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Understanding connectivity of pearl oyster populations within Tuamotu atoll semi-closed lagoons: cumulative insight from genetics and biophysical modelling approaches

Serge Andréfouet[1], Romain Le Gendre[2], Yoann Thomas[3], Alain Lo-Yat[4], Céline M. O. Reisser[4,5]

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

[2] IFREMER, UMR-9220 ENTROPIE, IRD, Université de la Réunion, CNRS, Université de la Nouvelle-Calédonie, Campus IRD, BP32078, Nouméa, New Caledonia.

[3] Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280 Plouzane, France

[4] UMR EIO, IFREMER Centre du Pacifique, Unité RMPF, BP49, Vairao, Tahiti, French Polynesia.

[5] MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Montpellier, France.

Abstract

Connectivity affects species demography, (meta)population dynamics, evolution, phylogeny and biogeography. Various methodological approaches are applied to measure connectivity. Biophysical modelling can explore systematically the influence of atmospheric, oceanic and ecological forcing, while genetics measures connectivity patterns within the sampling strategy limit. In the Pacific Ocean pearl farming lagoons, the activity relies on spat collecting of the black lipped pearl oyster *Pinctada margaritifera* occurring after the larval dispersal phase, which follows spawning from wild or farmed populations. Biophysical 3D modelling and genomic studies have both separately brought insights on within-lagoon connectivity and on the origin of spats. Here, we combined previous genetics results with new realistic biophysical modelling scenarios to elucidate connectivity in Ahe Atoll lagoon. When combined, we identified the weather sequence likely explaining the realized connectivity observations. We discuss the strengths, weaknesses, opportunities and threats of combining these two approaches considering specific pearl farming demographic connectivity questions

Key-words: connectivity matrix; population genomics; lagoon hydrodynamics; dispersal modelling; *Pinctada margaritifera*;

Introduction

The connectivity of marine populations has received considerable attention in the past 20 years (Cowen et al. 2007, Beker et al. 2007). 'Connectivity' embodies the study of a wide range of biophysical processes at a variety of spatial and temporal scale affecting demography, (meta)population dynamics, evolution, phylogeny and biogeography of species.

Understanding how individuals and their genes are exchanged in marine populations is strongly motivated by biodiversity conservation and fishery stock management (Fogarty and Botsford, 2007). Exchanges can occur through migration of juveniles or adults, or through larval dispersal phases. Despite significant advances in understanding marine connectivity, there is still a long path ahead before it becomes routinely possible to explain and predict connectivity of a given species, within a given environment and for a variety of demographic, ecological, and evolutionary time scales. Depending on the focus, a variety of methodological approaches has been applied to quantify the processes and scales that control connectivity (Lowe and Allendorf 2010). Tagging and microchemistry markers, hypervariable nuclear DNA sequencing and analyses, remote sensing observations of water masses, and biophysical models are all elements of the most advanced toolboxes. In particular, realistic biophysical models simulate water masses movement with 3D hydrodynamic models that are coupled in space and time with larvae behavior (e.g., swimming), adult and larvae physiology (e.g., energy use) and ecology (e.g., reproduction, nutrition, mortality) (Werner et al. 2007). Then, with on-growing interest in the past decade, genetic markers have further gained in power and application potential with the lowering of sequencing costs due to the development of next generation sequencing technologies and approaches such as reduced representation sequencing (DartSeq, RADseq, GBS), targeted sequencing (exome sequencing) or even whole genome sequencing. Using genome-wide markers can inform on a variety of connectivity scales, from parentage to population genetic analysis, including demographic parameters, such as the identification of adults reproducing in a population. These new genetic techniques push the limits of genetics for demographic connectivity studies previously highlighted in Lowe and Allendorf (2010).

The coupling of genetic studies and biophysical modelling have been previously used in various contexts such as population resilience facing anthropic perturbations (Timm et al 2020), marine conservation areas definition (Mertens et al 2018) and patterns of species introduction (Dawson et al 2005). It has also been used on various marine species, both mobile and sedentary (Baltazar-Soares et al 2018; Van Wynsberge et al. 2017; Alberto et al; 2011; Raitsos et al 2017; Davies et al 2015) as well as at various geographical scales. Genetics data can confirm the biophysical modelling predictions with a variety of metrics, which can include correlations between *Fst*-derived indicators, population allelic frequencies, genetic parentage data and biophysical indicators (Holsinger and Weir 2009, Alberto et al; 2011, Bode et al 2019, Boulanger et al 2020).

The aforementioned studies targeted coastal and halieutic communities that were open to the ocean. For isolated, physically closed populations living within an almost-locked water body presenting suitable habitats (Pinsky et al. 2012), it could be tempting to think that larval dispersal and ecological connectivity would be secondary order processes for the regulation of benthic populations, compared to reproduction, predation, competition, thermal stress, and so forth. The methodological challenges of characterizing connectivity within a fairly closed water body could also appear moderate compared to populations living in the open coastline and ocean. However, connectivity is not a negligible process in this type of system, especially in fisheries and aquaculture activities that depend on short-term processes such as recruitment or spat collection. The research community still needs to tackle substantial challenges before being able to create robust management tools for exploited populations even in semi-closed water bodies..

In semi-closed pearl farming atolls of the Central Pacific Ocean, the black lipped oyster *Pinctada margaritifera* oysters used for grafting and eventually for black pearl production can come from two sources. First, and this was historically the dominant pathway, larvae naturally spawned in the lagoon by wild populations are collected on artificial devices deployed in shallow waters. Spat collecting is not a granted activity and significant inter-annual and spatial variability are observed in most lagoons, with a trend towards decreasing success in the past decade. Second, when spat collecting is erratic, young adult oysters may be transferred from other atolls where spat collecting is efficient. These transfers have been common in the past three decades, before they become subjected to legal authorizations and their numbers decreased because of the risk of disease and epibionts transfer. With growing number of farms, the broodstock, laid around 2-10 meters deep in registered concessions, became numerically dominant in most exploited lagoons where the wild stock has been estimated. For instance, in Ahe atoll, the difference reaches much more than one order of magnitude, with ~666,000 *vs* ~14 million individuals in wild and farmed stock respectively (Thomas et al. 2014; Andréfouët et al. 2016). In theory, with a maximum legal density of 12,000 reared individuals per hectare, and despite a sex-ratio skewed towards male dominance (Andréfouët et al. 2016, Reisser et al. 2020), the reared broodstock should contribute to the larval pool, and collected spats could therefore have both wild and cultured origin (Thomas et al. 2014, 2016). In term of pearl farming management, the broad critical issues related to these processes are i) the maintenance of a stock able to provide spats, ii) the need to restock the part of the lagoon that could maximize larval dispersal to spat collector

locations, iii) the need to reserve suitable areas for spat collecting, and iv) the maintenance of the natural genetic diversity of oyster populations.

Previous biophysical models and genetic works have already investigated these questions. Specifically, for Ahe atoll lagoon in the Tuamotu archipelago, bio-physical 3D models have investigated the distribution of sink sectors according to different types of forcing, which included larval behavior (vertical swimming), pelagic larval duration (around 15-30 days, Sangare et al. 2020), type of stocks and their sex ratios, weather (for the realistic simulations of a specific period), climate regimes (for the simulations of standard recurrent situations) and lagoon sectorization (in often arbitrary management units), in addition to constraints inherent to the hydrodynamic model itself (e.g., spatial and vertical resolutions) (Thomas et al. 2012a, 2014, 2016). Both short term realistic events and long-term climatology approaches can be simulated. The results available thus far have hierarchized the level of influences of these different parameters. Results are presented with connectivity matrices that provide synoptic and synthetic views of the fluxes between sources and sinks sectors. For Ahe atoll, the results clearly show the range of demographic connectivity variations that can be expected, in particular according to the wind conditions, how some lagoon sectors can be more isolated than others because of long-term hydrodynamic forcing, and conversely, how some sectors are virtually permanent sinks for all source sectors (Thomas et al. 2012a, 2014, 2016).

In terms of using genetics, recently, Reisser et al. (2020) applied in Ahe atoll RAD sequencing to both wild and cultured individuals and to individuals recruited on spat collectors (Fig. 1). The analysis confirmed previous modelling results but also uncovered new patterns. In particular, it was confirmed that i) Ahe's wild population in the northeast lagoon is more isolated, ii) wild and cultured stocks from the southwest are mixed populations, iii) all spat collector samples were spawned from the wild population located in the northern part of the lagoon. These conclusions are unambiguous, and do not need further validation. The first two conclusions were congruent with biophysical model outputs and could be expected (Reisser et al. 2020). In this case, genetics validate the conclusions of the biophysics model. Both approaches, modelling and genetics appeared in agreement. In contrast, the third result was not expected, and if collected spats were the offspring of only wild populations, this is an extremely valuable information for management. The question is how representative is this latter result? Specifically, the sampling of collectors took place during a three-month period (02/2017-05/2017). After the period of collection, the sampled recruits unambiguously came from wild oysters, but would this conclusion be similar at a different sampling period? And

would it be the same conclusions for different collectors' locations? These questions have been raised by the authors, since temporal variability has been known to occur when sampling on collectors (Arnaud-Haond et al. 2008). It however become fundamental to check if a realistic biophysical simulation capture this pattern or not, and if the answer is yes, is it prevalent against other connectivity pathways? A challenge is therefore to better assess the possible synergies between genetics and biophysical modelling data to answer key pearl farming management, and connectivity questions. Specifically:

- Are there several populations, wild or cultured, within a given lagoon, and if so, how genetically different are they? Can they remain isolated?
- Where is the origin of spats and what are the adult population sources? In particular, in the context of numerically dominant farmed broodstock and decreasing wild stocks, is it possible to rely on the farmed stock for reproduction and spat collection?
- To what extent are the answers to these two questions explained by climate or weather conditions?

Within the very general context of using both biophysical models and genetics to study connectivity in marine/coastal environments, the objectives of this paper are to compare with a Strength-Weakness-Opportunity-Threat (SWOT) canvas, the relative merits and complementarities of the genetics and biophysical modelling approaches for pearl oyster farming management in semi-closed lagoon. . To guide us, we continue building on the Reisser et al. (2020) genetic data sets, and draw more systemically a parallel between the two approaches using new numerical experiments, at different spatial and temporal scales. The study eventually relies on combined genetics and modelling data with a level of resolution still seldom encountered in the literature, allowing to tackle representative pearl farming questions and clarify the avenues for integrated work for any atoll, and not just for Ahe atoll.

Material and Methods

Ahe atoll

Ahe atoll is located in the northwest Tuamotu. Since 2007, it has been the most studied pearl farming atoll (Andréfouët et al. 2012). The geomorphology of its lagoon is described in detail by Andréfouët et al. (2020). Useful information includes its surface area (145 km^2), maximum depth (71m) and volume (5.82 km^3). Ahe has a wide pass in the northwest section, as well as

numerous spillways allowing water exchanges between the ocean and the lagoon in the southern rim. The main lagoonal hydrodynamic structures are described in Dumas et al. (2012). *Pinctada margaritifera* stock was last surveyed and mapped in 2013 (Andréfouët et al. 2016). The most recent update on biophysical modelling work is described in Thomas et al. (2016), Sangare (2019) and Reisser et al. (2020).

Genetics data and results from Reisser et al. (2020)

We briefly describe here the sampling performed in 2017 for genetic analysis as it is detailed in Reisser et al. (2020). Natural and farmed populations were sampled throughout the lagoon respectively in 7 (N1-N7) and 6 (E1-E6) sites. Spat collectors (triplicates) were deployed from the second week of February to end of May 2017 in 5 locations (C1-C5). The Figure 1 shows the spatial distribution of the sampling sites. Site N1 was kept for the biophysical simulations but not for genetic analysis as only one specimen was found there and, furthermore, its sequencing failed (Reisser et al. 2020). After the sampling period, spats between 4 to 9 mm, unambiguously identified as *P. margaritifera* specimen, were kept and analyzed, yielding between 1 to 21 samples per spat collecting site.

Protocol for sample treatment and genetic processing is detailed in Reisser et al. (2020). In short, after sequencing, quality trimming, mapping sequences on the *P. margaritifera* genome and filtering, eventually, 13.408 loci were retained for population genetic analysis. All genetic indicators and metrics (heterozygosity among the different sites, inbreeding coefficients, relatedness indices, F-statistics, clustering) significantly showed the presence of two genetic clusters (Fig. 1): a first cluster regrouped all the exploited populations (E1-E6) and three natural populations from the southwestern part of the lagoon (N2, N3 and N4), and a second cluster regrouped the three natural populations from the northeastern part of the lagoon (N5, N6 and N7) and the collected spats in C1-C5 (Fig. 1). F_{st} values between each pair of sampled sites are provided in Reisser et al. (2020). Pairwise comparisons showed that the highest F_{st} values were reached when comparing the collected spats and members of the southwestern cluster. The analysis suggested that all the spats from all collectors only came from parents in the natural populations of the northeast lagoon.

New realistic biophysical modelling scenario

The simulations of Ahe lagoon larval dispersal performed by Reisser et al. (2020) were reprocessed to generate additional data and account for a possible variability of pelagic larval duration (PLD). After a spin-off period to initialize and stabilize realistically the conditions, the simulations performed with the MARS3D hydrodynamic model (Dumas et al. 2012) matched the collector field sampling exact same period (2017/01/25 to 2017/05/28) and used the actual real environmental conditions that occurred during the period (hence, a realistic scenario).

Since the exact spawning events that may have occurred before and during the genetic sampling periods are unknown, a systematic approach by using weekly virtual cohort was implemented. A series of 15 cohorts initiated at the beginning of every week are simulated to cover the sampling period, as in Reisser et al. (2020). Beginning of cohorts (and spawning day) are released once a week during 15 weeks, hence from 25/01/2017 to 03/05/2017.

Cohort's larvae (n=49000) are released at a depth of 5-10 meters, in a neighborhood (~350 meters radius) around the cells that contained the wild (N1-N7) and cultured (E1-E5) sampled stations. The number of larvae was based on computation time, low enough to have relatively fast simulations, and high enough to be able to capture rare hydrodynamic situations. This number is however several orders of magnitude lower than the number of larvae during a spawning event. However, unlike in Reisser et al. (2020) where PLD was set strictly at 25 days, PLD was considered here to be realistic if occurring within the 15-25 days range, based on Sangare et al. (2020) DEB simulations. Thus, the computed statistics are, for each weekly cohort, the sum of the larvae in the vicinity (<500m distance) of the sampled collectors from 15 to 25 days after spawning. In addition, are available for each collecting station, the standard deviation of the mean count, the day after spawning during which the maximum number of larvae is observed, and the value of this maximum. Hence, the statistics here are temporally more integrative than in Reisser et al. (2020). Each cohort C_i temporally overlaps by 18 days the preceding cohort C_{i-1}, and during this period, both cohorts are exposed to the same wind conditions.

Results are provided in the form of connectivity matrices, after that populations (natural or cultured) and collectors sampling stations were geographically ranked from west to east on the x and y-axes to detect more easily geographic trend in connectivity. To compare the similarities between cohort's connectivity matrices, a correlation matrix was computed. The Spearman rank correlation for non-normal data was used.

The export rate of simulated larvae into the ocean through the pass during the 25 days of each cohort and each source (N1-N7, E1-E6) are also monitored. Each particle that leaves the lagoon and does not re-enter, is removed from the larval pool to produce export (or retention) curve through time. These curves can also indicate which sources of larvae are less likely to provide spats if their export is high (or retention is low). High retention rates can indicate that larvae accumulate in some areas of the lagoon or do not circulate anymore close to the pass.

Wind data

The meteorological forcing used for the numerical experiments described above came from the ERA5 global reanalysis at 31km spatial resolution (Hersbach et al. 2020). Atmospheric fields (wind, pressure, temperature, solar fluxes) were then prescribed hourly to the hydrodynamic core (MARS3D) and wind was used to interpret the behavior of each cohort.

To help interpreting the differences between matrices, the wind conditions over Ahe during the sampling period are summarized in the form of a Progressive Vector Diagram (PVD) for each cohort dispersal period, and with a display of the time series of wind direction and speed versus cohort dispersal periods.

Comparison between genetics and biophysical modelling

We computed the Spearman rank correlation of each connectivity matrix with the Fst matrix provided by Reisser et al. (2020), after transformation as -1 x Fst, so that high genetic similarity pairs and high model connectivity pairs would be ranked similarly and correlated. The station N1 was removed for these analyses. Other metrics, like Fst/(1-Fst) described by Rousset (1997) or Alberto et al. (2011) were tested but results were similar to the simpler formulation above, possibly due to the limited spatial scale explored here (Rousset 1997), and are not shown.

Results

Environmental conditions

The PVD and time series of wind conditions at the time of the genetics sampling period are provided Figure 2. Two noteworthy wind episodes are visible, from day 21 to 25 (14-19 February) during which the wind shifted from east to northwest and increased from 5 to 18 $m.s^{-1}$. This episode is overlapped by cohorts 1 to 4. Then, a second similar episode, from day 87 to 91 (21-25 April), occurred. It is overlapped by cohorts 10 to 12. These two episodes correspond to a rapid shift from the east direction to northwest wind, with increasing speed, followed by a rapid return to east direction.

In addition, cohorts 13 to 15 are characterized by a gradual change of wind direction from east to north, with increased speed from 6 to 14 $m.s^{-1}$, occurring in the middle of cohort 13 (day 12 of cohort 13, or 1st May 2017, which correspond to day 5 of cohort 14). During the end of cohort 14 and beginning of cohort 15, the wind direction resumed progressively to the east.

Otherwise, the general pattern of the studied period consists in a moderate speed wind from the east, hence representative of tradewind conditions (Dutheil et al. 2020), and similar to several of the wind regimes identified in Thomas et al. (2014).

Connectivity matrices by cohorts and correlation

The connectivity matrices computed for each cohort are provided in Figure 3, and average and standard deviation matrices across all cohorts are provided in Figure 4. On several of the matrices, extreme values of connection between a specific source and a collector explains the standard deviation pattern. For example, for Cohort 1, the N4-C5 connection dominates. Some of these extremes are also recurrent between cohorts. For instance, this N4-C5 connection stands out in cohorts 1, 5, 7, 9 10 and 11 relatively to the other connections detected in each matrix. The E5-C4 connection also frequently stands-out (in cohorts 3, 6, 7, 8 and 11), while N7-C4 was also frequent albeit at a lower amplitude.

The Spearman correlation between connectivity matrices is summarized Figure 5. Non-significant cells are indicated, Significance was set at 0.01 alpha threshold. In terms of interpretation of correlation with F_{ST}, we considered that a positive and significant correlation indicates that the connectivity pattern correctly explains the genetic proximity between adults and recruits. Seven cells have negative correlations with F_{ST}, but with very low levels (Spearman correlation coefficient: min = -0.11; max = -0.004; mean = -0.05) and very low levels of significance (p-value: min = 0.37; max = 0.97; mean = 0.69) which makes them

uninterpretable. Several cohorts appear not significantly correlated with any of the others. These are cohorts 4, 10 and 15. Correlation of connectivity matrices with the F_{ST} matrix suggested stronger similarities with the connectivity generated by cohort 6, 10 and 15, with higher significance for cohorts 10 and 15 (Fig. 5). Highest correlations between F_{ST} and cohort connectivity metrics are thus observed for the same cohorts that are the most different from all others, namely cohorts 10 and 15.

The retention curves of each source of particles are shown Figure 6 for each cohort. The cohort 4 stands out with the highest similarities in retention among sources, with flat curves suggesting very high retention and possible accumulation in one area of the lagoon. All other cohorts, except cohort 15, are characterized by fast exports for several (1 to 4) sources, and lower exports for the other sources. As expected, the fastest exports are always reached for sources N1, N5, E2, E3, which are the closest to the pass, however, their ranking in term of export rates differ between cohorts. Periods of fast exports during 2 to 5 days are followed by curves that flatten afterwards. Cohort 15 exhibits an intermediate behavior which is between Cohort 4 and the others.

Discussion

The application discussed here and in Reisser et al. (2020) add new case studies to the list compiled few years ago by von der Heyden et al. (2014) on applications of genetics to marine management and conservation in the Indo-Pacific. The present application could be labelled as ‘stock management for mariculture application’ based on their classification. It is related to, and largely overlaps with other applications such as stock delineation and enhancement, identification of cryptic populations, management policy and spatial planning.

For pearl farming, the present work, at intra-lagoon scale differs from most of the earlier works that looked at the genetic diversity of lagoon oyster population, and the role of inter-islands transfers in population homogenization. These questions were tackled using mitochondrial and anonymous nuclear markers in Arnaud-Haond et al. (2003a, 2003b, 2004, 2008) and microsatellites in Lemer and Planes (2012, 2014). A single intra-lagoon work, in Takapoto Atoll, did compare the genetic differences between spat collectors from the same lagoon area; with a limited number of anonymous markers (Arnaud-Haond et al. 2008). They demonstrated, in their cases, the different origins of different cohorts even spatially close. This could be tracked to populations from different atolls that have been transferred in the

early years of pearl farming, and in the same time, comforted the idea that stochastic dispersal and recruitment within a single lagoon control its population structure.

Hereafter, we discuss the results and assess the information provided by both genetics and models in order to conclude on connectivity patterns during the studied period. Second, we more broadly discuss the two approaches using a SWOT canvas.

Does connectivity pathways inferred by biophysical modelling confirm connectivity pathways inferred by genetics? The case of cohorts 10 and 15 and the role of wind.

If we compare genetics, biophysical modelling results and wind data (Figs. 2-6), we can identify one interesting pattern that could link one cohort to the genetics results. Specifically, we first observe that all cohorts have a fairly similar pattern of dispersal based on correlations, except cohorts 4, and more markedly cohorts 10 and 15 (Fig. 5). Second, these two cohorts 10 and 15 also have the highest correlation with the F_{ST} matrix. These two cohorts are peculiar and match best the genetics. Logically, they would represent the connectivity conditions that were captured by genetics.

Cohort 15 corresponds to a change of wind direction pattern, with a gradual change from north to east during the cohort transport time (Fig. 2), a pattern occurring only during this cohort 15 throughout the studied period. Cohort 10 also experienced a fast wind shift, from east to west, then back to east. Other cohorts (1 to 4) also experienced similar shifts, with even more intensity, but their connectivity matrices did not compare well with the F_{ST} matrix. Connectivity matrices of Cohorts 1-4 were however similar to that of other cohorts (Fig. 5). Eventually, we hypothesize that the wind regime observed during cohort 15 could best explain the dispersal of offspring from the northeast part of the atoll to the western part (thus covering all spat collectors, being consistent with the collected genetic results), assuming spawning occurred between the end of cohort 14 and cohort 15.

(Lack of) insights from export rates

Export rates do not allow to identify a particular cohort that could be related to the genetics results. At least, it would be possible to discard cohorts if they had very high export rates for all sources and thus minimal chances of successful spat collecting. This is not the case here

and only one cohort actually showed high retention (cohort 4, Fig. 6), which is corroborated by a peak of strong western wind that accumulated the particles in the east of the lagoon.

Insights from bioenergetics modelling

Previous growth simulations of juveniles performed using a Dynamic Energy Budget (DEB) model (Sangare et al. 2019, 2020) for typical environmental conditions found in Ahe atoll at the time of the survey (chlorophyll a concentration at 0.5 $\mu g.l^{-1}$, and temperature at 29°C) (Thomas et al. 2016) suggest that the growth rate would be ~112 $\mu m.d^{-1}$ (see also for Raroia Atoll, Van Wynsberge et al 2020). One month after fixation on collectors, spat would have grown by 3.4 mm. The spats sampled during the experiments measured between 4 and 9 mm, hence suggesting that cohort 15 is unlikely to have produced the sampled spats. Even assuming an early fixation around mid-May, this would leave a maximum of only 2 weeks for growth before sampling while much more time would be needed. Therefore,, based on this discrepancy, cohort 10 appears to be a better candidate according to the size clue.

The combination of bio-physical methodologies and genetics therefore allows the precise identification of the weather sequence, during cohort 10, associated with the recruitment event. The contribution of bioenergetic modelling appears critical to better integrate the variability of environmental conditions on the life history traits of our species. This is a necessary perspective for a better understanding of the processes occurring after the larvae settlement.

Weaknesses of the genetics approach

The patterns uncovered by the genetics are real, but it is unclear if they unravel the complete story. The computed connectivity matrices and realistic simulations shows potentially a much more complex story than genetics alone. We keep in mind the warning by Lowe and Allendorf (2010) that assessing connectivity should be done within the larger demographic context of the focal population. As they pointed out: '*without that context, measures of dispersal—whether from genetic or observational data—are descriptive and cannot tell us whether and by what mechanisms populations are linked'*. We believe that it is very likely that available genetics data can miss part of the story. Several weak aspects of the genetic sampling performed in Ahe can pose problems and explain this statement.

First, biases can be related to the sampling of specimen on collectors. While genetic results of sampled spat are a clear indication of realized connectivity, the presence of only a few living recruits is only an indicator of the diversity of what could have settled but did not survive for a variety of reasons after few days or weeks. It is unknown and impossible to know if recruits coming from different sources were present at some point but died before the collector was withdraw from the water.

Second, the number of collectors was low. While their positions were strategically selected, they did not cover all the lagoon areas (Fig. 1), and the strategy (for instance, capturing connectivity during typical average tradewind conditions) could be challenged, and sub-optimal, if the weather conditions are unusual or submitted to events, as it was the case during part of the experiment in Ahe (Fig. 2). This latter point cannot however be improved, as weather prediction cannot be made with accuracy over large timespans necessary for sufficient sampling of spat.

Third, even if collector data were limited, all sources could be identified according to the sampling of natural and farmed populations in different lagoon areas. This is a very good aspect. However, it does not mean that all possible larvae origins have been captured. In our view, and even if the farmed population has a male-biased sex-ratio, it would be surprising that no offspring is produced by the 14 millions of farmed oysters. This is in agreement with Arnaud-Haond et al. (2004) who show a genetic homogenization of populations after translocation of spats between lagoons, and therefore the influence of farmed populations. The sampled populations in Reisser et al. (2020) were found to belong to two genetic clusters. As such, the origin of the collected individuals could only be addressed using these two clusters (Fig. 3A in Reisser et al. 2020), and while they were assigned to the northeastern cluster, it is still not clear which of the N5, N6 and N7 populations has produced the larvae that ended up in each of the related C1 to C5 collectors. This is unlike biophysical models that can track the individual trajectory of each released larvae.

Fourth, the questions about the contribution of the exploited stock to spawning and recruitment raised in Reisser et al (2020) also relied on the fact that the genetic signature of all natural individuals sampled in the northeastern lagoon did not show any introgression of the exploited stocks' genetic signature. Models indicate here that spawning of the exploited stocks located in the northeastern lagoon should provide larvae that would recruit back to the northeastern lagoon area. Considering the temporal heterogeneity of the composition of various cohorts, it is possible that the northeastern populations sampled for the genetic study

only represents a fraction of the diversity found in the lagoon, since sampling were made on isolated coral pinnacles. Indeed, one pinnacle could represent a single spawning event, so that all larvae that recruited on this pinnacle would be related and show a reduced diversity, which could lead to wrong conclusions. While this might be the case, it would still be surprising that three pinnacles (N5, N6 and N7) dispatched across the entire northeastern lagoon would all be related and come from the same cohort or different cohorts made by the same parents.

Weaknesses of the biophysical modelling approach

There are several weak points in the genetics data, yet, the observed results cannot be argued, even if they are partial. Hence, modeling should at least identify the patterns detected by genetics as plausible. If they are not detected, the failure of the model needs to be understood and critically assessed. In this case, several possible weaknesses of biophysical models in the context of pearl farming need to be investigated.

First, problems could come from inaccurate hydrodynamic forcing, due to insufficient resolution (x,y,z) or inadequate parameterization. Model validation is based on few key measurements in strategic locations (e.g., in the pass between lagoon and ocean), but it does not mean that all features are perfectly reproduced and that inaccuracies does not exist (Dumas et al. 2012).

Second, and actually much more difficult to constraint precisely, are the biological hypotheses related to the spawning time and the level of food quality during the dispersal phase. These uncertainties justified new on-going development of coupled biogeochemical and physical models that also integrate the physiology of oysters through DEB models (Fournier et al. 2012; Thomas et al. 2016, Sangare 2019; Sangare et al. 2020, Van Wynsberge et al. 2020). When coupled with environmental information (temperature, food), DEB models should provide better realism in term of spawning occurrences, and on the larval development rates in the water column during their pelagic life (Thomas et al., 2011a). Here, the sensitivity analysis performed by using cohorts and the knowledge of temperature conditions limit the problem of the spawning time definition, but food conditions were unknown and therefore not considered limited.

Third, and this is the major biophysical modeling gap when tackling connectivity, the stage of the fixation and the processes occurring directly on the experimental collectors are not considered. Hence, the analysts can deal only with a probability of recruitment based on the proximity of larvae to collectors at a time near to their PLD limit. It remains unclear how

reliable this proxy is when comparing it with genetics data. Experimental spat collectors data can be useful, but between the moment when a larvae gets close to a collector, as a model could describe it, and the moment when the potential subsequent recruit is counted by an observer, many fixation and lethal processes can interfere, and insufficient knowledge preclude their modelling. Indeed, an accurate recruitment model is still lacking and therefore cannot be coupled with the biophysical dispersal connectivity model.

Finally, checking the accuracy of the simulations using other means than genetics, in our Ahe experiment but also in general, are difficult. Besides the validation of the hydrodynamic model using some adequate physics observations (Dumas et al. 2012), in theory, numerical simulations of larval dispersal can be validated with different data sets including plankton sampling for larval abundance and swimming behavior, deployments of experimental collectors for recruits presence and abundance, and tagging for direct estimation of the population of origin. In the case of Lagrangian experiments, the measure of accuracy is, however, limited only to the congruence of spatial patterns and their relative distribution (Thomas et al. 2016), and cannot result from absolute abundance counts, because the initial number of gametes and larvae resulting from successful fecundation is most of the time unknown (but see Thomas et al. 2012a who could performed larval counts). Conversely, the number of 'numerical larvae' are known but is often set following computation time considerations and not necessarily with a realistic order of magnitude. In case of Eulerian approaches, it is possible to initialize the simulations with measured concentrations and follow the evolution through the flows in each point. In this case *in situ* and numerical concentrations have values in the same range (Thomas et al; 2012b). Finally, in addition to the logistical problem and costs of repetitively sampling larvae in the water column in numerous lagoon stations through a period long enough (Thomas et al. 2012b), there are inherent limitations, including the morphological and visual similarities between larvae within the *Pinctada* genus and the challenge to identify the *margaritifera* species (Thomas al. 2011b).

Coherence between genetics and biophysical model results

The patterns detected by genetics (Fig. 5) appear to be correlated with the connectivity matrices of specific cohorts (in particular cohorts 10 and 15). Hence, it can be concluded that the two approaches mutually reinforce each other at the scale of a short-term period and realistic scenario, but in this case the exact mechanism that have led to the genetics result cannot be ascertained using the biophysical model outputs. These observations and

conclusions reinforce the 'sweepstakes-chance matching hypothesis' of Hedgecock (1994) and already mentioned in a pearl farming context by Arnaud-Haond et al. (2008). Specifically, this means that surviving spats come from a fraction of a population that spawned in the right window of time and environmental conditions (Hedgecock 1994), which is exactly what the examination of genetics data, correlation of connectivity matrices (Fig. 5), and wind conditions suggest (Fig. 2).

On a longer time-frame, the modeling results by Thomas et al. (2014) based on forcing by wind regimes representative of inter-annual conditions, also converge with Reisser et al. (2020) who identified two genetic clusters separating the southwest and northeast wild populations. In the southwest, wild and farmed population appear similar. Reisser et al. (2020) discussed the peculiar northeastern wild population, isolated from all other populations due to a lack of west-east transfers and hypothetically a lack of local retention of larvae produced by the north eastern farmed stocks. All farmed populations appear similar throughout the lagoon, but the northeast wild and farmed population are genetically different. Since Thomas et al. (2014) have showed that in some conditions the north sector can be characterized by very limiting dispersal for both wild and farmed populations, this is a paradox. However, it also reinforces the strong conclusion that possibly mostly wild populations are able of effective spawning followed by successful fecundation.

Consequences for pearl farming management

The questions we initially aimed to tackle and presented in the Introduction were:

- Are there several populations, wild or cultured, within a lagoon, and if so, how genetically different are they? Can they remain isolated?
- Where is the origin of spats and what are the adult population sources? In particular, in the context of numerically dominant farmed broodstock and decreasing wild stocks, is it possible to rely in the farmed stock for reproduction and spat collection?
- To what extent are the answers to these two questions explained by climate or weather conditions?.

There are coherences and convergences between genetics and biophysical models and the results reply, but only partly, to these questions. Specifically, the genetics results raised questions on farmed stocks contribution to the larval pool, and then to the spat on collectors. As discussed above, we see the wild-only origin of spats and the complete absence of

individuals with an “exploited” genetic signature in the natural populations of the northeastern lagoon, despite the presence of exploited stocks in that area, as a paradox, considering the enormous population of farmed stock, even when characterized by a male-skewed sex ratio (Arnaud-Haond et al. 2004, Thomas et al. 2016). Contribution of reared stock to spats is null on the time period analyzed in Reisser et al. (2020) data sets, but this definitely needs further confirmation, with extended sampling driven by biophysical model scenarios, longer sampling periods and more studied atolls. If the findings from Reisser et al. (2020) are confirmed for other period and locations, the consequences would be significant in term of stock management and sustainability of the industry as it works today, without relying on hatchery but only on spat collecting. Managers will have to actively promote conservation of the existing wild stock, its reproduction, and restocking. In addition, eco-physiologists and modelers should also explicit the keys that block reproductive inputs from farmed stocks. This is likely at the gamete emission or fecundation or at the early stage of larval life (D-larvae) level that an answer lies. Finally, our computations also highlight the utility to confront the results using the environmental conditions (wind) as this factor contribute to identify with little doubts which cohorts corresponded to the genetic results.

The Ahe case study, and the studied period, does not provide alone a definitive answer to the three questions above but it is clear that we are on good track to move forward if similar experiments can be replicated in Ahe or elsewhere, especially if the *in situ* genetic sampling can be extended.

Promoting an interdisciplinary approach

The Figure 7 summarizes the main prerequisites, the outputs, and the possible inter-actions between the genetic and the biophysical modeling approaches for intra-lagoon connectivity study. We worked on *P. margaritifera* in atoll lagoons, but similar schemes can be developed for other model species. There are two main feedback loop in Figure 7: the possibility to validate biophysical models using genetics and the possibility to design sampling protocols for genetics using models. For long projects, several iterations can be possible. A cyclic complementary approach could benefit from:

1. Stratifying genetics study using biophysical models (site selection for sampling of stocks, location of collectors),

2. Duplicating Reisser et al. (2020) study in Ahe, but also for the atolls that are efficient spat producers, like Takapoto in French Polynesia or Manihiki in Cook Islands,
3. Integrating the conclusions into biophysical models (and go back to step 1),
4. Taking advantage of ancillary spat collectors sampling, notably by involving farmers as only them have access to year-long variability,
5. Being aware of inter-atoll transfers and conduct genetic sampling of the transferred lots,
6. Establish a library of wild stock samples per atoll sectors (identified by modeling).

Other challenges need to be considered, in particular the genericity of the approaches from one atoll to another, and the costs. For the pearl farming Tuamotu and Cook Island atolls, we believe that the main bottlenecks would be, as of 2020, related to the development of the biophysical models. As seen in Figure 7, it potentially requires much more planning, data collection in the field, satellite and model data (for weather and climate), and computing time than genetics. It is nevertheless clear that both approaches are highly specialized and require strong expertise. The references cited in Figure 7 also highlight the necessary developments for each prerequisite step. None is trivial, or cheap, especially for remote places. However, it is likely that both approaches will expand and will be used jointly on the near-future. In Fiji, new genetics approaches have already been successfully applied to discriminate the origins and levels of differentiation of different oyster populations (Lal et al. 2016). The present study echoes the review on 3D atoll hydrodynamic modeling for pearl farming by Andréfouët et al. (2006) which clarified for managers the necessary investments and the expected science and management benefits. Fifteen years later, models have been developed or are under development on five sites (namely Ahe, Takaroa, Raroia, and Mangareva in French Polynesia and Manihiki in the Cook Islands) thanks also to numerous field campaigns (Dumas et al. 2012, Le Gendre et al. in preparation, Andréfouët 2013, Andréfouët 2018). Similarly, we predict that the present study will also promote the combined routine used of genetics and biophysical modelling in the near future.

To summarize the discussion above, a SWOT table can be established as a take-home message (Table 1). Bio-physical modelling and genetics can be analyzed separately for their strength and weaknesses, but when they are combined, cumulative opportunities, but also threats can emerge. The threats, for managers, farmers, and scientists, would be to trust blindly the results without frequent calibration, validation, and critical analyses of the results.

Conclusion

According to Cowen et al. (2007), the core challenges and issues relevant to population connectivity can be parsed into four specific categories: observation, explanation, consequences, and application. Here, for the specific application of understanding larval dispersal and spat collecting efficiency in the context of black pearl farming, we used both genetics and biophysical modelling to observe, model and explain at lagoon scale the spatial and temporal distribution of larvae coming from wild and farmed oyster populations. At this stage, there are still many gaps before understanding and modeling accurately the different processes at stake in all conditions.

To increase its usefulness for management and the realism of the simulations, biophysical models are now facing major challenges, in particular i) how to accurately predict spawning, synchronous or asynchronous, that will trigger the beginning of the pelagic dispersal phase, and ii) how to accurately include the environment in the simulations of larval growth rate, in particular the trophic system and the levels of planktonic food. This is why on-going developments includes biogeochemical measurements (Rodier et al. 2021, Seceh et al. this issue) and the coupling with biogeochemical models to provide realistically, in space and time, food levels available for the oysters at every life stages. Further, coupling with full life-cycle Dynamic Energy Budget (DEB) models are required to simulate accurately the temporality of spawning in the various adult populations (Fournier et al. 2012; Sangare et al. 2020), and larval growth during dispersal phases (Thomas et al. 2016; Sangare 2019). The processes occurring during the juvenile phase, just after the attachment of the larvae to the collectors, now seem to be a fundamental element to elucidate and model.

For genetics sampling and analyses, the approach performed here and in Reisser et al. (2020) appears powerful, but insufficient sampling blurs the conclusions, even they appear to be coherent with biophysical models. It is likely that increased sampling efforts, temporally and spatially, will definitely answer the key questions we initially aimed to address here.

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Table 1: Table summary of the strengths, weaknesses, opportunities and threats of using jointly biophysical models and genetics.

Bio-physical models	**Genetics**
Strength	**Strength**
Process-based approach, allow a mechanistic understanding of larval pathways Scenario-testing approach, driven by management questions, can identify recurrent and outlier demographic connectivity patterns. Systematic sensitivity analysis is possible. Construction can be staged (e.g., hydrodynamic structures can be validated independently of biological input). Weather data easily available for present, hind- and forecast.	Address multiple-levels connectivity factors and processes. Identify unambiguously sources and sinks of connectivity, at different scale.
Weakness	**Weakness**
Bathymetry and hydrodynamics required. Construction need to be staged (e.g., hydrodynamic structures need to be validated first) Complexity and number of scenarios can increase rapidly. Computing time and computing facilities. Expertise required (hydrodynamic, computing, ecological modelling). Unknown accuracy of bio-physical outputs due to lack of biologic validation data; provide clues but not proofs.	Representativeness of sampling can be limited and sub-optimal, especially for demographic connectivity applications. Only assess connectivity for survivors of said connectivity. Sampling may not be possible (worst case). Cost of laboratory analysis and field sampling. Expertise required (genetics, statistics). Hind- and forecast are not possible.
Cumulative Opportunity	
Bio-physicals scenario can guide sampling for optimal spatio-temporal coverage, depending on the connectivity process at stake. Genetics data can validate the predictions of simulations if sampling is possible. Cycles of adaptive sampling and modelling can refine the conclusions (staged combined approach).	
Threats and cumulative threats	
The model sends the sampling in the wrong direction, because the model is inaccurate. Incomplete genetic sampling could push to wrong management decision. Inaccurate modelling could promote wrong management decision. Weather during sampling cannot be predicted hence there is a risk that sampling data may not be in line with model-driven specifications.	

Figures

Figure 1: Ahe map with sampling sites and patterns of connectivity by matching colors described in Reisser al al. (2020) according to genetics data. C1-C5: location of collectors, E1-E6: location of farmed population samples, N2-N7: location of natural wild population samples. N1 could not be used for genetics (n=1), but was used for biophysical modelling. From all the sampled stations (upper-left), Reisser et al. (2020) showed that all i) cultured stocks (E1-E6) were from the same population (upper right), ii) the southern wild population (N2-N4) could be related to the cultured stock while the north population (N5-N7) was different (lower right) and iii) all the juvenile spat found on collectors (C1-C5) were related to the wild population from the north.

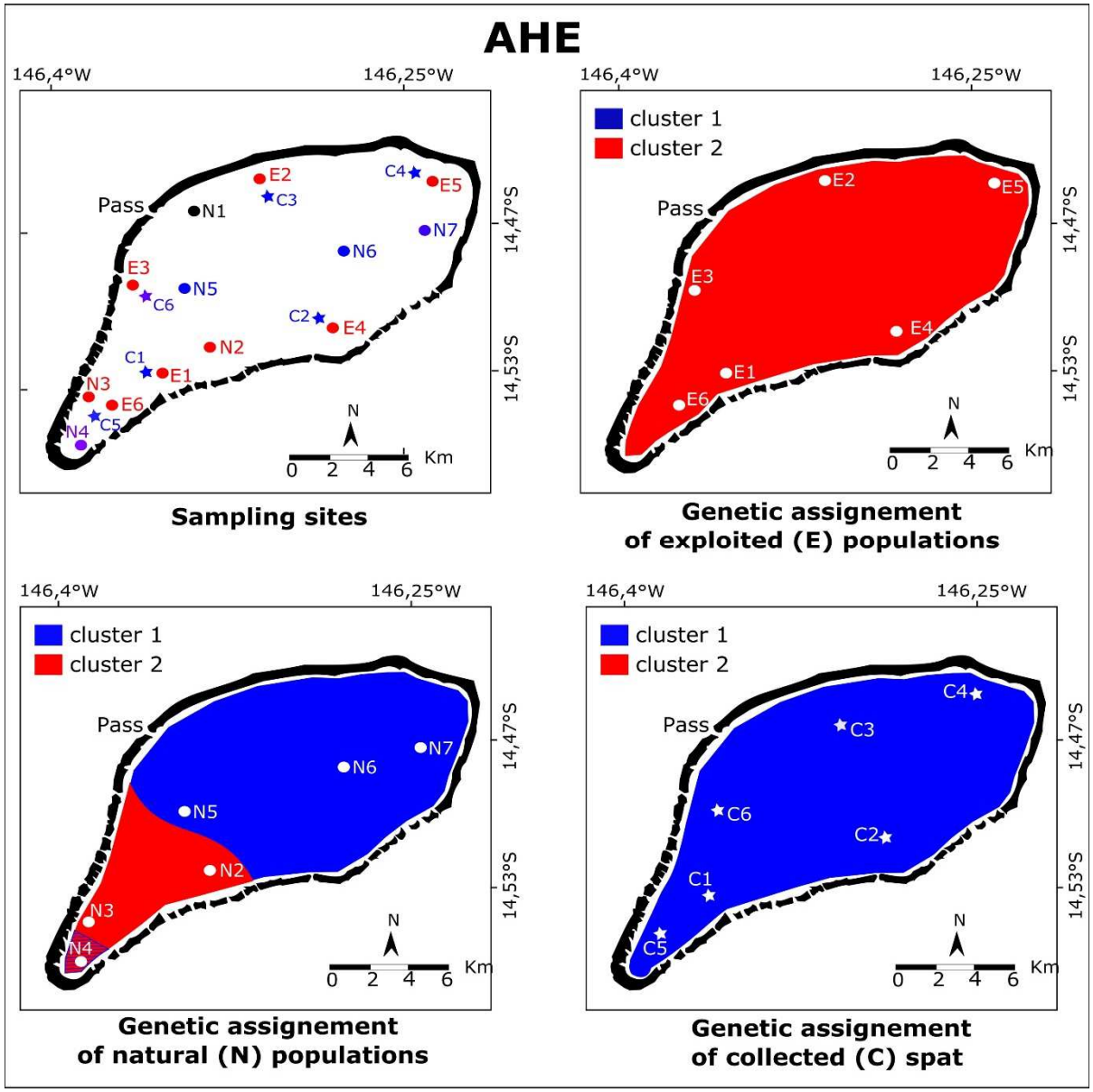

Figure 2: (a) the sequence of cohorts, (b) wind speed and direction time series and (c) progressive vector diagram for wind conditions during each cohort dispersal.

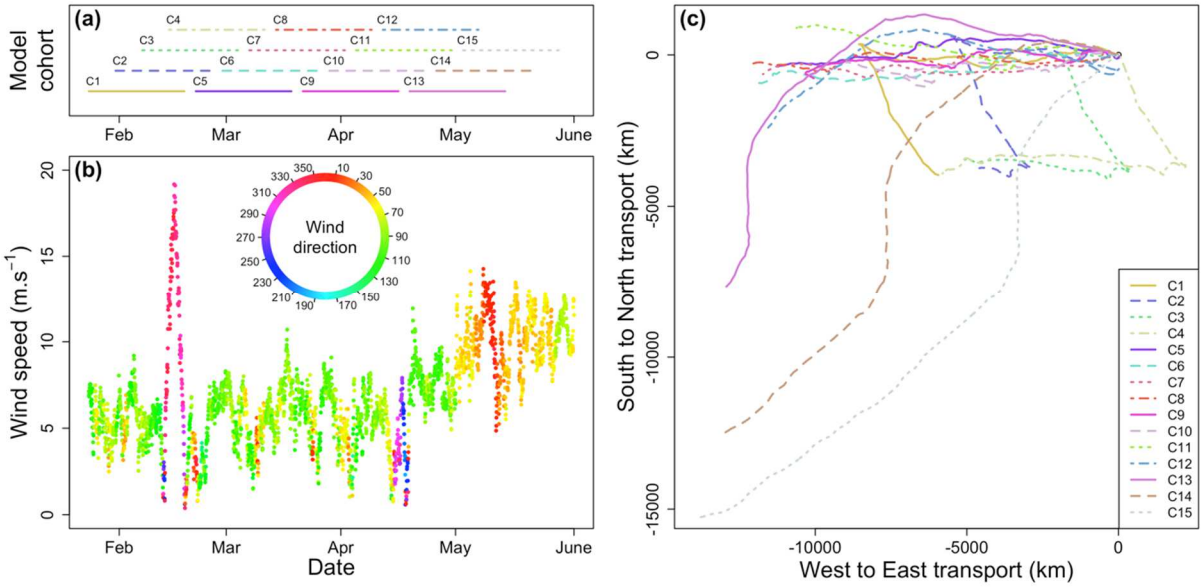

Figure 3: Connectivity matrices for each cohort. All color scales are identical and represent the cumulative number of particles coming from a given starting broodstock and crossing a given arrival collector. See figure 1 to refer to the spatial position of each station (natural populations: N1-N7; farmed populations: E1-E6) and collectors (C1-C5). Here, the stations are east-west sorted.

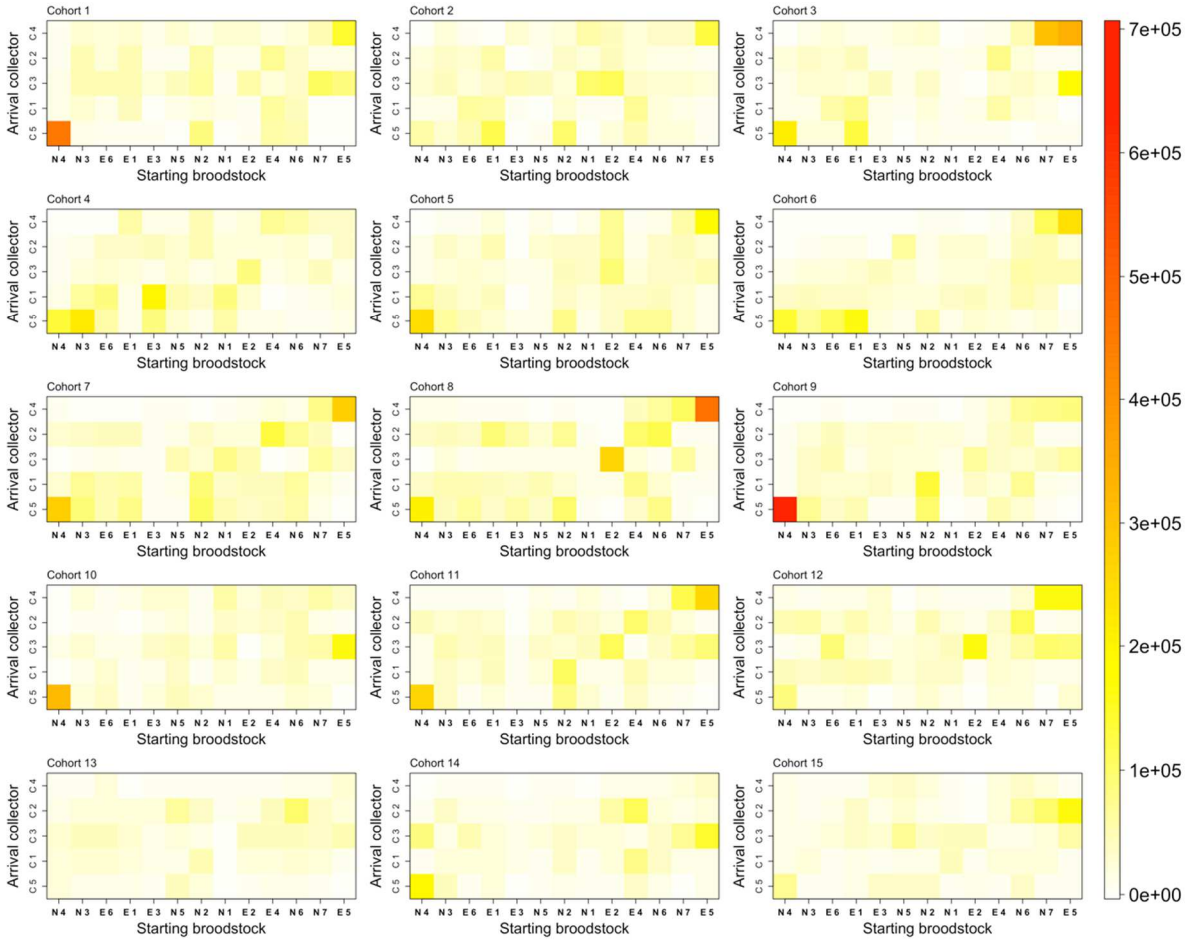

Figure 4: Average and standard deviation (cumulative number of individuals) for all the 15 cohort connectivity matrices presented Figure 3.

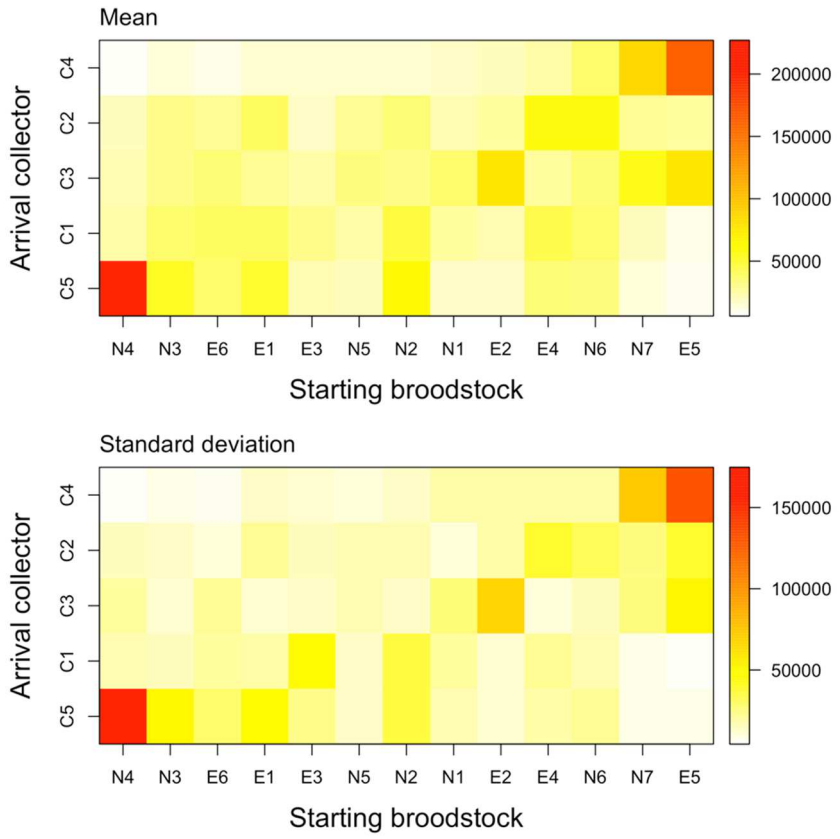

Figure 5: Spearman correlation between cohort connectivity matrices, and with the Fst matrix. Size and color (color bar) of the circle are related to the significance of the correlation ($p < 0.01$). cCells with a X are non-significant.

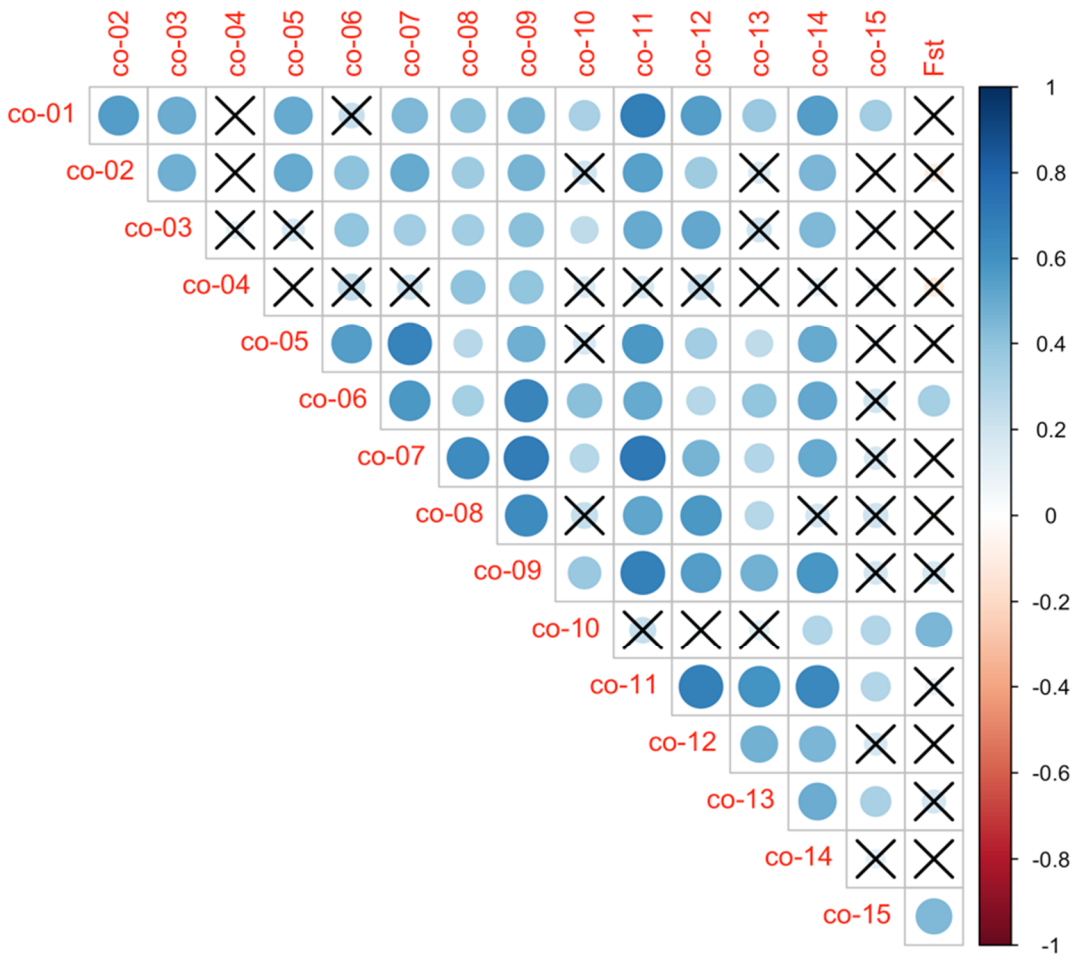

Figure 6: Retention of larvae in the lagoon for each sources (N1-N7, E1-E6) and for each cohort. The curves show the number of larvae still in the lagoon across time.

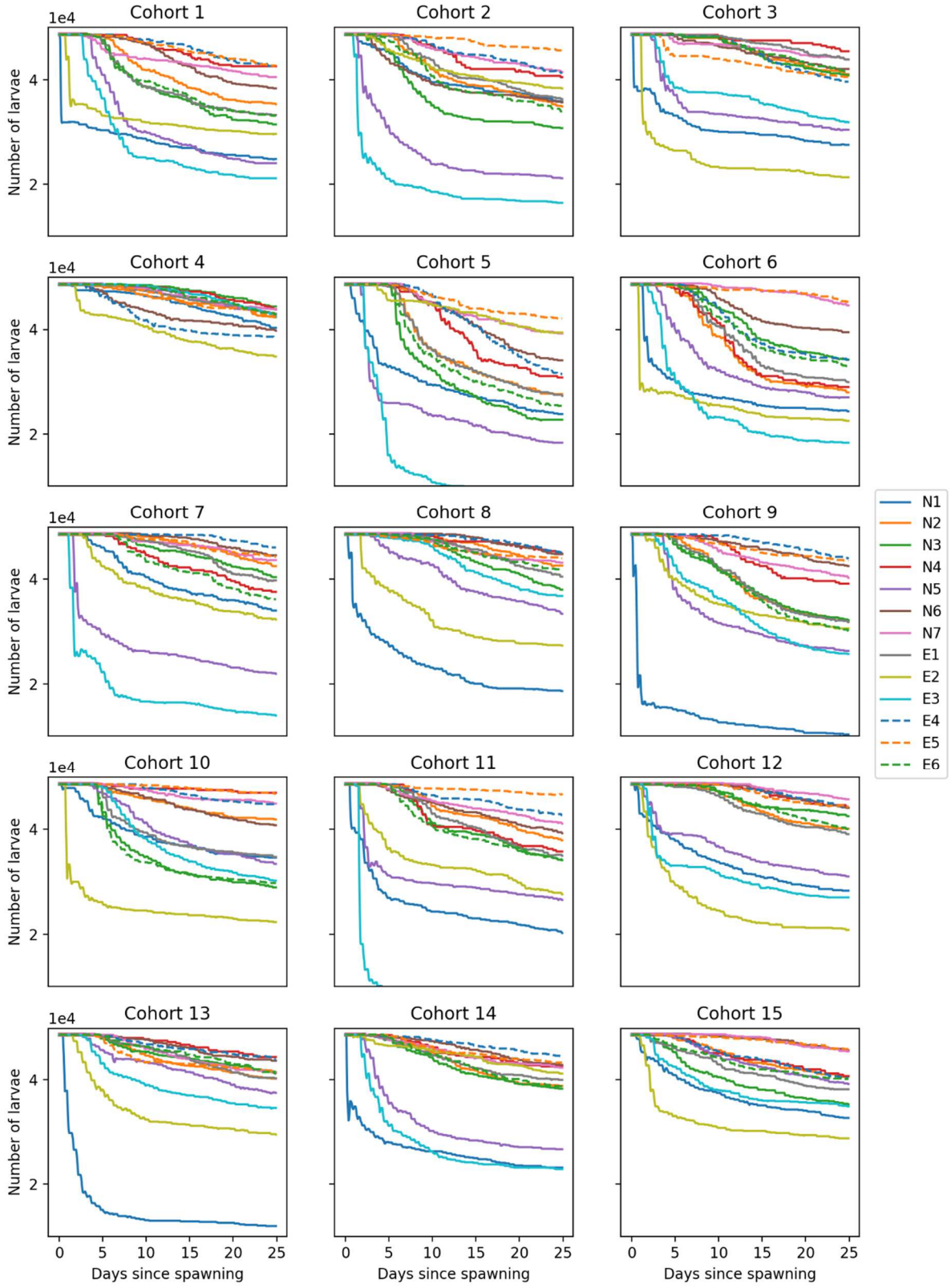

Figure 7 Flow chart summarizing the main prerequisites, the outputs, and the possible interactions between the genetic and the biophysical modelling approaches for intra-lagoon connectivity study. Numbers in parenthesis refer to examples of references for *Pinctada margaritifera* study in the context of Tuamotu atoll pearl farming: 1: Andréfouët al. (2020); 2: Dumas et al. (2012); 3: Dutheil et al. (2020); 4: Andréfouët et al; (2016); 5: Sangare et al. (2019); 6: Reisser et al. (2020); 7: Thomas et al. (2012a); 8: Thomas et al. (2016); 9: this study.