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ABSTRACT

Patterns of bivalve larvae dispersal in the deep Ahe atoll lagoon was studied by using a numerical 3D transport model (MARS3D) coupled with a vertical swimming sub-model, forced mainly by tide and wind-induced currents. The simulations were validated against observations of larval dispersal monitored several days throughout the lagoon. Connectivity matrices describing larval exchanges inside the lagoon were inferred. Larvae displayed a significant dispersal capacity at the lagoon scale, especially with dominant eastern winds. With southeastern winds, larvae mostly remained in their origin sector. The total export rate of the larvae, toward the ocean through the pass and shallow lagoon borders, was independent of the wind conditions, with 1% of the total concentration exported per day. However, the tide-driven currents efficiently flushed larvae in sectors close to the pass. Connectivity matrices suggest that the south and west sectors were more suitable for spat collecting and that central sectors would be efficient sanctuaries if genitors were accumulated.

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1. Introduction

More than 70% of the benthic invertebrates present a planktonic life stage during their larval development (Thorson, 1950). The settlement of these species, defined as the integration of juveniles in a population (Connell, 1985), is one of the main processes governing temporal variations and spatial structure of the adult populations (Ellien et al., 2004). Numerous studies are investigating the physical and biological factors that influence settlement and the consequences on adult population structure, larval dispersal, export rates, and spatial connectivity (Eckman, 1996; Grantham et al., 2003; Shanks et al., 2003; Cowen et al., 2007). In tropical ecosystems, significant research efforts have investigated the connectivity of populations through modelled larval dispersal between source input sectors and sink settlement locations, so as to protect, preserve and manage biodiversity (Roberts, 1997; Swearer et al., 1999; Botsford et al., 2009; Munday et al., 2009; Kool et al., 2010). Most of these efforts focussed on large-scale oceanic dispersal with coarse resolution model. Few studies have investigated realistically small coastal domains at high spatial resolution, and

even fewer the dispersal patterns within semi-closed water bodies like atoll lagoons (see review of atoll lagoon modelling in Andréfouët et al. (2006)). Atoll lagoons are generally saucer-shaped basins, with an average depth closer to 20–30 m, reaching ~70 m in its maximum. Atolls fine-scale topography may be complex, with frequent coral patches that reach vertically to the surface (pinnacles). Landscape is made of small islands and reef-flat spillways (*hoa*, less than 50 cm depth) distributed along the atoll rim in various possible configurations (Andréfouët et al., 2001a). Deeper passes through the rim, generally narrow (few tens of meters) with a few meters depth in its shallowest part, may be present in Tuamotu atolls. Flows though these passes is primarily modulated by tides. The moderate depth and semi-closed status of Western Tuamotu atolls suggest that lagoon circulation forcing can be dominated by either winds or waves (Andréfouët et al., 2006).

Like for all bentho-pelagic species in their own environment, diversity and structure of molluscan populations in atoll lagoons is highly dependent on local factors such as habitat type (substrate type, light intensity, depth, etc.) and water circulation and current (Pante et al., 2006). The abundance and distribution of adult populations would thus be dependent on the success of larval life and fixing process (Adjeroud et al., 2000). Larval dispersal processes have been studied at various spatial scales with population genetics (Siegel et al., 2003), *in situ* tracking of larval cohorts (McQuaid and Phillips, 2000) and by numerical modelling (Verdier-Bonnet et al., 1997; Edwards et al., 2006; Viard et al., 2006; North et al.,

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2008; Jolly et al., 2009). Some of these modelling exercises have quantified the effect of hydrological conditions on selected specie dispersal taking into account realistic estimates of mortality and larval behaviour (Levin, 2006). Specifically, even considering the low swimming capacity of invertebrate larvae in comparison to water speed and flow, it appeared that swimming behaviour, especially vertically, might significantly influence transport and dispersal (Shanks and Brink, 2005; Guizien et al., 2006; North et al., 2008).

In Ahe atoll, French Polynesia, recent studies put in evidence the lagoon-scale spatio-temporal heterogeneity of the bivalve larvae concentrations and the consequences for collection of the targeted black-lip pearl oyster for the local aquaculture industry (Thomas et al., 2012). In French Polynesian atoll lagoons, the black-lip pearl oyster (Pinctada margaritifera cumingii, Linné 1758) farming plays a major socio-economic role since the 1990s (Andréfouët and Charpy, 2012). The entire farming activity relies on the collection of black-lip pearl oyster juveniles on artificial collectors. However, collecting success has remained unpredictable with large spatiotemporal variations (Brié, 1999) and pearl farms activities remained vulnerable to steady availability of oysters. Andréfouët et al. (2006) recommended a spatially explicit numerical modelling approach to study and forecast spat collecting potential on Polynesian atoll lagoons. Dumas et al. (2012) made this recommendation a reality using the hydrodynamical model MARS3D (Lazure and Dumas, 2008) implemented for the deep atoll lagoon of Ahe atoll in French Polynesia. Here, we extend the hydrodynamical and circulation modelling work of Dumas et al. (2012) to the simulation and validation of bivalve larvae transport in Ahe atoll.

Specifically, the objectives of the present study are (1) to calibrate, integrate and validate a model of vertical swimming for the bivalve larvae, (2) to validate the transport model integrating the swimming sub-model with data acquired *in situ* and (3) to evaluate the intra-lagoonal connectivity patterns and quantify exchanges between potential sink and source sectors. The consequences of larval dispersal on pearl oyster settlement variability and aquaculture management are discussed.

2. Materials and methods

2.1. Study site

Ahe atoll is located in the North-western part of the French Polynesian Tuamotu Archipelago, 500 km North-East of Tahiti island (Fig. 1). Ahe lagoon covers 145 km² with a mean depth close to 40 m. One active pass is located in the western part of the lagoon and several reef-flat spillways (*hoa*, less than 50 cm depth) are distributed along the reef rim, mainly in the south and west part sectors (Dumas et al., 2012). The overall aperture is low, and Ahe can be defined as a semi-closed atoll.

Ahe is submitted to dominant easterly tradewinds, which are stronger from April to October. According to a meteorological station located in a nearby atoll (Dumas et al., 2012), the mean annual wind is around 6 m s⁻¹, from 107°, with a winter season, from April to October, showing southeastern wind trend (135°, 7 m s⁻¹) and a warm season with eastern winds (90°, 6 m s⁻¹). Ocean tidal amplitudes near Ahe atoll are small (around 40 cm) due to its proximity to an amphidromic point (Dumas et al., 2012).

2.2. Biological model description

Species P. margaritifera var. cumingii, known under the name: black-lip pearl oyster, is a molluscan from the Pteriidae family. P. margaritifera is found in the Indo-Pacific coral reef ecosystems, from the Red Sea to the Central America. This species is particularly abundant in the Polynesian Archipelago. The black-lip pearl oyster fixes itself mostly in lagoons, between 0 and 50 m depth, thanks to its byssus. Preferred substrates are coral on pinnacles and dead substrate, as well as debris from coral and mollusc shell on lagoon sandy bottom. The bulk of the natural stock was found below 30 m depth in the few atolls where the natural stock was assessed (e.g., Takapoto atoll, Zanini and Salvat, 2000). Maturity can be reached during the first year, followed by an important gonad development during the second year (Tranter, 1958; Thielley, 1993; Pouvreau et al., 2000). Gametogenesis is quick (1 month), and is observed throughout any given year with a significant asynchronism. Nonetheless, austral summer is the more favourable period (Pouvreau et al., 2000). At each spawning event, released gamets corresponds to 10% of the total flesh weight (Pouvreau et al., 2000). Females propagate up to 40–50 millions of eggs (50 μ m) at each spawn. Males propagate 10–100 time more spermatozoa (5 μ m). The first larval stage (D-larva, 80 µm), is reached after 24 h. A ciliate organ (the velum) allows swimming and feeding activities. The lifespan of the larval stage, observed in hatcheries averages 21 days for P. margaritifera (Doroudi and Southgate, 2003). However, depending on environmental conditions (e.g., temperature, food concentration), lifespan may vary from 15 to more than 30 days (Thomas et al., 2011). At the end of their development, larvae reach



Fig. 1. Location and general morphology of Ahe atoll, with positions of the sampling stations to study vertical cycles (V01 and V02), and lagoon wide concentrations (L01–L12).

230 μ m length on average. After metamorphosis, young spats (250 μ m) fixe themselves to the substratum with a byssus. The growth is fast, and juveniles reach 10–12 cm length after 2 years. Adult life duration may be more than 12 years, with a theoretical maximum length of 18 cm depending on atolls (Sims, 1994; Pouvreau and Prasil, 2001).

During our surveys, in 2007 and 2008, almost 10% of the Ahe lagoon area was dedicated to black-lip pearl oyster rearing (adult oysters, Fig. 1). The total stock of cultivated pearl oysters was estimated at 15 million individuals (Perliculture Service, pers. comm.). The extent of the wild population remains unknown. The exact position of each collection line is also unknown, but the extent and boundaries of each concession, and the number of lines per concession are registered. With nearly 1245 recorded spat collection stations (with a theoretical 600 collectors per station), distributed mainly in the western part of the lagoon, Ahe is one of the most important juvenile producers in French Polynesia.

2.3. The bio-physical larval transport model

Larval transport and dispersal were simulated with the 3-D hydrodynamic model MARS3D, which resolves the ocean dynamics equations (Lazure and Dumas, 2008). This model implements a set of partial differential equations resolved with finite differences. It simulates the ocean dynamics under the combined effect of tide, wind and thermal exchanges between the ocean and the atmosphere. The specifics of implementation for Ahe are explained by Dumas et al. (2012). In short, the model is constrained by a horizontal cell size of 100 m by 100 m, as a compromise between a correct representation of the physical structures governing the circulation (pass, bathymetric variations, hoa) and the calculation cost. The vertical spatial resolution of the model respects the range of water depths in Ahe lagoon with 23 sigmavertical layers. These sigma-vertical layers are tightened close to the bottom and to the surface in order to better represent velocity gradients in the interface layers. With maximum water flows observed in situ close to $2-3 \text{ m s}^{-1}$, a time step of 10 s was used, allowing model stability.

To model Ahe lagoon, four different levels of nesting were required. The first three levels are bi-dimensional horizontal approximation to describe the open boundary conditions of the atoll, including astronomical and meteorological tides. These are: Rank 0 for all the Polynesia (3 km grid); Rank 1 for the vicinity of Ahe and the nearby Manihi atolls (1 km grid): Rank 2 for a close-up on Ahe and Manihi atolls (300 m grid). The wider model is forced by a sea level signal harmonically composed from FES2004 (Lyard et al., 2006), accounting for an inverse barometric correction estimated from the NCEP Global Data Assimilation System (GDAS) pressure field. The barotropic mode (sea surface height and mean vertical velocity) along the open marine boundaries is thus provided by the immediately wider model of the embedment. Finally, the detailed inner hydrodynamic model has a spatial resolution of 100 m. It encompasses entirely the lagoon, the rim and the external slope. For the simulations presented here, water entrance through each hoa was forced during 6 h around the high tide with water flowing at 0.5 m s⁻¹, in agreement with to the mean velocity measured in situ. A complete description of the model and its validation can be found in Dumas et al. (2012).

The hydrodynamic model was coupled with an advection/dispersal module, itself integrating a model allowing reproducing the dial vertical swimming of the bivalve larvae. To summarise, the larval transport simulated Eulerian transport since the state variables were calculated at a fixed point. Larval distribution was thus described as a network of larval concentrations, transported as a function of time by the water flow network (as calculated by the dynamics equations) and by the vertical swimming displacement (as established by *in situ* observations). The larvae exported to impracticable sectors for farming activity, into the ocean, the pass or shallow waters (less than 5 m-deep), may be remobilized into the global larval pool *via* inbound exchanges through the pass and the *hoa*, or from the shallow waters to the deeper one.

Larval vertical displacement may result from three types of forcing: swimming, convection and turbulent mixing. *In situ* observations showed that bivalve larvae follow a dial migration toward the surface during the night and toward the bottom during the day (Thomas et al., 2012). The sub-model of vertical migration coupled to the transport model empirically simulated the vertical migration of the larvae depending on the swimming behaviour observed *in situ*. Here, no horizontal movement was introduced into the swimming model in agreement with the fact that oysters' larvae swim helicoidally with a limited horizontal displacement (North et al., 2008; Troost et al., 2008).

The swimming model simulates vertical displacement velocity of larvae as a function of the hour of the day, according to a sinusoid centred on 0, forcing a positive velocity during the night (going up) and a negative velocity (going down) during the day:

$$v = \alpha \sin(\omega t + \varphi) \tag{1}$$

with v the vertical velocity (m h⁻¹), α the half-amplitude of the sinusoid (m h⁻¹), ω the pulsation ($\omega = 2\pi/T$) (rad h⁻¹) with *T* the period, *t* the time (h) and φ the phase at the origin of the sinusoid (radian).

2.4. Larval transport model validation

2.4.1. Swimming model validation

Data used to calibrate/validate the vertical swimming model came from two deep stations, V01 and V02 (50 m deep), located in the west and the central-east part of the lagoon, respectively (Fig. 1). Water samplings were realised by pumping from a boat over the whole range of five layers (0–10, 10–20, 20–30, 30–40 and 40–50 m). A mesh retained larvae with a length between 40 and 250 μ m. Water was sampled from each layer with a continuous flow and a pipe diving speed of 1 m every 30 s, providing an average pumping rate of $43 \pm 41 \text{ m}^{-1}$. Each station was sampled every 4 h, from 8 h AM, during 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.

The swimming model was firstly calibrated into a 1-D model, simulating the concentration variations into five 10-m layers according to the hour and vertical velocity. The calibration step was made on three of the 24-h cycles, showing the smaller wind velocity in order to avoid the turbulences effect and to only consider the active displacement of the larvae. Next, the calibrated model was implemented into the 3-D model and validated for the entire 24-h cycles, with realistic conditions of wind and tide. No significant difference in global concentration being measured between the samples of each cycle, we considered a unique amount of larvae, without supply or diluting effect.

2.4.2. Lagoon scale validation

Validation data came from a larval sampling survey conducted throughout Ahe lagoon on 12 stations, L01–L12, during a 18 dayperiod in May 2007 (Fig. 1). Water sampling was realised every 2 days in the morning by pumping from a boat from the surface to 5 m above the bottom with a continuous flow rate and a pipe diving speed of 1 m every 10 s, providing an average pumping rate of $14 \pm 5 \, \mathrm{Im^{-1}}$. A mesh retained larvae with a length between 40 and 250 μ m. The 12 stations were sampled during the same day, with a delay of about 4 h between the first and the last station. That enabled to avoid the sampling of the same water mass. During this survey, a major spawning event occurred the 8 May and was

 Table 1

 Larval concentration observed the 8 May 2007, after the spawning event.

Station	Larval concentration $(\times 10^3 \text{ m}^{-3})$
L01	79.5
L02	9.8
L03	7.2
L04	3.6
L05	0
L06	10.1
L07	4.7
L08	4.2
L09	0
L10	8.0
L11	0
L12	4.7

identified on almost all the stations (Table 1). Larvae were morphologically very close to the pearl oyster and were assimilated to this specie. The cohort was isolated during the days following the spawning event, until the 26 May, by the modal decomposition method of Bhattacharya (software: FISAT-II, FAO-ICLAM, Italie, http://www.fao.org/fi/oldsite/STATIST/FISOFT/FISAT/index.htm).

For validation purposes, the initial larval concentration data recorded *in situ* on the twelve stations (Table 1) were interpolated and extrapolated to every cell of the transport model. On every cell of the model, the initial concentrations were considered homogenous along the water column. A spin-up period of 10 days before the spawning event was applied in order to stabilize the model. At every date of the sampling period, larval concentrations simulated on the 12 stations (1 cell for each station) were extracted and compared to *in situ* observations.

2.5. Connectivity measurement

The theoretical simulations described in the following section aimed to measure the connectivity level existing between different sectors of the Ahe lagoon by using the swimming bivalve larvae as tracers. For bentho-pelagic species, connectivity is dependent on the dispersal phase, from the spawning event to the end of the fixing process (including the choice of a substrate and the metamorphosis) (Cowen et al., 2007). Connectivity was measured here for a period corresponding to the larval lifespan before fixing which is 15–30 days. Therefore, the effect of the larval lifespan variability on connectivity was evaluated by running 30-days long simulations.

Twelve sectors were defined around the sampling stations (Fig. 2) and a specific tracer was associated for each sector to track larvae from one sector to another. For each sector, the initial local larval concentrations were of 100 m^{-3} , homogeneous in *x*, *y*, *z* directions. Indeed, the first larval stages (i.e. first 24 h), are less mobile and then are submitted to homogenisation. So, we considered here the veliger D-stage for initial condition, with homogeneous concentrations.

For these simulations, we defined three wind conditions: mean annual wind (107° globally E, 6 m s⁻¹), cold season mean wind (135° globally SE, 7 m s⁻¹) and warm season mean wind (90° E, 6 m s⁻¹). The mean annual wind was calculated from 2 years of daily recordings extracted from Takaroa meteorological station, an atoll 150 km west of Ahe. The cold and warm season trends were extracted from the same data set. Data were compared to the meteorological climatologies in this region to avoid using unusual conditions.

For the results, larval plume was observed every 5 days between t = 0 and 30 days. Larval dispersal was thus represented after 0, 5, 15 and 30 days for source Sectors 1, 3, 6, 10 and 12. These sectors were deemed representative of the different trends



Fig. 2. The 12 Sectors defined for the connectivity analysis.

observed by modelling. Connectivity was evaluated after 15, 20, 25 and 30 days, corresponding to the larval lifespan.

2.6. Data analyses

The goodness-of-fit of the swimming and transport models outputs (*Y*) vs in situ observations (*X*) was evaluated by linear regression and tested against the model Y = X at an alpha error threshold of 5%. The R^2 coefficient of determination evaluates the level of variance explained by the model.

A transition probability matrix formalised the connectivity synthetically. This matrix reflect the probability for a larvae emitted from a sector *i* at time *t* to be transported into the sector *j* after t + k, *k* being the larval lifespan (Paris et al., 2007). This probability was calculated as the ratio between the larval concentration coming from the sector *i* and measured into the sector *j* after t + k and the initial larval concentration into the sector *i* (North et al., 2008). In the results section, only the connectivity matrix for a lifespan of 20 days, corresponding to the mean larval lifespan, is presented. Auto-supply rate, corresponding to the probability for a larva to settle into its own source sector, was computed the same way. Self-recruitment was thus evaluated after 15, 20, 25 and 30 days.

The export rate for a given sector *i* corresponds to the proportion of the larvae that escaped from the system *via* the pass and *via* the rim shallow waters, below 5 m depth, which correspond to unsuitable sectors for farming activity. Nonetheless, larvae exported in these sectors may be remobilized into the global pool. The total export rate, *e*, was calculated with:

$$\boldsymbol{e} = (1 - \boldsymbol{r}) \tag{2}$$

with r the retention rate. r is defined as the ratio between the number of larvae coming from the i sector found in all other sectors than i at time t, and the initial number of larvae in the sector i. Export rate was extracted after 1, 2, 5, 10, 15, 20, 25 and 30 days of dispersal.

Multiple ANOVA with Tukey test were applied on arcsinus transformed data to test the effect of the various factors (*i.e.* time, sector) on connectivity and export rates.

3. Results

3.1. Model calibration and validation

The swimming model parameterization gave a maximal vertical velocity corresponding to a half-amplitude (α) of 1.5 m h⁻¹ or

0.42 mm s⁻¹ (Table 2). The model period, (*T* = 24 h) yielded a pulsation, ω , of 0.26 rad h⁻¹ and a phase at the origin, φ , of 1.45 rad. Consequently, maximal rising velocity occurred in the middle of the night, at 00:00, and the maximal descent velocity in the middle of the day, at 12:00.

At the exception of the V02 station in April 2007 (simulation B, Fig. 3), vertical migration was correctly reproduced by the swimming model, with a descent to the depths during the day and a rise towards the surface at night. The discrepancy for V02/April 2007 came from a poor match between the predicted day–night variations and the unusual observed stable concentrations.

For the large lagoon-scale validation, Fig. 4 shows the variations of simulated and measured concentrations averaged for the 12 stations during the 18 days period. The general trend was an exponential decrease of concentrations. The agreement was satisfactory (y = x; $R^2 = 0.55$; p < 0.0001), but we note an overestimation at the end of the simulations periods. Standard deviation of the mean, which was large at the beginning of the dispersal, for both observations and simulations, decreased with time, suggesting a homogenisation of concentrations lagoon-wide.

Details for each station are provided on Fig. 5. Overall, for the entire period, concentrations were under-estimated by the model $(y = 0.85x, R^2 = 0.50, p < 0.0001)$. The agreements were more satisfactory for the southern and central stations than in the north and east. For instance, for L01, the predictions were near perfect $(y = x, R^2 = 0.9, p < 0.0001)$ with quick decrease and stabilization to low concentration levels. For L03 $(y = x, R^2 = 0.8, p < 0.0001)$ the agreement was good, including for the peak of concentrations measured the 14th May 2007. Conversely, for L02, simulated concentrations were underestimated at the beginning of the period, before converging to observed value. For L04, simulated concentrations were overestimated at the beginning of the period, before converging. For L10, fairly stable simulations do not reproduce well the variability observed *in situ*. For L12, we report both under and overestimation in succession.

3.2. Intra-lagoon connectivity

3.2.1. Mean annual wind scenario

Year-round, the mean wind direction was 107°. Fig. 6 presents larval dispersal after 0, 5, 15 and 30 days for source Sectors 1, 3, 6, 10 and 12. In general, after day 15, homogenisation at the lagoon scale occurred despite contrasting situations before that day. From the western Sector 1, larvae propagated quickly to the north along the west side of the lagoon. Then they dispersed to the east first, and throughout the lagoon afterwards. From Sector 3, larvae propagated eastwards first then throughout the lagoon. From the central Sector 6, larvae dispersed towards the southeast, then the west, then after day 15 throughout the lagoon homogeneously. Conversely, larvae from Sector 10 remained in Sector 10 for about 15 days before dispersing. Finally, eastern Sector 12 larvae quickly dispersed westwards, both along the north and south shores, before diffusing in the entire lagoon.

The connectivity matrices (Fig. 7) summarised the level of exchanges between each of the 12 Sectors after 20 days of simulation. Anova and Tukey test were performed in order to characterise the spatio-temporal patterns. The four time-steps (15, 20, 25 and 30 days) appeared significantly different in average, with a

Table 2

Parameters of the vertical swimming model for the larvae.

Parameter	Symbol	Unit	Value
Half-amplitude	α	${\rm m}~{\rm h}^{-1}$	1.5
Period	Т	h	24
Pulsation	ω	$rad h^{-1}$	0.26
Phase	φ	rad	1.45



Fig. 3. Comparison between relative larval abundance measured for each vertical 10 m section during five 24-h cycles and simulated by the swimming model. (A) Station V01, April 2007; (B) Station V02, April 2007; (C) Station V01, August 2007; (D) Station V01, February 2008; (E) Station V02, February 2008.



Fig. 4. Average ± standard error larval concentrations evolution for 12 stations (L01–L12), observed and simulated from 8 to 26 May 2007.

decrease in exporting probability between source and arrival sectors (data not shown). Seven source groups with homogeneous exporting probability were found:

- Sector 9, in the east-centre of the lagoon, with a mean export probability of $8.5 \pm 0.9\%$, was a homogeneous source for all sectors.
- Sectors 6 and 12, in the centre and east of the lagoon, with a mean export probability of 7.7 ± 1.0%, were source for all sectors with higher probability of export to the western sectors (2, 3, 4, 5).
- Sectors 3, 7 and 8, in the west and south, with a mean export probability of 6.7 ± 1.0%, were source for all sectors with higher probability of export to the western sectors (2, 3, 4).



Fig. 5. Individual larval concentrations evolution per station (L01-L12), observed (black circle) and simulated (open circle) between the period: 8 to 26 May 2007.

- Sector 10, in the northeast, with a mean export probability of $5.9 \pm 1.2\%$, was source for all sectors, but with higher probabilities of export to the north sectors (4, 5, 10, 11).
- Sector 5, in the north, with a probability of $5.0 \pm 0.7\%$, was source for all sectors.
- Sectors 2 and 11, in the southwest and northeast, with a mean export probability of $4.7 \pm 1.0\%$, were small contributors, mainly for western and northeastern sector for respectively Sectors 2 and 11.
- Sectors 1 and 4, in the west and northwest, with a mean export probability of $3.3 \pm 0.5\%$, export homogeneously throughout the lagoon.

3.2.2. Winter wind scenario

In austral winter (June–September) winds were stronger and more south-easterly than year round. Mean wind direction was 135°. Larval dispersal in these conditions appeared significantly different than when considering an annual mean wind condition (see above) (Fig. 8). Indeed, for western and eastern sectors, larvae remained in their source sectors during the 30 days of simulation. For Sector 1 in the west, simulations reported a slight transport of larvae northwards along the western shore. Larvae from Sectors 3 and 6 displayed similar trends, concentrating in the centre of the lagoon, between the south and north shores. Larvae from these two sectors almost never reached the western sectors. Larvae from Sectors 10 and 12 also remained stable, with slight westwards transfer along the north shore.

The averaged export probabilities appeared significantly different between day 15, 25 and 30, with a decrease in export probability between source and arrival sectors (data not shown). But no significant differences were measured between day 15 and 20 and day 20 and 25. Five source groups with homogeneous exporting probability were extracted from the statistical analysis of the connectivity results (Fig. 7):

- Sectors 9 and 12, in the centre and east, with a mean export probability of 8.5 ± 3.4%, mainly exported to eastern sectors (9, 10, 11, 12) and partly by centre-north sectors (2, 4, 5, 6).



Fig. 6. Maps of larval concentration in Ahe lagoon, simulated by mean annual wind conditions (107°, 6 m s⁻¹), dispersed from the sectors: 1, 3, 6, 10 and 12, after 0, 5, 15 and 30 days of simulation.



Fig. 7. Connectivity matrices between the 12 Sectors, giving the export probability between source and arrival sectors after 20 days of simulations with mean annual wind (left) and winter wind (right).

- Sectors 3, 6 and 10, in the centre-west and north, with a mean export probability of $6.8 \pm 2.4\%$, mainly exported to western sectors (3, 4, 5, 6, 7, 8) but with a high retention in the eastern part of the lagoon (Sectors 9, 10, 11, 12) for the Sector 10.
- Sectors 5, 7, 8 and 11, in the north, south and east, with a mean export probability of 5.6 ± 2.0%. Sector 5 exports homogeneously in the lagoon, except to the Sector 1. Sectors 7 and 8 mainly export to the western sectors (2, 3, 4, 5, 6, 7, 8). Finally, Sector 11 is a source for the eastern sectors (9, 10, 11, 12).



Fig. 8. Maps of larval concentration in Ahe lagoon, simulated by winter wind conditions (135°, 7 m s⁻¹), dispersed from the sectors: 1, 3, 6, 10 and 12, after 0, 5, 15 and 30 days of simulation.

- Sector 2, in the southwest, with a mean export probability of $4.5 \pm 1.9\%$, highly retained larvae in the western part of the lagoon.
- Sectors 1 and 4, in the west and northwest, with a mean export probability of $3.6 \pm 2.7\%$. Sector 1 showed a high retention in the western sectors (1, 2, 3) and no export in the east. Sector 4 showed very small probability values, concentrated in the centre of the lagoon.

3.2.3. Summer wind scenario

In austral summer (October–May) the mean trade wind direction was 90° . Thus, close to the annual mean conditions, and indeed simulations showed for the summer similar patterns that what we previously described for the annual mean. Therefore, we hereafter discuss the mean annual and summer patterns *vs* the mean winter patterns.

3.2.4. Self-recruitment patterns

The connectivity matrix diagonal quantifies self-recruitment for each sector. It appeared significantly higher in winter wind conditions (p < 0.0001), with an average, between days 15 and 30, of 9% compared to 6.4% in mean annual condition. Winter self-recruitment was especially high in Sectors 1, 9, 10, 11 and 12 in the western and eastern sectors (Fig. 9). Conversely, the Sector 4 displayed the lowest self-recruitment rate with a 3.7% average. Self-recruitment decreased significantly between days 15 and 30 of the simulations for the mean annual condition (p < 0.0001), decreasing from 7.6% to 5.5% and not significantly from 11.1% to 7.3% for winter wind conditions.

3.3. Export

The mean export rate from the lagoon was not significantly different between each wind-dependent scenario (p > 0.05). It reached an average 28% after 30 days (Fig. 10, right). This export rate was variable across the lagoon (Fig. 10, left). Sector 4, displayed the highest export rate, with an average 45% between days 15 and 30 for the two wind conditions. For the mean annual wind scenario, Sector 4 showed significantly higher rates than a group of 6 Sectors: 1, 2, 7, 8, 9 and 12. The other sectors showed no significant difference. For the winter scenario, the Sector 4 was significantly higher than Sectors 1, 9, 10, 11, 12. These last 5 Sectors showed also significantly lower exporting rates than Sectors 2, 3, 6, 7 and 8. The largest differences between the two scenarios appeared in the eastern part of the lagoon. Indeed, the only significant differences between the two wind conditions were measured on Sectors 10 and 11, which showed higher export rates with mean annual wind. After 5 days of simulation (Fig. 10, right), the mean export rate obeyed to a linear trend, with a slope of 0.9% per day, thus suggesting that nearly 1% of the larvae were exported every day.

4. Discussion

4.1. Larval transport model validation

To the best of our knowledge, the present study presents for the first time in an atoll environment a validated model of bivalve larvae vertical migration, coupled with a hydrodynamic model.



Fig. 9. Left: average ± standard error self-recruitment probability between 15 and 30 days for the 12 different sectors, and according to the different wind conditions (mean annual, winter). Right: evolution of the self-recruitment probability averaged (±standard error) across the entire lagoon according to time (15, 20, 25 and 30 days) and according to the different wind conditions. Letters give significant differences between stations/time (Tukey test).



Fig. 10. Left: average ± standard error export rate between 15 and 30 days for the 12 different sectors and according to the different wind conditions (mean annual, winter). Right: evolution of the export rate averaged (±standard error) across the lagoon, according to time (15, 20, 25 and 30 days) and different wind conditions. Letters give significant differences between stations/time (Tukey test).

The vertical 1-D swimming model was validated locally with extensive in situ observations but it remains a first-order empirical model based on day-night cycles. It did not account for larval development stage. Larvae swimming abilities evolve during their development, in speed and direction (Troost et al., 2008) and Eq. (1) was not modulated accordingly. Furthermore, no changes were applied according to environmental factors such as salinity, temperature, food availability and hydrodynamic turbulences which are all factors influencing larval behaviour (Eckman et al., 1994; Dekshenieks et al., 1996). Here, the vertical swimming speed, with a maximal speed of 0.42 mm s⁻¹, was in agreement with previous works on bivalves species (Troost et al., 2008). The vertical swimming model simulations were also in good agreement with our observations, although some discrepancies were showed at station V02 in April 2007. Indeed, we measured high larval concentrations in deep layers at night, while a migration toward the surface was expected. In fact, wind speed during this survey was high at the beginning, over 8 m s⁻¹, from SE (130°), and decreased progressively to reach 4 m s⁻¹ from ENE (70°) at the end of the 24-h cycle. These wind conditions were the highest and the most variable that we encountered. Considering that larvae submitted to strong turbulent mixing may react by following a sinking strategy, this could likely explain the discrepancies between observation and simulations.

Once the hydrodynamic and the larval behaviour models were coupled, the study of larval dispersal by hydrodynamic transport and vertical periodic sinusoidal migration became possible. Results appeared realistic, being validated against data from a field

campaign that opportunistically bracketed a spawning event. Simulated and observed concentrations were in agreement across time, and the simulation of larvae dispersal was deemed satisfactory. The model seemed to reproduce correctly the progressive decrease of larval concentrations due to dilution and exports through the pass and along the water exchanges areas of the shoreline. An important standard deviation was observed at the beginning of the simulation for both observed and simulated concentrations. This variation was likely the consequence of spatial heterogeneity during the spawning event. The decrease of spatial variation, consistent with the lagoon scale homogenisation of concentrations (i.e., decrease in standard deviation) was well reproduced by the model. However, the model did not use a mortality rate. Larvae were expected to die due to predation and food deprivation (Eckman, 1996), but the good agreement between simulations and observations seemed to suggest that natural mortality could be very low in Ahe atoll, or that most mortality occur in the first 2 days of larval life. Indeed, mortality rates is highest in early life stages in the first couple of days (Pechenik, 1999) and in the last stages, due to higher predation and likely longer periods of starvation (Hofmann et al., 2004). Here: these early stages were not taken into account since capture and census in the field yielded larvae already 1-2 days old. Conversely, the expected actual higher mortality during the last stages could explain the general overestimation of simulated larval concentrations at the end of the simulated periods.

The agreement between simulations and observations was also satisfactory for most individual stations but several factors can explain the existing discrepancies. For station 12, discrepancies can be explained if the sampling missed the arrival of the cohort. Indeed, the source of larvae can be very local (Scheltema, 1986), and larvae may have been detected only after 1 or 2 days after the initial dispersal, which is likely what we captured in the field. Other sources of discrepancies are due to the spatial scale mismatch between *in situ* station (a point data) and simulated data. The later integrates values from the extent of a model grid cell, thus from a 10,000 m² area. Furthermore, larvae can form patches and groups that may aggregate at various space scales (Garland and Zimmer, 2002). For stations 4 and 5 located next to the pass, given the speed of the current and the extent of the influence of the pass in the lagoon (Dumas et al., 2012), small time lags between observations and models at these stations can also explain differences. All model values were extracted at 10 AM, but field data were measured between 8:00 and 12:00 AM. Finally, a likely source of discrepancy lied in the extraction of one cohort data from a pool of observations. The theoretical decomposition of modes in order to identify and monitor cohort's abundance is not necessarily free of errors.

The largest discrepancy observed between observations and simulation was observed close to the 20th of May, when observed larval concentrations decreased strongly in L05, 06, 08, 09 and 10, without increase elsewhere. This event was concomitant with a rainy period (7 mm day⁻¹), showing a decrease in temperature ($-2 \,^{\circ}$ C) and a decrease in insolation. The agreement between observation and simulation being satisfactory after this event, this could explain a large part of the discrepancy observed. Indeed, larvae might have migrated very close to the bottom (*i.e.* out of the sampling domain) during this rainy period.

4.2. Larval dispersal schematic diagram

Larval dispersal simulations provide a tool to diagnose the influence of environmental conditions (mostly wind) on the transport of larvae between sources and sinks sectors (including self-recruitment) and export rates. Simulations presented here revealed a strong dispersal potential within Ahe atoll lagoon, from one sector to the other, especially when the wind is blowing from the east (mean annual and summer period). Conversely, southeast wind, in winter, tends to increase self-retention, especially in the east and west sectors. If we simplify our 12-sector view into a 6-sector view based on the typology of behaviour highlighted in the result section, we obtain (Fig. 11):

- Sector Southwest (a, previously Sector 1): export larvae to the north and retain them in respectively easterlies and south-easterlies conditions.
- Sector West (b, previously Sectors 3, 4): facing the pass, it shows strong larval export and transport to the atoll centre in all type of wind conditions.
- Sector South (c, previously Sectors 2, 7, 8): with limited potential for transport, principally towards sector (b).
- Sector Centre (d, previously Sectors 6, 9): export larvae eastward and southward respectively in easterlies and south-easterlies conditions.
- Sector North (e, previously Sectors 5, 10, 11): export larvae westward in easterlies conditions, and display an almost exclusive retention during south-easterlies conditions.
- Sector East (f, previously Sectors 12): export rapidly larvae northwards and westwards, and exclusively northwards in respectively easterlies and south-easterlies conditions.

In short, wind coming from the east promotes larval transport between sectors and especially between east and west sectors. Concentrations are more easily homogenised lagoon-wide in these conditions. When the southeast winds blow, the situation is different. The limiting returning upwind deep flow (Dumas et al., 2012) promotes retention in the eastern and western sectors and limit export potential. This functioning is intimately related to the wind-dependent hydrodynamic behaviour of the atoll. In their study of the tidal flushing and wind driven circulation of Ahe atoll lagoon, Dumas et al. (2012), showed that the pass divided the lagoon in three main circulation cells located in the north, centre and south of the lagoon. When the wind blows from southeast, the three main cells are reinforced. The west and east sectors are more separated from the pass sector and their flushing time increase. This explains the strong retention (i.e. self-recruitment) measured in the western and eastern sectors. Furthermore, 95% of the Ahe atoll rim is completely closed to water exchanges. Only the pass and *hoa* are open to water exchanges. The flow in the pass is tide-driven. The flow in *hoa* are both tide and wave-driven, with an inflow only during a half tide cycle around high tide. Cumulated inflow through all the *hoa* is 10–20 times smaller than the volume exchanged through the main pass during the same time (Dumas et al., 2012). Since the only existing outflow that exists is through the pass, the atoll rim is thus a true boundary for larval dispersal.

4.3. Consequences for spat collection

Spatio-temporal variations in bivalve fixation (and thus on pearl oyster collecting) are theoretically dependant on the adults spatial distribution, spawning periods and occurrences, larval survival and thus environmental forcing and food availability, dispersal potential, potential chemical attraction and finally availability of suitable substrate for fixations when the larval development is completed (Rodriguez et al., 1993; Adjeroud et al., 2000; Pante et al., 2006). This study has clarified the dispersal potential of larvae coming from different sectors. In Ahe atoll lagoon, the stock of wild pearl oysters is unknown, but aquaculture farms alone raised in 2007 a substantial total of 15 millions adults spread across the lagoon, except in the eastern sectors that are unpractical for daily operations. The preferred sectors by professionals for spat collections are currently the western sectors.

In term of aquaculture management, this study provides clues to understand the variations in pearl oyster spat collecting success. Indeed, larvae displayed significant dispersal capacity at the lagoon scale, promoted at least by the wind-driven and tide-driven circulation. Our simulations suggest that in all conditions, the western sectors are best sectors to collect larvae. If the wind blows from the east, the western part of the lagoon is a sink, and if the wind comes from the southeast, most larvae are retained. Thus, there are fewer chances of shortages and loss year long, especially after the spawning periods. This potential is likely enhanced given the high concentrations of farms and concessions in this sector. The southern and central part of the lagoon appeared to be good sources of larvae for other sectors, with favourable self-recruitment rates as well. Since the central part of the lagoon is less used for farming activities, this sector could be an efficient sanctuary if genitors were accumulated there, as well-placed an additional source of larvae.

This study showed the capability of a 3D transport model to properly simulate the larval dispersal at the lagoon-scale. This provides a decision-support tool well tuned for the aquaculture application as described by Andréfouët et al. (2006). Indeed, circulation model outputs are technically effective for collecting spats and cost-effective for the industry when they identify suitable collecting areas without years of trials and errors by farmers. Dispersal model are only one part of the equation. Better knowledge of factors controlling recruitment variability will also enable to better understand the wild populations structure and to rationalise a collecting strategy for aquaculture. In particular, gametogenesis,



Fig. 11. Schematic view of larval exchanges according to the different eastern and south-eastern wind conditions and according to the different sectors (simplified here in 6 Sectors). Arrows widths are representative of exchange rates.

spawning and larval growth potential also determine spat collection variability (Fournier et al., 2012; Thomas et al., 2012). Coupling biology and physic-based approaches is now needed to perpetuate the pearl oyster aquaculture.

In addition to the general lagoon-scale wind-driven dispersal potential highlighted here, this study also revealed smaller-scale structures due to the influence of the pass, especially for the central northern sector. Given the small influence of the *hoa* in Ahe atoll, no other small-scale structural effects have been evidenced in Ahe. It is likely that lagoon coral pinnacles also have local-scale effects on larval survival, dispersal, retention and fixation but this scale was not considered here. Further work on geomorphologically different atolls could lead to highlight different regimes of water renewal, circulation and dispersal patterns (Andréfouët et al., 2001a,b). This warrants further investigation. It is however reasonable to state that for atolls with geomorphology and environmental forcing comparable to Ahe, the functioning will likely be very similar.

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