



The pearl oyster (*Pinctada margaritifera*) aquaculture in French Polynesia and the indirect impact of long-distance transfers and collection-culture site combinations on pearl quality traits

Chin-Long Ky^{a,*}, Floriane Broustal^a, Dan Potin^a, Cédrik Lo^b

^a Ifremer, UMR 241, EIO, Labex Corail, Centre du Pacifique, BP 49, 98719, Taravao, Tahiti, French Polynesia

^b Direction des Ressources Marines et Minières, BP 20, 98713, Papeete, Tahiti, French Polynesia



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ABSTRACT

In French Polynesia, the *P. margaritifera* pearl aquaculture industry is spread over a vast area, as large as Europe. All the oysters for this highly economically important activity are supplied from just a few collection lagoons, but they are grown in numerous sites across three archipelagos (Gambier, Society and Tuamotu). Many oyster transfers thus indirectly bring about grafting combinations mixing different geographic origins and production sites. This study aims to examine the impact of such graft combinations on cultured pearl quality traits. For this, six homogeneous and standardised experimental graft combinations (N = 6197) were conducted at commercial scale in the two growing locations the most frequently used in French Polynesia: Arutua atoll (Tuamotu) and Mangareva island (Gambier), using oysters supplied from the top three collection sites: Ahe, Takapoto and Mangareva lagoons. At harvest, four main pearl quality traits: nacre weight deposition speed, pearl colour components (darkness level and green overtone), grade and shape categories were recorded by a professional sorter from the Tahiti auction and compared. Results revealed effects of the combinations of oyster origin and grow-out location, with: 1) significant origin × site interaction for nacre weight deposition speed; 2) colour variation at intra- and inter-site scales, with Ahe origin producing the most dark pearls and Gambier highest rate of the attractive green coloured pearls; and 3) higher grade categories for the Gambier origin and rearing location. These oyster-site combination effects highlight the benefit for the Polynesian pearl industry of switching from a mono-site/ company production system to a new multi-site production strategy to maximize overall cultured pearl quality expression.

1. Introduction

Cultured pearl aquaculture in French Polynesia is unique. Firstly, pearls are the top export industry and the second economic resource after tourism. In 2017, 13416 tons of cultured pearls were exported around the world from French Polynesia, mainly to China (62%) and Japan (32%) (Fig. 1, source: Direction des Ressources Marines et Minières). From a socio-economic point of view, the industry sustains populations in atolls and islands and provides multiple source of sustainable income over generation. Secondly, the corresponding aquaculture is based on the exploitation of a single species, the black-lipped pearl oyster *Pinctada margaritifera* (family Pteriidae), in a territory covering a surface as large as Europe, compared with other "smaller" Pacific countries, such as Japan, where the three main *Pinctada* species are co-cultured (*P. fucata*, *P. maxima* and *P. margaritifera*). Thirdly, *P. margaritifera* is particularly abundant at the wild in French Polynesia

(Yukihira et al., 2000; Cunha et al., 2010). It occurs in the oligotrophic waters of coral reefs and atolls and is distributed across the Indian and Pacific Oceans, from the east coast of Africa to the west coast of America, as well as in the eastern Mediterranean Sea and the Ryukyu Archipelago. Due to its abundance in Polynesia, the supply for the pearl culture industry there is based on wild spat collection. To date this stock is mainly taken from three main excellent recruitment lagoons: Ahe and Takapoto atolls (Tuamotu archipelago), and Mangareva island (Gambier archipelago). Fourthly, the Polynesian pearl industry extends over a very large area, with numerous mainly small farms (family scale < 10 ha) and grow-out sites that are geographically distant and subject to disparate environmental regimes. Production sites are thus located across 26 atolls and islands, concern 556 producers and cover an exploited maritime area of 8050 ha. Expansion of this industry is limited by the means of transport between collection and production sites. Mangareva island (141 producers) and Arutua atoll (72

* Corresponding author.

E-mail address: chinky@ifremer.fr (C.-L. Ky).

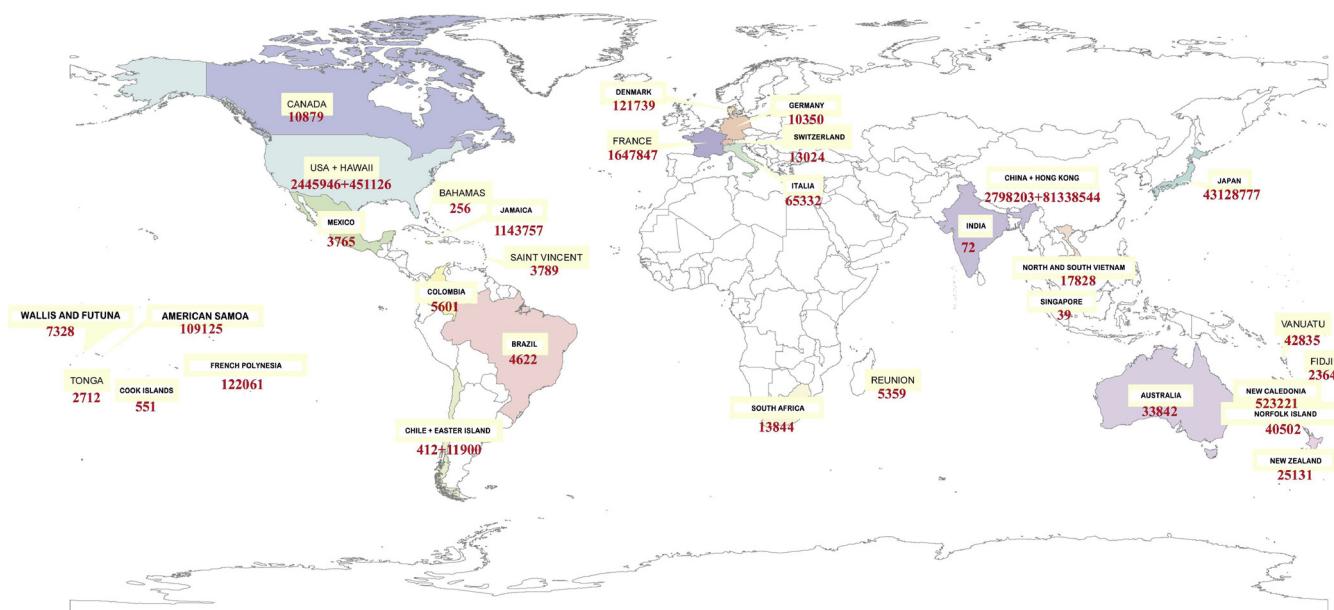


Fig. 1. Exported weight (kg) of Polynesian cultured pearls from *Pinctada margaritifera* to different countries of the world in 2017.

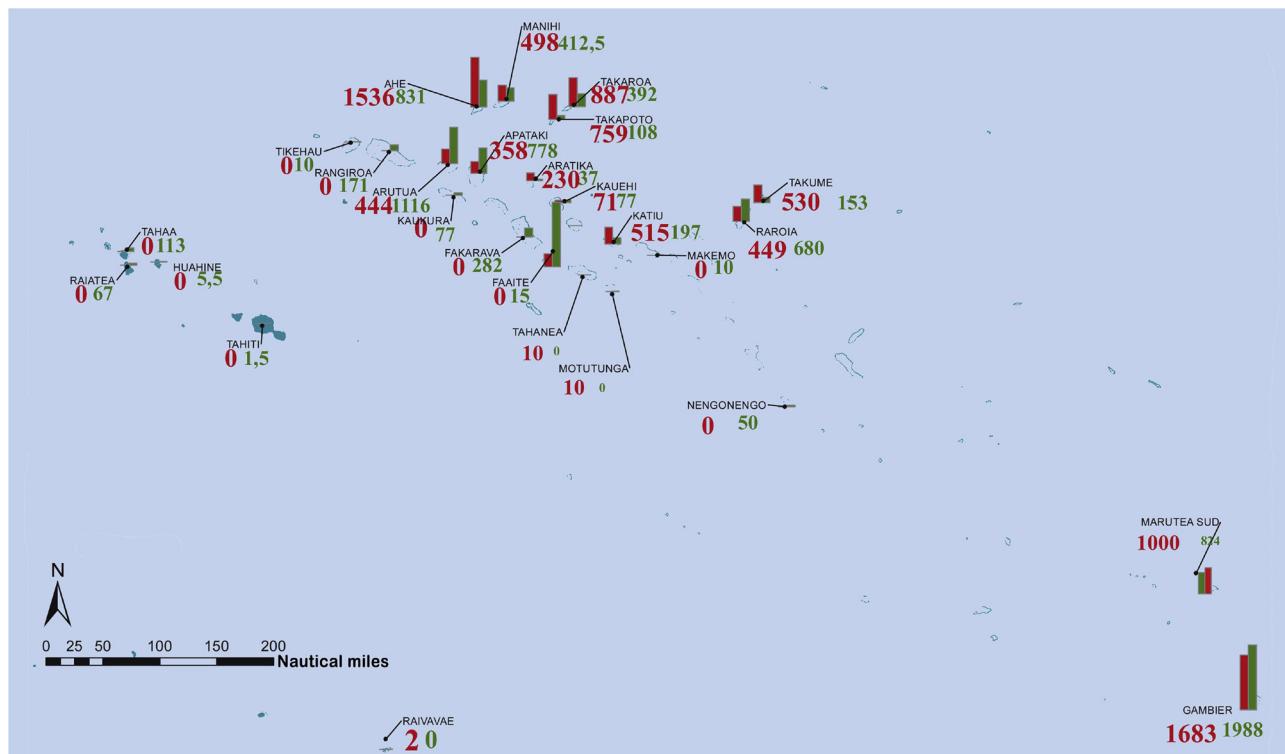


Fig. 2. Collection and production sites of the pearl industry in French Polynesia. Authorized areas (Ha) and number of collecting lines are respectively represented in red and green histograms (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

producers) are the top two production sites and represented 24.6% and 13.3% of the total area, respectively, in 2017 (Fig. 2, source: Direction des Ressources Marines et Minières). Thus, many oysters are transferred from collection sites to the numerous production sites.

Production of a cultured pearl with *P. margaritifera* requires two animals: a small piece of mantle tissue (a graft) is dissected from a donor oyster (consequently sacrificed) and inserted, together with a round bead of nacre (a nucleus), into the gonad of a recipient oyster (Gervis and Sims, 1992; Taylor and Strack, 2008). Over time, the tissue from the donor grows around the bead to produce a pearl sac, which

secretes successive nacreous layers onto the bead to produce a cultured pearl (Webster and Anderson, 1983; Landman et al., 2001; Kishore and Southgate, 2014a). Approximately 18 months after implantation, the pearl is harvested. Before sale, it is assessed for its quality. Five main factors are used to define pearl quality: size, shape, colour, lustre and surface quality. On the basis of these five factors, Tahitian cultured pearls were graded following the official classification, which uses an A, B, C, D and Rebut nomenclature (Tayale et al., 2012). Schematically, it has been shown that it is the donor oyster (rather than the recipient) that has the main influence over pearl quality traits, particularly colour

and lustre (Ky et al., 2013, 2017a and 2017b; Blay et al., 2017). By contrast, pearl size is mainly controlled by the recipient oyster and its biometric parameters (Le Pabic et al., 2016; Blay et al., 2017). Recently, donor-related genetic parameter estimates clearly demonstrated heritability for nacre weight and thickness, darkness and colour of pigmentation, surface defects and overall grade, which signifies a genetic basis for these traits in the donor oyster (Blay et al., 2018a). The interactions between donor and recipient in relation to the environment are highly complex. Specific variations in pearl quality traits among culture sites have already been observed, with distinctive "signatures" of certain sites, revealed by using a same donor phenotype grafted over six grow-out locations covering the three archipelagos (Ky et al., 2016a). However, differing environmental sensitivity between donors has been revealed, with some donors responsible for 20 to 36% of nacre weight determination (Ky et al., 2018a). Producing high quality pearls remains one of the main challenges for the future development of *P. margaritifera* aquaculture.

Understanding the influence of the donor origin and growing environment of the recipient in the realisation of cultured pearl quality traits is therefore particularly important in the context of the Polynesian pearl industry and for ensuring maximum production gains when multiple grow-out locations are used or when different markets with, for example different pearl colour preferences are targeted for the end product (Wada and Jerry, 2008). The objectives of this study were to examine the effects of different combinations of donor oyster origin and recipient growing site, which could be made as a consequence of animal transfer flows. We thus created combinations that involved the same/ different collection site for donors and recipients and rearing in same/ different culture site relative to the origin. For this, multiple graft experiments (totalling 6197 grafts) were realised at a commercial scale using donor oysters originating from the three main representative collection sites (Ahe, Takapoto and Mangareva) and grafted into recipients growing in the two main production lagoons (Arutua and Mangareva).

2. Materials and methods

2.1. Experimental animal origins

Wild *P. margaritifera* were collected as juveniles (spat stage) in the lagoons of Ahe atoll (AHE: 14°29'S, 148°20' W, Tuamotu archipelago, French Polynesia), Takapoto atoll (TKP: 14°32'S, 145°14' W, Tuamotu archipelago, French Polynesia) and Mangareva island (GMR: 23°07'S,

133°58' W, Gambier archipelago, French Polynesia) (Fig. 3). Passive techniques were employed for catching the spat, using commercial collectors made from plastic materials, to which planktonic mollusc larvae become attached fifteen to twenty days after their release. During the beginning of the main reproduction period (November to December in 2013), collectors were simultaneously deployed in the lagoons of Ahe, Takapoto and Mangareva. This provided a pool of pearl oysters of approximately the same age for the experimental graft. After 15 months (March 2015) of subsurface rearing (3–5 m below the surface) in the different collection sites, the juveniles (shell dorso-ventral measurements of 5.4 ± 1.8 cm) were removed from the spat collectors, pierced and tied together onto a CTN (Cord Technical Nakasai) rearing system, where they remained until their transfer to the grafting sites (Cabral et al., 1985). This rearing method involves drilling a small hole through the base of the shell in the dorso-posterior region, a process that does not affect the living tissues. The CTN were protected using plastic mesh to prevent predation in the lagoon. After 10 or more months of culture, the oysters were randomly transferred to two pearl farm production sites in Arutua atoll (ARX: 15°10'S, 146°49' W, Tuamotu Archipelago, French Polynesia) and Mangareva island (Fig. 3). Two months after transfer, oysters aging approximately 26–27 months (March 2016) and measuring at least 10 (for Ahe and Takapoto) and 8 cm (for Mangareva origin) in dorso-ventral measurement were taken from the rearing station, detached and stored ready to be used in the grafting procedure. Colourful donors were selected from the three geographic origins following a two-step procedure (Ky et al., 2017a). First, the grafted would choose a healthy pearl oyster based on the shell size and appearance (round shape suggesting a regular growth), the muscle resistance when opening the shells by using a speculum to open the valves, and then the appearance and colour of the visceral mass and gills (shiny appearance). Second, each oyster would be checked for its inner shell colour phenotype of the set of healthy pearl oysters. A dentist's mirror was inserted into the open oyster to be able to see the inner shell colouration, particularly the contact area (band colour) with the mantle at the edge of the shell. The recipient oysters used corresponded to Ahe and Mangareva origins in Arutua and Mangareva culture sites, respectively (Fig. 3).

2.2. Experimental graft design

In the Arutua culture site (Pommier Pearl farm), grafts (April 2015) were made using 38 donors from Ahe ($N = 929$ grafts), 52 from Takapoto ($N = 1288$ grafts) and 44 from Mangareva ($N = 880$ grafts)

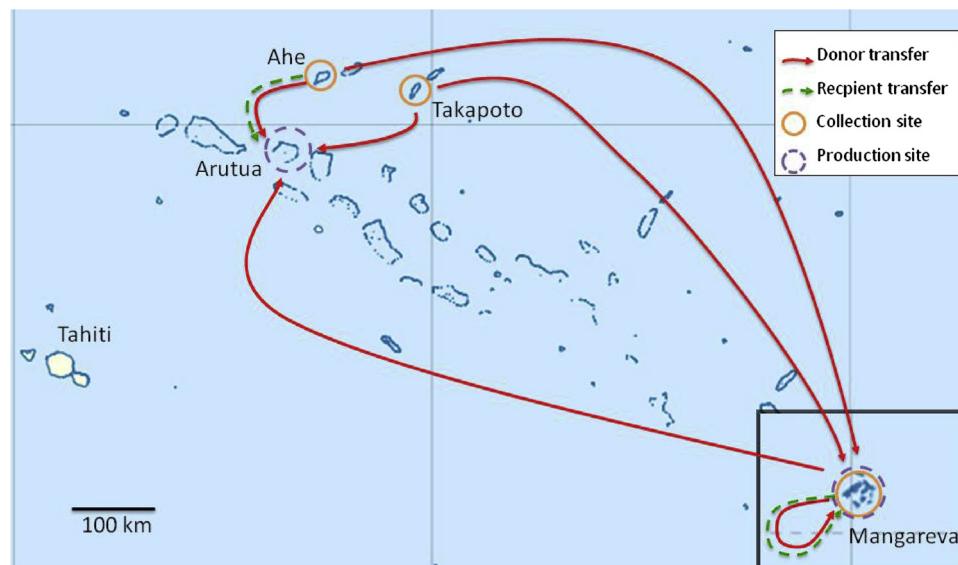


Fig. 3. Collection and production sites of the experimental design. The donor oysters of *P. margaritifera* were collected in Ahe, Takapoto and Mangareva lagoons, and transferred to the production sites of Arutua and Mangareva. Recipient oysters provided from Ahe for the Arutua culture site and from Mangareva for Mangareva culture site.

Table 1

Experimental grafts from *Pinctada margaritifera* performed in the lagoons of Arutua atoll (ARX) and Mangareva island (GMR), with donors originating from Ahe atoll (AHE), Takapoto atoll (TKP) and Mangareva (GMR). Graft characteristics are shown: number of donors selected, number of graft operations, rates and number of nuclei retained by the recipients, and cultured pearls scored respectively at 45 days post grafting and 20 months of culture. Values that significantly different ($p < 0.05$) among the donor origins within each culture site are indicated by the letters a and b.

Culture site	ARX			GMR		
Donor origins	AHE	TKP	GMR	AHE	TKP	GMR
Donor number	38	52	44	39	37	40
Graft number	929	1288	880	1160	1140	800
Retention rate (%) (number)	81.6 ^{ab} (758)	79.9 ^b (1029)	85.5 ^a (752)	85.8 ^b (995)	91.8 ^a (1047)	83.8 ^b (670)
Harvested pearl rate (%) (number)	52.5 (488)	61.8 (796)	61.4 (540)	84.1 (975)	69.8 (796)	74.5 (596)

(Table 1). Grafts were performed using 2.4 BU size nuclei (7.30 mm diameter, 0.59 g weight - Nucleus Bio, Hyakusyo Co., Japan), which consist of nacreous layers with thickness and hardness offering a specific gravity and thermal conductivity (Gervis and Sims, 1992). At 45 days post graft operation, recipient oysters were checked for nucleus retention, nucleus rejection and oyster mortality rate estimation as described in Ky et al. (2014). After this check and removal of the net retention bags, recipient oysters that had retained their nuclei (no bead detected in the bag) were drilled and randomly fixed to panel nets (in a panel net, oysters were attached to a plastic mesh with a monofilament fishing line). Each panel net was labelled according to the corresponding donor oyster (for traceability of donor and recipient). Pearl oysters were regularly cleaned (3 times) over the 20 months before the pearls were harvested and graded (January 2018).

In the Mangareva culture site (Regahiga pearl farm), all grafts were performed by the same expert technician who did this in the Arutua pearl farm. The number of donors and grafts were as followed: 39 donors from Ahe ($N = 1160$ grafts), 37 from Takapoto ($N = 1140$ grafts) and 40 from Mangareva ($N = 800$ grafts). Grafts were performed using a 1.8 BU size (5.45 mm diameter, 0.26 g weight - Nucleus Bio, Hyakusyo Co., Japan). All culture of grafted pearl oysters was done in panel nets as in the Arutua culture site, with the same washing frequency. The harvest took place in January 2017, 20 months after the graft.

2.3. Measurement of cultured pearl quality traits

At harvest, the cultured pearls were placed into a compartmented box that allowed traceability between sampled pearls and the corresponding oysters. Some *keshi* (small irregular shaped nacreous but non-nucleated pearls that form during the culture period after nuclei have been rejected) were also harvested, but not graded. Cultured pearls were then cleaned by ultrasonication in soapy water (hand washing) with a LEO 801 laboratory cleaner (2 L capacity, 80 W, 46 kHz) according to Ky et al. (2013). Cultured pearl quality traits: shape (13 categories), colour (dark green, light dark: medium pigmentation and light) and grade (A-C, D+, D, D1, D2 and Rebut) were evaluated visually (no magnification devices such as a jeweller's loupe were used) by a professional pearl quality evaluator at GIE Poe O Rikitea (Ky et al., 2016a). For the analyses on pearl shape, the 13 categories defined and sorted by the GIE (see Ky et al., 2016a) were grouped into four main shape categories: round (semi round SR, round near round RDNR and near semi round NSR), circle (circle short CRS and circle long CRL), baroque (semi baroque short SBQS, semi baroque long SBQL, baroque short BQS and baroque long BQL) and other shapes (oval OV, button BU, drop DP and top drop TD) (Table 2). Pearl size was assessed by nacre weight and thickness. These two components were measured as

described in Ky et al. (2013). As the nucleus size used for the graft was not the same between Arutua and Mangareva culture sites, nacre weight deposition speed is used as the unit: nacre weight. month⁻¹.

2.4. Statistical analysis

For the three qualitative variables, quality, colour and shape, χ^2 tests were used to detect differences according to donor origin and culture site. When differences according to origin were significant, pairwise comparisons were used with Bonferroni correction to find which origins were different for the categories studied. Kruskal-Wallis tests were used with quantitative variables, with post-hoc tests using Nemenyi correction when significant differences were detected. A multiple linear regression was performed to test site and origin effects as well as the interaction between these parameters. All analyses were performed using R© version 3.2.3 software (R foundation for Statistical Computing). The significant threshold was set at $p \leq 0.05$.

3. Results

3.1. Experimental graft

Overall the grafts made in both Arutua and Mangareva culture sites, the nucleus retention rate at 45 days post-grafting was 84.7% ($N = 5251$). In the Mangareva site, the retention rate was 87.5%, which was 5.5% more than in Arutua ($p < 0.001$). Intra-culture site comparisons showed that in Mangareva, the Takapoto donor origin had a significantly higher retention rate than the other donor origins: 91.8% compared with 83.8% for Mangareva origin ($p < 0.001$) and 85.8% for Ahe origin ($p < 0.001$) (Table 1). In the Arutua culture site, the retention rate for the Mangareva origin (85.5%) was significantly different from Takapoto (79.9%), while Ahe origin (81.6%) was not significantly different from either of the other two. Table 1 also gives the number of cultured pearls harvested according to the three donor origins and two culture sites.

3.2. Variation in nacre weight deposition speed

Intra-site comparison in the Arutua culture site showed that pearls with Takapoto and Mangareva donors had significantly higher nacre weight deposition speed than those with Ahe donors: + 23.3% (0.069 ± 0.032 g. month⁻¹ for Takapoto and Mangareva origins vs. 0.056 ± 0.024 g. month⁻¹ for Ahe origin) (Fig. 4). In the Mangareva culture site, Mangareva donors showed significantly higher nacre weight deposition speed compared with the other two origins: + 39.1% (0.039 ± 0.017 g. month⁻¹ for Mangareva origin vs. 0.028 ± 0.014 g. month⁻¹ for Ahe and Takapoto origins) (Fig. 4). As the correlation between nacre weight speed and nacre thickness deposition speed was 0.85 ($p < 0.001$); the same trends were observed for the variable nacre thickness.

The interaction between culture site effect and donor origin effect was tested with a multiple linear regression using nacre weight as a proxy for pearl quality. Culture site and donor origin both had significant effects ($p < 0.001$), as did the site \times origin interaction ($p < 0.001$).

3.3. Cultured pearl colour variation

Comparison among donor origins in the Arutua culture site revealed significantly different rates of light-coloured pearls among the three donor origins ($p < 0.001$): Mangareva (31.8%), Ahe (13.3%) and Takapoto (18.5%) (Fig. 5a). Differences observed for the proportions of dark pearls were also significant, with Ahe (47.6%), Takapoto (41.3%) and APK (27.0%). For light dark pearls, the Ahe (27.7%) was significantly different ($p < 0.05$) from Mangareva (35.9%). For green pearls, Mangareva donors produced significantly less (5.3%) than either

Table 2

Shape of *P. margaritifera* cultured pearls from the two culture sites (ARX and GMR) and the three donor origins (AHE, TKP and GMR). Data are expressed in percentages, with frequencies (N). Nomenclature of the 13 shape categories is given in the Materials and Methods section.

Culture site		ARX			GMR		
	Donor origins	AHE	TKP	GMR	AHE	TKP	GMR
Roundish	NRS	13.93 (68)	13.19 (105)	10.74 (58)	10.67 (104)	9.68 (77)	13.93 (83)
	SR	18.03 (88)	14.58 (116)	21.11 (114)	4.51 (44)	9.80 (78)	16.27 (97)
	RDNR	1.64 (8)	6.53 (52)	3.52 (19)	0.41 (4)	1.01 (8)	2.85 (17)
	Total	33.60 (164)	34.30 (273)	35.37 (191)	15.59 (152)	20.49 (163)	33.05 (197)
Circles	CRS	21.31 (104)	25.63 (204)	23.34 (126)	17.64 (172)	19.60 (156)	10.74 (64)
	CRL	17.42 (85)	14.95 (119)	21.30 (115)	25.44 (248)	23.12 (184)	20.13 (120)
	Total	38.73 (189)	40.58 (323)	44.64 (241)	43.08 (420)	42.72 (340)	30.87 (184)
Baroque like	SBQS	6.35 (31)	6.41 (51)	5.74 (31)	18.67 (182)	18.34 (146)	17.78 (106)
	SBQL	5.94 (29)	5.15 (41)	2.78 (15)	6.26 (61)	8.79 (70)	3.52 (21)
	BQS	4.71 (23)	3.01 (24)	2.22 (12)	7.49 (73)	1.76 (14)	1.00 (6)
	BQL	1.84 (9)	3.52 (28)	2.41 (13)	5.64 (55)	2.26 (18)	1.34 (8)
	Total	18.84 (92)	18.09 (144)	13.15 (71)	38.06 (371)	31.15 (248)	23.66 (141)
Others	OV	4.51 (22)	3.39 (27)	1.30 (7)	1.95 (19)	3.64 (29)	4.86 (29)
	BU	0.20 (1)	0.13 (1)	0.93 (5)	0.31 (3)	0.63 (5)	2.85 (17)
	TD	2.01 (9)	1.88 (15)	2.59 (14)	1.03 (10)	0.38 (3)	2.18 (13)
	DP	2.25 (11)	1.63 (13)	2.04 (11)	0 (0)	1.01 (8)	2.53 (15)
	Total	8.97 (43)	7.03 (56)	6.86 (37)	3.29 (32)	5.65 (45)	12.42 (74)

Ahe (11.4%) or Takapoto (9.4%) donors ($p < 0.001$ and $p = 0.01$, respectively).

Within the Mangareva culture site, the lowest rate of light-coloured pearls was observed with donors from Takapoto (21.9%), compared with both Ahe (29.4%; $p = 0.001$) and Mangareva (30.4%; $p = 0.001$) (Fig. 5a). By contrast, donors from Ahe (62.9%) and Takapoto (66.7%) produced darker pearls compared with Mangareva donors (37%) ($p < 0.001$). Mangareva (24.7%) donors produced higher proportions of green pearls in comparison to Ahe (5.8%) and Takapoto (5.3%) ($p < 0.001$). For the medium darkness level (light dark category), Ahe donors showed the lowest rate, with 1.8% in comparison to Takapoto (6.2%; $p < 0.001$) and Mangareva (7.9%; $p < 0.001$).

3.4. Cultured pearl grade variation

Within the Arutua culture site, rates of the six cultured pearl grades

were very similar, with few differences between the three origins (Fig. 5b). No significant differences were observed between Ahe and Takapoto donor origins. The Mangareva origin (24.3%) was significantly different ($p < 0.01$) from Takapoto (17.9%) for the D2 grade category. Mangareva origin also showed a significantly smaller Rebut category (5.5%), in comparison with Ahe (10.5%; $p < 0.001$) and Takapoto (10.6%; $p < 0.001$).

At the Mangareva culture site, more differences were observed among the three origins, with a tendency for better grades with Mangareva donors, followed by Takapoto and then Ahe (Fig. 5b). A significantly higher rate of A–C grade pearls was found with Mangareva donors (38.6%), in comparison to Ahe and Takapoto (average rate of 28.7%). In addition, the Rebut pearl category was also significantly lower for Mangareva donors (3.7%) than for Ahe (14.7%) and Takapoto (9.4%). Mangareva donors also led to a higher rate of the D⁺ pearl grade (9.9%), than Takapoto (4.2%) or Ahe (1.4%). By contrast, Ahe

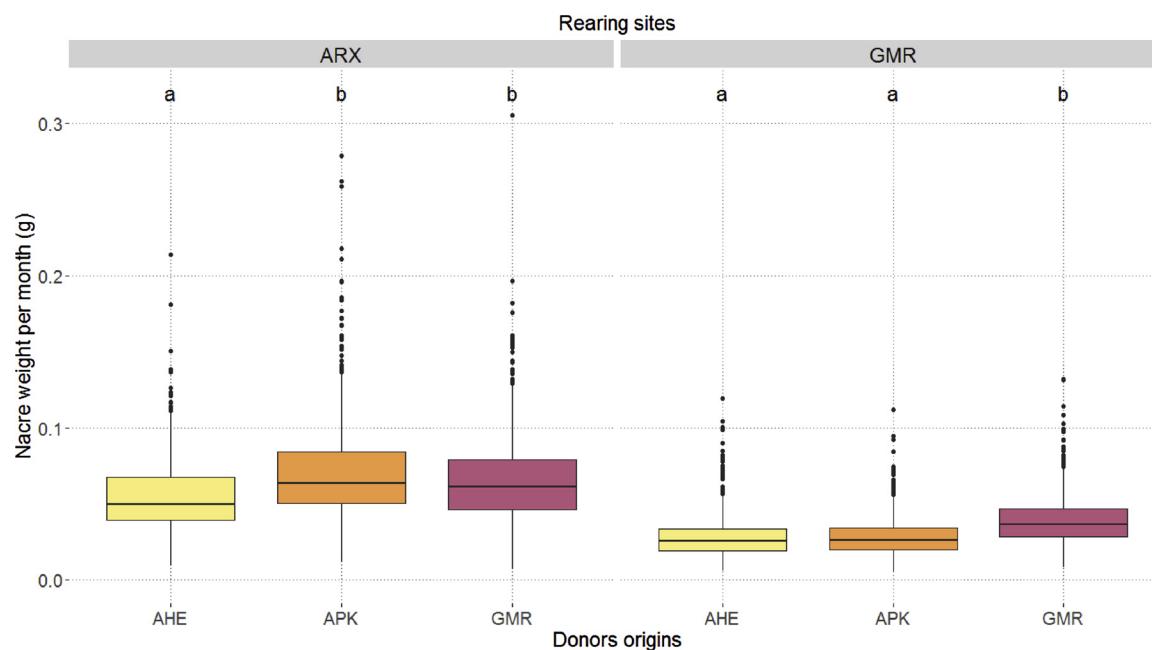


Fig. 4. Nacre weight deposition speed (nacre weight. month⁻¹) with donors of three *P. margaritifera* geographical origins (AHE, TKP and GMR) grafted in Arutua (ARX) and Mangareva (GMR) rearing sites. Each box-plot has the following six elements: 1) median (solid bar in the box-plot); 2) 25th to 75th percentile (rectangular box); 3) 1.5*interquartile range (non-outlier range of the box whiskers); 4) minimum and maximum values (extreme dots) and 5) outlier values (outside box whiskers). Letters (a and b) at the top indicate significant differences ($p < 0.05$) within rearing site between the three donor origins.

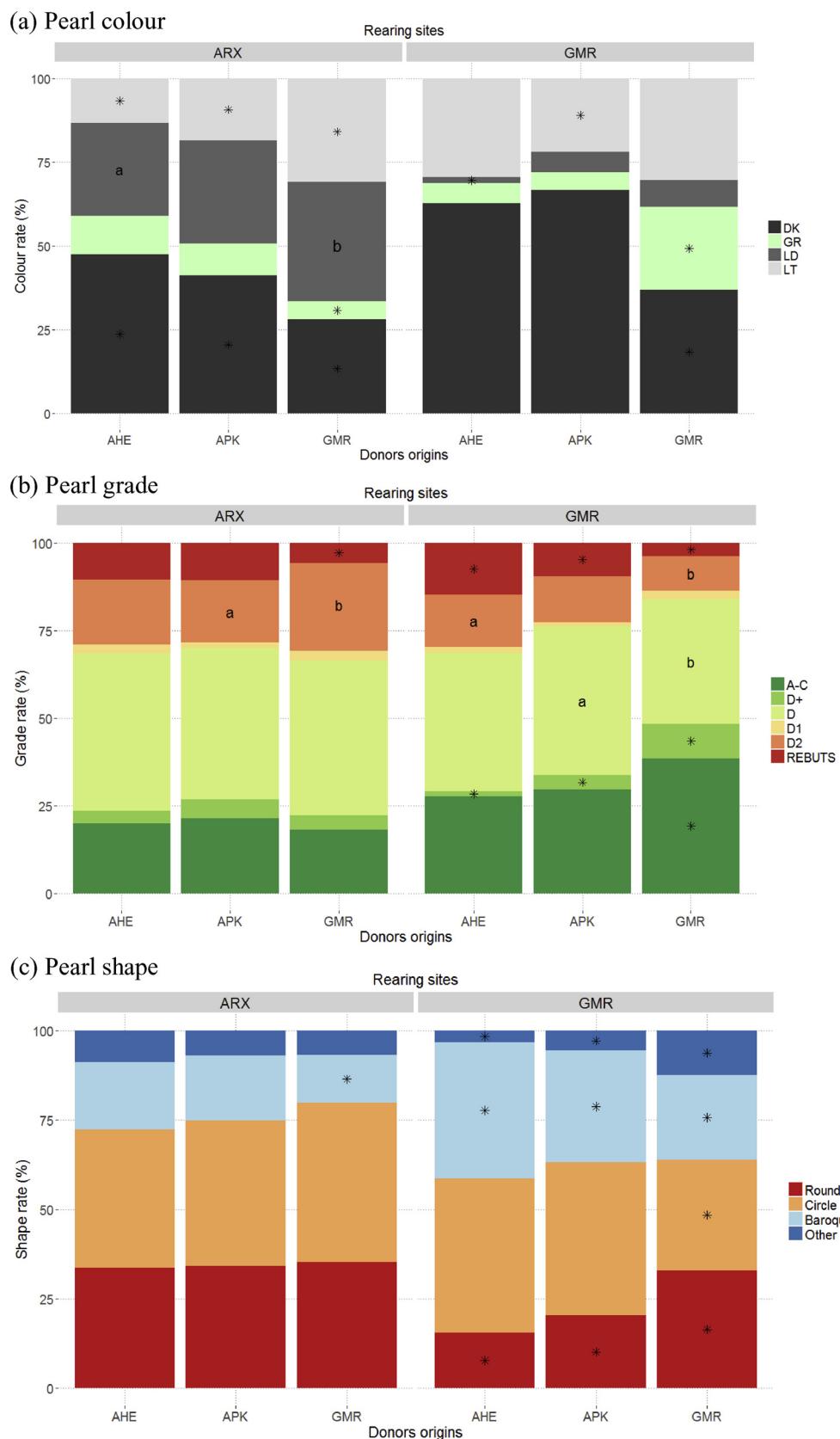


Fig. 5. Qualitative cultured pearl traits by rearing site and donor origin, assessed by the GIE Poe O Rikitea, following categories of: (a) colour (DK: Dark, GM: Green, LD: Light Dark [medium darkness], LT: Light), (b) grade and (c) shape. Asterisks (*) indicate a significant ($p < 0.05$) difference among donor origins for a trait category within the same rearing site. Letters (a and b) indicate two significantly different origins ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

donors showed the highest rate of the D2 grade (15.0%), which was significantly different ($p < 0.01$) from Mangareva donors (9.9%).

3.5. Cultured pearl shape variation

Within the Arutua culture site, shape variations were similar among donors of the three origins, with on average 34.4% round pearls, 34.3% circle pearls and 7.5% of other shaped pearls (Fig. 5c). The exception was the rate of baroque pearls (13.3%) from Mangareva donors, which was significantly lower than for the two other origins (average rate of 18.4%; $p < 0.05$).

For the Mangareva culture site, significant differences were found among all donor origins for all shape categories, except for circled pearls, for which Ahe and Takapoto origins displayed a similar rate (42.9% on average) that was significantly higher than for the Mangareva origin.

(30.9%). Proportions of round pearls were higher for Mangareva donors (33.1%) compared with Ahe (15.6%; $p < 0.001$) and Takapoto (20.5%; $p < 0.001$). The difference between Ahe and Takapoto donors was also significant ($p < 0.001$). For baroque-shaped pearls, Ahe origin (38.1%) showed a higher rate than Takapoto (31.2%) or Mangareva (23.7%). The highest rate of pearls in the other shape category was obtained with donors from Mangareva (12.4%) while Takapoto (5.7%) and Ahe (3.3%) lower proportions.

4. Discussion

Cultured pearl quality trait variations are known to be influenced by many factors, which could introduce bias in experimental grafts if they are not kept as homogeneous as possible, especially when making controlled comparisons. In the present study, donor oysters of the same age from three geographic origins were tested in two commercial culture sites, with the same pool of recipient oysters, which were also the same age. Indeed, pearl oyster age has been shown to be an important determining factor for good pearl production (Ky et al., 2017c), with donors aged between 12 and 18 months preferred. Pearl oysters of this age have a high potential for biomimetication and nacre deposition and are thus more likely to produce larger and higher quality cultured pearls than older donors (Blay et al., 2018b). In addition, culture methods were kept the same between the culture sites, as this is known to affect pearl grade and shape (Kishore and Southgate, 2016). External factors such as grafter skill and grafting season have also been shown to affect pearl shape, which is why the grafts were performed by the same technician to remove this source of variation (Ky et al., 2016b). These experimental standardisations made it possible to compare the effects of donor origin within a common rearing location and also to compare qualitative traits between culture sites.

Nacre weight deposition speed was greater in the AXR culture site (Tuamotu archipelago), than Mangareva (Gambier archipelago). This can mainly be explained by the contrasting temperature regimes of these two sites. Water temperature is a key parameter for bivalve shell growth (Nielsen, 1988; Laing, 2000) and higher temperatures have been observed to significantly increase pearl deposition rate and the number and thickness of nacre tablets deposited per day in both *P. margaritifera* (Latchere et al., 2018) and *P. fucata* (Muhammad et al., 2017). In terms of water temperature, the Gambier archipelago is characterised by contrasting seasons, with a large temperature range (22.3 °C–29.8 °C in 2017) due to its southern latitude, whereas North Tuamotu is less variable (25.7 °C–30.5 °C in 2017). Indeed, water temperature was already known to drive most growth and expression of genes encoding proteins implicated in the biomimetication process in *P. margaritifera* (Joubert et al., 2014). Inter-archipelago scale pearl variation had already been detected in a previous study (Ky et al., 2016a, 2016b), in which Tuamotu sites showed the higher values for pearl weight and size than Society and Gambier locations. This result also agrees with previous studies showing that cultured pearl size and

biometric parameters related to recipient oyster shell growth were higher for warmer sites with low seasonal water temperature variation relative to southern latitude sites (Le Pabic et al., 2016). Within each culture site, the present study shows evidence of a donor origin effect on growth of pearl and indicates the most appropriate donor-recipient combinations in terms of origins. Donor effect is already known at individual (Tayale et al., 2012) and family (Ky et al., 2013) scales. In addition, in a recent two-site experimental design, donor effect was found to be responsible for up to 20% of nacre weight and thickness determination, and donors showed significant sensitivity to the growing environment (Ky et al., 2018a).

For colour expression, each culture site had its specificity: a high proportion of dark and green pearls were obtained in Mangareva (Gambier archipelago), and light-coloured pearls in AXR (Tuamotu archipelago). Similar archipelago scale differences were also reported following a large standardised grafting experiment using the same donor phenotype across different sites (Ky et al., 2016a, 2016b). In the present study, significant effects on pearl colour of donor origins were observed within culture site when using donors selected for their inner shell colouration. These findings are reinforced by the heritability estimates for donor-derived pearl colour, which was relatively high for darkness level ($h^2 = 0.37$; 95% CI [0.30, 0.44]) (Blay et al., 2018a). In addition, pearl colour has been found to depend on individual donor oyster (Ky et al., 2017a), donor family effect (Ky et al., 2013) and has been reported to be influenced by the environmental conditions where the recipient oysters are grown (Snow et al., 2004; Alagarswami, 1987). Darkness level has already been found to be correlated with pearl nacre thickness and weight, with the palest pearls also being the smallest (Blay et al., 2014). Although the position on the donor mantle from which the graft was cut is known to influence pearl darkness level (Ky et al., 2018b), the differences observed in the present study could not be attributed to this factor because all grafts were taken (by the same grafter in both culture sites) from the middle section of the mantle, as is the usual practice in commercial grafting.

For cultured pearl grade, differences were observed at an inter-archipelago scale, with the Mangareva site systematically producing the highest rate of good quality pearls compared with the Arutua site, for the same donor origin. These differences could be due to environmental effect, and also to the contrasting temperature regime between the two culture sites. Pearl grade is based on the evaluation of surface defects and lustre. High temperature and its associated environmental factors, such as low levels of dissolved oxygen, lower salinity due to summer rainfall and toxic blooms of algae and bacteria could affect the first nacreous materials deposited on the nucleus surface and contribute to a greater number of surface defects (Cuif et al., 2011; Southgate and Lucas, 2008). Lack of lustre is often observed in the Tuamotu archipelago, where water temperature variation is lower than in Gambier. Snow et al. (2004) hypothesized that pearls with a brilliant lustre are produced by consistent and regular crystal formation in the winter season. This has been confirmed by a recent study by Latchere et al. (2018), where high water temperature stimulates both shell and nacre deposition rates. By contrast, low water temperature led to thinner nacre tablets, a lower number of tablets deposited per day and therefore affected pearl grade through better lustre and fewer defects. Mantle tissue derived from the donor has been shown to have determining effects on cultured pearl surface and grade quality traits (Tayale et al., 2012). Although this relationship is not understood in detail, *P. maxima* donor mantle tissue, was seen to produce pearls with a smoother surface (i.e. a higher grade) than *P. margaritifera* donor tissue, regardless of the receiving pearl oyster species (McGinty et al., 2010), thus underlining the role played by the donor oyster in this trait.

A donor origin effect was found for pearl shape, especially in combination with the Mangareva culture site, where more contrast between the different shape categories was observed. Shape determination is known to be mostly driven by recipient oysters and their interactions with the environment. Indeed, Blay et al. (2018a) showed

that pearl shape and presence/ absence of circle(s) showed low heritability values attributable to the donor ($h^2 = 0.02$; 95% CI [0.00, 0.06] and $h^2 = 0.05$; 95% CI [0.01, 0.10], respectively). Shape category differences between site could not be explained by cultural practices (panel net rearing system, washing frequencies, season of graft and harvest), because they were standardised in both sites in the present study. By contrast, other factors may play a key role in pearl shape differences among culture sites, especially those impacting the recipient oysters, which had different origins in the present study. Kishore et al. (2014b) hypothesised that secretion of an increased number of byssal threads by oysters (to anchor them to various substrates), as a response to a greater degree of water agitation, may influence resulting pearl shape. Indeed, a thick and rigid byssus root thread could, for example, physically impinge on the pearl-sac causing disruption of regular nacre deposition.

5. Conclusions

With 26 culture sites supplied from 5 main collection sites, the French Polynesian pearl industry is dependent on oyster transfers (at an inter-atoll, inter-island or even inter-archipelago scale). The consequence of these transfer flows creates combinations of oysters from different geographic origins. By standardising grafting procedures and animal age, this study revealed evidence of favourable and unfavourable combinations of donor and rearing site on the pearl quality trait determination. This opens the way for deliberate selection of the most appropriate origin/ rearing location combinations to maximize gain in the production process. These results will be helpful for the French Polynesian pearl industry. A wise strategy to increase pearl quality could be to rear pearl oysters in different locations at different stages of their culture: first in Arutua to increase nacre deposition rate and thus pearl size; then, in a second step, in Mangareva to enhance colour and grade. Adoption of such new culture management strategies to increase pearl quality would require investment to switch from a mono-site pearl culture system on a single farm (1 producer in 1 site) to a multi-site system (1 producer in multiple sites) but would represent a step towards modernising the pearl industry in French Polynesia.

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References

- Alagarswami, K., 1987. Cultured Pearls-Production and Quality. Marine Fisheries Research Institute (Eds.), Pearl Culture, Cochin, pp. 105–113.
- Blay, C., Sham Koua, M., Vonau, V., Tetumu, R., Cabral, P., Ky, C.-L., 2014. Influence of nacre deposition rate on cultured pearl grade and colour in the black-lipped pearl oyster *Pinctada margaritifera* using farmed donor families. *Aqu. Inter.* 22 (2), 937–953.
- Blay, C., Planes, S., Ky, C.-L., 2017. Donor and recipient contribution to phenotypic traits and the expression of biomineralisation genes in the pearl oyster model *Pinctada margaritifera*. *Sci. Rep.* 7 (1), 1–12 2696.
- Blay, C., Planes, S., Ky, C.-L., 2018a. Crossing phenotype heritability and candidate gene expression in grafted black-lipped pearl oyster *Pinctada margaritifera*, an animal chimera. *J. Heredity.* <https://doi.org/10.1093/jhered/esy015>, in press.
- Blay, C., Planes, S., Ky, C.-L., 2018b. Optimal age of the donor graft tissue in relation to cultured pearl phenotypes in the mollusc, *Pinctada margaritifera*. *PLoS One.* <https://doi.org/10.1371/journal.pone.0198505>.
- Cabral, O., Mizuno, K., Tuaru, A., 1985. In: Delesalle, B., Galzin, R., Salvat, B., La Croix, C., Wolf, A.E., Thiebaut, N., Poli, G. (Eds.), Preliminary Data on Spat Collection of Mother of Pearl (*Pinctada margaritifera*) in French Polynesia. Proc. 5th. Int. Coral Reef Congress Vol. 5 International Association for Biological Oceanography, Tahiti, pp. 177–182.
- Cuif, J.P., Dauphin, Y., Howard, L., Nouet, J., Rouzière, S., Salomé, M., 2011. Is the pearl layer a reversed shell? A re-examination of the theory of pearl formation through physical characterizations of pearl and shell development stages in *Pinctada margaritifera*. *Aquat. Liv. Res.* 23, 277–284.
- Cunha, R.L., Blanc, F., Bonhomme, F., Arnaud-Haond, S., 2010. Evolutionary patterns in pearl oysters of the Genus *Pinctada* (Bivalvia: pteriidae). *Mar. Biotechnol.* 13 (2), 181–192.
- Gervis, M.H., Sims, N., 1992. The biology and culture of pearl oysters (Bivalvia: pteriidae). Overseas development administration and international center for living aquatic resources management. Manila 1992, 3–38.
- Joubert, C., Linard, C., Le Moullac, G., Soyez, C., Saulnier, D., Teaniniuraitemoana, V., Ky, C.L., Gueguen, Y., 2014. Temperature and food influence shell growth and mantle gene expression of shell matrix protein in the Pearl Oyster *Pinctada margaritifera*. *PLoS One* 9 (8), e103944. <https://doi.org/10.1371/journal.pone.0103944>.
- Kishore, P., Southgate, P.C., 2014a. A detailed description of pearl-sac development in the black-lip pearl oyster, *Pinctada margaritifera* (Linnaeus 1758). *Aquac. Res.* <https://doi.org/10.1111/are.12674>.
- Kishore, P., Southgate, P.C., 2016. The effect of different culture methods on the quality of round pearls produced by the black-lip pearl oyster *Pinctada margaritifera* (Linnaeus, 1758). *Aquaculture* 451, 65–71.
- Kishore, P., Hunter, J., Zeng, C., Southgate, P.C., 2014b. The effects of different culture apparatuses and current velocities on byssus production by the black-lip pearl oyster, *Pinctada margaritifera*. *Aquaculture* 434, 74–77.
- Ky, C.L., Blay, C., Sham-Koua, M., Vanaa, V., Lo, C., Cabral, P., 2013. Family effect on cultured pearl quality in black-lipped pearl oyster *Pinctada margaritifera* and insights for genetic improvement. *Aquat. Liv. Res.* 26, 133–145.
- Ky, C.-L., Molinari, N., Moe, E., Pommier, S., 2014. Impact of season and grafter skill on nucleus retention and pearl oyster mortality rate in *Pinctada margaritifera* aquaculture. *Aqua. Inter.* 22 (5), 1689–1701.
- Ky, C.-L., Okura, R., Nakasai, S., Devaux, D., 2016a. Quality trait signature at archipelago scale of the cultured pearls produced by the black-lipped pearl oyster (*Pinctada margaritifera* var. *cumingi*) in French Polynesia. *J. Shellfish Res.* 35 (4), 827–835.
- Ky, C.L., Nakasai, S., Molinari, N., Devaux, D., 2016b. Influence of grafter skill and season on cultured pearl shape, circles and rejects in *Pinctada margaritifera* aquaculture in Mangareva lagoon. *Aquaculture* 435, 361–370.
- Ky, C.L., Lo, C., Planes, S., 2017a. Mono- and polychromatic inner shell phenotype diversity in *Pinctada margaritifera* donor pearl oysters and its relation with cultured pearl colour. *Aquaculture* 468, 199–205.
- Ky, C.L., Le Pabic, L., Sham Koua, M., Molinari, N., Nakasai, S., Devaux, D., 2017b. Is pearl colour produced from *Pinctada margaritifera* predictable through shell phenotypes and rearing environments selections? *Aqua. Res.* 48 (3), 1041–1057.
- Ky, C.L., Demmer, J., Blay, C., Lo, C., 2017c. Age-dependence of cultured pearl grade and colour in the black-lipped pearl oyster *Pinctada margaritifera*. *Aquat. Res.* 48 (3), 955–968.
- Ky, C.L., Broustal, F., Sham Koua, M., Quillien, V., Beliaeoff, B., 2018a. Donor effect on cultured pearl nacre development and shell matrix gene expression in *Pinctada margaritifera* reared in different field sites. *Aquat. Res.* 49 (5), 1934–1943.
- Ky, C.-L., Nakasai, S., Parrad, S., Broustal, F., Devaux, D., Louis, P., 2018b. Variation in cultured pearl quality traits in relation to position of saibo cutting on the mantle of black-lipped pearl oyster *Pinctada margaritifera*. *Aquaculture* 493, 85–92.
- Laing, I., 2000. Effect of temperature and ration on growth and condition of king scallop (*Pecten maximus*) spat. *Aquaculture* 183, 325–334.
- Landman, N.H., Mikkelsen, P.M., Bieler, R., Bronson, B., 2001. Pearls, a Natural History. American Museum of Natural History and Harry N. Abrams, Inc., New York, pp. 32–54.
- Latchere, O., Mehn, V., Gaertner-Mazouni, N., Le Moullac, G., Fievet, J., Belliard, C., Cabral, P., Saulnier, D., 2018. Influence of water temperature and food on the last stages of cultured pearl mineralization from the black-lip pearl oyster *Pinctada margaritifera*. *PLoS One.* <https://doi.org/10.1371/journal.pone.0193863>.
- Le Pabic, L., Parrad, P., Sham Koua, M., Nakasai, S., Saulnier, D., Devaux, D., Ky, C.L., 2016. Culture site dependence on pearl size realization in *Pinctada margaritifera* in relation to recipient oyster growth and mantle graft biomimetic gene expression using the same donor phenotype. *Estuarine Coastal Shelf Sci.* 182, 294–303.
- McGinty, E.L., Evans, B.S., Taylor, J.U.U., Jerry, D.R., 2010. Xenografts and pearl production in two pearl oyster species, *P. Maxima* and *P. margaritifera*: effect on pearl quality and a key to understanding genetic contribution. *Aquaculture* 302, 175–181.
- Muhammad, G., Atsumi, T., Sunardi Komaru, A., 2017. Nacre growth and thickness of Akoya pearls from Japanese and Hybrid *Pinctada fucata* in response to the aquaculture temperature condition in Ago Bay. *Japan. Aquaculture* 477, 35–42.
- Nielson, M.V., 1988. The effect of temperature on the shell length growth of juvenile *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 123, 227–234.
- Snow, M., Pring, A., Self, P., Losic, D., Shapter, J., 2004. The origin of the colour of pearls in iridescence from nano-composite structures of the nacre. *Am. Mineral.* 89, 1353–1358.
- Southgate, P.C., Lucas, J.S., 2008. The Pearl Oyster Elsevier, vol. 2008 Oxford 575 pp.
- Tayale, A., Gueguen, Y., Treguier, C., Le Grand, J., Cochennec-Laureau, N., Montagnani, C., Ky, C.-L., 2012. Evidence of donor effect on cultured pearl quality from a duplicated grafting experiment on *Pinctada margaritifera* using wild donors. *Aquat. Living Resour.* 25 (3), 269–280.
- Taylor, J.J., Strack, E., 2008. Pearl production. In: Southgate, P.C., Lucas, J.S. (Eds.), The Pearl Oyster. Elsevier, Amsterdam, pp. 273–302.
- Wada, K.T., Jerry, D.R., 2008. Population genetics and stock improvement. In: Southgate, P.C., Lucas, J. (Eds.), The Pearl Oyster. Elsevier, Oxford, pp. 437–471.
- Webster, R., Anderson, B.W., 1983. Gems, Their Sources, Descriptions and Identification, Butterworths, London, pp. 505–506.
- Yukihira, H., Lucas, J.S., Klumpp, D.W., 2000. Comparative effects of temperature on suspension feeding and energy budgets of the pearl oysters *Pinctada margaritifera* and *P. Maxima*. *Mar. Ecol. Prog. Ser.* 195, 179–188.