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Mismatch between the ecological processes driving early life-stage dynamics of bivalves at two contrasting French Polynesian lagoons

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Abstract :

The pearl-farming industry depends mostly on the natural recruitment of pearl oysters. Little is known about the relative influence of different ecological processes on the natural recruitment of pearl oysters across biogeographical scales. Spatio-temporal dynamics of bivalve larvae and spats were described at Ahe and Mangareva, 1500 km apart across French Polynesia. We quantified the effect of candidate environmental predictors on the dynamics of larvae. Both lagoons showed similar temporal dynamics with twice more larvae and 6 times more spat in Ahe. Pinctada maculata spat were more abundant than for P. margaritifera at both lagoons. While the temporal dynamics in larvae abundance were best explained by a positive effect of temperature in Ahe, the dynamics in Mangareva were poorly predicted by the environmental variables, meaning bivalve early-life stages perform better in Ahe than Mangareva suggesting a mismatch between the relevant environmental forces driving larval dynamics at these two contrasting lagoons.

Highlights

► Six months of simultaneous surveys of bivalve larvae and spat dynamics in 2 contrasting lagoons. ► Higher abundance of larvae and spat associated with higher water temperature and phytoplankton levels in Ahe Atoll. ► While temperature was the main driver of larval dynamics in Ahe, no environmental drivers were detected in Mangareva. ► *Pinctada maculata* spats win the competition for space on the collectors in both locations during the 6 months survey. ► Mismatch between environmental predictors of larvae dynamics between contrasting atolls.

Keywords : Bivalve larvae, Spat, Dynamics, Atoll, Pinctada margaritifera, P, maculata

1. Introduction

Within 40 years, the pearl industry involving the black-lip oyster *Pinctada margaritifera* became the 2nd main economic activity of French Polynesia, after tourism. While in some countries the production of bivalve spats depends on hatchery production (James et al., 1994; Monteforte et al. 1994; Rose et al. 1994; Southgate et al. 1997; Velasco et al. 2011), the French Polynesian pearl industry relies almost entirely on spat collection in the natural environment (Andréfouët et al. 2012). This spat supply provides the seed to grow adult oysters needed for producing pearls. Thus far, however, little is known about the ecological processes underlying the dynamics of pearl oyster larvae and recruits, complicating our ability to manage pearl-farming activities at both local and regional scales. To that end, it is useful to (1) describe spatio-temporal patterns in the abundance of early-life stages of bivalves, and to (2) quantify the effects of relevant environmental drivers at both local and biogeographical scales.

The early life-stage dynamics of species with planktonic larvae, including most bivalves, respond to a complex mix of biotic and abiotic factors, often difficult to separate. Some studies *in situ* and in hatcheries showed that common biotic factors include the abundance and distribution of the wild and farmed stocks (Underwood & Fairweather, 1989; Pineda et al. 2007; Andréfouët et al. 2016; Thomas et al. 2016), the availability and quality of food (Strathmann, 1985; Hofmann et al. 2004; Martínez-Fernández et al. 2006; Marshall et al. 2010; Thomas et al. 2012b), the survival rates of larvae (Rumrill, 1990; Troost et al. 2008, 2009) and spat (Gosselin & Qian, 1997; Hunt & Scheibling, 1997; Friedman et al. 1998, 2000; Oengpepa et al. 2006), and the intra- and inter-specific competition for food and space (Petersen, 1984; Avendaño et al. 2013). Abiotic factors commonly cited are the hydrodynamic regime (Knights et al. 2006; Thomas et al. 2012a), the water temperature (Chícharo et al. 2001; Ehteshami et al. 2010), the salinity and the turbidity (Friedman et al. 1998, 1999; O'Connor et al. 2004), the type of substrates to settle (Friedman et al. 1996, 1998; Saucedo et al. 2005) and the wind speed and direction (Garland et al. 2002; Thomas et al. 2012a; Thomas et al. 2012b; Fournier et al. 2012; Hoyer et al. 2014).

To attempt to better understand the influence of some of these factors on the dynamics of the early stages of bivalve molluscs, we monitored during 6 months the abundance of bivalve larvae (without distinction of species) as well as the spat recruitment of *P. margaritifera* and its competitor *P. maculata*. Monitoring was conducted synchronously at Ahe and Mangareva, two islands with high pearl-farming activity, located 9° latitude apart at opposite ends of French Polynesia. The contrast of the sites should thus allow us to test the differential effects of relevant environmental drivers on the production of bivalves across different lagoons.

2. Materials and Methods

2.1 Sampling sites

The Ahe Atoll (14°28.889'S, 146°18.509'W, Fig. 1A, B) has a semi-closed lagoon with an area of 142 km² and a mean depth of 41 m. The lagoon contains multiple pinnacles separated by basins of up to 70-m depth, rendering an overall honeycomb-like pattern. The average renewal time of the lagoon has been estimated at 250 days (Dumas et al. 2012). The island of Mangareva (23°6.872'S, 134°56.613'W, Fig. 1A, C) has a deep (60 m) and large lagoon (433 km²) patched with small peaks that resulted from the relicts of the ancient caldera (Bonvallot et al. 1993). The reef rim has a 90 km perimeter with emergent parts only in the north and north-east zones of the lagoon (Pirazzoli, 1984). Although hydrodynamic data are lacking for Mangareva, water exchange between the lagoon and the open ocean is assumed to be greater than at Ahe Atoll because of Mangareva's more open reef system.

In both lagoons, 3 stations were sampled for the concentrations of bivalve larvae and chlorophyll-*a* (Chl-*a*, a proxy for bivalve's food). In Ahe, A1, A6, A8 (Fig. 1B) where chosen along the longest axis of the lagoon. Mangareva is 3 times larger than Ahe and for logistic reasons, the sampled stations M1, M3, M4 (Fig. 1C) were chosen in the area where most of the farmers usually collect the spats they use for pearls production.

2.2 Measurement of environmental variables

For the duration of the study, we gathered data on potentially important environmental variables (Chl-*a,* seawater temperature, and wind speed and direction) to describe variability in conditions between and within lagoons and over time, and to investigate potential drivers of larvae dynamics at each lagoon. As shown by Fournier et al (2012), Thomas et al (2014, 2016), those variables are key parameters for phytoplankton production and for the growth, reproduction and dispersion of the bivalves.

Chl-*a* was sampled every week at 3 stations in Ahe (Fig. 1B; A1, A6 and A8) and Mangareva (Fig. 1C; M1, M3 and M4). Chl-*a* was measured from seawater samples collected using a Niskin bottle deployed at 5-m depth. 300 ml of water were filtered using 25-mm diameter Whatman GFF filters (0.7-µm pore size) to retain total Chl-*a*. Filters were frozen at -20°C in the dark until laboratory analyses. To extract the Chl-*a*, filters were soaked overnight in 6 ml of 96% ethanol. We used a Turner Trilogy fluorometer with a non-acidification method to determine the concentration of the extracted Chl-*a* (µg l^{-1}) (Welshemeyer, 1994).

Seawater temperature was recorded every 2 hours using one logger (iBCod22L) immersed at 5-m depth at stations A6 in Ahe and M1 in Mangareva (Fig. 1B and 1C). Hourly-recorded wind speed and direction data recorded in Takaroa Atoll (~120 km east of Ahe) and Mangareva were provided by Météo France.

2.3 Sampling of bivalve larvae

To compare the abundance and dynamics of bivalve larvae and spats in Ahe and Mangareva, samplings were done simultaneously in both locations between November 2012 and May 2013, the period of highest reproduction activity in the region (Pouvreau et al. 2000; Fournier et al. 2012).

The bivalve larvae were sampled weekly at 3 stations in Ahe (Fig. 1B; A1, A6, A8) and Mangareva (Fig. 1C; M1, M3, M4). Sampling was done between November 10th 2012 and April 27th 2013 in Ahe, and between November 5th 2012 and April 22nd 2013 in Mangareva (25 weeks of sampling in both islands). We collected larvae by submerging a plankton net (40-µm mesh, 35-cm aperture) 5 m above the seafloor (to avoid lifting sediment) and then slowly lifting to the surface. The filtered volume was computed based on the net aperture and site-specific depth measurements. The filtrate was passed through a 400-µm mesh to exclude material larger than bivalves' larvae, and then preserved in 72% ethanol. One lift of plankton net was done each week at each station.

In the laboratory, each sample was homogeneously spread on a Petri dish with a layer of 72% ethanol and digitalized with a high-resolution scanner (Epson perfection 4990 Photo, 9600 dpi). Using ImageJ v.1.48 software, we counted all bivalve larvae and measured the area projected by each individual in 4 randomly subsampled images representing 5% of the Petri dish area. The total abundance of larvae (number m^{-3}) was computed by extrapolation to the full Petri dish area and standardized by the volume of filtered seawater. The larvae lengths were estimated based on the diameter of the circle resulting from the equivalent surface-area projected by each individuals' digital image. Note that it was not possible to discriminate between bivalve species at this early stage of development. Therefore, these data represent estimates of the overall bivalve larvae productivity.

2.4 Sampling of bivalve spats

The bivalve spats were sampled at each lagoon during the same time period of larvae sampling. Collectors where deployed during 6-week intervals at 8 stations in Ahe (Fig. 1B; A1-A8) and 4 stations in Mangareva (Fig. 1C; M1-M4). The stations locations were set to cover

the whole lagoon at Ahe. At Mangareva, they cover the portion of the lagoon where most of the farmers collect the spats. The number of sampled stations were limited to 4 due to logistic issues but the number of stations per area where comparable to Ahe. Also, the spat abundance was standardized according to collectors number and length. This sampling scheme yielded 4 retrievals for each lagoon (R1-R4). 25-cm long experimental collectors were used, as those used by farmers, which were attached in triplicate along a horizontal rope and immersed in the lagoon at 5-m depth. Each collector was made of a thin, black polypropylene mesh, knitted along a polyethylene rope. After retrieving collectors, they were stored in 72% ethanol for preserving the samples until processing. In the laboratory, spats were detached from the collectors and sorted into three taxonomic categories: *P. margaritifera*, *P. maculata* and "other bivalve spat". If abundance was extremely high, the subsampling and weight extrapolation method was used to count and measure the spat. The abundance (standardized by collector length, number m^{-1}) and length (mm) of *P. margaritifera* and *P. maculata* spat were estimated with the same method used for larvae.

2.5 Data analyses

The data were analyzed using R (R Core Team, 2019). To examine variability in larvae/spat abundance and environmental variables between lagoons, among stations, and across time, either non-parametric (Mann-Whitney M-W or Kruskal-Wallis K-W, with posthoc Dunn test) or parametric (ANOVA with pairwise posthoc) tests were used, depending on whether assumptions of normality and variance homocedasticity were met.

To examine the influence of island and environmental variables (i.e., temperature, Chl-*a*, wind strength, and wind direction) on the temporal variability in abundance of larvae, generalized linear models (GLM, Poisson error distribution) were used. Models were tested including all combinations of explanatory variables and ranked them based on Akaike's information criterion corrected for small sample size (*AIC*c) using the R package *MuMIn* (Barton, 2020). Given that most of the larvae in the samples were small, likely falling within the 1-week age class, we included 1-week time lag in the analyses. Because wind direction (expressed in units of degree) is a circular variable, it was decomposed into the continuous sine (east-west axis) and cosine (north-south axis) components. Before inclusion in the models, each environmental variable was standardized by subtracting the mean and dividing by standard deviation (i.e., z-score) to allow direct comparison between the model coefficients. Independent model selection protocols were run for each atoll because of a strong collinearity between this factor and the environmental variables (variance inflation factor, $VIF = 12.08$). While we also

examined relationships between environmental variables and the spat records, no significant effects were detected, which is possibly an artefact of the reduced sample size of this time series.

3. Results

3.1 Environmental variables

The mean (± standard error) lagoon water temperature was significantly higher in Ahe (29.3 ± 0.01°C) than Mangareva (27.4 ± 0.01°C) (Fig. 2A; Table 1). The mean concentration of total Chl-*a* (i.e., particles > 0.7 µm) was higher in Ahe (0.32 ± 0.02 µg l^{-1}) than Mangareva (0.25 ± 0.02 µg l^{-1}) (Fig. 2B; Table 1). In Ahe, mean total Chl-*a* was higher in station A1 than in A6 and A8 while no significant difference was detected among Mangareva stations (Table 2). The overall wind speed was also higher in Ahe (5.5 ± 0.5 m s^{-1}) than Mangareva (2.9 ± 0.5 m s^{-1}) (Fig. 2C; Table 1). The dominant wind came from the East in Ahe (103.6 ± 13.1°) while the wind direction was mostly from the South-South-East in Mangareva (164.0 ± 18.4°) (Table 1).

3.2 Larvae of bivalves

3.2.1 Abundance and distribution

Considering the 25 sampling weeks, the mean abundance of bivalve larvae was significantly higher in Ahe (5,196 ± 499 larvae m^{-3}) than in Mangareva (2,886 ± 153 larvae m^{-3}) (Table 1). There also was intra-lagoon variability at both sites. In Ahe, larvae were significantly more abundant at station A1 than at A6. A8 was not significantly different from A1 and A6 (Table 2). In Mangareva, larval abundance was significantly higher at M1 than at M4. No significant difference was detected neither between M1 and M3 nor M3 and M4 (Table 2).

At both lagoons, larvae were always present in all stations and throughout the duration of the study. The highest abundance levels were recorded between December 2012 and February 2013 (Fig. 3). In Ahe, several abundance peaks occured at station A1 (December 22nd, January 5th and 19th, February 16th, March 23rd and April 27th) (Fig. 3A), while in Mangareva station M1 contributed with the highest peaks (December 10th, January 7th, February 2nd and March 3rd) (Fig. 3B).

3.2.2 Size and distribution

The mean length of larvae in Ahe (114.0 ± 2.3 µm) was significantly higher than in Mangareva (99.4 ± 1.5 µm) (Table 1). Considering the 25 weeks of sampling, the size-frequency distribution of larvae revealed that the smallest individuals (< 150 µm) were the most common at both atolls (Fig. 4). These smallest larvae were 5 times more abundant than the other sizes (>150 to 350 µm) pooled together.

3.2.3 Environmental influence on larvae abundance

Overall, the higher abundance documented in Ahe than Mangareva correlated with the generally higher chlorophyll-*a*, temperature, wind speed, and easterly winds (Fig. 2). Our models revealed a mismatch on the environmental processes driving the temporal dynamics of larvae at each lagoon. Among the competing models tested for Ahe, the top-ranked model indicated a strong positive effect of seawater temperature and a weaker negative effect of the sine component of wind direction (i.e., easterly winds favored larvae abundance). chlorophyll-*a* and the cosine component of wind direction were present in the top-ranked model, but their influence was minor (Fig. 5A coefficients; Table S1). While the second-ranked model suggested a negative effect of wind speed, the relative support for this model ($w\text{AIC}_c = 0.27$) was substantially lower than for the top-ranked model ($w\text{AIC}_c = 0.73$). The deviance explained by the top-ranked model was 16.21%.

For Mangareva, the top-ranked model explained a higher proportion of the variability of larval abundance (27.65%) than the top-ranked model for Ahe. However, the relative contribution of the different environmental variables suggested by this model was inconclusive. The top-ranked model indicated a weak positive effect of the cosine component of the wind direction (i.e., southerly), and weak negative effects of chlorophyll-a, temperature, the wind direction-sine component, and wind speed (Fig. 5B; Table S1).

3.3 Spat

3.3.1 Abundance and distribution

The variability in spat abundance depended on the time of retrieval, the sampling station, the lagoon, and the species considered (Figs. 6-7). For *P. margaritifera*, recruitment was higher in Ahe (3.7 ± 0.4 spat m^{-1}) than Mangareva (1.9 ± 0.3 spat m^{-1}). In Ahe, *P. margaritifera* spat were more abundant at the retrievals R2 and R3 (5.2 ± 0.8 spat m^{-1}) than at R1 and R4 (1.5 ± 0.3 spat m^{-1}) (Fig. 6A; M-W, $p = 0.001$). During the period of highest recruitment (R2 and R3), the abundance varied by up to 5 times between stations, with generally more spats in the western sectors (station A1 to A4). Recruitment was lowest and more homogeneously distributed for

R4 (Fig. 6A). In Mangareva (Fig. 6B), the spats were more abundant at the retrievals R1 and R2 (3.7 ± 0.5 spat m^{-1}) than at R3 and R4 (0.1 ± 0.1 spat m^{-1}) (M-W, p = 0.0002). During these first two harvests, spat were twice more abundant at station M4 than at the other stations.

Overall, *P. maculata* was 91 times more abundant than *P. margaritifera*. The differences between lagoons and the temporal dynamics of both species, however, followed similar patterns (Figs. 6-7). Considering *P. maculata*, recruitment was higher in Ahe (472.7 ± 58.4 spat m^{-1}) than Mangareva (37.0 ± 7.1 spat m^{-1}) (Table 1). In Ahe (Fig 7A), recruitment was highest during periods R1 (868.5 ± 260.0 spat m^{-1}), R2 (590.4 ± 55.3 spat m^{-1}) and R3 (382.6 ± 140.4 spat m^{-1}), and lowest on R4 (49.3 ± 18.8 spat m^{-1}) (K-W, p = 0.0004). At station A2, the abundances reached more than 2 000 spat m^{-1} at R1. In Mangareva (Fig. 7B), the spats were more abundant at R1 (100.0 ± 23.3 spat m^{-1}) and R2 (42.3 ± 12.4 spat m^{-1}) than at R3 (2.0 ± 0.3 spat m^{-1}) and R4 (3.7 ± 1.2 spat m^{-1}) (K-W, p = 0.007). The maximum was recorded during R1 at station M4 (167.3 spat m^{-1}). Spat were twice more abundant at M4 than in the other stations.

3.3.2 Size

P. margaritifera

In Ahe (Fig. 8A), the mean spat length was significantly different across retrieval times (ANOVA, $p < 0.05$), except for R2 and R4, which had similar mean lengths (2.4 and 2.6 mm). The maximum mean length was 2.9 mm at R3. In Mangareva (Fig. 8B), the smallest (1.9 mm) and largest (3.8 mm) spats were collected at R1 and R3, respectively.

P. maculata

In Ahe (Fig. 9A), the largest mean length of *P. maculata* spat was found at R3 and R4 (3.6 and 3.8 mm). Spats collected at R1 and R2 were the smallest (2.3 mm). In Mangareva (Fig. 9B), the smallest spat size is also seen at R1 and R2 (2.0 mm). The biggest were collected at R3 and R4 (respectively, 5.4 and 4.3 mm).

4. Discussion

The objective of our study was to understand the processes involved in the dynamics of early stage bivalve populations by monitoring their spatio-temporal variations of abundance in two contrasting islands. Our results showed that the abundances of larvae and spat reflected the geographical and environmental contrast with higher number of these early stages in Ahe than in Mangareva. The analyses suggest that while the dynamics of early-life stages of bivalves can be explained by environmental predictors in the closed lagoon of Ahe, the potential importance

of environmental drivers seems to be weakened in the more open lagoon of Mangareva. Notably, our data show that the degree of openness between lagoons might explain larval retention and spat availability. Additionally, we found that *P. maculata* spats dominated *P. margaritifera* in both locations.

4.1 Larval dynamics

Larvae were present at both islands throughout the duration of the study, although with greater abundance peaks occurring between late December 2012 and mid-February 2013. The presence of larvae abundance peaks in the warm season is a well-identified phenomenon that encompasses all the species living in the reef ecosystem (e.g., Chao et al. 1995; Counihan et al. 2001; Wilson et al. 2003; Lo-Yat et al. 2011). With a more abundant food and with rising temperatures, the spawners meet the right conditions to mature quickly and spawn. Although the spawning period of *P. margaritifera* has also been documented during the warm season (Fournier et al. 2012), this species can spawn year-round if the level of phytoplankton is sufficient to reach gonad maturation. This phenomenon is well known since its description for tropical bivalves by Pouvreau et al. (2000) in Takapoto Atoll, and by Thomas et al. (2012a) and Fournier et al. (2012) in Ahe. Therefore, the pearl oysters are able to spawn asynchronously in different parts of the lagoon if the abundance and the availability of phytoplankton are not uniform over time and space (Thomas et al. 2012b,). The ability to spawn no matter the season, the potential multiple spawning area and the different dispersal patterns that spread-out the larvae after spawning episodes could explain the permanent presence of bivalve larvae throughout the 25 weeks of sampling in Ahe and Mangareva.

Our linear models (Fig. 5) revealed in Ahe lagoon a positive effect of seawater temperature and chlorophyll-*a* on the abundance of larvae. The variations were almost synchronous, illustrating the dependence of larvae on theses variables (Fig. 2). Conversely in Mangareva, the model indicated weak and negative effects of chlorophyll-a and temperature, showing a poorly predicted larval dynamics by these environmental variables by methods used in this study. This strongly suggests a mismatch between the ecological processes driving the early-life stage dynamics between Ahe and Mangareva. Mangareva is quite an atypical high island, with a deep and large lagoon surrounded by a reef-rim almost entirely submerged in the southern half of the island. Although no hydrodynamic data are available, this geomorphological conformation may suggest that the exchanges between lagoon and ocean waters are probably higher than at the lagoon in Ahe. Therefore, the export of larvae to the open ocean might prevail in Mangareva contrasting with the low exportation of bivalve larvae (5.2

%) estimated for Ahe Lagoon by Thomas et al. (2014). The more important loss rate of larvae in Mangareva could be an important factor contributing to the smaller population size in that lagoon.

The spatial distribution of larvae in Ahe and Mangareva showed multimodal pattern with several peaks of abundance. The abundance peaks were particularly obvious for stations A1 and M1 (Fig. 3). Considering the weekly variations of mean abundance of larvae (Fig. 2E), the abundance peaks occurred every 8 to 10 weeks in Ahe (see white arrows in Fig. 2E) and about 8 to 6 weeks in Mangareva (black arrows in Fig. 2E). These intervals between larval abundance peaks could be the "redevelopment phase" defined by Wilson et al. (1967) as the time for females of bivalves to reach again a new ripe condition after a spawning episode. This maturation time of 6 to 10 weeks corresponds with the 8 weeks estimated by Fournier (2011) based on a dynamic energy budget (DEB) model developed for *P. margaritifera* in Ahe. Looking back at the raw data (Fig. 2E), the intermediate abundance peaks between the hypothetical major spawning episodes as defined previously, suggest asynchronic reproduction activities of different aggregations within the same lagoon. However, the intermediate abundance peaks could also mean that the redevelopment phase is shorter or longer than 8 and 9 weeks. Indeed, Pouvreau et al. (2000) analyzed the gonad index of *P. margaritifera* in Takapoto Atoll over 1 year and detected up to 5 spawning events for 2-3-year old females. These events occurred every 4 to 12 weeks. For the 1-year old oysters, 2 peaks were found with an interval of 16 weeks. In Ahe, Sangare et al. (2020) also examined gonad index of 2 populations of 2-years old *P. margaritifera*. During the 6 months monitoring, 3 to 4 spawning events were recorded and were separated by 5 to 12 weeks. In Mangareva, Le Moullac et al. (2012) used the same method and found 3 significant reproductive events for 2-year old oysters. The abundance peaks occurred every 12 weeks. The discrepancies could be due to the different methods used: observation of larval abundance vs. histologic gonadal index. Regardless of the method, all the results show the opportunistic strategy of *P. margaritifera* with gonads potentially ready to mature for spawning all year long. All the studies cited here consider food and temperature as the main drivers to trigger spawning events but none have explored yet other factors like the lunar cycle, tide or water turbulence. In fact, the reproduction success of bivalves is multifactorial and it remains difficult to estimate the contribution of each of them.

Larval abundance averaged over the whole period was about two times higher in Ahe than Mangareva. This observation is linked to environmental parameters such as water temperature, wind and Chlorophyll-*a*, which were significantly higher in Ahe than in Mangareva during 6 months of measurements. Overall, the warmer temperatures experienced

by individuals in Ahe (29.3 °C) than Mangareve (27.4 °C) were closer to the species physiological thermal optimum at which growth and reproduction are highest (Le Moullac et al. 2016; Sangare et al. 2020; Doroudi and Southgate 1999; 2003; Thomas et al. 2011). Although situated in the optimal range for a good larval development, the difference could explain the lower productivity in Mangareva.

It is likely that these warmer temperatures also have a positive impact on the growth and production of phytoplankton, as suggested by the higher concentration of chlorophyll-*a* in Ahe (0.32 µg l-1) than in Mangareva (0.25 µg l-1). The wind blew almost twice more strongly in Ahe, promoting the circulation of water layers and contributing to nutrient enrichment. Indeed, the wind drives an overturning circulation of waters, with surface currents flowing downwind and returning deep layers upwelled windward (Dumas et al. 2012). The nutrients resulting from the mineralization of the organic matter are thus resurfaced. The enrichment of the water column favors phytoplankton production and therefore enhances growth and reproduction of bivalves. The influence of wind on phytoplankton abundance and on the reproduction of *P. margaritifera* has been particularly studied in Ahe by Fournier et al. (2012). More food available and more adequate water temperature could drive to a more efficient larval production, survivorship and growth.

The difference in the larval productivity between Ahe and Mangareva is probably also linked to the abundance and to the productivity of the reared and wild broodstock. Working on biophysical larval transport models, Thomas et al. (2014; 2016) showed in Ahe that the productivity of spawning sites explains 59% of the variance of the potential connectivity. In other words, the oyster broodstock is among one of the main drivers of the larval productivity. In Ahe, the wild and reared stocks were estimated to be 666 000 and 14.3 million oysters, respectively (Thomas et al. 2014; Andréfouët et al. 2016). Unfortunately, no stock evaluation has been done in Mangareva. A rough estimation could be computed for the reared stock, based on the 1 281 ha of official authorized concessions surfaces (*Direction des ressources marines de la Polynésie française*, personal communication). With 12 000 oysters/ha (which is the maximum quota of grafted oysters allowed by the authorities), we could estimate to 15.3 million oysters the reared stock in Mangareva. This value is comparable to the one estimated in Ahe. Although wild-stock data are lacking for Mangareva, this result could suggest the broodstosks might not be the main factor explaining the twice higher larval abundance in Ahe, and other processes warrant further examination (e.g., environmental and hydrophysical factors, larval performance, etc.). Importantly, the semi-submerged barrier reef in Mangareva might allow for

more larval exportation to the open ocean than in Ahe. This loss of larvae for the lagoon system could therefore also explain the lower larval abundance in Mangareva.

The size frequency distribution (Fig. 4) shows that the smallest larvae (< 150 µm) were dominant in both locations and across time. This was confirmed by the distribution of larvae by size classes where, in both islands and whatever the stations, the smallest larvae are 5 times more numerous than the other sizes all pooled together. These results illustrate the r-reproductive strategy of bivalves and more generally, of benthic species (MacArthur & Wilson, 1967; Ruiz et al. 1992). The fertilization and the larval phase happen in open water, which is potentially an unstable and unpredictable environment. Egg and larvae production are maximized as quickly as possible to compensate possibly the high rate of mortality during the larval phase. The results could show age dependent mortality or variance among different species of bivalves. The species were not identified, then none of these hypotheses can be favored.

Comparing the stations within each island, the bivalve larvae were found more abundant at station A1 in Ahe. This could be explained by higher concentrations of Chlorophyll-*a* at this station (Table 2). A1 is situated in the South West of the atoll where is concentrated the biggest part of the wild broodstock (Andréfouët et al. 2016), in addition of the reared stock available in this area. With an easterly wind dominating throughout the studied period, the water circulation (Dumas et al. 2012) promotes local areas that retain food and larvae (Thomas et al. 2012a). In Mangareva, larvae were generally more abundant at M1 station, where chlorophyll-a concentration was not significantly different from the other stations (Table 2). M1 is separated from the other stations by a physical boundary formed by a ridge of caldera of an ancient volcano, now submerged. M3 and M4 stations were relatively close to each other, so it is unsurprising that the larval abundances were similar between these locations. The separation between M1 and the other stations possibly dictates local differences in the hydrodynamic conditions that could explain the differences in larval abundance. But as no hydrodynamic studies have been done in Mangareva, it is still not possible to test this hypothesis.

4.2 Spat dynamics

Considering all the species of bivalves, the spat were 6 times more numerous in Ahe than in Mangareva. It is likely that the warmer temperatures and higher food availability of Ahe, which favored larval production, would also drive the higher spat abundance.

P. maculata spat dominated all the sampled collectors, regardless of the island or the stations in the island. *P. maculata* spat were up to 2 000 times more abundant than *P.*

margaritifera spat in station A1 in Ahe. The competitive dominance of *P. maculata* can be explained by its faster colonization and growth rates, compared to *P. margaritifera*. At each harvest after the same immersion time, collectors are colonized by larger *P. maculata* spat than *P. margaritifera* spat. It is unclear, however, what the output of this competition would be after the evaluated 6-month period. Because *P. maculata* reaches a smaller maximum size than *P. margaritifera* (5 versus 20 cm, respectively), it is possible that the later might be a stronger competitor in the longer term.

At an individual level, the reproductive performance seems higher for *P. maculata*. Thielley (1993) demonstrated that *P. maculata* could mature very quickly and spawn throughout the year, like *P. margaritifera*. However, no comparison is available to evaluate more precisely the spawning performances of the two species. It is probable that the sexual maturity of *P. maculata* occurs before they reach 1 year old, meaning earlier than *P. margaritifera* (after 1 to 2 years). The reproductive success of *P. maculata* is also explained by a sex-ratio favorable to female unlike *P. margaritifera* where male dominates (unpublished results). Finally, *P. maculata* is dominating because it might tolerates a wider range of environmental conditions than *P. margaritifera*, but little work on the comparative life histories of these species is available.

At both islands, similar temporal dynamics in the abundance of *P. maculata* and *P. margaritifera* spat were found, despite vastly different levels of abundance between them. In Mangareva, spat settlement was considerably reduced after March, probably due to an early reduction in water temperature. In Ahe, the "good" season lasted longer, with larval settlement extending until April.

Also temporal dynamics in spat body size were identified, with both species *P. margaritifera* and *P. maculata* showing the largest individuals recruiting on the same collection period in Ahe and Mangareva. This contrasted with the abundance of spat, which decreased sharply during the same periods. This suggests that during periods of low abundance, the few spat have more space and probably less trophic competitors than during periods of high abundance. Under these conditions, the spat grow faster and larger. This could likely be an example of density-dependence effect in bivalves' growth (Jensen et al. 1993; David et al. 1997).

In Ahe, considering all the species together, the stations that collected more spats were A1, A2, A3 and to a less extend A4. A4 is under the influence of the import/export flux generated by the pass. Thus, this station might be less productive as noticed by Thomas et al. (2012b). In contrast to A4, A1, A2 and A3 stations were in the southern part of the atoll, where

the spawners, chlorophyll-*a* and larvae were most abundant. These conditions are therefore extremely favourable to the settlement of the spat. As discussed for the larvae, it is likely that the hydrodynamic functioning of the atoll is a key element to explain spat dynamics (Thomas et al. 2012a).

Unlike Ahe, in Mangareva the abundance of spats did not well correlate with the abundance of larvae. For instance, spat collection at M4 station was approximately two times higher than at every other station, even though the sampled larval abundance there was low. Local larval retention at station M4 thus appears to be higher than at the other stations, were larvae were abundant and spat recruitment low. The general disconnect between larvae and spats abundance detected in Mangareva is likely explained by the openness of the lagoon system, relative to that of Ahe (Thomas et al. 2014). Other hypotheses could explain the results such as different larvae and spat behavior and conditions, differential predators and mortality pressure in water and on collectors, differential collector biofilm development that could favor or not the settlement of spats, chance in movement of competent larval clouds. The sampling method could also introduce bias in the results and could be improve by more sampling sites in Mangareva to extend the studied area. Future works could also compare lagoons with different degree of openness because each lagoon is geomorphologically different, meaning differences in hydrodynamic patterns, habitats, food resources, larval exportation and loss, etc. Therefore, spat collection sites for farmers or broodstock restocking areas in MPA design should be specific to each island.

5. Conclusion

The geographical and environmental contrast between Ahe and Mangareva were reflected in the larval and spat dynamics. Interestingly, however, while the early-stage dynamics of bivalves followed similar temporal dynamics at these two contrasting atolls, a mismatch between the ecological drivers was detected. In Ahe, the combination of higher mean temperatures (within the range for an optimal growth) and the higher mean Chlorophyll-*a* concentration could explain the twice more abundant larvae and the 6 times more abundant spat in this atoll, compared to Mangareva. But temperature and food abundance are insufficient to explain the higher abundance of larvae and recruits of Ahe, because the spawners' stocks and the hydrodynamics might also contribute to the larval dispersion and settlement in Ahe.

Numerically, the productivity of Ahe could be truly benefical for pearl farmers of this atoll, because the availability of spat of *P. margaritifera* could be relatively more important than in Mangareva. It is well-known that shortages of spat are a real problem in French

Polynesia where the pearl industry rests entirely on natural spat collection. Similarly, the faster larval and spat growth in Ahe means that the production cycle of pearl is shorter than in Mangareva (*Direction des ressources marines de la Polynésie française*, personal communication). This represents a saving of time and money for the pearl farmers of Ahe. However, the pearls produced in Mangareva are known for their quite unique range or combination of colors and also for their remarkable luster compared to pearls of the Tuamotu atolls. This could potentially give a better commercial value to the pearls of Mangareva. Usually the more common hypothesis emitted by the locals to explain these particularities are the food quality (supposedly due to the enrichment of the lagoon by the terrigenous particles) and the low growth rate of the pearl oysters (which would be due to a general physiological slowdown of the mollusk).

Our results show that *Pinctada maculata* spat were far more numerous than *P. margaritifera* in all the samples from both sites. Such an ecological dominance could be explained by a more productive reproduction mode of *P. maculata* and perhaps a more flexible metabolism compared to *P. margaritifera*.

6. Acknowledgments

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7. References

Andréfouët, S., Charpy, L., Lo-Yat, A., & Lo, C. (2012). Recent research for pearl oyster aquaculture management in French Polynesia. *Marine pollution bulletin*,65(10), 407-414.

Andréfouët, S, et al. 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.

Barton, K., 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn.

Bonvallot, J., Dupon, J. F., Vigneron, E., Gay, J. C., Morhange, C., Ollier, C., Peugniez, G., Reitel B. & Yon-Cassat, F. (1993). Atlas de la Polynésie française. *Orstom éditions*, 112 planches.

Chao, S. M., Chen, C. P., & Alexander, P. S. (1995). Reproductive cycles of tropical sea cucumbers (Echinodermata: Holothuroidea) in southern Taiwan. *Marine Biology*, 122(2), 289-295.

Chícharo, L., & Chícharo, M. A. (2001). Effects of environmental conditions on planktonic abundances, benthic recruitment and growth rates of the bivalve mollusc *Ruditapesdecussatus* in a Portuguese coastal lagoon. *Fisheries research*,*53*(3), 235-250.

Counihan R, McNamara D.C., Souter D. C., Jebreen E. J., Preston N. P., Johnson C. R., Degnan B. M. (2001) Pattern, synchrony and predictability of spawning of the tropical abalone *Haliotis asinina* from Heron Reef, Australia. *Marine Ecology Progress Series* 213:193–202

David, P., Berthou, P., Noel, P., & Jarne, P. (1997). Patchy recruitment patterns in marine invertebrates: a spatial test of the density-dependent hypothesis in the bivalve *Spisula ovalis*. Oecologia, 111(3), 331-340.

Doroudi, M. S., Southgate, P. C., & Mayer, R. J. (1999). The combined effects of temperature and salinity on embryos and larvae of the black-lip pearl oyster, *Pinctada margaritifera* (L.). Aquaculture Research, 30(4), 271-277.

Doroudi, M. S., & Southgate, P. C. (2003). Embryonic and larval development of *Pinctada margaritifera* (Linnaeus, 1758). *Molluscan Research*, *23*(2), 101-107.

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*(10), 425-440.

Ehteshami, F., Christianus, A., & Rameshi, H. (2010). Effects of location and time of *Pinctada margaritifera* spat transfer from hatchery, on its growth and mortality in the sea. Aquaculture, 306(1-4), 85-91.

Fournier, J. (2011). Étude du régime alimentaire et du déterminisme environnemental de la reproduction des huîtres perlières *Pinctada margaritifera* sur l'atoll d'Ahe, Archipel des Tuamotu-Gambier, Polynésie française (*Doctoral dissertation, Université de Polynésie française*).

Fournier, J., Levesque, E., Pouvreau, S., Le Pennec, M., & Le Moullac, G. (2012). Influence of plankton concentration on gametogenesis and spawning of the black lip pearl oyster *Pinctada margaritifera* in Ahe atoll lagoon (Tuamotu archipelago, French Polynesia). *Marine pollution bulletin*, *65*(10), 463-470.

Friedman, K. J., Bell, J., 1996. Effects of different substrata and protective mesh bags on collection of spat of the pearl oysters, *Pinctada margaritifera* (Linnaeus, 1758) and *Pinctada maculata* (Gould, 1850). J. Shellfish Res., 15(3): 535-541.

Friedman K. J., Bell, J. D., Tiroba, G., 1998. Availability of wild spat of the blacklip pearl oyster, *Pinctada margaritifera*, from "open" reef systems in Solomon Islands. Aquaculture, 167: 283-299.

Friedman, K. J., & Bell, J. D. (1999). Variation in abundance of blacklip pearl oyster (*Pinctada margaritifera* Linne.) spat from inshore and offshore reefs in Solomon Islands. *Aquaculture, 178*(3), 273-291.

Friedman, K. J., Bell, J., 2000. Shorter immersion times increase yields of the blacklip pearl oyster, *Pinctada margaritifera* (Linne.), from spat collectors in Solomon Islands, Aquaculture (187)3-4

Garland, E. D., Zimmer, C. A., & Lentz, S. J. (2002). Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. *Limnology and Oceanography*, *47*(3), 803-817.

Gosselin, L. A., & Qian, P. Y. (1997). Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series*, *146*(1), 265-282.

Hoyer, A. B., Wittmann, M. E., Chandra, S., SChladow, S. G., & Rueda, F. J. (2014). A 3D individual-based aquatic transport model for the assessment of the potential dispersal of planktonic larvae of an invasive bivalve. *Journal of environmental management*, *145*, 330-340.

Hunt, H. L., & Scheibling, R. E. (1997). Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series*, *155*, 269-301.

James, P. S. B. R., & Narasimham, K. A. (1994). Saltwater pearl fisheries and pearl culture in India: An update. *Aquaculture Magazine*, 20(4), 41-49.

Jensen, K. T. (1993). Density-dependent growth in cockles (*Cerastoderma edule*): evidence from interannual comparisons. Journal of the Marine Biological Association of the United Kingdom, 73(2), 333-342.

Knights, A. M., Crowe, T. P., & Burnell, G. (2006). Mechanisms of larval transport: vertical distribution of bivalve larvae varies with tidal conditions. *Marine Ecology Progress Series*, *326*, 167-174.

Le Moullac, G., Tiapari, J., Teissier, H., Martinez, E., & Cochard, J. C. (2012). Growth and gonad development of the tropical black-lip pearl oyster, *Pinctada margaritifera* (L.), in the Gambier archipelago (French Polynesia). *Aquaculture International*, *20*(2), 305-315.

Le Moullac, G., Soyez, C., Latchere, O., Vidal-Dupiol, J., Fremery, J., Saulnier, D., Lo-Yat, A., Belliard, C., Mazouni-Gaertner, N. & Gueguen, Y. (2016). *Pinctada margaritifera* responses to temperature and pH: Acclimation capabilities and physiological limits. Estuarine, Coastal and Shelf Science, 182, 261-269.

Lo-Yat, A., Simpson, S. D., Meekan, M., Lecchini, D., Martinez, E., & Galzin, R. (2011). Extreme climatic events reduce ocean productivity and larval supply in a tropical reef ecosystem. *Global Change Biology*, 17(4), 1695-1702.

MacArthur, R. H., & Wilson, E. O. (1967). The theory of island biogeography Princeton University Press. Princeton, NJ, 203.

Marshall, R., McKinley, S., & Pearce, C. M. (2010). Effects of nutrition on larval growth and survival in bivalves. *Reviews in Aquaculture*, *2*(1), 33-55.

Martínez-Fernández, E., Acosta-Salmón, H., & Southgate, P. C. (2006). The nutritional value of seven species of tropical microalgae for black-lip pearl oyster (*Pinctada margaritifera*, L.) larvae. *Aquaculture*, *257*(1), 491-503.

Monteforte, M., & Garcia-Gasca, A. (1994). Spat collection studies on pearl oysters *Pinctada mazatlanica* and *Pteria sterna* (Bivalvia, Pteriidae) in Bahia de La Paz, South Baja California, Mexico. *Hydrobiologia*, *291*(1), 21-34.

O'Connor, W. A., & Lawler, N. F. (2004). Salinity and temperature tolerance of embryos and juveniles of the pearl oyster, *Pinctada imbricata* Röding. Aquaculture, 229(1-4), 493-506.

Oengpepa, C., Hawes, I., Lane, I., Friedman, K., & Bell, J. (2006). Long-term variability in spat collections of the blacklip pearl oyster (*Pinctada margaritifera*) in Solomon Islands. Journal of Shellfish Research, 25(3), 955-958.

Petersen, J. H. (1984). Larval settlement behavior in competing species: Mytilus californianus Conrad and *M. edulis* L. *Journal of Experimental Marine Biology and Ecology*, *82*(2), 147-159.

Pineda, J., Hare, J.A., & Sponaugle S. (2007). Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography 20(3)*:22–39.

Pirazzoli, P. A. (1984). Cartographie des hauts fonds par télédétection dans l'archipel des Gambier (Polynésie française). *Espace géographique*, *13*(3), 277-284.

Pouvreau, S., Gangnery, A., Tiapari, J., Lagarde, F., Garnier, M., & Bodoy, A. (2000). Gametogenic cycle and reproductive effort of the tropical blacklip pearl oyster, *Pinctada margaritifera* (Bivalvia: Pteriidae), cultivated in Takapoto atoll (French Polynesia). *Aquatic Living Resources*, 13(01), 37-48.

R Core Team (2019). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. https://www.R-project.org/.

Rose, R. A., & Baker, S. B. (1994). Larval and spat culture of the Western Australian silver-or goldlip pearl oyster, *Pinctada maxima* Jameson (Mollusca: Pteriidae). *Aquaculture*, 126(1), 35-50.

Ruiz, C., Abad, M., Sedano, F., Garcia-Martin, L. O., & Lopez, J. S. (1992). Influence of seasonal environmental changes on the gamete production and biochemical composition of *Crassostrea gigas* (Thunberg) in suspended culture in El Grove, Galicia, Spain. Journal of Experimental Marine Biology and Ecology, 155(2), 249-262.

Rumrill, S. S. (1990). Natural mortality of marine invertebrate larvae. *Ophelia*, *32*(1-2), 163-198.

Sangare, N., Lo-Yat, A., Le Moullac, G., Pecquerie, L., Thomas, Y., Lefebvre, S., Le Gendre, R., 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

Saucedo, P. E., Bervera-Leon, H., Monteforte, M., Southgate, P. C., & Monsalvo-Spencer, P. (2005). Factors influencing recruitment of hatchery reared pearl oyster (*Pinctada mazatlanica*; Hanley 1856) spat. Journal of Shellfish Research, 24(1), 215-219.

Southgate, P. C., & Beer, A. C. (1997). Hatchery and early nursery culture of the blacklip pearl oyster (*Pinctada margaritifera* L.). *Journal of Shellfish Research*, *16*(2).

Strathmann, R. R. (1985). Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annual review of ecology and systematics*, 339-361.

Thielley, M. (1993). Étude cytologique de la gamétogenèse, de la sex-ratio et du cycle de reproduction chez l'huître perlière *Pinctada margaritifera* (L) var. Cumingii (Jameson),(mollusques, bivalves). Comparaison avec le cycle de *Pinctada maculata* (Gould). (*Doctoral dissertation, Université Française du Pacifique*).

Thomas, Y., Dumas, F., & Andréfouët, S. (2014). Larval Dispersal Modeling of Pearl *Oyster Pinctada margaritifera* following Realistic Environmental and Biological Forcing in Ahe Atoll Lagoon. *PloS one*, *9*(4).

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.

Thomas, Y., Garen, P., & Pouvreau, S. (2011). Application of a bioenergetic growth model to larvae of the pearl oyster *Pinctada margaritifera* L. *Journal of Sea Research*, *66*(4), 331-339.

Thomas, Y., Garen, P., Bennett, A., Le Pennec, M., & Clavier, J. (2012b). Multi-scale distribution and dynamics of bivalve larvae in a deep atoll lagoon (Ahe, French Polynesia). *Marine Pollution Bulletin*, *65*(10), 453-462.

Thomas, Y., Le Gendre, R., Garen, P., Dumas, F., & Andréfouët, S. (2012a). Bivalve larvae transport and connectivity within the Ahe atoll lagoon (Tuamotu Archipelago), with application to pearl oyster aquaculture management. *Marine Pollution Bulletin*, *65*(10), 441-452.

Troost, K., Gelderman, E., Kamermans, P., Smaal, A. C., & Wolff, W. J. (2009). Effects of an increasing filter feeder stock on larval abundance in the Oosterschelde estuary (SW Netherlands). *Journal of Sea Research*, *61*(3), 153-164.

Troost, K., Kamermans, P., & Wolff, W. J. (2008). Larviphagy in native bivalves and an introduced oyster. *Journal of Sea Research*, *60*(3), 157-163.

Underwood, A. J., & Fairweather, P. G. (1989). Supply-side ecology and benthic marine assemblages. *Trends in Ecology & Evolution*, *4*(1), 16-20.

Velasco, L.A., Barros, J., Trujillo, C., Gomez, J., Arias, L.M., HERNANDEZ, R., ROJAS, J., LOVATELLI, A. and SARKIS, S., 2011. *State of shellfish aquaculture on the Caribbean coast of Colombia and potential site for a regional hatchery facility.* FAO, Rome (Italy), mailto:publications-sales@fao.org].

Wilson, B. R., & Hodgkin, E. P. (1967). A comparative account of the reproductive cycles of five species of marine mussels (Bivalvia: Mytilidae) in the vicinity of Fremantle, Western Australia. *Marine and Freshwater Research*, 18(2), 175-204.

Wilson, J. R., & Harrison, P. L. (2003). Spawning patterns of scleractinian corals at the Solitary Islands-a high latitude coral community in eastern Australia. *Marine Ecology Progress Series*, 260(115), 23.

Figures

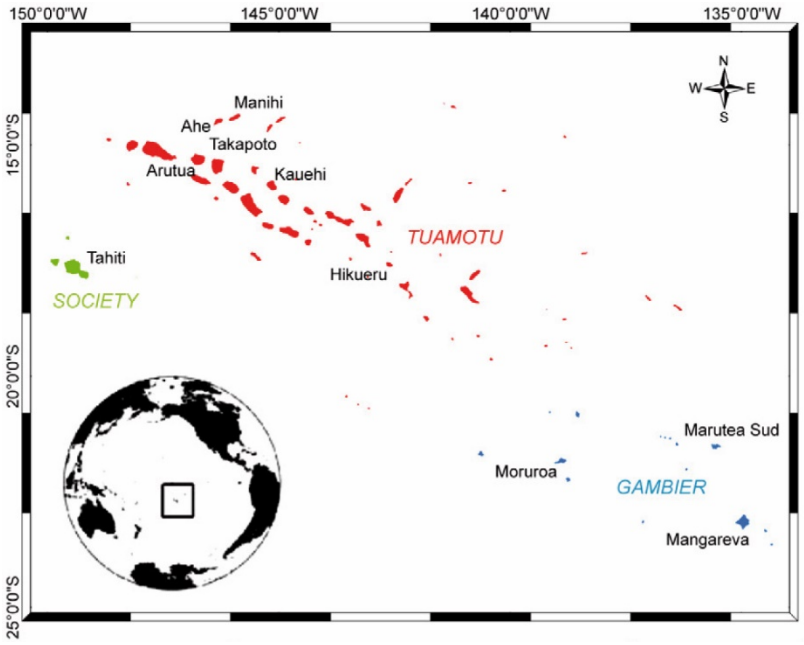

Fig. 1A In French Polynesia, Ahe Atoll is located in the North West of the Tuamotu archipelago. Mangareva high island belongs to the Gambier archipelago.

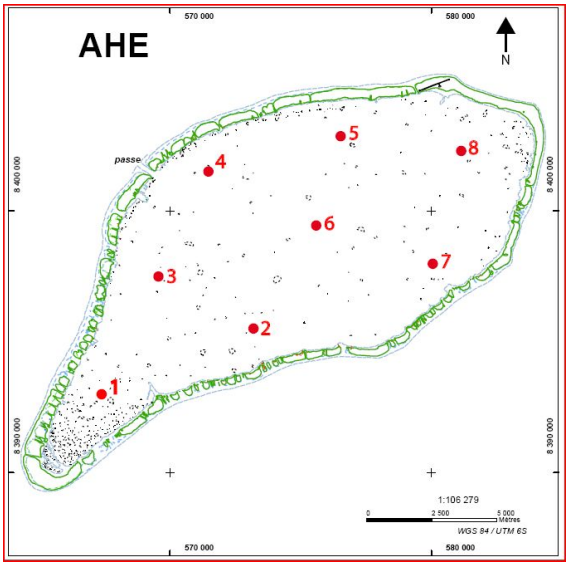

Fig. 1B Ahe stations are labeled A1 through A8. The spats were sampled every 6 weeks in the 8 stations. Larvae of bivalves, regardless of species, and chlorophyll-*a* were sampled weekly at sites A1, A6 and A8. One temperature logger was immersed at 5-m depth at site A6. The sampling period run from 10/11/2012 to 27/04/2013.

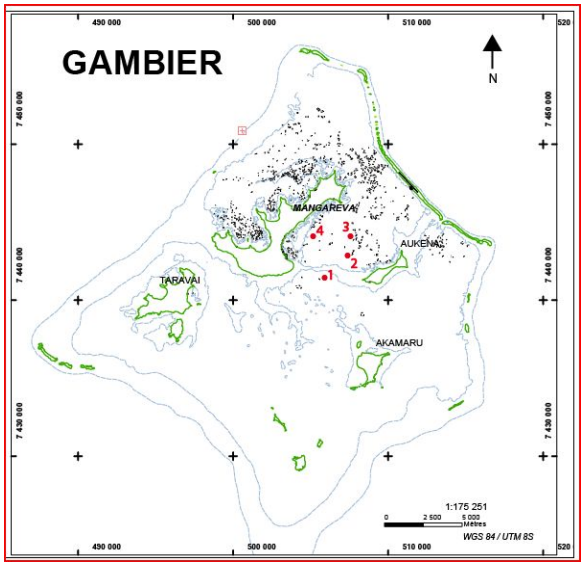

Fig. 1C Mangareva stations are labeled M1 through M4. The spats were sampled every 6 weeks in the 4 stations. Larvae of bivalves, regardless of species, and chlorophyll-*a* were collected weekly at sites M1, M3 and M4. One temperature logger was immersed at 5-m depth at site M1. The sampling period run from 5/11/2012 to 22/04/2013.

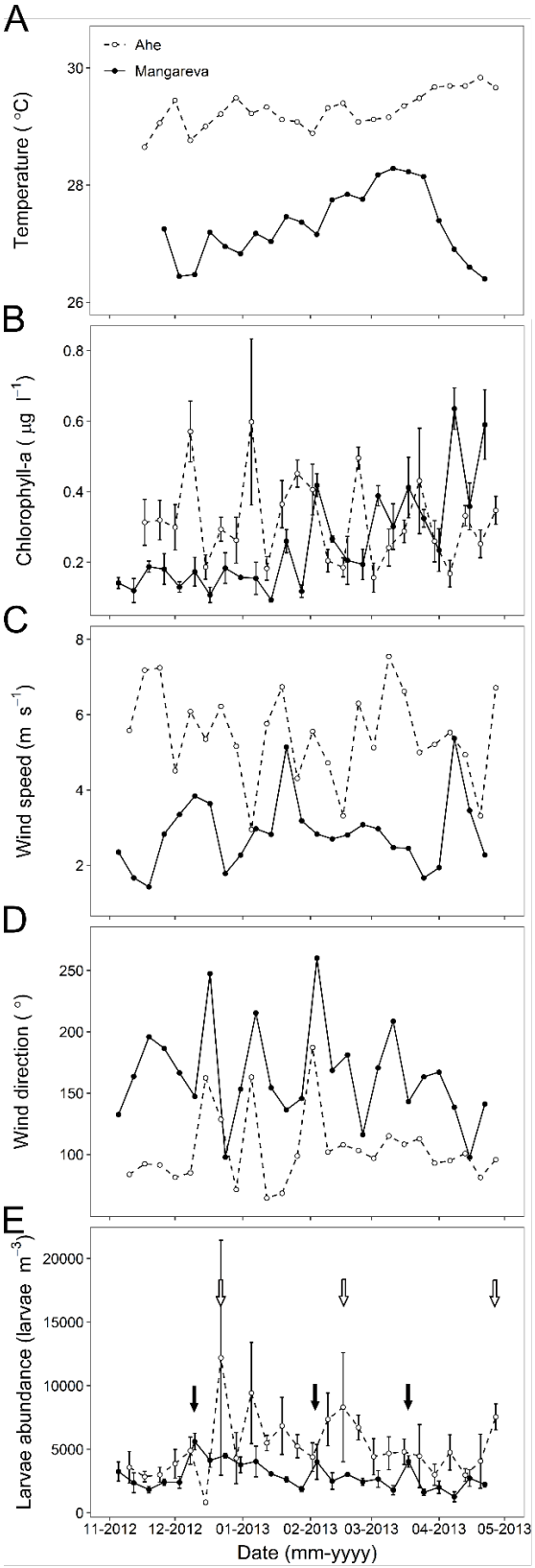

Fig. 2 Weekly variations of mean value of lagoon water temperature (**A**), total chlorophyll a>0.7µm concentration (**B**), wind speed (**C**), wind direction (**D**) and bivalve larval abundance (**E**) in Ahe and Mangareva. Sampling period is 25 weeks from 10/11/2012 to 27/04/2013 in Ahe and from 5/11/2012 to 22/04/2013 in Mangareva. Standard error bars are shown where available. Larval abundance peaks are marked on the chart (**E)** with white arrows for Ahe and black arrows for Mangareva.

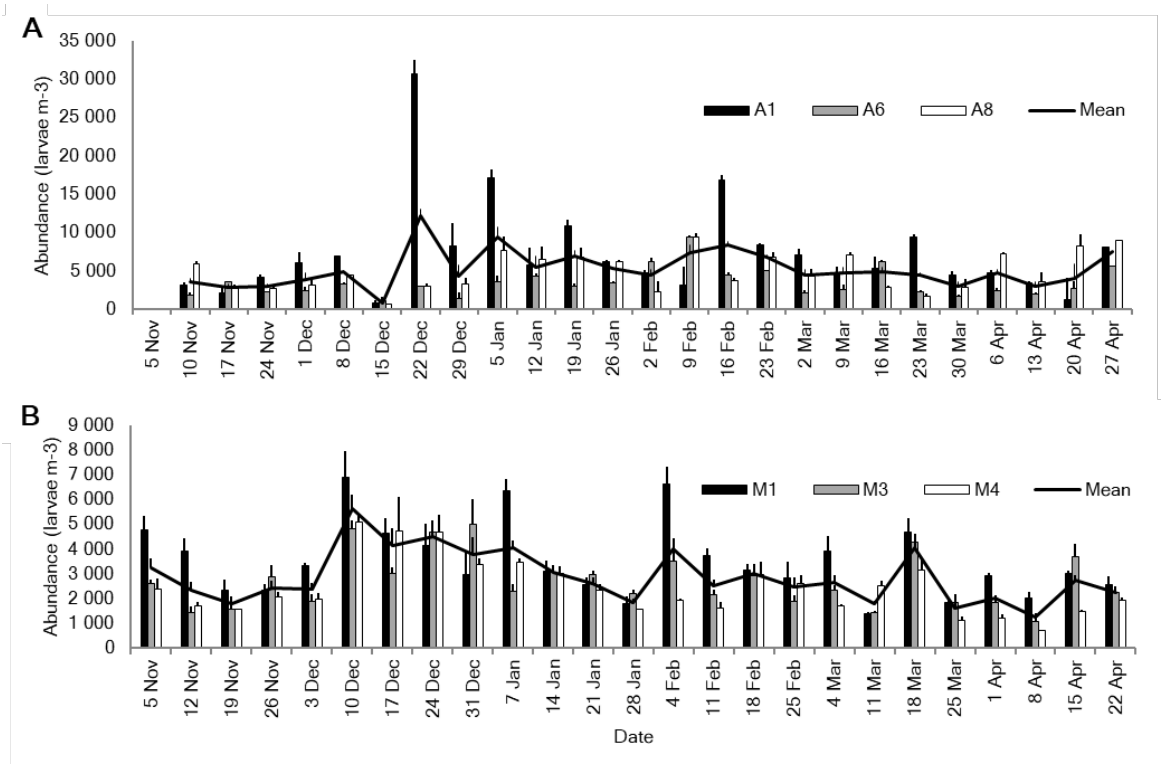

Fig. 3 Total larval abundance distribution in Ahe (**A**) and Mangareva (**B**) with standard error bars. In Ahe, stations A1, A6 and A8 were sampled weekly from 10/11/2012 to 27/04/2013. In Mangareva, M1, M3 and M4 were sampled similarly from 5/11/2012 to 22/04/2013. Data means are also plotted (black line).

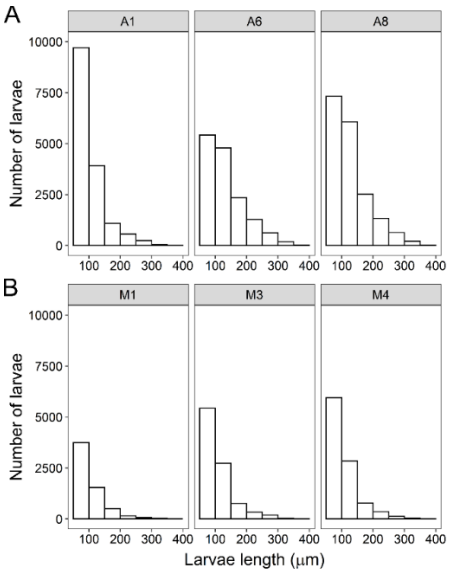

Fig. 4 Distribution of larvae by size classes in Ahe A1, A6, A8 stations (**A**) and Mangareva M1, M3, M4 (**B**). The 48 819 measured larvae in Ahe and 25 037 in Mangareva were caught during the 25 sampling weeks.

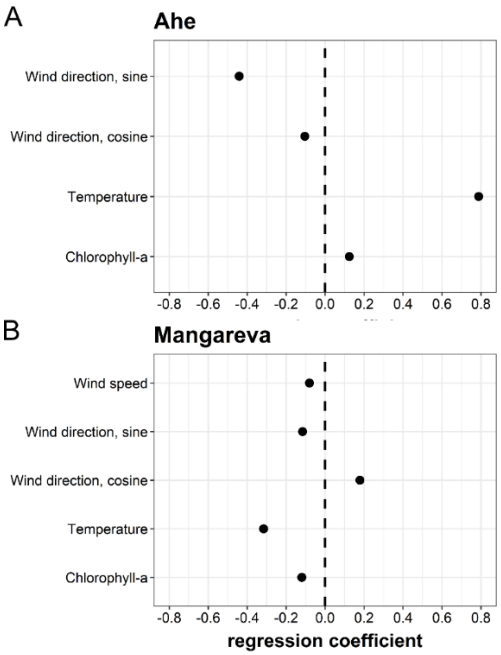

Fig. 5 Effect plots derived from the top-ranked generalized linear models (Poisson error distribution) describing the influence of environmental variables (i.e., temperature, Chl-*a*, wind strength, and wind direction expressed as sine and cosine components) on the temporal variability in abundance of larvae in Ahe (**A**) and Mangareva (**B**). Mean regression coefficients are depicted by the points, with standard errors too small to see. Table S1 provides the details of every candidate model tested.

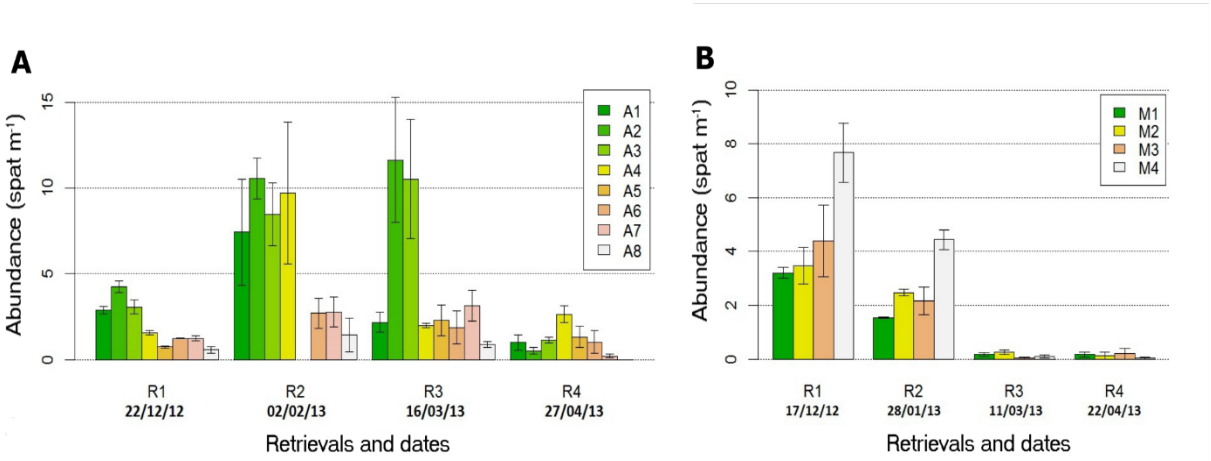

Fig. 6 *P. margaritifera* spat abundance per meter of collector at 8 stations (A1 to A8) in Ahe (**A**) and at 4 stations (M1 to M4) in Mangareva (**B**). Collectors were retrieved 4 times (R1 to R4) every 6 weeks. Standard error represented.

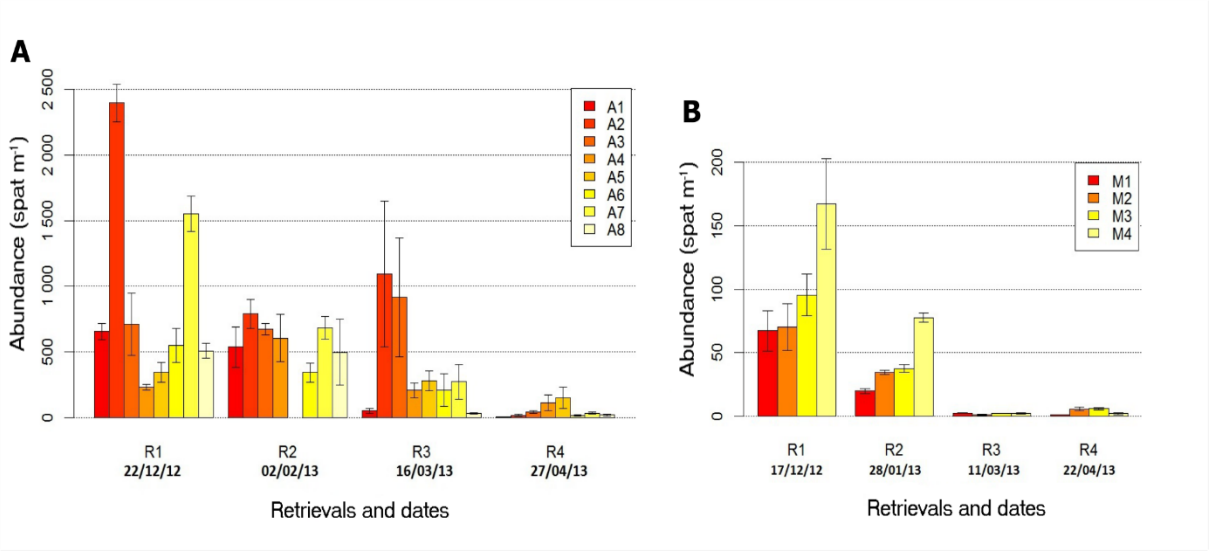

Fig. 7 *P. maculata* spat abundance per meter of collector at 8 stations (A1 to A8) in Ahe (**A**) and at 4 stations (M1 to M4) in Mangareva (**B**). Collectors were retrieved 4 times (R1 to R4) every 6 weeks. Standard error represented.

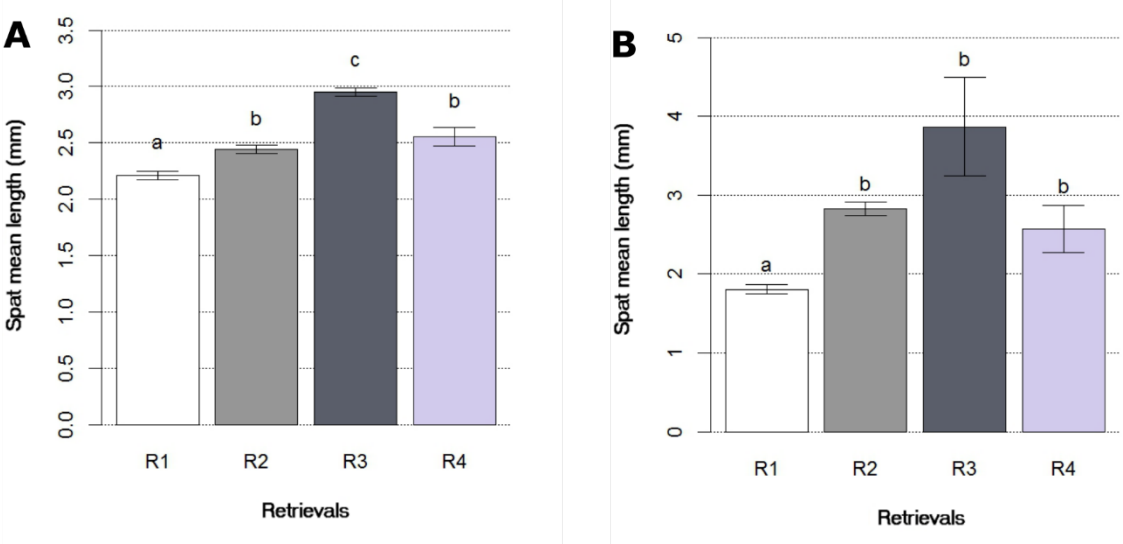

Fig. 8. Mean length of *P. margaritifera* spat in Ahe (**A**) and Mangareva (**B**). Collectors were retrieved 4 times (R1 to R4) every 6 weeks. The highest mean is 3.8 mm for R3 in Mangareva. Standard error and significance represented (a, b, c).

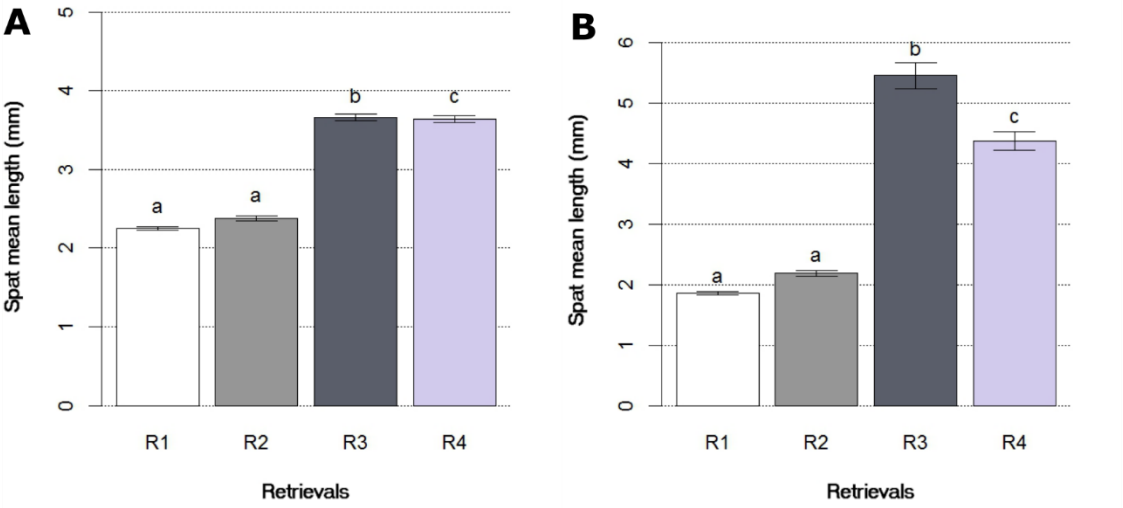

Fig. 9. Mean length of *P. maculata* spat in Ahe (**A**) and Mangareva (**B**). Collectors were retrieved 4 times (R1 to R4) every 6 weeks. The highest mean is 5.4 mm for R3 in Mangareva. Standard error and significance represented (a, b, c).

	Unit	Ahe	Mangareva	Significance
Environmental parameters				
Mean water temperature	°C	29.3 ± 0.01 (n=1 944)	27.4 ± 0.01 (n=1 764)	* (p<0.0001) M-W
Mean wind speed	m s^{-1}	5.5 ± 0.5 (n=175)	2.9 ± 0.5 (n=175)	* (p<0,0001) M-W
Mean wind direction	degree	103.6 ± 13.1 (n=175)	164.0 ± 18.4 (n=175)	*(p<0,0001) M-W
Mean Chl-*a* (>0.7 µm)	µg l^{-1}	0.32 ± 0.02 (n=72)	0.25 ± 0.02 (n=74)	* (p<0,0001) M-W
Bivalve larvae & spat				
Mean larval abundance	larvae m^{-3}	5 196 ±499 (n=75)	2 886 ±153 (n=75)	* (p<0,0001) M-W
Mean larval length	µm	114.0 ±2.3 (n=75)	99.4 ±1.5 (n=74)	*(p=0.003) M-W
Mean spat abundance	spat m^{-1}	645.9 ±72.2 (n=92)	107.9 ±21.3 (n=48)	* (p<0,0001) M-W
including *P. margaritifera*	spat m^{-1}	3.7 ±0.4 (n=92)	1.9 ±0.3 (n=48)	*(p=0.008) M-W
P. maculata	spat m^{-1}	472.7 ±58.4 (n=92)	37.0 ±7.1 (n=48)	*(p<0,0001) M-W
Others	spat m^{-1}	169.5 ±24.5 (n=92)	69.0 ±17.8 (n=48)	* (p<0,0001) M-W
Mean spat length	mm	3.0 ±0.02 (n=14 800)	2.5±0.03 (n=3 491)	*(p<0,0001) M-W
including *P. margaritifera*	mm	2.5 ±0.02 (n=2 069)	2.2 ±0.05 (n=512)	* (p<0,0001) M-W
P. maculata	mm	3.1 ±0.02 (n=12 731)	2.5 ±0.04 (n=2 979)	* (p<0,0001) M-W

Table 1. Environmental, larval and spat data in Ahe and Mangareva. Sampling location and periods are as in Fig.1. Means are given with the standard error and the number of data (n). The symbol (*) tags significant differences between means, with p-values from a Mann-Whitney (M-W) test. Alpha error=5%. For both locations, we used Météo-France's wind data. Note that for Ahe, we used wind data from Takaroa, which is the nearest atoll with a weather station.

	Station	**Mean abundance (larvae m-3)**	**Group Dunn test**	**Significance**	**Mean total Chl-*a* (µg l^{-1})**	**Group Dunn test**	**Significance**
Ahe	A1	7 325 ±1 264 (n=25)	a	* (p=0.002) K-W	0.39±0.04 (n=24)	e	* (p=0.013) K-W
	A6	3 408 ±380 (n=25)	b		0.25±0.02 (n=24)	f	
	A8	4 856 ±489 (n=25)	ab		0.29±0.03 (n=24)	ef	
Mangareva	M1	3 511 ±297 (n=25)	c	* (p=0.019) K-W	0.26±0.03 (n=25)		(p=0.771) K-W
	M3	2 710 ±220 (n=25)	cd		0.24±0.03 (n=25)		
	M4	2 438 ±230 (n=25)	d		0.25±0.03 (n=24)		

Table 2 Larval abundance and total Chl-a concentration tests between stations in Ahe and Mangareva. Sampling location and periods are as in Fig.1. Means are given with the standard error and the number of samples (n). Dunn post-hoc test performed when significant differences (*) occurred after a Kruskal-Wallis (K-W) test. p-values obtained with alpha error=5%.

Supplementary material

Table S1. Ranking of models testing the relationships between all combinations of environmental variables (chlorophyll-*a*, seawater temperature, and wind speed and direction) and the temporal dynamics of larvae abundance (1-week time lag). LL = log-likelihood; k = number of model parameters; ΔAIC_c = difference in Akaike's information criterion (corrected for small sample size) between the current and top-ranked models; $wAIC_c$ = AIC_c weight (~ model relative probability); Int = intercept; Chl-*a* = chlorophyll-*a*; Temp = temperature; WS = wind speed; WD_{sin} = wind direction, sine component; WD_{cos} = wind direction, cosine component.

Model	k	LL	AIC_c	ΔAIC_c	$wAIC_c$
Ahe					
Int + Chl-*a* + Temp + WD_{sin} + WD_{cos}	5	-76889.32	153789.60	0.00	0.73
Int + Chl-*a* + Temp + WS + WD_{sin} + WD_{cos}	6	-76889.11	153791.57	1.97	0.27
Int + Temp + WS + WD_{sin} + WD_{cos}	5	-78262.42	156535.80	2746.20	0.00
Int + Temp + WD_{sin} + WD_{cos}	4	-78268.68	156545.99	2756.39	0.00
Int + Chla-*a* + Temp + WS	4	-83049.22	166107.06	12317.46	0.00
Int + Chl-*a* + WS + WD_{sin} + WD_{cos}	5	-83505.68	167022.31	13232.72	0.00
Int + Chl-*a* + Temp	3	-83887.11	167780.59	13990.99	0.00
Int + Chl-*a* + WD_{sin} + WD_{cos}	4	-85163.85	170336.32	16546.72	0.00
Int + WS + WD_{sin} + WD_{cos}	4	-85567.69	171144.00	17354.40	0.00
Int + Temp + WS	3	-85669.52	171345.41	17555.81	0.00
Int + Chl-*a* + WS	3	-85881.55	171769.48	17979.88	0.00
Int + Temp	2	-87057.07	174118.32	20328.72	0.00
Int + WD_{sin} + WD_{cos}	3	-87663.13	175332.63	21543.03	0.00
Int + Chl-*a*	2	-88257.25	176518.68	22729.08	0.00
Int + WS	2	-88353.01	176710.20	22920.60	0.00
Int	1	-91691.93	183385.92	29596.32	0.00
Mangareva					
Int + Chl-*a* + Temp + WS + WD_{sin} + WD_{cos}	6	-13246.22	26506.02	0.00	1.00
Int + Chl-*a* + Temp + WD_{sin} + WD_{cos}	5	-13315.90	26642.90	136.88	0.00
Int + Temp + WS + WD_{sin} + WD_{cos}	5	-13755.07	27521.25	1015.23	0.00
Int + Temp + WD_{sin} + WD_{cos}	4	-13890.24	27789.22	1283.20	0.00
Int + Chl-*a* + Temp + WS	4	-14352.01	28712.75	2206.73	0.00
Int + Chl-*a* + WS + WD_{sin} + WD_{cos}	5	-14468.22	28947.55	2441.53	0.00
Int + Chl-*a* + WD_{sin} + WD_{cos}	4	-14501.42	29011.57	2505.55	0.00
Int + Chl-*a* + Temp	3	-14545.43	29097.29	2591.27	0.00
Int + Temp + WS	3	-15042.41	30091.26	3585.24	0.00
Int + Temp	2	-15363.83	30731.87	4225.84	0.00
Int + WS + WD_{sin} + WD_{cos}	4	-16089.75	32188.24	5682.22	0.00
Int + WD_{sin} + WD_{cos}	3	-16152.40	32311.24	5805.21	0.00
Int + Chl-*a* + WS	3	-16276.95	32560.33	6054.31	0.00
Int + Chl-*a*	2	-16291.92	32588.04	6082.02	0.00
Int + WS	2	-18166.19	36336.59	9830.57	0.00
Int	1	-18196.24	36394.54	9888.52	0.00