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Revisiting wild stocks of black lip oyster *Pinctada margaritifera* in the Tuamotu Archipelago: the case of Ahe and Takaroa atolls and implications for the cultured pearl industry

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Abstract :

Spat collecting of the black lip oyster (*Pinctada margaritifera*) is the foundation of cultured black pearl production, the second source of income for French Polynesia. To understand spat collecting temporal and spatial variations, larval supply and its origin need to be characterized. To achieve this, it is necessary to account for the stock of oysters, its distribution and population characteristics (size distribution, sex-ratio). While the farmed stock in concessions can be easily characterized, the wild stock is elusive. Here, we investigate the distribution and population structure of the wild stock of Ahe and Takaroa atolls using fine-scale bathymetry and *in situ* census data. Stocks were surprisingly low (~666,000 and ~1,030,000 oysters for Ahe and Takaroa respectively) considering these two atolls have both been very successful spat collecting atolls in the past. Furthermore, in Ahe atoll, wild populations are aging with a dominant but small female population. Comparison with the cultured stock population (~14 millions oysters) and its dominant young male population suggests that to maximize larval supply and spat collecting on the long term, it would be useful to increase the number of females in selected sanctuaries. We discuss the implication of our findings for the long-term management of stocks and for spat collection in pearl farming atolls, and for on-going numerical modelling studies on larval dispersal.

Keywords : Invertebrate population, Aquaculture, Spat collecting, French Polynesia, Atoll bathymetry, Wild stock assessment

lagoons. The harvesting of wild oysters using SCUBA is prohibited in French Polynesia since 1988, and Tahitian culture pearl production is now founded on natural spat collection only. However, spat collection is not a granted activity. Farmers experience erratic spatial and temporal variations (Brié 1999). Although this remains unquantified, they have observed over the years lower collection rates in some atolls, like in Takapoto atoll, once a very productive source of spats.

New decision-support tools explore spat collecting potential with larval dispersal and survival models. Three-dimensional models of larval dispersal were validated for Ahe atoll by Thomas et al. (2012, 2014, 2016) using the hydrodynamic model of Dumas et al. (2012). Research on Takaroa is following the same path (Tedesco 2015). Ahe atoll, and in a less extent Takaroa atoll, are now the two main French Polynesia atolls for research on *P. margaritifera* aquaculture and lagoon environment (Andréfouët et al. 2012a). In addition to factors such as collecting locations, methodology, food availability, and climate which are all required to understand variations in spat collecting (Andréfouët et al. 2012b, Thomas et al. 2016), it is also necessary to assess, or re-assess, the natural benthic wild stock of oysters found in a lagoon, and the farmed stock. Both stocks can theoretically contribute to the pool of *P. margaritifera* larvae that recruit on spat collectors. To realistically refine dispersal models, it is necessary to use in input of the model a map of the stock distribution, as the source of the reproductive material released in the water (Thomas et al. 2016).

Here, we map distribution and population structure of the wild stock of Ahe and Takaroa using fine-scale bathymetric models of the entire lagoons and *in situ* census data. We discuss the implication of our findings for the long-term management of stocks in order to sustain spat collecting activity in Ahe, Takaroa and also for other atolls. Before, however, we provide after this introduction a short review on past stock assessment methods and data, which are mostly available in grey literature written in French. This review helps understanding what is novel in our approach, and provides background information useful to discuss our results.

A short review on pearl oyster stock assessment in Central Pacific atolls

Historically, since early in the 19th century, *P. margaritifera* were collected in the wild to use the nacre locally and internationally in various ways (marquetry, jewellery, crafting fishing hooks, etc.). By the end of the century, the button industry was the main driver. Several Tuamotu atoll lagoons were famous for their high abundance of stocks which allowed a production of up to 1000 tons of shells a year, like in Hikueru atoll. The harvests, mostly by free-diving, took place on different lagoons every year, with rotational closure promoting seasonal migrations of islanders from one atoll to another at the diving season, and a way of life that lasted for decades. Around 4500 fishers were active in 1905 (Le Pennec 2010). In the mid-19th century, around 500 tons of shells were exported outside French Polynesia each year. Highest exports ever recorded occurred in 1919 and 1924 with 1200 and 1350 tons respectively (Archipol, 2000), followed by World War II years which increased the demand for nacre.

Harvesting did effect the perception of stock sustainability and concerns were voiced as early as 1850. Some atolls were closed to fishing in 1868, and many lagoons were deemed depleted early in the 20th century. Only five lagoons were opened to fishing in 1904 (Hikueru, Takaroa, Takapoto, Takume, Marutea Sud). Due to the 1919, 1924, and Second World War high nacre production, it was suggested that populations probably never fully recovered (Intes, 1993). After the war, Hikueru for instance yielded only around 150-200 tons of shells in the 1950s (Archipol, 2000). By the early 1960s, it seemed that most atolls were depleted (Domard 1962), although Zanini (1999) argued that these statements can be valid only if it is assumed that all lagoons had a high stock to start with, an hypothesis which was not supported by the most recent stock assessments of the late 1990s. Eventually, depleted or not, the rise of the polyester button industry, the collapse of the market export in the 1950-1960s, and the simultaneous development of new economical activities in the Tuamotu resulted in decline in fishing and catches, offering a surrogate moratorium in large parts of the fishery. Exploitation for the nacre continued in the 1970s, but at a very low production and export rates.

One of the new French Polynesia rising economic activities of the early 1970s was black pearl production, and the attention turned again on *P. margaritifera* stocks. The new industry prompted a number of stock assessments in a variety of atolls and islands during the 1980-1990s. Several scattered localized density measurements have been performed earlier, but without deriving lagoon-scale trends or stocks. Between 1982-1985, the atolls of Takapoto, Manihi, Hikueru, Scilly (protected since 1971) were systematically surveyed to infer a stock (Intes and Coeroli, 1985). Cheffort (1996) also surveyed Mopelia, Manihi, Takapoto and Takaroa in 1990 but did not infer a total stock. This first wave of lagoon-scale stock assessments benefited from better means and techniques, including SCUBA and acoustic bathymetry, and from the realization that surveys needed to be stratified by geomorphology, habitat types and depth (Intes, 1993). Intes and Coreoli (1985) reported that the highest densities were found between 20-40m deep in Scilly and Takapoto atolls, with average densities around 1000 oysters per hectare, although very high densities (~3,000 - 5,000 ha^{-1}) were found in few specific hard-substrate habitat and geomorphic locations (Intes and Coeroli, 1985; Intes et al. 1985). Stocks (without confidence intervals provided) were estimated at 5.5 and 7.5 millions individuals in Scilly (80 km^2) and Takapoto (76 km^2) respectively (Intes et al. 1985). In contrast, Manihi and Hikueru had average densities an order of magnitude lower and no aggregations despite suitable habitats. Densities collapsed deeper than 40 meters in all atolls with few oysters recorded. Later, other studies on lagoon resources reported similar low density in Fakarava and Tikehau (Kronen et al. 2008). No oysters were also found below 36m in the Cook Islands atolls where surveys also took place for similar reasons than in French Polynesia (Sims 1992).

Zanini (1999) provided the second wave of French Polynesia stock assessment (1995-1997). He surveyed, or re-surveyed Marutea Sud, Nengo-Nengo, Aratika, Manihi, Taenga and Takapoto atolls with, when oysters were present, an estimate of the total stock using a double-stratification sampling scheme based on depth and bottom-type. He also reported (with mean ± 95% confidence interval when feasible) very contrasted situation with extremely small population of wild oysters in Taenga (about 5000 oysters in a 166 km^2 lagoon)) and Nengo-nengo (about 20,000 oysters for 66 km^2), moderate stock in Aratika and Manihi (with 0.56 ± 0.36 million for 150 km^2 and 1.5 ± 0.5 millions oysters for 195 km^2, respectively), a high stock in Takapoto (4.3 ± 0.67 million, 76 km^2) and finally, Marutea Sud (108 km^2) hosted the highest population with 12.1 ± 1.8 million oysters (Table 1). In Takapoto and Marutea Sud, oyster densities were the highest between 30 and 40 meters (respectively 8.2 and 23.0 oysters per 100 m^{-2}). Combined with the large area covered by this depth range, most of the stock was deeper than 30 meters. In atolls with very low or low stock (Taenga, Aratika, Manihi), the top (0-10 m) of pinnacles were oyster high-density hot-spot, with next to nothing in other locations. However, the small surface area of pinnacles did not yield large stocks.

Only Takapoto and Manihi atolls experienced multiple surveys during the 1982-1999 period. Takapoto was one of the main spat providers for the Tahitian culture pearl industry and Manihi the location of the first commercial farm. In Takapoto, Intes and Coeroli (1985) reported a total of 5.5 millions individuals in 1982-1983, but the atoll experienced a massive mortality of bivalves in 1985-1986 (Cabral, 1989, Richard 1987). No stock assessments were done immediately after this event. However, Cheffort and Zanini (1997) revisiting data collected in 1990 and processing them like in Zanini (1999), estimated the 1990's stock at 10.1 ± 1.7 million individuals. Finally, in 1995, Zanini (1999) reported highest densities between 30 and 40 m, with an average of ~800 oysters per hectare. This depth layer was rugose and rich in small coral heads, making 50% of the estimated stock but the stock was down again at 4.3 ± 0.67 million individuals. Zanini (1999) also reported partial mortalities at depth in 1997 in the most confined part of the lagoon. Differences in numbers are likely partially explained by different methods and different diving sites, but the fluctuations also likely reflect the effects of mortalities (partial, between 1990 and 1997) as well as a high reproduction success and relatively quick reconstitution of the stock (between 1986 and 1990) in a closed lagoon. In Manihi, in 1982, Intes et al. (1982) did not estimate a stock but reported a low density, with oysters found mostly on pinnacles. Cheffort and Zanini (1997) (revisiting data collected in 1990 and processing them like in Zanini (1999)), and Zanini (1999) reported in 1990 and 1997 respectively 0.7 ± 0.3 and 1.5 ± 0.5 million individuals for Manihi. Temporal data suggest that population can grow fast, but are also subject to frequent mortalities although the biophysical processes involved remain poorly known (Andréfouët et al. 2015).

Today, spat collecting is the object of interdisciplinary work that combines *in situ* experiments (e.g., collecting experiments) with numerical modelling of larval dispersal (Thomas et al. 2012, 2014, 2016). To realistically refine dispersal models, it is necessary to use in input of the model a map of the stock distribution, as the source of the reproductive material released in the water (Thomas et al. 2016). However, none of the early studies has provided a map of the stock in any lagoon. Farmed stock is easily mapped because they are found on concessions that are registered at the French Polynesia "Direction des Ressources Marines et Minières" (DRMM), the technical governmental authority in charge of the management of the concessions. Moreover, there is an upper limit to the number of oysters that can be farmed limited to 12,000 grafted oysters per hectare (but up to 2 or 3 times this number considering both grafted and non-grafted individuals), and most functioning farms reach that limit. In contrast, the wild stock is less straightforward to map. The various techniques employed by Intes et al. (1985), Zanini (1999), Zanini and Salvat (2000) and Sims (1992) in Cook Islands provided stock estimates with confidence intervals, but no maps.

Material and Methods

Study sites

Ahe atoll has been recently the focus of numerous biophysical investigations and is probably now one of the most studied atoll in the world (Andréfouët et al. 2012a). It is located in the northwestern part of the Tuamotu Archipelago by 14°48'S – 146°30'W (Fig. 1a). The lagoon is a 142-km^2 deep, semi-closed (i.e., with a narrow pass, but with a low ratio of functional reef flats and spillways along the rim, Andréfouët et al. 2001a, 2001b), water body with an average depth of 41 m, reaching up to 70 m depth. As such, it is much deeper than most atolls previously investigated in the 1980-1990s for wild stock assessment. Numerous pinnacles dot the lagoon surface. The lagoon bathymetry was mapped after interpolation of tide-corrected, east-west acoustic continuous parallel tracks acquired every 50 meters in 2008, and completed by denser coverage near pinnacles and in the pass. This data set revealed the morphology of the lagoon, including the deeper areas made of honeycomb-like cellular structures (Fig. 1a). The southwestern part of the lagoon is much shallower than the rest of the lagoon.

Takaroa atoll is also part of the north-western Tuamotu, located by 14°27'S – 144°57'W (Fig. 1b). Its lagoon is also semi-closed, but much shallower and smaller than Ahe reaching 85 km^2 with an average and a maximum depth of 26 and 47.5 meters respectively. The bathymetry was mapped in the same way as Ahe, in 2008-2009 (Fig. 1b). Numerous pinnacles dot the lagoon surface, but Takaroa do not present the honeycomb deep structures found in Ahe lagoon.

According to Piquenot (1900), Ranson (1952) and Domard (1962), Ahe has never been a heavily fished atoll, with one maximum yield at 100 tons of shells, and rather below 50 tons otherwise. It ranked 16th in a list of 27 atolls sorted according to their maximum known nacre production (Domard 1962). Its stock was flagged as declining by the early 1960s. However, Ahe has been a very successful collecting atoll since the 1980s, and a hub as oyster provider for other atolls, suggesting that its stock has recovered at some point. In contrast with Ahe, Takaroa has been one of the historical center of nacre fishing, ranking 6th according to its maximum production (300 tons), and regularly above 100 tons per year (Domard 1962). Takaroa was still considered a productive atoll in the early 1960s. Later, Takaroa, like Ahe, has played a fundamental role for spat collecting and as oyster providers for farming in other locations. Ahe has never been the subject of any density or stock assessment. Takaroa was investigated in 1990 (Cheffort-Lachart, 1994, 1996), but data are scarce and report a mean density of 1.2 oyster per $100m^{-2}$ for 54 random locations throughout the lagoon.

Both atoll lagoons are largely covered by pearl farming concessions (Andréfouët et al. 2014b). Delimited concessions are granted to farm and grow oysters but spat collection stations can be set anywhere. In the narrow and shallow Takaroa atoll, concessions are widespread except in the north part of the lagoon and on the deepest areas. In Ahe, concessions are also widespread along the border of the lagoon and avoid the central deepest areas, but spat collection lines and farmed oysters are especially dense in the southwest part of the lagoon.

In Ahe, Thomas et al. (2016) conservatively estimated the reared, farmed, stock at more than 14 millions oysters, using as baseline the legal density of 12,000 grafted oysters per hectare of concessions. A map of the concession, and farmed stocks is provided in Thomas et al. (2016, supplemental material).

P. margaritifera is a protandrous hermaphrodite. Typically, oysters below 8 cm or less than 2 year old are male and then shift as female when growing larger after 2 y.o. (Chavez-Villalba et al., 2011). Since reared oysters are generally not large (shell size below 14 cm), the reared population is about 90% male (i.e., about 1.4 millions females and 12.6 millions males, in Ahe lagoon after the frequency distribution of relative size of males and females from Chavez-Villalba et al. (2011)). Using in the same way the frequency distribution and the size-structure of the wild stock, we inferred the ratio of female *vs* male individuals in the wild population (estimated below).

In situ ***census and sampling design for wild stock assessment***

Ahe was visited in May 2013 with the R/V Alis that conducted a number of surveys and experiments for one month in the lagoon. Part of the tasks was to assess the wild stock with 2 dives per day between 0 and 60 meters for the deepest ones. No existing information on stock structure existed to drive the sampling, but the bathymetry was available before the survey. Therefore, we conducted first a series of exploratory dives at different depth and on different locations (lagoon floor, pinnacles, lagoon slopes) to quickly assess the range of configurations and decide where and how we needed to focus our efforts. Surprisingly, and unlike what was described for Takapoto and several other atolls by historical researches, virtually no oysters were found below 20 meters. Densities were very small, with some of these exploratory dives yielding zero counts. Furthermore, all deep dives below 45 meters showed a sand bottom without hard substrate or relief. The slopes of the deep honeycomb structures were also fine carbonate sand with some thin cyanobacteria films.

Considering these findings, we used a timed plotless belt-transect protocol based on three divers counting oysters for 5 minutes at fixed depth ranges. Similar technique has been recently successfully employed to survey green snails on forereefs (Andréfouët et al. 2014a). When diving around pinnacles or along the lagoon slope, timed searches were performed in the 50-40, 40-30, 30-20, 20-10, 10-5 and <5 meters depth range. On flat lagoon floor, without slope to ascend progressively, several searches were performed at the same depths following a square-dive profile. Also, when reaching the shallows, we performed additional searches in the 10-0 m depth range, since there was no dive-time constraints at this depth. The swims were performed at 1 to 2m above the bottom, for a belt-width of about 2 meters, at constant very slow speed that was frequently calibrated when circling around vertical pinnacles where the exact covered distance could be measured afterward on very high resolution (1 meter) satellite imagery. The belt–transect was swim along an approximately 5-meter-wide corridor of constant depth that could be vertical or horizontal depending on the relief. The corridor could include patch of hard-bottom and sand. The directions taken by each diver on the bottom was random, except along pinnacles where they had to follow the slope (or wall) clockwise or anti-clockwise randomly. Slow swimming speed and short distance to the bottom authorized scanning underneath rocks and overhangs to detect even small hidden individuals (Fig. 2). The horizontally-projected surface covered by each 5’ search period was approximately 200 m^2, with calibration tests ranging between 180 to 250 m^2, but most around 200 m^2 once similar pace was acquired by all divers. No significant current was ever met that could have affected this coverage since the pass and its vicinity was not surveyed.

Each oyster was measured in its greatest length. Depth and substrate (soft or hard-bottom) was recorded. A total of 47 stations were performed in Ahe with this method (Fig. 1).

For Takaroa, the census protocol was similar to the timed plotless belt-transect of Ahe, after that a series of exploratory dives was performed. These dives suggested similar patterns as in Ahe main lagoon, with mostly a shallow scattered stock. A team of three divers operated from the shore with a small boat and surveyed 22 stations in September 2013 (Fig. 1b). However, the size of the oysters was not recorded.

Results

Density by depth level in Ahe : main lagoon* vs *southwestern lagoon

Densities in Ahe were measured in the 60-0 m depth range on 47 stations covering the entire lagoon and different geomorphological zone (inner slope, pinnacles, lagoon floor, deep ridges) (Fig. 1). Most dives took place in a mix of soft and hard-bottom in various proportions, except on the upper horizon of pinnacles that were entirely hard-bottom (old eroded corals, corals, coralline algae, and making overhangs). Almost all oysters were found on hard-substrate. No oysters were recorded below 50 meters, since the lagoon floor was systematically covered by fine sand. There was a clear increasing oyster density gradient from 40m to the surface (see Fig. 3a).

In Ahe, two regions had to be considered: the main lagoon, and the shallower western lagoon (stations 24, 26, 36, 36, 37, 40, 42, 43, 45 in Fig. 1a). Large differences were indeed measured in oyster population density and structure between these two areas. In the main lagoon, the highest densities were found in the 10-5 m depth range, reaching an average of 1.87 oysters per 100.m^{-2}. The southwest lagoon also displayed highest densities in the 10-5 meter range, however, densities reached an average of 8.42 oysters per 100.m^{-2}, four times more than in the rest of the lagoon (Fig. 3).

The population structure of Ahe (Fig. 3b) is contrasted between the two parts of the lagoon (Fig. 3c). In the main lagoon, the distribution is skewed towards larger, older, oysters with a 17-cm mode. It appears that 74% of the population is above 14 cm (Fig. 3c). In contrast, the population of the southwest lagoon shows a normal distribution, much smaller and centered around 12-13 cm, with 38% of the population above 14 cm (Fig. 3c). The limited numbers of small oysters is partly explained by a census done by visual assessments, and many juveniles can be missed.

Using Chavez-Villalba et al. (2011) frequency distribution of relative size of males and females and the size-structure of the wild stock (Fig. 3b), we found that this stock is about 30% female (i.e., ~198,000 females and ~468,500 males), and spatially contrasted as well. Indeed, the proportion of females is 36% in the main lagoon (i.e., ~151,100 females and

~267700 males) and only 19% in the southwest lagoon (i.e., ~46,900 females and ~200,800 males).

Density by depth level in Takaroa

Densities in Takaroa were measured in the 35-0 m depth range on 22 stations covering the entire lagoon and different geomorphological zone (inner slope, pinnacles, lagoon floor, deep ridges) (Fig. 1b). No oysters were recorded below 30 meters (Fig. 4). Above this limit, there was a clear gradient of increasing oyster density with decreasing depth, similar to Ahe (see Fig. 4, by 5-meter intervals). The highest densities were found in the 10-0 m depth range, reaching an average of 4.6 oysters par 100.m^{-2}. Unlike Ahe, there were no obvious spatial patterns within the lagoon, the stations with the highest overall (all depth-ranges included) densities were found throughout the lagoon with, for the top-five densities, stations 15, 17, 9, 14, 2 by decreasing order (Fig. 2).

Stocks in Ahe and Takaroa

The stock (in number of individuals) in Ahe was computed, and mapped (Fig. 5a) by considering two regions. For the main lagoon (94.11 km^2, between 0 and 50 meters, after masking out the pass), the stock was estimated considering the density per depth strata shown as black bars in Figure 3a and the surface area of each depth strata. For the western lagoon (5.98 km^2), stock was estimated in the 20-0m depth range considering the density per depth strata shown as grey bars in Figure 3a and the surface area of each depth strata. The total stock was estimated at around 666,000 oysters with 418,857 ± 67,437 and 247,682 ± 65,687 oysters for the main lagoon and the southwestern lagoon respectively (mean ± 95% confidence interval).

The stock (in number of individuals) in Takaroa between 0 and 30 meters (62.59 km^2, after masking out the pass) was estimated and mapped (Fig. 5b) considering the density per depth strata shown Figure 4, and the surface area of each depth strata. We found that the wild stock was around 1,031,045 ± 226,364 oysters (mean ± 95% confidence interval).

Discussion

Similarity between atolls and studies

The distribution of the wild stock was not what we anticipated considering the most studied atoll, Takapoto, and the history of good spat collection on both Ahe and Takaroa. We expected a larger stock, especially in Ahe. However, the patterns seen in Ahe main lagoon and Takaroa are close to what Zanini (1999) described for Aratika and Manihi atolls. These four atolls are characterized by higher densities in shallow water than in deep waters, especially on the slopes of pinnacles. Aratika, also known for a good history of spat collection, hosted a small wild stock concentrated on the upper 20 meters of pinnacles. Manihi is characterized by the same type of population but its size and the extent of the 20-40 m depth strata yielded a stock similar to what we found for Takaroa.

The Ahe southwest lagoon was similar to Takapoto for densities, but not for depth since it is a shallow basin. Ahe is the only atoll with a marked geographical heterogeneity in density (Fig. 3a). All atolls studied since 1982 were heterogeneous in density according to depth and geomorphology strata (e.g., pinnacles *vs* lagoon floor), but none seemed to have one basin or geographical part of the lagoon that contrasted with another part of the lagoon. This was described for the high Mangareva island and its lagoon (Intès et al. 1985, Zanini 1999), but not for atolls.

The few historical inter-atoll dataset collected, in a similar time period and with similar methods, suggest that atolls can be very different in terms of spatial distribution of densities and overall stocks. Here, we conclude that Ahe and Takaroa are part of a group of atolls with natural specific characteristics in terms of stocks, one of them being shallow high densities. They join Aratika and Manihi as described by Zanini (1999). Zanini (1999) did not propose a functional typology of atoll regarding the wild stock of oysters, but with Ahe and Takaroa as two additional atolls to sharpen the picture, it is possible to highlight four groups of atolls across a gradient of population number (Table 1), and their characteristics, keeping in mind that the stocks have been estimated at different time across a 30-year period. Cook Islands atolls are included (Penrhyn, Suvarrow, Manihiki), with ten French Polynesia atolls. The range of lagoon size is 35-200 km^2. These groups of atolls are not defined with a rigorous multivariate analysis, but only report next to the stock number the key qualitative characteristics that are common to all atolls of the group.

Without additional atolls and knowledge, the purpose of this Table 1 is to confirm that there is no clear combination of macro-factors (such as aperture to the ocean, size, maximum or average depth) that could simply explain the different stock abundance. For instance, “no pass and semi-open” are characteristics that describe both the most depauperate and the most stocked lagoon. In contrast, abundance of hard structures in the lagoon floor is a necessary condition for a high stock (Zanini and Salvat 2000). The presence of suitable habitats at depth, the extent of pinnacles, the extent of the different depth zones, and the hydrodynamic regime (controlling larval export but also mortalities) are all abiotic factors, together or independently, that can contribute to high stock. Food supplies, which can vary per atoll, are also a limitation for adult reproduction (Fournier et al. 2012), larval development and survival; and eventually adult stock survival.

The choice of a stock assessment method

The method applied here was different than Intes et al. (1985), Sims (1992) or Zanini (1999). These previous studies used few bathymetric, parallel, regularly spaced, transects across the lagoon to infer a statistical distribution of depth range and bottom-types to weight the estimate of stock per depth and habitat strata. Dive sites were picked up at random and data analysis took into account *a posteriori* these two strata. Although statistically correct, the main issue with this technique to infer the total stock is that the actual entire distribution of depth and habitat remains unknown for most of the lagoon. Obviously, the denser the network of bathymetric transects, the better, but some atolls (Aratika, Manihi) had only 7 transects. Here, we could use detailed bathymetric maps at 50-meter resolution and we sought for census and density data a systematic coverage throughout the lagoon with random selection within a given sector. The bathymetric map provided an exhaustive and precise mean to infer the stock spatially, after that densities have been estimated by depth range throughout the lagoon. Because interpolation was part of the depth mapping process, these maps have some uncharacterized residual errors, but their impact for the stock value is likely minor compared to the deviation due to the natural variation of the stock.

In previous work, the proportion in the lagoon of up to three habitat types were inferred from the examination of acoustic track, but the errors also remain unquantified, despite all precautions took by past investigators to have confidence in their results (Zanini 1999). Similar to the bathymetry shortcomings, the proportion of habitats was measured only for a limited number of transects, and during the dives themselves. Stratification by habitat-types makes sense especially when densities are high, but here, we did not separate depth from substrate as Zanini and Salvat (2000) in Takapoto. This was not necessary because in Ahe and Takaroa, densities were systematically low, and habitats types were found roughly organized by depth and geomorphology.

Mapping habitat types is an inherently difficult time-consuming task even by remote sensing. The average depth of most lagoons precludes using directly optical remote sensing satellite images to map them entirely, and acoustic data would be needed. This is in contrast with the estimation of stocks for shallow species like giant clams where remote sensing is a necessary part of the protocol (Andréfouët et al. 2005). Therefore, the approach of using only bathymetry for *P. margaritifera* stock could be interesting and cost-effective even in complex lagoons where habitat types vary within the same depth range. We did not have the raw data from Zanini and Salvat (2000) to compare stock computations using a depth-only stratification with their double depth-substrate stratification but this would be an interesting exercise considering the high densities they have observed. Another significant advantage to work by bathymetric levels only is that when scuba-divers need to account for the different types of bottom and their rugosity, the sampling protocol can be greatly complexified and variable. Furthermore, it is impossible to select the right protocol until the actual bottom types have been seen (Zanini 1999).

To summarize, the variety of existing lagoon and oyster population configurations suggests that the stock assessment sampling method can not be fixed in advance for any given atoll. Stratification by depth will be always useful. As such, measuring accurately and at high resolution the bathymetry of complete lagoons could be a priority in the coming years. Mapping bathymetry with mono-beam acoustic sounder like in Ahe and Takaroa was doable, but using portable multi-beam systems for systematic mapping of several atolls would likely be more cost-effective on the long run, especially for larger pearl-farming atolls like Raroia or Arutua (Andréfouët et al. 2006). Bottom-type stratification can be necessary for high-density population found on hard-bottom, especially if these hard-bottoms are widespread at depth, unlike Ahe or Takaroa. In that case, 2D bottom-type mapping at depth will be required, and based on acoustic methods too, simultaneously with bathymetric mapping. Finally, the oyster census protocol (belt-transect, fixed length or timed) will depend also on depth, type of bottom and density and need to be devised after a number of exploratory surveys.

Reasons for a low density, shallow stock?

Both Ahe and Takaroa are characterized by a shallow and, especially for Ahe, a fairly limited wild stock. This is surprising for atolls that have been recently the French Polynesia main suppliers of spat for many atolls and islands. We expected patterns more inline with Takapoto instead of Manihi where spat collection has never been very successful. Is fishing a possible explanation for the low stock in Ahe and Takaroa? It is today illegal to harvest wild oysters in French Polynesia, but this may still happen when oysters are needed during the presence of a grafter in a farm. However, poaching can not explain the population structure we observed, with large shells in the shallows. These shells, when they had reached the size for grafting (10-12 cm), would have been the primary targets for any poacher. There is also no reason why a poacher would decimate the stock below 30 meters and leave alone the shallow stock. Furthermore, fishing deep oysters to graft them, then leave them in the shallow afterwards, is more likely to lead to mortality than fishing shallow oysters. Thus, we discarded fishing as the explanation of the low stocks.

Another hypothesis that could explain the low density in the deeper areas would be depth-specific mass mortality, as it was reported for the most confined part of Takapoto in 1997 (Zanini 1999). Such events have been also reported in Tatakoto, and also for Ahe and Takaroa, but for farmed, and thus shallow, oysters (Andréfouët et al. 2015). We did not see in Ahe or Takaroa natural amount of dead shells to confirm mortality, only artificial ones when farmers dump discarded shells in the lagoon (Andréfouët et al. 2014b). Furthermore, many other bivalves were found in the 10-40 meters depth-range, including large population of, for instance, *Spondylus varius.* If mortality was an explanation, it would have to be *Pinctada margaritifera* specific in addition to be depth specific. Finaly, we can imagine that all bivalves could have been impacted by some events, as in Takapoto in 1986 (Richard 1987) or Hikueru atoll in 1994 (Adjeroud et al. 2000). But then, all bivalve population would have recovered except *P. margaritifera* population. At this stage, we can only make conjunctures to explain the inverted density *vs* depth pattern observed in Ahe and Takaroa (Fig. 3a and 4).

Consequences for Tahitian cultured pearl industry and management

There is no doubt that past and present exploitations have an influence on present *P. margaritifera* population structure. In the past, the fishing of oysters for the nacre had profound effects at their time as discussed by Piquenot (1900), Ranson (1952) and Domard (1962). Today, *P. margaritifera* aquaculture also generates impacts.

First impact of aquaculture is that farmed oysters contribute, genetically and demographycally, to the pool of wild oysters. The translocation of spats and adult oysters between atolls since 30 years have created, for now, higher genetic heterogeneity of wild oysters in farmed lagoons than unfarmed lagoons, including Takaroa (Lemer and Planes, 2012). In Ahe, the reared, farmed, stock includes 14 millions oysters. Thus, there are in the lagoon, at least, around 100 times more farmed oysters than wild oysters. In these conditions, one can not expect anymore the wild stock in Ahe to be purely from wild origin. For instance, the Ahe western lagoon is a very dense area of farming and collecting lines. The density of oysters hanging on baskets and lines is at its maximum. The area is a maze of buoys, lines, and farms, within and outside concessions (Andréfouët et al. 2014b). Furthermore, this location is, in terms of intra-lagoon connectivity, a natural sink for larvae (Thomas et al. 2012, 2014, 2016). Tradewinds tend to push sub-surface larvae coming from other locations to the west. Not surprisingly, we found the highest densities of wild oysters, and one third of the stock in this small area, with a large fraction of small oysters (Fig. 3b). There is little doubt that this "wild" stock is also maintained by the reproduction of the farmed oysters of this sector, and not just by the import of larvae from other lagoon sectors. In fact, it is well possible that nowadays farmed oysters reproduction cycles may be prevalent compared to the reproduction cycle of wild *P. margaritifera*.

Considering the likelihood that both stocks contribute to the larval pool, management decisions that are taken to sustain spat collecting need to consider the two stocks. Practically, the objective would be to maximize the reproduction potential of a lagoon so that larvae remain steadily available for spat collection. Reproduction between reared oysters is most likely to be more effective at 12,000 grafted oysters per hectare than for 100 scattered wild oysters per hectare. However, the sex-ratio of reared and wild populations needs to be taken into account to fully assess the reproduction potential. We found that the wild stock is about 30% female (i.e., ~198,000 females and ~468,500 males). It was spatially contrasted with 36% females in the main lagoon (i.e., ~151,100 females and ~267700 males) and only 19% in the southwest lagoon (i.e., ~46,900 females and ~200,800 males). Conversely, the farmed stock is about 90% male everywhere (i.e., about 1.4 millions females and 12.6 millions males). Independently of the origin of the current wild stock, in both atolls, it seems timely to implement replenishment and restocking programs to maximize dense areas of balanced sex-ratio. In other words, it is recommanded to stock females (i.e., large adults) where their density is low againt males. This could be critical to maximize reproduction success, high larval density; and maintain spat collection on the long term. Obviously, other factors could impact this startegy, including predation on adults and larvae, or competiton for instance.

This study has provided an update on pearl oyster population structure and distribution in Ahe and Takaroa lagoons. Thomas et al. (2016), in a companion paper, has demonstarted the influence of a good parameterization of the stock when modeling larval dispersal. Numerical 3D modelling, despite its complexity and the volume of required data, is necessary to move forward and tackle new management challenges. Other atolls will be targeted in a near future. For atolls where spat collecting is still effective (like in Takume), the stock needs to be assessed, monitored and protected, since there is virtually no recent data for most atolls. We remain cautious that the methodology for stock assessment applied here could be sub-optimal for different lagoons, with different population distribution. Further, since biophysical spatially explicit modelling tools are currently developped for pear farming management, and considering the patchiness of populations (at least in Ahe, with two different lagoons in terms of density and sex-ratio), future population dynamics and ecophysiological studies could have to integrate a spatial component in their design.

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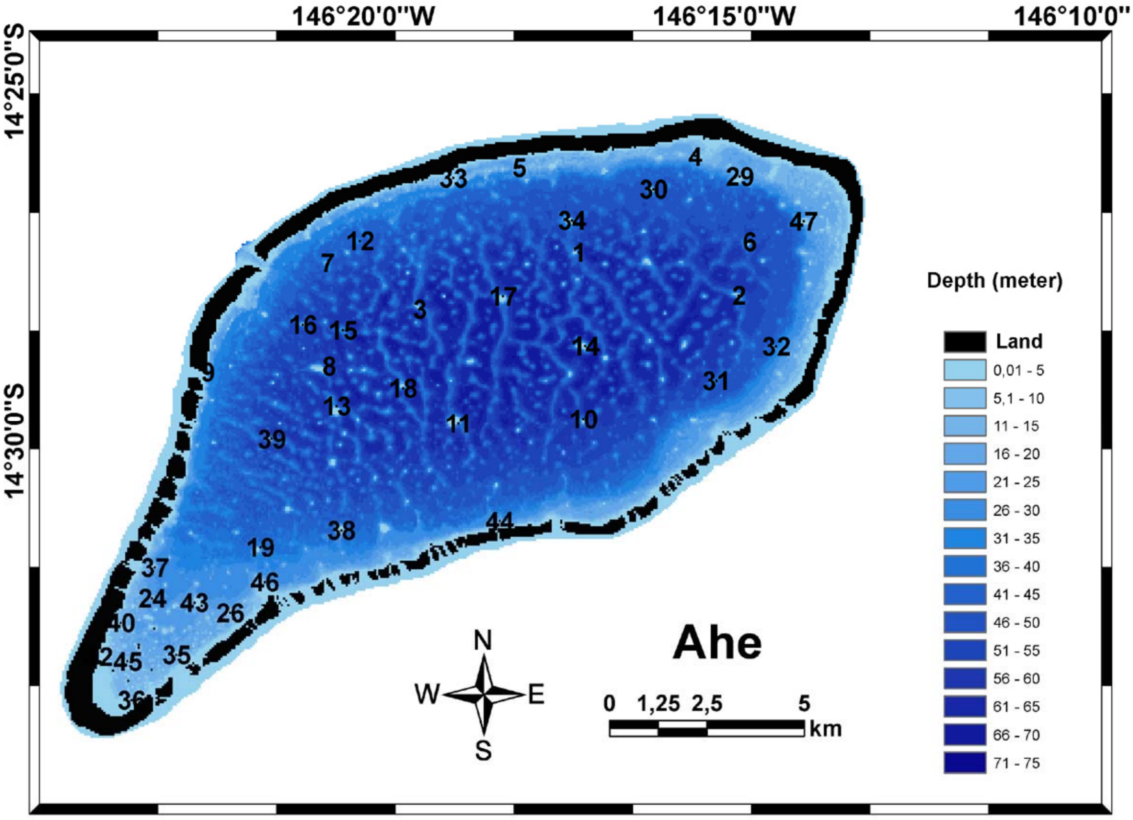
FIGURES



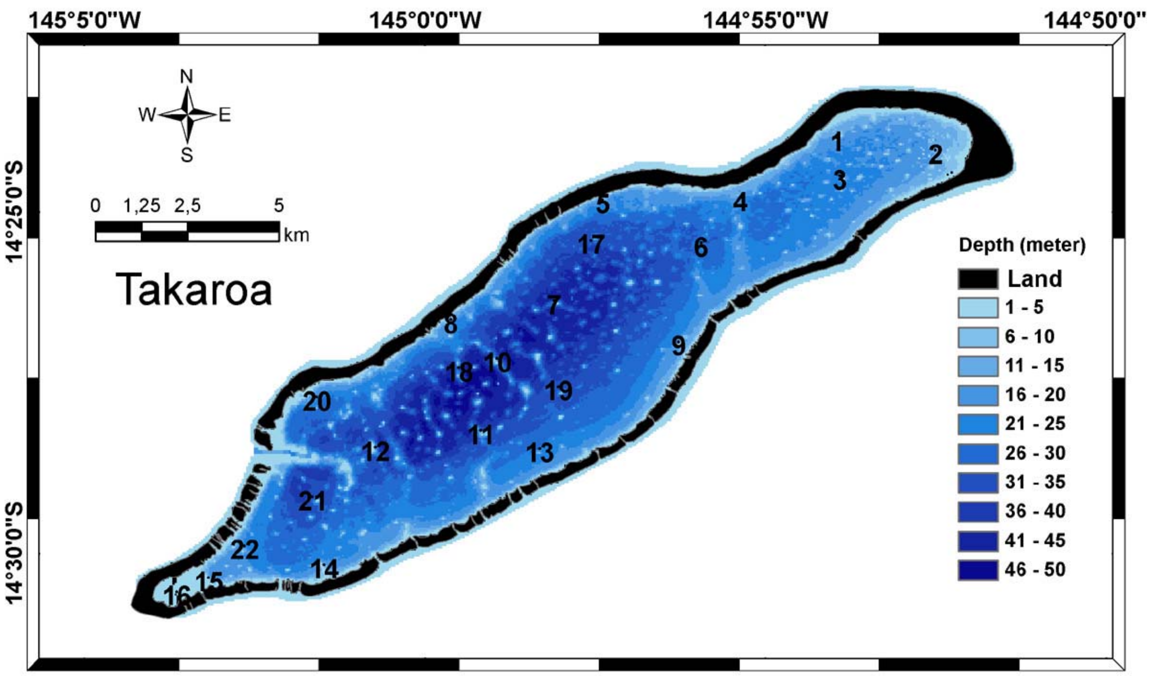


Figure 1: Bathymetry map for Ahe atoll (top) and Takaroa atoll (bottom).

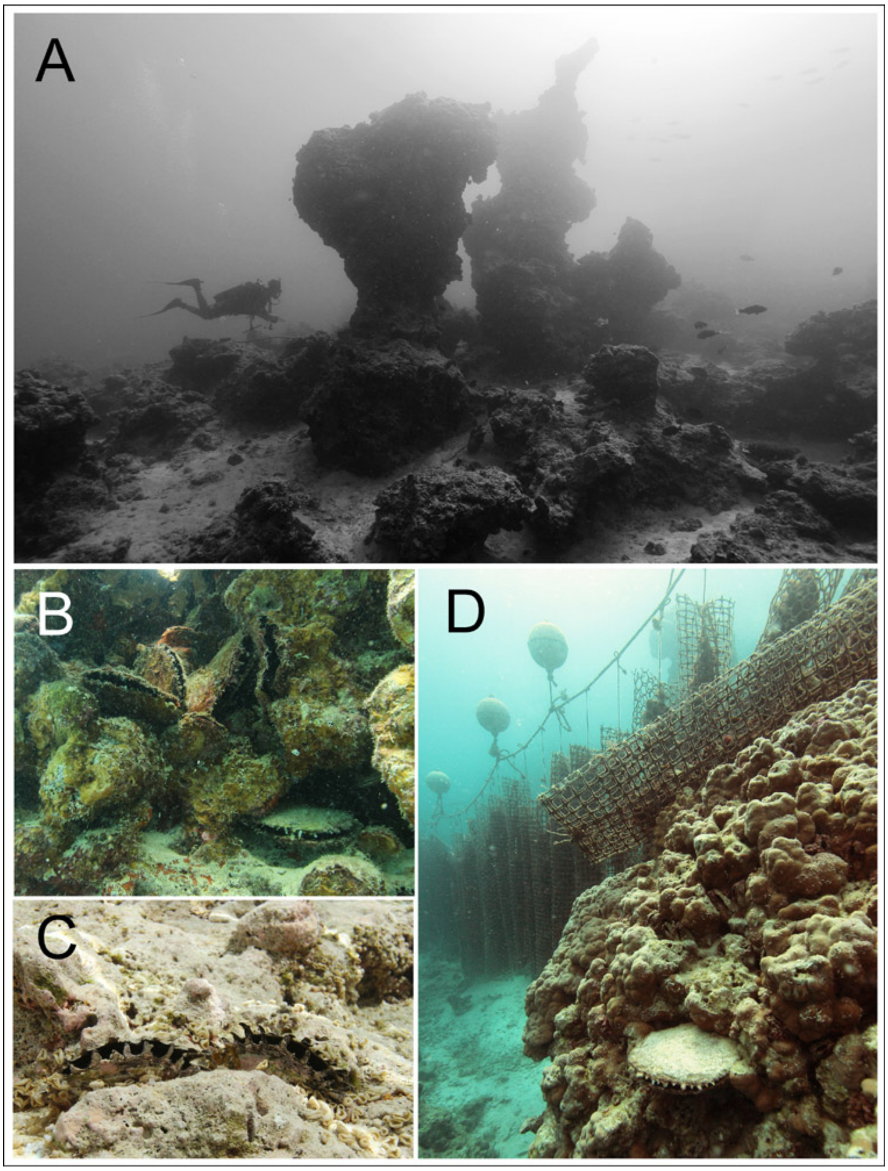


Figure 2: A) Ahe lagoon configuration on the north lagoon slope, in the 20-15m depth range, with dominant hard and rugose substrates. B) A cluster of adult *Pinctada margaritifera* hidden under shallow overhangs in the Ahe southwest lagoon. C) Juvenile oysters settled on a coralline substrate on the top of a pinnacle of Ahe main lagoon. D) In Ahe southwest lagoon, a lonely *P. margaritifera* has settled on a coral colony behind which thousands of farmed oysters on baskets are hanging.

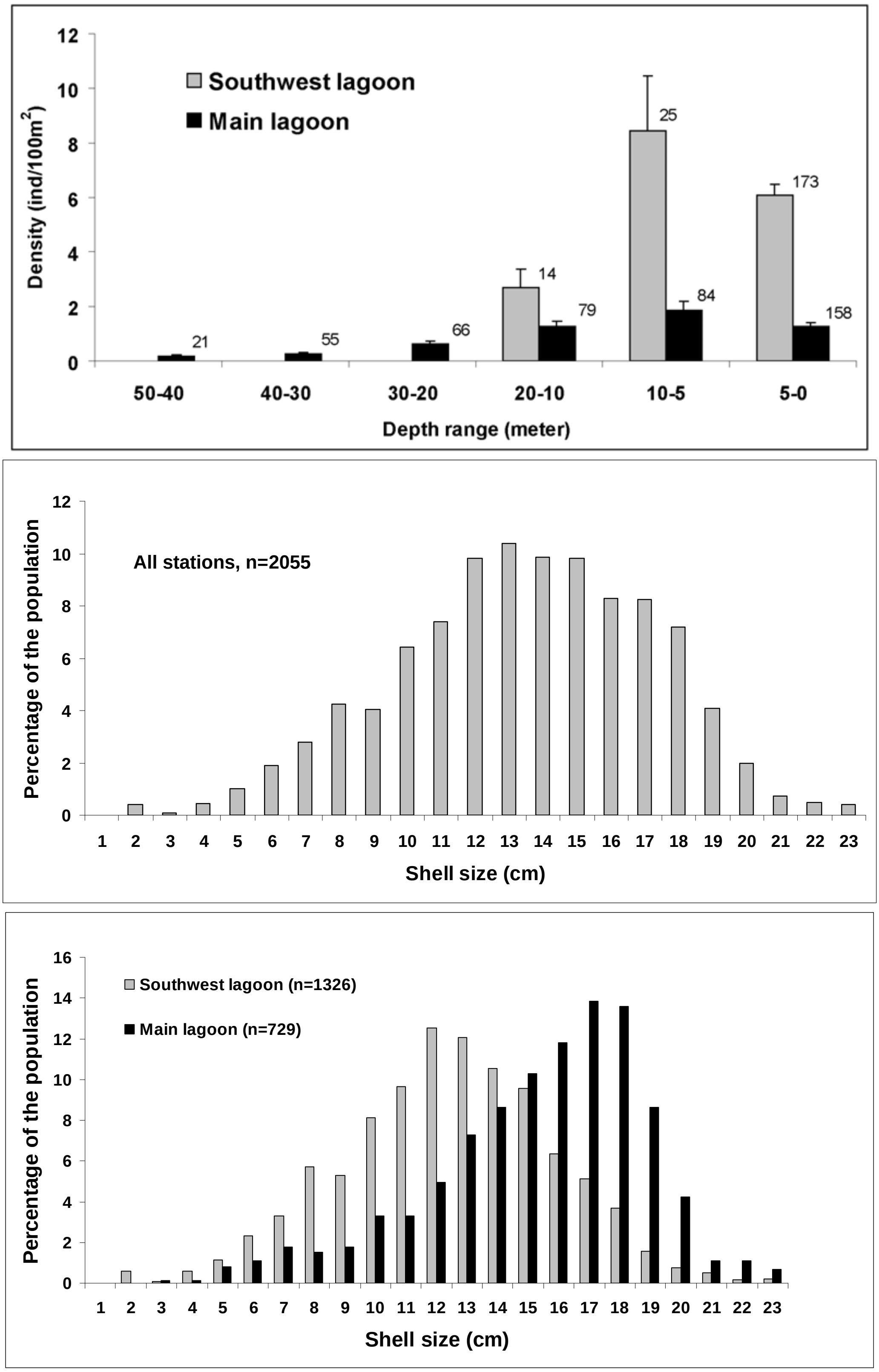


Figure 3: Top: Ahe atoll oyster population structure: density per depth strata for the main and southwest lagoon. Error bars are standard deviations. Numbers are sample sizes. Middle: Total population size structure (middle). Bottom: population size structure for the main and southwest lagoon.

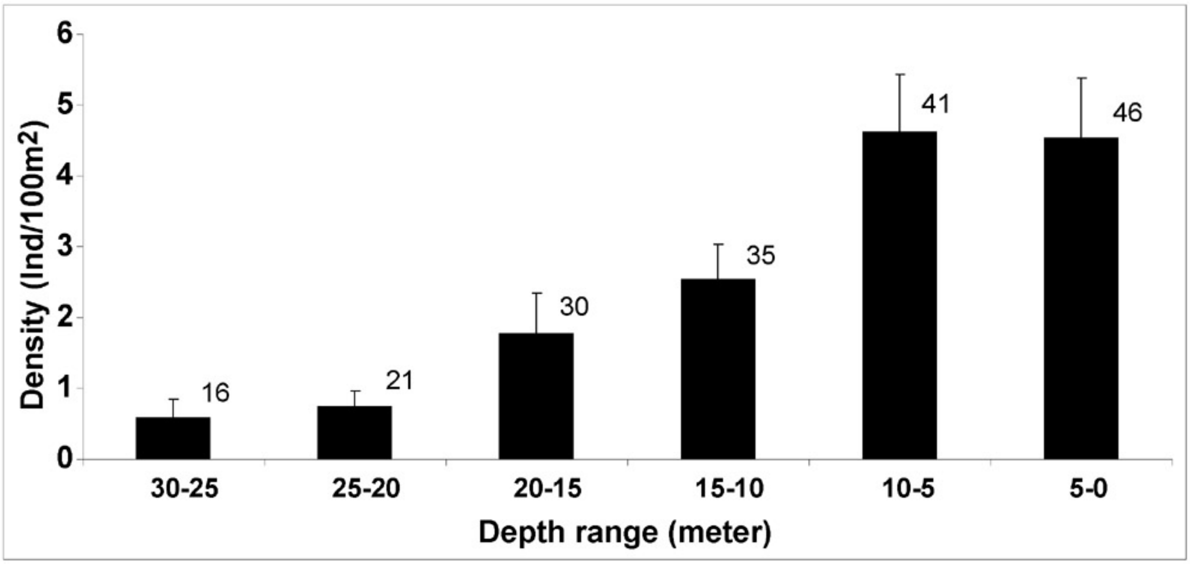


Figure 4: Takaroa atoll oyster mean density per depth strata. Error bars are standard deviations. Numbers are sample sizes.

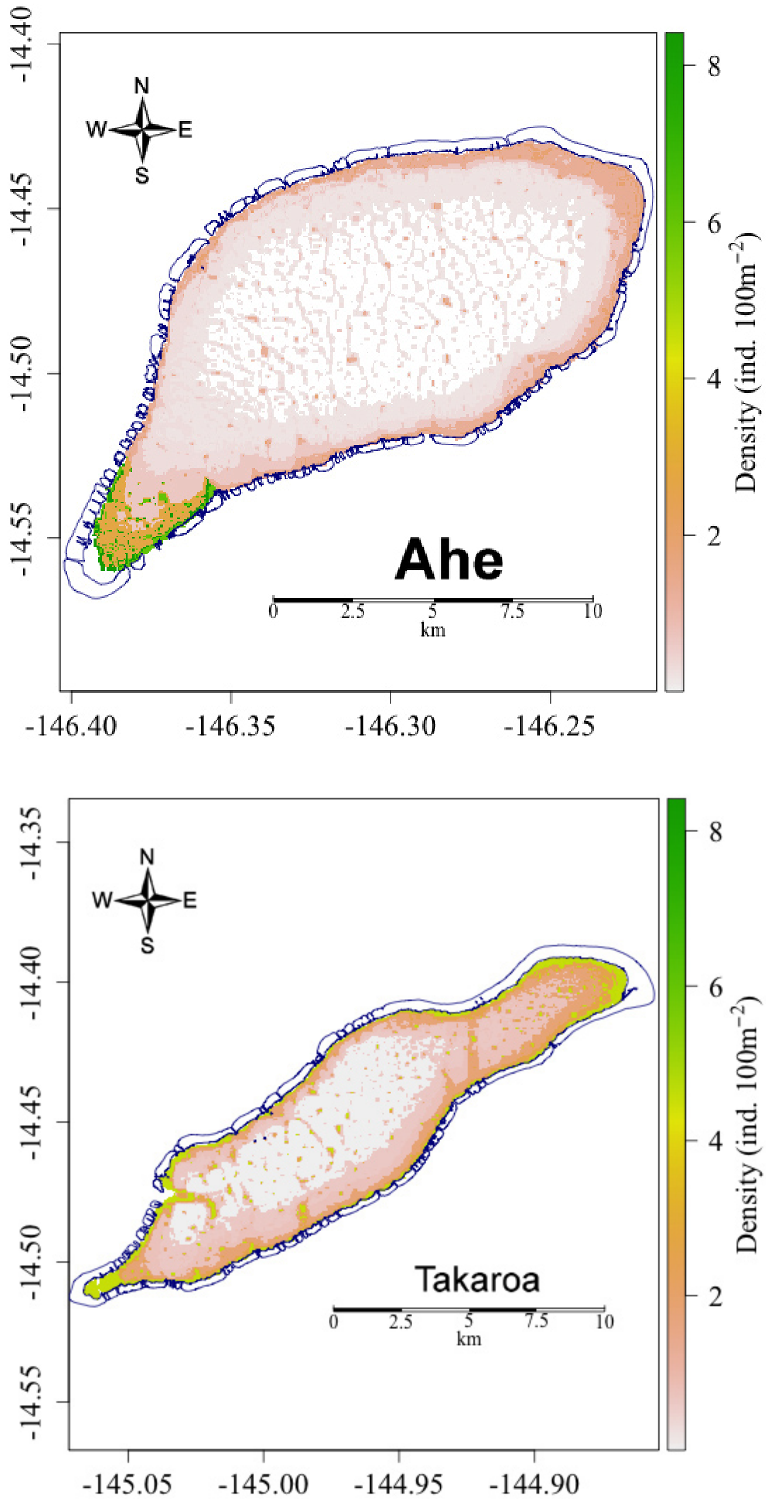


Figure 5: Map of total stock in Ahe atoll (top) and Takaroa atoll (bottom).

Table 1: Ranking of studied atolls according to their estimated stock at the time of their surveys (1982-2013 period). The common characteristics of atolls within a group are indicated. [a] Zanini (1999), [b] Cheffort-Lachhar (1996), [c] Intes et al. (1985), [d] Sims (1992), [e] this study.

Group	Stock	Atoll	Density	Habitat	Geomorphology/aperture	Lagoon size (km^2)
1	<50.000 individuals.	Nengo-Nengo [a], Taenga [a]	No clear pattern, random.		No pass, semi-open	70-170
2	<2 million individuals	Ahe [e], Aratika [a], Mopelia [b], Suvarrow [d], Manihi [a], Takaroa [e]	Highest densities in 0-10m depth range and/or pinnacles;	Mixed bottom types on lagoon floor between 10-40 m	Pass, semi-closed	30-165
3	between 2-10 million individuals	Manihiki [d], Scilly [c], Takopoto[a], Penrhyn [d]	Highest densities in 20-40m depth range	Dominance of hard-bottom on lagoon floor	No pass	45-195
4	> 10 million individuals	Marutea Sud [a]	Highest densities in 30-50m depth range	Dominance of hard-bottom on lagoon floor	No pass, semi-open	115

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