



Editorial

Recent research for pearl oyster aquaculture management in French Polynesia

1. Introduction

The papers on Ahe Atoll (Fig. 1) compiled in this volume release fresh scientific information relevant for a fairly specific human activity, currently developed mostly in the South Pacific and especially in atolls: black pearl aquaculture. Pearl farming is a commercial activity more than a century-old. It includes the farming of white and gold pearls in Asia and Australia, in both fresh and marine waters. Conversely, black pearl farming is more recent, and mostly associated with Pacific Islands where the production is the highest, and especially from French Polynesia which has dominated the market for the past 20 years (Southgate and Lucas, 2008).

As a human activity conducted in natural lagoon environments, the general topic is of interest for *Marine Pollution Bulletin*. This journal has published papers on a wide array of topics describing the marine environment, its use by human activities, and the related impacts. The suite of manuscripts presented on this special issue on “Ahe Atoll and Pearl Oyster Aquaculture in the Tuamotu Archipelago” investigated Ahe Atoll’s oceanic wave regime, lagoon hydrodynamics, oyster larval dispersal, reproduction of oysters, lagoon hydrology, phytoplankton and zooplankton communities, oyster’s diet, planktonic food webs, and impacts of the farming activity on the lagoon sediments and picoplankton communities. Several of the papers published in this volume tackle subjects that are generally published in journals specialized in aquaculture and biology, but with the huge emergence of aquaculture in recent decades has come greater recognition that the practice is commonly accompanied by deleterious changes. The papers here include eco-physiological papers focused on the pearl oyster *Pinctada margaritifera* and the description of plankton communities. However, all the papers are connected (see below a synthesis of the results) and collectively provide a multidisciplinary and integrated view of a lagoon ecosystem which is seldom available. We are pleased that these papers are published side by side in this issue, for the benefits of scientists and managers interested by human activities in lagoon environments.

2. The aquaculture of pearl oyster in French Polynesia

Black pearl production in French Polynesia tropical lagoons turned in 40 years from the status of a South Seas adventure to the status of an industry, as the second source of income for the country at the end of 1990s, after tourism. In the best years (Fig. 2), black pearl represented 60 MUS\$ of income for a country of 250,000 inhabitants. Beyond the magnificent jewel, beyond

the beauty of the myriad of colors, lusters and shapes, beyond the prized value, beyond the unique human culture and know-how found around pearl farms, black pearls are fascinating for scientists because they represent the ultimate product of both an exploited lagoon ecosystem and an exploited bivalve, the black lip oyster *Pinctada margaritifera* (Linnaeus, 1758) var. *cumingii* (Jameson, 1901).

Pearl production has always been challenging for the suite of numerous factors and processes that need to be understood and mastered before a black pearl materialize in the hand of a farmer. Throughout the 19th and first half of the 20th century, *P. margaritifera* oysters were harvested by free-divers only for the nacre, and button, industry. Sometimes, natural black pearls were found. In French Polynesia, in 1961, the first attempt to graft oysters with the goal of producing cultivated round pearls was successfully achieved in Hikueru atoll by Jean-Marie Domard and Churoku Muroi. The first farm was established in Manihi atoll in 1968. The two following decades saw the slow rise of a new commercial activity with production in Tuamotu and Gambier archipelagos (e.g., Marutea Sud), with black pearls acquiring the status of high quality gems in international jewellery markets. By the end of the eighties, both archipelagos experienced a black pearl rush, with thousands of Polynesian and foreigners workers returning to remote atolls. Hundreds of new concessions were granted per year on a variety of lagoons. Production rose quickly. Experiments of all kind followed to achieve the most efficient collecting and farming possible, often in logistically challenging remote conditions. Spat collecting was critical. Indeed, the pearl industry required before all the provision of oysters. They were initially harvested from wild stocks, and spat collecting developed rapidly in suitable lagoons to steadily provide to farmers the oysters needed for grafting. Enhanced farming practices yielded an average successful rate of 300–400 sellable pearls for 1000 grafted oysters. On the other hand, transfers of oysters between atolls were frequent, making local populations and lagoons vulnerable to extinction, diseases, and spread of invasive epibionts species. Dedicated governmental services were created to manage and monitor the environmental and socio-economic consequences of what was virtually an entire new field of economic activity coming out of the blue of the Tuamotu and Gambier lagoons. Quickly, despite the growing empirical knowledge developing among farmers, better knowledge of lagoon ecosystem functioning and suitability for pearl farming were needed. This included better knowledge on the physiology of *P. margaritifera*. Scientific research programs were launched, and both lagoon ecosystems and organisms came under the scrutiny of applied and fundamental studies.

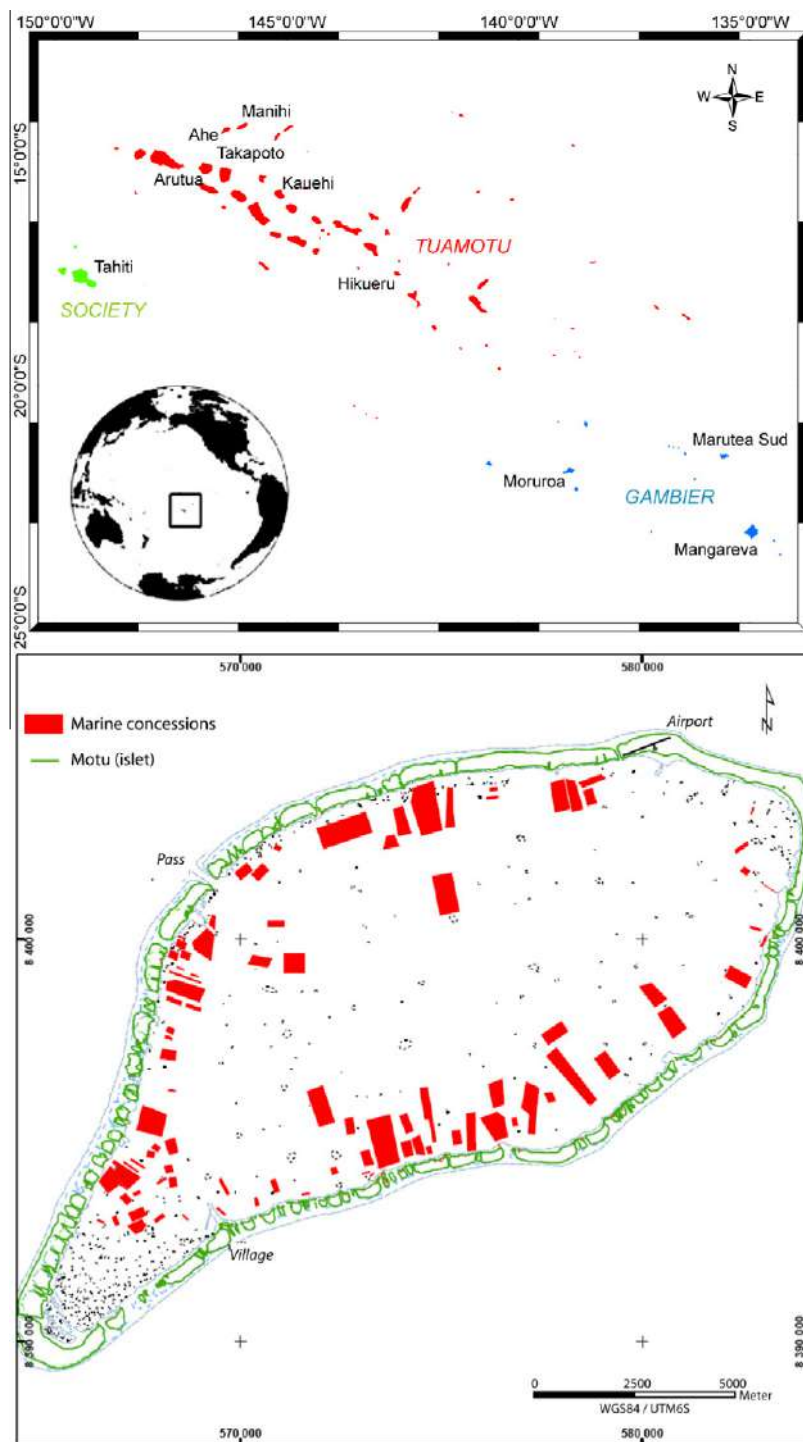


Fig. 1. Top: location map of French Polynesia and Ahe atoll, as well as other sites mentioned in the text. Bottom: map of marine concessions in Ahe atoll, as in 2012. To be compared with the same map in Andréfouët et al. (2006).

In 2011, time came to take a pause and look at the evolution of the situation 20 years after the industry boom. It was also time to assess the status of knowledge and what would be the new priorities. Indeed, like a natural ecosystem, the French Polynesia black pearl industry has reached its climax, collapsed, and is now in a recovery stage. The official numbers from the *Institut de la Statistique de Polynésie Française* (ISPF) show the changes in total exported production, monetary value per gram and total number of concessions since these variables are monitored (Figs. 2 and 3).

Prices collapsed in the year 2000s, due primarily to overproduction of lowest quality pearls and poor management and control of the commercial distribution towards international Asian, American and European markets. Prices plummeted from around 100US\$ per gram in 1985 down to less than 5US\$ in 2010. Consequently, the number of concessions decreased steadily throughout the Tuamotu and Gambier. In 2010, respectively 425, 102 and 28 concessions were granted for respectively Tuamotu, Gambier (mostly in Mangareva, a high island with a wide lagoon) and Society Archipelagos, thus a total of 555 concessions. In 2011, the last available overall

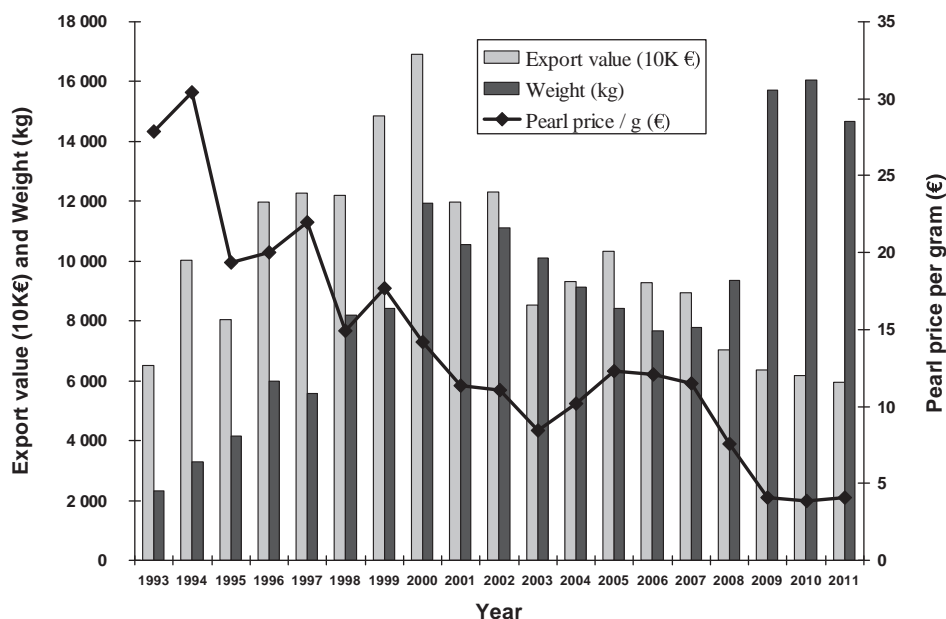


Fig. 2. Evolution from 1993 to 2011 of key indicators: total export value, total weight, and price per gram. Data source: Institut Polynésien de la Statistique.

number is 541. In 1999, 2745 concessions were active. Small family businesses took a heavy toll with the collapse of the prices. They represented in 2011 80% of the farms for 20% of the export market. The total concession area is now limited to 10000 hectares all lagoons included. In 2011, this represented 26 atolls and 4 islands. Among them, 15 atolls are collecting atolls.

The industry is now trying to rebuild the equilibrium between offer and demand, with the hope that curves of prices per pearl and per gram will rise. Pearl quality is closely monitored for exportation. Eleven millions pearls have been controlled in 2010, which represented 18.3 tons. Low quality pearls are destroyed and farmers receive a fixed rate of 0.5 US\$ per destroyed gram as a compensation. In 2010, 400 kg of these poor quality pearls have been disregarded. In addition, commercial promotion and selling networks are also restructured.

The aquaculture of black pearl in French Polynesia has thus modified the livelihoods of thousands of islanders in the past 30 years. It has also reshaped the atollscapes, with numerous farms,

buildings, pontoons and boats appearing and disappearing along shores and coral pinnacles. Tens of thousands of buoys and millions of hanging lines dot the lagoons, spread in the official 10000 hectares of concessions all over French Polynesia. Millions of oysters have been artificially hanging in the water column instead of living on deep atoll floors. Naturally separated oyster populations have been mixed, and species of sponges, anemones (in particular *Aiptasia pallida*) and other epibionts have been introduced in lagoons. Massive local and widespread mortalities have occurred that remain poorly explained due to insufficient *in situ* monitoring of environmental conditions, given the remoteness of atolls and associated monitoring costs. The exact ecological impact of the pearl industry remains unknown to date and will likely be a future direction of investigation. In the past, however, research programs investigated how the lagoon ecosystem carrying capacities could sustain the industry, what could be the best aquaculture practices, and what were the sanitary risks for the cultivated stocks. We review hereafter these past axes of research.

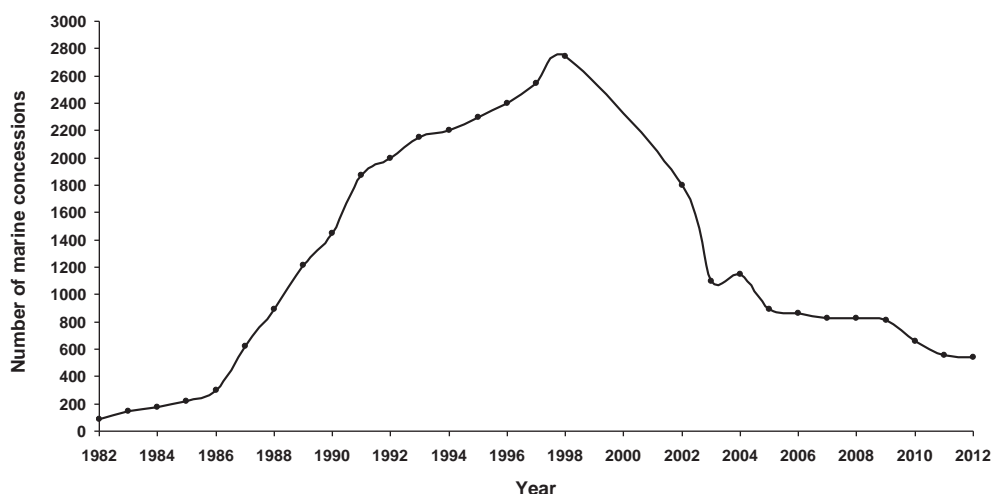


Fig. 3. Thirty years of evolution in number of pearl farming and collecting marine concessions in French Polynesia.

3. Past research on pearl oyster and atoll lagoons

From the early 1980s till to date, research activities have accompanied the black pearl industry. The *Etablissement pour la Valorisation des Activités Aquacoles et Marines* (EVAAM) was created in 1983 to assist farmers and to develop the market. This is in addition to all the empirical individual research activities taking place in farms to enhance spat collecting, grafting, and farming. Initially, research was not seen as a priority by professionals. Confidentiality of knowledge ruled between farmers. However, massive mortalities in 1985–1986 in Takapoto Atoll showed that virtually nothing was known on the interactions between *P. margaritifera* and its environment, its capacity to resist to environmental stressors, and possible pathogens. These assessments were beyond the capacities of farmers alone and new research programs were needed.

Atoll have been studied for decades in French Polynesia and elsewhere, but not always with a focus imposed by one bivalve species and black pearl production. The ATOLL, CYEL, and TYPATOLL projects in particular have looked at general aspects of the ecology and functioning of various atoll lagoons, some specifically selected for their lack of human activities (Dufour and Harmelin-Vivien, 1997). Besides description of planktonic and benthic communities, scientists looked very early at primary production, nutrient limitations and organic matter recycling in both the water column and sediments (Sournia and Ricard, 1975; Charpy and Charpy-Roubaud, 1990; Delesalle and Sournia, 1992; Dufour et al., 2001). The atolls used for nuclear tests (Moruroa and Fangatau) were also intensively studied (Guille et al., 1993; Tartinville et al., 1997). Finfish fisheries were investigated in Tikehau Atoll (Intes et al., 1995). Stocks of giant clams have been studied since at least Salvat (1967) and are still of objects of investigations in the Eastern Tuamotu (Andréfouët et al., 2005; Gilbert et al., 2006). Ciguatera poisoning has also been a major concern for human population health in French Polynesia (Bagnis et al., 1985). Finally, the geology and geomorphology of atolls have been studied and mapped under the light of late Holocene sea level variations, lithospheric processes, and exposure to dominant swell (McNutt and Menard, 1978; Pirazzoli et al., 1988; Andréfouët et al., 2001a).

The *Programme General de Recherche sur la Nacre* (PGRN, standing for Nacre General Research Program), was launched in 1990 and reoriented the research performed on atolls towards black pearl aquaculture issues. The focus set by scientists was primarily on understanding the trophic capacity of the lagoons, and the ecophysiological and metabolic capacities of oysters (feeding regime, growth, reproduction, respiration) as well as its resistance to temperature and high population density stress. The pilot atoll was Takapoto, where a field station allowed running long term *in situ* experiments. In selected lagoons, a network of stations was set with volunteering farmers to monitor environmental conditions (Pouvreau and Prasil, 2001). In addition, research on aquaculture practices focused on the processing of oysters and lines to clean epibionts and trophic competitors. The PGRN aimed to disseminate results to farmers by various means: on site training, newsletters in both French and Tahitian, meetings etc. The program also led to numerous doctoral studies conducted in the new French Polynesia university, and yielded an abundant scientific literature (e.g., Charpy, 1996; Niquil et al., 1998; Zanini and Salvat, 2000; Buestel and Pouvreau, 2000; Torréton et al., 2002). These papers clarified the dominant planktonic communities, trophic flux and limiting nutrients found in atoll lagoons, and their variations according to atoll morphology and hydrodynamic regime (Charpy et al., 1997; Andréfouët et al., 2001b; Dufour et al., 2001).

This first coordinated research, which terminated in October 1999, provided practical advice to farmers to optimize densities, collecting methods, and epibiont clean-ups. It also enhanced knowledge on the biology and ecophysiology of *P. margaritifera* (Pouvreau et al., 2000a,b). It clarified the links between Takapoto environment and oyster physiology and sources of food. A major conclusion was that lagoons (at least Takapoto Atoll) were not food-limiting given their current loads of cultivated animals (Niquil et al., 2001). In atoll lagoons, organic particles < 5 µm (heterotrophic bacteria, autotrophic bacteria and phytoplankton < 5 µm) generally represented more than 70% of the living carbon biomass whereas particles between 5 µm and 200 µm (protozoan, phytoplankton > 5 µm, appendiculates and metazoan larvae) represent less than 30%. PGRN demonstrated that the low retention efficiency of the dominant < 5 µm planktonic communities by *P. margaritifera* was largely offset by the efficient grazing of the larger size-fraction plankton and protozoan (Loret et al., 2000a,b), and by exceptionally high pumping rates (Pouvreau et al., 1999, 2000c; Yukihiro et al., 1998). However, not all aspects of the planktonic food chain were understood, including the role of various zooplankton compartments and the influence of possible competitors.

The PGRN recommendations for a second phase of research were to investigate the risks related to pathogen spreads, the process controlling the quality of the pearl (in particular those controlling the color and mineralization and the influence of the type of nucleus used), and also the influence of environmental parameters on spat collection. Indeed the success of this activity remained highly variable in space and time (Andréfouët et al. 2006). After the PGRN, researches were not anymore necessarily coordinated within a single program. Instead, the *Service de la Perliculture* (Pearl Aquaculture Service) managed since 2002 individual actions with the various research organisms involved in the activities.

Numerous programs were launched in the past five years, using a variety of source of funding. In 2008 and 2009, the PERDUR project aimed for a better resource sustainability and farmers profits (Hui et al., 2011; Thomas et al., 2011a; Yaroshewski, 2011). The ADEQUA research consortium was launched in 2008 to coordinate during 4 years the activities related to the understanding of the quality of the pearl (e.g., Joubert et al., 2010; Linard et al., 2011; Montagnani et al., 2011). Meantime, the project REGENPERL specifically looked at physiologic (Le Moullac et al., 2011) and genetic aspects (Lemer and Planes, 2012) and a network dedicated to the monitoring of sanitary conditions was developed. Larval dispersal in Ahe atoll was studied, and the larval ecology of *P. margaritifera* was characterized leading to the development of a bioenergetic growth model (Thomas et al., 2011b). Finally, late 2007, a European Community funded project was launched under the auspices of the *Service de la Perliculture* to investigate in Ahe Atoll and Takarua Atoll the trophic regime of oysters and the hydrodynamic forcing on spat collection. The compilation of papers published in this special issue and summarized below present the main finding of this project for Ahe Atoll.

4. New results from Ahe atoll

Ahe Atoll was selected by a European Fund for Development project for its major position in the hierarchy of pearl and spat producers. Ahe atoll is located in the North-western part of the Tuamotu Archipelago, 500 km North-East of Tahiti. Its lagoon covers 145 km² with a mean depth close to 40 m and a maximum depth of around 70 m. One active pass is located in the western part of the lagoon and several reef-flat spillways (hoa, less than 50 cm depth) are distributed along the reef rim, mainly in the south and west part sectors (Dumas et al., 2012). The overall aperture is low, and Ahe can be defined as a semi-closed atoll.

In May 2012, 77 farms were registered. They covered 1188 hectares of lagoonal space (Fig. 1). In December 2007, these numbers were respectively 83 farms and 1320 hectares, illustrating the continuous decrease of the activity. The number of authorized collecting stations was 1050 in May 2012, each about 200 m long. The total number of cultivated oysters could represent up to 15 millions oysters.

The bulk of the Ahe project was accomplished between 2008 and 2010, with field work occurring from mid-2008 to end of 2009. Three different activities took place. First, using numerical tools never applied before in the Tuamotu atolls, the objective was to characterize the circulation of the lagoon to understand better the source of variability in spat collecting. Second, the objectives were to characterize the planktonic communities of Ahe lagoon at different seasons also using new investigation approaches never used before in Tuamotu atoll lagoons. As much as possible, the influence of pearl farming on planktonic communities was assessed. Third, biology and ecophysiology of oysters at adult and larval stages was investigated. Reproduction, grazing and larval dispersal were monitored *in situ* in several periods under different environmental conditions. This third project component benefited from additional source of funding.

The hydrodynamic component of the project had two main sub-components following Andréfouët et al. (2006) recommendations: an oceanic and a lagoon sub-component. The oceanic and atmospheric forcing of the atoll was classically studied using meteorological data and model. However, the wave regime of the atoll was characterized at high spatial resolution (5 km) using both wave numerical model and satellite altimetry data (Andréfouët et al., 2012). The study shows that Ahe atoll experienced an atypical wave regime, with lower wave height year round than other Tuamotu atolls. This is due to the level of protection of the atoll provided by south Tuamotu atolls. The consequences are that Ahe's lagoon renewal rate is controlled by tide, and not waves. To precisely study the circulation and renewal rates of Ahe's lagoon, Dumas et al. (2012) implemented a high resolution (100 m) 3D numerical model using the Mars3D software and assumptions, using finite difference techniques in a sigma coordinate framework. The model was calibrated and validated using one year of intensive field data acquisition. It provided simulated quantitative data on the three main residual barotropic structures inside the lagoon, under different wind conditions. This demonstrated that the pass played a major role in the hydroscape of the lagoon. It defined areas of high flushing rates, areas of dilution and areas of retention. Circulation is driven by wind. Wind (generally from the east and south-east directions) creates a general overturning circulation parallel to the wind direction and contributes to bring nutrients to the downwind upwelling areas.

The 3D model was fully used by Thomas et al. (2012a) to complete with connectivity matrices and dispersal scenarios the mapping of the distribution and the dynamics of bivalve larvae as observed *in situ* (Thomas et al., 2012b). Models were run under climatological and realistic wind condition scenarios. The connectivity modelling provided maps of the most suitable areas for spat collection under different weather conditions. The hydrodynamic 3D model was refined for this objective by using a vertical swimming sub-model validated *in situ* (Thomas et al., 2012b).

Larval dispersal is itself the consequences of the factors that control the reproduction of oysters. Fournier et al. (2012a) investigated in Ahe Atoll the influence of natural plankton concentration on maturation and spawning of *P. margaritifera*, during a 4 months survey. Plankton concentration (chlorophyll a) and microscope counts were compared with oysters reproduction activity, measured with gonadic index, gonado-visceral dry weights and histology. Fournier et al. (2012a) concluded that gametogenesis rate was

mainly related to plankton concentration and that spawning occurred when maximal gonad storage was reached. The main spawning synchronizing factor was plankton concentration. Understanding at least the chlorophyll spatio-temporal variations are thus a priority for predicting the timing of spawning. In their sampling stations, Fournier et al. (2012a) reported that plankton concentration fluctuations were mainly related to the wind regime, and to the overturning circulation and upwelling effects described by Dumas et al. (2012).

The hydrology of the lagoon was characterized during the larval experiments (Thomas et al., 2010), during the hydrodynamic surveys (Dumas et al., 2012) and during the plankton surveys (Charpy et al., 2012). Because different depth limits and stations were considered, and because of the fairly high wind regime experienced during each field period, conclusions were not always in agreement between studies in terms of stratification. Neither Charpy et al. (2012) and Thomas et al. (2010) reported stratification for any of their campaigns. However, according to Dumas et al. (2012), slight thermal and salinity stratifications can occur. The general overturning circulation evidenced by Dumas et al. is likely to be responsible for the mixing of the lagoon water body. In light to medium wind conditions, the overturning circulation weakens, allowing the development of a slight vertical stratification. In more intense wind, the circulation is strong enough to prevent stratification, by upwelling to windward of the bottom cold water and downwelling to leeward of the surface warm water.

Charpy et al. (2012) reported on the general hydrologic characteristics of the lagoon, and compared them to previously studied atolls. The vertical and spatial distribution observed on phytoplankton biomass (extracted chlorophyll) in Ahe was fairly homogeneous, with a significant increase in the southwest of the lagoon under windy conditions. Phytoplankton biomass was also in the same range as other atoll lagoons, as well as nutrient concentrations. Nitrogen is probably the first limiting factor for phytoplankton production (DIN: P ratio <3) but N-enrichment by benthic N₂-fixing cyanobacteria needs to be precisely investigated. The benthic interface was assumed to deliver only up to 28% of the nitrogen phytoplankton demanded. Lefebvre et al. (2012) refine the assessment of spatio-temporal variability through estimations of photosynthetic parameters (using pulse amplitude modulation fluorometry) and primary production (¹³C incorporation) measurements of the size structured phytoplankton biomass (<2 µm and >2 µm), in addition to traditional incubation of carbon isotopes. Primary production was dominated by the picophytoplankton, but its biomass specific primary productivity was lower than in other atoll lagoons. They showed significant spatial (sites) and temporal (seasonal and day to day) effects on the measured processes for the two size fractions of phytoplankton. The variables size fraction of the phytoplankton, water temperature, season, the interaction term station * fraction and site, explained significantly the variance of the data set using redundancy analysis. However, no significant trends over depth were observed in the range of 0–20 m. A consistent clear spatial pattern was found with the south and north sites different from the two central stations for most of the measured variables. This pattern was explained by the different barotropic cells highlighted by Dumas et al. (2012) in their hydrodynamic study. Lefebvre et al. (2012) hypothesized the existence of a fast regeneration mechanism of nitrogen through pulses, a process that fuels the larger phytoplankton's production better than the picophytoplankton one. Sediment interface and cultured oysters were good candidates to explain, at least partly, the fast regeneration processes of nitrogen organic material. A precise spatial evaluation of the cultured pearl oyster stock remain necessary for future studies, as well as measurements of nutrient ambient conditions, preferentially with flux methods using carbon

and nitrogen tracers rather than measurement of nutrient stocks that are rapidly assimilated and transformed by autotrophs (Furnas et al., 2005).

Charpy et al. (2012) suggests that relatively low particulate organic carbon content compared to other lagoons localized at the same latitude could reflect the impact of pearl oyster aquaculture. However, this impact does not appear on phytoplankton biomass. Indeed, as shown by Fournier et al. (2012b), oysters do not feed directly on phytoplankton, but rather graze heterotrophic plankton. Fournier et al. (2012b) refined the knowledge on *P. margaritifera* diet by demonstrating with the flow through chamber method that the main factor influencing clearance rates of pearl oysters was the biovolume of planktonic particles. Thus, the diet of *P. margaritifera* was mainly driven by fluctuation of the relative biomass of the nano- micro- planktonic communities. Both heterotrophic nano- and micro-plankton represented an important part of the diet of *P. margaritifera* depending on their relative biomass in the water column. The picoplankton communities displayed the lowest clearance rates but represented however a detectable contribution to the diet. Whether or not this selective grazing may induce a change in plankton assemblage in cultivated lagoons compared to uncultivated ones remain unknown.

Pearl farming could impact lagoons in different ways. First, the population of oysters hanging on lines may induce changes in the planktonic communities but this remains unproven to date. Second, lines hanging above the lagoon floors can modify the flux of material at the sediment interface. Gaertner-Mazouni et al. (2012) quantified benthic nutrient fluxes and sedimentation rates for two stations located under pearl oyster frames, and two control stations away from the pearl culture facility. They concluded that aquaculture increased sedimentation rates but probably by modification of local currents and not by the release of additional organic material. No organic enrichment in sediments was demonstrated. Conversely, they showed that maximum values of benthic nitrogen fluxes were recorded in stations directly under the influence of pearl oyster culture. These benthic nitrogen fluxes could contribute up to 28% of the nitrogen demand in the water column. Third, human populations around farms could directly impact the lagoon. Bouvy et al. (2012a) concluded from faecal indicator bacteria that there was no evidence that human sewage had any impact on picoplankton throughout the atoll. They concluded that Ahe atoll belongs to the type of unproductive aquatic system, without high external inputs of inorganic nutrients issuing from human activities, as defined by Duarte and Agusti (1998).

Three papers in this issue refine knowledge of planktonic communities of atoll lagoons. First, Bouvy et al. (2012b) investigate with one survey per atoll the virioplankton and bacterioplankton in Ahe and Takarua atolls, in comparison with the surrounding oligotrophic ocean. The role of virioplankton in lagoons was unknown while viruses are the numerically dominant biological entities in the ocean and viral infection is a major structuring process in the dynamics of marine microbial communities. For instance, viral lysis of autotrophic and heterotrophic microorganisms influences the rate of nutrient cycling through microbial food webs. Most virioplankton in the environment infect bacterioplankton and, in general, the distributions of viral populations often mirror the bacterial distributions. However, Bouvy et al. (2012b) suggest that the distribution patterns of virioplankton are apparently not coupled in Ahe and Takarua. Fractions of infected bacterial cells were all extremely low, among the lowest recorded in both marine and freshwater systems. Differences between atolls occurred, with a mean virus-to-bacteria ratio significantly lower in Ahe than in Takarua. This is consistent with the hypothesis that this ratio is likely to increase in environments that favor fast bacterial growth given the estimated longer residence times in Takarua compared to Ahe.

Michotey et al. (2012) investigated the prokaryotes communities of Ahe lagoon using molecular techniques. Heterotrophic prokaryotes are important for the mineralization of organic matter and they are the only one able to use directly dissolved organic matter (DOM). The produced prokaryotic biomass is grazed by nanoplankton (nanoflagellates and ciliates), that is successively consumed by micro-zooplankton and organisms of higher trophic level that in turn produce DOM. This microbial loop allows the transfer of energy to the higher levels of the trophic web by recycling of organic matter. All sequences retrieved by Michotey et al. (2012) were affiliated within bacterial (*Cyanobacteria*, and heterotrophic *Proteobacteria* and *Flavobacteria*) or archaeal superkingdoms. Communities and operational taxonomic units were analysed according to dry/rainy seasons and free-living/particle-attached state. Variations of these communities were also assessed in relation to an oceanic-lagoon gradient, and inside the lagoons at different locations and depth. Bacterial density was higher in the lagoon compared to ocean and a seasonal trend was observed. No spatial pattern of bacterial abundance and diversity within the lagoon was detected, nor the influence of the planktonic/attached states was noticed. Archaeal abundance showed seasonal tendency and particle-prevalence, but no differences between lagoon and oceanic location was observed. The spatio-temporal pervasiveness found by Michotey et al. (2012) for the heterotrophic groups (*Marinovum*, *Flavobacteria* and *Erytrobacter*) confirms that in Ahe atoll, the microbial loop can be predominant (Pagano et al., 2012) and the community is heterotrophic.

Finally, Pagano et al. (2012) completed within Ahe lagoon the assessment of planktonic communities and food webs by investigating during three periods the space-time variations of metazooplankton communities and their abundance according to environmental (salinity, temperature, wind), and trophic factors (phytoplankton, bacteria, heterotrophic nanoflagellates, and ciliates) distribution. Zooplankton plays a major role in the functioning, productivity and food webs of aquatic ecosystems. Zooplanktonic organisms have an herbivorous-detritivorous diet and can exert a strong grazing pressure on phytoplanktonic biomass. Zooplankton, including larvae of *P. margaritifera*, are themselves a food source for organisms of the upper trophic levels such as planktivorous fish and carnivorous invertebrates. In Ahe, the meroplankton, mainly bivalve and gastropod larvae, was dominant. Holoplankton was dominated by copepods. Results highlighted the wind influence on the horizontal distribution of the zooplankton communities that are consistent with the hydrodynamic structures described by Dumas et al. (2012). The metazooplankton was bottom-up controlled by trophic resources. Then, the low nanophytoplankton biomass in contrast to the high abundance of picophytoplankton, nanoflagellates and nano-particle grazers confirmed the importance of the microbial loop in the planktonic food web of Ahe lagoon. The dominance of bivalve larvae suggested potential major community change arising from aquaculture activities, but the influence of the wild populations could not be discarded.

5. Conclusion and perspectives

Following Takapoto Atoll in the nineties during the PGRN program, Ahe Atoll has been since 2007 the main research site for black pearl aquaculture in French Polynesia. As briefly presented above and in detail in this issue, new methods applied to both old and new questions provided a wealth of fresh results on atoll lagoon environments, oyster ecophysiology, planktonic communities and trophic relationships. In particular, the detailed study of the lagoon circulation provided the spatial and hydrodynamic context of the biological observations. This yielded a first integrated view of the lagoon biophysical functioning, which now needs to

be refined and modelled more extensively. Indeed, the next steps consist in coupling the hydrodynamic larval dispersal model with a larval bioenergetic growth model (Thomas et al., 2011b). The result would be a model of larval dispersal taking into account currents but also environmental and food conditions. Development of a bioenergetic growth model is also planned for adults. A series of experiments in Ahe Atoll planned in 2012–2013 will collect new data to meet these goals, also using new methodological approaches.

Another objective for French Polynesias is to expand the research to other lagoons where natural spat collection occurs. A priority is Mangareva Island in the Gambier Archipelago. Mangareva consists of a large deep lagoon surrounding several small high islands where black pearl farming is still active and productive. On-going projects will investigate larval dispersal and *Pinctada margaritifera* ecophysiology in very different environmental and hydrodynamic conditions than those found in Ahe or Takapoto. It is also planned to monitor occurrences of spawning events using the condition index (ratio of wet weight of the visceral mass to shell weight) (Le Moullac et al., 2012). Together, spawning monitoring and larval dispersal modelling will enhance the accuracy of the spat collecting forecast system that French Polynesia aimed at.

All these future activities on Ahe and Mangareva are currently planned in the POLYPERL (2012–2014) and BIODIPERL (2012–2013) recently funded projects. Finally, we point out that the professionals involved in pearl farming in the various atolls and islands are generally supportive of research activities. Their support is essential, and a great motivation, to conduct the researches presented here elsewhere. Therefore, on the long run, additional atolls should be studied, such as Arutua and Kaeuhi. The modelling, environmental and ecophysiological work pioneered in Ahe should provide for these atolls an objective foundation to establish spatial zoning plans in their lagoons. For the benefits of farmers, space and concessions would be allocated according to the most optimal areas for collecting larvae, and for growing juvenile oysters and grafted adults.

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