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The giant clam *Tridacna maxima* communities of three French Polynesia islands: comparison of their population sizes and structures at early stages of their exploitation

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Several lagoons of the atolls of Tuamotu Archipelago and volcanic islands of the Australes Archipelago (French Polynesia) are characterized by enormous populations of the clam *Tridacna maxima*, a species considered as endangered in many locations worldwide. Even if this resource can still be considered as virtually intact, the growing harvesting pressure to feed Tahiti's market (up to 50 t of wet matter y^{-1}), combined with the relatively small size of these lagoons, will soon call for management action to sustain a fishery that currently targets a large, virtually pristine stock. Hence, we present *T. maxima* population sizes and structures for two atolls (Fangatau and Tatakoto) and one island (Tubuai), where high clam densities and population sizes have promoted a small-scale, but growing, commercial fishery since the late 1990s. We followed an earlier pilot study, in which a combination of remote sensing and *in situ* data provided an estimate of the Fangatau clam population size (23.6 ± 5.3 million clams, mean ± 95% confidence interval, for 4.05 km^2 of mapped lagoon). We obtain 88.3 ± 10.5 and 47.5 ± 5.2 million clams for Tatakoto (mapped area of 11.46 km^2) and Tubuai (mapped area of 16.3 km^2), respectively. Accounting for contrasted length frequency distribution curves and one common size–weight relationship, the total biomasses are 1485 ± 177 t, 1162 ± 272 t, and 2173 ± 232 t of commercial flesh for Tatakoto, Fangatau, and Tubuai, respectively. In addition, given the legal restriction on collecting clams smaller than 12 cm, the legally harvestable biomasses are 958 ± 114 t, 1038 ± 247 t, and 1971 ± 210 t of flesh for Tatakoto, Fangatau, and Tubuai, respectively. The ratio between legal and total stock is much smaller for Tatakoto because this atoll is dominated by small clams, unlike the other two sites. The differences in population size and structure are discussed in terms of natural environment (habitats, degree of aperture to the ocean, temperature variations), providing insights on the natural variability between two similar systems (Tatakoto and Fangatau), and between different systems (the two atolls and the volcanic island of Tubuai), suggesting that future management schemes will have to be optimized locally.

Keywords: coral reef, fishery, French Polynesia, giant clam, marine resource management, remote sensing.

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Introduction

There is a remarkable abundance and dominance of the tridacnid clam *Tridacna maxima* (Röding, 1798) in French Polynesia atolls and island lagoons. Andréfouët *et al.* (2005b) reviewed the published values, and mentioned a value of 224 clams m^{-2} in Reao Atoll (Salvat, 1971). In addition, Andréfouët *et al.* (2005b) reported 23.6 ± 5.3 million clams (mean ± 95% confidence interval) in the mapped lagoon of Fangatau Atoll (4.05 km^2), and Gilbert *et al.*

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(2005) report up to 544 clams m^{-2} on the nearby Tatakoto Atoll, a unique site now designated as a no-take-area. Fangatau and Tatakoto atolls therefore have the biggest giant clam densities observed anywhere in the world. Many locations worldwide (e.g. Papua New Guinea, Samoa, Fiji), and lagoons of some of the islands of French Polynesia or the western Tuamotu atolls, have much lower densities with, at best, a few clams m^{-2} (Copland and Lucas, 1988; Lucas, 1994; Green and Craig, 1999; Andréfouët *et al.*, 2005b). One exception to this statement could be Tubuai Island, in the Australes Archipelago in the south of French Polynesia, for which previous unpublished reports have mentioned high densities of clams throughout the lagoon and barrier reef system. In addition, Tubuai Island appears to have been the main provider of clam flesh to the Tahiti market since the late 1990s. In 2002, sales of giant clams in the Tahiti market were estimated by the Service de la Pêche de Polynésie française (French Polynesia Fisheries agency, or SPE) to be about 50 t of wet matter y^{-1}.

It is unclear whether the high population densities of clams accumulated in spatially limited shallow lagoonal areas of Fangatau, Tatakoto, and Tubuai can sustain fishery activities. To clarify the potential, SPE funded a multidisciplinary programme from 2002 to assess the population size and structure, growth rates, genetics, and aquaculture potential of *T. maxima* at these three sites. Here we present the results of *T. maxima* population size and structure. The work follows the pilot stock assessment achieved at Fangatau Atoll using *in situ* and remote sensing data (Andréfouët *et al.*, 2005b). While Andréfouët *et al.* (2005b) focused on only one atoll, here we compare the clam population size and structure at Fangatau, Tatakoto, and Tubuai. It is also a prelude to a final manuscript that will present for the same sites the management models and actions required to sustain the fisheries on a long term. Comparison between the three sites provides more insights on the natural variability between two similar systems (Tatakoto and Fangatau atolls) and between different systems (the two atolls and the volcanic island of Tubuai). The differences in population size and structure are discussed in terms of natural environment (habitats, degree of aperture to the ocean, and temperature variations).

Material and methods

Study sites

Fangatau and Tatakoto atolls, two of the 77 atolls of the Tuamotu Archipelago (French Polynesia), are both in the remote eastern part of this archipelago (Figure 1). These closed lagoons without deep passes connecting to the ocean belong to the same morphological type, and have fairly similar rim structure. Rims are closed in the north by vegetated land, and semi-open in the south, with a succession of vegetated islets and several shallow spillways (Andréfouët *et al.*, 2001). They nevertheless slightly differ in terms of surface area and total opening to the ocean (Table 1), Tatakoto being the largest and more open. Both lagoons are dotted by numerous intertidal or subtidal carbonate structures locally called "mapiko", which are made of an accumulation of cemented or loose *T. maxima* shells.

Most inhabitants of the two islands live on the higher grounds of the western side of the atolls. Fangatau and Tatakoto villages have ~130 and ~250 inhabitants, respectively. There are no tourist activities on either atoll. Incomes are from fishing, coconut groves for copra exportation and, more recently, from *T. maxima* harvesting. In 2004, commercial clam flesh (muscle, mantle, plus gonad) exports towards Papeete's market in Tahiti reached 5.5 t for Fangatau and >16 t for Tatakoto. These numbers represent approximately half the estimated annual French Polynesia clam market (~50 t y^{-1}).

Tubuai is a high volcanic island in the central part of the Australes Archipelago (Figure 1). It is the largest island of the archipelago, with 45 km^2 of land, and the second most populated, with ~1900 inhabitants. Its lagoon (90 km^2) is open to the ocean, and water is continuously flushed through five shallow passes and through the barrier reef flats that surround the island entirely. Mapikos also occur in the lagoon, indicating that giant clams are quite abundant. Tourism there is at an early stage of development, and agriculture is the major commercial activity. The *T. maxima* fishery is developing quickly, with activities spread among three villages, making it difficult to monitor clam flesh exportation. However, a recent survey estimated that ~30 t of clam flesh were exported to Tahiti in 2003. Tubuai, Tatakoto, and Fangatau together account for almost the entire French Polynesian clam market.

Remote sensing

Andréfouët *et al.* (2005b) showed for Fangatau Atoll how the use of remote sensing data delivered better stock estimates of clams. Fangatau lagoon habitats and geomorphology were mapped using a variety of remote sensing data, including a mosaic of aerial photographs, a digital photograph acquired from the International Space Station, and one Landsat 7 digital image. The conclusion of that study was that none of the sensors were optimal for assessment of habitat structure at Fangatau Atoll, even if they were very useful in constraining the clam stock assessment. Based on their experiences from other habitat mapping exercises (Andréfouët *et al.*, 2003, 2004), Andréfouët *et al.* (2005b) recommended the use of high spatial resolution sensors (<4 m), geodetically rectified at a precision of a few metres, with at least four spectral bands, including a near-infrared band that allowed better identification of above-water features and sea surface glint correction. Therefore, Tatakoto Atoll and Tubuai Island were surveyed and mapped using a suite of Quickbird images acquired in 2004 at 2.5 m resolution. Here, we use the results for Fangatau Atoll achieved using the mosaic of aerial photographs at 1.5 m resolution (Andréfouët *et al.*, 2005b).

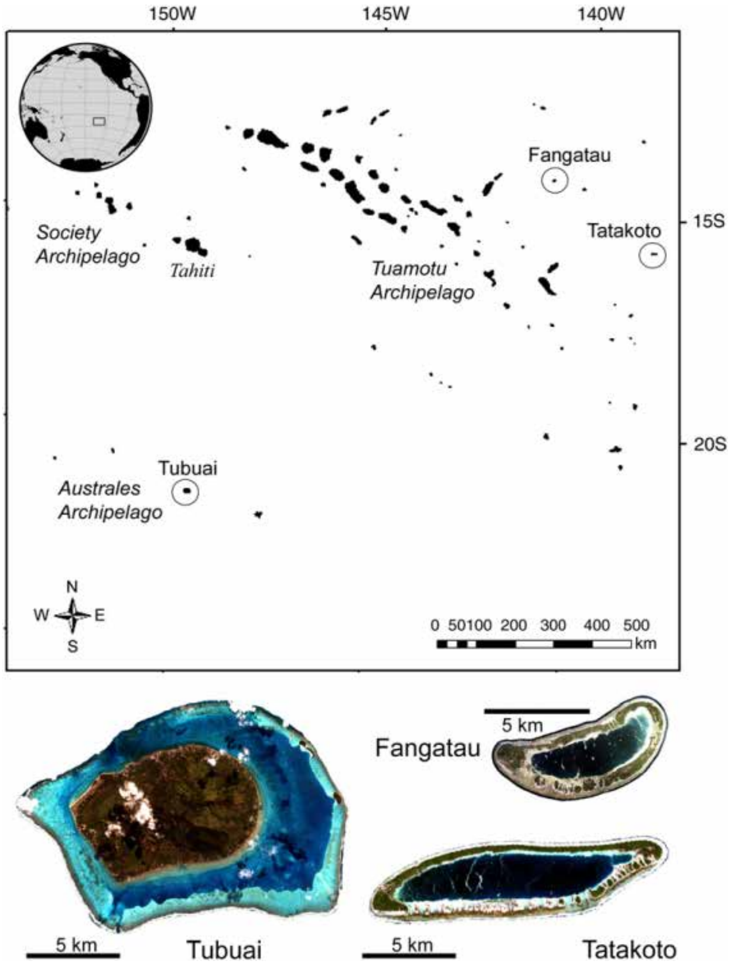

Figure 1. Location of Fangatau, Tatakoto, and Tubuai in French Polynesia, and a true colour composite image of each island made from aerial photographs (Fangatau) or Quickbird satellite images (Tatakoto and Tubuai).

The Quickbird images were used to stratify *in situ* surveys. Both representative areas and areas with peculiar features (in terms of colour and texture) were flagged for *in situ* assessment. In addition, as in Andréfouët *et al.* (2005b) for Fangatau Atoll, sites were selected to account for different geomorphological units (reef flats, slopes, ridges, lagoon floor patches, and mapikos for atolls; fringing reef, barrier reef, coral patches, ridges for Tubuai), exposure to wind and swell, proportional presence of hard and soft substratum, distance to the coast and to the villages, logistics, and finally time devoted for the surveys (one week at Tatakoto and Fangatau, ten days at Tubuai). As good weather prevailed during all surveys, all preselected zones were investigated, and two sites were measured per zone.

In situ data collection for habitat mapping was constrained differently depending on atoll and island configuration. Indeed, clam beds are a significant feature of atoll lagoon habitats, as at Fangatau (Andréfouët *et al.*, 2005b). For each atoll site, two 20-m transects provided benthic cover data. Cover of live clams, dead clams, rubble, live coral, dead coral, sponge, macroalgae, and encrusting coralline algae were noted using the Line Intersect Transect (LIT) method (English *et al.*, 1997). Transect directions were random (i.e. not necessarily parallel or perpendicular to the reef front), within the sampling zone.

Three 0.25-m^2 quadrats were surveyed to assess the density of clams in areas of high clam occurrence (Andréfouët *et al.*, 2005b). Quadrats were placed randomly within the zone and depth range captured by the transects. Quadrat data served both the population size assessment and the population structure description, because the size of each clam present in each quadrat was measured. Quadrat area was limited to 0.25 m^2 because of the impressive clam density (up to 500 clams m^{-2}, all sizes included). A team of scuba-divers collected data for sites 2–10 m deep, and a snorkelling team collected data in the shallows along reef crest and mapiko edges.

Table 1. Main morphometric parameters for Tatakoto, Fangatau, and Tubuai (after Andréfouët *et al.*, 2005a). Those authors provide a consistent database computed using Landsat 7 images for all French Polynesian islands, useful for comparisons with other sites (Table 3). Values computed using the highest resolution Quickbird image specifically for this study (cf. text) are slightly different because of differences in spatial resolution. The total area includes land. Total aperture is the sum of the width of the submerged spillways divided by the perimeter of the island. For Tubuai, completely surrounded by a submerged barrier reef, the aperture is 100%. The lagoon area in atolls includes the shallow inner slope, the deep lagoon, mapikos, and pinnacles. For Tubuai, the lagoon area includes the deep lagoon, fringing reefs, patch reefs, barrier reef flats, passes, and sedimentary terraces.

Island	Total area (km^2)	Perimeter (km)	Lagoon area (km^2)	Total aperture (%)
Fangatau	24.51	20.33	7.91	6.37
Tatakoto	44.53	30.96	17.66	12.07
Tubuai	168.42	47.62	90.88	100

On the wide reef flats of the Tubuai barrier reef and in its lagoon, we expected a great variety of habitats with clams not as dominant as in the atolls. In atolls, habitat characterization was achieved using LIT data collected primarily to measure clam cover (see above), as at Fangatau (Andréfouët *et al.*, 2005b). At Tubuai, habitat characterization was achieved using a reefscape approach: a rapid semi-quantitative evaluation of benthic cover (sand, rubble, rocky floor, pavement, live coral, dead coral, algae) and architecture (topography, complexity, coral growth form) of areas generally covering $\sim 10 \times 10$ m. Then, in a second stage, clam densities were measured in these habitats using 1-m-wide belt transects. Transects' orientations were random. Transect depth and length were selected according to the type of habitat (and therefore the range of clam cover) and current (which can be very strong on barrier reef flats). Some sites described in term of habitat were not sampled because we found that clams were absent. At Tubuai, we ran transects 1 m wide by 5, 10, and 30 m long. All live clams were counted and their lengths measured. Therefore, in contrast with the situation at Fangatau and Tatakoto, density within the sampling zone was estimated directly. In the atolls, the cover of clams from the transect method is needed to weight the estimation of clam density, because density is measured on high cover areas only.

The data collected for habitat description, either LIT (atolls) or reefscape (Tubuai), offer the possibility to cluster the different sites using a measure of similarity. Data from Tatakoto transects and Tubuai reefscape description were clustered into benthic habitats by hierarchical clustering based on Bray–Curtis similarity. For Fangatau, transect data were clustered into different benthic habitats by principal component analysis (PCA), and subsequent hierarchical clustering was performed on the PCA scores (Ward method; Andréfouët *et al.*, 2005). This eventually provided a hierarchical typology (dendrogram) of habitats. As in Green and Craig (1999) and Andréfouët *et al.* (2005b), *T. maxima* population size was estimated by compiling the mean clam density in each habitat (*in situ* data), measuring the total area of each habitat (from the remote sensing image classification, see below), multiplying each area by the mean density for that habitat, and summing these totals for an overall population estimate. Final selection of the habitat typology used to compute the total population of clams depended on differences in clam density differences between habitats. The most interesting pattern is found when live clam densities' differences are maximized between habitats and the intra-class variance minimized as well. However, we added the strong ancillary constraint that those habitats can be mapped accurately using Quickbird data.

Length measurements from quadrats and transects were used to plot clam length frequency distribution for each island, for the different habitats within the island, and considering two depth strata ("shallow" and "deep", which roughly corresponded to what is above and below ~1-m depth, and what has been surveyed by snorkelling or by SCUBA, respectively).

Size–weight relationship and biomass estimates

During the first survey at Fangatau, two relationships with length were established: total biomass (shell and flesh) and flesh biomass. Additionally, at Tatakoto, we measured also the subfraction of the flesh biomass that makes the edible (commercial) flesh biomass (i.e. mantle, gonad, muscle), working under the hypothesis that a unique length–weight relationship would be valid for all sites in French Polynesia. We checked this assumption by running an ANCOVAR analysis (Zar, 1984), log-transforming the variables.

The biomass (total, flesh, commercial flesh) per island is computed by compiling the population size and structure for each habitat. Summing these totals by length and habitat gives an overall population commercial biomass estimate:

$$\mathrm{BcT} = \sum_{i=1}^{n} \mathrm{Bc}_i = \sum_{i=1}^{n} \sum_{j=1}^{26} n_i F_{ij} P_j,$$

where BcT is the total commercial biomass (in g), n the number of habitats, Bc_i the commercial flesh weight for habitat i (g), n_i the number of clams in habitat i, F_{ij} the proportion of clams of shell length j in habitat i, P_j the flesh weight for shell length j (g), and 26 is the maximum shell length (in cm) observed in the field.

Supervised image classification

The Quickbird images of Tubuai and Tatakoto were processed as in Andréfouët *et al.* (2005b). For Fangatau, we used the habitat map generated and processed from aerial photographs documented in Andréfouët *et al.* (2005b). For Tatakoto and Tubuai, deep lagoon waters and land areas were masked out. Once the relevant habitats were defined (see above), they were mapped using an iterative combination of *a priori* and *a posteriori* contextual editing and supervised classification. Sedimentary areas (coral sand, shallow, or deep) were added to the Tatakoto and

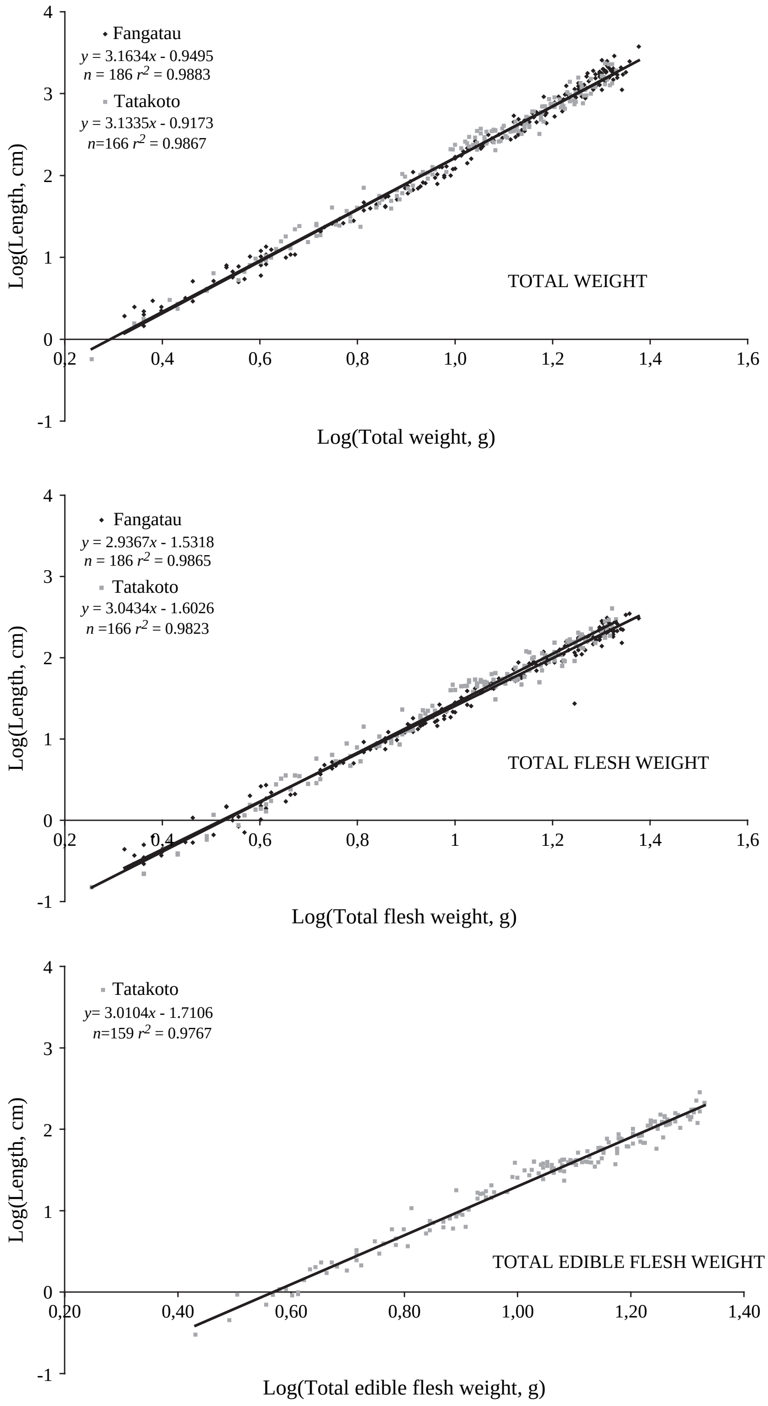

Figure 2. Size–weight relationships. Top panel, total weight (shell + flesh) plotted against length for Tatakoto and Fangatau. Middle panel, total flesh plotted against length for Tatakoto and Fangatau. Bottom panel, total edible flesh plotted against length for Tatakoto, the only site where such measurements are available.

Tubuai habitat typology for mapping purposes although virtually no clams occur in such areas.

Results

General survey

In all, 59, 63, and 97 sites were investigated for community structure assessment at Fangatau (Andréfouët *et al.*, 2005b), Tatakoto, and Tubuai, respectively. From the 396 quadrats surveyed at Fangatau, the 281 quadrats at Tatakoto and the 327 belt-transects at Tubuai, 3781, 6389, and 6400 clams were measured at Fangatau, Tatakoto, and Tubuai, respectively.

For Fangatau and Tatakoto, 186 and 165 clams, respectively, were used to establish the length–weight relationships (Figure 2). ANCOVAR revealed no significant differences between atolls in the relationships between total weight and length, on slopes ($F_{0.05,\ 3.86} = 0.48$) or elevations ($F_{0.05,\ 3.86} = 0.07$; upper panel of Figure 2). Conversely, differences were significant for the relationships between total flesh weight and length (slope, $F_{0.05,\ 3.86} = 6.92$; elevation, $F_{0.05,\ 3.86} = 11.77$; Figure 2, central panel). This is due to us having measured gonad mass during different fertility periods at the two atolls.

The shell is the major contributor of the total weight (83%), flesh (17%), and edible flesh (gonad, 3%; mantle + muscle, 9%) being lesser contributors. The ratio of flesh weight to total weight is 0.17, a value similar to the 0.14 given by Salvat (1972). Richard (1977) reported a range of 0.15–0.20 that depended on mean clam length. The differences reported here between studies are therefore

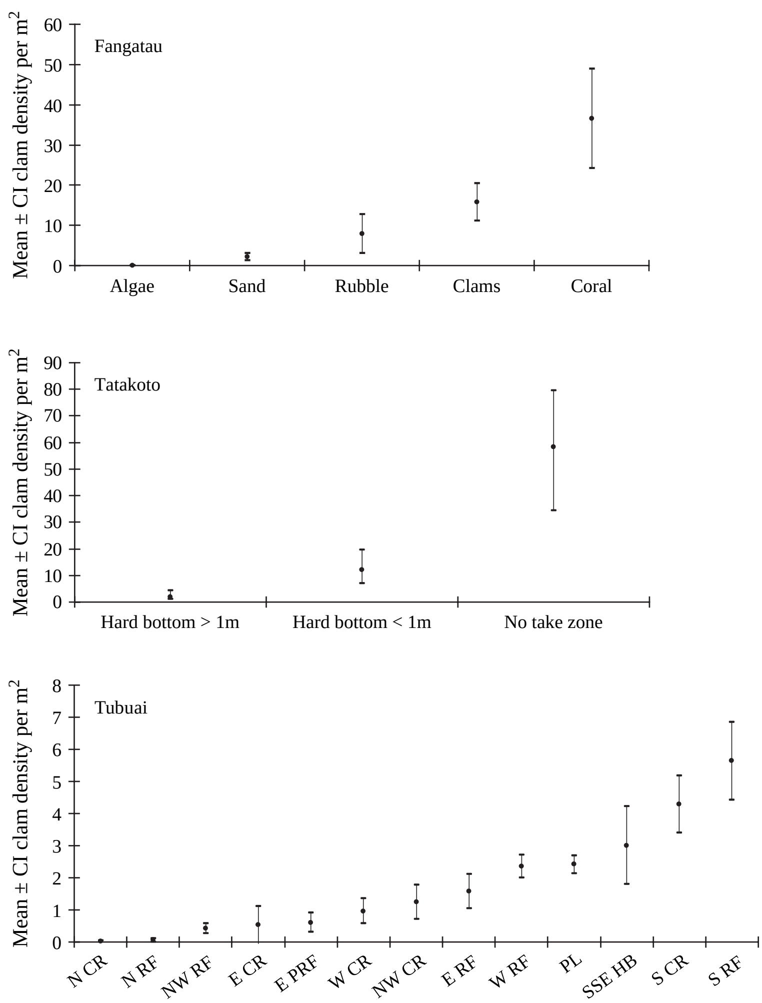

Figure 3. Clam density (mean ± 95% confidence intervals, CI) for Fangatau (top panel), Tatakoto (middle), and Tubuai (bottom) for each mapped habitat classes. For Tubuai, habitat classes are defined according to geomorphology (RF, reef flat; CR, crest; PRF, patch on reef flat; PL, patch in lagoon; HB, hard bottom), and exposure (N, north; E, east; S, south; W, west; NW, northwest; SSE, south-southeast). Note the different scales on the *y*-axes.

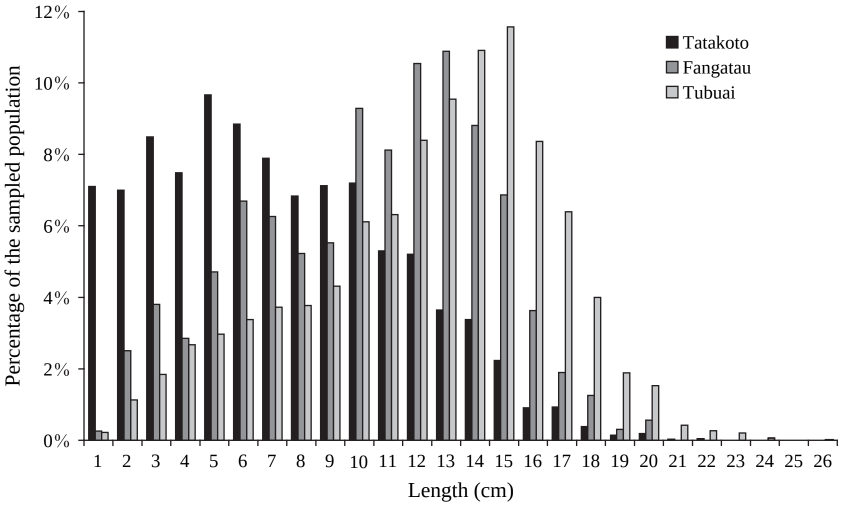

Figure 4. Size frequency plots for the sampled clam population at Fangatau ($n = 3781$), Tatakoto ($n = 6389$), and Tubuai ($n = 6400$).

probably explained by differences in the mean length of the sampled population and different epibiont loads, which vary from place to place.

For Tatakoto and Fangatau biomass estimates, site-specific length–weight relationships were used. However, Figure 2 shows that relationships between length and flesh weight are very close for the two atolls, even if the test was negative. Therefore, in the case of missing data, we assumed that a single common relationship would be of value for inter-site generalization. As no relationships between edible flesh weight and length were available specifically for Fangatau and Tubuai, Tatakoto's relationship was applied (Figure 2, lower panel). Finally, Tatakoto's relationship between total flesh weight and length was also applied to Tubuai.

Habitat typologies

Surprisingly, habitat structures varied substantially between the two atolls. Between Tubuai and the atolls, habitats also appeared to be very different, but this result was expected. At Fangatau, we found five classes of well-contrasted habitats with significantly different clam densities (Andréfouët *et al.*, 2005b). They were generically labelled as "Coral", "Clams", "Sand", "Rubble", and "Algae". At Tatakoto, the pattern differed. In the eastern lagoon, there were mounds of high clam densities where the habitats were structured by the clams, as at Fangatau, but this pattern was not evident elsewhere. Data on benthic cover showed a much higher coral cover (mainly branching corals *Acropora* spp., and inner crests of massive *Porites* colonies), a lack of *Caulerpa bikinensis* at depth, but a significant presence of *Caulerpa urvilliana* on the western side of the atoll, along the slopes of the structures and the lagoon floor. Tatakoto habitats for clams comprise a networked structure of ridges and patches at depth (<2–10 m), extensively covered by branching corals and, in the western lagoon, by caulerpas. There was no such pattern at Fangatau. Consequently, at Tatakoto, the habitats could not be clearly defined thematically, geographically, and spectrally but rather as a continuous gradient of habitats with similar cover type and fuzzy boundaries, which are more difficult to map accurately (Andréfouët *et al.*, 2000).

At Tatakoto, there were very high clam densities per m^2 (58.1 ± 21.2) on the eastern mapikos and subsurface mounds of live clams, although such observations were limited to the area that has been classified recently as no-take area (Gilbert *et al.*, 2005). Clam densities were high (12.0 ± 7.6) on the edges of mapikos and inner reef flats, where clams were often under the canopy of branching

Table 2. Population sizes and biomasses for the total population and for the legally harvestable population (≥12 cm) at the three islands. Total weight includes flesh and shell. Commercial flesh includes only the fraction that is sold, i.e. mantles, adductors, and gonads.

Island	Total clam population (millions)	Clam population ≥12 cm (millions)	Total weight (t)	Total flesh weight (t)	Total commercial flesh weight (t)	Commercial flesh weight, clams ≥12 cm (t)
Fangatau	23.6 ± 5.3	14.3 ± 3.3	9 194 ± 2 158	1 491 ± 350	1 162 ± 272	1 038 ± 247
Tatakoto	88.3 ± 10.5	17.6 ± 2.1	13 135 ± 1 573	2 166 ± 259	1 485 ± 177	958 ± 114
Tubuai	47.5 ± 5.2	30.5 ± 3.3	19 729 ± 2 109	3 197 ± 342	2 173 ± 232	1 971 ± 210

Acropora spp., with some massive *Porites* corals, caulerpas, dead clams, and sediment. Densities were moderate (1.9 ± 2.4) at depth along the slopes of the structures. Therefore, the Tatakoto typology of mappable habitats that maximized inter-class density and minimized intra-class density is limited to three classes, contrasting the five found at Fangatau (Figure 3). These three classes are referred to as "No-take zone", "Hard bottom <1 m", and "Hard bottom >1 m". Further, we added different sedimentary areas for mapping purposes (i.e. representing as exhaustively as possible the lagoon bed), but the clam density on these areas was zero. Unmapped areas were too deep to see the bottom with optical remote sensing images, i.e. deeper than 15 m.

On the Tubuai reef flats, as in many reef systems structured primarily by wave energy, the habitat typology was well defined in terms of benthic cover and architecture. There was no significant zone of fleshy algae, except on some narrow rocky fringing sections, where there were no clams. Seven lagoon and barrier reef habitats could be clearly defined based on hierarchical clustering of topography, complexity, pavement, sand, rubble, small boulder, large boulder, dead encrusted coral, live coral, and macroalgae

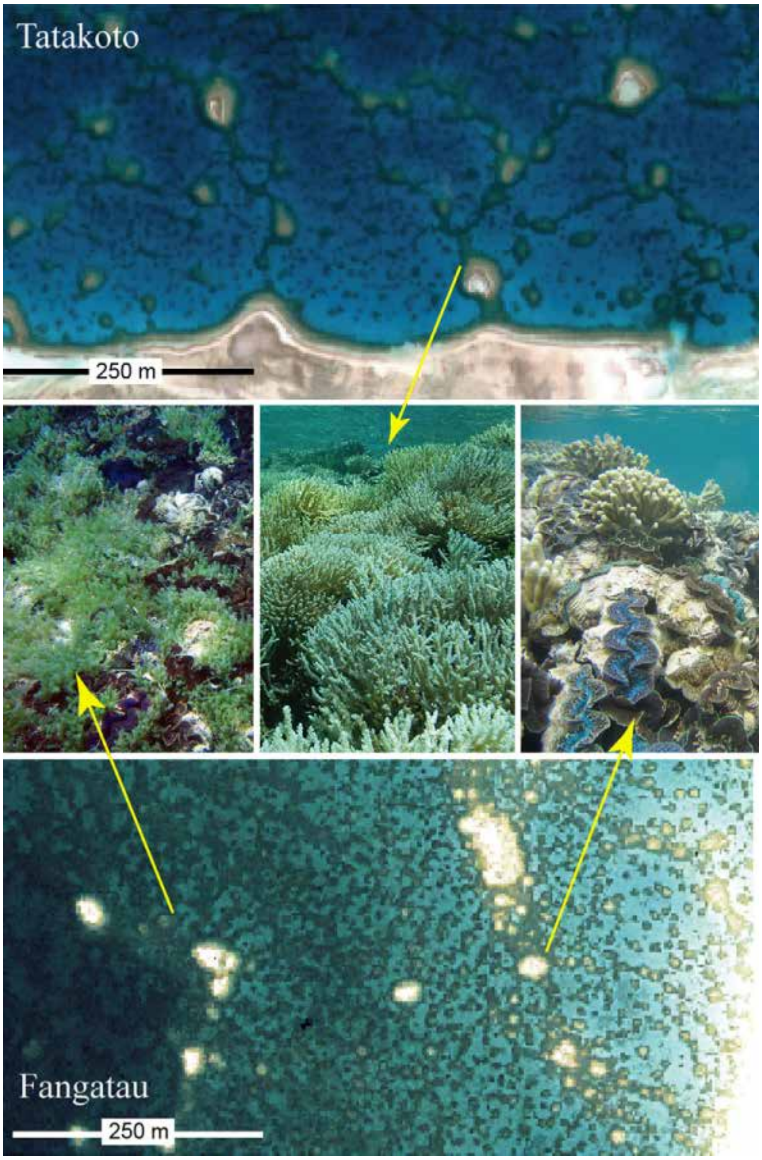

Figure 5. Differences in habitat structure between Fangatau and Tatakoto. Top panel, Tatakoto's habitat structure from Quickbird satellite images, with networks of coral ridges and patches. Bottom panel, Fangatau's habitat structures with isolated clam mounts shifting to *Caulerpa bikinensis* meadows deeper than 5–6 m.

(fleshy and encrusting). However, the initial habitat typologies did not provide an optimal gradient in clam density, mean density extrema being 1.5–4 clams m^{-2}. A better gradient was achieved when we pooled data from the different sampling zones based on their exposure and geomorphology. For geomorphology, we considered barrier reef crests, barrier reef flats, lagoonal patch reefs, back barrier reef, patch reefs, and hard-bottom alleys on the sedimentary accumulation of the back barrier reef. For exposure, we considered east, north, west, and south directions for the barrier reef sites but no exposure for lagoon patch reefs. Combining geomorphology and exposure provided 13 classes of interest, with mean clam density extrema between 0 and 6 clams m^{-2} (Figure 3). A similar density range could be achieved by combining the seven-habitat typology with exposure, but mapping habitat is more complex and less accurate than mapping geomorphology, so we used this 13-class geomorphology + exposure typology to map Tubuai clam density. A large part of the lagoon (71.54 km^2) is mapped as "no clam area" because it is sedimentary, with virtually no clams.

Population size, size frequency distribution, and biomass

Given the surface areas of each habitat class and the average clam density in each, we estimated a total of 88.3 ± 10.5 and 47.5 ± 5.2 million clams (mean ± 95% confidence interval) present at Tatakoto (mapped area of 11.46 km^2) and Tubuai (mapped area of 16.3 km^2), respectively. Andréfouët *et al.* (2005b) estimated the Fangatau clam population at 23.6 ± 5.3 million clams, for 4.05 km^2 of mapped lagoon.

Size frequency plots for each island are given in Figure 4. Tatakoto stands out from Fangatau and Tubuai with a main mode at 5 cm, highlighting the importance of small clams there. In contrast, the main modes at Tubuai and Fangatau were at 15 cm and 13 cm, respectively. Tubuai had the largest clams, up to 26 cm.

Total biomass (flesh + shell) and commercial flesh (gonad + muscle + mantle) are detailed in Table 2, for each island. We also include in the Table the fraction that corresponds to the population size (≥12 cm) that can be legally exploited in French Polynesia.

Discussion

Habitat differences

Differences in habitat structure between the three sites are important because they have implications in terms of community structure and in methods to be deployed, both *in situ* and to process remote sensing images. Although the two atolls are geomorphologically similar, geographically close, and influenced by the same oceanic and atmospheric environments, the organizations of their lagoon habitats differ (Figure 5). At Fangatau, we mapped five well-defined habitats easily, even with aerial photographs. Conversely, at Tatakoto the gradient of seven habitats was not only

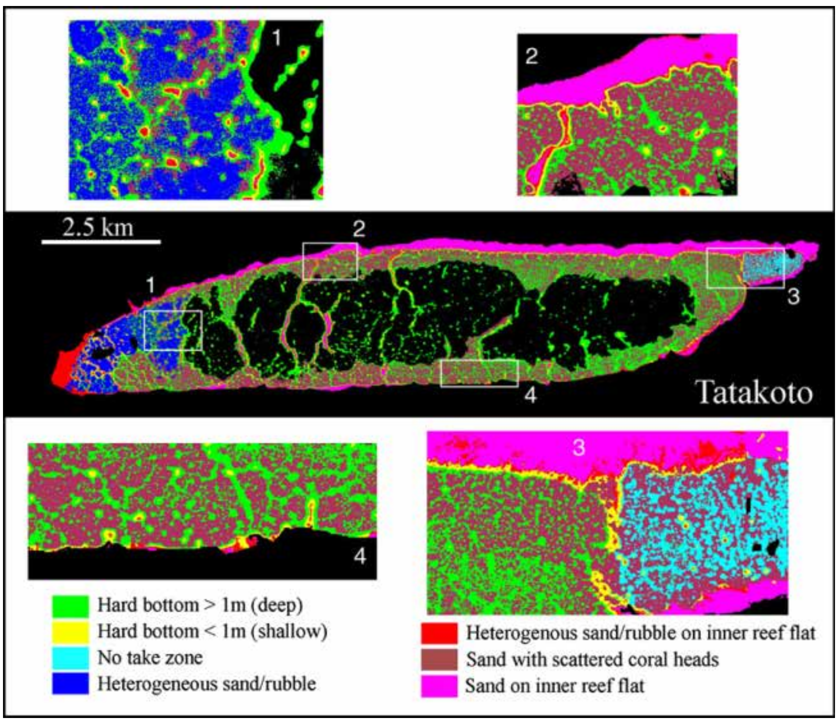

Figure 6. Tatakoto habitat map with enlargements.

more subtly defined, but also differently organized in terms of clam density and cover. Coral cover at Tatakoto is very high (up to 60% coral cover for 21% of the stations; an average of 0.37 ± 0.21 for all stations), a situation not present at Fangatau. Only three classes with significantly different clam densities could be mapped at Tatakoto, including the remarkable eastern area of submerged dome-shaped mapikos that was classified as a single unique habitat (and now administratively designed as a no-take area; Gilbert *et al.*, 2005). In contrast, the high volcanic island of Tubuai with its barrier reef offered a large variety of habitats defined by geomorphology and exposure, well

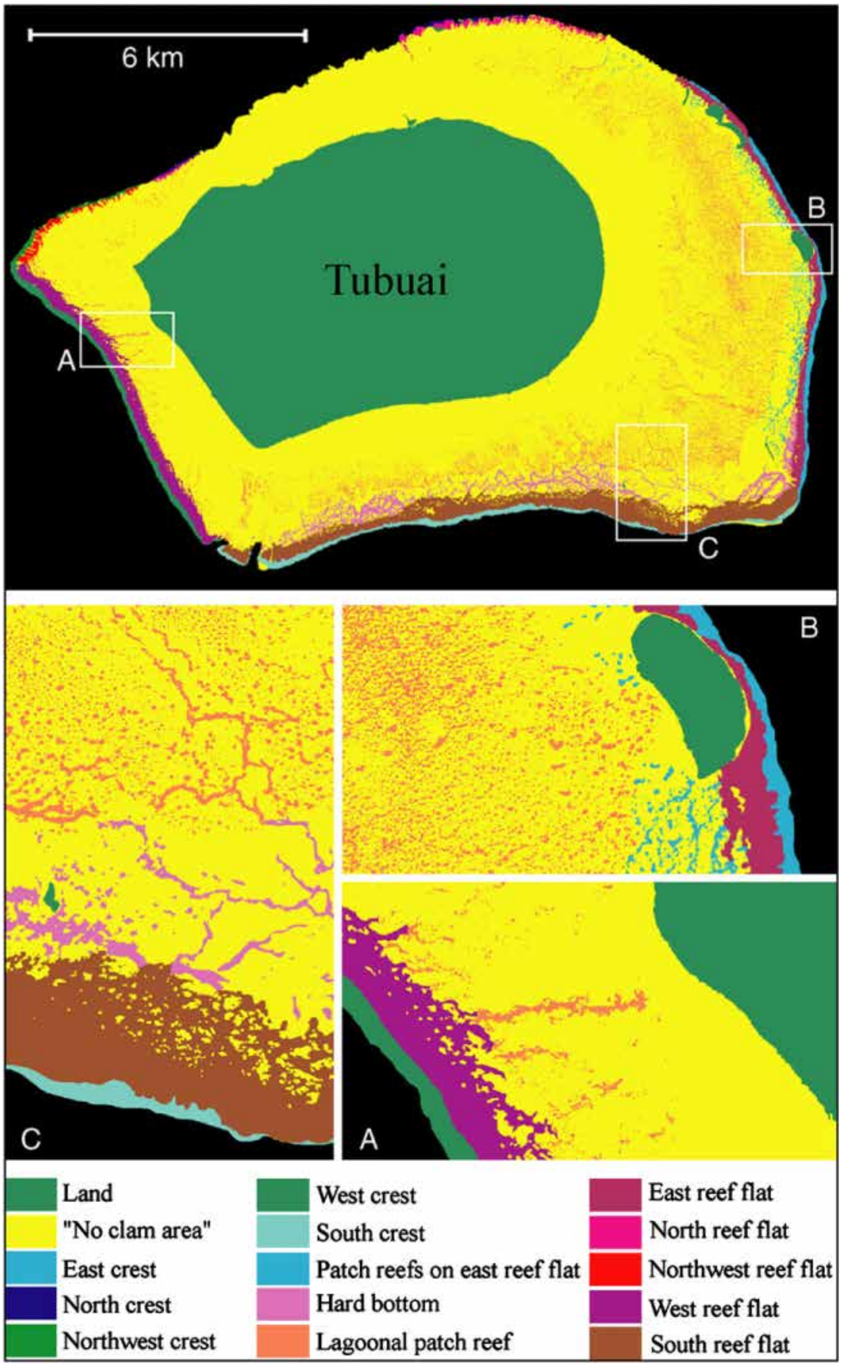

Figure 7. Tubuai habitat map with enlargements.

contrasted in terms of densities, although densities were 6−10 times lower than at the atolls. The lesson from the three islands regarding habitat mapping is that each may be unique and may provide a unique configuration, even if they belong to the same system as the two atolls. Each site may need a specific habitat typology to fine-tune the spatial distribution of clam density and to take advantage of synoptic remote sensing images. Blind generalization from one site to another could provide poor map product and, therefore, poor upscaling of clam population properties. Finally, even if the habitat typology may seem thematically coarse, these coarse classes are mapped using very high spatial resolution images, so the spatial details and the outlines are excellent (Figures 6 and 7) and contribute to the precise estimation of stock sizes. The estimates would be degraded if data of coarser spatial resolution were to be used (Andréfouët *et al.*, 2005b).

We do not have accuracy assessment data for Tatakoto (Figure 6), but this is not really required to trust the product. Indeed, the level of confusion is small, because one class is spatially constrained to the eastern side of the atoll (*a priori* contextual editing). The two other hard-bottom classes are dependent on depth. Therefore, *a posteriori* contextual editing can be used to limit misclassification of deep pixels. Finally, four soft-bottom classes (sand) were mapped, but they are not relevant in terms of stock size because of the absence of clams there. They were added only to enhance habitat and geomorphology diversity representation. These sandy areas can be easily differentiated between each other by *a posteriori* contextual editing, because they belong to different geomorphological zones. Similarly, the Tubuai habitat map (Figure 7) is very robust in terms of misclassification, because habitat classes are geomorphology- and exposure-dependent. Such characteristics alone allow removal of virtually all confusion and classification error by virtue of the masking process (i.e. contextual editing). For instance, a barrier reef flat pixel exposed to the north and classified as a patch reef pixel is an obvious error that is easy to correct. We also lacked formal accuracy assessment for Tubuai because of a lack of time to collect hundreds of accuracy assessment points, but our "geomorphology + exposure" habitat typology prevented generation of substantial errors. The use of topological rules to improve coral reef maps and to facilitate discussion of their accuracy has been presented in Andréfouët and Guzman (2005).

Differences in clam micro-distribution

The densities and clam spatial organizations reported differ significantly among islands (Figure 8). Three microstructures can be identified: regular, clustered, and random (Orensanz *et al.*, 2006). In general, Fangatau and eastern Tatakoto have regular carpets of high clam density, sometimes organized in three-dimensional structure, the understory of clams providing the substratum for new clam settlement. At Tatakoto, the thickets of branching coral tended to break the regular structure into clustered clams, in a much patchier way than at Fangatau. Finally at Tubuai, even at highest densities, clams were isolated and randomly embedded in the coral, pavement, or rocky floor substrata.

These differences in spatial distribution pose problems when collecting field data for a programme as unique as this. It is difficult to design a unique survey technique

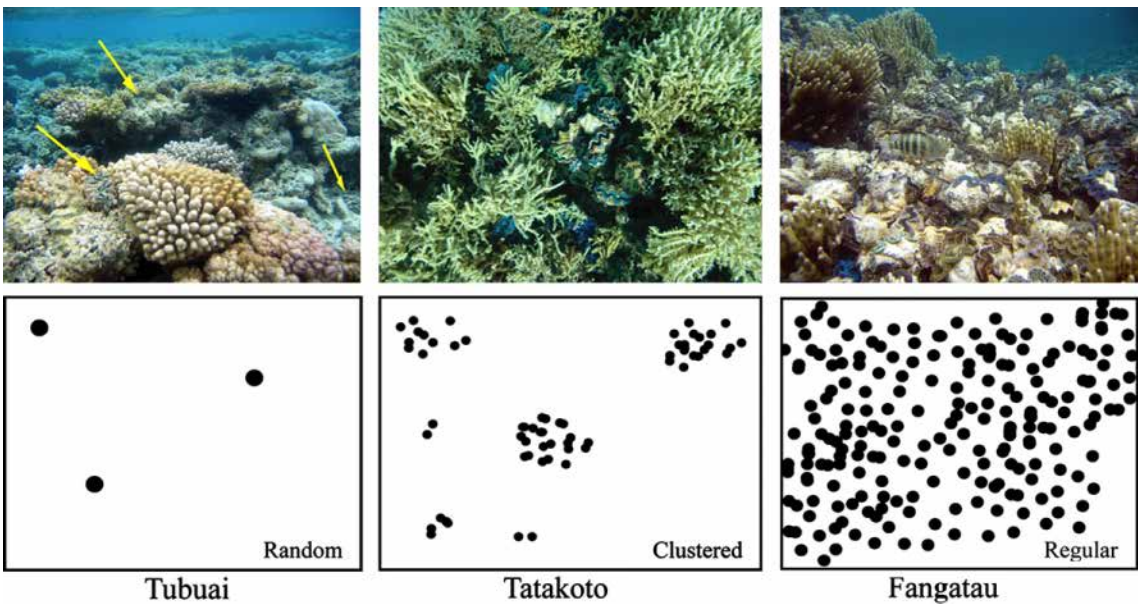

Figure 8. Differences of clam micro-distribution between the three islands. Left, Tubuai with random population. Middle, Tatakoto with clustered aggregates of clams. Right, Fangatau with regular continuous field of clams.

optimized for all sites. Therefore, it is justifiable to shift from one method to another among and between sites where differences in density and patchiness of several orders of magnitude are observed. Given the low density encountered at Tubuai, 30-m-long belt transects are required, but generalizing this method to atolls would be impractical. It would take days to complete a single transect in areas where clam density was measured at up to 500 m^{-2}. The transect + quadrat approach is suitable for high density, even patchy, areas. Conversely, the 0.25-m^2 quadrat method applied at the atolls significantly underestimates actual density if applied to Tubuai's densities (unpublished data). Moreover, even if Tubuai's densities appear small compared with those of the atolls, they are still one or two orders of magnitude greater than at most coral reefs of the Indo-Pacific. Calibration experiments may be required to identify trends before running a complete survey in areas of low to moderate densities.

Between-island population comparison

Tatakoto, Fangatau, and Tubuai lagoons clearly have the largest stocks of giant clam ever assessed in French Polynesia. Table 3 reports previously published observations, though the methodology of some works differed from that used here, making comparisons difficult.

Population structure at the two atolls appears to differ. In terms of total population size, the 23.6 million clams at Fangatau are well short of the 88.3 million at Tatakoto. Tatakoto's average density is approximately twice that of Fangatau's, a difference explained by the abundance of small clams at Tatakoto. The eastern part of Tatakoto contributes 40% of the atoll's clam population while covering only 0.16 km^2 (1.4% of the mapped area), and there the population distribution is skewed towards small clams. Only 4% of the clams there reach more than 12 cm long, compared with 14% and 24% for the two other Tatakoto hard-substratum habitat classes. The size−density structure of Figure 9 is derived from a situation of highly aggregated clams, where spatial competition is probably the main factor affecting shell length. Recruitment there tends to be enhanced on living clams, which comprise most of the substratum, and the subsequent competition for space, leading to competition for light, is doubtless responsible for the early mortality in that clam population. The pattern of larger *T. maxima* shell size in the deeper lagoon areas of Tatakoto and Fangatau (Figure 10) has also been reported at the Cook Islands atolls (Sims and Howard, 1988; Table 4). As at Aitutaki, a well-fished atoll of the Cook Islands, greater clam mortality in the shallower water of Fangatau and Tatakoto lagoons can certainly be attributed to heavier fishing pressure. Moreover, shallow clams are more susceptible to ultraviolet and temperature stress when water renewal is less, as for instance when water levels are low in the lagoon. Greater natural predation by octopus and molluscivorous fish in the shallows could be another

Table 3. Review of estimates of available giant clam (*T. maxima*) population size for French Polynesia. Surface and aperture data come from Landsat data presented in Andréfouët *et al.* (2005a). Total aperture is the sum of the width of the submerged spillways divided by the perimeter of the island. For Tubuai, completely surrounded by a submerged barrier reef, the aperture is 100%. The lagoon area in atolls includes the shallow inner slope, the deep lagoon, mapikos, and pinnacles. For Tubuai, the lagoon area includes the deep lagoon, fringing reefs, patch reefs, barrier reef flats, passes, and sedimentary terraces.

Parameter	Anaa	Takapoto					Reao	Fangatau	Tatakoto	Tubuai
Reference	Laurent (2001)	Richard (1982)	Richard (1989)	Richard and Duval (1993)	Addessi (1999)	Laurent (2001)	Salvat (1971)	Andréfouët *et al.* (2005b)	This study	This study
Locality	Central Tuamotu Archipelago	Eastern Tuamotu Archipelago	Western Tuamotu Archipelago	Western Tuamotu Archipelago	Western Tuamotu Archipelago	Western Tuamotu Archipelago	Eastern Tuamotu Archipelago	Eastern Tuamotu Archipelago	Eastern Tuamotu Archipelago	Central Australes Archipelago
Population size (millions)	0.26 ± 0.13	14	11.5	10.6 ± 0.42	1.98 ± 1.21	1.29 ± 0.65	11.3	23.6 ± 5.3	88.3 ± 10.5	47.5 ± 5.2
Total lagoon area (km^2)	91.14			77.45			38.96	7.91	17.66	90.88
Total aperture (%)	18.59			2.83			4.96	6.37	12.07	100

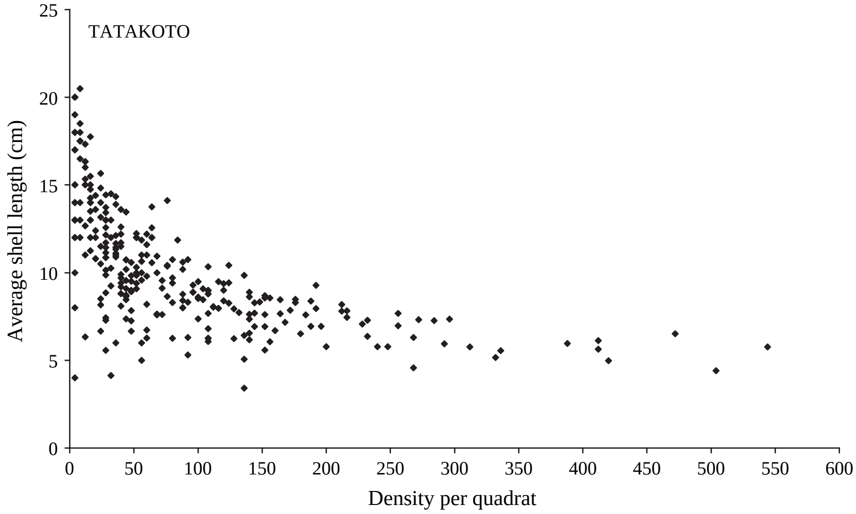

Figure 9. Relationship between average clam size and clam density for every quadrat surveyed at Tatakoto in April 2004.

explanation (Sims and Howard, 1988), but we have no proof of this.

The main causative factor of Tatakoto juvenile abundance is not fully understood. Aquaculture experiments in progress on both atolls suggest that spat collection on artificial supports is more successful at Tatakoto, with more frequent recruitment. Time-series of temperature measurements in these closed lagoons at a similar depth range (Figure 11) reveal inter-atoll differences, spikes of cool water entering more frequently at Tatakoto, in both cool and warm seasons. Aquaculture experiments also show that settlement appears to be timed to coincide with lagoon water cooling events, in turn the consequence of oceanic water entering the lagoon. Fangatau's lagoon is less open to the ocean, making it more likely that the thermal stresses that trigger spawning more frequently at Tatakoto are the consequence of a difference in degree of aperture. Further, the fact that Tatakoto is more open than Fangatau along its southern rim provides a physical explanation for the higher frequency of spawning at Tatakoto, which in turn would then result in greater abundance of small clams. At this stage, this hypothesis is being tested by ongoing monitoring of both thermal variations and recruitment rates in the different lagoon areas.

Tubuai clam populations are different from those of the atolls. First, densities are much lower (Figure 3), about 6−10 times lower in terms of the habitats with the greatest densities at each island (Figure 3). Moreover, clams attain larger size at Tubuai (Figure 4). Size frequency plots per habitat at Tubuai do not reveal striking spatial differences, even though several of the habitats are well defined spatially through explicitly accounting for exposure. In addition, size frequency histograms between shallow and deep regions are less contrasted than at the atolls (Figure 10). The presence of larger clams and a similar community structure in shallow and deeper areas at Tubuai can be explained by the low densities, which do not promote competition for space, in contrast to the situation at the atolls.

Differences in biomass

The 12-cm threshold is a French Polynesian legal minimum size limit for clam collection. Only clams living in shallower water (<1.5 m) are generally collected; 52% of Fangatau clams in such depths are of legal size, but just 20% of Tatakoto clams at the same depth are of legal size. However, despite such differences in population and demography, the two atolls yield remarkably similar commercial quantities of clam flesh, 364 ± 85 t and 307 ± 69 t from Fangatau and Tatakoto, respectively.

At Tubuai, total biomass is 2173 ± 232 t of edible flesh from 47.5 million clams. Of this, again considering the 12 cm limit plus the fact that local fishers also gather clams from deeper water (up to 10 m), the commercial stock flesh weight would be 1971 ± 210 t. The high proportion of total stock that is legal there can be explained by the dominance of large clams in Tubuai lagoon (Figure 4). Tubuai commercial biomass is therefore six times higher than at Tatakoto and Fangatau, for a clam population that is double that at Fangatau and half that at Tatakoto, and for densities 6−10 times less than at the atolls.

From clam community structure to resource management

Besides international requirements for exporting *T. maxima* (it is listed in Appendix 2 of the Convention on the International Trade of Endangered Species, CITES), local French Polynesian conservation action includes the establishment of no-take areas (Gilbert *et al.*, 2005), the development of

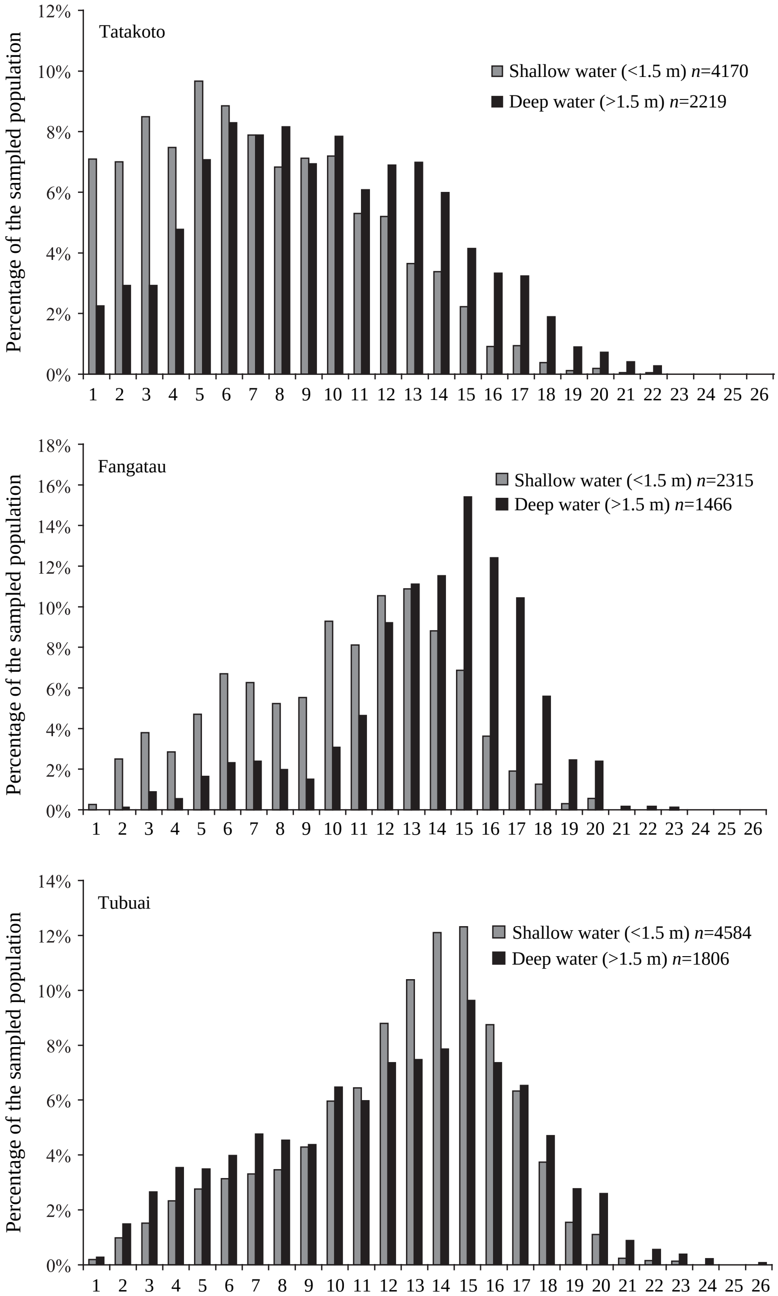

Figure 10. Fangatau, Tatakoto, and Tubuai size frequency distributions in shallow and deep areas.

clam aquaculture capacity, and maintaining the minimum shell length before capture at 12 cm. However, the fact that the fishery is multi-island means that more elaborate management schemes for the species need to be devised and put in place. The societal importance of the fisheries is so high on these lightly populated islands that it is crucial to address quickly the long-term sustainability of clam stocks, including at the same time promoting better ecosystem conservation of the waters in which the clams live.

In situ monitoring of clam growth, natural mortality, and recruitment, and of exports from Tatakoto, Fangatau, and Tubuai wild stocks is in progress; new and better data will soon be available to support management actions. The contribution to total mortality (Z) of natural (M) and fishing mortality (F) will soon be clarified. Currently, as in Green and Craig (1999), Z is estimated using a length-converted catch curve (Pauly, 1983) based on length frequency data from the targeted shallow waters of the lagoons

Table 4. Mean shell length in different depth strata for different islands of French Polynesia and the Cook Islands. Survey year is shown in parenthesis. Moorea data from Wagner (2001) and Cook Islands' data from Sims and Howard (1988).

Island	Depth strata (m)	Mean shell length (cm)	Number of clams (n)
French Polynesia			
Fangatau (2003)	<1.5	10.3	2 315
	>1.5	13.8	1 466
	All	11.7	3 781
Tatakoto (2004)	<1.5	7.2	4 170
	>1.5	9.6	2 219
	All	8.0	6 389
Tubuai (2004)	<1.5	12.4	4 594
	>1.5	12.1	1 806
	All	12.3	6 400
Moorea (2001)	All	6.3	291
Cook Islands			
Aitutaki (1998)	Reef flat	7.9	275
	Lagoon	12.4	104
	All	9.1	379
Manihiki (1998)	<6	10.6	56
	>6	12.7	181
	All	12.2	237
Suvarrow (1998)	<6	5.9	142
	>6	6.8	54
	All	6.2	196

(Figure 10). These preliminary analyses yield total mortalities (Z) of 0.39, 0.34, and 0.25, respectively, for Tatakoto, Fangatau, and Tubuai. For Rose Atoll in Samoa, Green and Craig (1999) found a low total mortality ($Z = 0.23-0.30$), equal to the natural mortality ($M = 0.3$) for a site that is protected and probably safe from poaching. Estimates of M based on *in situ* observations for each of our sites are not yet available, but if it is constant at the atolls and similar to the value at Rose Atoll, we can only conclude that our shallow atoll communities ($Z = 0.34-0.39$) have already reached a stage where the impact of fishing is noticeable. At Tubuai, however, the situation is not so critical ($Z = 0.25$).

Besides local community adherence to laws, plus political will, other information such as clam population spatial structure as shown by the habitat maps presented here will be important in communicating better with politicians and local residents. The importance of knowledge of the dynamics and spatial structure of the populations has been stressed already (Orensanz and Jamieson, 1998; Smith, 2003; Smith and Rago, 2004). Traditional Polynesian societies used to manage resource exploitation through spatial schemes, using practices such as rotational harvesting (*rahui* in the Polynesian language). Future ideas for management plans that will be evaluated in the near future may promote these old techniques, but the selection of areas to protect and the time required to let the communities recover can now be based on a wealth of robust biological data that have already shown that each island needs to be considered separately.

Conclusion and perspectives

The study aimed at detailing the community structure of three natural clam populations of three Polynesian islands. Such detailed assessments are seldom available for tropical areas, but are a necessary prerequisite to being able to manage effectively the growing micro-fisheries that started just a few years ago on each island. The unique clam resources and ecosystems described here, especially at atolls with

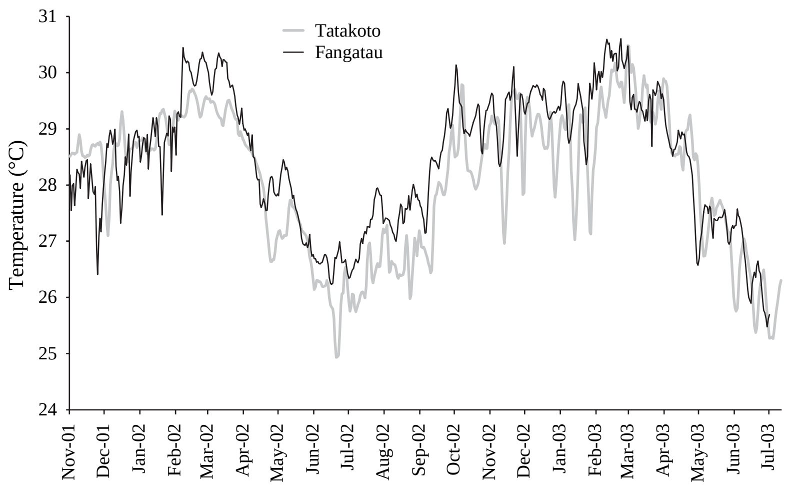

Figure 11. Temperature time-series at Fangatau and Tatakoto. Each curve is the average of an almost continuous time-series of three temperature sensors located in different areas and depths in each lagoon. Note the more frequent and intense intrusion of cold water into Tatakoto lagoon.

unusually large densities, require careful long-term management, and SPE is dedicated to the endeavour. The three islands investigated here are not the only islands where clams are fished heavily, but lessons learnt from these three sites may be useful in planning management action at other sites, and the first lesson is that each site may well be unique. Ecologically, the data have revealed that each site has its own specific characteristics, with differing habitat and clam population structure. Even similar systems that are close geographically, though isolated from nearby islands, and still exposed to the same forcing environments display important differences in their clam populations.

The future is now clearly to work with local inhabitants to monitor fishing pressure, and to evaluate the results of ongoing monitoring of clam natural mortality in order to optimize for each island the action required to sustain these fisheries in the long term. Since we surveyed and analysed the situation at Tubuai, Fangatau, and Tatakoto, we have looked also at two more atolls (Reao and Pukarua, eastern Tuamotu) and another Australes island (Raivavae), with a view to conducting stock analyses using the same techniques described here (remote sensing combined with *in situ* stratified sampling). Preliminary results show even more variation between locations and island types, so over the next 1–2 years we will focus on analysing these differences in order to maximize the relevance and efficiency of management actions that will be proposed.

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