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Original Article

Understanding consequences of adaptive monitoring protocols on data consistency: application to the monitoring of giant clam densities impacted by massive mortalities in Tuamotu atolls, French Polynesia

Stéphane Georget[1], Simon Van Wynsberge[1‡], and Serge Andréfouët[2]*

[1]*Institut de Recherche pour le Développement, UMR 9220 ENTROPIE (Institut de Recherche pour le Développement, Université de la Réunion, Centre National de la Recherche Scientifique), 98713 Arue, French Polynesia*
[2]*Institut de Recherche pour le Développement, UMR 9220 ENTROPIE (Institut de Recherche pour le Développement, Université de la Réunion, Centre National de la Recherche Scientifique), 98848 Nouméa, New Caledonia*

**Corresponding author: tel: + 687 26 07 87; e-mail: serge.andrefouet@ird.fr.*
[‡]Present address: IFREMER, Unité de Recherche Lagons, Ecosystèmes et Aquaculture Durable, 98848 Nouméa, New Caledonia.

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During long-term monitoring, protocols suitable in the initial context may have to change afterward because of unforeseen events. The outcome for management can be important if the consequences of changing protocols are not understood. In Tuamotu Archipelago atolls, French Polynesia, the density of giant clams (*Tridacna maxima*) has been monitored for 12 years, but massive mortalities and collapsing densities forced to shift from a line-intercept transects and quadrats (LIT-Q) method to a belt-transect (BT) method. We investigated with a simulation approach the conditions (density, size structure, aggregation of giant clam populations) under which the two methods provided different results. A statistical model relating the BT density to the LIT-Q density was validated using new field data acquired on the same sites with both protocols, on two atolls. The BT method usually provided higher estimates of density than the LIT-Q method, but the opposite was found for very high densities. The shape of the relationship between measurements depended on population size structure and on aggregation. Revisiting with the model the historical LIT-Q densities suggested that densities have been underestimated in the past but previously detected trends in population trajectories remained valid. The implication of these findings for management are discussed.

Keywords: belt-transect, ecological monitoring, fishery, line-intersect transects, mass mortality, quadrats, sampling methods, time series, *Tridacna maxima*.

Introduction

In ecosystem and resource management, knowledge of long-term temporal trends of abundance, density, and size structure are needed to guide decisions (Hilborn and Walters, 2013). In fishery management, monitoring abundances is critical to pinpoint overexploitation (Worm *et al.*, 2009) and assess indirect or direct anthropogenic and climate change effects on resources (Koenigstein *et al.*, 2016). Long-term monitoring, however, can be affected by unforeseen events, which can impair the suitability of the initial sampling protocol. The need to adapt the sampling protocols to these changes may be even more acute when the monitoring objectives were very precise, aiming at detecting subtle changes. For instance, the detailed Level 3 protocol by Hill and Wilkinson (2004) to monitor coral reefs can be prone to frequent switches in sampling protocols to adapt to new conditions. However, the consequences of switching protocols on data quality and time-series consistency must be understood. In some instances, rebuilding coherent time series of fishery catches was problematic for this reason and became a huge effort (Léopold *et al.*, 2017).

In benthic density surveys, among the factors that drive the choice of sampling method stands density itself. Indeed, when density is high or patchy, methods that cover small areas are usually implemented (e.g. quadrat-based methods with generally a stratification factor, which can be for instance per habitat type, or depth, etc.). In contrast, when density is low, sampling methods that cover wide areas are required [e.g. manta-tow or long belt-transects (BT)]. For instance, in Indo-Pacific Islands, monitoring protocols for benthic invertebrates have covered a wide range of methods based on expected range of densities, aggregations, and habitat types (Andréfouët *et al.*, 2009; Kronen *et al.*, 2009). Methods for the same type of resource frequently varied spatially from one sampling area to another, posing sometimes comparison problems (Van Wynsberge *et al.*, 2016). For a given area, taxa that are affected by high and fast fluctuations of abundances over time (either naturally or human induced) can be problematic to monitor when the initial method becomes prohibitively time consuming, subject to biases, or too imprecise.

An example where adaptive monitoring was required was for monitoring giant clam (*Tridacna maxima*) density in Tuamotu Archipelago, French Polynesia. *Tridacna maxima* is a gregarious species, but the observed degree of aggregation is variable between lagoons (Gilbert *et al.*, 2006). Most giant clams monitoring protocols worldwide would use 50–100 m long BT considering the typical densities which are of the order of few tens of individuals per hectare (Van Wynsberge *et al.*, 2016). However, in the Tuamotu Archipelago, surveys performed in semi-closed atolls in the early 1970s, and then in 2004 and 2005 revealed densities reaching several tens or hundreds of individuals per square metre. The maximum was recorded in Tatakoto atoll at 544 ind.m^{-2} (Gilbert *et al.*, 2005). The BT method would have been too time consuming at such high densities. Therefore, short (20 m) line-intercept transects (LIT) and quadrats (Q) were jointly used to assess the stock in these high density areas (Gilbert *et al.*, 2006). This LIT-Q method (see "Material and methods" section for a comprehensive description) was initially suitable for a patchy distribution of resource, with high density patches. Unfortunately, densities in several lagoons collapsed in the wake of mass mortality events due to unusual weather conditions (Andréfouët *et al.*, 2013; Van Wynsberge and Andréfouët, 2017). After these events, maximum densities could reach only a few individuals per square metre at best, and preliminary trials suggested that the BT method was now more accurate than LIT-Q (Andréfouët, Wabnitz, Remoissenet and Van Wynsberge, unpublished data). Moreover, BT was not anymore a time-consuming affair. For consistency sake, revisiting surveys between 2012 and 2017 still used LIT-Q, but BT was used for new sites. However, the shift to a different protocol prompted to question the temporal and spatial consistency of the estimated densities. To understand the possible biases, we suggest that simulations and modelling should bring critical insights to reconstruct consistent time-series, as if they were performed only with BT.

In this study, we first investigate with a simulation approach whether the BT method and the LIT-Q method provide different density estimates depending on (i) the true value of the density, (ii) the giant clam aggregation levels, and (iii) the population size structure. Then, we investigated how the historical LIT-Q estimates could be corrected in order to be compared with recently acquired BT data. For this purpose, a statistical model that expresses the BT density as a function of the LIT-Q density was developed and validated by new field data acquired with both protocols. The historical estimates of two atolls are then revisited. We discuss the practical implications for management and, rather than recommending one method or another; we reinforce the idea that long-term monitoring should frequently question the validity of their protocol, especially through rigorous and innovative modelling.

Material and methods

Description of LIT-Q and BT sampling method

The BT method consisted of counting and measuring to the nearest centimetre every clam (N_b) located in a belt of 1-m width (l) and variable length (L; between 5 and 20 m in this study). The calculation of the density D_{BT} was straightforward from Equation (1).

$$D_{BT} = \frac{N_b}{L * 1} \quad (1)$$

The LIT-Q method combined LIT to estimate the percentage cover of living clams (C), with three quadrats of 0.25 m^2 (50 × 50 cm) placed on clams' patches along the LIT. When density of giant clams was very high along the entire transects (tens to hundreds of individuals per square metre as found in Andréfouët *et al.*, 2005), quadrat locations were near random. With the fall of densities (down to <1 ind.m^{-2}), quadrats had to be placed where giant clams could be found. Clams within quadrats were counted and measured to the nearest centimetre. $D_{LIT\text{-}Q}$ was calculated from Equation (2).

$$D_{LIT-Q} = C * \frac{\sum D_i}{3} \quad (2)$$

where D_i is the density calculated in quadrat i (ind.m^{-2}).

To avoid overestimating densities, clams overlapping BT and quadrat limits are only counted for two edges chosen beforehand.

Study sites and giant clam field sampling

Field data used in this study came from three semi-closed atolls located in Tuamotu Archipelago (French Polynesia): Tatakoto (18°39′S–139°36′O), Reao (18°30′S–136°22′O), and Fakahina (16°0′S–141°51′O) (Figure 1). Their lagoons (11.5, 44.1, and 17.8 km^2, respectively) are only connected to the ocean by way of several shallow channels that bisect half of the rim.

For each lagoon, giant clam surveys were performed at a number of stations. A station is defined as a set of transects (either LIT-Q or BT), located 5–20 m apart. The number of transects per station (usually 3 or 4) could vary between stations and between field trips.

Tatakoto atoll

In March 2017, the two sampling methods (BT and LIT-Q) were both used to estimate giant clam density for 37 transects (Figure 1, Table 1). This dataset is used for model validation purpose.

Regarding the historical reconstruction, several precautions were needed. Indeed, the initial survey of giant clams was performed in 2004. A stratified random sampling was used: stations were chosen randomly inside preliminary habitat classes identified by remote sensing. More details can be found in Gilbert *et al.* (2006). Sampling methods used for this initial survey were mostly

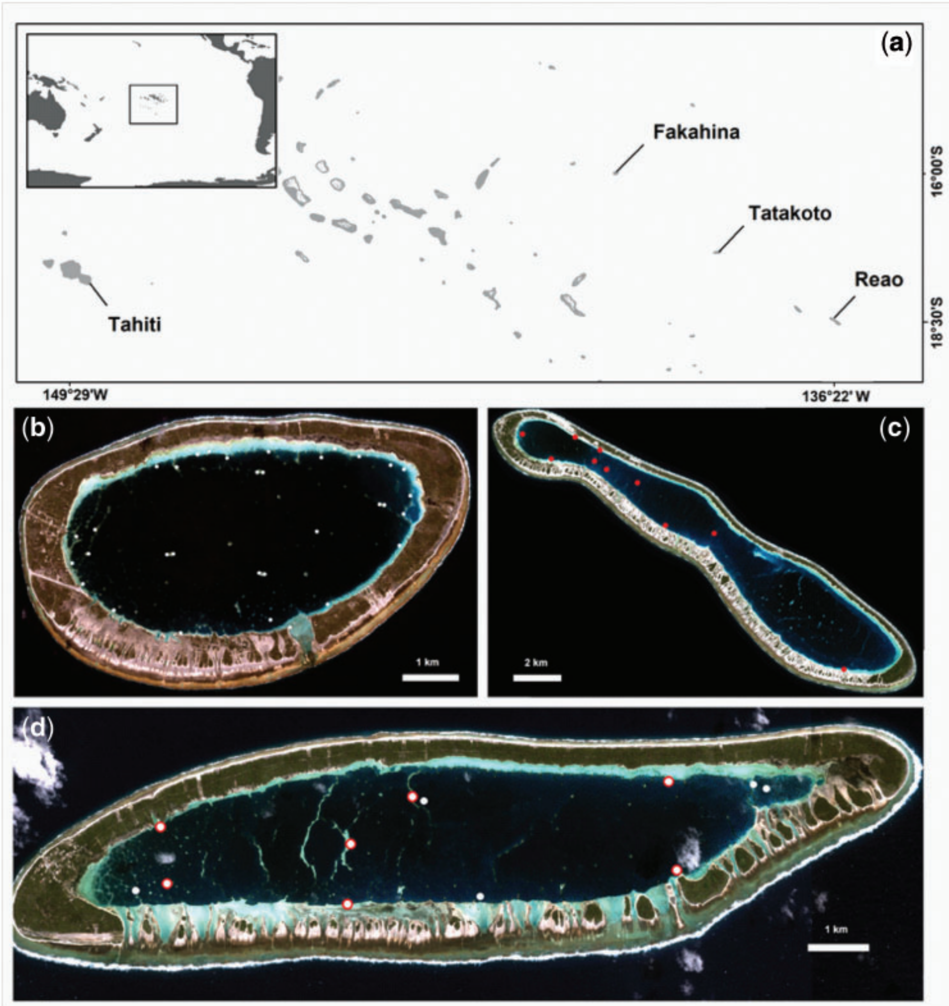

Figure 1. Site location and field sampling design for giant clam surveys. (a) Location of Fakahina, Tatakoto, and Reao in French Polynesia. (b–d) Satellite view of each atoll and sampling design for Fakahina (b), Reao (c), and Tatakoto (d). Red dots indicate stations repetitively sampled during the decade and used in this study. Triangles indicate stations repetitively sampled during the decade and used in this study. Circles locate stations where both methods were used during the same field trip. Hexagons refers to stations that cumulate properties of triangle-marked-stations and circle-marked-stations.

the LIT-Q method, except for some transects where the BT method was used (Supplementary Table S1). Subsequent surveys took place throughout the decade, using the LIT-Q method. Because of logistical constraints, including difficulties to bring scuba diving equipment on site, these subsequent surveys were performed only for a subset of the shallowest stations sampled during the first survey. In addition, new stations could replace previous stations due to specific new inquiries (e.g. estimating the recruitment in a given sector), thus the surveyed stations were not always the same as for the first survey (Supplementary Table S1). Therefore, to revisit the trajectory of historical densities, we selected seven stations that were consistently surveyed in April 2004, January 2012, November 2012, July 2013, October 2013, October 2014, and June 2016 (Figure 1). These stations were all located in the 0.5–2 m depth range, and were always sampled using the LIT-Q method.

Reao atoll

The first survey of giant clams at Reao was performed in 2005, with a sampling design following the method descried in Gilbert *et al.* (2006). The BT method was used for most stations, while LIT-Q was applied for the few others (Supplementary Table S2). A subset of stations sampled during the first survey was visited again in July 2010, December 2013, April 2016, and September 2016, but the sampling methods were not always similar to the initial survey (Supplementary Table S2).

For the historical reconstruction, we therefore selected ten stations that were consistently surveyed during all field trips (Table 1). These stations were all located in the 0.5–2 m depth range, and most of them are located in the north-western part of the lagoon (Figure 1). These ten stations and the five field trips represented 175 transects, among which 164 were sampled using the BT method, and 11 with the LIT-Q method.

Fakahina atoll

Fakahina was first surveyed in May 2017. The sampling design followed the method described in Gilbert *et al.* (2006), and involved the BT method on 48 stations (Supplementary Table S3).

Table 1. Field data used in this study to validate the statistical model described in "Modelling BT-density from LIT-Q-density" section.

Atoll	Field trip	Station	Method	Number of transects
Tatakoto	March 2017	13b_25_25	LIT-Q and BT	4
Tatakoto	March 2017	1b_16	LIT-Q and BT	2
Tatakoto	March 2017	20b_21	LIT-Q and BT	2
Tatakoto	March 2017	23b_30	LIT-Q and BT	4
Tatakoto	March 2017	25b_28	LIT-Q and BT	4
Tatakoto	March 2017	30b_15	LIT-Q and BT	3
Tatakoto	March 2017	31b_6	LIT-Q and BT	3
Tatakoto	March 2017	4b_19	LIT-Q and BT	3
Tatakoto	March 2017	8	LIT-Q and BT	3
Tatakoto	March 2017	11	LIT-Q and BT	3
Tatakoto	March 2017	14	LIT-Q and BT	3
Tatakoto	March 2017	17	LIT-Q and BT	3
Fakahina	May 2017	A01	LIT-Q and BT	1
Fakahina	May 2017	A03	LIT-Q and BT	1
Fakahina	May 2017	A04	LIT-Q and BT	1
Fakahina	May 2017	A05	LIT-Q and BT	2
Fakahina	May 2017	A06_A07	LIT-Q and BT	3
Fakahina	May 2017	A08	LIT-Q and BT	1
Fakahina	May 2017	A09	LIT-Q and BT	2
Fakahina	May 2017	A10	LIT-Q and BT	2
Fakahina	May 2017	A11	LIT-Q and BT	2
Fakahina	May 2017	A13	LIT-Q and BT	2
Fakahina	May 2017	A14	LIT-Q and BT	2
Fakahina	May 2017	A16	LIT-Q and BT	2
Fakahina	May 2017	A18	LIT-Q and BT	1
Fakahina	May 2017	A21	LIT-Q and BT	2
Fakahina	May 2017	A22	LIT-Q and BT	2
Fakahina	May 2017	A23	LIT-Q and BT	2
Fakahina	May 2017	A28	LIT-Q and BT	2
Fakahina	May 2017	A29	LIT-Q and BT	2
Fakahina	May 2017	A30	LIT-Q and BT	2
Fakahina	May 2017	A31	LIT-Q and BT	2
Fakahina	May 2017	A32	LIT-Q and BT	1
Fakahina	May 2017	A33	LIT-Q and BT	2
Fakahina	May 2017	A34	LIT-Q and BT	2
Fakahina	May 2017	A35	LIT-Q and BT	2
Fakahina	May 2017	A36	LIT-Q and BT	2
Fakahina	May 2017	A37	LIT-Q and BT	2
Fakahina	May 2017	A38	LIT-Q and BT	2
Fakahina	May 2017	A39	LIT-Q and BT	2
Fakahina	May 2017	A43	LIT-Q and BT	2
Fakahina	May 2017	A49	LIT-Q and BT	2

However, for 31 stations (55 transects), the two methods (BT and LIT-Q) were performed specifically for this study and to allow comparing the two methods.

Sampling simulations

All sampling simulations were performed in the R.3.3.2 environment (R Core Team, 2015).

Parameters considered in simulations

We tested the effect of three parameters on giant clam density estimates. First, we tested if the true value of density may affect the congruence of estimates provided by the LIT-Q and the BT methods, as suggested by preliminary field tests performed in November 2014 and November 2015 at Tatakoto. Second, we tested the effect of the size of individuals. Third, we tested the effect of the spatial aggregation of individuals, as other studies have pinpoint aggregation as a key parameter (Burnham *et al.*, 1980; Miller and Ambrose, 2000; McGarvey *et al.*, 2016).

Simulation of giant clam distributions along transects

Density estimation at transect scale using the LIT-Q and BT methods were simulated for 13 440 combinations of density, size structure, and aggregation configuration. For each simulation, clams were placed inside the sampling area (>10 m by 1m) at various densities and according to the selected size frequency distribution and aggregation level (Figure 2). Specifically:

- Twenty-four values were considered for density (i.e. from 1 to 20 ind.m^{-2} in step of 1 ind.m^{-2}, and 50, 100, 150, and 200 ind.m^{-2}), to cover most of density values encountered in historical surveys.
- Forty size frequency distributions were considered. These size frequency distributions were those observed during historical surveys performed at Tatakoto and Reao with the LIT-Q method.
- Aggregation was simulated by precluding clams to be randomly located throughout the total available area (A_s) by constraining them to be distributed only in a subpart (A_p) of the area (Figure 2a). In practice, we randomly placed in the area different numbers of 0.5m-radius circles (thereafter named "patches") inside which clams could be randomly positioned. From 10 to 90 patches (in step of 20 patches) were considered. An aggregation index I_a was defined. It is independent of density in order to discriminate the respective effect of aggregation and densities on estimates. We did not quantify aggregation with existing autocorrelation indices (e.g. Moran's or Geary's indices) because we found them unstable at low density (Supplementary Figure S1). Instead, the surface area covered by all patches (A_p) was calculated using the `gIntersection` and `gArea` functions of package `rgeos`. The aggregation level associated with each simulation was quantified by the index I_a from Equation (3).

$$I_a = 1 - \frac{A_p}{A_s} \tag{3}$$

I_a stands between 0 and 1. Values close to 0 corresponded to a random distribution (i.e. clams could be placed anywhere in the area) whereas values close to 1 corresponded to highly aggregated distributions (i.e. all clams were placed in the same part of the area).

Estimating density using BT and LIT-Q methods

For each simulated configuration of giant clam distribution, density was calculated using both BT and LIT-Q methods (Figure 2).

The calculation of BT density was entirely computerized by placing a 10m-long and 1m-wide rectangle in the centre of the sampling area and by enumerating clams in the rectangle using the `gIntersection` function of package `rgeos`, and Equation (1).

To calculate the LIT-Q density, a LIT was systematically placed at the centre of the area and the giant clam percentage cover [C in Equation (2)] was calculated using the `gIntersection` and `gLength` functions of package `rgeos`. The positioning of the

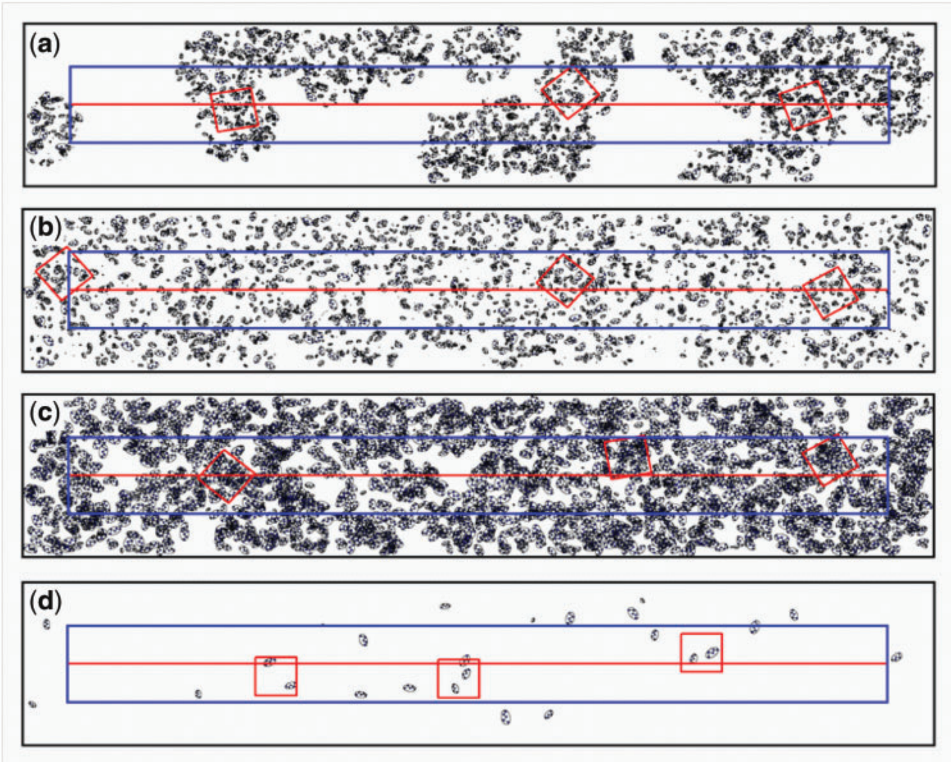

Figure 2. Example of four simulations among the 11 280 performed in this study. (a) Density in the area was set to 100 ind.m^{-2}, size frequency distribution was oriented toward small individuals, and clams were aggregated ($I_a = 0.46$). Estimating density with the BT method (D_{BT}; thick black line) and the LIT-Q method ($D_{LIT\text{-}Q}$; thin dashed line) provided estimates of 97.2 and 40.5 ind.m^{-2}, respectively. (b) Similar configurations than panel (a), but clams were randomly distributed ($I_a = 0.05$). D_{BT} was 100.2 ind.m^{-2} and $D_{LIT\text{-}Q}$ was 29.1 ind.m^{-2}. (c) Density was set to 100 ind.m^{-2}, size frequency distribution was oriented toward big individuals, and clams were randomly distributed ($I_a = 0.06$). D_{BT} was 98.2 ind.m^{-2} and $D_{LIT\text{-}Q}$ was 86.6 ind.m^{-2}. (d) Similar configurations than panel (c), except that density was set to 1 ind.m^{-2}. D_{BT} was 1.2 ind.m^{-2} and $D_{LIT\text{-}Q}$ was 0.18 ind.m^{-2}.

three quadrats was user-interactive using the `locator` function of package `graphics`. Quadrats were placed for each configuration independently by two users (SG and SVW). After several trials testing automatic quadrat placements following different rules, this interactive process was deemed the most efficient to simulate the behaviour of surveyors in the field. Density inside quadrats was calculated following the same protocol as for the BT, with $D_{LIT\text{-}Q}$ Equation (2).

Clams that overlapped the rectangle or quadrat limits (respectively for BT and LIT-Q quadrats) were included in the count only for respectively one and two of the borders to accurately replicate the field protocol.

Modelling BT density from LIT-Q density

To check if historical LIT-Q estimates could be corrected and expressed as BT data, we designed a three-step model that expressed BT density as a function of LIT-Q density.

Model structure and parameterization

Here, we describe how the model was parameterized on the basis of BT density and LIT-Q density estimated in controlled conditions (simulations). Given the non-linear relationship between BT density, LIT-Q density, and I_a that we achieved in preliminary tests (see also "Results" section), we expressed BT density as a function of LIT-Q density and I_a on the basis of a generalized additive model (GAM) using the `gam` function of package `mgcv` [Equation (4)]. Because size structures were also found to influence results, a specific model was fitted for each simulated size structure.

$$D_{BT} \sim s(D_{LIT-Q}, k = 15, \quad bs = \langle\langle \text{ cr } \rangle\rangle) + te(D_{LIT-Q}, I_a) \quad (4)$$

Where $s()$ is a smooth function defined by a degree of freedom k. The $bs =$ "cr" argument indicates that a cubic regression spline function was used, to allow for a more complex curve shape. This was suitable for the low LIT-Q density values that were more present in our sample scheme. A coercion parameter te [see Wood (2017) for details] was also included to take into account the interaction of $D_{LIT\text{-}Q}$ and I_a in the model.

Model validation

To evaluate if the model parameterized on the basis of simulated data can be reliably used to correct density estimated in the field, we compared the values of D_{BT} estimated by the model and D_{BT} estimated in the field, for similar conditions of $D_{LIT\text{-}Q}$, and size structure. This validation step was based on transects for which the two methods were performed, in Tatakoto (37 transects) and Fakahina (55 transects) (Figure 1, Table 2). For aggregation, no quantitative estimation of I_a was routinely performed in the field, hence the value of I_a in Equation (4) was set to a fixed value that

Table 2. Field data used to monitor giant clam densities along the decade at Reao.

Stations	Aug. 2005	July 2010	Dec. 2013	Apr. 2016	Sept. 2016
S48	BT	BT	LIT-Q and BT[a]	BT	BT
S45	BT	BT	LIT-Q and BT[a]	BT	BT
S44	BT	BT	LIT-Q and BT[a]	BT	BT
S43	BT	BT	LIT-Q and BT[a]	BT	BT
S41	BT	BT	BT	BT	BT
S39	BT	BT	BT	BT	BT
S33	BT	BT	BT	BT	BT
S30	BT	BT	BT	BT	BT
S26	BT	BT	BT	BT	BT
S12	BT	BT	BT	BT	BT

Data sampled with the LIT-Q method were corrected using the statistical model described in "Modelling BT-density from LIT-Q-density" section.
[a]The two sampling methods were used on different transects.

remained the same in all subsequent analyses. This value was set so that model output fitted the best with field densities globally, over all simulations.

For each size structure, the model was used to estimate D_{BT} from observed $D_{LIT\text{-}Q}$. This modelled BT density ($D_{BT,pred}$) was then compared with the measured BT density ($D_{BT,obs}$) by a coefficient of determination denoted R^2 and calculated from Equation (5).

$$R2 = \frac{\sum(D_{BT,obs} - D_{BT,pred})2}{\sum(D_{BT,obs} - D_{BT,obs})} \quad (5)$$

Revisiting historical densities

The model was first parameterized with simulated data (see "Model structure and parameterization" section) and validated with *in situ* data (see "Model validation" section), then it was used to revisit the historical LIT-Q densities estimated at Tatakoto and Reao. For each transect surveyed during the past decade, the size structure was extracted and the `predict.gam()` function of `mgcv` package was applied to the historical LIT-Q densities. Aggregation was unknown in the historical surveys, and was set constant following the method described in the previous section.

Results

Modelling BT density from LIT-Q density

Simulations of giant clam distributions and sampling methods yielded BT and LIT-Q densities that were different for a given configuration. Interestingly, the shape of the relationship between D_{BT} and $D_{LIT\text{-}Q}$ was not linear: the BT method usually provided higher estimates of density than the LIT-Q method, but the opposite was found for very high densities (>100 ind.m^{-2}, Figure 3). Very different shapes were also found depending on size structures (Figure 3). Aggregation also influenced the relationship and the two methods agreed more in the case of high aggregations.

Model predictions agreed better with field data when I_a [see Equation (4)] was set at 0.8. For 70.2% of the historical size structures that were simulated, the observed value of D_{BT} fell in the prediction interval of the modelled D_{BT}. For 6.4% of the cases, the model overestimated density, and for 23.4% it underestimated field values. Overall, the model explained 76.5% ($R^2 = 0.765$) of the D_{BT} variance measured during fieldwork.

Revisiting historical densities and collapse

The modelled historical densities were significantly higher than the field values for all the Tatakoto surveys and the Reao survey of December 2013 (Mann–Whitney test, $p < 0.001$) (Figure 4). These results suggest that densities have probably been underestimated at Tatakoto and Reao between 2004 and 2013. However, even after adjustments, the collapse of density evidenced at Tatakoto by previous studies remained comparable. Previous LIT-Q data yielded a 98% decrease overall for the entire lagoon between April 2004 and June 2016, while the adjusted value suggested an 86% decrease for the subset of historical transects considered for this analysis.

Discussion

Differences of densities found between methods and explaining factors

According to our results, the BT method and the LIT-Q method could provide sensibly different density estimates under certain conditions. As expected from field observations, the difference between the two methods was greater for low densities. The primary explanation is that giant clam cover along the LIT [parameter C in Equation (2)] is underestimated at low densities. Ultimately, for very low densities, the giant clam cover was frequently nil because the LIT did not overlap any clam. Conversely, simulations suggested that LIT-Q densities were higher than BT densities for very high densities and high cover. This was not foreseen from field work. Based on our field experience, it is possible that at such very high densities, the surveyor just targeted very high density areas to lay his quadrats, not necessarily the highest density spots. In our simulations, the whole area is visible on screen, and it seemed less a problem for the two operators (SG and SVW) to precisely identify on the computer screen the locations of the highest densities and lay the quadrats there.

The size of giant clams also partly explained the lack of agreement between methods. This is rather easily explained as large individuals tend to increase cover [C in Equation (2)] more than small individuals. To the best of our knowledge, the potential bias induced by size of individuals on cover estimates has not been addressed in the literature, likely because cover is a metric used for estimating the relative proportion of benthic components (e.g. coral cover, algae) and more rarely used for estimating species abundance. The use of cover to infer abundance [Equation (2)] was of particular concern to us because long-live bivalve species such as giant clams continue to grow until death and sampled individuals could measure anywhere from 1 cm to several decimetres.

Finally, spatial aggregation is also a well-known factor challenging the reliability of sampling methods (Burnham *et al.*, 1980; Miller and Ambrose, 2000; McGarvey *et al.*, 2016). Our study evidenced the potential effect of aggregation on LIT-Q density estimates. We found that for densities <100 ind.m^{-2}, high aggregation tends to reduce the difference between the LIT-Q and the BT methods. This is probably because in the LIT-Q method, quadrats are not randomly placed, but target dense patches of giant clam. The more the clams are aggregated, the higher the density in quadrats, and thus the higher the LIT-Q density. Differences between the LIT-Q and the BT methods are reduced for density <100 ind.m^{-2}, but increases when density is very high (>200 ind.m^2) (Figure 3).

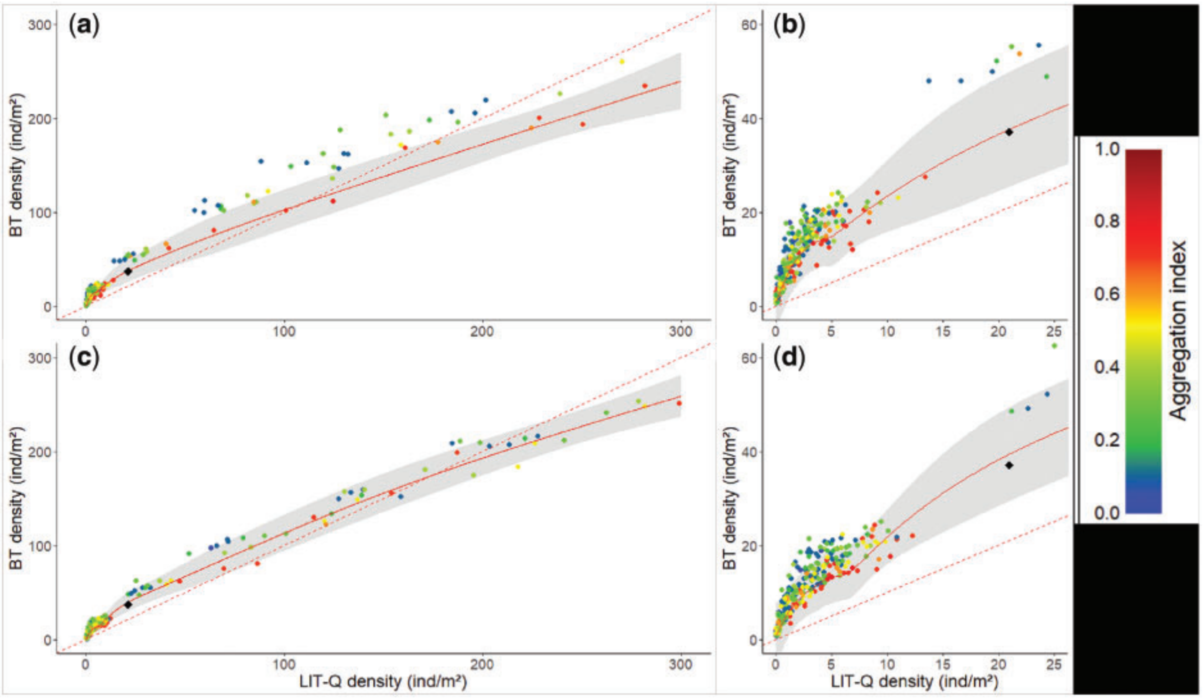

Figure 3. Comparison between LIT-Q and BT densities for two size structures among the 40 historical size structures used in this study. Plots (b) and (d) are enlargements of plots (a) and (c), respectively for low densities (from 0 to 25 ind.m^{-2}). Coloured points are the result of simulations (see "Study sites and giant clam field sampling" section). The colour of each point is reflecting the aggregation index [I_a, see Equation (3)] considered for the simulation. The dashed red line (equation $y = x$) indicates equality between the two methods. The black square corresponds to the field data obtained for the size structure considered. The red line is a smooth line obtained by the GAM for I_a = 0.8, which has been selected for estimating historical densities (see "Sampling simulations" section). The prediction interval associated is represented by the grey area.

To date, only few studies have attempted to design sampling protocols adapted for aggregated populations (Paschoal *et al.*, 2013). Smith *et al.* (2003) tested the relevance of adaptive cluster sampling methods for aggregated populations of freshwater mussel populations along the Cacapon River, West Virginia. They found that the efficiency of the method decreased with increasing density. Thus, Smith *et al.* (2003) recommended this method for rare populations only. These adaptive cluster sampling methods cannot be recommended for monitoring giant clams in Tuamotu Archipelago, where densities are high compared with freshwater mussel populations. Kermorvant *et al.* (2017) compared a stratified random sampling St(RS) with a spatially balanced generalized random tessellation stratified (GRTS) design for monitoring aggregated manila clams in Arcachon Bay, France. The authors recommended the use of GRTS for bay-scale assessments. Our study focused on method comparison at transect scale only, not at lagoon-scale, but Kermorvant *et al.* (2017) results could be used to monitor giant clams at lagoon scale. In our case, the stratification is based on habitats mapped using satellite imagery and depth (Andréfouët *et al.*, 2005). The distribution of sampling sites within each strata could be provided by GRTS.

Can we accurately correct the historical LIT-Q estimates?

This study combined simulations with field data to calibrate and validate a model that predict BT density from LIT-Q density. Field data alone could not offer an exhaustive dataset to establish a reliable statistical model, especially for some configurations observed in the past but vanishing due to mass mortalities (e.g. densities >300 ind.m^{-2} and size structures dominated by small 1–4 cm individuals) (Van Wynsberge and Andréfouët, 2017). The simulation approach was not limited by these constraints and allowed modulating the different factors independently of each other and understand their respective effects. However, confronting model outputs with actual field data was required to validate the model. The agreement between model predictions and field data ($R^2 = 0.765$) was deemed sufficiently satisfactory to use the model for correcting historical LIT-Q densities.

Despite these encouraging results, our modelling approach encountered several difficulties. First, because of time constraints, simulations could only be performed for 40 size structures encountered in field data, but not for all of them. For validation, we therefore compared model prediction and field data that had close, but not exactly the same, size structures. It is expected that the accuracy between model predictions and field data will increase after that all observed size structures can be simulated.

Second, the aggregation index could not be estimated *in situ*. Aggregation was set to maximize the adequacy between model prediction and field data. This process provided an estimation of 0.8 for the aggregation index. While this value is not unrealistic, the model would certainly gain in accuracy if aggregation could be quantified during fieldwork. Quantifying the extent by which individuals are aggregated is rarely integrated in sampling protocols and to our knowledge, few methods are proposed [but see McGarvey *et al.* (2010)].

Finally, owing to an interactive procedure, the simulation approach implemented in our study reproduced and formalized the

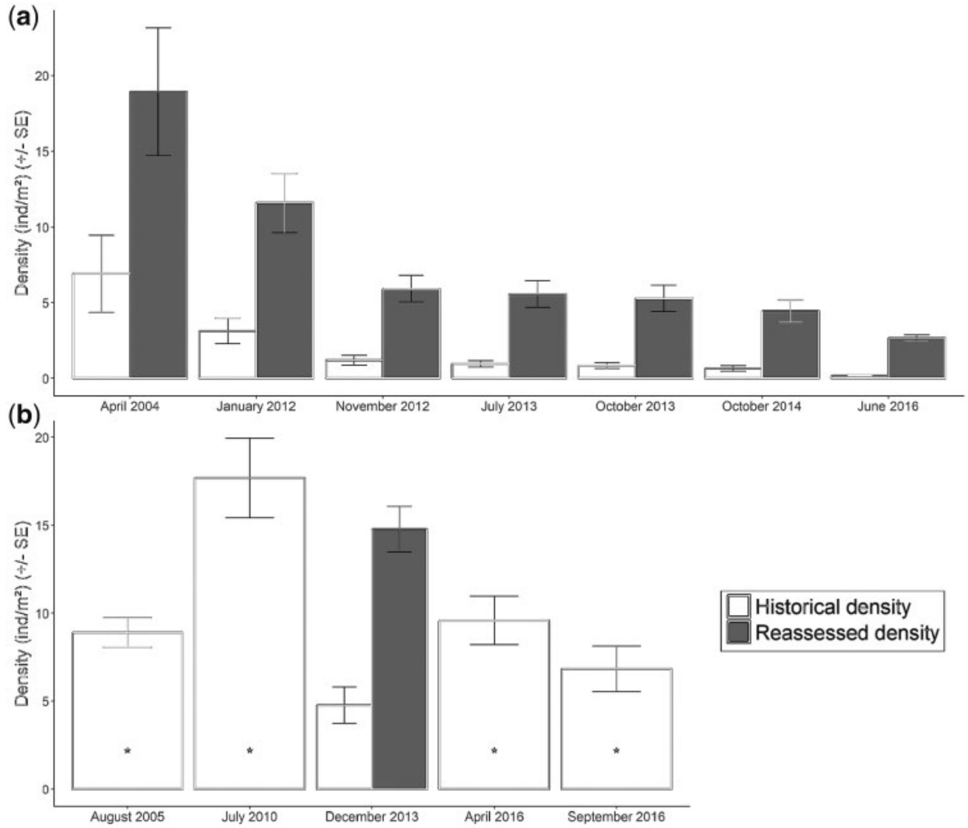

Figure 4. Barplot of historical (white bar) and reassessed (dark-grey bar) clam densities (±standard error) for the two atoll lagoons studied (Tatakoto and Reao, respectively, a and b) and for each sampling campaign considered. The "*" symbol in white bars indicates that BT method was used hence densities were not corrected. For each sampling campaign and atoll, the corrected density appeared significantly higher than the historical density (Mann–Whitney test, $p < 0.001$).

behaviour of surveyors when they choose haphazardly the location of quadrats. It is difficult to ascertain if the interactive on-screen selection of quadrat location mimicked exactly the behaviours during *in situ* surveys, but we believe it is close considering our results. This computing modelling approach for haphazard sampling site selection is an interesting alternative when straightforward methods for random sampling [see Smith *et al.* (2017) for a review] could not be used.

Consequences for giant clam fishery management

Tatakoto atoll

During the past decade, giant clam densities and stocks at Tatakoto were used to model population dynamics and predict the sustainability of the fishery under various management strategies. Management measures included no-catch closure area, size limitation, and quotas (Van Wynsberge *et al.*, 2013, 2018). The latest population model was initialized with stocks falling in the 2004 stock confidence interval, and was validated on the basis of densities estimated during the January 2012, November 2012, October 2013, and October 2014 field trips. In the present study, we highlight that giant clam density may be higher than previously expected by a factor from 2.5 to 12 depending on the field trip considered (Figure 4). Clarifying precisely the extent by which these differences in densities (and stock) may have changed the overall population dynamics is not a trivial task, but there is a very limited probability that the main previous findings for Tatakoto could be discarded. There are two reasons for this.

First, each scenario considered in the stochastic population model developed by Van Wynsberge *et al.* (2018) involved 100 simulations, each holding different values of initial stock (but still falling in the 2004 stock confidence interval). The results were very consistent across simulations.

Second, the main conclusions of Van Wynsberge *et al.* (2018) were that quotas were the most effective management measure to slow down the decrease of giant clam stocks at Tatakoto, whereas closure areas were the least effective. The effectiveness of closure area was poor in this context because closing areas only displaced fishing effort to adjacent open areas. Displacement had a negligible effect on stocks since they remained high at Tatakoto compared with the fishing pressure. These conclusions were mainly driven by the high density context found at Tatakoto, and thus, they are likely to remain valid when considering the corrected (and highest) densities of giant clams provided here.

Reao atoll

During the past few years, management measures at Reao were less strict than at Tatakoto, because the decline of densities did not appear to have the same magnitude as in Tatakoto. However, after correcting the December 2013 LIT-Q densities, the decreasing trend from 2013 to 2016 became more significant and worrisome. The decrease of densities in 2016 was triggered by a bleaching event that has been well monitored and documented by local inhabitants and the local fishery department, and in the scientific literature as well (Van Wynsberge and Andréfouët, 2017; Andréfouët *et al.*, 2018). The present study suggests that densities decreased by 35% between December 2013 and April 2016 for the subset of stations that we have considered for the reconstruction. If this decreasing trend is confirmed, additional management measures may be required.

Lessons learned

The objective of this study was not to determine which method (either LIT-Q or BT) should be preconized for long-term monitoring. Instead, this study aims at reinforcing the idea that long-term monitoring should question the validity of their protocol on the long run (Figure 3) especially if some conditions (density, size structure, aggregation) have changed. Coupling simulations and field work can help understanding the possible biases.

The long-term monitoring of giant clams in Tuamotu Archipelago brings lessons that can be of interest for other resources monitoring. In practice, for many, often data poor, insular fisheries, quotas are frequently set on the basis of a percentage of stocks. These decisions are strongly dependent on the sampling method used. For Tatakoto, absolute values of density were affected by the method used but the temporal trends, in contrast, remained similar. Therefore, formulating management decision on the basis of temporal trends instead of the most recent absolute estimation of stocks seems sensible.

Second, we encourage population model studies to systematically perform sensitivity analyses and assess the effects of a possibly underestimated or overestimated density and stock.

Third, it seems that correcting surveys *a posteriori* is not optimal and greater effort should be deployed *a priori* to test the validity of a new method, and the effects of density, size, aggregation, or other population parameters that could be relevant for the case at stake. Despite the advantages, testing methods by simulation is not trivial. It requires dedicated, costly, and time-consuming field sampling with multiple sampling to include each methods, programing skills and, non-trivial and sometime laborious modelling steps. Keeping in mind that each survey may potentially be the first of a long time series (even if not planned at the time) it will help design protocols that take the population parameters into account. Here we demonstrated that the LIT-Q method became biased for estimating densities for some configurations due to inaccurate estimation of giant clam cover along the LIT. The LIT-Q method is therefore not recommended, except for very high densities. This conclusion probably applies to other methods that use cover to infer abundance. Considering the decrease of densities that occurred during the past decade at the studied sites, the BT method is now recommended for future surveys of giant clams at Reao and Tatakoto.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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