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A systematic prioritization approach for identifying suitable pearl oyster restocking zones following a mass mortality event in Takaroa Atoll, French Polynesia

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Abstract :

Oyster farming for black pearl production is central in French Polynesia. It is the second source of national income and provides substantial job opportunities, notably in remote atolls. However, this sector has been undermined by successive crises, such as mass-mortalities of wild and farmed oyster stocks that have impacted entire lagoons. An option to revive the activity consists of reintroducing oysters in strategic benthic locations selected to maximize reproduction and dispersal of larvae throughout the lagoon, hence promoting recolonization and spat collection for farming. For Takaroa, a Tuamotu atoll recently impacted by mortalities, a systematic prioritization approach identified these restocking sites, using environmental and socio-economic criteria such as: location of suitable habitats for oyster settlement, larval connectivity estimated from hydrodynamic circulation model, farming waste accumulation, and opportunity cost to fishers and farmers who lose access to restocking areas. This approach provides managers with a portfolio of restocking options.

Highlights

► Identification of pearl oyster restocking zones after a mass mortality event ► Spatial criteria uses connectivity, depth, fishery and pearl farming attributes. ► Systematic planning offers solutions for aquaculture management strategies. ► Systematic planning is a decision support tool useful for remote lagoon management.

Keywords : Spatial planning, Marxan, Connectivity, Aquaculture, Pinctada margaritifera, French Polynesia

1 Introduction

In French Polynesia, the farming of the *Pinctada margaritifera* black-lipped oyster for black pearl production is an important component of the economy, particularly for remote atolls where this sector is the main source of employment and income in households (Le Pennec et al., 2009). In Tuamotu-Gambier archipelagos, one in two people live from the pearl industry, fishery or coprah exploitation (ISPF, 2018) despite it has been weakened by successive economic and production crises (IEOM, 2020). This sector is also exposed to a number of environmental drivers and mass-mortality events. The latter are likely of multi factor origins, including, high sea surface temperature, low wave energy and low wind speed, as characterized for several semi-closed lagoons (Andréfouët et al., 2015). These conditions can promote anoxia in the deeper layers of the lagoon water column, phytoplanktonic blooms or thermal stress for oysters.

The process of oyster farming in Tuamotu Gambier classically starts with spat collection to allow the provision of *Pinctada margaritifera* oysters. Then, juvenile oysters are reared until they are large enough for grafting. Eventually, it is possible to harvest black pearls from the grafted oysters. The whole process takes at least 3 to 4 years in the fastest pace. It is expected that both farmed and wild oyster stocks yield spats, although according to recent studies in Ahe Atoll (Andréfouët et al., 2021; Reisser et al., 2020), spats seem to be originating from the wild stock only. In any case, in atolls impacted by massive mortalities, neither the farmed nor the wild stock will no longer contribute to spat collection if both populations are gone.

At the very beginning of the black pearl industry in French Polynesia, Takaroa Atoll (Tuamotu Archipelago) (Figure 1) was once one of the most productive lagoons in terms of both pearl and spat production, with as many as 81 million spats or oysters exported to other lagoons between 1985 and 2015 (DRM, unpublished data). Mass-mortality events in this atoll were first recorded in 2000-2001 among farmed oysters in shallow water (Andréfouët et al., 2015). In 2013-2014, mortalities occurred massively among both farmed and wild oysters at all depth. This led to a quick decline of farming activities and a 24% decrease in the local population between 2012 and 2017 (census data from ISPF, 2017), owing to the lack of economic opportunities. Seven years after the mortality, as in 2021, the farming activity remains moribund, with *in situ* monitoring of farmed oysters suggesting slow growth (~0.04 $mm.d^{-1}$, less than half the expected growth) and relatively low reproductive effort (Monaco et al., 2021). Nevertheless, there are good signs of recovery as all oysters brought into the lagoon remain alive and grow, and it is expected that spat collection could take place again, provided that enough mature adult oysters, male and female, are able to spawn in the lagoon.

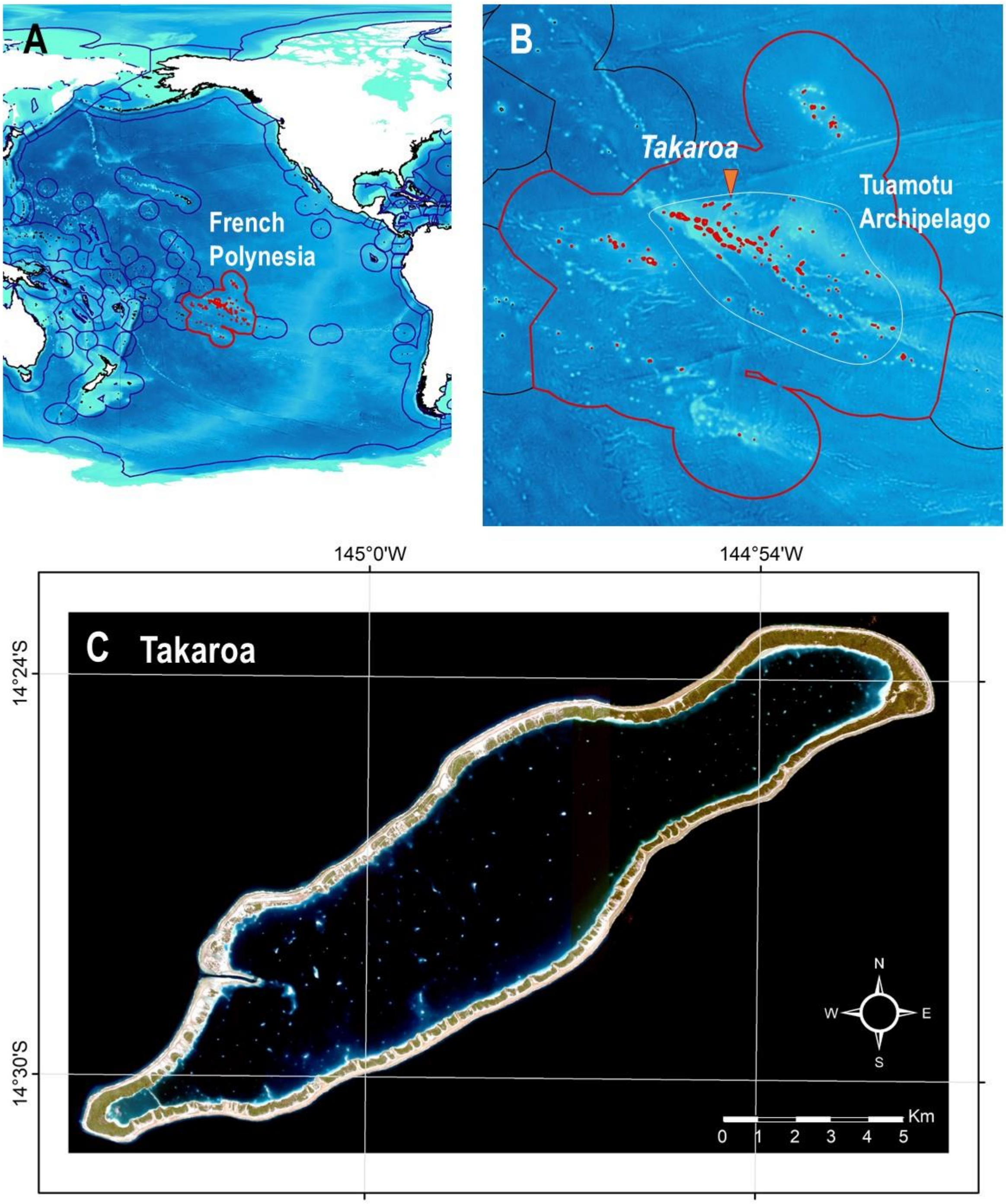

Figure 1. Maps of the study site. (A) French Polynesia economic exclusive zone in the Pacific Ocean; (B) Location of Takaroa Atoll in the Tuamotu Archipelago; (C) Takaroa Atoll. Source of Ocean bathymetry: ETOPO1 (2011), source of Quickbird satellite image: DigitalGlobe (now Maxar) 2008.

In order to revitalize the wild stock and eventually, strengthen the potential for spat collection in Takaroa, it has been suggested to restock the lagoon by either using imported adult oysters from healthier and productive atolls, in particular the neighboring Takapoto atoll, and/or releasing available adult farmed oysters after pearl production. Restocking is a process that has never been thought for entire atolls thus far. It will consist in placing enough oysters of various sizes and ages to create high density patches of oyster population of balanced sex-ratio, at the bottom of the lagoon in suitable areas. A number of *a priori* criteria need to be considered to define and search for the best suitable sites. These are:

i) Selected locations should maximize chances of settlement and survival of restocked oysters at suitable depth range. The different locations for restocking should represent the areas where natural stock was present before the mortality, and also be able to collectively resist to environmental disturbances. This latter criteria means in particular having oysters in a variety of depth zones, with some populations less vulnerable to anoxia and others less vulnerable to overheating in shallow waters;

ii) Selected locations should maximize larval dispersal and spat collection potentials throughout the lagoon. This means that restocking areas should include the best source areas able to maximize connectivity with all lagoon sectors in standard hydrodynamic conditions of dispersal;

iii) If they are seen as sanctuaries, selected locations can be forbidden to other usages by legal decree, therefore they should also avoid impacting important existing activities as much as possible, in particular fishing, which is very important for food security and recreational activity in this remote atoll. Tourism and related recreational lagoonal activity are not present in Takaroa.

iv) Conversely, selected locations should be naturally suitable for oysters to grow, away from human disturbances, including farming itself which modifies the substrate through waste accumulation, moorings etc. Wastes generated by pearl farming have become a significant issue. Indeed, spat collection and adult oyster rearing require a significant amount of immersed equipment such as lines, ropes, buoys, baskets, *etc.*, that eventually sink and are lost if not regularly maintained. As in many pearl farming lagoons, such as the Ahe Atoll (Andréfouët et al., 2014), in three decades, Takaroa lagoon has accumulated significant amounts of waste that have sunk at the bottom of the lagoon, as evidenced in a survey coordinated by the technical service in charge of pearl farming management, *Direction des Ressources Marines* (DRM). For restocking, it is necessary to avoid areas with high presence of wastes because these wastes are subjected to movements in case of storms, and are likely to tear out benthic organisms, including transplanted ones. Cleaning of these areas by DRM and the farmers may also be detrimental to restocked populations if they end up among or on top of derelict gears, a situation that we have observed (SA, pers. obs).

The aforementioned list of criteria to select restocking locations refers to both areas to include or avoid. The choice of best restocking locations can therefore be formalized as a spatial optimization problem that can be well tackled with spatial systematic prioritization tool. The relevant data on environmental parameters and socio economic uses of the lagoon were collected during a survey carried out in Takaroa in 2019 or made available through previous studies. Hereafter, we detail the different data sets collected for Takaroa Atoll and the spatial planning scenarios. The results are discussed more broadly in terms of pearl farming management perspectives, for Takaroa and beyond.

2 Material and methods

2.1 Study site

Takaroa is one of the most northwestern atolls in the Tuamotu Archipelago, located at 14.27°S latitude and 145°W longitude (Figure 1). The lagoon has a 86 km^2 surface area, with a maximum and average depths of 47.5 m and 25 m, respectively (Andréfouët al., 2020). It is a semi-closed atoll, as its only connections to the ocean are a single narrow 170 m-long and

20 m deep straight pass, and multiple '*hoa'* (local name for shallow water passages between the ocean and the lagoon, across the atoll rim). The only village is located near the pass and accounts for the majority of the 674 inhabitants based on the 2017 census (ISPF, 2017). Among them, 480 persons are in the 10-60 age group, which corresponds to the potential fishing-age population.

2.2 Data mobilized for Takaroa Atoll

In this study, the environmental parameters considered were: i) the lagoon bathymetry, ii) oyster distribution before the 2013 mortality, iii) the known locations of waste accumulations and (iv) the lagoon areas that represent the best spawning sources able to disperse larvae throughout the entire lagoon. As for socio-economic parameters, we based our analysis on v) the artisanal fishing activity inside the lagoon) and vi) the most recent map of oyster farm concessions. All these necessary data layers are detailed hereafter.

Bathymetry

Lagoon bathymetry was previously surveyed using a mono-beam sounder, and a gridded product at 60 m resolution was interpolated, refined with the positioning of the very shallow top of pinnacles (locally called '*karena*') that could not be directly surveyed but were identified on very high resolution satellite imagery at 2.4 m resolution (Figure 1C). The bathymetric product is described in Andréfouët et al. (2020).

Wild oyster stock distribution and suitable depth

In Takaroa, dive surveys undertaken in 2013 estimated the wild oyster stock to be one million individuals (Andréfouët et al., 2016). Using the bathymetry data presented above, the stock density measured *in situ* at 22 stations were then generalized to the entire lagoon according to a depth-density relationship. The highest abundance of wild stocks was found between 5 m and 25 m deep, so this depth range was then used to represent suitable habitat for oysters in this study, including lagoon slopes covered by sand or hard bottoms as well as isolated coral pinnacles in the deep lagoon. Including the full depth range of oyster occurrences, either living on soft or hard-bottoms, has also the potential to limit the effect of the disturbances that can affect oysters according to their depth. While a mass mortality, (following a phytoplanktonic bloom for instance as the one that occurred in 2013-2014), can kill oysters at all depth, other processes, such as surface warming or deep anoxia can result in more depth-specific effects.

Distribution of artisanal fishing grounds

Map-based fishery surveys were conducted with 44 active and regular fishers in August 2019, in order to map and quantify fishing catch, following the methodology described in André et al. (2021b). In short, fishers individually answered a targeted questionnaire to locate all their fishing grounds on a high spatial resolution satellite image-derived map. For each fishing ground, the temporal frequency of fishing activity and amount of catches were documented. Answers were compiled, mapped and analyzed using Geographical Information Systems (GIS) tools, to infer an estimate of the annual yield per fishing ground.

Hydrodynamic model and connectivity matrices

Characterizing the connectivity of marine species in water bodies, through the biophysical modelling of larval dispersal has become a useful approach in spatial ecology and spatial planning, and it has been applied in Tuamotu atoll lagoons since about a decade (Thomas et al., 2012a, 2014; Andréfouët et al., 2021). A previous study has focused on modelling the hydrodynamic circulation within Takaroa lagoon, according to tide and wind regimes (Tedesco, 2015). The model architecture and specifications were similar to those described for Ahe Atoll by Dumas et al. (2012) and Thomas et al. (2014). In short, the lagoon hydrodynamic model has a spatial resolution of 100 m. It encompasses the entire lagoon, the rim and most of the external slope. On the vertical axis, 23 sigma layers were distributed to represent both the bottom and the surface boundary layers.

Using ERA-Interim data from January 1979 until December 2011, Thomas et al. (2014) described the main wind regimes occurring during a 30-day period for the north-western Tuamotu. A total of 12 wind regimes represented the overall variability appropriately. These regimes mostly have an eastern direction, although average speed and frequency of occurrences vary (Thomas et al., 2014). During these regimes, hydrodynamic simulations by Tedesco (2015) show that the lagoon is structured in two main gyres separated by a jet from the pass during rising tides (Figure 2A). For our objectives, we considered the dominant wind regimes, and considered a subset of regimes covering the wider range of mean wind direction (Figure 2C), but acknowledge that the hydrodynamic pattern may change during short-term conditions (Tedesco, 2015). The wind regimes 3, 8, 9 and 12 were selected from Thomas et al. (2014) and used to estimate larval dispersal and connectivity.

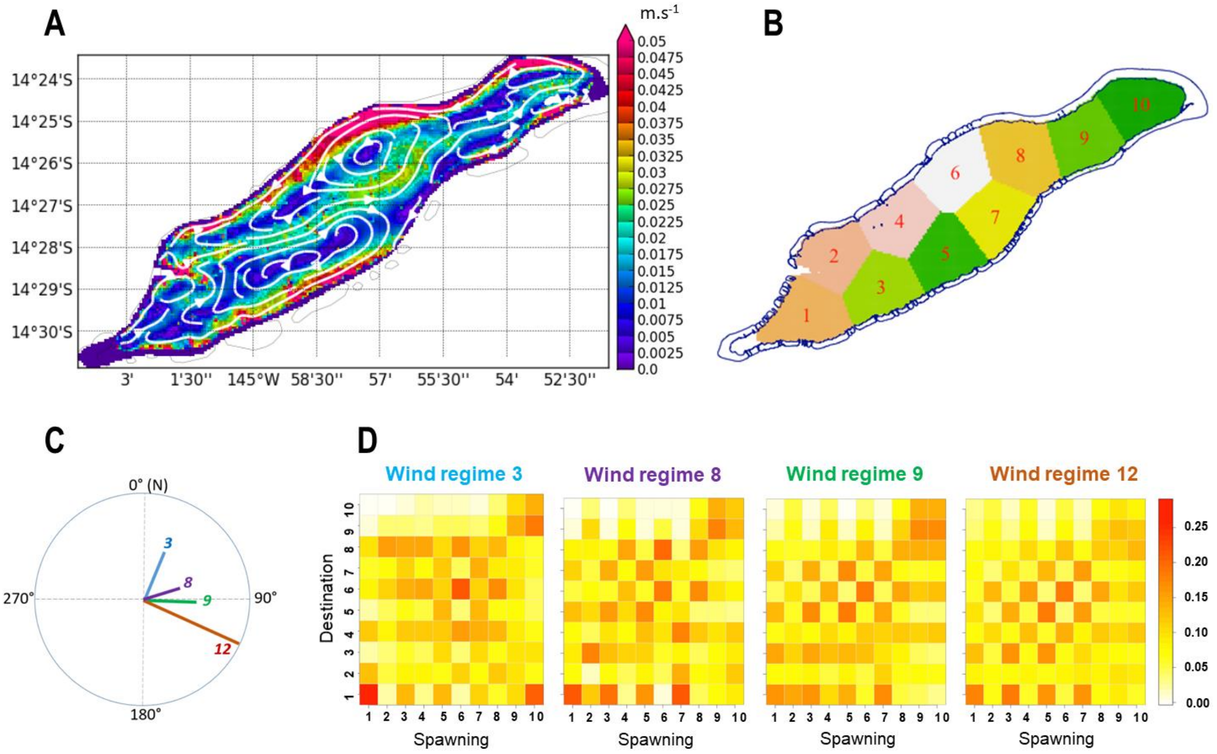

Figure 2. Hydrodynamic circulation modelling and connectivity matrices in Takaroa. (A) Representation of depth-averaged current speed (color bar, m.s^{-1}) and direction (white line) considering a trade wind regime direction 107 degrees, speed 6 m.s^{-1} blowing for 30 days. Two circulation cells dominate the circulation, anticlockwise in the north and clockwise in the south. Note that the highest speed is along the edge of the atoll rim, which should promote higher dispersal from these areas. (B) Ten sub-zones in the lagoon are defined to compute connectivity between each of them. (C) Simplified wind rose representing the mean direction and speed of the four representative wind regimes (3, 8, 9 and 12 as described in Thomas et al. (2014)). Circle radius = 7.6 m.s^{-1} or the mean wind speed of regime 12. The direction of the wind is from the external tip of the trait towards the center, hence all regimes are east dominant, with north (regime 3) to south (12) variations. Connectivity is computed for these 4 regimes. (D) Potential connectivity matrices between the ten different sub-zones, as a function of spawning i (x-axis) and destination j (y-axis) sub-zones, under the four wind regimes presented in C and for pelagic larval duration = 15 days. To interpret these matrices, for instance, larvae from sub-zones 9 and 10 in wind regime 8 and 9 are mostly found still in the same sub-zones after 15 days, but this trend disappear with wind regime 12. Spawning sub-zones 3, 5, 6 and 7 generate high scores in various destination sub-zones (hence the checkerboard pattern here).

Based on the hydrodynamic model, connectivity matrices were computed following the methods described by Thomas et al. (2012a, 2014) for Ahe Atoll. Here, we considered only the connectivity computed for the wild oyster stock, which results in larval release close to the bottom of the lagoon, where restocking will take place. More specifically, Takaroa lagoon was split into ten sub-zones with equal surface areas (Figure 2B) and connectivity matrices between these sub-zones allowed characterization of the dispersal potential for oyster spat under the four selected wind regimes. Among the simulations by Tedesco (2015), which explored the sensitivity of potential connectivity matrices to pelagic larval duration (Thomas et al., 2014), we considered that a pelagic oyster larval duration of 15 days was appropriate given the temperature and phytoplanktonic food conditions typical of Takaroa under normal conditions (Sangare et al., 2020) (Figure 2CD). The measure of connectivity between two sub-zones i and j is the ratio between the number of larvae in the destination location j after 15 days of dispersal originating from the spawning site i, and the total number of larvae emitted in the spawning site i. In other words, these connectivity matrices display what proportion of spats from any given sub-zone (spawning site) would be broadcasted to the other sub-zones (destination sites), from which we infer the connectivity potential of each sub-zone. The same number of larvae were emitted for each sub-zone (as in Thomas et al. 2014). We used these matrices as indicators of connectivity potential between each sub-zone, and specifically to identify the sub-zones that have the highest capacity to disperse larvae in all sub-zones, including themselves. Then, a semi-quantitative index of connectivity ranked the spawning sub-zones based on how many different destination sub-zones they reach with a high level of probability (>0.15, *sensu* Thomas et al. 2014) across the four wind regimes.

Macro-waste distribution

The amount of waste was assessed in a deep central portion of the lagoon in 2015, by means of scuba-diving searches and photography (Figure 3B). The survey produced a semi-quantitative map of the accumulation of waste in this lagoon central zone (DRM, unpublished data). We interpreted this waste map with a suitability index for oyster restocking, assuming that substrates with a large amount of waste were not favorable for restocking because they are potentially mobile.

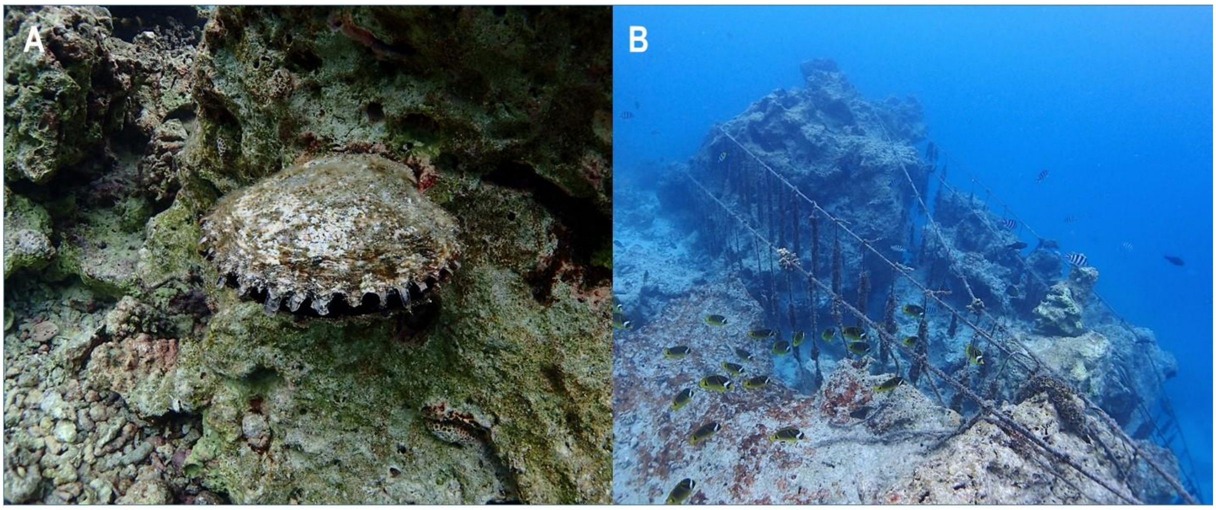

Figure 3. (A) Wild black-lipped oyster *Pinctada margaritifera* on a *karena* in Takaroa lagoon. (B) Example of moderate amount of pearl farming waste (sunk collection lines, as in 2019) accumulated in the Takaroa lagoon. Such ropes like these can move and tear out benthic organisms, including transplanted ones.

Pearl farming concessions

Active concessions are inventoried every year by DRM, including by means of field controls. For this study, we used a 2021 updated map of active concessions in Takaroa provided by DRM. It was estimated that pearl farming concessions occupied 326 ha of the lagoon surface area, a very low value compared to historical data available for the atoll before the mass-mortality events.

2.3 Systematic site-selection scenarios

To implement SCP analyses, we defined planning units (PU) by a regular grid of hexagonal cells, to ensure the best perimeter – surface area ratio (Ardron et al., 2010). PU sizes were set at 25 ha to best suit spatial patterns of oyster concessions, fishing grounds and 5-25 m isobaths contours (Van Wynsberge et al., 2015). PU contours were trimmed when necessary, to match the external shape of the layer of oyster suitable depth. As a result, a total of 406 PU were defined in the lagoon surface area > 5 m depth, representing an 8490 ha study site.

The restocking site selection procedure identified the set of PUs that altogether provide the best solution (or sets of solutions). For this, to guide this site-selection we used prioritization scenarios, where it is necessary to define the objectives to reach (what to include) and the costs (what to avoid).

Here, the parameter describing suitable habitat for oyster restocking was considered as an objective. It was used with different levels of quantitative targets, through the surface area of suitable habitat included in the solution (e.g., 10, 20, or 30% of the area of suitable habitats has to be included in the solution, as an objective).

The next four aforementioned parameters (section 2.2) were considered as ‘costs’ following the SCP terminology since they must be minimized in the selected solution. In other words, the scenario had to avoid, or minimize the inclusion of areas of i) concessions, ii) wastes, iii) sub-zones of lesser connectivity potential and iv) high fishing activity. Loss of fishing zones for fishers and loss of concession areas for pearl farmers are socio-economic opportunity costs, *sensu* Naidoo et al. (2006).

A systematic prioritization analysis was conducted using the Marxan © toolbox (Ball et al., 2009). Based on a minimum objective function, the goal of this exercise was to represent a given proportion (for instance 30%) of the surface area favorable for oyster restocking in a solution that minimizes the aforementioned costs.

These four layers of cost, namely fishery catch, connectivity, waste and concessions, were combined to obtain a unique layer of cumulative cost. To allow comparable values between cost layers (l), the value of each PU (k) in a given layer ($c_{l,k}$) was normalized by the maximum value reached in the layer: $c_{l,max}$ (Eq. (1)). Hence the normalized cost for any PU in any layer ranged from 0 to 1. Then, the cumulative cost (C_k) was calculated for each PU as the addition of the PU normalized cost across the four layers (Eq. (1)).

$$C_k = \sum_{l=1}^{4} \frac{c_{l,k}}{c_{l,max}} \qquad (1)$$

Additional Marxan parameter settings were tuned. The Boundary length modifier (BLM) was set at 0 because no compactness was deemed necessary for the PUs selected for restocking. The Species penalty factor (Spf), in which increasing value compels the solution to meet the exact objective instead of just approaching it, but often at the expense of a higher cost, was tested following the methodology from Ardron et al. (2010).

Number of runs per scenario was set at 100 after trials showing a fast convergence of solutions. Each run provides a solution that is as set of selected PUs. The most commonly used Marxan outputs are the 'best solution', which is the least costly solution across all runs, and the 'selection frequency' of PUs, which indicates how many times in *n* runs a given PU is part of the solution. In this study we used selection frequency outputs.

To provide the total cost *St* reached by each scenario and target *t*, *St* was calculated as the sum across each PU (*k*) of cumulative cost C_k multiplied by the selection frequency (f_k) (Eq. (2)).

$$S_t = \sum_{k=1}^{406} f_k * C_k \qquad (2)$$

2.4 Values assigned to the objective and cost layers

Prior to the computation of the different site selection scenarios, each PU was assigned a value for each objective and cost layer. For this, the following parameterization was applied:

- Layer of suitable habitat for oyster, as an objective, which translates here into the 5-25 m depth range. Each PU was assigned the value of the surface area at this depth range within the PU;

- Layer of connectivity sub-zones, as a cost: each PU was assigned with coefficients ranging from 0 if it belongs to sub-zones of high dispersal potential, to 1 if it belongs to sub-zones with low dispersal potential.

- Layer of pearl farming wastes, as a cost: each PU was assigned with coefficients ranging from 0 for areas without waste detected or not surveyed, to 1, corresponding to areas with the highest rates of waste accumulation;

- Layer of active concessions as of 2021, as a cost. Each PU was assigned the value of the surface area occupied by concessions within the PU;

- Layer of total fishery catch, as a cost. It was obtained by calculating the annual catch density (in $kg.km^{-2}$) of each fishing ground, then by intersecting the fishing grounds by the PU grid. The amount of catch within each fragmented fishing ground was recalculated from catch densities and the obtained surface areas from the intersected fishing grounds. Finally, these amounts were summed within each PU to get the annual catch per PU. This was conducted following the methodology described in André et al., 2021b. Resulting values were Log-transformed to reduce skewness of catch distribution per PU.

3 Results

Data aggregation, and assignment of objectives and cost values by PU revealed a complex Takaroa lagoon despite its small surface area (Figure 4).

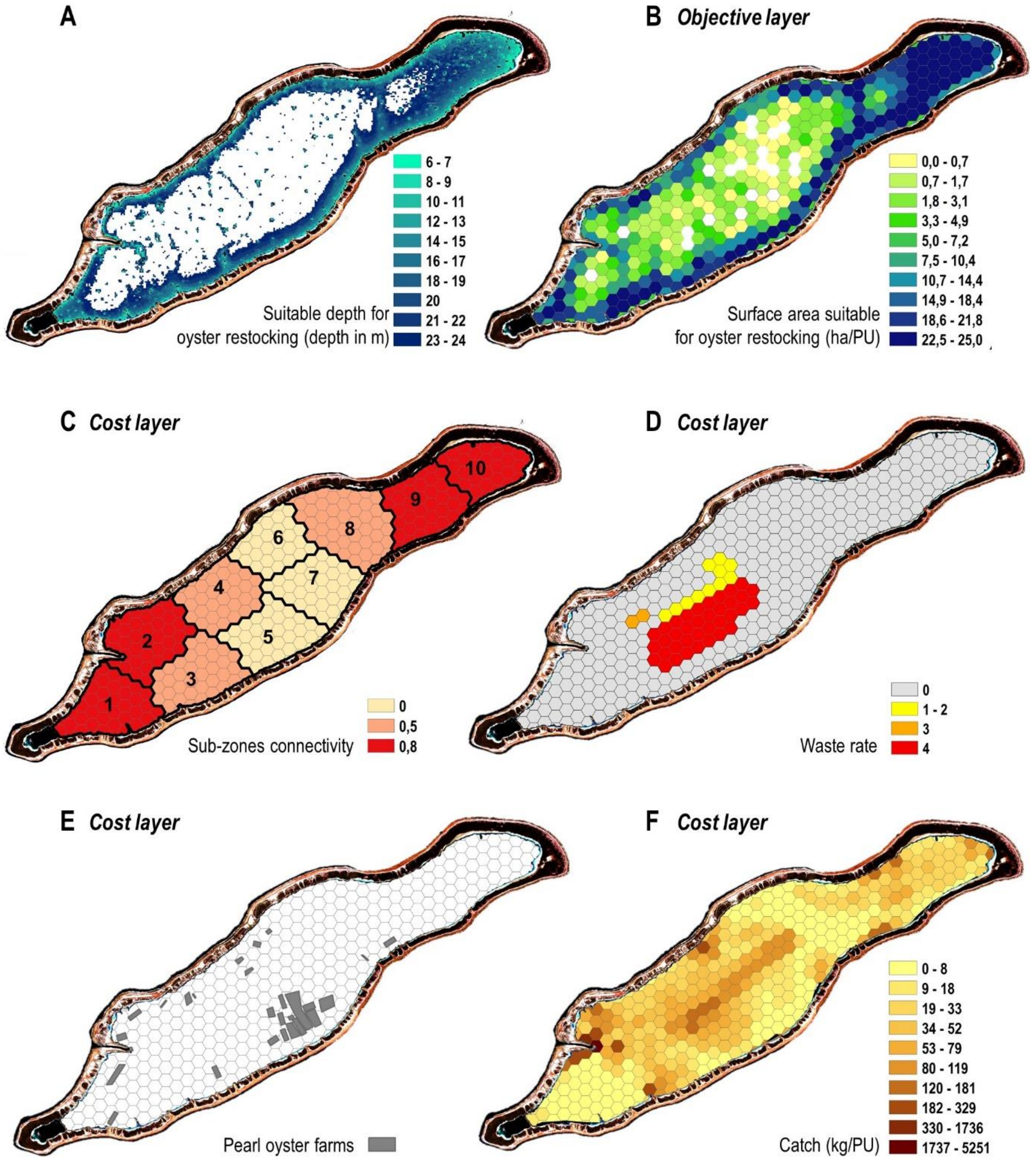

Figure 4. Spatial layers used for the systematic prioritization analysis. (A) The 5-25 depth range representing the maximum extent of the potential restocking areas. (B) Surface area of suitable depth for potential restocking present in each planning units (PU). Depth is here a proxy to represent the habitat of oysters. This layer is used as the objective layer for the systematic prioritization analysis. (C-F) Cost layers used for the prioritization analysis: (C) connectivity costs with high costs assigned to low connectivity sub-zones; (D) costs for waste abundance; (E) cost for farm concessions; (F) opportunity costs using fishery catch aggregated by PU.

The 5-25 m depth map shows that the main favorable areas for oyster restocking were expectedly located on flats and slopes around the shores of the lagoon, but some suitable depth also available in the center of the lagoon due to '*karena*', totalizing 3870 ha (Figure 4A). Once intersected with each PU, the surface area at this depth was known per PU (Figure 4B).

Connectivity between sub-zones shows high dispersal potential for sub-zones 5, 6 and 7 (Figure 4C). Medium rates of dispersal potential were found for sub-zones 3, 4 and 8, and the lowest rates were found for sub-zones 1, 2, 9 and 10. Costs assigned to the PUs within each of these set of sub-zones were accordingly equal to 0, 0.5 and 0.8, respectively.

Wastes from oyster farming in the center of the lagoon ranked from very high abundance (cost = 4) to medium (cost = 1-3), whereas the rest of the lagoon was considered zero (Figure 4D).

Most of the current farming concessions were mainly located along the southeast lagoon. Some additional concessions were near the pass and some small ones along the north-west coast (Figure 4E).

The fishery survey indicated that the 44 fishers used the entire lagoon space, albeit with considerable variation in catch rates among fishers. The zone encompassing the pass, which is also near the village, yielded the highest catch, with 5251 $kg.y^{-1}$ in a PU. Medium levels of catch values were found in the north of the lagoon, along the north-west coast and in the center of the lagoon, where many fishers use spear-gun on '*karena*' as well as line and troll fishing from a boat. The total catch for the lagoon was estimated at ~22 t per year (Figure 4F).

Combining the four normalized cost layers provided a resulting cost layer that shows high cost levels in the center of the lagoon (mainly due to waste and fishing activity), near the pass (mainly due to fishing), and in the north (due to low connectivity sub-zones) (Figure 5A).

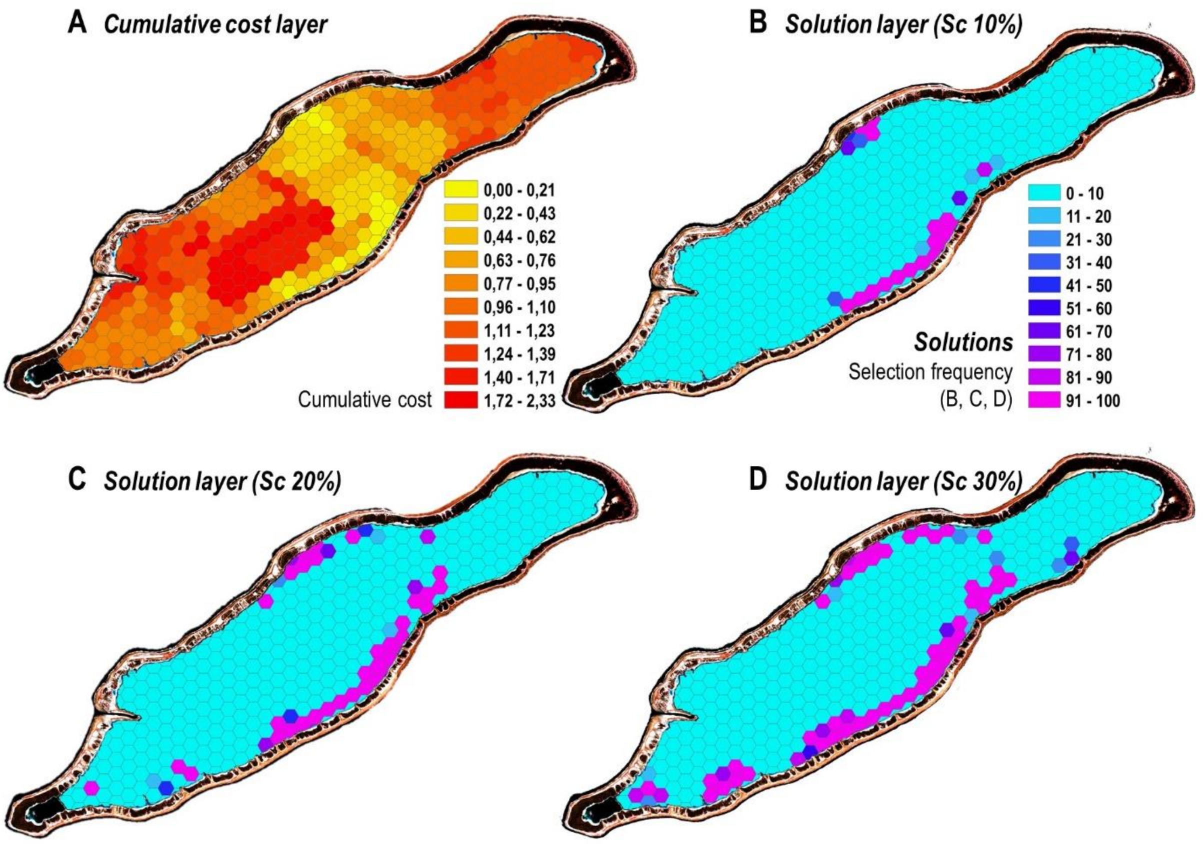

Figure 5. (A) Cumulative cost, resulting from the four types of cost summed by PU (see Figure 4). This cost layer was used for the systematic prioritization analysis. B-C-D are solutions to Scenario 1, 2 and 3 with targets of respectively 10%, 20%, and 30% representation of the 5-25 m depth range.

Calibration tests showed that setting Spf at 5 resulted in a satisfying compromise between achieving or almost achieving the target for the three scenarios (see Table 1: shortfall ≤1.1 ha), while still ensuring minimized costs. PU selection frequency is displayed in Figure 5 for the three scenarios.

Table 1. Description of the three scenarios with increasing targets, associated specie penalty factor (Spf), resulting shortfall (as the area that is missing to totally fulfil the 10, 20 or 30% representation target) and total cost of the solution (no unit).

Scenarios	**Target values**		**Spf**	**Shortfall to reach the target**	**Solution cost**
	relative	absolute			
1	10 %	387 ha	5	0 - 0.9 ha	3.91
2	20 %	774 ha	5	0 - 1.1 ha	14.82
3	30 %	1,161 ha	5	0 - 0.6 ha	29.66

All the different scenarios identified candidate sites (PU) for oyster restocking, with an incremental number of PU expectedly matching the increasing targets. Selection frequency was > 80-90 (pink colors) for many PUs located in the north and south sides of the middle section of the lagoon (Figure 5BCD). The pattern of solutions indicates that the south-central border is particularly suitable for restocking. Other possibilities were also identified at lower frequency (purplish colors), offering flexibility to managers for deciding different schemes of implementation when these options will be discussed with pearl farmers.

4 Discussion

In response to concerns raised by the pearl producers on 'what can be done to restore the initial spat collection levels?' and at the request of DRM, this study helps identifying practical management solutions, by combining pearl farming criteria, while also integrating other concerns. The highlighted solutions (Figure 5) provide a baseline for further discussions on restocking options in Takaroa lagoon for stakeholders. To our knowledge, the use of a systematic spatial prioritization toolbox for such a purpose has never been reported. This study constitutes an original contribution to the panel of management or conservation questions addressed by the general field of systematic conservation planning in tropical island environments (André et al., 2021a), because it integrates pearl farming related issues for the first time.

With more diverse criteria than most conservation plans for wild species, our study is consistent with the recommendations by André et al. (2021a) for the Pacific Islands. These authors identified a lack of planning studies taking into consideration local specific activities, such as black pearl farming, and invertebrate resources. Specifically for the Tuamotu

Archipelago, a previous systematic conservation planning study actually already addressed a local question, which was on how to conserve giant clam stocks and limit fishing while maintaining equitable conservation costs on different atolls (Kabbadj et al., 2018). This first application was in line with typical spatial planning exercises and goals that often balance biodiversity and resource conservation with fishery opportunity costs. In the case of Takaroa here, the planning question was motivated by the reboot of an aquaculture activity impacted by oyster population mortalities, an application more rarely put forward in a systematic planning context to our knowledge.

Specifically for the management of pearl oyster farming, our analysis is a first step towards the identification of favorable restocking zones. The restocking question is acute for Takaroa, but also in several places where a decline in spat collection has been reported by farmers, like in Ahe Atoll. Besides potential environmental changes, the decline in several atolls could be explained by the combined aging of the wild populations and the skewed sex-ratio due to the protandric nature of the species (Andréfouët et al., 2016), and by the growing suspicion that spat production could be dominated by gametes released by the natural stock, and not by the farmed stock (Andréfouët et al., 2021; Reisser et al., 2020). Altogether, the principles of the methodology put forward here are likely to be useful for a variety of lagoons in the future. It could be part of the management portfolio of DRM in French Polynesia, and possibly other countries where pearl farming based on spat collection also takes place, such as Cook Islands and Fiji (Lal et al., 2020).

To apply these tools effectively, however, data are needed. Takaroa is already well studied compared to most other pearl-growing areas, nevertheless, several aspects could be improved. Here, we used a limited data set to parameterize the best areas susceptible to maximize larval dispersal throughout the lagoon. This is reasonable because we used climatologic information and dispersal forced by typical trade wind regimes, which represented fairly typical present-day situations. However, other configurations exist, in wind patterns (including fast reversals not captured in the wind regime statistical analysis), but also in pelagic larval duration, larval food supply in the lagoon, temperature, and so forth (Thomas et al., 2014; 2016).

Future similar exercises to identify restocking areas will give more weight to connectivity than the other parameters, as it is a fundamental criterion for an efficient restocking to reach ultimately an efficient spat collection rate. Refined analyses will take into account additional environmental condition scenarios, including wind regimes and higher spatial resolution of connectivity matrices, prior to making final recommendations for the selection of restocking sites. Since new wind regime data also became available recently (Dutheil et al., 2020), the future simulations will be forced by these conditions. Nevertheless, we do not expect significant changes compared to the present results because these updated regimes remain dominated by easterly wind directions. Additionally, the 2013 stock data were used here to estimate the location of suitable habitat and depth for restocking, but there may have also been some changes in substrate that could question the assumptions we made here. This could warrant further investigations and if some recruitment has occurred since 2014. New empirical observations on wild oyster stock abundance could be relevant to update our parameterization.

For other sites, other data could be thought of, but they were deemed secondary for Takaroa considering the local livelihoods and the atoll economic activity (no tourism for instance), and considering data immediately or rapidly available or the cost to acquire new ones. For instance, in-water fish census could be used to complement the fishery-survey, but this data set is not currently available for Takaroa and would require the funding of a significant expedition to be collected. Recently, we also investigated how ciguatera could be an important criterion to take into account to lower the cost of conservation for fishers (André et al., 2021b). Indeed, in many Pacific Islands, ciguatera poisoning outbreaks are frequently reported. They result from the ingestion of poisonous marine products due to harmful microalgal blooms producing toxins that further bioaccumulate in the food web. However, unlike what is observed in areas where ciguatera risk represents a major driver for fisher's use of the lagoon (André et al., 2021b; Chinain et al., 2010 and 2020), in the case of Takaroa, very few cases were actually reported. Therefore, although the ciguatera criteria was not considered in the present study, it can be highly relevant elsewhere, especially in ciguatera-prone areas and, hence, should be integrated in future similar exercises. Finally, the waste survey was incomplete, as the surveys did not cover the entire lagoon; but it definitely allows to discard some areas. It also corresponds to the most used zone for spat collection in the past. Extended lagoon waste assessment and some bottom cleaning are on the DRM's agenda and as work progresses, the map of waste is expected to better cover the Takaroa lagoon, but also others.

To apply our methodologies specifically to other pearl farming locations, the oyster suitable depth range is probably necessary, so bathymetric data on the study site is an essential prerequisite to map the stock across the lagoon (Andréfouët et al., 2016). Taking into account the socio-economic parameters is important for the success of the project and according to the study site; it can include tourism frequentation or infrastructure development (ports, moorings, hotels, airstrips), in addition to fisheries. Additional environmental parameters could also be considered when relevant, such as pollution (induced by these developments). Then, connectivity matrices are critical if the goal, as here, is efficient restocking that allows for the oyster larvae produced to disperse as widely as possible throughout the lagoon. But we are aware that hydrodynamic circulation modelling and computation of connectivity matrices are complex and costly to produce, especially if some *in situ* validation data are expected, through lagoon physical measurements, or through larval census (Aucan et al., 2021, Thomas et al., 2012b). In the sites without data or with very little opportunities to collect data, favorable locations for restocking could be identified more empirically by the identification of where high densities of live oysters occur, potentially spotted with the help of fishers and oyster farmers. This is interesting only if mass mortalities have not already wiped out the populations. Furthermore, this leaves no guaranty that these sites are effective to maximize connectivity with other areas.

In conclusion, this study provides a new canvas that paves the way for better integration of different types of spatial data and to develop new approaches for sustainable management of pearl farming lagoons in the South Pacific. Although the scope of this manuscript is limited to one atoll, the spatial planning approach used in this study should also help inform management measures in other island contexts where there is need to protect biodiversity, or optimize the benefits for multiple stakeholders in using the marine resources in different ways, while minimizing the effects of human activities on these measures. The systematic planning approach described in the present paper should be particularly useful for harmonizing biodiversity conservation with the fishing and aquaculture operations that provide livelihoods for island communities.

Data statement

Data is available from the authors on request.

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