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

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18

1 **Abstract**

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

22 **Keywords**

23 Pearl oyster; *Pinctada margaritifera*; Graft combinations; Pearl quality traits; Environment

24

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, 134,16 tons of cultured pearls were exported around the world from French Polynesia, mainly to China (62%) and Japan (32%) (Figure 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 hectares. Expansion of this industry is limited by the means of transport between collection and production sites. Mangareva island (141 producers) and Arutua atoll (72 producers) are the top two production sites and represented 24.6% and 13.3%

1 of the total area, respectively, in 2017 (Figure 2, source: Direction des Ressources Marines et
2 Minières). Thus, many oysters are transferred from collection sites to the numerous
3 production sites.

4 Production of a cultured pearl with *P. margaritifera* requires two animals: a small
5 piece of mantle tissue (a graft) is dissected from a donor oyster (consequently sacrificed) and
6 inserted, together with a round bead of nacre (a nucleus), into the gonad of a recipient oyster
7 (Gervis and Sims, 1992; Taylor and Strack, 2008). Over time, the tissue from the donor grows
8 around the bead to produce a pearl sac, which secretes successive nacreous layers onto the
9 bead to produce a cultured pearl (Webster and Anderson 1983; Landman et al., 2001; Kishore
10 and Southgate, 2014a). Approximately 18 months after implantation, the pearl is harvested.
11 Before sale, it is assessed for its quality. Five main factors are used to define pearl quality:
12 size, shape, colour, lustre and surface quality. On the basis of these five factors, Tahitian
13 cultured pearls were graded following the official classification, which uses an A, B, C, D and
14 *Rebut* nomenclature (Tayale et al., 2012). Schematically, it has been shown that it is the donor
15 oyster (rather than the recipient) that has the main influence over pearl quality traits,
16 particularly colour and lustre (Ky et al., 2013, 2017a and 2017b; Blay et al., 2017). By
17 contrast, pearl size is mainly controlled by the recipient oyster and its biometric parameters
18 (Le Pabic et al., 2016; Blay et al., 2017). Recently, donor-related genetic parameter estimates
19 clearly demonstrated heritability for nacre weight and thickness, darkness and colour of
20 pigmentation, surface defects and overall grade, which signifies a genetic basis for these traits
21 in the donor oyster (Blay et al., 2018a). The interactions between donor and recipient in
22 relation to the environment are highly complex. Specific variations in pearl quality traits
23 among culture sites have already been observed, with distinctive "signatures" of certain sites,
24 revealed by using a same donor phenotype grafted over six grow-out locations covering the
25 three archipelagos (Ky et al., 2016a). However, differing environmental sensitivity between

1 donors has been revealed, with some donors responsible for 20 to 36% of nacre weight
2 determination (Ky et al., 2018a). Producing high quality pearls remains one of the main
3 challenges for the future development of *P. margaritifera* aquaculture.

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

17

1 2. Materials and methods

2 2.1. Experimental animal origins

3 Wild *P. margaritifera* were collected as juveniles (spat stage) in the lagoons of Ahe
4 atoll (AHE: 14°29'S, 148°20' W, Tuamotu archipelago, French Polynesia), Takapoto atoll
5 (TKP: 14°32'S, 145°14' W, Tuamotu archipelago, French Polynesia) and Mangareva island
6 (GMR: 23°07'S, 133°58' W, Gambier archipelago, French Polynesia) (Figure 3). Passive
7 techniques were employed for catching the spat, using commercial collectors made from
8 plastic materials, to which planktonic mollusc larvae become attached fifteen to twenty days
9 after their release. During the beginning of the main reproduction period (November to
10 December in 2013), collectors were simultaneously deployed in the lagoons of Ahe, Takapoto
11 and Mangareva. This provided a pool of pearl oysters of approximately the same age for the
12 experimental graft. After 15 months (March 2015) of subsurface rearing (3–5 m below the
13 surface) in the different collection sites, the juveniles (shell dorso-ventral measurements of
14 5.4 ± 1.8 cm) were removed from the spat collectors, pierced and tied together onto a CTN
15 (Cord Technical Nakasai) rearing system, where they remained until their transfer to the
16 grafting sites (Cabral *et al.*, 1985). This rearing method involves drilling a small hole through
17 the base of the shell in the dorso-posterior region, a process that does not affect the living
18 tissues. The CTN were protected using plastic mesh to prevent predation in the lagoon. After
19 10 or more months of culture, the oysters were randomly transferred to two pearl farm
20 production sites in Arutua atoll (ARX: 15°10'S, 146°49' W, Tuamotu Archipelago, French
21 Polynesia) and Mangareva island (Figure 3). Two months after transfer, oysters aging
22 approximately 26–27 months (March 2016) and measuring at least 10 (for Ahe and Takapoto)
23 and 8 cm (for Mangareva origin) in dorso-ventral measurement were taken from the rearing
24 station, detached and stored ready to be used in the grafting procedure. Colourful donors were

1 selected from the three geographic origins following a two-step procedure (Ky et al., 2017a).
2 First, the grafter would choose a healthy pearl oyster based on the shell size and appearance
3 (round shape suggesting a regular growth), the muscle resistance when opening the shells by
4 using a speculum to open the valves, and then the appearance and colour of the visceral mass
5 and gills (shiny appearance). Second, each oyster would be checked for its inner shell colour
6 phenotype of the set of healthy pearl oysters. A dentist's mirror was inserted into the open
7 oyster to be able to see the inner shell colouration, particularly the contact area (band colour)
8 with the mantle at the edge of the shell. The recipient oysters used corresponded to **Ahe and**
9 **Mangareva** origins in **Arutua and Mangareva** culture sites, respectively (**Figure 3**).

10 **2.2. Experimental graft design**

11 In the **Arutua** culture site (Pommier Pearl farm), grafts (April 2015) were made using
12 38 donors from **Ahe** (N = 929 grafts), 52 from **Takapoto** (N = 1288 grafts) and 44 from
13 **Mangareva** (N = 880 grafts) (Table 1). Grafts were performed using 2.4 BU size nuclei (7.30
14 mm diameter, 0.59 g weight - Nucleus Bio, Hyakusyo Co., Japan), which consist of nacreous
15 layers with thickness and hardness offering a specific gravity and thermal conductivity
16 **particularly suited to pearl culture** (Gervis and Sims, 1992). At 45 days post graft operation,
17 recipient oysters were checked for nucleus retention, nucleus rejection and oyster mortality
18 rate estimation as described in Ky et al. (2014). After this check and removal of the net
19 retention bags, recipient oysters that had retained their nuclei (no bead detected in the bag)
20 were drilled and randomly fixed to panel nets (in a panel net, oysters were attached to a
21 plastic mesh with a monofilament fishing line). Each panel net was labelled according to the
22 corresponding donor oyster (for traceability of donor and recipient). Pearl oysters were
23 regularly cleaned (3 times) over the 20 months before the pearls were harvested and graded
24 (January 2018).

1 In the **Mangareva** culture site (Regahiga pearl farm), all grafts were performed by the same
2 expert technician who did this in the **Arutua** pearl farm. The number of donors and grafts were
3 as followed: 39 donors from **Ahe** (N = 1160 grafts), 37 from **Takapoto** (N = 1140 grafts) and
4 40 from **Mangareva** (N = 800 grafts). Grafts were performed using a 1.8 BU size (5.45 mm
5 diameter, 0.26 g weight - Nucleus Bio, Hyakusyo Co., Japan). All culture of grafted pearl
6 oysters was done in panel nets as in the **Arutua** culture site, with the same washing frequency.
7 The harvest took place in January 2017, 20 months after the graft.

8 **2.3. Measurement of cultured pearl quality traits**

9 At harvest, the cultured pearls were placed into a compartmented box that allowed
10 traceability between sampled pearls and the corresponding oysters. Some *keshi* (small
11 irregular shaped nacreous but non-nucleated pearls that form during the culture period after
12 nuclei have been rejected) were also harvested, but not graded. Cultured pearls were then
13 cleaned by ultrasonication in soapy water (hand washing) with a LEO 801 laboratory cleaner
14 (2L capacity, 80 W, 46 kHz) according to Ky et al. (2013). Cultured pearl quality traits: shape
15 (13 categories), colour (dark, green, light dark: medium pigmentation and light) and grade (A-
16 C, D+, D, D1, D2 and Rebut) were evaluated visually (no magnification devices such as a
17 jeweller's loupe were used) by a professional pearl quality evaluator at GIE Poe O Rikitea
18 (Ky et al., 2016a). For the analyses on pearl shape, the 13 categories defined and sorted by the
19 GIE (see Ky et al., 2016a) were grouped into four main shape categories: round (semi round
20 SR, round near round RDNR and near semi round NSR), circle (circle short CRS and circle
21 long CRL), baroque (semi baroque short SBQS, semi baroque long SBQL, baroque short
22 BQS and baroque long BQL) and other shapes (oval OV, button BU, drop DP and top drop
23 TD) (Table 2). Pearl size was assessed by nacre weight and thickness. These two components
24 were measured as described in Ky et al. (2013). As the nucleus size used for the graft was not

1 the same between Arutua and Mangareva culture sites, nacre weight deposition speed is used
2 as the unit: nacre weight. month⁻¹.

3 **2.4. Statistical analysis**

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

13

1 3. Results

2 3.1. Experimental graft

3 Overall the grafts made in both Arutua and Mangareva culture sites, the nucleus
4 retention rate at 45 days post-grafting was 84.7% (N = 5251). In the Mangareva site, the
5 retention rate was 87.5%, which was 5.5% more than in Arutua ($p < 0.001$). Intra-culture site
6 comparisons showed that in Mangareva, the Takapoto donor origin had a significantly higher
7 retention rate than the other donor origins: 91.8% compared with 83.8% for Mangareva origin
8 ($p < 0.001$) and 85.8% for Ahe origin ($p < 0.001$) (Table 1). In the Arutua culture site, the
9 retention rate for the Mangareva origin (85.5%) was significantly different from Takapoto
10 (79.9%), while Ahe origin (81.6%) was not significantly different from either of the other
11 two. Table 1 also gives the number of cultured pearls harvested according to the three donor
12 origins and two culture sites.

13 3.2. Variation in nacre weight deposition speed

14 Intra-site comparison in the Arutua culture site showed that pearls with Takapoto and
15 Mangareva donors had significantly higher nacre weight deposition speed than those with
16 Ahe donors: + 23.3 % (0.069 ± 0.032 g. month⁻¹ for Takapoto and Mangareva origins vs.
17 0.056 ± 0.024 g. month⁻¹ for Ahe origin) (Figure 4). In the Mangareva culture site, Mangareva
18 donors showed significantly higher nacre weight deposition speed compared with the other
19 two origins: + 39.1 % (0.039 ± 0.017 g. month⁻¹ for Mangareva origin vs. 0.028 ± 0.014 g.
20 month⁻¹ for Ahe and Takapoto origins) (Figure 4). As the correlation between nacre weight
21 speed and nacre thickness deposition speed was 0.85 ($p < 0.001$); the same trends were
22 observed for the variable nacre thickness.

23 The interaction between culture site effect and donor origin effect was tested with a
24 multiple linear regression using nacre weight as a proxy for pearl quality. Culture site and

1 donor origin both had significant effects ($p < 0.001$), as did the site \times origin interaction
2 ($p < 0.001$).

3 **3.3. Cultured pearl colour variation**

4 Comparison among donor origins in the **Arutua** culture site revealed significantly
5 different rates of light-coloured pearls among the three donor origins ($p < 0.001$): **Mangareva**
6 (31.8%), **Ahe** (13.3%) and **Takapoto** (18.5%) (Figure 5a). Differences observed for the
7 proportions of dark pearls were also significant, with **Ahe** (47.6%), **Takapoto** (41.3%) and
8 **APK** (27.0%). For light dark pearls, the **Ahe** (27.7%) was significantly different ($p < 0.05$)
9 from **Mangareva** (35.9%). For green pearls, **Mangareva** donors produced significantly less
10 (5.3%) than either **Ahe** (11.4%) or **Takapoto** (9.4%) donors ($p < 0.001$ and $p = 0.01$,
11 respectively).

12 Within the **Mangareva** culture site, the lowest rate of light-coloured pearls was
13 observed with donors from **Takapoto** (21.9%), compared with both **Ahe** (29.4%; $p = 0.001$)
14 and **Mangareva** (30.4%; $p = 0.001$) (Figure 5a). By contrast, donors from **Ahe** (62.9%) and
15 **Takapoto** (66.7%) produced darker pearls with higher rates of dark coloured pearls compared
16 with **Mangareva** donors (37%) ($p < 0.001$). **Mangareva** (24.7%) donors produced higher
17 proportions of green pearls in comparison to **Ahe** (5.8%) and **Takapoto** (5.3%) ($p < 0.001$).
18 For the medium darkness level (light dark category), **Ahe** donors showed the lowest rate, with
19 1.8% in comparison to **Takapoto** (6.2%; $p < 0.001$) and **Mangareva** (7.9%; $p < 0.001$).

20 **3.4. Cultured pearl grade variation**

21 Within the **Arutua** culture site, rates of the six cultured pearl grades were very similar,
22 with few differences between the three origins (Figure 5b). No significant differences were
23 observed between **Ahe** and **Takapoto** donor origins. The **Mangareva** origin (24.3%) was
24 significantly different ($p < 0.01$) from **Takapoto** (17.9%) for the D2 grade category.

1 **Mangareva** origin also showed a significantly smaller Rebut category (5.5%), in comparison
2 with **Ahe** (10.5%; $p < 0.001$) and **Takapoto** (10.6%; $p < 0.001$).

3 At the **Mangareva** culture site, more differences were observed among the three
4 origins, with a tendency for better grades with **Mangareva** donors, followed by **Takapoto** and
5 then **Ahe** (Figure 5b). A significantly higher rate of A-C grade pearls was found with
6 **Mangareva** donors (38.6 %), in comparison to **Ahe** and **Takapoto** (average rate of 28.7%). In
7 addition, the Rebut pearl category was also significantly lower for **Mangareva** donors (3.7%)
8 than for **Ahe** (14.7%) and **Takapoto** (9.4%). **Mangareva** donors also led to a higher rate of the
9 D⁺ pearl grade (9.9%), than **Takapoto** (4.2%) or **Ahe** (1.4%). By contrast, **Ahe** donors showed
10 the highest rate of the D2 grade (15.0%), which was significantly different ($p < 0.01$) from
11 **Mangareva** donors (9.9%).

12 **3.5. Cultured pearl shape variation**

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

18 For the **Mangareva** culture site, significant differences were found among all donor
19 origins for all shape categories, except for circled pearls, for which **Ahe** and **Takapoto** origins
20 displayed a similar rate (42.9% on average) that was significantly higher than for the
21 **Mangareva** origin
22 (30.9%). Proportions of round pearls were higher for **Mangareva** donors (33.1%) compared
23 with **Ahe** (15.6%; $p < 0.001$) and **Takapoto** (20.5%; $p < 0.001$). The difference between **Ahe**
24 and **Takapoto** donors was also significant ($p < 0.001$). For baroque-shaped pearls, **Ahe** origin
25 (38.1%) showed a higher rate than **Takapoto** (31.2%) or **Mangareva** (23.7%). The highest rate

- 1 of pearls in the other shape category was obtained with donors from **Mangareva** (12.4%)
- 2 while **Takapoto** (5.7%) and **Ahe** (3.3%) lower proportions.

1 4. Discussion

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

17 ~~In the process of pearl production, the grafted mantle tissue proliferates around the nucleus to~~
18 ~~form a layer of secretory tissue, which then deposits successive sheets of nacre onto the~~
19 ~~nucleus (Cochennee-Laureau et al., 2010). Effects of donor origin and their potential are thus~~
20 ~~carried into the pearl formation stage through the graft process as the graft develops to form a~~
21 ~~pearl sac.~~

22 Nacre weight deposition speed was greater in the AXR culture site (Tuamotu
23 archipelago), than Mangareva (Gambier archipelago). This can mainly be explained by the
24 contrasting temperature regimes of these two sites. Water temperature is a key parameter for
25 bivalve shell growth (Nielsen et al., 1988; Laing, 2000) and higher temperatures have been

1 observed to significantly increase pearl deposition rate and the number and thickness of nacre
2 tablets deposited per day in both *P. margaritifera* (Latchere et al., 2018) and *P. fucata*
3 (Muhammad et al., 2017). In terms of water temperature, the Gambier archipelago is
4 characterised by contrasting seasons, with a large temperature range (22.3°C to 29.8°C in
5 2017) due to its southern latitude, whereas North Tuamotu is less variable (25.7°C to 30.5°C
6 in 2017). Indeed, water temperature was already known to drive most growth and expression
7 of genes encoding proteins implicated in the biomineralisation process in *P. margaritifera*
8 (Joubert et al., 2014). Inter-archipelago scale pearl variation had already been detected in a
9 previous study (Ky et al., 2016), in which Tuamotu sites showed the higher values for pearl
10 weight and size than Society and Gambier locations. This result also agrees with previous
11 studies showing that cultured pearl size and biometric parameters related to recipient oyster
12 shell growth were higher for warmer sites with low seasonal water temperature variation
13 relative to southern latitude sites (Le Pabic et al., 2016). Within each culture site, the present
14 study shows evidence of a donor origin effect on growth of pearl and indicates the most
15 appropriate donor-recipient combinations in terms of origins. Donor effect is already known
16 at individual (Tayale et al., 2012) and family (Ky et al., 2013) scales. In addition, in a recent
17 two-site experimental design, donor effect was found to be responsible for up to 20% of nacre
18 weight and thickness determination, and donors showed significant sensitivity to the growing
19 environment (Ky et al., 2018a).

20 For colour expression, each culture site had its specificity: a high proportion of dark
21 and green pearls were obtained in Mangareva (Gambier archipelago), and light-coloured
22 pearls in AXR (Tuamotu archipelago). Similar archipelago scale differences were also
23 reported following a large standardised grafting experiment using the same donor phenotype
24 across different sites (Ky et al., 2016). In the present study, significant effects on pearl colour
25 of donor origins were observed within culture site when using donors selected randomly for

1 their inner shell colouration. These findings are reinforced by the heritability estimates for
2 donor-derived pearl colour, which was relatively high for darkness level ($h^2 = 0.37$; 95% CI
3 [0.30, 0.44]) (Blay et al., 2018a). In addition, pearl colour has been found to depend on
4 individual donor oyster (Ky et al., 2017a), donor family effect (Ky et al., 2013) and has been
5 reported to be influenced by the environmental conditions where the recipient oysters are
6 grown (Snow et al., 2004; Alagarwami 1987). Under controlled laboratory conditions,
7 however, visual colour and the darkness level were previously found not to be dependent on
8 either microalgal concentration or water temperature (Latchere et al., 2018). Darkness level
9 has already been found to be correlated with pearl nacre thickness and weight, with the palest
10 pearls also being the smallest (Blay et al., 2014). Although the position on the donor mantle
11 from which the graft was cut is known to influence pearl darkness level (Ky et al., 2018b), the
12 differences observed in the present study could not be attributed to this factor because all
13 grafts were taken (by the same grafter in both culture sites) from the middle section of the
14 mantle, as is the usual practice in commercial grafting.

15 For cultured pearl grade, differences were observed at an inter-archipelago scale, with
16 the Mangareva site systematically producing the highest rate of good quality pearls compared
17 with the Arutua site, for the same donor origin. These differences could be due to
18 environmental effect, and also to the contrasting temperature regime between the two culture
19 sites. Pearl grade is based on the evaluation of surface defects and lustre. High temperature
20 and its associated environmental factors, such as low levels of dissolved oxygen, lower
21 salinity due to summer rainfall and toxic blooms of algae and bacteria which could affect the
22 first nacreous materials deposited on the nucleus surface and contribute to a greater number of
23 surface defects (Cuif et al., 2011; Southgate and Lucas, 2008). Lack of lustre is often
24 observed in the Tuamotu archipelago, where water temperature variation is lower than in
25 Gambier. Snow et al. (2004) hypothesized that pearls with a brilliant lustre are produced by

1 consistent and regular crystal formation in the winter season. This has been confirmed by a
2 recent study **made** by Latchere et al. (2018), where high water temperature stimulates both
3 shell and **nacre** deposition rates. By contrast, low water temperature led to thinner nacre
4 tablets, a lower number of tablets deposited per day and therefore affected pearl grade through
5 better lustre and fewer defects. Mantle tissue derived from the donor has been shown to have
6 determining effects on cultured pearl surface and grade quality traits (Tayale et al., 2012).
7 Although this relationship is not understood in detail, *P. maxima* donor mantle tissue, was
8 seen to produce pearls with a smoother surface **complexation** (*i.e.* a higher grade) than *P.*
9 *margaritifera* donor tissue, regardless of the receiving pearl oyster species **into which this**
10 **tissue was grafted** (McGinty et al., 2010), thus underlining the role played by the donor oyster
11 in this trait.

12 A donor origin effect was found for pearl shape, especially in combination with the
13 **Mangareva** culture site, where more contrast between the different shape categories was
14 observed. Shape determination is known to be mostly driven by recipient oysters and their
15 interactions with the environment. Indeed, Blay et al. (2018a) showed that pearl shape and
16 presence/ absence of circle(s) showed low heritability values attributable to the donor ($h^2 =$
17 0.02 ; 95% CI [0.00, 0.06] and $h^2 = 0.05$; 95% CI [0.01, 0.10], respectively). **Shape category**
18 **differences between site could not be explained by cultural practices (panel net rearing**
19 **system, washing frequencies, season of graft and harvest), because they were standardised in**
20 **both sites in the present study.** By contrast, other **factors** may play a key role in pearl shape
21 differences among culture sites, especially those impacting the recipient oysters, which had
22 different origins in the present study. Kishore et al. (2014b) hypothesised that secretion of an
23 increased number of byssal threads by oysters (to anchor them to various substrates), as a
24 response to a greater degree of water agitation, may influence resulting pearl shape. Indeed, a

1 thick and rigid byssus root thread could, for example, physically impinge on the pearl-sac
2 causing disruption of regular nacre deposition.

3 **5. Conclusions**

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

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24 Polynesia), for their generous assistance.

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

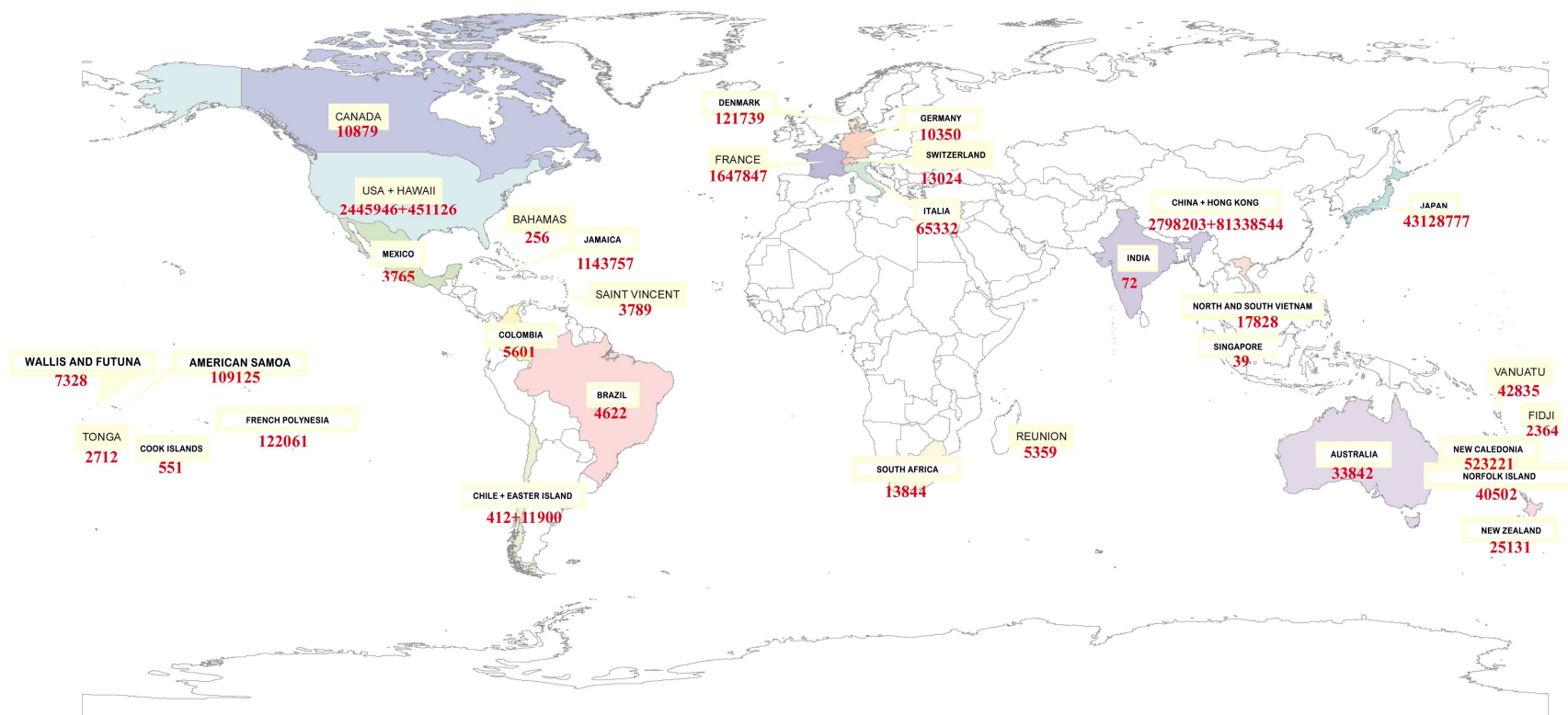


Figure 2. Collection and production sites of the pearl industry in French Polynesia. Authorized areas (Ha) and number of collecting lines are respectively represented in red and green histograms.

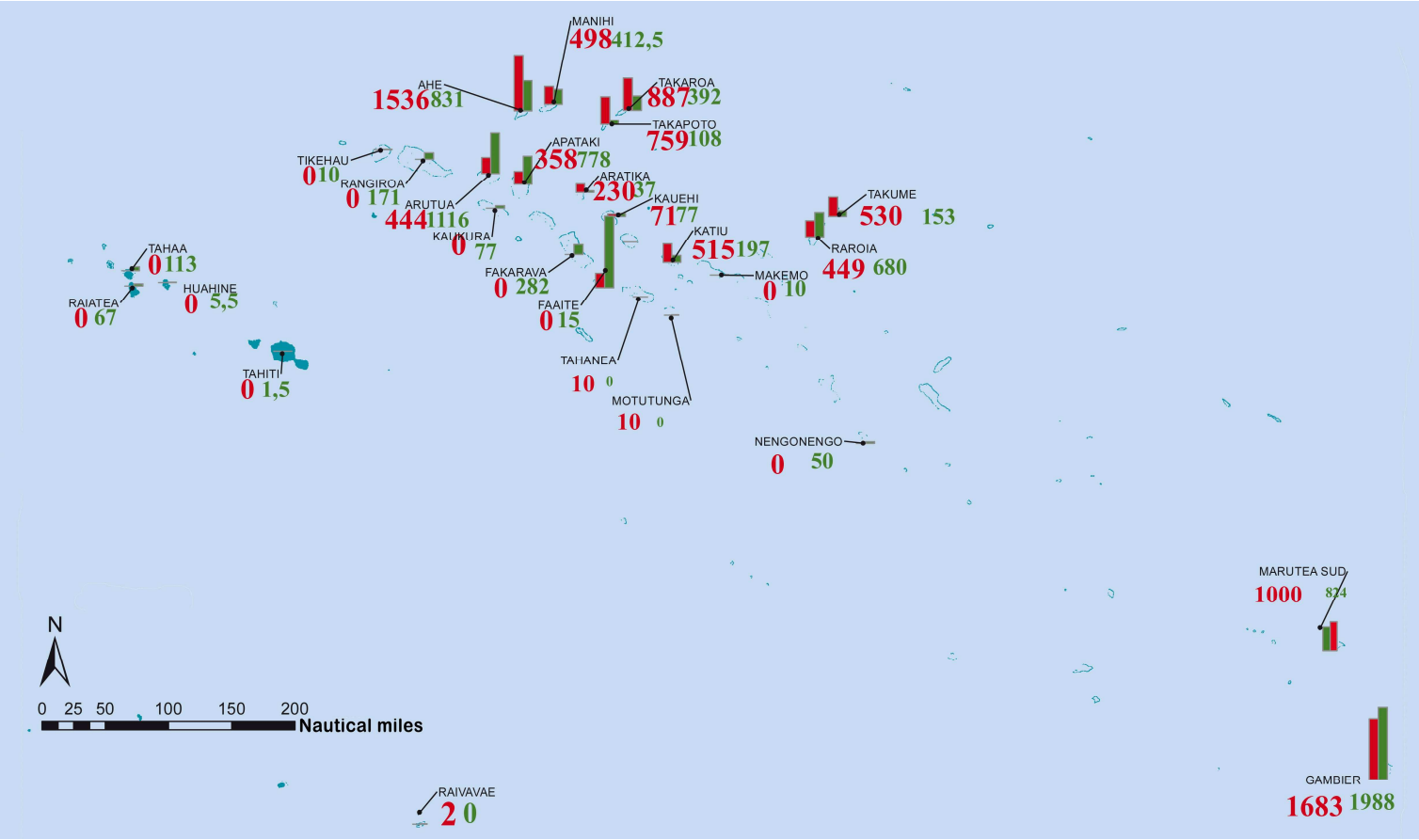


Figure 3. Collection and production sites of the experimental design. The donor oysters of *P. margaritifera* were collected in Ahe, Takapoto and Mangareva lagoons, and transferred to the production sites of Arutua and Mangareva. Recipient oysters provided from Ahe for the Arutua culture site and from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

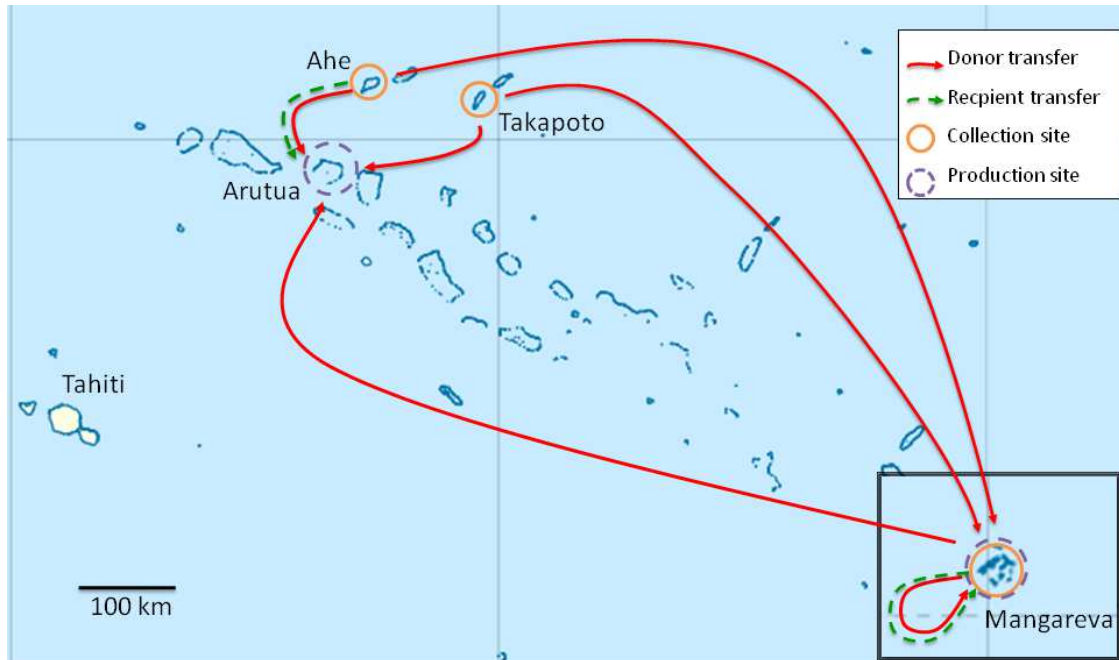
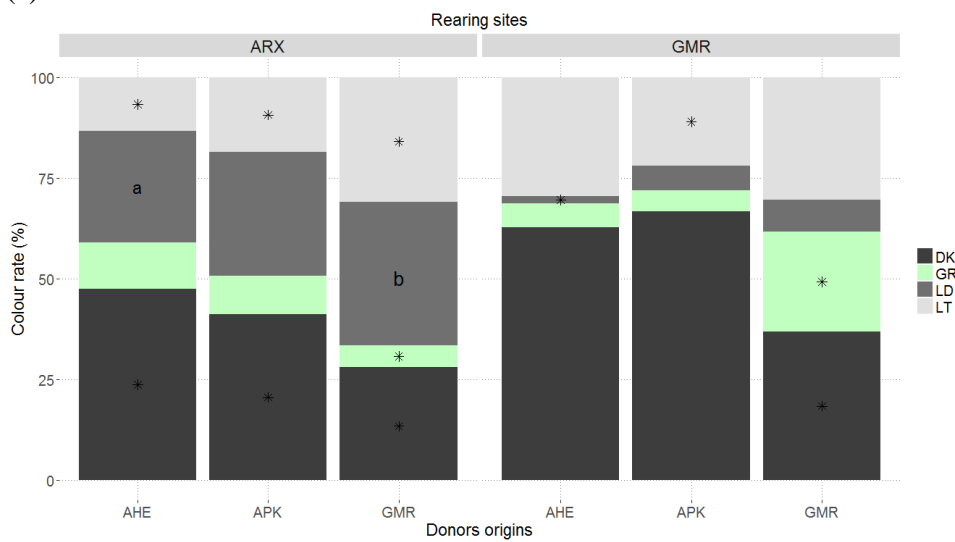


Figure 4. Nacre weight deposition speed (nacre weight. month⁻¹) with donors of three *P. margaritifera* geographical origins (AHE, TKP and GMR) grafted in Arutua (ARX) and Mangareva (GMR) rearing sites. Each box-plot has the following six elements: 1) median (solid bar in the box-plot); 2) 25th to 75th 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.

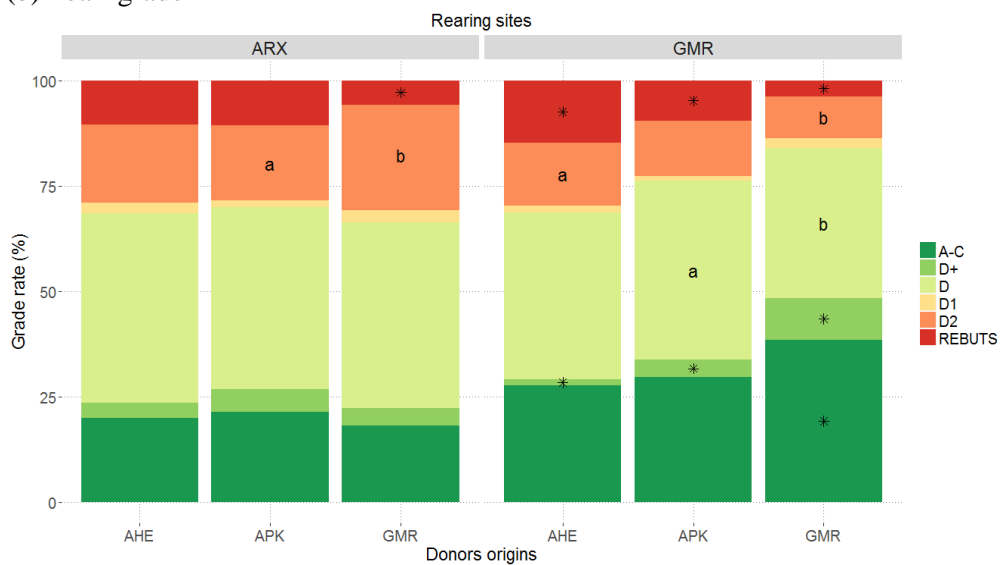


Figure 5. Qualitative cultured pearl traits by rearing site and donor origin, assessed by the GIE Poe O Rikitea, following categories of: (a) colour (DK: Dark, GM: Green, LD: Light Dark [medium darkness], LT: Light), (b) grade and (c) shape. Asterisks (*) indicate a significant ($p < 0.05$) difference among donor origins for a trait category within the same rearing site. Letters (a and b) indicate two significantly different origins ($p < 0.05$).

(a) Pearl colour



(b) Pearl grade



(c) Pearl shape

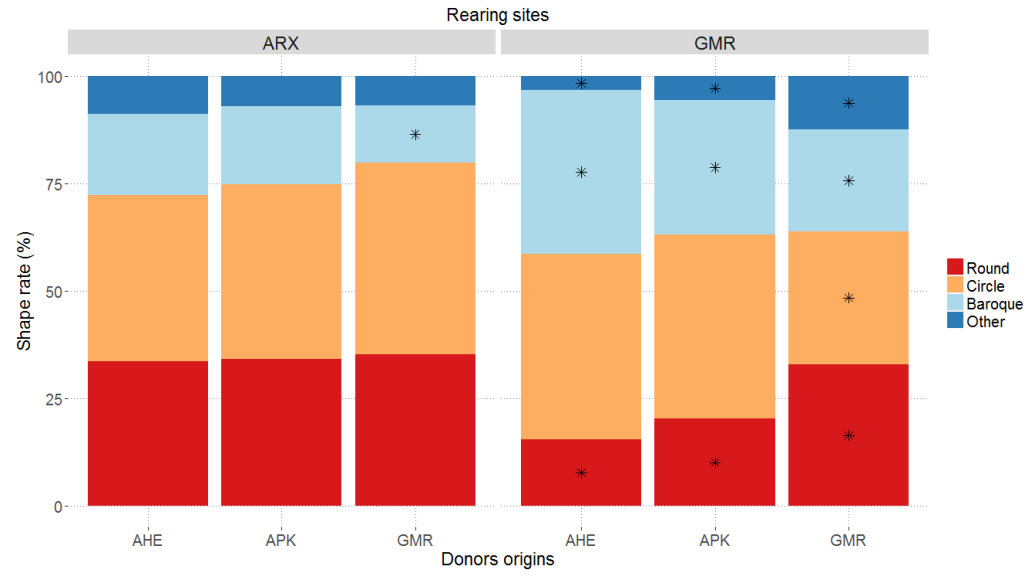


Table 1. Experimental grafts from *Pinctada margaritifera* performed in the lagoons of Arutua atoll (ARX) and Mangareva island (GMR), with donors originating from Ahe atoll (AHE), Takapoto atoll (TKP) and Mangareva (GMR). Graft characteristics are shown: number of donors selected, number of graft operations, 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 (%) | 81.6 ^{ab} | 79.9 ^b | 85.5 ^a | 85.8 ^b | 91.8 ^a | 83.8 ^b |
| (number) | (758) | (1029) | (752) | (995) | (1047) | (670) |
| Harvested pearl rate (%) | 52.5 | 61.8 | 61.4 | 84.1 | 69.8 | 74.5 |
| (number) | (488) | (796) | (540) | (975) | (796) | (596) |

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) |