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Natural stocks of *Pinctada margaritifera* pearl oysters in Tuamotu and Gambier lagoons: New assessments, temporal evolutions, and consequences for the French Polynesia pearl farming industry

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Abstract :

Knowledge of the status of the black-lipped pearl oyster Pinctada margaritifera populations is critical for the sustainability of the French Polynesia black pearl farming industry. Indeed, this activity relies on collection of spat settling out of the water column, which is inherently related to the abundance of in situ benthic stocks and their reproductive capacities. From surveys performed between 2016 and 2021, we present new stock assessments of natural wild oyster populations from four contrasted pearl farming lagoons (Gambier, Takapoto, Raroia, Takume). Also using Ahe atoll historical data, we first highlight how results vary with the methods (Direct, Zonal and Cokriging) used to scale in situ density measurements to lagoon-scale stocks. Takapoto and Gambier populations were also previously surveyed at least twice since the 1980s, allowing to demonstrate with field data clear changes in stock distributions and population structures. The consequences of our findings are discussed to provide recommendations for stock monitoring and management in the future.

Keywords : Sustainability, Aquaculture, Stock assessment, Habitat mapping, Population dynamics

Introduction

The exploitation of black-lipped pearl oysters, *Pinctada margaritifera* (Linné), has represented since the nineteenth century one of the main sources of income in French Polynesia (Intès, 1984; Intès and Coeroli, 1985). Andréfouët et al. (2016) and Le Pennec et al. (2010) compiled from various sources the historical information regarding the exploitation of this oyster for its shell during the 1800-1960 period, and the stock assessments that followed 1980 in relation to the booming pearl farming industry. In short, this species was first exploited for its shell and occasionally to harvest natural pearls. Traditionally, Polynesians used pearl oyster shells to make hooks and lures, and for ornamental purposes, but harvests of the wild stock were then unimportant (Intès, 1982a; Zanini, 1999). The first known significant export of *P. margaritifera* shells occurred in 1802 from the Gambier archipelago (Laval, 1968), motivated by the button manufactures and for marquetry (Intès, 1982a). The trade developed and was in full swing by the years 1820-1850 with America or Australia, but the exported quantities were not well described (Intès and Coeroli, 1985). By 1870, several biologists have already warned the local communities about the potential decline of benthic *Pinctada margaritifera* if fishing pressure remained intense and proposed recommendations to mitigate its effects, but no conservation measures were implemented (Intès, 1995). Germain Bouchon Brandely was the first biologist to initiate experiments on spat collection by using *miki miki* (*Pemphis acidula*) bundles (Anonym, 1887 *in* Intès, 1984). These experiments were successful and allowed to pearl farmers to source newly settled oysters direct from the abundant pool of larvae, but natural stocks were still insufficient for harvests and no restocking through spat collection took place. Eventually, at the end of the 19th century and early in the 20th century, custom services started to track the amount of exported mother-of-pearl (Intès, 1982a) and conservation measures were implemented with limited period for diving and fishing, minimum legal size, maximum numbers of divers, harvest quota per atoll and in some cases complete closure. The demand for shells decreased drastically after World War II, but technical improvements (outboard motors, masks, fins, etc.) and enhanced inter-island transports in 1950 worsened the situation in most fished lagoons. Eventually, very low market demand and new livelihood opportunities in Tuamotu (employment in logistical support for nuclear testing) provided some respite to oyster stocks in the mid-1960s.

In 1963, Jean-Marie Domard with the collaboration of Japanese experts attempted to graft *Pinctada margaritifera* in Hikueru atoll and Bora Bora Island to produce black round pearls. These experiments were successful, and the first private pearl farm was created in Manihi atoll in 1966. Following this pioneer event, pearl farming slowly developed during 15 years with several farms and atolls increasingly devoted to pearl production. Consequently, the demand for adult oysters grew immediately in order to supply to pearl farmers sufficient raw material, in the form of ready-to-graft oysters. Without any nurseries at the time, the supply of pearl farms depended on spat collections and mostly (80%) on direct harvest of natural stocks until 1983. In 1983, the Tahitian cultured pearls became most valuable French Polynesia export, in declared value (Intès and Coeroli, 1985). In 1988, harvest of natural oysters using SCUBA diving was banned and pearl farms have been critically dependent on spat collection since then (Andréfouët et al., 2016).

Spat collection is an integral part of pearl production, with some farms and even entire atolls diversifying their activity to concentrate on this part of the farming process. In such case, some producers concentrate on collection of spats, the juveniles being sold to other farmers. Today, without spat collection, the industry would not have sufficient raw material for implantation of seed pearl and the industry would quickly collapse. The risk is well perceived, as farmers experiment both inter-annual and long-term temporal and spatial variations. Many variables can explain the fluctuations in success of spat collection, including professional (types of collectors, depth and location of collectors, etc.), climate (temperature, wind and wave forcing), hydrodynamics (currents and exports of larvae to the ocean) and biological variations (food availability for adults, larvae and juveniles, fertile adult abundances, and spawning periods) (Brié, 1999; Andréfouët et al., 2012; Fournier et al., 2012; Thomas et al.; 2012; Thomas et al., 2016). The amount of oysters available in a lagoon depends on two populations: 1) the farmed stock, located in hanging lines and baskets in the water column and for which a census can be estimated through the extent of farming concessions (Thomas et al., 2016), and 2) the benthic wild stock which of less well documented abundance. The benthic component of the stock (density and distribution) can be approximated with dedicated surveys (Intès, 1982a; Zanini and Salvat, 2000; Andréfouët et al., 2016). Theoretically, both stocks can contribute to the pool of larvae, and to the amount of spat collected, but the efficiency of this process depends first on the reproductive capacities of each stock. Andréfouët et al. (2016) discussed for Ahe and Takaroa atolls how the patchy distribution, low density, and skewed sex ratio of the total wild stock do not really allow science to infer a strong reproductive capacity and contribution to spat collection in comparison to the amount and density of farmed stocks, which are one or two orders of magnitude higher than the wild stock. Yet, Reisser et al. (2020) showed with genetic data for Ahe atoll that all sampled spats originated from the benthic *in situ* stock population. While this experiment needs to be reproduced (Andréfouët et al., 2021), this conclusion likely explains the low, irregular, decreasing and sometimes null level events of spat collection recently experienced by farmers, considering 1) the fact that the farmed stock is mostly male, and 2) the wild stock status is generally spatially scattered and at low density. It seems that there is a thin line between spat collection success and failure, and stock reproduction through its abundance, sex-ratio, and fertility, is an important part of the equation.

Another factor explaining low spat collection, is the evidence that wild stocks can collapse rapidly following lagoon mortality events (Andréfouët et al., 2015) but conversely recover very slowly, as experienced in the past in Takapoto (Zanini and Salvat, 2000), and recently in Takaroa in 2013-2014 (Rodier et al., 2019). The recovery of the populations to the point that spat collection becomes effective again seems to take at least a decade. Indeed, in Takapoto, spat collection took about 15 years to effectively recover to a level suitable for farmers, following the last observed mortality in 1998 (DRM, pers. obs.). Similarly, Monaco et al. (2021) suggested that Takaroa atoll oyster population is still not in a physiologically optimal state 5 years after the 2013-2014 mortality event, even with the present environmental conditions considered to be suitable.

Therefore, knowledge of the status of the wild benthic stocks of pearl oysters on which pearl farming relies is an important piece of information for the management of these lagoons. As explained above, it is a key piece of information to help understand variation in spat collection abundance. But it is also a mandatory information for the computation of realistic larval dispersal scenarios that also help understand spat collection variations using analytical methods (Thomas et al., 2016, Andréfouët et al., 2021). Further, both larval dispersal modelling results and stock information can help take decision for restocking, should this measure be necessary (André et al., 2022a).

Since the beginning of the pearl farming era, the reasons to characterize the wild stocks have thus evolved, to fulfill professional and management needs. The motivation was first to understand the number of wild oysters that could be harvested when this was allowed, to the understanding of spat collection variability, its modelling, and finally to take management decisions, including for restocking. The stock assessment methods have also evolved, from Intès (1982a), to Zanini (1999) and to Andréfouët et al. (2016), the main differences and enhancements being the use of spatially explicit data such as bathymetric maps and the improvement of sampling designs. The methodological differences likely hinder the capacity to compare in time the total stock estimates for sites that have been assessed multiple times in the past 40 years, but some information could be reasonably compared with confidence, such as *in situ* densities, or the distribution of the stock across the depth range.

The objective of this paper is to update our knowledge of the wild stock data in Takapoto, Raroia and Takume atolls and in Gambier, and discuss, for Takapoto and Gambier, two historical sites, their temporal evolutions. In addition, we add a methodological component by comparing several approaches that are permitted by either the precise knowledge of depth (Takapoto, Raroia, Takume), or by the availability of a detailed habitat map for Gambier. Data from the 2013 survey in Ahe atoll (Andréfouët et al., 2016) are also re-used here for method comparison. The pool of results is discussed considering the need for pearl farming management in the future, allowing us to make some recommendations for the atolls studied, but also for other sites as well.

Material and methods

Study sites

Here, we focus primarily on three atolls (Raroia, Takume and Takapoto) and one island (Gambier) for which new stock assessments were performed after 2016. We also revisit the results from a 2013 survey achieved on Ahe atoll (Andréfouët et al., 2016) for method comparison purposes. Historically, among our five study sites, Takapoto and Gambier were both studied several times (see next section). The main characteristics of each study site are summarized in Table 1.

Table 1. Main characteristics of each studied atoll and Gambier Island. Bathymetry data were extracted from Andréfouët et al. (2020), data were not available for Gambier, so the stock analysis was performed by habitat and not by depth strata. DL: with deep lagoon; no DL: without deep lagoon.

Study site	Type of lagoon	Latitude & Longitude	Sampling period & duration	Depth strata	Surface area of depth strata (km²)	Maximum depth (m)	Average depth (m)
Ahe	Semi-closed	14°48′S 146°30′W	05/2013 3 weeks	0-71 0-10 10-50	144.63 7.41 88.27	71	40.6
Raroia	Semi-open	16°01′S 142°26′W	12/2018 3 weeks	0-68 0-10 10-40	367.95 12.87 226.72	68	32.2
Gambier	Open	23°07’S 134°58’W	11/2019, 02/2020 2 weeks	DL No DL	470.66 139.87	NA	NA
Takapoto	Closed	14°37’S 145°12’W	11/2021 2 weeks	0-43 0-10 10-40	78.64 7.02 67.29	43	24.8

Takume	Semi-closed	15°48′S 142°12′W	07/2016 1 week	0-58 0-10 10-30	40.98 2.94 37.75	58	20.4

Ahe, Raroia, Takume, and Takapoto atolls are located in the northwestern part of the Tuamotu Archipelago (cf. Figure 1). Following Takapoto that was intensively studied between 1982-1996 (Salvat 2018), Ahe, since 2008, is the most studied pearl farming atoll in French Polynesia (Andréfouët et al., 2012). Raroia, 724 km east of Tahiti, is the largest of the atolls studied here and has received little recent attention from the scientific community. Numerous pinnacles dot the lagoon (1,618 if we include those located less than 20m deep). Takume is the nearest atoll to Raroia. It is the smallest, shallowest, and least studied site here. Finally, the Gambier lagoon is a vast geomorphologically complex system, which cannot be compared directly to the much simpler atoll study sites. Pearl farming is a prominent activity and Gambier is one of the main French Polynesia farming sites (André et al., 2022b). The Gambier lagoon is surrounded by a barrier reef system but is very open to the ocean. The lagoon includes a series of patch reefs and wide fringing reefs found around a series of volcanic islands, the main one being Mangareva. The Gambier lagoon can be described as a series of different basins and lagoons with their own hydrodynamic regime. Pearl farming occurs mostly in the basins west and east of Mangareva Island, and in the channel immediately south of Mangareva and Aukena islands. Spat collection takes place only east of Mangareva Island, and in the south channel.

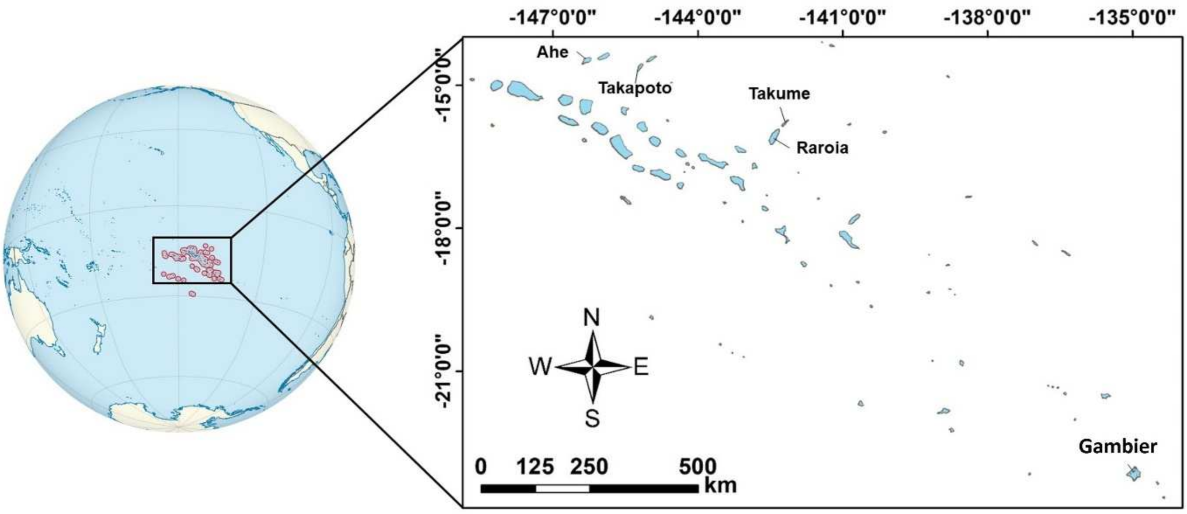

Figure 1. Location of French Polynesia on a world map (in red). The box is an enlargement of the Tuamotu-Gambier Archipelago. Studied atolls are located north of the Tuamotu Archipelago while Gambier is on the southeastern part of the archipelago.

Historical stock assessments (Takapoto and Gambier)

Andréfouët et al. (2016) provided a summary of the past studies on stock assessments for all sites ever studied. Most of these reports are from the grey literature and were first compiled by Zanini (1999). Briefly, in the context of pearl farming, two waves of surveys performed by SCUBA took place, specifically in the early to mid-1980s, and between 1995 and 1998 (Zanini, 1999), with generally an improving statistical approach employed between the two periods. All historical surveys were done without a complete knowledge of the bathymetry of the studied lagoons, but only using few depth profiles across the lagoons (Andréfouët et al., 2016). Without this knowledge, the studies report first local densities, and in some cases extrapolate to an overall stock per lagoon by making inferences on the distribution of depth ranges, and in some cases bottom types (hard *vs* soft bottom), across the lagoon (Intès, 1993; Zanini and Savat, 2000). This is unlike the most recent surveys (2013-2021) that we report here and for which exhaustive high spatial resolution depth data could be secured, including through the use of multi-beam sounders (Andréfouët et al., 2020). Also, several historical studies, but not all, have reported on the size structure of the stock, including for Takapoto and Gambier (Zanini, 1999 and references within).

Takapoto was one of the first atoll where pearl farming experiments took place. The first attempt to assess the *Pinctada margaritifera* stock was done in 1982 by Intès (1982b), with a result at approximately 7.5 million individuals (no confidence interval provided). In 1985, Takapoto experimented a massive oyster mortality event which halted pearl farming for a long while but density data from 1990 (Cheffort, 1996) and revisited by Cheffort and Zanini (1997) yielded a stock estimated at 10.1 ± 1.7 million individuals (mean ± CI 95%). Several stock assessment studies were subsequently carried out and the latest report was from a 1995 survey on 65 sites, yielding 4.3 ± 0.67 million individuals (Zanini and Salvat, 2000), suggesting a 57% decrease between 1990 and 1995. Takapoto had another partial mortality event in 1998 and it was only in 2012 that spat collection became very productive again. The historical surveys reported highest densities between 30 and 40m depth (see Table 1 in Zanini and Salvat, 2000, 8.2 ± 1.84 ind.100m^{-2}) compared for instance to the 0-10m depth range (1.0 ± 0.80 ind.100m^{-2}) although it is not clear if these historical surveys also included the very shallow top of pinnacles within the 1 or 2-meter depth range. Size structures were measured in 1983 (reported in Intès, 1995), 1989-1990 (Cabral, 1990; Cheffort, 1996) and 1995 (Zanini, 1999), suggesting two modes at 11 and 17cm in 1983 and for all the most recent historical data, a single prominent mode around 11-14cm.

Gambier archipelago was studied twice at the end of the 19th century. Intès and Coeroli (1982) counted pearl oysters on 29 stations mostly located in the northeast lagoon but did not infer a total stock. Pearl oyster densities varied horizontally and vertically. Indeed, oysters were much more abundant at the Aukena sill and south of it, while densities were very low in the north. Higher densities were found in the 0-10m depth range, and values subsequently decreased with depth. Zanini (1999) sampled 41 sites in 1996 within two private concessions: Taku (4 km²) located north of Mangareva Island; and the concession of Aukena (43 km²), a zone encompassing the Aukena island, the sill and deeper surrounding waters. Similarly to Intès and Coeroli (1982), Zanini (1999) observed higher densities on the sill where there was a decreasing oyster density gradient from the surface down to 50m depth. The stock was estimated at 10,000 ± 7,700 individuals and 580,000 ± 360,000 for Taku and Aukena, respectively. Finally, they also measured the sizes of the individuals. Size distribution displayed two marked modes at around 11 and 17cm.

In situ census and population data

In term of site selection and sampling strategy, several criteria need to be considered: 1) it is necessary to have a grid as regular as possible, without gaps but in practice, quickly modified according to depth and pinnacles specifically. This criterion is also imposed by the larval dispersal models implemented for several of these lagoons (for Ahe, see Thomas et al., 2016 for instance), that require a spatial parameterization of the existing stock without large gaps; 2) time in the field, as all sites are remote and *in situ* work was limited to 3 continuous weeks in the best-case scenario (Raroia, Table 1); and 3) depth and scuba-diving decompression constraints, hence 40 meters was the maximum depth for the surveys after 2016. The 40 m served as a generic indication of the sampled max depth; 3) it is necessary to have a spatial coverage of the entire lagoon as homogeneous as possible, without gaps. In addition, we tried to revisit historical sites although none of the historical studies precisely provided latitude/longitude coordinates, as these surveys were done before or at the beginning of the hand-held GPS era. Hence published maps were used as an indication of where the historical survey sites were. These maps were generally imprecise but could be useful if pinnacles and other lagoon-mark were indicated. However, it is impossible to say that we revisited accurately the location of previous sites, and thus we did not attempt to assess temporal differences at the scale of a station.

At all sites surveyed between 2018 and 2021, in the 40 to 2-meter depth range, densities were measured by SCUBA using 5 minutes long timed plotless belt-transect census, which represent around 200 m^2 in low oyster density areas (Andréfouët et al., 2016). This was estimated by calibrating the distance covered using GPS and by ensuring that divers swam slowly at constant speed, while surveying a ~4m wide corridor. In high density area in which the divers have to slow down and sometime stop, the area covered is adjusted *a posteriori* considering the actual distance covered in 5 minutes. One of us (SA) was noting when adjustments on the surveyed distance were necessary and the amount of required corrections. In very shallow areas, less than 2 m deep, belt transects were performed by snorkeling after deploying a 30m-long tape meter and divers surveyed a ~1m wide corridor each side (a total of 2 m width).

The census is performed by depth strata, meaning that at each 10m depth interval (40-30, 30-20, 20-10, 10-2, and 2-0), a 5-minute census is performed by each diver, as they swim in duo or in quartet. Exact depth within each depth range can be random, with one diver for instance swimming at 28m and another at 22m.

All oysters whether found on the sand or attached to a hard-bottom were systemically measured along their greater length with a 30-cm metal ruler at a precision of 1 to 2cm, depending on how the oyster is positioned and reachable. Records were taken by depth range. Depending on the needs, the size structure can thus be inferred afterwards per station, per depth range and per lagoon. Here, we primarily focus on lagoon-scale population structures.

Bathymetry and habitat map data

When available, bathymetry is used for 1) site selection, 2) scaling the stock from field sites to the entire lagoon. To estimate from the measured densities the overall stock per lagoon using field data, we took advantage of the bathymetry data available for all the study sites, except Gambier. Details on the atoll bathymetry data are provided in Andréfouët et al. (2020). For Raroia and Takapoto, the bathymetry was fully or partially available prior to the field campaigns, allowing to precisely select the diving sites to sample the different depth ranges. For Takume and the Gambier lagoon, this knowledge was not available before the survey took place.

For all stock estimates methods presented hereafter, it is necessary to limit the overestimation of the stocks due to a shallow lagoon border effect. This is necessary when high densities that were measured for instance on pinnacles are also assigned to the upper shallow inner slope of the lagoon, where much fewer oysters are actually present due to its sedimentary nature and possibly due to higher variation of temperature and the exposure to stress (e.g., predators). To avoid this effect, the shallowest sedimentary lagoon edges are not included and were masked out. This correction is especially necessary on the north side of some atolls where the shallow inner sedimentary slope tends to be quite wide.

For Gambier, a full high-resolution coverage of bathymetry was not available at the time of this study (this is in progress), but a detailed habitat map was available (André et al., 2022b). As the survey showed that significant densities were found on only two habitat types and very low densities elsewhere, it became obvious that the habitat map could be used to scale-up the stock. This is the same principles that allowed scaling giant clam stock in other Tuamotu atolls. For this, it is required to have density per habitat and the surface area of each habitat (Andréfouët et al., 2005).

Stock estimates using a density-bathymetry relationship

This method is referred hereafter as the 'Direct Method' and was performed for Ahe, Raroia, Takapoto and Takume atolls. For this, the surface area of each depth strata is estimated using the bathymetry maps and ArcGIS© (v. 10.8.1) software. From the oyster census data, the mean densities (d_m, in individuals per 100 m²) and confidence intervals for each depth strata were calculated, and the stock was estimated by multiplying the mean density for each depth stratum by the surface area (SA) of these strata. Unlike Andréfouët et al. (2016) who used all the sampled depth strata, the range of densities and a sensitivity analysis showed that using only two strata was adequate for all atolls, namely the 0-10m and the 10-40m strata. Stocks were therefore estimated using equation 1:

$$Stock = \frac{d_m\,(0-10\ m) \times SA\,(0-10\ m)}{100} + \frac{d_m\,(>10\ m) \times SA\,(>10\ m)}{100} \qquad \text{(eq.1)}$$

In this Direct method, for the depth range that was not sampled (>40m), two strategies are possible: first, this deep domain was considered to be without oysters; second, the densities observed in the 10-40m depth range were also assigned to the domain deeper than 40m. These two options allow for a sensitivity analysis in order to estimate the future need for sampling deeper than 40m.

A similar but zone-specific method, hence termed hereafter 'Zonal Method', was additionally used for those study sites that exhibited, for similar depth ranges, significant differences in density across their lagoons. In this case, within each zone, the mean densities were calculated for each depth strata and the stocks per zone were calculated as with the Direct method. The total stock was estimated by summing the stock estimates across the zones. This strategy was in fact already applied by Andréfouët et al. (2016) for Ahe atoll which was characterized by two different lagoon zones, each with contrasted densities and population structures. This was applied here to Raroia and Gambier, which displayed strong gradients of densities at similar depth between different lagoon zones or habitats. The definition of the limits of these zones was case-specific and explained in the Result sections.

For both the Direct and Zonal methods, the uncertainty is computed by the estimates of the standard error (SE) of the density obtained from the measurements (for the whole lagoon or for each zone). The total uncertainty is simply the SE applied to all points, hence SE multiplied by the surface areas (of the whole lagoon, or of each zone). Assuming a normal distribution for the density data, a confidence interval is provided (as in Andréfouët et al., 2016).

Stock estimates by cokriging of density data

Densities measured on every field station can also be used by a spatial interpolation method to directly derive a map. This third method was attempted here considering the variations that we noticed on the density results. Indeed, first, there was a clear spatial correlation pattern between depth and density, at both close range (e.g., along the slope of a pinnacle) and long range (between distant stations at different depth). It was also clear that between stations, densities per depth range were sometimes quite different, but not according to a random spatial pattern. Instead, changes were rather occurring by spatially coherent zones within the lagoonal space. For instance, in Ahe, the change occurred between the southwest lagoon and the east lagoon (Andréfouët et al., 2016). In Raroia, the gradient was more subtle, but it was clear that densities were lower within a 4 km radius of the pass and village than elsewhere, while densities on the south-central lagoon were higher than the lagoon average. In Takapoto, conversely, no clear trends could be seen between different lagoon zones, except a decreasing density in the far north (see in Results, Figure 2). Therefore, we hypothesized that an interpolation method of the density data applicable across a lagoon presenting spatial variations and trends in the depth-density relationships could provide results more reflective of actual abundance, without the need to define zones *a priori* as in the Zonal Method. For this, cokriging was identified as a useful option.

Cokriging is a geostatistical, multivariate method used to interpolate a variable X, for which the number of samples may be small, using a covariable Y which is possibly but not necessarily known on every point and that is correlated to X. Cokriging uses the same principles of kriging, applied to both X and Y, and it requires an analysis of the cross-correlation between X and Y. For more details on the concept and formula of the kriging method, the reader may refer to Carr (1985) and Matheron (1971) for the early work, but numerous textbooks and examples exist in a variety of fields. In short, kriging will assess based on a set of data the regression between the variable of interest (density in our case) and the spatial coordinates as the explanatory variables, but the errors are specifically minimized by using some auto-correlation model. Kriging thus requires a characterization of the auto-correlation of the variables of interest, which is done by examining systematically the differences between all the pairs of sampled stations *versus* their distances. The resulting plot is an empirical semivariogram (or possibly covariance) cloud that can be fitted with some predefined auto-correlation models. Then, various kriging algorithms (based on assumptions on the mean value over the domain) also exist. The kriging algorithm and auto-correlation model are used to predict the variable across the spatial domain, using also the Y variable in the case of cokriging. However, it may be difficult to foresee which type of kriging and auto-correlation model is optimal especially when data are sparse (like in our case, Figure 2). A systematic screening of different models may help, the ultimate criteria being to minimize errors for known data points and try to reproduce well the range of data. Indeed, kriging typically underestimates extremes (high values are predicted too low and low values are predicted too high). Many options are possible when modelling the semivariogram or covariance plot, that can help improve the results.

Using *in situ* data, a kriging/cokriging result also estimates the error, based on the differences between predicted and observed values. Unlike the Simple and Zonal method (see above sections), for Kriging, an error is computed for all points of the domain using the prediction model. Prediction error statistics are calculated either with a validation data set independent of the training data set, or by cross-validation approach (e.g., leave-one-out method). The best model should have the standardized mean close to zero, the smallest root-mean-squared prediction error (RMS, expressed in the same unit as the variable of interest), the average standard error (ASE) nearest the root-mean-squared prediction error (RMS), and the standardized root-mean-squared prediction error (RMSS, no unit) close to 1.

Here, for the atolls for which bathymetry is available, we interpolated density data using the cokriging method and bathymetry data as covariate. Interpolations were done using the cokriging package of the Geostatistical Wizard Tool in the ArcGIS© (v. 10.8.1) software. For all the study sites, different kriging algorithms (simple, ordinary and universal) and autocorrelation models were systematically tested and the combination providing the best prediction error statistics were selected for reference. The prediction standard error map computed by cross-validation was used to estimate the 95% confidence interval (IC95%) uncertainty for entire lagoons assuming that data obeyed a normal distribution. In this case, a factor 2 is applied to the sum of standard errors at all points to compute IC95%.

In the cokriging method, for the depth range that was not sampled (>40m), two post-processing strategies were possible. First, this deep domain was considered without oysters and forced to zero regardless of the interpolation results. Second, the results of the interpolations are kept 'as is'.

Results

Density of pearl oysters in atolls

Densities were measured on 39 stations in Takapoto (~0.50 stations/km²), 62 in Raroia (~0.17 stations/km²) and 24 in Takume (~0.59 stations/km²) (Figure 2). The Figure 2 also provides the 47 stations of Ahe atoll (~0.32 stations/km²) surveyed in 2013. For all the studied atolls, densities were higher near the surface (0-10 m) while fewer oysters were found in deeper waters (Figure 3). Highest average densities were found in Takapoto, reaching 30 individuals per 100 m². In Takapoto, the top of pinnacles had remarkable densities, with one pinnacle having a record pearl oyster density of 108.33 individuals per 100 m² (Figure 2). Raroia atoll had the lowest densities overall with values not exceeding 3.88 individuals per 100 m² (Figure 2) and with a mean density of approximately 1 individual/100m². Densities were fairly homogeneous in Takapoto and Takume lagoons while a strong spatial heterogeneity can be observed in Raroia, as it was the case in Ahe (Figure 2).

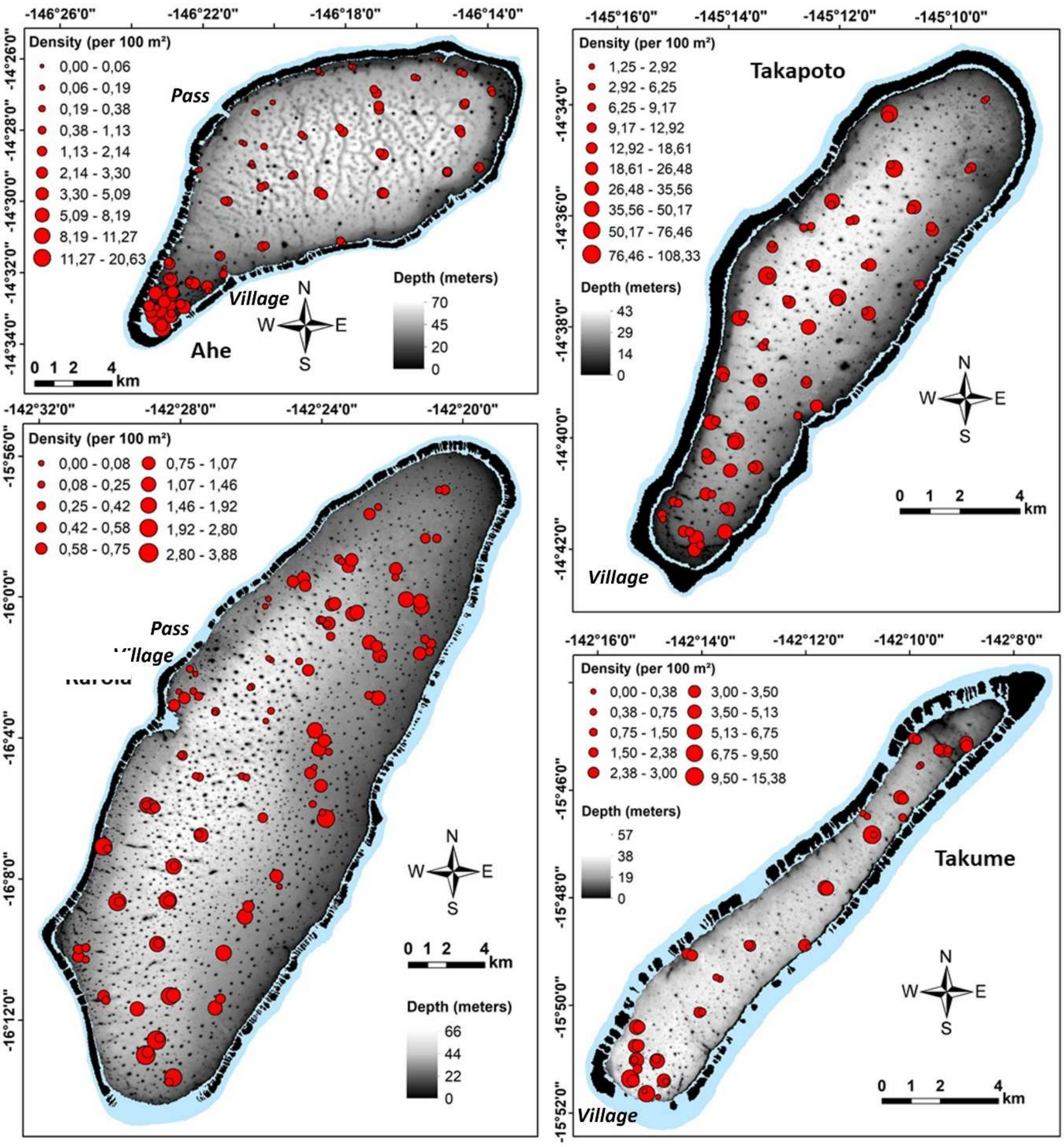

Figure 2. Pearl oyster densities (per 100 m²) overlaid on bathymetry maps for Ahe, Raroia, Takapoto and Takume atolls. Data collected between 0-10m and below 10m depth appeared in the figure and are separated here, explaining why some points may overlap. The atoll rim is represented in light blue and the atoll rim land (the islets, or *motu*) is black. Passes and villages are indicated. Ahe and Raroia displayed high variations of densities at similar depth between different lagoon zones.

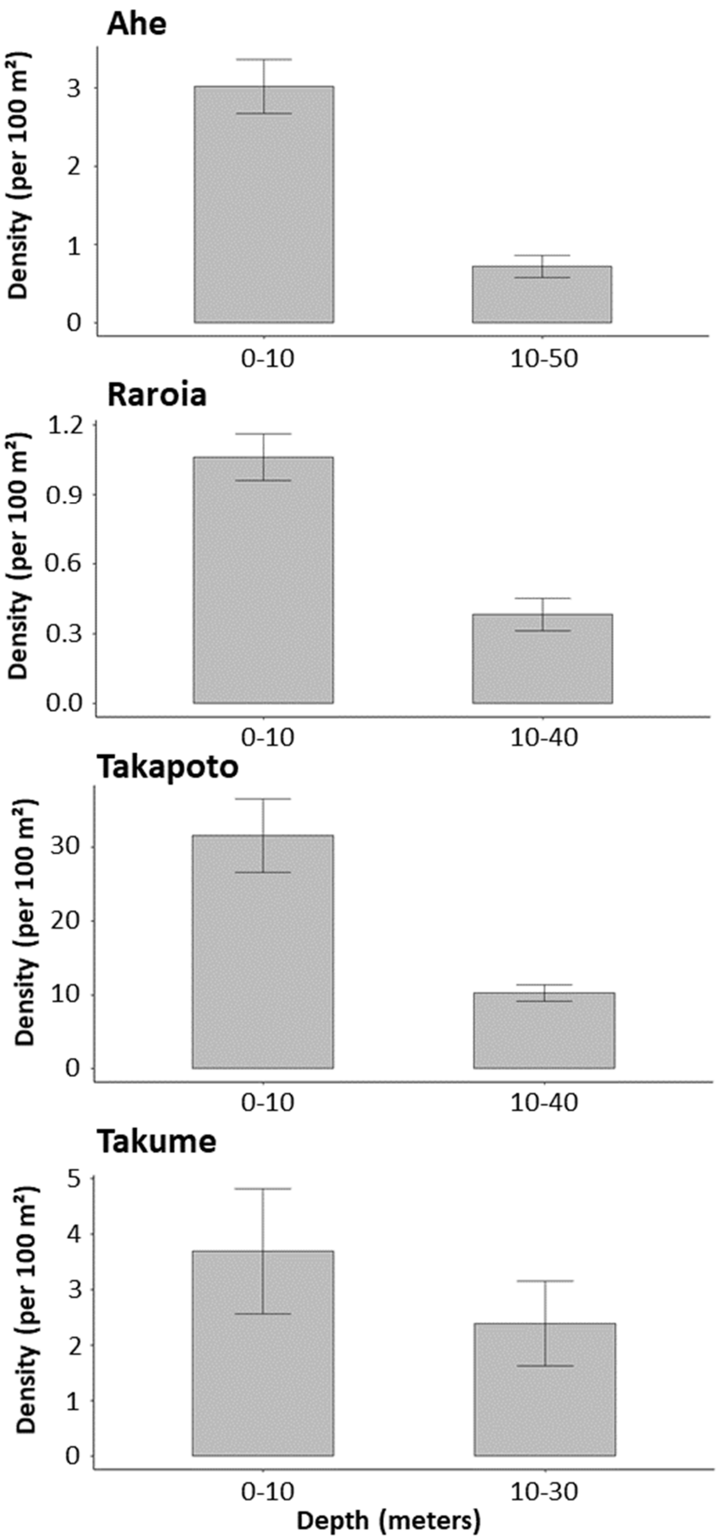

Figure 3. Density per depth strata using the standard method for Ahe, Raroia, Takapoto and Takume atolls. Error bars correspond to the ± 95% confidence interval.

Density of pearl oysters in Gambier

Density data were collected in the 0-50m depth range on 64 stations (~0.14 stations/km²) covering ~2/3 of the lagoon (Figure 4). There was a clear zonal pattern within the lagoon with high densities mainly found 1) in a shallow zone between Mangareva and Aukena and extending just north of Aukena; 2) in the patch reefs located south of Mangareva and Aukena (Figure 4). Elsewhere, densities were null or very low. The highest densities, in Zone 1, reached 30.36 oysters per 100 m².

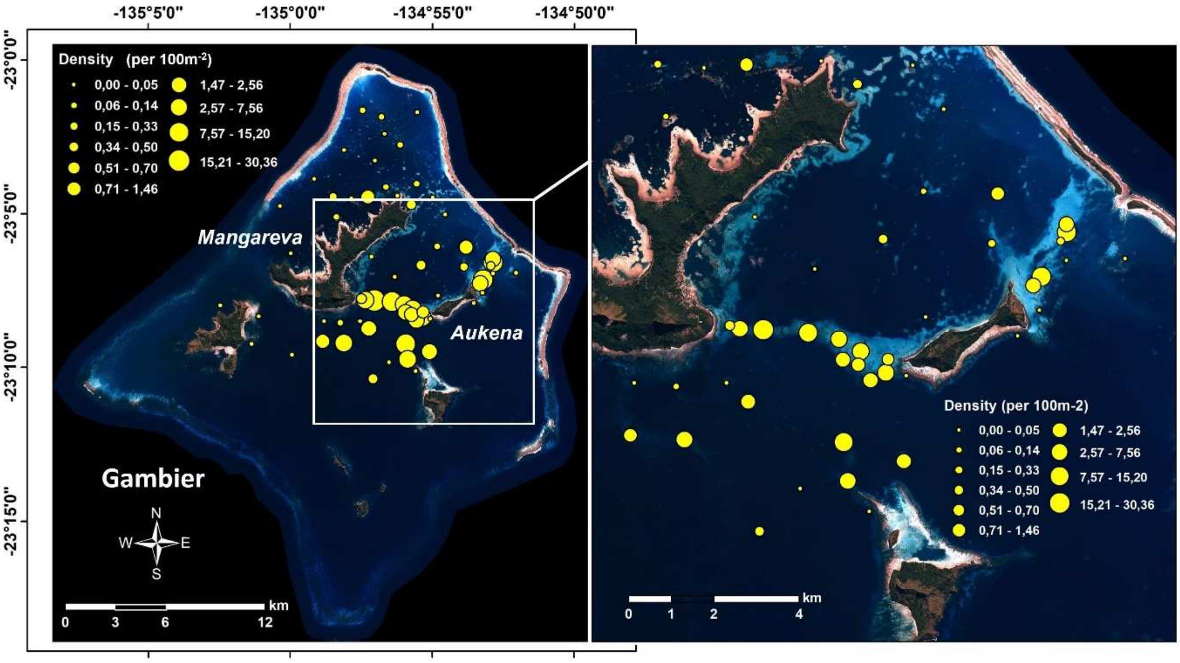

Figure 4. Map of Gambier and enlargement showing the location of the highest density survey sites around the islands of Mangareva and Aukena. Densities were high on two specific areas: the shallow zone that extends west and east of Aukena, and on the patch reefs found in the lagoon south of Mangareva and Aukena. These patch reefs are not visible here on the satellite imagery as they are around 10m depth but see Figure 9 for the habitat map. The stock is calculated for the entire lagoon (see text) not just for the enlargement on the right.

Cokriging results

We present first the results of the cokriging method that was applied to all sites where depth data were available, because cokriging has been used to refine the zonal method for Raroia. After testing different models on each site, the parameterization providing the best results are listed in Table 2. Results presenting the best slope in the scatterplot of predicted values versus true values were selected, meaning when the blue line (the fitted line through the scatter of points) is the closest to the 1:1 line (the gray line) (see Figure 5). The best statistical results shown Figure 5 varied widely between atolls, from good predictions in Ahe, mediocre in Raroia and Takapoto, and very poor in Takume, where the predicted values all fall within the same narrow interval. The corresponding prediction map results are shown Figure 6.

Table 2. Cokriging input parameters that provided the best results for each study sites.

Study site	Cokriging type	Models
Ahe	Simple	Exponential
Raroia	Simple	Exponential
		Hole effect
Takapoto	Simple	Stable
		Exponential
Takume	Simple	Rational
		Quadratic

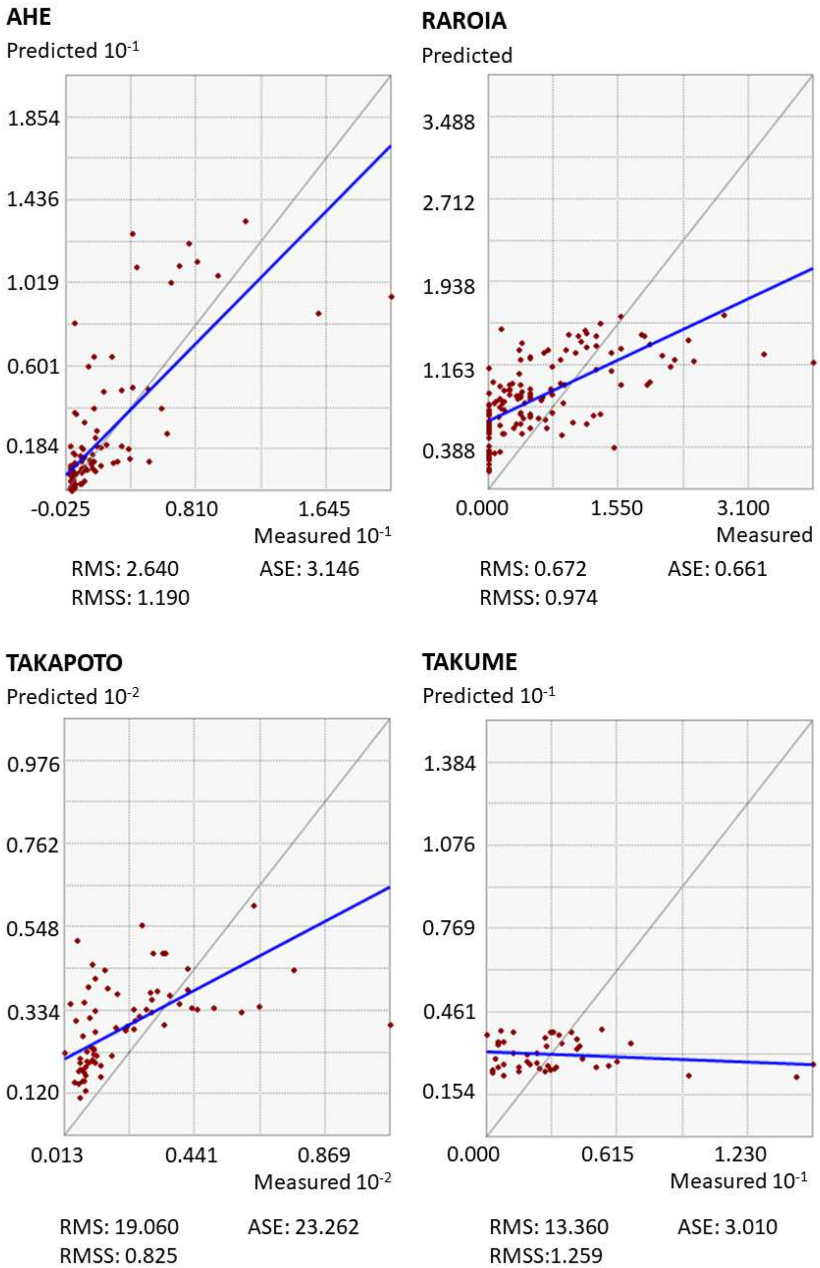

Figure 5. Scatterplot of predicted values versus true values as generated by ArcGIS©. Statistic values resulting from the cokriging interpolation are presented below each corresponding plot. RMS: Root-Mean Square; ASE: Average Standard Error; RMSS: Root Mean Square Standardized. The best results for each study site are shown here.

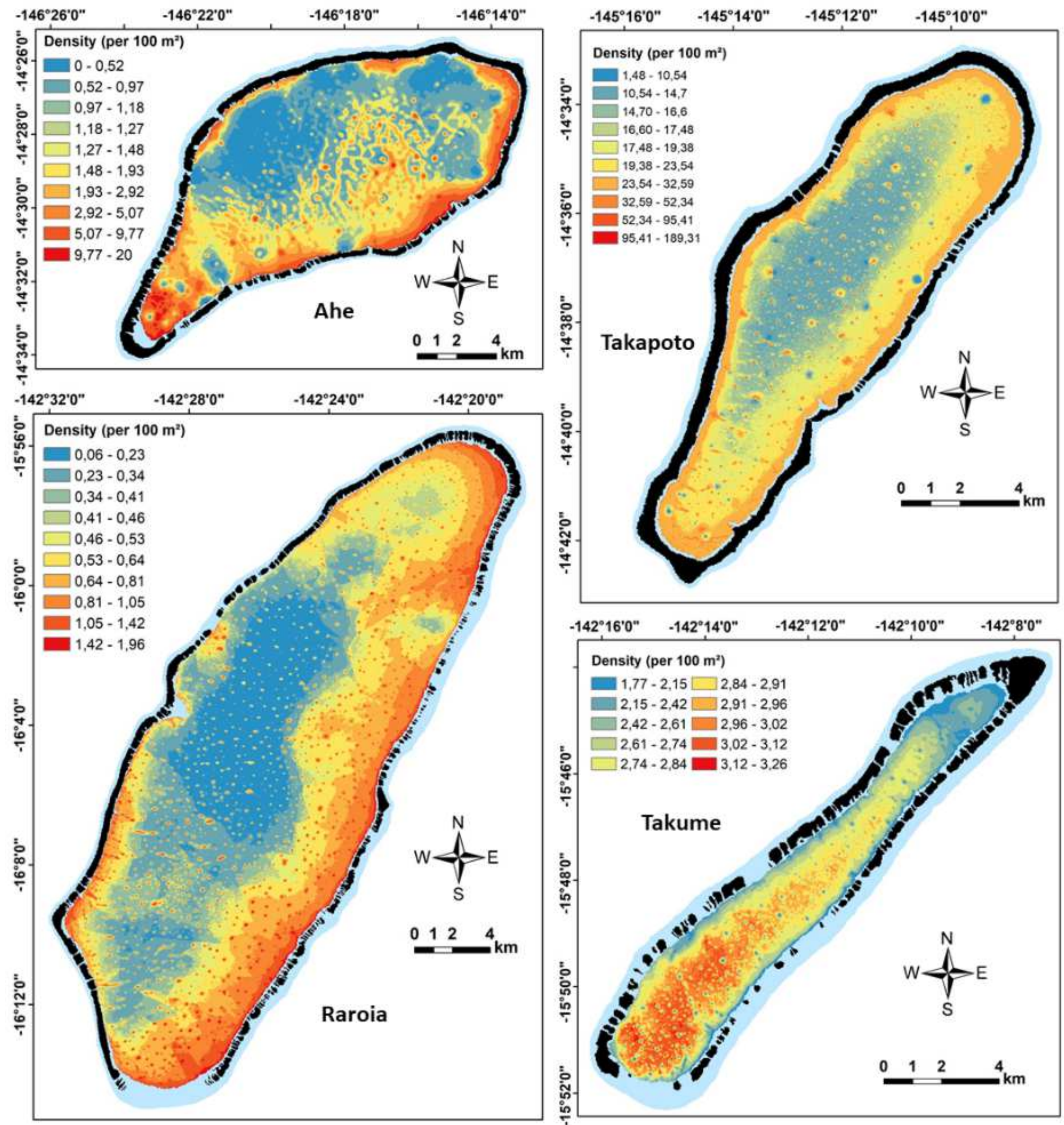

Figure 6. Density prediction map for Ahe, Raroia, Takapoto and Takume with the best results achieved using the cokriging interpolation method. The areas deeper than the sampled domain are shown here with the interpolation result, and not forced to zero. A version of the product exists where this deep domain is forced to zero.

Zonal method results

The zonal method was used for Ahe (2 zones) and Raroia (3 zones), considering also two depth strata. It was also used for Gambier, but considering two habitat types as the different zones.

In Ahe, the two zones were geomorphologically well separated (Andréfouët et al., 2016). In Raroia, the limits were not spatially so obvious (Figure 2), and to define the Raroia zones, we thresholded the results of a cokriging map by a 3, 4 and 5-class slicing of the density range as performed by the Jens method implemented in ArcGIS© (v. 10.8.1). We kept the 3-class slicing (Figure 7) as it provided maximum density differences between zones (Figure 8). The two first zones corresponded well to the low-density area located close to the pass/village; and to the high-density area located south. The third zone corresponded to the rest of the lagoon (Figure 7).

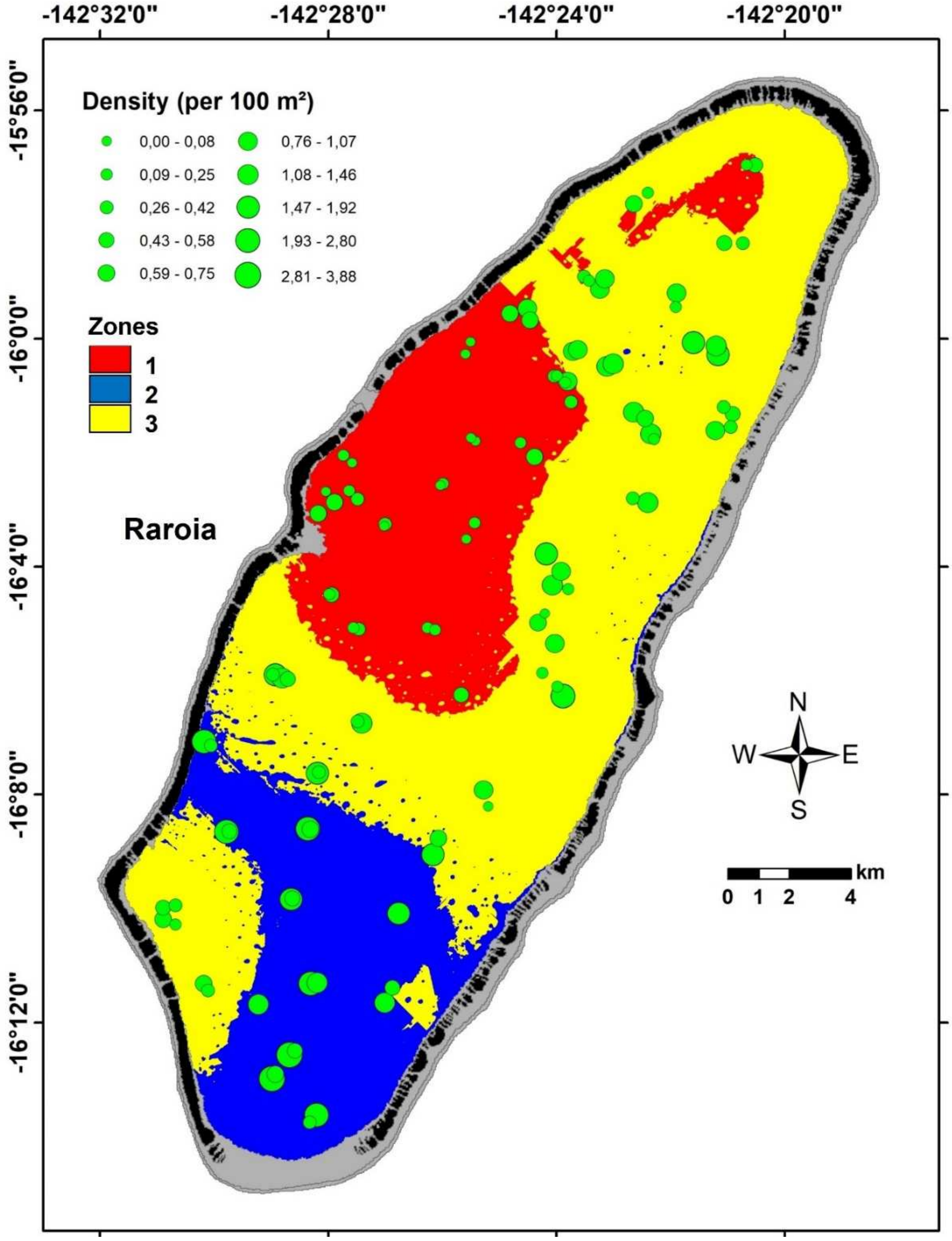

Figure 7. From a first cokriging map product, the interpolated densities were thresholded in 3 classes of increasing densities, providing the 3 zones shown here. The density field data are overlaid on top of the three zones. Three masks closely matching the limits of these three zones were created to estimate the oyster stock using the Zonal Method with the density statistics shown Figure 8.

The oyster densities for Ahe and Raroia and for each zone and depth strata are shown Figure 8.

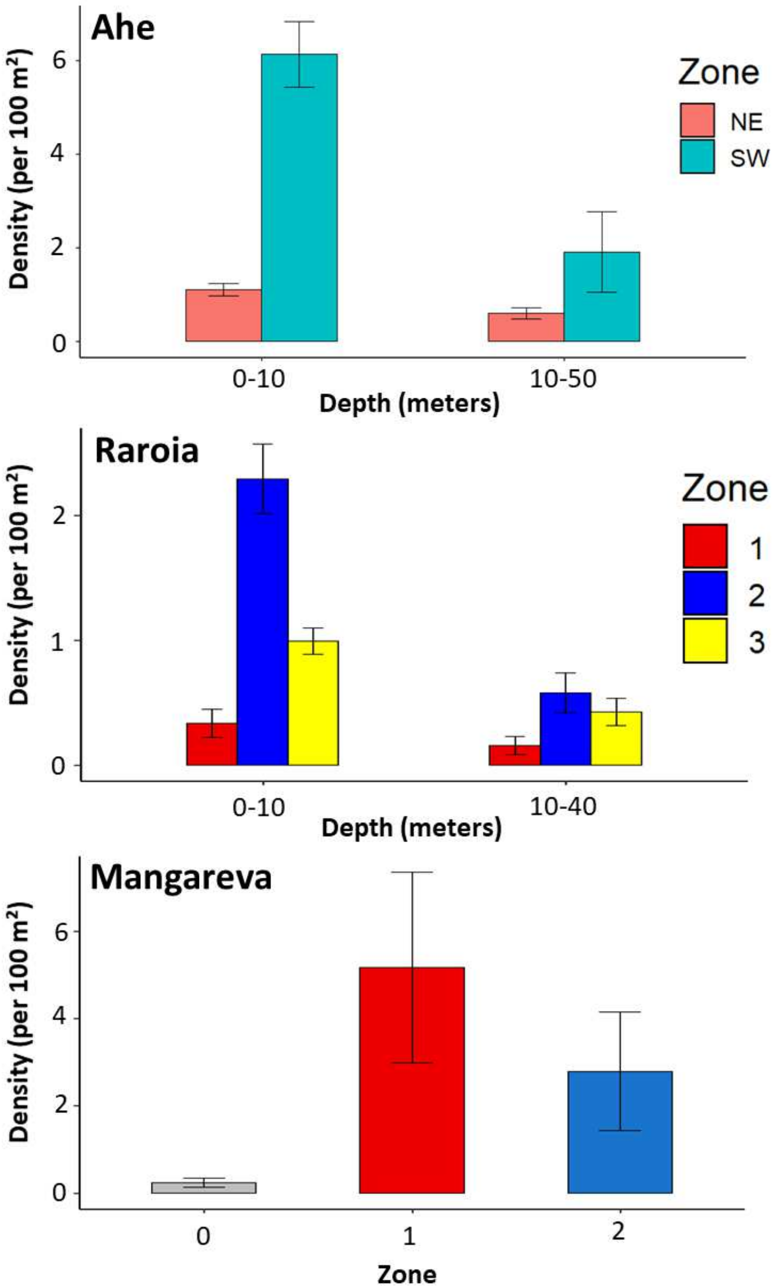

Figure 8. Top: Density per depth strata for the northeast (NE) and southwest (SW) zones of Ahe. Middle: Density per depth strata for the three zones of Raroia. Bottom: Density per zone for Gambier; zone 1 corresponds to the sill; zone 2 is composed of patch reefs; and zone 0 is the rest of the lagoon (see Figure 9). Error bars correspond to the ± 95% confidence interval. The bar colors refer to the mapped classes in Figure 7 and 9.

For Gambier, the density per habitat is shown Figure 8. The habitat map in Figure 9 directly provided the two zones of interests. The rest of the lagoon was considered homogeneous in densities, using the data collected on all other habitats at all depth range.

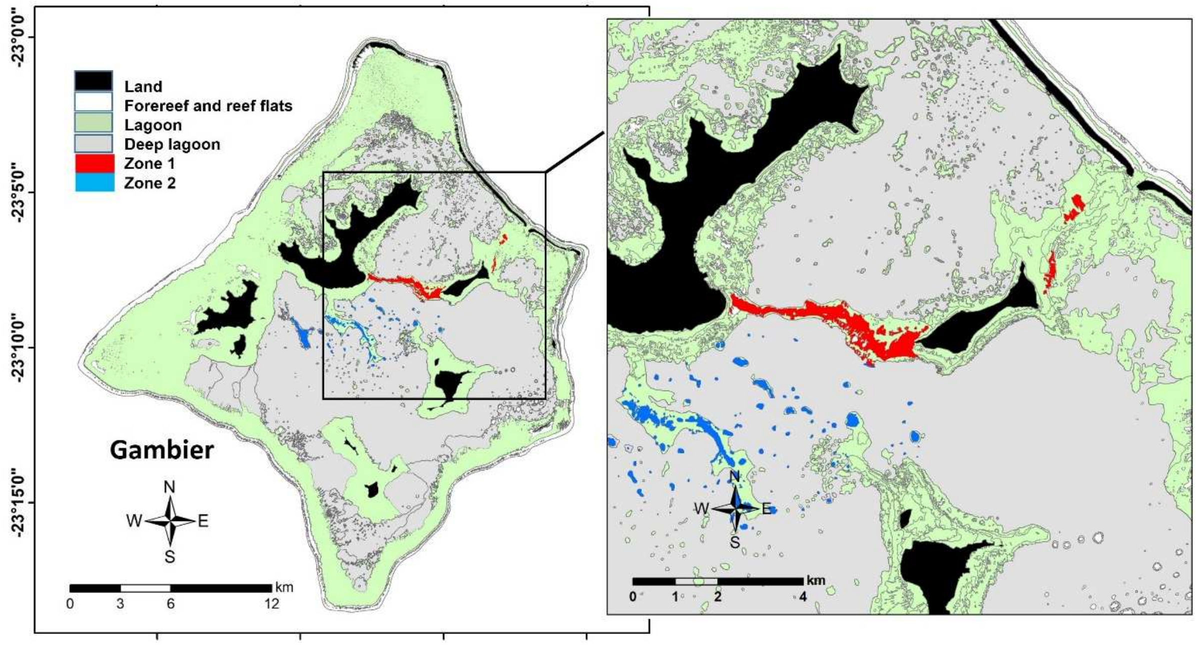

Figure 9. From the detailed high spatial resolution Gambier habitat map presented in André et al. (2022b), the two habitats with the highest oyster densities (Figure 4) are kept apart from the main lagoon to define a total of 3 zones with contrasted densities (see Figure 8). The third low density zone can be used in two versions, by including or not the deep lagoon, even in the south (Figure 4).

Direct method results

For all the atoll sites, an estimate of the stock can be provided considering the two depth strata and their average density computed from the entire field data set (Figure 3). The spatial distribution of the densities according to the Direct Method are shown Figure 10.

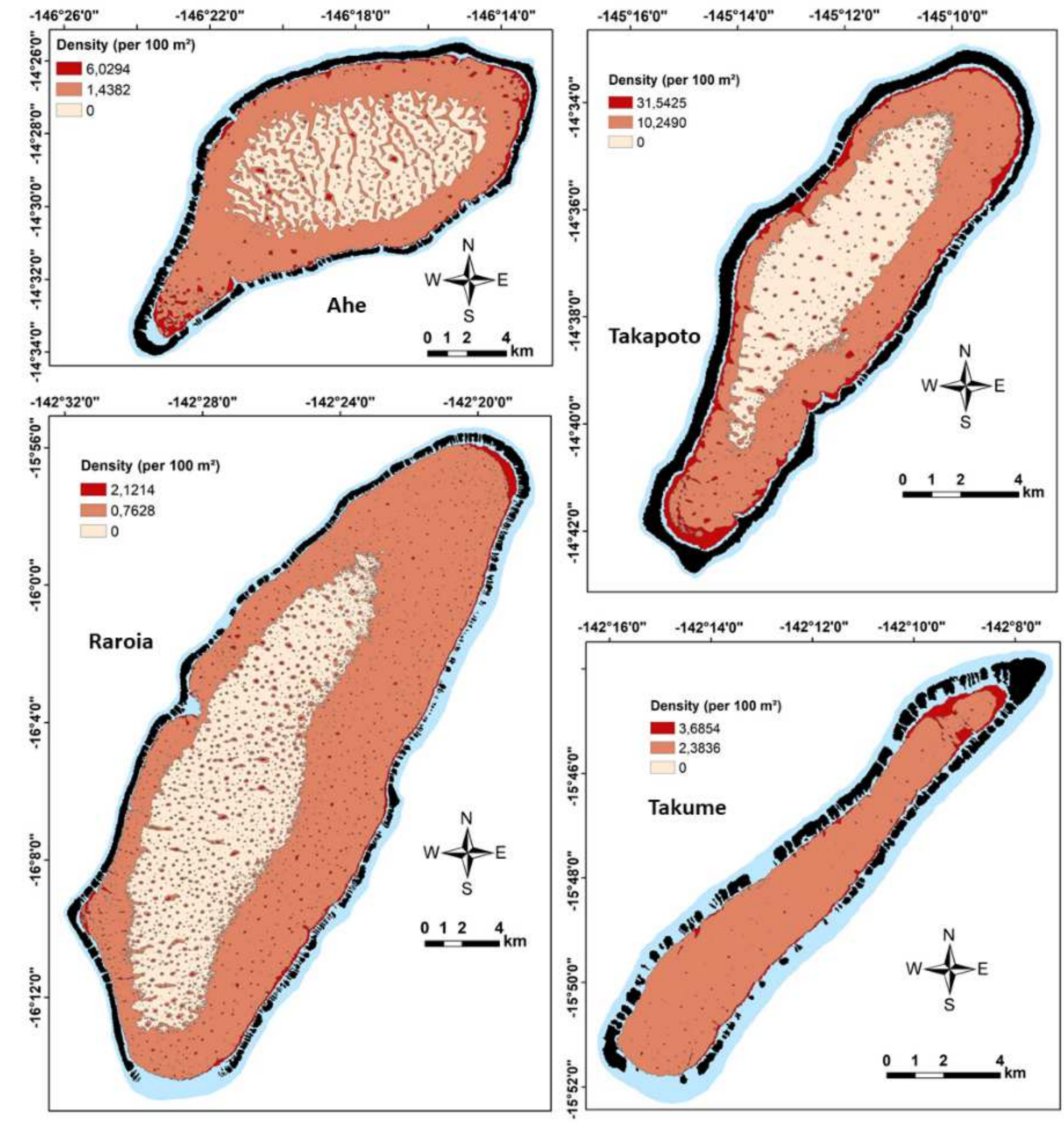

Figure 10. Map of densities and distribution of the stock in Ahe, Raroia, Takapoto and Takume atolls using the Direct Method on two depth strata. Here, the deep non-sampled area is shown with a stock forced at zero for the 4 atolls. For Takume, this non-sampled area deeper than 40m is very small (3175m²).

Synthesis of stock estimates

To summarize, the stocks (in number of individuals) in Ahe, Raroia, Takapoto and Takume were estimated and mapped using at least two methods: a Direct density-bathymetry relationship (Figure 10) and the Cokriging method (Figure 6). Then, a third Zonal Method was also performed for Ahe, Raroia and Gambier as densities varied spatially according to different zones or habitats. Finally, results are also provided depending on if the deep non-sampled domain was forced to zero or weighted with the 0-40m density. The Table 3 provides all the corresponding stock estimates. We note that the IC95% estimated for all cokriging products were often very high (Figure 5). The highest stock was estimated for Takapoto atoll, even if it is not the largest of the studied lagoons. The least abundant oyster population was in Gambier, as its stock was estimated at 460,779 ± 152,883 if we consider the sampled lagoon only. The estimate can be pushed to 1,231,114 ± 501,891 (Table 3) if we take into account the entire lagoon (deep and shallow lagoon, see Figure 9).

Table 3. Stock size of pearl oysters according to the method used. IC95% is the 95% confidence interval. In bold, the values that are kept as references. For Takume, the non-sampled area deeper than 40m is very small (3175m²), and the results are very close with or without zeroing the stock deeper than 40m.

Atoll Deep lagoon forced to 0	Method	Stock	IC95%
Raroia	Direct	2,002,572	158,562
	Cokriging	1,719,334	1,430,558
	Zonal	**1,109,003**	**182,184**
Takapoto	Direct	**9,107,344**	**817,826**
	Cokriging	11,880,094	17,567,642
Ahe	Direct	857,975	127,372
	Cokriging	2,001,138	5,816,592
	Zonal	**772,074**	**108,459**
Takume	Direct	**1,008,283**	**290,925**
	Cokriging	1,244,562	47,860
Gambier	Zonal	**460,779**	**152,883**
Atoll Deep lagoon density not forced to 0			
Raroia	Direct	2,887,882	234,488
	Cokriging	2,047,258	1,949,840
Takapoto	Direct	9,462,491	852,456
	Cokriging	16,505,111	24,182,928
Ahe	Direct	1,190,843	191,948
	Cokriging	2,454,620	7,728,984
Takume	Direct	1,008,359	290,949
	Cokriging	1,244,562	47,878
Gambier	Zonal	1,231,114	501,891

Oyster populations size structures

For all atolls and in Gambier, few oysters < 4cm were recorded and this can be explained by the difficulty to find these small oysters even when swimming slowly. Between 1,057 and 2,516 oysters were measured on each site to plot the lagoon-scale population size structure (Figure 11). Size structures of *P. margaritifera* populations varied according to the atoll or island studied (Figure 11). In Gambier, the distribution is skewed towards smaller and younger oysters with an 8-cm mode. Repeated peaks at 8, 10 and 12cm suggest different cohorts arriving each year in the 4, 5 and 6 years preceding the survey, if we refer to the age-size curve in Chavez-Villalba et al. (2011). In Takapoto, the oyster size distribution was centered around 11-12cm, with the largest oysters only reaching 18cm. The size distribution was normal for the entire Ahe atoll, with a single 13-cm mode. Keep in mind however, that Andréfouët et al. (2016) showed that the oyster population on the two Ahe zones were characterized by very different size structures: the northeast lagoon population was centered at 17 cm and the southwest population was more abundant and centered around 12cm. In Takume and Raroia atolls, pearl oysters were larger, and older, than in the other sites, with a 17-cm and a 20-cm mode, respectively (Figure 11), but similar to the Ahe northeast lagoon. Maximum sizes reached also 24 and 26cm for Takume and Raroia respectively. Conversely, these atolls show a deficit in small sizes with respectively only 7.9 and 5.7% of the population below the 10 cm threshold (against 21.3% for Ahe, 41.5% for Takapoto and 60.2% in Gambier).

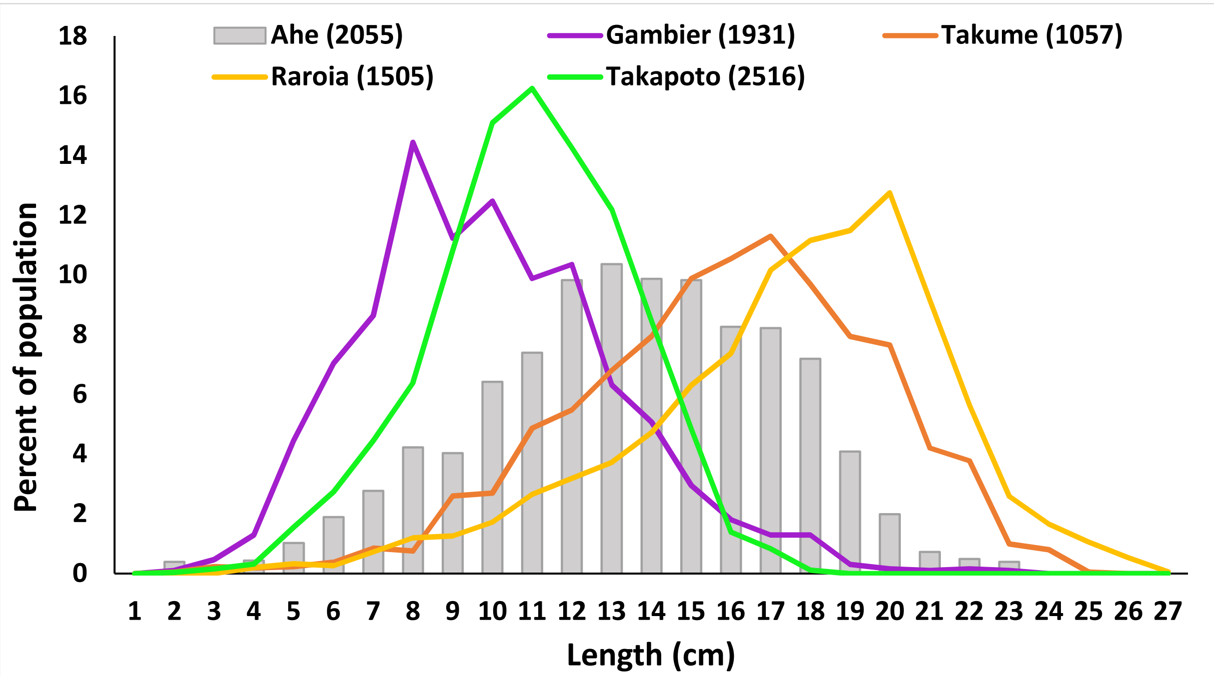

Figure 11. Size structure for the oyster populations of Ahe (grey bars), Gambier, Takume, Raroia and Takapoto (all shown as curves for better visibility). The number of measured oysters are in parenthesis next to the site name.

Discussion

Critical analysis of stock assessment methods

Stock abundance estimates varied substantially depending on the method used in scaling lagoonal estimates. With the Zonal method, estimates were lower than with the other methods. Conversely, cokriging systematically estimated larger stocks than the other methods, especially in Takapoto where the interpolation computed a stock almost twice as large as that estimated with the Direct method (Table 3).

The three different methods were all based on the variation of oyster densities with depth. The Direct method used a simple bathymetry-density relationship. We decided to apply this method with only two depth strata (0-10m and > 10m) instead of Andréfouët et al. (2016) who estimated a stock for Ahe and Takaroa with six depth strata. Indeed, little difference is observed between stock abundance results computed with different number of strata if we consider the 95% confidence interval.

The refinement that is brought by the Zonal method certainly avoids the spatial over-generalization of local results, in particular some very high densities found on some pinnacles. The bathymetry-density relationships are adapted to the zone considered, and the consequences are a systematic lowering of estimated total stock than with the Direct method. The particular case of Gambier, where a habitat-based zonal method is used, shows that every site can be different in term of the best approach to use. Here, this reflects in particular the uniqueness, among all our sites, of the configuration of the shallow sill between Mangareva and Aukena islands where the dominant substrate (pavement with turf algae) is apparently extremely suitable for oysters (Figure 12). This habitat was never found in Tuamotu atolls where the reefal configurations are different (Figure 12). Similar pavement on top of the patch reef of the Gambier Zone 2 also correlates with the high density found there. While atypical for our oyster stock assessments, the habitat-based zonal approach has been however quite common to assess the stocks of other mollusks such as giant clams or green snails, including in French Polynesia (Andréfouët et al., 2005; Gilbert et al., 2006; Andréfouët et al., 2014).

Density data from Takapoto and Takume were not sufficiently gradual across the lagoon to suggest the existence of different zones, so the Zonal method was not used there. One could suggest that the sampling effort can explain the lack of perceived zones, but considering that each lagoon is sampled in order to achieve a maximum coverage across each lagoon (Figure 2), despite sometimes a low density of sampling stations per km^2, it is unlikely that zones as they are apparent in Ahe southwest lagoon (high density zone), or around the pass/village of Raroia (low density zone) or on the Mangareva-Aukena sill (high density) could be missed.

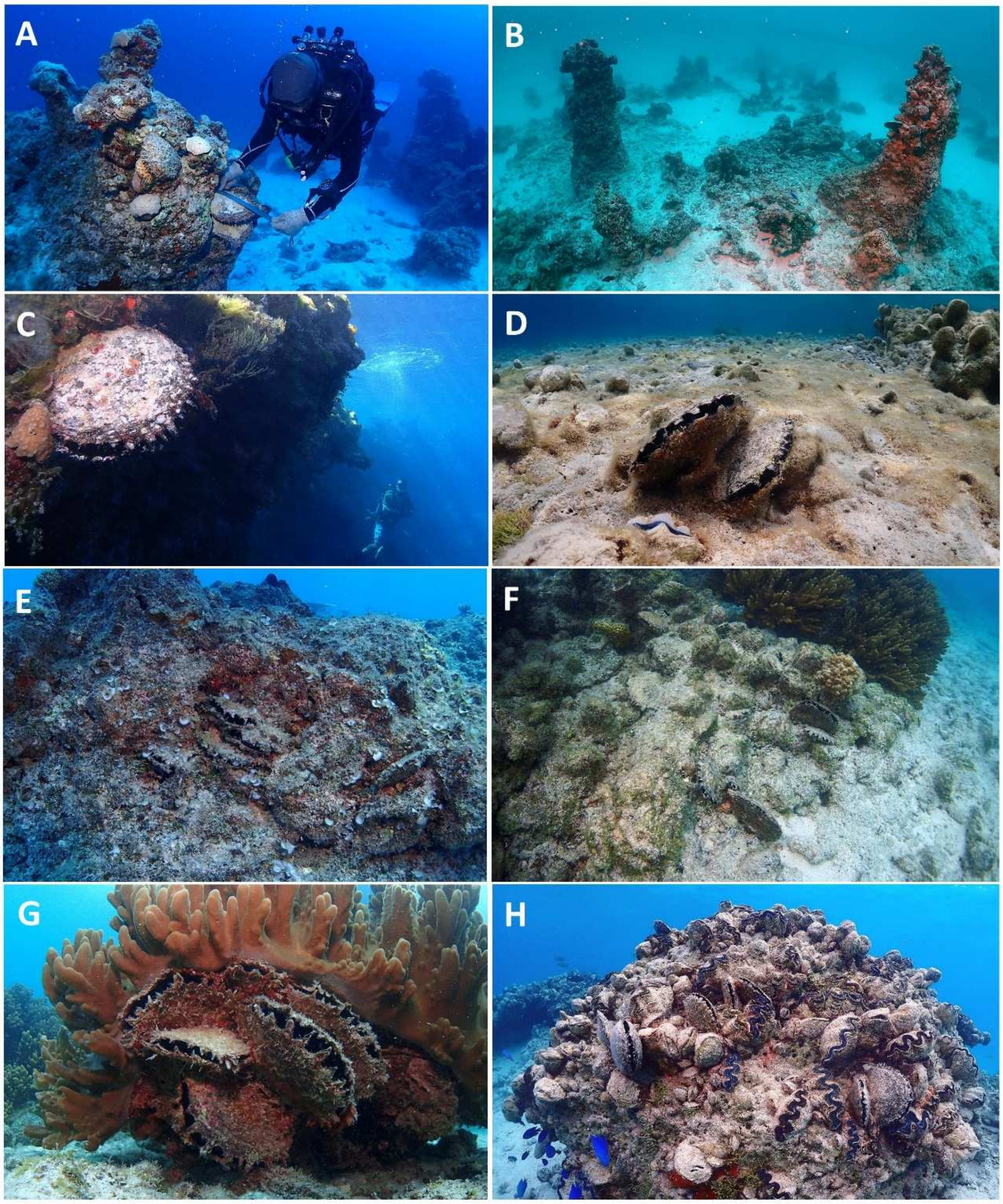

Figure 12. Different type of lagoon configurations where oyster census took place. A: Deep Raroia lagoon (~30m) with small eroded structures on sandy bottom, and low oyster density, B: Similar habitat is found on part of the Takapoto lagoon, in the 30-40m depth zone, C: Vertical pinnacles in Raroia atoll where highest oyster densities were found in the 0-10m upper depth zone, D: low relief pavement and turf algae make the summit of Takapoto patch reefs and pinnacles, where high densities of small oysters were found (mode at 8cm), E: In Gambier, example of the distribution of oysters for the high-density Zone 2 (Figure 9), F: In Gambier, example of the distribution of oysters for the high-density, mid-depth (5-15m) Zone 1, growing on pavement and hard substrate with turf algae (Figure 9), G: In Gambier, example of frequent shallow (0-2m) cluster of oysters for the high-density Zone 1 growing on covered (here by soft coral) rock eroded structures, H: In Takapoto, in the 0-10m depth zone around the shallow lagoon edge and pinnacles, oysters grow in high densities on hard substrate, often associated with giant clams.

These zones were however the reasons for which we investigate the cokriging method, as a solution to avoid a potentially arbitrary pre-segmentation of the lagoons, in order to define these zones. The results considering the prediction errors prove to be variable depending on each site. Further, ordinary kriging, which allows variable mean across the studied domain and data, be theoretically better than the simple kriging considering the trend in some data set, but this approach performed more poorly than the simple approach. This may be explained by a data set which was too limited for all atolls despite our sampling efforts, in addition to local specificities on densities. Indeed, typically, lagoons with low contrast of density between sampling stations, at all depth, would yield poor results in terms of statistical fit (see Takume, Figure 5), although the mean stock estimates are acceptable when compared to the Direct method (see Takume, Table 3). Statistical fits were better in lagoons that have a wide density range like in Takapoto (1 to 108 ind./100m²) (Figure 5). Generally, and as expected with kriging methods, high densities were underestimated by the cokriging models (Figure 5), and there was a general (slight) overestimation of the low densities in deep waters, which eventually yields widely overestimated stocks due to the large surface areas of the deep (>40m) waters in Ahe, Raroia or Takapoto (Table 3). This can be tampered by zeroing the stock >40m but even in this case the stock is too high in the deeper sampled layers. As such, the estimates provided by the cokriging approach cannot be reliably used, and the best results are eventually those provided by the Zonal, or Direct approach, despite their simplicity. However, biases may also exist with these simple methods. For instance, medium to high densities found on top of some pinnacles cannot be directly extrapolated to the 0-10m depth range of the entire lagoon, in particular along the atoll rim inner slope. These corrections can be done after processing or before by taking into account a mask avoiding the treatment of these zones.

To conclude, depending on the method used and the characteristics of the density data, results can vary substantially (Table 3). Stock estimates computed by the Direct and Zonal approaches seem more realistic than with the Cokriging method. Following a precautionary approach, these conservative estimates were kept as references for the future. In order to have a better prediction of densities by interpolation, it is also better to have a large number of sampling stations (for reference, we achieved ~025-0.45 stations/km² for Takapoto, but we suggest ~5-10 times this density), but this is typically difficult to achieve in remote lagoons investigated with short-term expeditions. We conclude that cokriging methods will remain inadequate for the type of sampling effort we can typically afford in these remote locations. Cokriging can however be useful to segment the lagoon and define zones. In our case, the presence of different zones was quite obvious in the Raroia, Ahe and Gambier sites, although exact limits for Raroia were not that obvious to infer. When a segmentation became necessary, a preliminary cokriging interpolation was helpful here to define the different zones (see Raroia, Figure 7) when they were not as obvious as for Ahe or Gambier. Kriging methods could become suitable with more sampling sites, especially in the deep areas. Our logistical constraints in remote atolls without decompression chamber facilities nearby in particular limit performing deep dives, which will most likely uncover null or very limited stocks deeper than 40m. Using underwater drones to carry out deep explorations has been suggested, but this poses a number of logistical constraints on their own. In conclusion, the choice of a stock assessment method is case-dependent, following the type of study sites and on its oyster density distribution. Each case is unique.

Comparison with historical studies for Takapoto and Gambier

Our results (densities, size structure and stock estimates) were compared to the results of previous studies (summarized in Table 4) carried out in Takapoto atoll and Gambier. These results are from grey literature reports, in French language, except for Zanini and Salvat (2000).

Table 4. Review of pearl oyster key historical data in Takapoto and Gambier. NA=not available.

Island/Atoll	References	Sampling period	Mean density (ind./100 m²)	Stock (number of individuals)
Gambier	Intès and Coeroli (1985)	1982	1.82 ± 1.02	NA
	Zanini (1999)	1995	5.30 ± 0.83	Taku: 10,000 ± 7,700 Aukena: 580,000 ± 360,000
Takapoto	Intès (1982)	1982	9.57 ± 2.09	7.5 millions
	Cabral (1990)	1989-1990	12.00	NA
	Cheffort and Zanini (1997)	1990	NA	10.1 ± 1.7 millions
	Zanini (1999)	1995	5.30 ± 0.83	4.3 ± 0.7 millions
	Addessi (1997)	1997	NA	4.3 ± 3.7 millions

In Takapoto atoll, the pearl oyster size structure was consistent over time, with a normal distribution population centered on an 11-cm mode. No oysters > 20 cm were ever reported between 1990-2021, while the maximum size observed in 1982 and 1987 was 22 and 20 cm, respectively (Cheffort, 1988; Intès, 1995). Based on Chavez-Villalba et al. (2011), a sex-ratio of 1:1 is reached for a pool of individuals around 16-cm long, hence the present Takapoto wild stock would be predominantly male. However, it may be difficult to estimate a precise sex ratio by size structure analysis as Takapoto pearl oysters were known for their unusual small sizes and slower growth (Pouvreau and Prasil, 2001; Zanini 1999).

In Takapoto, densities were similar from 1982 to 1990 but they seemed to have decreased by 1995 (Zanini and Salvat, 2000). Since that date, the mean density has increased sharply and is now about 4 times that of 1990 (~21 ind./100m² in 2021). Another difference is the depth-density relationship. Namely, all the studies carried out from 1982 to 1995 found low densities on the 0-10m depth range, increased values until 30m, and then a decrease again beyond 30 m (Intès and Coeroli, 1985, Zanini and Salvat, 2000). Here, our 2021 results show an inverse density-depth trend compared to these past results, with low density below 10m and high density on the top of pinnacles, *kaoa* (reefs that grow perpendicular to the shore), and shallow patch reefs (Figure 3). This shift is explained by the increase of the shallow densities, and not by the decrease of the deeper densities, as Zanini and Salvat (2000) and our recent surveys both report similar average densities below 10 meters.

The Takapoto stock that we report here is one the highest ever estimated, with a value of 9,107,344 ± 817,826 individuals. In 1982, the stock was estimated at 7.5 million individuals (Intès, 1995), then increased to 10.1 ± 1.7 million individuals in 1990 (Cheffort and Zanini, 1997) before decreasing to approximately 4.3 million individuals in 1995-1996 (Zanini, 1995; Addessi, 1997; Zanini and Salvat, 2000). The 1995-2021 increase is too large to be just a methodological artefact. Despite the high density in the 0-10m range, the deep stock is still dominant. Indeed, the surface area of zones deeper than 10m is approximately 10 times higher than shallow zones. Hence, we conclude that the situation in Takapoto is now very different than almost 30 years ago but mostly for the shallow area that today is equivalent to ~1/3 of the deeper stock (~2.2 million oysters).

In Gambier archipelago, the historical reports and our observations are consistent in term of stock location and densities. All studies since 1982 agree that the area between Mangareva and Aukena has much higher densities than elsewhere. Elsewhere, for all surveys, densities were very low to null, including in the north of the lagoon. This area is where the oysters came from when the mollusks were exploited for their shells, early on since the nineteenth century. Unfortunately, there are no available *in situ* density measurements from this period and this area, but the amount of exports suggest that the stock in the north lagoon was substantial before it collapsed (Intès, 1982a), and obviously without recovery despite several decades at rest.

One aspect that did change in Gambier between 1995 and 2021 is the size distribution of the population. Specifically, large oysters were rare in 2019-2020 in the field, while in 1995 the percentage of the stock at size 10-12cm and at size 16-18cm were similar (Zanini, 1999). Instead, our results show a single 8-cm mode, and the majority of oysters (73.4%) were in the 7-13cm range. We note however that Zanini (1999) measured only 200 specimens (against 1931 in our case) and may have under-represented the smallest specimen. Nevertheless, from our data, these characteristics classify Gambier as the pearl farming site with the smallest individuals, just before Takapoto (Figure 11). Most likely, the Gambier population sex ratio is severely unbalanced with 96% of the population below the 16cm-threshold for which the proportion of male and females is equal according to Chavez-Villalba et al. (2011). Combined with a low estimated stock (460,779 ± 152,883 individuals), the auspices for the next years of spat collection do not seem very good. However, we believe it is necessary to reassess with new histological sampling the proportion of males and female gonads in Gambier individuals across the observed population size spectrum. This would be necessary for Takapoto too.

Finally, the overall stock that we estimated in Gambier cannot be really compared with any historical results, since only Zanini (1999) inferred a stock in Gambier, and only for two-sub-areas, which were concessions of Taku and Aukena belonging to the Wan farm. We note however that the stock was estimated at 10,000 ± 7,700 individuals for Taku and 580,000 ± 360,000 in Aukena, i.e. a total of 590 000 for the two zones (Table 4). This mean value is similar to our estimate (460,779 ± 152,883 individuals) that, however, was computed for the whole sampled lagoon, and not two sub-areas. It is therefore tempting to suggest that the overall stock has decreased since it is equivalent, and less, than what was found in 1995 in two concessions only.

Consequences for pearl oyster stock management

The atolls and island studied here displayed different pearl oyster densities, population size structures, and stocks that also all show variations in time at the decadal scale at least for Takapoto and Gambier. The abundance and status of a pearl oyster stock cannot be simply related and hierarchized based on some static macro-factors (e.g., lagoon size, presence of pass, etc.) considering for instance the sizes of Takapoto and Raroia, or the presence/absence of pass in our study sites. Other mechanisms and determinant factors are involved such as favorable habitats, depth, hydrodynamic processes, and, most likely but more difficult to track and characterize, the history of the sites (mass mortalities, periods without exploitations, periods of intensive exploitation, etc.). Therefore, it seems unrealistic to try to infer from our case studies a general model for all pearl farming sites that could predict stocks and their evolutions (and also spat collection which is the ultimate key issue) based on a series of simple variables. Instead, it seems more sensible to follow in the future a per-atoll approach that should include per-lagoon population dynamics monitoring, associated with the long-term monitoring of local environmental variables and, importantly, pearl farming activities themselves as the number of breaded pearl oysters is related to spat collection success. Management decisions could then be better optimized when some decisions are required.

In term of management, which actions can the French Polynesia pearl farming management entity (DRM) really take to help sustain spat collection? We list hereafter the actions that can be helpful based on our results. Obviously, these actions could be enhanced by the knowledge and monitoring of the farmed stocks, which is much larger than the wild stock, typically one or two orders of magnitude larger (Thomas et al., 2016). Despite its smaller size compared to farmed stocks, the importance of the wild benthic stock cannot be ignored since the study by Reisser et al. (2020) who suggested that only the wild stock contributed to spat collection. Management decisions can include:

1) Asses regularly (every 4 years) the population size structures, in order to monitor the arrival of new cohorts and the renewal of the wild population and assess its mortality. The monitoring could continue from a subset of the sites already surveyed here. A survey stratified by depth should also be necessary in order to help identify periods of changes in the population *vs* depth relationships, as they occurred in Takapoto between 1995 and 2021. In a short future, the monitoring of wild oyster stock will include a new site (Apataki Atoll) and revisit a previous site (Takaroa) after a mass mortality event occurring in 2013-2014 and where the stock is considered depleted.
2) Assess the actual sex ratio of the populations, especially the populations characterized by a small size dominance (Takapoto and Gambier, Figure 11). Updated per-lagoon curves relating age and growth/size, and the percentage of female-male reproductive material at different size-ages will be critical to infer the reproductive capacity of the stock (as done in Thomas et al., 2016 for instance). Changes in temperature regimes that are predicted with global warming are also most likely to affect growth and reproductive capacities differently per lagoon depending on their locations (Sangare et al., 2020), and updating the previous knowledge (Chavez-Villalba et al., 2011) seems sensible. The case of Gambier in particular should be a priority considering the importance of this site for the industry.

3) Promote restocking in lagoons where spat collection has lowered, and where there are signs of unbalance (with dominance of very large oysters like in Raroia, but also with small oysters like in Gambier) that need to be counteracted, or too low population abundance (as in Gambier). However, restocking decisions need also some information on larval dispersal for a variety of environmental conditions, such as wind regimes (André et al., 2022a), and not only knowledge of stock distribution and abundance. Evaluating how many oysters are needed is also a challenge. Trying to reach the historical levels, for instance pre-pearl farming, is impaired by the simple fact that we don't know what the past stocks were. Some extrapolations could be possible by trying to use shell exports data collected in the nineteen centuries during several decades (Intès 1982a). For this, several challenges exist, the first one being the conversion of bulk shell weight into number of individuals after assuming a size structure for the harvested specimen.
4) Unusual years of low spat collection could be related to inter-annual changes of environmental conditions rather than stock issues but deciphering the relative influence of both set of factors is possible only with time series of spat collection data, associated to stock and environmental variation knowledge (temperature, chlorophyll a, planktonic communities, etc.). These time-series do not exist thus far. This will be achievable only through the participation of farmers. DRM and farmers critically need to develop a partnership for data sharing, for the benefits of all.
5) In the case of recent massive mortalities, to be useful, restocking need to be performed only when the environmental conditions are again optimal, which may take years as in Takaroa Atoll (Monaco et al., 2021). However, the environmental monitoring and characterization is itself a challenging costly task in remote lagoons, and there are no real cost-effective solutions. Nevertheless, environmental monitoring of a series of key parameters (temperature, chlorophyll, plankton communities) remains a priority with *in situ* or remote sensing technology if doable (Van Wynsberge et al., 2017, 2020; Lefebvre et al., 2022). Obviously, identification of the reasons of the mortality (such as pathogens) should be tremendously useful.
6) Remarkable locations of high wild stock abundance, such as the sill between Mangareva and Aukena in Gambier need to receive attention from managers, and possibly protection. Activities that may affect these sites should be avoided or forbidden.

The series of aforementioned actions related to the management of the *Pinctada margaritifera* wild stocks are certainly challenges for DRM staff, for the farmers and for the scientists involved in this activity. These are only one aspect of the whole black pearl farming context, which also includes many other issues (such as lagoon pollution and clean-up, enhancement of pearl quality, climate change, etc.). The stock-related actions are however critical to plan for a sustainable pearl farming industry.

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