The MANA (MANagement of Atolls, 2017–2022) project for pearl oyster aquaculture management in the Central Pacific Ocean using modelling approaches: Overview of first results

Andréfouët Serge ^{1,*}, Lo-Yat Alain ², Lefebvre Sebastien ³, Bionaz Océane ¹, Liao Vetea ⁴

¹ UMR-9220 ENTROPIE (Institut de Recherche pour le Développement, Université de la Réunion, Ifremer, CNRS, Université de la Nouvelle-Calédonie), 101, promenade Roger-Laroque Anse Vata, BP A5, 98848 Noumea, New Caledonia

² UMR241 Ecosystèmes Insulaires Océaniens (EIO), Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Centre du Pacifique, Unité Ressources Marines en Polynésie Française. BP. 49, 98725 Vairao, Tahiti, French Polynesia

³ Université de Lille/Station Marine de Wimereux, UMR LOG 'Laboratoire d'Océanologie et

Géosciences' (Univ-Lille/CNRS/ULCO 8187), 28 avenue Foch, 62930 Wimereux, France

⁴ Direction des Ressources Marines, BP 20, 98713 Papeete, French Polynesia

* Corresponding author : Serge Andréfouët, email address : serge.andrefouet@ird.fr

Abstract :

This editorial presents results of the MANA (MANagement of Atolls) project compiled in the form of a Marine Pollution Bulletin collection of 14 articles. MANA is a project funded by the French Agence National pour la Recherche that specifically addresses the development of knowledge and management tools for pearl farming atolls, with a focus on the spat collecting activity in French Polynesia. The 14 papers cover the range of thematic tasks described in the initial project, including atoll geomorphology and bathymetry, climate forcing, atoll lagoon and rim hydrodynamics, typology of atolls, evaluation of remote sensing data for monitoring atoll lagoons, and development of numerical models and spatially-explicit tools that altogether have contributed to the applied objectives. In addition, this editorial draws an update on the pearl farming industry in French Polynesia with the latest statistics, and discusses the next targeted priorities for research programs focusing on pearl farming atolls.

Keywords : Black pearl farming, Aquaculture, French Polynesia, Atoll, Biogeochemistry, Hydrodynamics

Introduction

This editorial presents results of the MANA (MANagement of Atolls) project compiled in the form of a Marine Pollution Bulletin collection of articles available at

www.sciencedirect.com/journal/marine-pollution-bulletin/special-issue/10H4HPG4SF3._In a nutshell, MANA aims to develop numerical models and products relevant for the management of black pearl farming lagoons in the central Pacific Ocean, in particular in French Polynesia. Here, we first update with fresh publicly available statistics the presentation of the Polynesian pearl farming industry made in 2012 at the occasion of another paper collection that focused on results achieved mostly for one single pearl farming site, in Ahe Atoll (Andréfouët et al. 2012, https://www.sciencedirect.com/journal/marine-pollution-bulletin/vol/65/issue/10). We also draw hereafter a brief summary in term of research programs that took place between these two collections to explain the genesis of the MANA project.

The links between the 14 published papers, their relevance, and their contribution to the overall MANA project goals are described following the project organization in 7 tasks, among which 6 are scientific tasks. The 14 studies are representative of these 6 tasks. Throughout, we also refer to these tasks when mentioning the papers already published elsewhere. The collection of papers is both methodological and thematical, addressing processes related to pearl farming in its environment. Perspectives are discussed at the end of the editorial, with a conclusion on the benefits that the development of numerical tools are expected to bring for the management of pearl farming lagoons.

Pearl oyster farming in French Polynesia after 40 years of activity: a vulnerable situation

Since 1961 and the first attempt by Jean-Marie Domard and Churoku Muroi to graft *Pinctada margaritifera* (Linnaeus, 1758) var. *cumingi* black-lipped oysters to produce cultivated round black pearls in Hikueru atoll, pearl farming has developed since the late 1980s into one of the main sources of local income in French Polynesia. This success has motivated private and government enterprises to develop a similar activity in other countries, such as Cook Islands or Fiji. This was possible because in places like Tuamotu and Gambier lagoons, successful oyster spat collecting allowed to provide to farmers the necessary animals, without relying on hatcheries. The latest official number, as in 2020, shows that French Polynesia exports represented a 64 million \notin value. These positive statements however hide a now 40-year-long chaotic pearl farming history, made of an energetic full-of-promise childhood, a difficult adolescence, and a fragile adulthood. Indeed, while it seems that today a relative stability has been reached since 2009 in term of incomes, price per gram, exports (Figure 1), and number

of marine concessions (Figure 2), this stability has followed a period of steady decline and crisis that itself followed a period of initially very lucrative, and anarchic, 'black pearl rush' in 1982-1998 (Figures 1, 2).

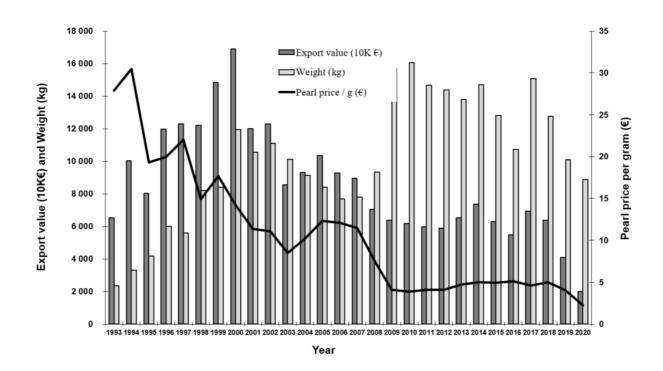


Figure 1: Evolution from 1993 to 2020 of key indicators of the pearl farming industry: total export value, total exported weight, and price per gram (Data source: Institut de la Statistique de la Polynésie française, http://www.ispf.pf). The decline after 1993 of the price per gram of pearl is clearly visible, as well as the relative stability after 2009, albeit at a low level far from the initial value.

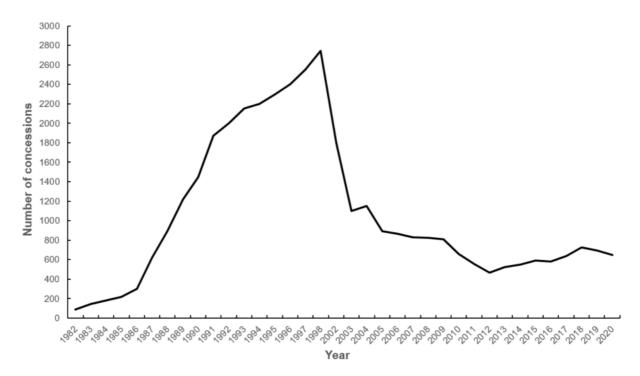


Figure 2: Evolution in the number of pearl farming concessions in French Polynesia during the past thirty eight years (Data source: Direction des Ressources Marines de la Polynésie française,). The periods of growth (1982-1998, itself in 3 periods1982-1986, 1987-1991 and 1992-1998), steep decline (1999-2003), and overall slow decline (2004-2020) are clearly visible.

Pearl farming is not an easy task. Often conducted in logistically challenging remote conditions, the activity rely first on the successful production and growth of millions of juvenile oysters, through spat collecting. This phase is necessary to steadily provide the oysters needed for grafting. However, collecting is consistently efficient in a limited number of lagoons, and for a given lagoon also proved to be erratic from one year to another, which means that farmers need to constantly adapt to maintain their oyster supplying chain. Atolls that have a good spat production have exported, and continue to do so, to other lagoons. These transfers are now subjected to authorizations in particular to limit the spread of pathogens and invading epibiont species such as the *Aiptasia pallida* anemone that has seriously impacted lagoons. The grafting of adult oysters is a critical step, and achieving 300-400 sellable pearls for 1000 grafted oysters is a good rate. The pearl farming activity is labour but also space intensive. On the management side, since the early boom of pearl farming, dedicated governmental services manage and monitor the activity. The now Direction des Ressources Marines (DRM) currently oversight legal implementations of governmental decisions and monitor lagoons with a focus on achieving balance between sustainability and profitability of the activity, and environmental sustainability of the lagoons and its resources. The task is humongous as, in 2020, the activity is represented in 28 atolls and islands, among which 15 atolls are spat collecting atolls. As in 2021, the total area allowed for the farming activity is

limited to 10000 hectares all lagoons included, and including the areas for spat collecting. Dedicated spat collecting areas have been legally defined like in Ahe Atoll or Gambier Island.

Despite the government oversight, the initial crisis of the early 2000s is largely explained by the lack of vision, at all management and commercial levels, of the consequences of a massive overproduction which itself brought lot of low quality pearls to the market. In a decade, the initial high quality gem niche market turned into a saturated market yielding an average price down to, as in the last 5 years, 2 to $5 \in$ per gram of pearl. It was around 100US\$ per gram in 1985. This represents a ~20-fold decrease that bankrupted many of the small family-run farms. The situation seems stabilized today when looking at the Figures 1 and 2 but in fact it remains excessively fragile due to the same problem of poor quality and overproduction at the scale of the country. The French Polynesia government does not fully address this situation by using long-term, strong, quality-control measures that are unpopular with many farmers and wholesalers. Furthermore, several factors out of the control of French Polynesia stakeholders also make this industry vulnerable. Namely, environmental problems affecting spat collecting, and fragile international markets can very quickly compromise the benefits of a relatively good year.

Recent examples of 'external' disturbances range from the political situation in Hong-Kong (a primary buying market) to the Covid pandemic which restricted international travels for both foreign grafters required to maintain the production and buyers that usually visit French Polynesia at the time of auctions organized by group of farmers. Conversely, purely 'internal' problems occurred with environmental issues related to algal bloom and benthic mortality events that have plagued entire lagoons in the past (Andréfouët et al. 2015). Recently, Takaroa Atoll, usually one of the main producer of both spats and pearls, was subjected to such disturbance (Rodier et al. 2019). The bloom completely shut down the activity in 2013-2014, and the effects are still felt today, with a now moribund activity. On the other hand, atolls that were impacted in the past by mortalities, such as Takapoto in the late 1980s, eventually bounced back and became again excellent spat producers ~20 years later. However, the pressure put by farmers in term of spat collection on these renewed El Dorado-like lagoons may mean that their maximum carrying capacity (Aubert et al. 2019) is close to be reached, and that they are at socio-economical and environmental risks in front of diseases outbreaks, invading lethal species, dystrophic events, and more frequent heatwaves.

To conclude and summarize this overview, DRM, farmers and scientists are continuously facing a highly dynamic pearl farming landscape that is fuelled and impacted by both the wider international context and by the intrinsic diversity of the range of situations, present and historical, displayed by the suite of exploited lagoons spread in a 2 million-km² territory and exposed to different weather and climate.

Recent research on pearl oyster and atoll lagoons, and the genesis of the MANA project

In the past, despite the growing empirical knowledge developed by farmers, there was a fast awareness that better scientific knowledge of lagoon ecosystem was needed. Since the late 1980s research programs have looked at a variety of processes such as the physiology of P. margaritifera, genetics and adaptation at atoll population scales, lagoon ecosystem trophic carrying capacities, lagoon hydrodynamics, aquaculture practices and processes controlling the quality of pearls, and influence of environmental parameters on larval and adult ecology and their modelling through Dynamic Energy Budget approaches. In late 2007, a European Fund for Development (FED) project was launched, with one folder targeting Ahe and Takaroa Atolls' trophic regime and the hydrodynamical forcing on spat collection. Ahe Atoll in particular has been the main studied site since 2007 and results of the FED project were presented in the aforementioned Marine Pollution Bulletin special collection (Andréfouët et al. 2012, https://www.sciencedirect.com/journal/marine-pollution-bulletin/vol/65/issue/10). In 2012, the ANR-funded (ANR=Agence National de la Recherche, The French national research agency) POLYPERL project continued some of the previous activities on aquaculture practice, genetics, ecophysiology, hydrodynamics, mainly in Ahe atoll but also with pilot studies in Gambier, a high island. The project also investigated ex situ the influence of ocean acidification on shell growth and pearl quality. It also had a social science multi-site component to assess the sustainability of pearl farming. The project conducted new wild oysters stock assessments, an activity that was neglected for 15 years (Zanini 1999) and revealed unbalanced sex ratio in aging populations due to the species protandric life cycle. Some of these researches have been reviewed in Gueguen et al. (2016) for another special issue (https://www.sciencedirect.com/journal/estuarine-coastal-and-shelfscience/vol/182/part/PB). Since these 2012 and 2016 reviews, new work have investigated the

environmental impact of the micro-plastics that pearl farming have generated in lagoons (Gardon et al. 2021). Due to the abundance of derelict macro-gears also generated by farming (Andréfouët et al. 2014), the cleaning-up of lagoons and promotion of green practices are new management focus as well. Thus far, cleaning and removal of macro waste is left at the stage

of feasibility and inventories in French Polynesia but it was partially implemented in Manihiki Atoll in Cook Islands.

Following a workshop conducted in June 2014 and the conclusion that understanding spat collecting variability remained a priority, it was decided to not pursue a wide multidisciplinary project like POLYPERL in order to avoid scattering efforts and funds in too many disconnected components. Instead, it was decided to re-focus on lagoon hydrodynamics and biophysical modelling with a dedicated large integrative project, and investigate a new set of geomorphologically diverse lagoons as well. Therefore, MANA (meaning spiritual energy of power and strength in Polynesian culture, and standing here for MANagement of Atolls) is a project selected for funding by ANR in 2016 that is broadly dedicated to the development of tools for the management of exploited atoll lagoons facing a changing environment. Specifically, it addresses closed and open atoll lagoons dedicated to pearl farming in the Central Pacific Ocean, an area vulnerable and exposed to global change, but with limited adaptation capabilities (Bell et al. 2011). The 5-year project (01/2017-03/2022) is articulated around 7 interconnected main tasks (Figure 3), namely: Task1: Project coordination; Task2: Regional-scale atoll typology, Task3: Lagoon 3D circulation modelling; Task4: Lagoon coupled bio-physical modelling; Task5: Lagoon field data collection; Task6: Regional-scale environmental forcing and climate change; Task7: Decision support tools. Hence, the scientific tasks (T2-T6) are coordinated (T1) to converge towards an applied T7 task.

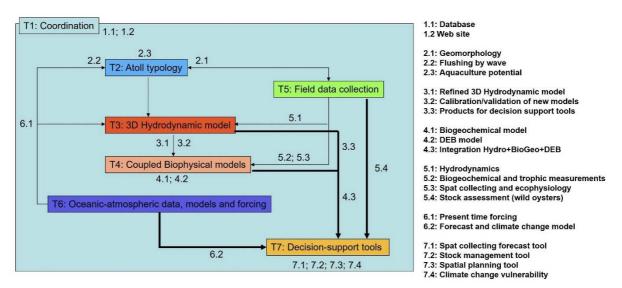


Figure 3: Architecture of the MANA project, with the pre-defined main task and their links on the flow chart, and the sub-tasks listed on the right inside. The papers of the special issue, and others already published elsewhere as well, illustrate most of these sub-tasks

The main characteristic and objective of the project is the development of management tools and products from enhanced biophysical numerical models of pearl farming lagoons. The concept was to develop 3D circulation models for two new sites (Raroia in Tuamotu Archipelago, and Manihiki in Cook island), and to develop new biophysical capacities and applications for two atolls already benefiting from existing circulation models (Ahe and Takaroa), specifically through their coupling with DEB and biogeochemical models. Great importance was given to the calibration and validation of these 3D circulation models using adequate field data, including multibeam bathymetry, hydrobiological observations, and an array of deployed sensors during periods long enough to cover various meso-scale forcing conditions (up to 10 months). Adequate logistics was available through the simultaneous use of a large number of sensors (for temperature, pressure and currents) provided by DRM and the use of the R/V ALIS, a 30 m long research vessel normally based in New Caledonia in the Western Pacific but transiting to French Polynesia for the field campaigns. Eventually, the data and models were expected to provide fresh information on meso-scale oceanic and atmospheric regimes, forcing conditions at the ocean-lagoon interface, atoll geomorphology, lagoon hydrodynamics, oyster population structures, larval dispersal potential within lagoons, and wild oyster restocking scenarios, all informations useful in the context of spatial planning and management of farming lagoons.

New results from the ANR MANA project

This special issue aims to present some key methodological developments and thematic results available as in early-2022. Some results have already been published elsewhere, and more will be published following the on-going analyses. This issue includes 14 original studies (Table 1). The Table 1 lists the task and sub-task titles and numbers used in Figure 3 to locate each study within the frame of the project. The sub-task numbers in Figure 3 are associated to all MANA references cited hereafter, published in this issue or elsewhere.

Reference	Theme	Task &
		Sub-task
Andréfouët et al. (2020)	Atoll lagoon bathymetry and geomorphology	2.1
Andréfouët et al. (2022)	Periodicity of wave driven lagoon renewal	2.2, 2.3
Aucan et al. (2021)	Wave-driven flows across Raroia atoll rim	2.2, 5.1
Monaco et al. (2021)	DEB modelling and oyster population recovery in Takaroa Atoll	4.1
Seceh et al. (2021)	Biogeochemical model development (0D)	4.1
Lefebvre et al. (2022)	Chlorophyll monitoring in Ahe Atoll with remote sensing	4.2, 2.3, 5.2
Van Wynsberge et al.	Temperature monitoring in Raroia Atoll lagoon using remote	5.1
(2020)	sensing	

Grenz et al. (2021)	Sediment interface biogeochemical measurements in Ahe Atoll	5.2
Rodier et al. (2021)	Pelagic biogeochemical measurements in Ahe Atoll	5.2
Lo-Yat et al. (2022)	Larvae and spat dynamics in Ahe Atoll vs Gambier Island	5.3
Dutheil et al. (2020)	Wind regime of Central Pacific Ocean	6.1, 6.2
Dutheil et al. (2021)	Wave regime of Central Pacific Ocean	6.1
Andréfouët et al. (2021)	Larval dispersal with modeling and genetics in Ahe Atoll	7.1
André et al. (2022)	Lagoon Spatial Planning	7.3

Table 1: List of studies published in the Special MANA issue, with their main theme and ranked according to their task and sub-task numbers as listed in Figure 3.

The MANA project is hierarchical, with thematically and spatially imbricated suite of Tasks (Figure 3). The largest Task, geographically speaking (Task 6), looked at the meso-scale oceanic and atmospheric environment that both constrain the functioning of lagoons through the action of waves (for its action on lagoon water renewal) and wind (for its action on locally generated oceanic waves and on the circulation of the lagoon). As such Dutheil et al. (2020, Task 6.1, 6.2) and Dutheil et al. (2021, Task 6.1) computed the different wind and wave regimes that French Polynesia and Cook islands experimented in the past decades. Wind data (1980-2016) came from various models (WRF, ERA-5) and wave data (2000-2017) were sourced from WaveWatchIII simulations at 50 and 5-km resolution. Following Dutheil et al. (2019), use of climate change models (CIMP5 projections under the RCP8.5 scenario for the late 21st century) allowed to make projections for the future wind regimes. Results suggest only minor increase in wind velocity (15% on average), and small shifts between regimes in directions and frequencies. To match the oyster pelagic larval duration, regional wind regimes were computed also considering a time-scale of 30 days, and the extraction around selected atolls showed regimes variation from one atoll to another. The nine identified regional 30-day regimes will serve as references for lagoon connectivity models forced by climatological conditions. The wave climate was studied differently and focused on three different spatial scales considering the local effects that atolls have on wave distributions. Results showed for the first time the continuous geographic variation of wave regimes across the archipelagos, for 83 atolls, and for the 8 directions around any given atoll. Unlike wind regimes that were more homogeneous and continuous at meso-scale, wave regimes characterized smaller geographic sectors with breaks due to the shadowing effects of atolls within archipelagos, to the point that each atoll can be a separate case when looking at the variation of wave regimes along its 8 sectors.

The individual characterization of each atoll based on its exposure to wave was investigated further considering this time also the effect of the atoll rim geomorphology, and the periodicity of the wave-driven flows across each rim sector. A total of 73 Central Pacific Ocean atolls was studied (Andréfouët et al. 2021a, Task 2.2 and 2.3). WaveWatch III simulations at 5 km resolution were used for this characterization. Different theoretical water renewal metrics inferred from the wave-driven inflows allowed to typify groups of atolls characterized by different frequencies of renewal rate as described by a wavelet spectral analysis. The combination of hydrodynamically semi-closed geomorphology and wave regimes identified the historically highly productive spat collector atolls at the end of a spectrum of renewal functional group. The wavelet spectral analysis of renewal metrics thus opens the possibility to identify and study functionally-representative atolls in the context of pearl farming, and the possible changes in forcing that they may have experienced in the past. This also has implications to understand why some atolls have been more subjected to mass mortalities than others.

Lagoons can be defined by their exposure to meso-scale oceanic and atmospheric processes, but they are also inherently different according to their size, depth and rugosity for which coral pinnacles are important local drivers of the abundance and richness of living communities. For seven atolls with a history of pearl farming and for which high resolution bathymetry was available, we quantitatively compared their lagoon geomorphology and discussed the possible geological processes that could explain their specificities (Andréfouët et al. 2020, Task 2.1). Knowledge of bathymetry is necessary to develop numerical simulation models and additional atolls (Kaeuhi, Arutua, etc.) will be added to this database in the future.

Development of numerical circulation models require bathymetry, but also the collection of data for calibration and validation. The MANA project has instrumented in particular Raroia Atoll, with a large array of sensors deployed for up to 10 months. Raroia was a newly studied atoll in the context of pearl farming, and its geomorphology is the most complex of all studied atolls thus far (Andréfouët et al. 2020, Task 2.1). It is also the largest (368 km²). As such, it is expected that hydrodynamical processes vary significantly within the lagoon and around the atoll. Numerous temperature and pressure sensors, and five ADCP current meters were deployed in strategic locations, outside the lagoon, in the deep pass, in shallow *hoa* and in the lagoon. Aucan et al. (2021, Task 2.2, 5.1) proposes a model to estimate wave-driven water flows across *hoa* after comparing the *in situ* data collected in three different rim and *hoa* geomorphological configurations. This step is also necessary for the lagoon circulation model developments and future tests on different atolls will confirm the generic application of Raroia inflow models to other types of rims.

Also using Raroia data, Van Wynsberge et al. (2020, Task 5.1) continued their initial work (Van Wynsberg et al. 2017, Task 5.1) aiming to assess if it is possible to monitor Sea Surface Temperature in lagoons using satellite data. Temperature is an important variable for pearl oyster development and survival at all life stages (Sangare et al. 2020, Task 4.2). Monitoring with satellites the sea surface temperature (SST) is an attractive option if the measurements are accurate enough to model oyster growth and larval survival in the lagoon. Two SST public products (namely MUR and G1SST) were compared with the 18 temperature sensors deployed in Raroia lagoon and oceanic slopes. SST values and outputs from DEB simulations were in very close agreement between each data source, suggesting that G1SST and particularly MUR can be used cost-effectively to monitor large lagoons and force physiological simulations. However, numerous caveats are raised: generalisations to smaller and more closed atolls are not granted. Extrapolations above the thermal range processed for Raroia in the case of heatwave or global warming are also not granted before additional tests can be conducted. Because the SST products merge different data sets to limit cloud cover effects and filter out outliers, artefacts can occur with oceanic values assigned to the lagoon during some days. Finally, MUR SST actually reflects temperature at depth and it is not always suitable to represent the condition of cultured or shallow wild oysters.

In situ measurements are also directly useful to validate numerical spatial models. The refinement of existing hydrodynamical models (Ahe, Takaroa) and development of new ones (Raroia, Manihiki) are unfortunately not included in this issue, but will be published later (Le Gendre et al. in prep., Task 3.1, 3.2, 5.1). Models, and associated tools (particle tracking, etc.) can be used to compute analytically lagoon metrics (e.g., renewal time) and hydrodynamic lagoonal structures in standard wind and wave regime conditions. They also offer the possibility to simulate the conditions during specific past realistic periods, in particular when biological data were collected (Thomas et al. 2016). An example of such application is provided in Andréfouët et al. (2021b, Task 7.1). The hydrodynamical model of Ahe Atoll was used in a realistic hindcast scenario to compare for a specific period of time the connectivity inferred by the model and by the genetic signatures of farmed, wild and spat populations (Reisser et al. 2020, Task 7.1). The connectivity pattern shown by genetics cannot be questioned, but the model allows to investigate other connectivity pathways that cannot be captured by the limited genetics sampling. Both approaches complement each other. Reisser et al. (2020, Task 7.1)'s findings unexpectedly suggested that all sampled spat only came

from the wild population. No similarities were found with the much more abundant farmed population. This is critical information for the sustainability of the industry as it became clear few years ago that in Ahe Atoll the wild stock alone cannot be reproductively efficient to sustain spat collecting on the long term (Andréfouët et al. 2016). However, these conclusions from a limited sampling warrant additional tests, in Ahe, and also in other atolls. Output from models can bring useful clues on where to sample if new samplings for genetic analyses are performed.

Working with spat collectors scattered in a lagoon and deployed for different periods of time is an option to understand connectivity. More generally, larval census and spat census in lagoons can reveal the role of environmental factors controlling the early life stage of oysters. Lo-Yat et al. (2021, Task 5.3) revisit previous simultaneous larval and spat census in Ahe atoll and Gambier Island. They empirically evaluate for these contrasting lagoons the role of environmental variables (temperature, chl a, wind) in explaining larval and spat abundances during a 25 week-period. While the early-stage dynamics of bivalves followed similar temporal dynamics at these two contrasting sites, Ahe and Mangareva had different environmental drivers, with Ahe being much more responsive to temperature and chl a than Mangareva. Although not all factors were included in the analysis (including hydrodynamics), the different responses to variables re-emphasize that lagoons can have specific bio-physical functioning and pearl farming dynamics, which can require specific management.

One case study also highlights the peculiar trajectory that atoll lagoons can experiment, which may call for island-specific management actions. Following an unusually long harmful algal bloom in 2013-2014, Takaroa Atoll experienced a mass mortality that still seems to impact the pearl oyster population 5 years later. Indeed, in Monaco et al. (2021, Task 4.1), DEB simulation results (Sangare et al. 2020, Task 4.1) were compared against the oyster growth rates and reproduction measured *in situ* during 6 months in 2019. The environmental conditions (temperature, chl a) were suitable but growth was sub-optimal, suggesting despite positive news (almost no mortalities observed in 6 months) that the oysters' physiological maintenance costs were too high. In fact, despite abundant chl a levels, it was concluded by Monaco et al. (2021) that oysters were still nutritionally deprived five years after the algal bloom. Two consequences arose: first, it remains necessary to better characterize the spatiotemporal variation of phytoplankton communities and food sources, as it was done in Ahe in 2008-2009 (e.g., Lefebvre et al. 2012, Michotey et al. 2012), and go beyond the chl a > 2 μ m

proxy routinely used in models to represent the food that adult oysters should ingest (Thomas et al. 2016, Sangare et al. 2020, Task 4.1). For instance, continued presence in 2019 of toxic phytoplanktonic organisms (Rodier et al. 2019) could be a factor to explain the paradox. Micro-plastics could also be responsible of the poor use of apparently abundant food (Gardon et al. 2021). Further, Monaco et al. (2021) recommend to restructure the DEB model to be able to use these different phytoplankton components and to represent them adequately in the oyster feeding and maintenance components. These improvements should be coupled with the continuous monitoring of the environment.

Four papers contribute to a better understanding of the lagoon biogeochemical functioning and ultimately foster the development of biophysical models for pearl farming lagoons. Similar to the setup of 3D circulation models that require specific in situ data for calibration and validation (see above), biogeochemical models need specific deployment and data, both pelagic and benthic. The recycling and pathways of key elements (carbon, oxygen, dissolved nutrients) remain poorly documented in atolls and are relevant in the context of pearl farming that directly depends on lagoon production, and contribute retroactively to matter recycling through oysters nutrition, respiration and excretion. Considering the existing gaps, new data were collected in 2017 in Ahe Atoll by Grenz et al. (2021, Task 5.2), Rodier et al. (2021, Task 5.2) and Lefebvre et al. (2022, Task 2.3, 4.2, 5.2). Grenz et al. (2021) investigated the exchanges of oxygen and nutrient at the sediment-water interface by means of transparent and dark benthic chambers deployed in less than 20 meter deep, where the light regime is optimal. They quantified how the sediment water interface combines daylight production controlled by microphytobenthic algae and bacterial degradation of organic matter at night. The ratio (>1) between gross oxygen production and the sediment oxygen demand pointed out to the autotrophic state of the sediment water interface in Ahe lagoon. The balance between the processes at the sediment interface promotes the recycling of nutrients and contribute to the release of oxygen in the lagoon. Rodier et al. (2021) focus on water column processes, namely on carbon production for the sized-fractioned phytoplankton ($<2\mu m$, $>2\mu m$) relevant for oysters nutrition (see also Lefebvre et al. 202) and on the never studied nitrogen (ammonium and nitrite-nitrate) uptake and. They also looked at phytoplankton total stock, and types of communities present during the survey. They worked in hydrodynamically distinct areas of the lagoon, following Dumas et al. (2012). Phytoplanktonic biomass and primary production was dominated by the $<2\mu m$ fraction throughout the lagoon, but the nanophytoplankton contribution was far from negligible (~25%). Nitrogen uptakes were more balanced between

fractions. Results show the general importance of regenerated production and the fast internal nutrient recycling which controls a relatively high productivity, but also the spatial heterogeneity of biogeochemical processes across the Ahe lagoon, in the standard trade wind conditions that prevailed during the experiment. Similar conclusions can be expected for other large and structurally complex lagoons (Andréfouët et al. 2020, Task 2.1). Using the results from these two in situ studies, Seceh et al. (2021, Task 4.1) initiated the new biogeochemical ECO3M-Atoll model, which in addition to the previous models for tropical lagoons (Faure et al. 2010), also included compartments for both sized-fractioned phytoplankton ($<2\mu m$, $>2\mu m$) relevant for oysters nutrition. The model describes both the carbon and nitrogen cycles and consists of six compartments that use either carbon or nitrogen concentrations: pico and nano phytoplankton, bacteria, detritic particulate organic matter, and labile dissolved organic matter. In addition, inorganic matter compartment contains ammonium, nitrate + nitrite (NOx), and dissolved oxygen. Chlorophyll a, which is a diagnostic variable and the key variable ultimately expected from the model for pearl farming application, is calculated from the pico and nano phytoplankton's internal N/C ratio. The 0D (non-spatial) version of the model was used to assess first how pico and nano-planktonic biomass could be predicted according to different hypotheses on nitrogen sources and cycling, some that remain to be explored in the field. Nitrogen uptake and primary production from both fractions were in the range of observed values. Finally, in order to bridge gaps between too few in situ data and abundant modelling data, the mapping of lagoonal chlorophyll concentrations from high resolution satellite sensors was attempted by Lefebvre et al. (2022, Task 2.3, 4.2, 5.2) to provide regular snapshot of the trophic conditions of Ahe Atoll deep lagoon, and how it affects oyster life-traits in space and time. A time-series of 153 Landsat images was processed with standard ocean colour algorithms. In situ validation data and cross-comparison with other space missions allowed to perform a robust assessment of a never-seen-before spatiotemporal view of chl a variation, from 2013 to 2021. Seasonal changes were confirmed, but long-term changes in these cycles were also apparent. Intra-lagoon spatial variations are also discussed in relation to the atoll hydrodynamics and oyster populations. Indeed, to take advantage of the chl a time series, a bioenergetic modeling exercise estimated how the oyster life history traits also changed during the studied period, for three lagoon locations already studied by Sangare et al. (2020). The outputs highlighted the variations in pelagic larval duration (11 to 28 days), time to reach commercial size (20 to 35 months) and reproductive outputs (0.8 to 1.7 event year¹). After these four studies, the next biogeochemical steps will be the coupling of the biogeochemical model with a 3D hydrodynamical model and a DEB model. Such integration will allow better control and understanding on, for instance, larval dispersal simulations.

The last study of the special issue by André et al. (2022, Task 7.3) illustrates one of the tool envisioned by the MANA project for managers, namely marine spatial planning for lagoons experiencing pearl farming issues. The 'lagoon spatial planning' case study is Takaroa Atoll that have experienced, as explained above, a mass mortality event in 2013 and 2014 that stopped all farming activities, till today (Rodier et al. 2021, Task 5.2; Monaco et al. 2021, Task 4.1). The planning exercise investigated how to identify restocking areas using a variety of spatial criteria, including oyster habitat suitability, bathymetry, intra-lagoon connectivity, fishing activity, existing farming concessions, and accumulation of pearl farming wastes. The spatial optimization problem to solve, with areas to include to meet the objectives and others to not-include to avoid impacting other activities is a classical systematic planning exercise, but it is the first time to our knowledge that it was applied to a pearl farming lagoon. The exercise requires significant amount of data that may not be easily available elsewhere. As such, it also reinforces the need to continue the acquisition of baseline data in pearl farming sites, especially the key ones. Some to acquire may have to be acquired only once (bathymetry) while others could be revisited from time to time using DRM staff with technical expertise (stock assessment, waste surveys). Finally, others require significant expertise and can be acquired only through large projects like MANA (data for hydrodynamic or DEB modelling, larval dispersal, etc.).

The challenge of transferring new scientific knowledge to pearl farmers

Transferring new data and knowledge to managers and pearl farmers is a challenge. There are recurrent complaints by the professionals that scientific knowledge and new results published in scientific peer-reviewed English language journals are simply not accessible due their format and language, not vulgarized enough, or outdated since it may take years before some results get published. All these criticisms are unfortunately basically right. The problem of indepth transfers and discussions on new results is even more acute considering that farmers are located in remote and not easily accessible places.

In the past, DRM and its overarching ministry always had various initiatives to transfer valuable information to professionals: yearly scheduled meeting dedicated to the farming industry, seminars at the end of a given project, publication of newsletters, on-site information meeting open to all when DRM agents are visiting a farming site. New management

committee now established on almost all farming islands and atolls also offer a one-stop location to disseminate information, should the committee expand further the dissemination to all farmers during their own subsequent local meetings.

For the MANA project, a specific effort was launched to disseminate new knowledge and results to the pearl farming community at the end of the project. For this, a 60-page special issue of the newsletter *Te Reko Parau* (or the *Voice of the oyster*) will be released in 2022 (past issues can accessed @ http://www.ressources-marines.gov.pf/cdi/te-reko-parau/). Its content was discussed with DRM and selected farmers, and will include a series of fact sheets on 4 broad topics related to the MANA project: Climate and hydrodynamics of lagoons; Oyster Biology; Applications; and Synthesis (Figure 4). The 20 fact-sheets include both overview and general knowledge reminders (on *P. margaritifera* lifecycles for instance) and fresh knowledge often not yet published in peer review journals (such as results of hydrodynamic and larval dispersal models, or stock assessments). Hence, this *Te Reko Parau* special issue will be a vulgarization issue complementary both to the present special issue, and to future peer-reviewed publications as well.

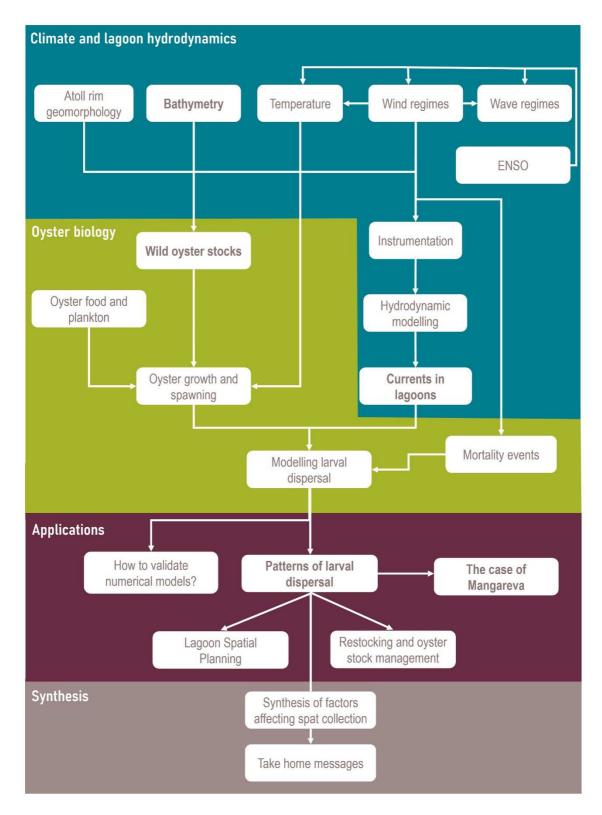


Figure 4: Architecture of the information flow and items that are the objects of a specific vulgarization publication aimed at professionals and edited by DRM. Items in bold are presenting results for specific sites (Raroia, Ahe, Takaroa, Takapoto, etc), for instance bathymetry, stock assessments or larval dispersal results, while others are generic. The arrows point to the influence of some factors to others, for instance the wind and wave climates control lagoon circulation, and themselves they all influence the oyster biology or larval dispersal. This overall canvas should help farmers better realize why some aspects of this flow chart are scientifically studied.

Short and long term atoll modelling perspectives for pearl farming

The results presented in this special issue mark methodological steps towards new multi-atoll knowledge and towards the finalization of the products and tools that the MANA project must deliver at its completion. For instance, the provisions of connectivity matrices for each studied atoll and each wind regime (Dutheil et al. 2021) should be delivered at the end of the project. These results are necessary for DRM to be able to select optimal restocking and collecting zones. The results will also serve spatial planning scenarios that, by design, integrate other activities and constraints like artisanal fishing (André et al. 2022, Task 7.3). André et al. (2021b, Task 7.3) reported that pearl farming has not been included in any of the systematic planning scenarios discussed thus far for Pacific islands. However, case studies now include applications relevant to pearl farming for Gambier and Takaroa (André et al. 2022, Task 7.3). Last field surveys, that were delayed by the COVID pandemic or planed at the end of the year 2021, include additional stock assessment (in Gambier, Takapoto, Takaroa and Apataki). The initial coupling of DEB and biogeochemical model with the 3D circulation model of Ahe Atoll are part of completed or almost completed PhD theses (Sangare 2019, Task 4.2, 4.3), and finalization of realistic modelling scenarios are on-going.

On the long term, in line with MANA biophysical coupled model developments, and should further experiment, in situ and numerical, are planned, it must be pointed out that their calibration and the validation of the outputs is getting increasingly complex, costly, and risky. For instance, the accurate and rigorous validation of the various components of a realistic dispersal scenario should include simultaneous measurements of adults' reproduction status, hydrodynamical and hydrobiological conditions, and larval densities and sizes in the lagoon. All this should ideally be monitored during several weeks to be able to capture the dispersal of a cohort throughout its pelagic larval duration, until their recruitment on an array of experimental spat collectors, and possibly on several pearl farming atolls. Ideally, several periods throughout a year should be investigated, at least during the warm and fresh seasons that are empirically known to yield different spat collecting successes. Finally, a tight spatial sampling design can be required to characterize entire lagoons and capture their inner variability. The deployment and subsequent analyses of such ambitious field program would quickly become in remote areas a significant costly logistical challenge, representing the functioning cost of the entire MANA project. The risk is that it is also possible to not capture any strong signal in the case of limited spawning. The integration of other approaches, such as

genetics, can offer powerful validation but it also poses sampling challenges on their own (Andréfouët et al. 2021b, Task 7.1).

Because using for management model outputs without any form of validation is out of the question, the risks, costs and practical aspects of field work for model validation need to be carefully balanced. Some aspects of the model outputs need to be rigorously validated with field observations, while others could be assessed through sensitivity analyses. Nevertheless, to develop models on new lagoons, the first foundation steps are to characterize the hydrodynamical patterns under different wind and waves conditions. This can lead to operational physics-based only products immediately useful for lagoon management. Conversely, operational use of coupled 3D biophysical models with a DEB and/or biogeochemical remains even today a distant perspectives and require much more work, including for validation. Unfortunately, thus far, it has been difficult for DRM and scientists to collect in space and time vast amount of data through the farmers themselves. This type of participatory science is certainly to be developed in the future, but how to achieve it remains unclear due to the limited logistics and free time available on most farms.

Beyond the topics at the epicentre of the MANA developments (Figure 3), further aspects need to be included in the future that were not seen at the launch of the MANA project. For instance, the growing evidences that micro-plastics could affect reproductive potential, and possibly other physiological processes at all life stages as well, need to be considered. The characterization of the micro-plastic load of pearl farming lagoons and its implications for oyster populations has started recently (Gardon et al. 2021) and, if impacts are confirmed, it can be predicted that it will be an additional component to include in both physiological and biophysical models, possibly even with a higher priority than climate change scenarios.

Eventually, DRM in French Polynesia and other management entities such as the Ministry of Marine Resources in Cook Islands should benefit from numerical models through different avenues, after the completion of the scientific calibration/validation tasks and proof-of-concept case studies such as those presented in this special issue. Numerical models allow to:

 Revisit the past: hindcasting specific past events and periods can bring critical clues for understanding variation in spat collecting abrupt or gradual, mass mortalities due algal blooms or anoxia, and revisit some biological or physical data collected in the past but lacking environmental context. Note that these tools can be used beyond the case of black pearl farming, as similar problems have plagued non farming lagoons and other resources such as giant clams (Adjeroud et al. 2003, Andréfouët et al. 2013, Andréfouët et al. 2015).

- Manage *Pinctada margaritifera* stocks: pearl farming need oysters, and the question of the sustainability of the stock is a top priority. The first application of the numerical tools, in their simpler former (3D circulation) or in their more sophisticated version (3D coupled biophysical) is to guide the identification of restocking areas, in order to use locations that allow maximum dispersal and survival (André et al. 2022). This activity needs to be coordinated with *in situ* stock assessment that could be conducted every 4 or 5 years for instance. If a pearl farming site has been hit by a massive disturbance, such as Takaroa in 2013-2014, it is also necessary to monitor if the conditions are adequate again before restocking (Monaco et al. 2021). Enhanced DEB models (at individual or ecosystem scale) can help checking if the environmental conditions are suitable to meet the growth and reproduction levels necessary for sustainable farming.
- Better monitor the lagoons, with an adaptive approach: To enhance in situ monitoring, results from numerical modelling also allows to better define where sampling should take place, since hydrodynamical structures or connectivity pathways can be inferred from the model outputs. Hydrodynamical models require cal/val data, and physical data acquisition are required. Deploying instruments for several months to one year is challenging but allows capturing a range of events and processes that can be representative of most conditions. Several studies presented here investigated different ways to increase the spatio-temporal coverage of biophysical monitoring. Both sea surface temperature and chl a are key variables to keep looking at, using remote sensing data when suitable, namely for deep and large lagoons as discussed in Van Wynsberge et al. (2021) and Lefebvre et al. (2022). Finally, we recognize that it will be probably impossible to monitor in situ or remotely all lagoons. Therefore, a sub-selection of representative sites is sound, yet, it must be necessary to be able to change priorities quickly due to unseen circumstances. Adaptive approaches are required considering the likely future occurrences of heatwaves, algal blooms and mortalities. Thus far, scientific monitoring has always been deployed a step too late during the heavy environmental crisis reported for pearl farming sites.
- Prioritize zones and foster multi-activity spatial planning: spatial biophysical models help characterize the spatial dynamics of a lagoon submitted to different oceanic and atmospheric forcing that are also dynamics. A lagoon is constantly changing, but standard

recurrent behaviours can emerge in the form of 'biophysical regimes'. The spatial patterns occurring during these frequent regimes can be used to define areas reserved for farming or spat collecting, or conversely to define areas on which no farming-related activities can occur. Depending on the lagoon, other activities, such as fishing or tourism, can also play a major role and spatial planning is necessary to optimize the use of a lagoon, at least by presenting to all parties the challenges at stake in a spatially-explicit way. It is expected that outputs from biophysical models will increasingly contribute to these plans, still often conducted on an *ad hoc* basis.

• Forecast the future of lagoons: predicting what would be the spat collecting potential in a year from now, understanding how warmer a lagoon will be in 30 years, or anticipating the evolution of atolls under sea level rise in 100 years are legitimate questions for farmers, managers, and for all the people of the Central Pacific Ocean islands and atolls. However, as of today, and similar to weather predictions, the short time scale questions (e.g., prediction of spat collecting from one year to the next, or even season to the next) remain extremely difficult. The products mentioned just above can provide probabilities of the occurrence of different physical regimes that should lead to specific dispersal patterns. Yet, without precise knowledge of food conditions and physiological status of oyster populations, uncertainty levels are high.

In conclusion, among the five main types of applications of biophysical numerical models listed above, four are already happening or are close to happen (Revisit the past, Monitor better the lagoons, Manage *Pinctada margaritifera* stocks, Prioritize zones and foster multi-activity spatial planning) as demonstrated by the papers of this special issue. The last application (Forecast the future of lagoons) drives several of the developments required for other applications, but its operationalization still remains a far perspective.

Acknowledgements

This study was funded by grant ANR-16-CE32-0004 MANA (Management of Atolls project). MALIS 1 and MALIS 2, two oceanographic cruises in Raroia Atoll on board R/V Alis (https://doi.org/10.17600/18000582) made this work possible. It was also co-funded by the *Direction des Ressources Marines* OTI project, *Contrat de Projet* France-French Polynesia, Program 123, Action 2, 2015-2020. We acknowledge the implications of Pat Hutching and Bruce Richardson as MPB editors in supervising this special issue as well as the

MPB/Elsevier staff for their help. We are also grateful to inhabitants, farmers, and mayors of all the studied sites for their help during fieldwork. Last but not least, many thanks to the 27 reviewers who accepted to share their expertise and improve each paper of this special issue.

References

- Adjeroud, M., Andréfouët, S., Payri, C., 2001. Mass mortality of macrobenthic communities in the lagoon of Hikueru atoll (French Polynesia): Coral Reefs 19, 287–291. https://doi.org/10.1007/PL00006962
- André, L.V., Van Wynsberge, S., Chinain, M., Andréfouët, S., 2021a. An appraisal of systematic conservation planning for Pacific Ocean Tropical Islands coastal environments. Marine Pollution Bulletin 165, 112131. https://doi.org/10.1016/j.marpolbul.2021.112131
- André, L.V., Van Wynsberge, S., Chinain, M., Gatti, C.M.I., Dempsey, A., Andréfouët, S., 2021b. A framework for mapping local knowledge on ciguatera and artisanal fisheries to inform systematic conservation planning. ICES Journal of Marine Science fsab016. https://doi.org/10.1093/icesjms/fsab016
- André, L.V., Chinain, Gatti, C.M., Liao, V., Van Wynsberge, S., M., Tedesco, P., Andréfouët, S., 2022. A systematic prioritization approach for identifying suitable pearl oyster restocking zones following a mass mortality event in Takaroa Atoll, French Polynesia. Marine Pollution Bulletin, 11347, <u>https://doi.org/10.1016/j.marpolbul.2022.113472</u>
- Andréfouët, S., Charpy, L., Lo-Yat, A., Lo, C., 2012. Recent research for pearl oyster aquaculture management in French Polynesia. Marine Pollution Bulletin 65, 407–414. https://doi.org/10.1016/j.marpolbul.2012.06.021
- Andréfouët, S., Van Wynsberge, S., Gaertner-Mazouni, N., Menkes, C., Gilbert, A., Remoissenet, G., 2013. Climate variability and massive mortalities challenge giant clam conservation and management efforts in French Polynesia atolls. Biological Conservation 160, 190–199. https://doi.org/10.1016/j.biocon.2013.01.017
- Andréfouët, S., Thomas, Y., Lo, C., 2014. Amount and type of derelict gear from the declining black pearl oyster aquaculture in Ahe atoll lagoon, French Polynesia. Marine Pollution Bulletin 83, 224–230. https://doi.org/10.1016/j.marpolbul.2014.03.048
- Andréfouët, S., Dutheil, C., Menkes, C.E., Bador, M., Lengaigne, M., 2015. Mass mortality events in atoll lagoons: environmental control and increased future vulnerability. Global Change Biology 21, 195–205.
- Andréfouët, S., Thomas, Y., Dumas, F., Lo, C., 2016. Revisiting wild stocks of black lip oyster Pinctada margaritifera in the Tuamotu Archipelago: The case of Ahe and Takaroa atolls and implications for the cultured pearl industry. Estuarine, Coastal and Shelf Science 182, 243–253. https://doi.org/10.1016/j.ecss.2016.06.013
- Andréfouët, S., Van Wynsberge, S., Kabbadj, L., Wabnitz, C.C.C., Menkes, C., Tamata, T., Pahuatini, M., Tetairekie, I., Teaka, I., Scha, T.A., Teaka, T., Remoissenet, G., 2018. Adaptive management for the sustainable exploitation of lagoon resources in remote islands: lessons from a massive El Niño-induced giant clam bleaching event in the Tuamotu atolls (French Polynesia). Envir. Conserv. 45, 30–40. https://doi.org/10.1017/S0376892917000212
- Andréfouët, S., Genthon, P., Pelletier, B., Le Gendre, R., Friot, C., Smith, R., Liao, V., 2020. The lagoon geomorphology of pearl farming atolls in the Central Pacific Ocean revisited using detailed bathymetry data. Marine Pollution Bulletin 160, 111580. https://doi.org/10.1016/j.marpolbul.2020.111580

- Andréfouët, S., Le Gendre, R., Thomas, Y., Lo-Yat, A., Reisser, C.M.O., 2021. Understanding connectivity of pearl oyster populations within Tuamotu atoll semiclosed lagoons: Cumulative insight from genetics and biophysical modelling approaches. Marine Pollution Bulletin 167, 112324. https://doi.org/10.1016/j.marpolbul.2021.112324
- Andréfouët, S., Desclaux, T., Buttin, J., Swen, J., Aucan, J., Le Gendre, R., Liao, V., 2022. Periodicity of wave-driven flows and lagoon water renewal for 73 Central Pacific Ocean atolls Marine Pollution Bulletin. in press.
- Aucan, J., Desclaux, T., Le Gendre, R., Liao, V., Andréfouët, S., 2021. Tide and wave driven flow across the rim reef of the atoll of Raroia (Tuamotu, French Polynesia). Marine Pollution Bulletin 171, 112718. https://doi.org/10.1016/j.marpolbul.2021.112718
- Bell, J.D., Adams, T.J. Johnson, J.E. Hobday, A.J. Gupta, A.Sen. 2011. Chap. 1. Pacific Communities, Fisheries, Aquaculture and Climate Change: An Introduction. In Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change; Bell, J. D., Johnson, J.E., Hobday, A.J., Eds.; Secretariat of the Pacific Community: Noumea, New Caledonia,; pp 1–48.
- Dumas, F., Le Gendre, R., Thomas, Y., Andréfouët, S., 2012. Tidal flushing and wind driven circulation of Ahe atoll lagoon (Tuamotu Archipelago, French Polynesia) from in situ observations and numerical modelling. Marine Pollution Bulletin 65, 425–440. https://doi.org/10.1016/j.marpolbul.2012.05.041
- Dutheil, C., Andrefouët, S., Jullien, S., Le Gendre, R., Aucan, J., Menkes, C., 2020. Characterization of south central Pacific Ocean wind regimes in present and future climate for pearl farming application. Marine Pollution Bulletin 160, 111584. https://doi.org/10.1016/j.marpolbul.2020.111584
- Dutheil, C., Bador, M., Lengaigne, M., Lefèvre, J., Jourdain, N.C., Vialard, J., Jullien, S., Peltier, A., Menkes, C., 2019. Impact of surface temperature biases on climate change projections of the South Pacific Convergence Zone. Clim Dyn 53, 3197–3219. https://doi.org/10.1007/s00382-019-04692-6
- Dutheil, C., Jullien, S., Aucan, J., Menkes, C., Le Gendre, R., Andréfouët, S., 2021. The wave regimes of the Central Pacific Ocean with a focus on pearl farming atolls. Marine Pollution Bulletin 162, 111751. https://doi.org/10.1016/j.marpolbul.2020.111751
- Faure, V., Pinazo, C., Torréton, J.-P., Jacquet, S., 2010. Modelling the spatial and temporal variability of the SW lagoon of New Caledonia I: A new biogeochemical model based on microbial loop recycling. Marine Pollution Bulletin 61, 465–479. https://doi.org/10.1016/j.marpolbul.2010.06.041
- Gardon, T., El Rakwe, M., Paul-Pont, I., Le Luyer, J., Thomas, L., Prado, E., Boukerma, K., Cassone, A.-L., Quillien, V., Soyez, C., Costes, L., Crusot, M., Dreanno, C., Le Moullac, G., Huvet, A., 2021. Microplastics contamination in pearl-farming lagoons of French Polynesia. Journal of Hazardous Materials 419, 126396. https://doi.org/10.1016/j.jhazmat.2021.126396
- Grenz, C., Rodier, M., Seceh, C., Varillon, D., Haumani, G., Pinazo, C., 2021. Benthic nutrients and oxygen fluxes at the water sediment interface in a pearl farming atoll (Ahe, Tuamotu, French Polynesia). Marine Pollution Bulletin 173, 112963. https://doi.org/10.1016/j.marpolbul.2021.112963
- Gueguen, Y., Gaertner-Mazouni, N., Lo, C., Le Moullac, G., 2016. Integrated management of pearl culture in French Polynesia in the context of global change: Synopsis of existing results. Estuarine, Coastal and Shelf Science 182, 229–234. https://doi.org/10.1016/j.ecss.2016.07.010
- Le Moullac, G., Soyez, C., Vidal-Dupiol, J., Belliard, C., Fievet, J., Sham-Koua, M., Lo-Yat, A., Saulnier, D., Gaertner-Mazouni, N., Gueguen, Y., 2016. Impact of pCO2 on the

energy, reproduction and growth of the shell of the pearl oyster *Pinctada margaritifera*. Estuarine, Coastal and Shelf Science 182, 274–282. https://doi.org/10.1016/j.ecss.2016.03.011

- Lefebvre, S., Claquin, P., Orvain, F., Véron, B., Charpy, L., 2012. Spatial and temporal dynamics of size-structured photosynthetic parameters (PAM) and primary production (13C) of pico- and nano-phytoplankton in an atoll lagoon. Marine Pollution Bulletin 65, 478–489. https://doi.org/10.1016/j.marpolbul.2012.04.011
- Lefebvre, S., Verpoorter, C., Rodier, M., Sangare, N., Andréfouët, S. Remote sensing provides new insights on phytoplankton biomass dynamics and black pearl oyster life history-traits in a Pacific Ocean deep atoll. Submitted to Marine Pollution Bulletin
- Lo-Yat, A., et al. Mismatch between the ecological processes driving early life-stage dynamics of bivalves at two contrasting French Polynesian lagoons. Marine Pollution Bulletin en revision
- Michotey, V., Guasco, S., Boeuf, D., Morezzi, N., Durieux, B., Charpy, L., Bonin, P., 2012. Spatio-temporal diversity of free-living and particle-attached prokaryotes in the tropical lagoon of Ahe atoll (Tuamotu Archipelago) and its surrounding oceanic waters. Marine Pollution Bulletin 65, 525–537. https://doi.org/10.1016/j.marpolbul.2012.01.009
- Monaco, C.J., Sangare, N., Le Moullac, G., Basset, C., Belliard, C., Mizuno, K., Smith, D.L., Lo-Yat, A., 2021. Dynamic Energy Budget model suggests feeding constraints and physiological stress in black-lip pearl oysters, 5 years post mass-mortality event. Marine Pollution Bulletin 167, 112329. https://doi.org/10.1016/j.marpolbul.2021.112329
- Pagano, M., Rodier, M., Guillaumot, C., Thomas, Y., Henry, K., Andréfouët, S., 2017. Ocean-lagoon water and plankton exchanges in a semi-closed pearl farming atoll lagoon (Ahe, Tuamotu archipelago, French Polynesia). Estuarine, Coastal and Shelf Science 191, 60–73. https://doi.org/10.1016/j.ecss.2017.04.017
- Reisser, C.M.O., Gendre, R.L., Chupeau, C., Lo-Yat, A., Planes, S., Andréfouët, S., 2020. Population Connectivity and Genetic Assessment of Exploited and Natural Populations of Pearl Oysters within a French Polynesian Atoll Lagoon. Genes 11, 426. https://doi.org/10.3390/genes11040426
- Rodier, M., Longo, S., Henry, K., Ung, A., Lo-Yat, A., Darius, H., Viallon, J., Beker, B., Delesalle, B., Chinain, M., 2019. Diversity and toxic potential of algal bloom-forming species from Takaroa lagoon (Tuamotu, French Polynesia): a field and mesocosm study. Aquat. Microb. Ecol. 83, 15–34. https://doi.org/10.3354/ame01900
- Rodier, M., Pinazo, C., Seceh, C., Varillon, D., 2021. Pelagic stocks and carbon and nitrogen uptake in a pearl farming atoll (Ahe, French Polynesia). Marine Pollution Bulletin 167, 112352. https://doi.org/10.1016/j.marpolbul.2021.112352
- Sangare, N., Lo-Yat, A., Le Moullac, G., Pecquerie, L., Thomas, Y., Beliaeff, B., Andréfouët, S., 2019. Estimation of physical and physiological performances of blacklip pearl oyster larvae in view of DEB modeling and recruitment assessment. Journal of Experimental Marine Biology and Ecology 512, 42–50. https://doi.org/10.1016/j.jembe.2018.12.008
- Sangare, N., Lo-Yat, A., Moullac, G.L., Pecquerie, L., Thomas, Y., Lefebvre, S., Gendre, R.L., Beliaeff, B., Andréfouët, S., 2020. Impact of environmental variability on *Pinctada margaritifera* life-history traits: A full life cycle deb modeling approach. Ecological Modelling 423, 109006. https://doi.org/10.1016/j.ecolmodel.2020.109006
- Seceh, C., Pinazo, C., Rodier, M., Lajaunie-Salla, K., Mazoyer, C., Grenz, C., Le Gendre, R., 2021. Biogeochemical model of nitrogen cycling in Ahe (French Polynesia), a South Pacific coral atoll with pearl farming. Marine Pollution Bulletin 169, 112526. https://doi.org/10.1016/j.marpolbul.2021.112526

- Thomas, Y., Dumas, F., Andréfouët, S., 2016. Larval connectivity of pearl oyster through biophysical modelling; evidence of food limitation and broodstock effect. Estuarine, Coastal and Shelf Science 182, 283–293. https://doi.org/10.1016/j.ecss.2016.03.010
- Van Wynsberge, S., Menkes, C., Le Gendre, R., Passfield, T., Andréfouët, S., 2017. Are Sea Surface Temperature satellite measurements reliable proxies of lagoon temperature in the South Pacific? Estuarine, Coastal and Shelf Science 199, 117–124. https://doi.org/10.1016/j.ecss.2017.09.033
- Van Wynsberge, S., Le Gendre, R., Sangare, N., Aucan, J., Menkes, C., Liao, V., Andréfouët, S., 2020. Monitoring pearl farming lagoon temperature with global high resolution satellite-derived products: An evaluation using Raroia Atoll, French Polynesia. Marine Pollution Bulletin 160, 111576. https://doi.org/10.1016/j.marpolbul.2020.111576
- Zanini, J., 1999. Stocks naturels de nacres *Pinctada margaritifera* de Polynésie française. PhD thesis. École Pratique des Hautes Études, Perpignan, 199 p.