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Yoann Thomas, P. Garen, A. Bennett, M. Le Pennec, Jacques Clavier. Multi-scale distribution and dynamics of bivalve larvae in a deep atoll lagoon (Ahe, French Polynesia). *Marine Pollution Bulletin*, 2012, 65 (10-12), pp.453-462. 10.1016/j.marpolbul.2011.12.028 . hal-00671058

HAL Id: hal-00671058

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Submitted on 7 Jan 2023

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Multi-scale distribution and dynamics of bivalve larvae in a deep atoll lagoon (Ahe, French Polynesia)

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Abstract:

Bivalve larvae and hydrographic parameters were sampled over a range of spatio-temporal scales in a deep atoll lagoon. Bivalve larvae abundances were very high throughout the year: 18,550 m⁻³ in average. Larvae were (i) concentrated at mid-depth with nocturnal ascent and diurnal descent, (ii) heterogeneously dispersed at the lagoon scale, (iii) subject to day-to-day variation in abundance and (iv) transferred between different parts of the lagoon providing evidence of intra-lagoonal connectivity. The primacy of physical factors was seen on large spatial scale with the diluting effect of water renewal and transfers by hydrodynamics. On smaller spatial scale, the primacy of biological processes was recognised, with larval swimming activity leading to diel vertical migration correlated with food concentration. Variations in larval abundance were driven by bivalve reproductive activity correlated with meteorological conditions (*i.e.* windy periods). Finally, relationship between bivalve larvae patterns and pearl oyster (*Pinctada margaritifera*) settlement structuring is discussed.

Highlights

► Bivalve larvae distribution patterns were studied in a deep atoll lagoon. ► Bivalve larvae abundances were very high throughout the year. ► The primacy of physical factors was seen on large spatial scale. ► Biological processes (swimming, spawning) were recognised to drive small-scale patterns. ► We demonstrated the relationship between larvae abundance and *Pinctada margaritifera* settlement.

Keywords: Bivalve larvae ; Distribution patterns ; Vertical migration ; *Pinctada margaritifera* settlement ; Deep atoll lagoon ; French Polynesia

1 Introduction

The majority of marine invertebrates have a planktonic larval stage at the beginning of their lives. This planktonic step appears to be a key determinant for adult distribution and abundance since the distribution and abundance of sessile populations are determined by a combination of pre- and post-settlement factors (Olson and Olson 1989; Cowen et al., 2000; Levin 2006). Besides endogenous factors, like feeding capacity and metabolic processes

(Pace et al., 2006), bivalve larval growth and survival depend on external pressures from predation (Troost et al., 2009) and a wide variety of environmental factors, *i.e.* temperature, salinity, food quality and availability (Eckman 1996; Doroudi et al., 1999; Powell et al., 2002; Hofmann et al., 2004). Moreover, as for all zooplankton communities, bivalve larvae distributions exhibit spatial patterns (Pinel-Alloul 1995; Avois-Jacquet 2002). These patterns are generated and maintained by physical factors, like hydrodynamics, and biological processes such as larval swimming activity (Haury et al., 1978; Garland et al., 2002; Masson et al., 2004; Badylak and Philips 2008). Since zooplankton distributions and environmental processes are ‘scale-dependent’, a range of spatial and temporal scales should be considered for studying zooplankton variability and understanding its driving mechanisms (Borcard et al., 2004).

The determinants of marine population dispersal remains one of the fundamental challenges for marine ecology and oceanography (Cowen et al., 2006). In tropical ecosystems, numerous studies address fish or coral larval dispersal, mainly to understand the connectivity between source and recipient sectors so as to protect, preserve and manage biodiversity (Roberts 1997; Swearer et al., 1999; Botsford et al., 2009; Munday et al., 2009). In atoll lagoons, the diversity and structure of mollusc populations are highly related to local factors like substrate types or hydrodynamic conditions (Pante et al., 2006). Nonetheless, most of the mechanisms explaining abundance and distribution variability of adult populations remain obscure and could be attributed to larval development success and settlement processes (Adjeroud et al., 2000).

In French Polynesian atoll lagoons, reared stocks of the black-lip pearl oyster (*Pinctada margaritifera*, Linné, 1756) are added to wild populations, increasing the abundances of bivalves. Pearl oyster farming plays a major socio-economic role in French Polynesia with 81 million euros in exports and about 5000 jobs in 2008 (ISPF, 2008). This activity is entirely sustained by the wild collection of juveniles on artificial collectors, although the levels of spat collected are unpredictable. Efficient management of *P. margaritifera* production requires the ability to understand distribution of larvae, and identify suitable zones for spat collection. Among the 15 French Polynesia collecting atolls, Ahe atoll is one of the main producers of *P. margaritifera* juveniles and was chosen as a reference site to study bivalve larvae ecology.

The goals of this study were to quantify the spatio-temporal heterogeneity of bivalve larvae abundances, and develop plausible scenarios involving physical or biological mechanisms to explain observed patterns of variation. The link between larval patterns and *P. margaritifera* settlement variability is discussed.

2 Material and methods

2.1 Sampling site

Ahe atoll is located in the northwestern part of the French Polynesian Tuamotu Archipelago, 500 km northeast of Tahiti Island (Fig. 1). Ahe lagoon has a 145 km² area with a mean depth close to 40 m. Ahe is defined as a semi-enclosed atoll with a mean residence time of 34 days (Pagès and Andrefouet 2001; Dumas et al., this issue). One active pass is located in the western part of the lagoon and several reef-flat spillways (less than 50 cm depth) are distributed along the reef rim, mainly in the south and west part of the lagoon (Andréfouët and Yamano this issue). Almost 10 % of the Ahe lagoon area is dedicated to black-lip pearl oyster rearing. The total stock of cultivated pearl oysters, located in breeding line and excluding spat on collectors, is judged to be 15 million individuals (Perliculture Service, pers. comm.), although the extent of the wild population remains unknown. With nearly 1240 spat collection stations and with 600 collectors per station, Ahe is one of the most important producers of pearl oyster juveniles in French Polynesia.

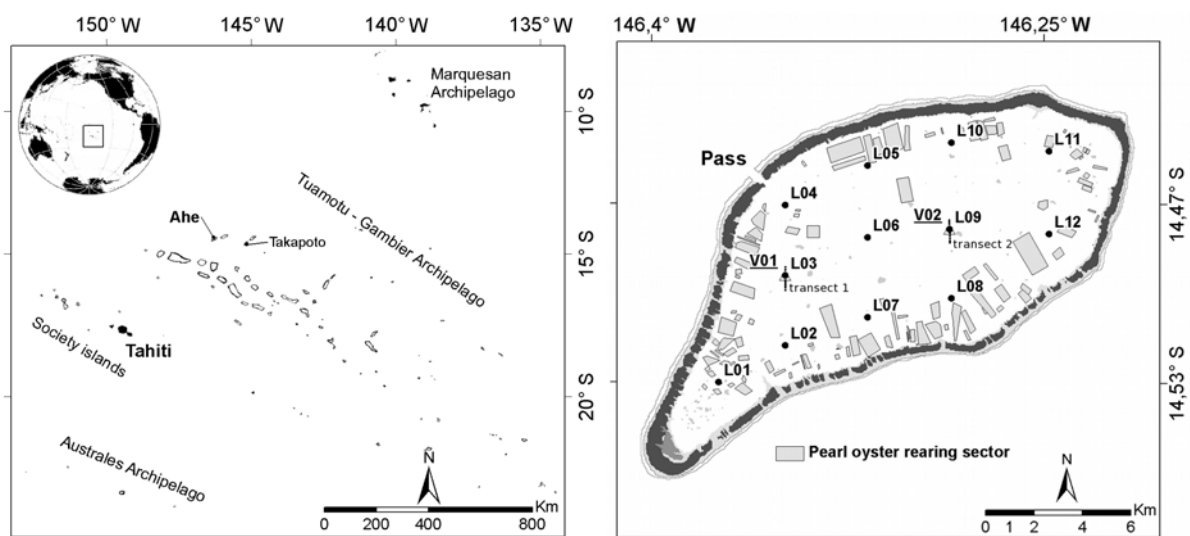


Fig. 1 Left: Localization of the Ahe lagoon. Right: Morphology of the Ahe lagoon and positions of the sampling stations in the lagoon; 'L': lagoon scale, 'V': vertical scale (24-h cycles), 'Transect': local scale

2.2 *Sampling design*

A multi-scale spatial and temporal approach was developed to assess larval abundance and size distribution and hydrographic parameters at local (i.e. horizontal and vertical) and lagoon scales, according to nycthemeral, day-to-day and seasonal dynamics.

Day-to-day lagoon-scale sampling: Sampling was made at twelve stations (L01 to L12) distributed throughout the lagoon (Fig. 1). Stations were visited successively every two days in the morning, from L12 to L01. Water was sampled at each station from the surface to 5 m above the bottom. To assess the seasonal dynamics, four surveys were carried out, in April-May 2007, July-August 2007, November 2007 and February-March 2008. For technical reasons, day-to-day samplings were of different durations: 29, 15, 20 and 29 days during these periods, respectively.

Local transect: Two north south transects (Fig. 1) of ten stations separated by 100 m were sampled in the west and the central-east part of the lagoon, respectively. Water was sampled on each station from the surface to 5 m above the bottom. The two transects were successively sampled at 24-h interval. Three transect samplings surveys were carried out, in April 2007, May 2007 and July 2007, giving a total of 6 profiles; 3 for each transect.

24-h cycle vertical sampling: Two deep stations, V01 and V02 (50 m deep), located in the west and the central-east part of the lagoon, respectively (Fig. 1), were sampled over the whole range of five layers (0-10, 10-20, 20-30, 30-40 and 40-50 m). Each station was sampled with a frequency of 4 h from 08:00 h over a 24-h cycle. The two stations were successively visited at a 24-h interval. These day/night cycles were studied in April 2007, July 2007 and February 2008, giving a total of six cycles; 3 for each station.

2.3 *Zooplankton sampling method*

Plankton was sampled from a boat by pumping at an average flow rate of $5 \text{ m}^3 \text{ h}^{-1}$. A pipe of 32 mm diameter was connected to the pump and immersed to the sampling depth. The mean sample volumes were of 560, 740 and 430 litres for each of the lagoonal, transect and vertical samples, respectively. Pumped water was prefiltered on a $250 \mu\text{m}$ mesh and plankton was retained on a $40 \mu\text{m}$ mesh. Samples were immediately preserved in 72 % ethanol.

In the laboratory, each sample was transferred into a 16 cm diameter glass dish and spread evenly. Three transversal bands covering the dish width and disposed at the first quarter, middle and third quarter of the dish diameter were scanned at 6400 ppp with an Epson V750Pro scanner. The sum of the three scanned surfaces corresponded to 6 % of the total dish surface and therefore to 6 % of the total sample. On each scan, bivalve larvae were visually enumerated and automatically measured using NIVision® image analysing software. The major axis of the adjusted ellipse was used to describe larval size. In 2007, the specific identification of bivalve larvae was difficult and did not allow *P. margaritifera* and *Pinctada maculata* (Gould, 1850) to be distinguished (Paugam et al., 2006), thus no species distinction could be made at the larval stage for this study.

2.4 *Experimental spat collection*

We studied black-lip pearl oyster settlement concurrently with planktonic bivalve larvae distribution, in order to assess any direct links between them. Three experimental collectors, of the type used in the industry (i.e. loops of black flat polypropylene, knitted onto a 30 cm monofilament polyethylene line), were immersed at 6 depths (5, 10, 15, 25, 35 and 45 m) at 2 stations (V01 and V02) for 6 weeks in April-May 2007, July-August 2007, November-December 2007 and February-March 2008. In the laboratory, spat were retrieved from the collectors and fixed in a 72 % ethanol solution. Three groups: *P. margaritifera*, *P. maculata* and ‘other bivalves’ spat were identified and enumerated.

2.5 *Environmental parameters*

Vertical profiles of salinity (practical salinity unit), temperature (°C) and *in vivo* chlorophyll *a* ($\mu\text{g l}^{-1}$), were carried out *in situ* with a multi-parameter probe (SBE S19Plus, Sea-Bird Electronics, Inc.) at each sampling station. Hourly wind direction and velocity were obtained from Takaroa atoll meteorological station (Météo France data) located about 120 km east of Ahe (145°3'4''W, 14°28'57''S). Wind direction and velocity were recorded in the field with a mobile anemometer during the 24-h cycles. A detailed description of spatial and temporal variation of environmental parameters can be found in Thomas et al., (2010).

2.6 *Data analysis*

Median size was used to characterize the population of larvae species. Knowing the median size provides a first description of community composition by inferring the

developmental stage and species structure. The coefficient of variation ($CV = \sigma / \mu$) was calculated for larval abundance and size so as to quantify the degree of variability on various scales. To represent lagoon scales patterns, data were standardized by the standard score: $z = (V - \mu) / \sigma$ where V is the median size value or larval concentration. After $\log(x + 1)$ transformation of abundances for data normalization and variance homogenisation, one-way ANOVA was applied to test the effects of space and time at the different scales. A post hoc Scheffé's pair-wise multiple comparison test was performed when significant differences were detected.

A Hierarchical Cluster Analysis (HCA), using similarity coefficient (*i.e.* Pearson correlation coefficient), was performed on all the daily abundances and median sizes ($n = 1200$), to identify homogeneous groups of stations at the lagoon scale in order to ease result interpretations.

Spearman correlations were used to test the relationships between bivalve larvae abundances and environmental parameters. Since all the data of the 4 sampling campaigns were introduced to calculate the correlation coefficient, the distribution of the data did not reach the normality. This has motivated the choose of the Spearman's rank correlation coefficient, which makes the coefficient less sensitive to non-normality in distributions. Finally, the mean depth distribution of the larvae (ZCM), described by Fortier and Leggett (Fortier and Leggett 1982), was calculated for the 24-h cycles:

$$ZCM = \sum c_i d_i$$

where c_i is the concentration frequency at the i th depth interval and d_i is equal to the mid-depth of the i th interval.

3 Results and discussion

3.1 Vertical structure and dynamics

Bivalve larvae abundances were heterogeneously distributed through the water column ($p < 0.001$) (Table 1, Fig. 2a). Larvae were concentrated between 15 and 35 m depth. The mean CV calculated on the whole vertical profile was 38 %. In addition, the population median size was unevenly distributed, with the largest larvae between 15 and 35 m depth (Fig. 2b).

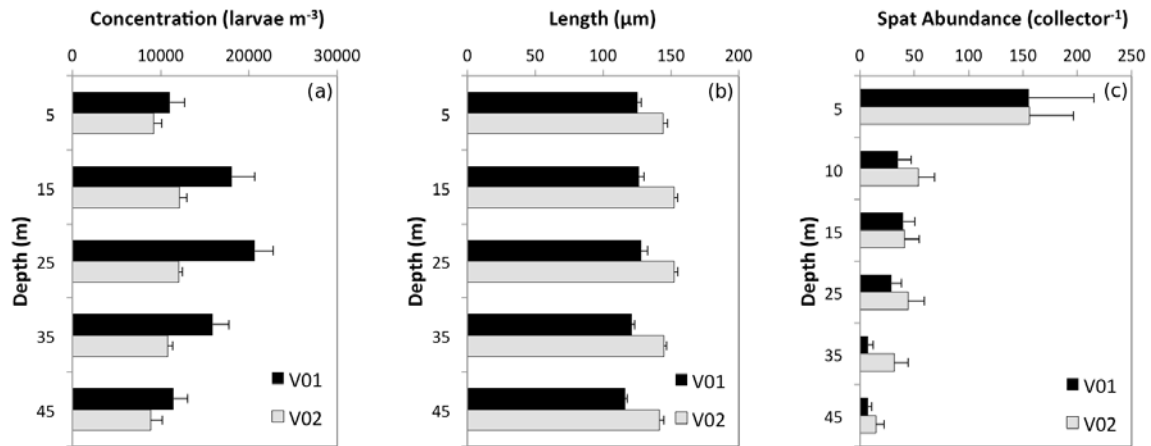


Fig. 2 Vertical patterns of (a) bivalve larvae abundance, (b) bivalve larvae median size and (c) *P. margaritifera* spat settlement density at the two stations V01 and V02. Data correspond to averages \pm standard error, calculated on the three sampling periods: April-May 2007, July-August 2007 and February-March 2008.

Table 1. Results of the one-way ANOVA tests. In the comments column, numbers give the depth level (m) or the survey number (1: April-May, 2: July-August, 3: November and 4: February-March), and the letters give the homogenous groups.

Parameter	Factor	DF	F	p	Comment
Larval concentration	Station	1	18.03	< 0.0001	V01 > V02
	Depth	4	5.55	0.0003	5a 15bc 25c 35abc 45ab
	Hour	5	0.42	0.836	=
Larval median size	Station	1	150.52	< 0.0001	V01 < V02
	Depth	4	4.76	0.001	5ab 15a 25a 35ab 45b
	Hour	5	0.60	0.732	=
<i>P. margaritifera</i> spat density	Station	1	8.53	0.006	V01 < V02
	Survey	3	5.18	0.004	1a 2b 3b 4ab
	Depth	5	9.57	< 0.0001	5a 10ab 15abc 25bc 35c 45c
<i>P. maculata</i> spat density	Station	1	1.97	0.169	V01 = V02
	Survey	3	6.40	0.001	1a 2b 3ab 4a
	Depth	5	7.91	< 0.0001	5ab 10a 15a 25ab 35c 45bc
Other bivalves spat density	Station	1	10.317	0.003	V01 < V02
	Survey	3	11.15	< 0.0001	1a 2c 3ab 4bc
	Depth	5	8.63	< 0.0001	5a 10a 15a 25a 35a 45b

Larvae exhibited vertical migration according to the day/night cycles (Fig. 3, 4). No significant effect of the hour of the day was measured on the total concentration (Table 1), demonstrating the homogeneity of total abundances during the surveys. Larval abundances increased in the deeper layer during the day until 16:00 h and then increased in the upper layers until midnight. This cycle was mainly observed in the upper 10 m layer where larval concentration was systematically higher at night than during the day (Fig. 3). A slight variation of the mean depth distribution, ZCM, was measured with 26.5 m during the day and 23 at night (Fig. 4). This pattern implies nocturnal ascent and daytime descent but was disrupted by windy conditions, mainly during the two first surveys on the V02 station where day/night migration was not clear due to winds of 5.8 and 7.6 m s⁻¹, respectively, comparing to the 3.8, 3.8, 3.7 and 4.1 m s⁻¹ measured during the 4 others surveys. No specific pattern could be identified in the median size (data not shown) according to 24-h dynamics.

The vertical heterogeneity of bivalve larvae abundance observed in Ahe atoll is in agreement with a previous study in the Takapoto lagoon, with maximum larval concentration at mid-depth (pers. comm. Garen). Similar patterns were described for bivalve larvae by Garland et al. (2002) in an inner-shelf of North Carolina (USA) and by Raby et al. (1994) in the Baie des Chaleurs, Quebec, Canada. Various stimuli were suggested that might explain the vertical swimming behaviour of bivalve larvae, like salinity or temperature discontinuity, light intensity, food availability or avoidance of predators (Raby et al., 1994; Knights et al., 2006). In Ahe lagoon, the vertical distribution was positively correlated with temperature and food concentration (*i.e.* Chl *a in vivo*) (Table 2). These results must be considered cautiously because correlations are not causal relationships. Nonetheless, temperature (or saline) discontinuities may have a significant influence on the vertical swimming ability (*i.e.* speed) of bivalve larvae (*see e.g.* Deksheniaks et al., 1996). But this influence was always described with high variation levels in T or S and mostly for species from temperate area. That is why; specific experimental protocols need to be developed to better know the effect of various T and S gradients on tropical species larvae. However, autotrophic communities and bivalve larvae seem to follow similar diel dynamics, apparently driven by light intensity, as suggested by the day/night pattern observed. This swimming behaviour is however hampered by windy conditions, probably due to water column homogenisation. No specific pattern was observed in median sizes of larval cohorts during the 24-h cycles studied. Species-specific larval behaviour at this stage could instead be invoked to describe the vertical distribution (Baker 2003).

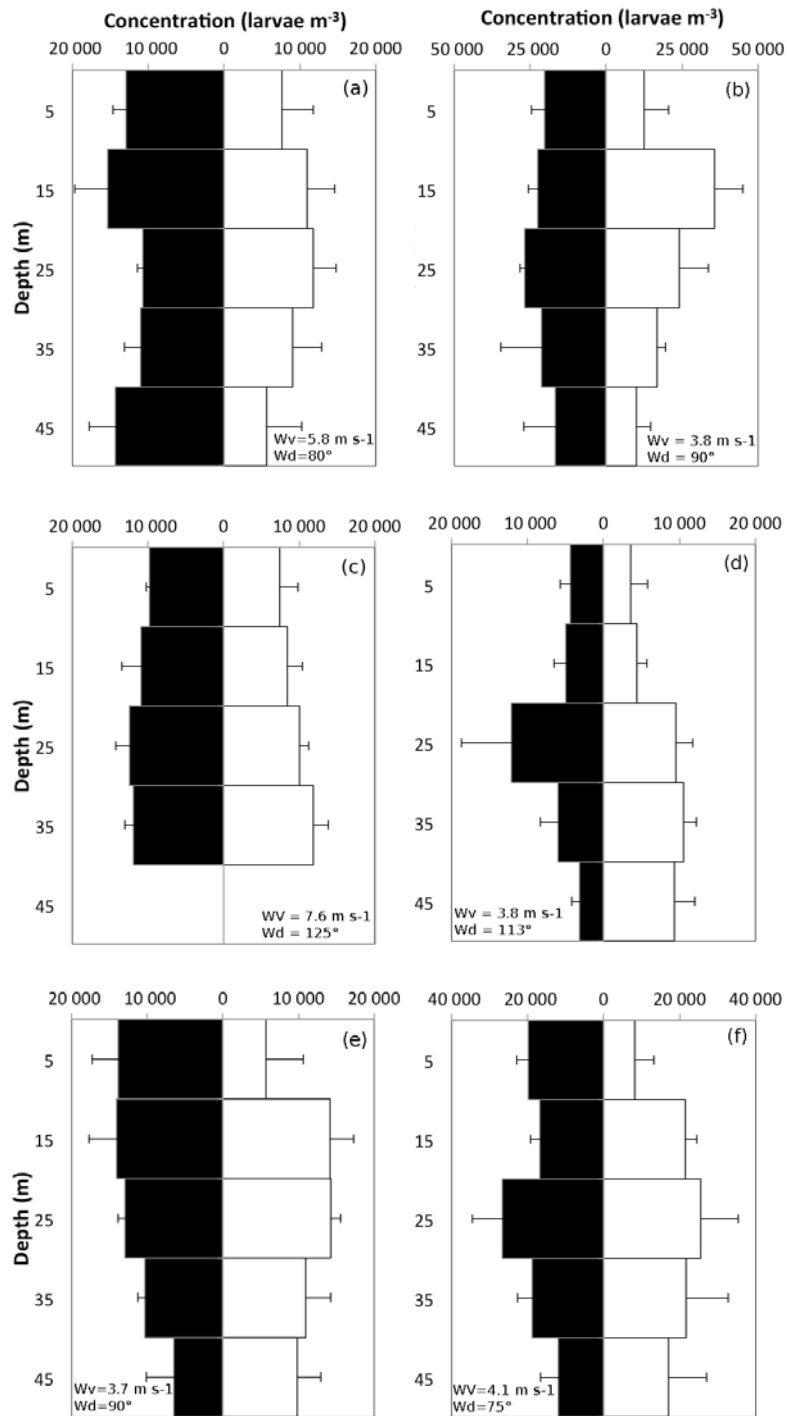


Fig. 3 Vertical distribution of bivalve larvae concentration (\pm standard error) during the day (open) and at night (black): (a) V02-April 07, (b) V01-April 07, (c) V02-July 07, (d) V01-July 07, (e) V02-February 08 and (f) V01-February 08. Day means correspond to 4 measurements: 08:00, 12:00, 16:00 and 08:00 the second day and night means to 3 measurements: 20:00, 00:00 and 04:00. Wind velocity (Wv) and direction (Wd) are indicated on the plots.

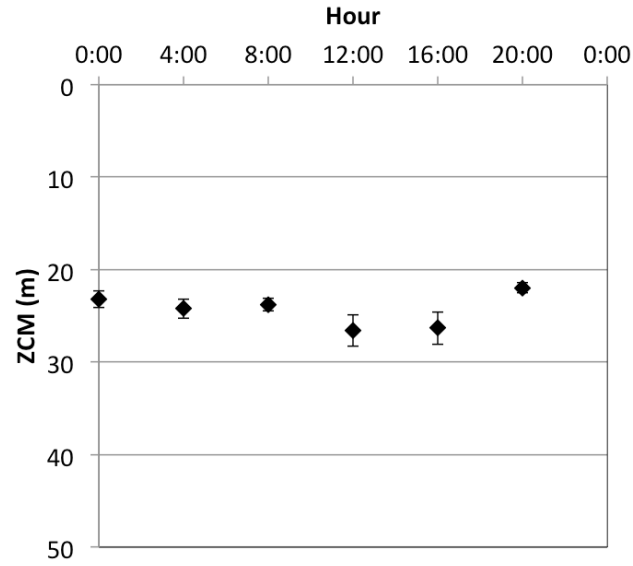


Fig. 4 Diel variation of the mean depth distribution of the larvae, ZCM. Data correspond to the averages \pm standard error calculated on the overall 24-h cycles data set.

Table 2. Spearman correlation among the studied environmental parameters (LARV = larval abundance, SAL = Salinity, TEMP = temperature, Chl *a* = *in vivo* Chlorophyll-a, Dist pass = distance from pass, Dist east-reef = distance from eastern reef and WV = wind velocity) according to the three spatial scales studied (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Scale		LARV	SAL	TEMP	Chl <i>a</i>	Dist pass
Lagoon	SAL	0.04				
	TEMP	0.06	-0.06			
	CHLA	0.07	0.30***	0.37***		
	Dist pass	0.42***	0.03	-0.09*	0.08*	
	Dist east-reef	-0.37***	0.02	0.01	-0.16***	-0.85***
	WV	0.04	0.17***	0.13**	0.12**	-
Transect	SAL	-0.39**				
	TEMP	0.02	-0.59***			
	CHLA	0.30*	-0.16	0.14		
	Dist pass	0.07	0.05	-0.26*	0.34**	
	Dist east-reef	-0.19	-0.06	0.24	-0.29*	-0.75***
Vertical	SAL	-0.33***	-			
	TEMP	0.43***	-0.33***	-		
	CHLA	0.14*	0.01	-0.14	-	

3.2 Large-scale distribution and dynamics

Bivalve larvae were present in the plankton of Ahe lagoon at each of the sampling periods. The average abundance ranged from $15.8 \pm 0.6 \times 10^3 \text{ m}^{-3}$ in November 2007 to $21.3 \pm 1.1 \times 10^3 \text{ m}^{-3}$ in April-May 2007 (Table 3). This constant presence is in agreement with the continuous reproductive patterns described for tropical bivalves (Pouvreau et al., 2000). Average concentrations were higher than in other atolls. In addition, bivalve larvae contribute to a large part of the zooplankton abundance in the Ahe lagoon with a contribution of $53.3 \pm 13.2 \%$ to the abundance (Pagano et al., this issue). In their study of Tikehau lagoon (French Polynesia), Blanchot et al. (1989) reported a mean bivalve larvae concentration of $0.9 \times 10^3 \text{ m}^{-3}$, ranging from 0.2×10^3 to $1.9 \times 10^3 \text{ m}^{-3}$, and corresponding to 6 % of the plankton abundance. An average concentration of $2.1 \times 10^3 \text{ m}^{-3}$, ranging from 0.3×10^3 to $35.4 \times 10^3 \text{ m}^{-3}$ was measured in the Takapoto lagoon (French Polynesia) (Garen, unpublished data).

Table 3. Water temperature, bivalve larvae concentration: mean \pm standard error (n); and spat density of *P. margaritifera*, *P. maculata* and other bivalve species on collectors: mean of 6 depths \pm standard error (n , relative proportion) during four survey periods (letters indicate significant differences between surveys: $p < 0.05$)

		April-May	July-Aug.	Nov.	Feb-March	
Water temperature (°C)		29.3 ± 0.001^a ($> 10^4$)	27.2 ± 0.001^b ($> 10^4$)	28.2 ± 0.001^c ($> 10^4$)	28.6 ± 0.001^d ($> 10^4$)	
Bivalve larvae ($\times 10^3 \text{ m}^{-3}$)		21.3 ± 1.1^a (194)	17.4 ± 0.8^{ab} (96)	15.8 ± 0.6^b (132)	19.7 ± 0.9^{ab} (180)	
Spat (collector ⁻¹)	V01	<i>P. margaritifera</i>	35 ± 7^a (12, 0.52)	11 ± 6^b (6, 1.5)	15 ± 8^{ab} (6, 0.39)	88 ± 35^a (14, 2.12)
		<i>P. maculata</i>	5853 ± 2188^a (8, 86.50)	570 ± 166^b (6, 78.01)	3238 ± 1568^{ab} (6, 80.76)	3742 ± 1149^{ab} (6, 90.27)
		Other bivalves	879 ± 198^a (8, 12.98)	150 ± 52^b (6, 20.49)	756 ± 259^{ab} (6, 18.85)	315 ± 117^{ab} (6, 7.61)
	V02	<i>P. margaritifera</i>	61 ± 13^a (12, 1.64)	81 ± 49^a (6, 4.65)	42 ± 18^a (6, 0.99)	49 ± 18^a (12, 0.75)
		<i>P. maculata</i>	2408 ± 1007^b (8, 65.04)	1369 ± 585^b (6, 78.99)	3017 ± 1177^b (6, 71.61)	5941 ± 1755^a (8, 91.29)
		Other bivalves	1233 ± 288^a (8, 33.32)	284 ± 67^c (6, 16.37)	1154 ± 335^{ab} (6, 27.40)	518 ± 118^b (8, 7.96)

The larval concentration in Ahe lagoon appeared also very high compared with other ecosystems. A coastal lagoon of southern Portugal had an average bivalve larvae concentration around $4.7 \times 10^3 \text{ m}^{-3}$ (Chicharo and Chicharo 2000), and the inner-shelf off North Carolina yielded $9.8 \times 10^3 \text{ m}^{-3}$ (Garland et al., 2002).

The abundant population of adults in Ahe lagoon certainly explain the permanent larval abundance, which is also modulated, by larval mortality due to predation, export, and starvation. In Ahe, only the reared *P. margaritifera* stock numbers are well known (circa 15×10^6 individuals), not including oysters on collectors that are breeders from the age of approximately 6 months to 1 year. Although no data are available on the wild bivalve populations in Ahe lagoon, 6 bivalve species are likely present given their abundance in other Polynesian atoll lagoons: *Arca ventricosa* (Lamarck, 1819), *Pinctada maculata*, *Crassostrea cucullata* (Born, 1778), *Spondylus varians* (Sowerby, 1829), *Chama iostoma* (Conrad, 1837) and *Tridacna maxima* (Röding, 1798). An evaluation of the wild population broodstocks should be made in Ahe lagoon to evaluate the relative contribution of these species to the entire bivalve community. Our spat settlement measurement suggest that *P. maculata* would be dominant since it accounts for almost 80 % of the total density (see below). Nonetheless, species selectivity of collectors is unknown and it would be hazardous to draw any direct conclusion about wild stock from this result.

During our surveys, the variability of larval abundance appeared lower on the local scale than on the large scale. Larval abundance was constant or exhibited gradient shape along the two transects (Fig. 5). This observation meant that interpretation mistakes due to small-scale patchy patterns were minimized.

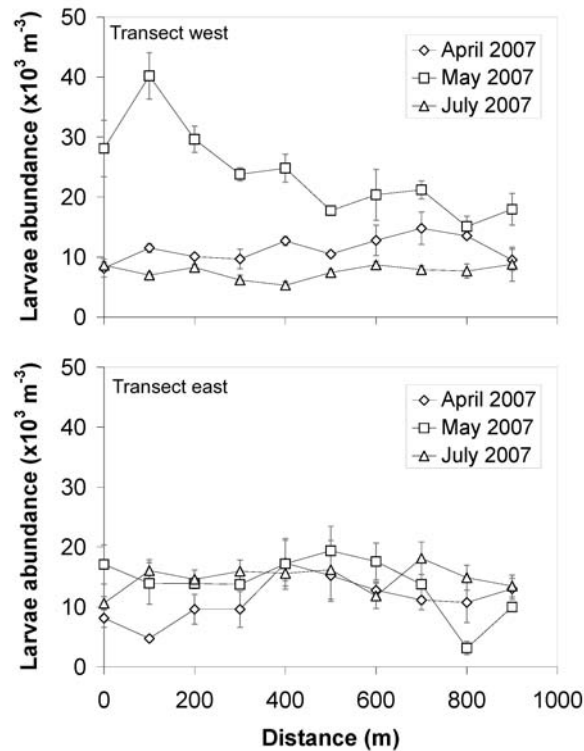


Fig. 5 Bivalve larvae abundance variation (mean \pm standard error) along the west (up) and east (down) transects, during three sampling surveys

Bivalve larvae abundances were heterogeneously distributed at the lagoon scale (Fig. 6), with a general pattern showing (i) a low concentration area in front of the pass, (ii) a high concentration area along the east reef rim and (iii) a more variable concentration area in the southwest sector. The extent of the southern high concentration sector was the most variable feature, with a minimal area during the August survey, which was the windiest period, and a shift of the ‘poorest’ area towards the west coast of the lagoon. A significant east-west gradient was revealed for the median size of bivalve larvae cohorts, showing higher values in the eastern sector at every survey (Fig. 6). A similar large-scale pattern was described by Carleton & Doherty (1998) in the Taiaroa lagoon, with different zooplankton assemblages in windward and leeward parts of the lagoon, which they interpreted as a result of both hydrodynamic circulation and species-specific behaviour.

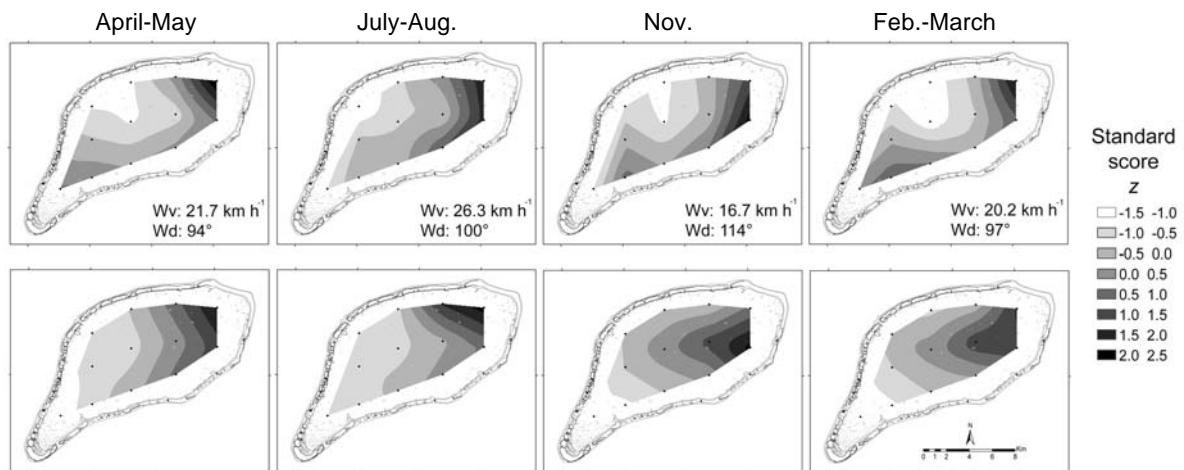


Fig. 6 Spatial variation of bivalve larvae abundance (up) and bivalve larvae median size (down), in the four surveys: (a) April-May 2007, (b) August 2007, (c) November 2007 and (d) February-March 2008. All data were standardized (standard score z). Mean wind velocity (Wv) and wind direction (Wd) are indicated on the maps

Ahe should be regarded as a deep lagoon, with a 40 m average depth and maximum depth over 70 m. In such deep lagoons, circulation patterns are mostly wind-driven, with surface circulation going downwind and a ‘compensatory’ upwind current of deep water (Atkinson et al., 1981). Since the majority of larvae were actually distributed in deep layers, the vertical distribution of bivalve larvae could explain some of the observed large-scale patterns, the larvae being subjected to the ‘compensatory’ upwind current leading to high larval concentration along the eastern reef rim. This observation is confirmed by the study of Pagano et al. (this issue) in the Ahe lagoon, describing heterogeneity in zooplankton assemblage, with species showing a migratory behaviour concentrated in the western part of the atoll and a high concentration of bivalve larvae in the eastern part by windy conditions. The large-scale pattern could also be related to the broodstock distribution, as the majority of the cultivated broodstock is located close to the reef rim around the lagoon. The central part of the lagoon has deep waters, with few reefs suitable as adult habitat (Adjeroud et al., 2000; Pante et al., 2006). Nonetheless, the high transport potential for larvae observed in our study (see below) and confirmed by the modelling study of Thomas et al. (this issue) on the larval transport and connectivity in the Ahe lagoon, seem to minimize the effect of the broodstock location, mainly by eastern winds.

In atoll lagoons, tide residual transport and direct influence on planktonic communities exhibit a general low pattern and are mostly confined to the vicinity of the pass (Tartinville et

al., 1997). In our study, the diluting effect of the pass was obvious and corroborated by the positive correlation between larval abundances and distance from the pass (Table 2). Stations L04, L05 and L06, located in front of the pass, and extended toward the east, were mainly submitted to this diluting effect.

The hierarchical cluster analysis (HCA) allowed 4 groups of stations with similar abundance and median size patterns and dynamics to be identified (Fig. 7): a western confined sector A, corresponding to the L01 station; a sector B, separated in two groups: one in front of the pass covering the L02, L03 and L04 station and a second in southeast, covering the stations L08, L09 and L12; an extended north sector, C, covering the stations L05, L06, L10 and L11; and a small south sector, D, corresponding to the station L07. HCA did not provide any explanation or interpretation, so the results need to be considered carefully. Indeed, as our HCA analysis did not include weighting by location proximity, the spatial and temporal continuity of two-day step data used for the HCA may induce positive spatial autocorrelations (Schabenberger and Gotway 2005). This analyse is mainly used to simplify the short-time scale patterns presentation and interpretation.

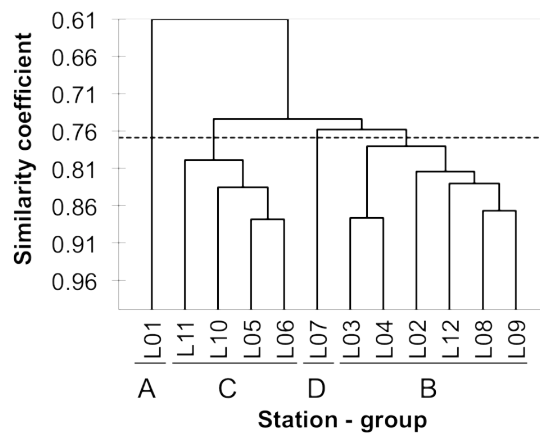


Fig. 7 Dendrogram extracted from the hierarchical cluster analysis.

Short time-scale variations were recorded in wind velocity, mostly during the three first surveys (Fig. 8a). In addition, high day-to-day variations in phytoplankton biomass were observed, concurrent to stratification/mixing events, showing higher concentration in the deeper layers (Fig. 8b). The bivalve larvae abundances and median size variations are presented on Fig. 8c and d with a two-day step frequency, according to the four groups identified by the hierarchical cluster analysis: A, B, C and D. The mean coefficients of

variation calculated for sectors A, B, C and D were 101, 30, 32 and 54 %, respectively. These high levels of variation were mainly supported by the first and last surveys. Four successive increases in abundance were then observed with increasing intensity during the fourth survey in sector A (Fig. 8c). A specific event occurred during the first survey, on 8 May, with a synchronous increase in the four sectors. The abundance rise recorded in sector A also appeared delayed in the adjacent D area, as seen during the first survey, after the 8 May, and during the last survey, after the second and third ‘larval blooms’, on 19 and 25 February.

The ‘larval blooms’ observed during the first and last surveys were correlated with high wind occurrence, leading to the homogenisation of the water column that was recorded through the Chl *a in vivo* measurement (Fig. 8b). As revealed by the day-to-day recording, abundance variations appeared to be mostly sustained by punctual increases, which were dominant in sector A. These events were related to a decrease in median size and could then be linked to spawning events. The southwest zone can, therefore, be considered as a ‘source area’ for larvae, sustained by multiple ‘spawning events’ identified by the simultaneous increase in abundance and decrease in median size. Indeed, this sector gathers an important pearl oyster stock and several reefs suitable as adult habitat. Nevertheless, bivalve larvae abundance decreased rapidly after these ‘spawning events’ in L01 and reached lower values than in other areas, providing evidence of export. This west-east transfer through the southern part of the lagoon is supported by the delay of abundance rises described between sectors A and D (Fig. 8c). Furthermore, westward extension of the B and C groups shows evidence of east-west transfers.

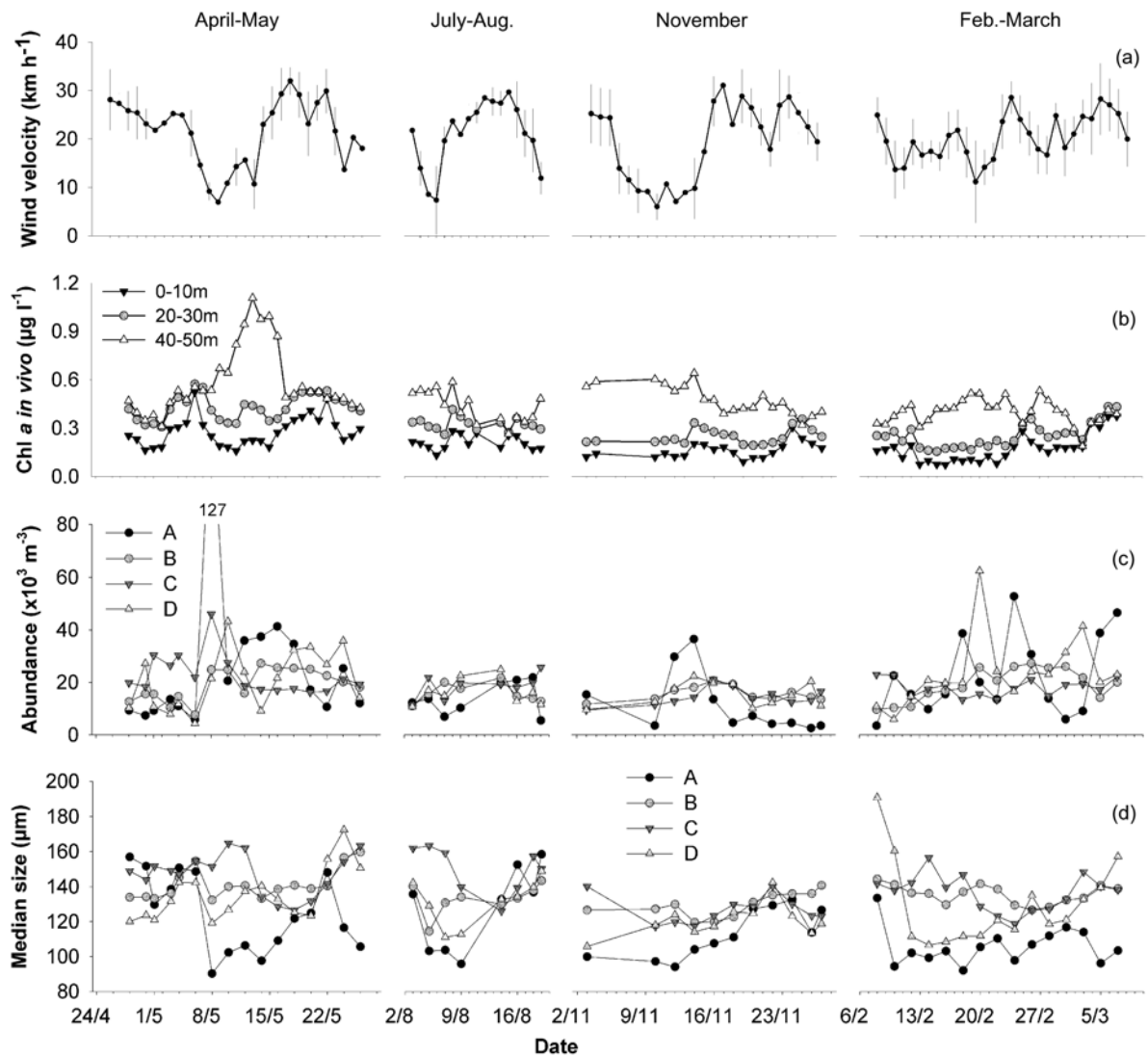


Fig. 8 Day-to-day variation in wind velocity, Chl *a in vivo* concentration by 10 m depth layers, abundance of bivalve larvae and median size of bivalve larvae for the four groups of stations: A, B, C and D, during the four surveys: April-May 2007, August 2007, November 2007 and February-March 2008

A system like the counter-rotating bodies of water described by Atkinson et al. (1981) in the Enewetak atoll lagoon could explain these east-west transfers without north-south communication. Indeed, this kind of functioning has been recently described in Ahe lagoon by Dumas et al. (this issue), with the stream function displaying three main barotropic circulation structures: a flat clockwise cell along the southern rim, an anticlockwise circulation cell in the middle of the atoll, and a clockwise circulation loop along the northern rim. In addition, a high connectivity level between sectors of the Ahe lagoon has been recently confirmed by Thomas et al. (this issue), through a 3D modelling study of the larval

transport. Indeed, they showed that the west-east transfer of larvae was supported by eastern winds, observed during the summer period, and related to the activation of a compensatory current in the deep layers. For winds coming from the southeast, mainly observed during the winter, a lower compensatory current, induced by a low fetch, implies higher retention of the larvae in their origin area.

3.3 *Bivalve larvae patterns related to environmental factors*

Correlations between environmental parameters and bivalve larvae abundances at the three spatial scales studied are presented in Table 2. Spatio-temporal variability of environmental parameters such as the temperature, salinity and phytoplanktonic communities in the Ahe lagoon were described by Thomas et al., (2010). Distances from the pass and from the eastern reef were added to the analysis in order to extract the effects of water renewal and geomorphology.

At the lagoon scale, larval abundances revealed a significant positive correlation with distance from the pass and negative correlation with distance from the eastern reef. At the local scale (*i.e.* transects), larval abundance showed significant positive correlation with Chl *a* *in vivo* and negative correlation with salinity. Finally, at the vertical scale, larval abundance exhibited a significant positive correlation with temperature and *in vivo* Chl *a*, and a negative correlation with salinity.

Maximal larval concentrations were recorded during the warmest periods. As already mentioned, this pattern must largely be related to oyster broodstock reproductive activity that, despite continuous reproduction, reaches a maximum during warm periods (Pouvreau et al., 2000). Reproductive pattern itself appeared closely linked to hydro-biological and/or meteorological events on a short time-scale, according to the synchronous ‘spawning events’ correlated with high wind occurrences recorded during the first and last surveys (**Erreur ! Source du renvoi introuvable.**). Bivalve molluscs are known to have stress-induced reproductive triggers (Fujikura et al., 2007). Windy conditions could, therefore, provide a physical stress factor that triggers reproduction by current modification, water mixing or the consequent modification of hydro-biological parameters (*e.g.* food concentration and/or availability). Indeed, Fournier et al., (This issue) showed recently that *P. margaritifera*

developed a clear opportunistic strategy of reproduction in which gametogenesis rate and spawning are directly related to plankton concentration, itself correlated to the wind speed.

The spatial patterns described in our study showed significant heterogeneity, in agreement with the ‘multiple driving force hypothesis’ described by Pinel-Alloul (1995), and defined as the combination of biotic and abiotic factors controlling environmental heterogeneity. We demonstrated the primacy of abiotic factors controlling bivalve larvae heterogeneity at a large spatial scale and a greater importance of biological processes at smaller scales. At the lagoon scale, bivalve larvae abundances were then positively correlated with the distance from the pass, indicating a significant diluting effect. In addition, abundances were negatively correlated with the distance from the eastern reef, which could partly be related to hydrodynamic effects on retention or through the effect of the compensatory current in deep layers (Thomas et al., this issue). At last, the large scale heterogeneity in larval concentration may be related to the trophic resource heterogeneity described by Thomas et al. (2010) and the opportunistic strategy of reproduction of *P. margaritifera* described by Fournier et al. (this issue), with higher plankton concentration close to the east and west reefs, corresponding to the sectors most concentrated in larvae. On the smallest scales, larval abundances were significantly correlated with temperature, salinity and food concentration, and exhibited vertical swimming behaviour leading to vertical structuring of abundances.

3.4 *Bivalve species settlement patterns*

P. margaritifera spat appeared largely under-represented on collectors, with a relative proportion of 1.6 % compared with 80.3 % and 18.1 % for the *P. maculata* and ‘other bivalves’, respectively (Table 3). *P. margaritifera* spat settlement on artificial collectors showed a low but significant difference ($p = 0.044$) between the two stations, with higher densities at V02 (Table 3). The maximum *P. margaritifera* spat recruitment was recorded at 5 m depth with a strong decrease below this layer (Fig. 2). No significant seasonal difference was recorded at the V02 station, and maxima were recorded in April-May and February-March at V01.

P. maculata spat showed maximum density in the first 25 m (data not shown). No significant difference was recorded between stations ($p > 0.05$), both showed lower abundances in August and higher during warm periods in April and February.

‘Other bivalves’ showed significantly lower density at 45 m (data not shown) with higher abundances at V02. The same seasonal trend was recorded at both stations, showing maxima during the first and third surveys.

Several studies indicate spatial and temporal variability of benthic invertebrate larvae settlement over a wide range of scales (Porri et al., 2008). Beside the substrate selection, most studies explain this temporal and spatial variation by two related factors: hydrodynamics and larval supply (Friedman and Bell 1999). In our case, significant spatio-temporal variations were found for the *P. margaritifera* spat settlement. The two collecting stations exhibited different patterns: the eastern sector showing no seasonal variation, but higher settlement performances, and the western stations showing a more seasonal pattern, with higher performances during warm periods. These observations could be related to the distribution of bivalve larvae cohorts on a large scale, with high concentrations in the east and a more variable southwest area. The larval phase of *P. margaritifera* has a duration of 3-4 weeks in the laboratory (Southgate and Beer 1997). Larvae could, therefore, be exported from the southwest sector to an area with higher residence time until they reach the competent stage necessary for settlement (Le Pennec et al., 2003). Higher larval median sizes found in the eastern part of the lagoon and east-to-west connectivity in the western part of the lagoon measured during eastern wind periods corroborate this observation. As observed during the July-August survey, the windiest conditions coincided with lowest settlement westward and increasing settlement eastward, indicating that windy conditions provide favourable circumstances for west to east transport.

Vertical heterogeneity was found with maximum *P. margaritifera* settlement at 5 m depth, which is in agreement with previous studies and industry recommendations (Friedman and Bell 1999). However these observations differ from those made in Takapoto lagoon, where more than half of the wild stock was found in the 30-40 m depth layer (Zanini and Salvat 2000). Specific behaviour related to artificial substrates (*i.e.* collectors) might explain the characteristics of oysters in Ahe atoll, as chemical cues (*e.g.* biofilm coverage) and substrate type (*i.e.* deep colour, roughness) are key parameters determining attractiveness for settlement (Doroudi and Southgate 2002; Su et al., 2007), and may be depth-dependent. In addition, *P. margaritifera* spat appeared to be particularly under-represented, mainly in comparison with

P. maculata spat. Inter-specific competition could, therefore, contribute to a part of the spatio-temporal variation in settlement on collectors.

4 Conclusion

Despite the low variability of hydro-biological parameters commonly assumed in atoll lagoons, we recorded significant heterogeneity of bivalve larvae abundances in the range of the spatio-temporal scales we examined. According to the ‘measured heterogeneity’ concept, defined as the product of the observer’s perspective (Pinel-Alloul 1995), bivalve larvae appeared (i) concentrated at mid-depth with nocturnal ascent and daytime descent, (ii) heterogeneously dispersed at the lagoon scale, (iii) exhibited day-to-day abundance variations and (iv) transferred between sectors of the lagoon. These transfers provide evidence for intra-lagoonal connectivity and, therefore, for potential source and sink sectors. According to the ‘functional heterogeneity’ concept (Pinel-Alloul 1995), which arises from the ecological interactions between ecological entities and their environment, we identified (i) the primacy of physical factors at a large spatial scale, with the diluting effect of renewal and large-scale hydrodynamic transfers, and (ii) the primacy of biological processes at smaller scales, showing larval swimming activity leading to vertical migrations positively correlated with food concentration. Small time-scale abundance variations also appeared to be driven by reproductive activity, itself correlated with meteorological conditions (*i.e.* windy periods). Finally, we demonstrated the positive relationship between bivalve larvae abundance and *P. margaritifera* settlement abundance. However, only species identification at larval stages should provide more information between small-scale larval patterns and spat settlement. To this end, whole mount *in situ* hybridisation technique recently developed to allow the discrimination of closely-related pearl oyster larvae species found in the French Polynesian atolls (Thomas et al., 2011), might be a relevant tool.

Acknowledgments

This study was funded by the Institut Français de Recherche pour l’Exploitation de la Mer (Ifremer) and the French Polynesian government (research delegation) with technical support of the Service de la Perliculture. Authors wish to express their gratitude to the Ifremer and Service de la Perliculture staff for their efficient help during sample collection. We also thank the Pa’umotu: the Maifano family for their effective assistance on Ahe atoll. We thank H. McCombie for her helpful comments and English revision.

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