inhabitants. Clearly, large clams are of high symbolic value in Tuamotu and Gambier, and they are widely fished. During our visits, inhabitants were proud to show large shells in their homes (Fig. 2). They were also very interested to know where we had seen large shells and at which depth. Large shells are traditionally offered as prized gifts to officials and families, and this custom is still current. Large clams are obviously still collected, especially around atolls that are easy to reach (Fig. 6). This is probably the reason that we observed a higher number of clams on the remote Temoe atoll and Acteon Group (with the exception of Tenararo), compared with populated locations (Fig. 4).

Conservation measures need to be promoted to maintain the *T. squamosa* population in the Tuamotu and Gambier atolls. These could include the introduction of upper size limits of clams that can be collected as an extension of the current measure that prohibits the collection of clams smaller than 12 cm. This limit is obviously

Figure 6. *Tridacna squamosa* collected around Hao atoll in one day, to be used as gifts. Photograph courtesy of M. Philip Foster (Hao atoll).

a measure aimed to protect the smaller *T. maxima* (Van Wynsberge *et al.* 2013). It also indirectly protects juvenile *T. squamosa*, but not the prized large adults. However, this regulation is well known and well respected throughout French Polynesia, which means that the concept of both a minimum and a maximum size for all giant clams could be easily understood, promoting compliance. A 25-cm limit could be a good threshold to limit large *T. squamosa* clam collection, while not disturbing the habits of fishermen in the Austral islands who typically collect *T. maxima* between 12 and 20 cm (and sometimes more) for their 'meat' where these bivalves commonly reach larger sizes (Gilbert *et al*. 2006).

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Supplemental data

Supplementary file 1. List of photographic records and live samples (*) collected in the Tuamotu and Gambier archipelagos.

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