Aquaculture Reports 34 (2024) 101917

Contents lists available at ScienceDirect

Aquaculture Reports

journal homepage: www.elsevier.com/locate/aqrep

Progress towards development of a unique pearl culture technology for red abalone (*Haliotis rufescens*) in Chile

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ARTICLE INFO

Keywords:
Abalone
Pearl oysters
Mantle tissue
Biomineralization
Pearl culture
Latin America

ABSTRACT

Abalone pearl farming is an aquaculture activity with great potential for future growth and diversification of the global pearl sector, which has been dominated for decades by pearls of marine pearl oysters of the genus *Pinctada*. Despite this potential, there is a significant lack of knowledge regarding methods for nucleus (bead) seeding and the process of pearl formation in abalone, compared to the well-studied pearl oyster model. To address this problem, this review first compares the main anatomical differences and similarities between both groups of mollusks, particularly those associated with the structure and role of mantle tissue on the synthesis of $CaCO_3$ compounds that integrate the inner nacreous layer. The iridescence (orient) and color properties of nacre in a cultured pearl is particularly related to the microstructure of aragonite crystals during biomineralization in each mollusk group. We then analyze the advantages and disadvantages of the adoption in abalone of methods originally developed for pearl oysters to produce bead-seeded pearls and half-pearls (or mabé pearls). For the red abalone *Haliotis rufescens* in particular, updated information on commercial production of both bead-seeded and mabé pearls is provided as a case of success for Latin America (Chile). Finally, the current status and future prospects for abalone pearl farming are discussed, assessing technology gaps and challenges to be addressed for the pearl sector to achieve its full potential, particularly for Latin America.

1. Introduction

Historically, three species of pearl oysters of the genus *Pinctada* (*Pinctada fucata*, *Pinctada margaritifera*, and *Pinctada maxima*) have sustained the culture of marine pearls worldwide (Southgate et al., 2008; Zhu et al., 2019). In the last few years, this aquaculture activity generated an average of US$ 300 million per year in many South Eastern Asian and South Pacific nations, such as Japan, Australia and French Polynesia (Southgate, 2021; Saucedo et al., 2023). Additionally, the culture of marine pearls created export income and jobs for the locals and improved livelihood opportunities for coastal communities (Saidi et al., 2017; Johnston et al., 2020). However, overproduction of cultured pearls in the last two decades has caused estimated declines of 40 to 60% in average production and output values of commercial pearls, particularly in the Akoya and Tahitian pearl segments (Shor, 2007; Saucedo et al., 2023). One strategy to prevent this and help the pearl sector diversify globally is the production of pearls from other mollusk species, but in colors and tones different from those of pearl oysters. This is the case with cultured pearls from abalone (*Haliotis* spp.), whose unique pattern of iridescence and metallic colors is valued by jewelers and gemmologists (Homkrajae et al., 2023) and could offer a competitive edge over pearl oysters (Wentzell, 1998; Hutchins, 2005; Monteforte and Bervera, 2010; Rojas-Figueroa et al., 2019).

Among the more than 70 species of abalone that exist in the world, about 15 are farmed through aquaculture, since abalone fisheries drastically declined from early 2000s due to overfishing, diseases and global climate change (Morales-Bojórquez et al., 2008; Nguyen et al., 2022). For most species, the meat (muscle) is an expensive, gourmet product that is exported to many countries as canned medallion (Cook, 2016; FAO, 2021, 2022). In 2019, China was the largest producer of abalone

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https://doi.org/10.1016/j.aqrep.2024.101917
Received 25 October 2023; Received in revised form 31 December 2023; Accepted 2 January 2024
Available online 9 January 2024

(*Haliotis discus hannai* and *Haliotis diversicolor*), reaching 89% of global production (>180,000 tones) (Nguyen et al., 2022) (Table 1). The remaining world production was mostly supplied by South Korea (9.1% from *H. discus hannai*), South Africa (0.8% from *Haliotis midae*) and Australia (0.2% from *Halitis rubra* and *Haliotis laevigata*). Other countries that yielded < 0.15% of abalone global production in 2019 are listed in Table 1.

In Latin America, some abalone species are currently farmed to produce other economically-valuable goods, such as pearls, following dual-crop models that use both the meat and pearls (Monteforte and Bervera, 2010; Araya et al., 2016). Mexico and Chile have successfully adopted this model in the last two decades. For example, of the five abalone species distributed in Mexico in the Eastern Pacific coast, the red abalone *H. rufescens* is used for the commercial production of canned medallion and half-pearls (or mabé pearls) (Monteforte and Bervera, 2010). Chile has two abalone species that were introduced in the 1980s (*H. rufescens* and *H. discus hannai*) (Flores-Aguilar et al., 2007), with exports of *H. rufescens* reaching 317 tons in 2020 from the Atacama, Coquimbo, Valparaíso and Los Lagos regions (Sernapesca, 2020). This has opened an opportunity window for the abalone sector in Chile to expand, not only because of the well-established demand for meat, but because of the added value that pearl culture may represent in a global market with little competition (Saucedo et al., 2023).

Table 1
Global abalone (*Haliotis spp.*) production by aquaculture and country in 2019.

Country	Species	Common Name	Total Production (tones)	Total Production (%)
China	*H. discus hannai*	Pacific abalone; green abalone	180,267	88.9 *
	H. diversicolor	Variously coloured abalone		
South Korea	*H. discus hannai*	Pacific abalone	18,436	9.1 *
South Africa	*H. midae*	South African abalone	1675	0.82 *
Australia	*H. rubra* *H. laevigata*	Blacklip abalone Smooth abalone	424	0.21 *
Chile	*H. rufescens*	Red abalone	300	0.15 *
United States	*H. fulgens*	Blue abalone	220	0.11 * *
	H. rufescens	Red abalone		
Taiwan	*H. diversicolor*	Var. coloured abalone	220	0.11 * *
	H. discus hannai	Pacific abalone		
Philippines	*H. asinina*	Ass's-ear abalone	220	0.11 * *
Thailand	*H. diversicolor*	Var. coloured abalone	220	0.11 * *
New Zealand	*H. iris*	Paua	100	0.05 * *
Iceland	*H. rufescens*	Red abalone	100	0.05 * *
Canada	*H. kamtschatkana*	Pinto abalone	100	0.05 * *
Oman	*H. mariae*	Omani abalone	100	0.05 * *
Mexico	*H. rufescens* *H. fulgens* *H. corrugata*	Red abalone Blue abalone Yellow abalone	< 100	–
France	*H. tuberculata*	Green ormer	< 100	–

*Data calculated as a percentage of the sum of the countries mentioned above (Cook 2014; FAO Aquaculture News, 2021; Nguyen et al., 2022)
* *Data estimated as an approximate percentage of production, establishing 0.1% for small scale and 0.05% for smaller scale.

Despite the potential of abalone for pearl culture, there is still a lack of knowledge in this mollusk group organism regarding methods for nucleus (bead) seeding and process of pearl formation, compared to the well-studied pearl oyster model (Saucedo et al., 2015; Araya et al., 2016). To address this problem, this review first compares the main anatomical differences and similarities between both groups of mollusks, particularly those associated with the structure and role of mantle tissue on the synthesis of $CaCO_3$ compounds that integrate the nacreous layer. The iridescence (orient) and color properties of nacre in a cultured pearl is related to the microstructure of aragonite crystals during biomineralization in each mollusk group. We then analyze the advantages and disadvantages of the adoption in abalone (Gastropoda: Haliotidae) of the techniques originally developed for pearl oysters (Bivalvia: Pteriidae) to produce cultured pearls (referred to as bead-seeded pearls in this review) and mabé pearls. For the red abalone *H. rufescens* in particular, updated information on commercial production of cultured pearls is provided as a case of success for Latin America (Chile). Finally, the current status and future prospects for abalone pearl farming are discussed, assessing technology gaps and challenges to be addressed for the pearl sector to achieve its full potential.

2. Anatomical structure and role of mantle tissue

Evolution has favoured a wide morphological variety in shell-producing mollusks, including the Scaphopoda (tusk shells), Polyplacophora (chitons), Bivalvia (oysters, scallops, clams, mussels), and Gastropoda (snails) (Ponder et al., 2019). These taxa all have in common that their shells are formed by mantle tissue, which regulates important specialized functions, including sensory capacity, storage and mobilization of energy reserves and synthesis of $CaCO_3$ compounds to form the shell (Fougerouse et al., 2008). This last process is known as biomineralization (Simkiss and Wilbur, 2012; Nudelman, 2015). Mantle tissue is also responsible for the defense mechanism of the mollusk by encapsulating within mother-of-pearl material (nacre) any external particle or parasite that comes into contact with internal body tissues (Acosta-Salmon and Southgate, 2006). This process produces a natural pearl.

The class Bivalvia has been well studied with regard to overall mantle structure and shell (nacre) formation, mostly in pearl oysters (Levi et al., 1998; Dauphin et al., 2008), and to a lesser extent, in freshwater mussels (Checa, 2000; Van Phuc et al., 2011). In general, two large and thin mantle folds (one for each valve of the shell) cover and protect the internal organs. Macroscopically, both folds are separated ventrally, anteriorly and posteriorly, but merge dorsally along the hinge. Structurally, four distinctive mantle regions or zones are recognized in pearl oysters of the genus *Pinctada*: (1) Marginal, divided into the outer, middle, and inner lobes; (2) Pallial, where the pallial artery and nerve are located; (3) Central, adhered to the visceral mass and adductor muscle; (4) Isthmus, dorsally fused to the hinge (Fougerouse et al., 2008; Awaji and Machii, 2011) (Fig. 1A). The lobes from the marginal zone participate in forming the three constitutive layers of the shell: periostracum (a thin proteinaceous layer facing the external shell), prismatic (a thick layer in the middle), and nacreous (facing the visceral mass). An inner nacreous layer is only present in three mollusk classes: Bivalvia, Gastropoda and Cephalopoda.

Microscopically, the structure of mantle tissue is basically the same in all pearl oyster species (Fig. 1A), although there may be cells of different types and sizes depending on the particular process they regulate. In the marginal zone, the outer epithelium is aligned with a monolayer of columnar cells and large secretory cells (containing acid mucopolysaccharides, carbohydrates, proteins and calcium granules), which are associated with the formation and regeneration of the shell and nacreous compounds (García-Gasca et al., 1994; Awaji and Machii, 2011). The rest of the marginal zone is formed of connective tissue with muscle fibers (longitudinal, radial), nerves and blood cells (Jabbour

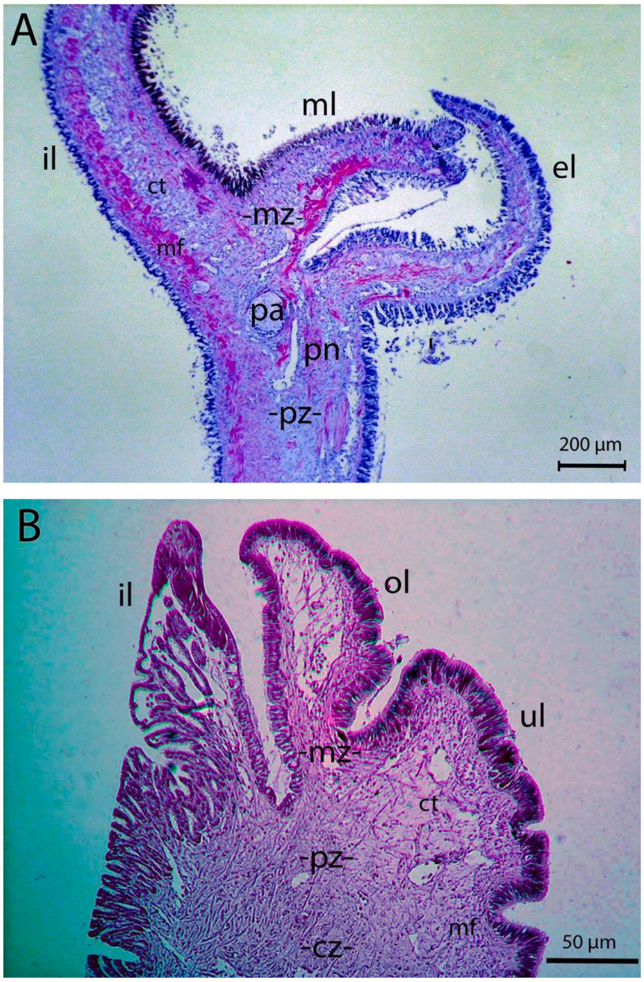

Fig. 1. Histological comparison of mantle tissue of the pearl oyster *Pinctada margaritifera* (A) and the red abalone *Haliotis rufescens* (B). Photo A is a transversal section (10 ×) stained with hematoxylin-eosin, showing the marginal zone (–mz–) with its internal lobe (il), middle lobe (ml), and external lobe (el) and the pallial zone (–pz–) with its pallial artery (pa) and pallial nerve (pn) and. A wide layer of connective tissue (ct) and muscle fibers (mf) is clearly visible in the –mz–. Photo B is a transversal Section (4 ×) of mantle tissue stained with hematoxylin-eosin, showing the marginal zone (–mz–) with the outer lobe (ol) and inner lobe (il) well developed, as well as a third small, and presumably, undeveloped lobe (ul). The pallial zone (–pz–) and central zone (–cz–) can also be observed. While the pallial artery and pallial nerve are not evident in the photo, a large area of ct and mf is observed. Photo A by Hector Acosta-Salmon; photo B courtesy of Alejandro Rojas-Figueroa.

et al., 1992). Close to the pallial zone, the pallial nerve and pallial artery are surrounded by connective tissue, ciliated cells and melanin pigments. The central zone is composed of many secretory cells that participate in both protein and glycogen synthesis (García-Gasca et al., 1994).

Among the Gastropoda, the abalone is the best studied model with regard to mantle structure and role on the formation and structural properties of the shell and nacreous layer (Lin and Meyers, 2005; Heinemann et al., 2011). A cytological study of mantle tissue of *H. tuberculata* revealed that the marginal zone ends with the division into two lobes only (Sud et al., 2002), instead of the three lobes present in bivalves (Fougerouse et al., 2008). Preliminary findings by Sáez-Saavedra (2024) not only support this feature, but suggest that a third lobe in *H. rufescens* is presumably undeveloped or rudimentary (Fig. 1B). Although this may have some implications for the preparation of mantle tissue for the seeding surgery, the feature has yet to be confirmed. The inner mantle epithelium in the marginal zone regulates ion exchange with the environment and consists of glandular cells and ciliated or unciliated non-glandular cells (Sud et al., 2002). In contrast, the outer epithelium is divided into a tubular area (covered by secretory tubules that control shell pigmentation and participate in forming the calcite layer) and a large area beyond the tubular zone (aligned with secretory-ciliated cells that participate in forming the aragonite nacreous layer) (Budd et al., 2014). The periostracal groove, near the pallial and central zones, has a columnar epithelium with numerous cilia and secretory cells involved in protein expression during shell formation (Jolly et al., 2004; Lin and Meyers, 2005; Heinemann et al., 2011) (Fig. 1B).

In summary, some differences in overall structure of mantle tissue appear evident between abalone and pearl oysters, particularly those suggesting the existence of a poorly developed or rudimentary lobe in the marginal mantle region of abalone. Given the importance of the correct preparation of mantle tissue for the seeding surgery, confirming this likelihood by histological, histochemical, ultrastructural and molecular tools is necessary.

3. Biomolecules controlling nacre synthesis and structure during biomineralization

The physiological process by which a living organism develops a mineralized framework of calcareous compounds (e.g. calcite, aragonite, vaterite, barite, hydroxyapatite, celestite) from the intake of environmental elements and ions is called 'biomineralization' (Simkiss and Wilbur, 2012; Nudelman, 2015). The evolutionary development of this mechanism has allowed organisms such as corals, sponges, echinoderms and mollusks to create calcareous structures that are unique in their macro- and micro-architecture and provide mechanical support and protection (Müller, 2011; Marin et al., 2012). The molluscan shell is a good example of such a protective structure.

In bivalve mollusks, biomineralization is controlled by the outer mantle epithelium and involves important interactions between organic matrix components and inorganic ions that integrate all the shell layers (Levi et al., 1998; Checa, 2018). While the organic matrix is composed of 1–2% polysaccharides, proteins, glycoproteins and lipids, most shell precursor ions in the inorganic matrix, constituting ~99% of the shell weight, are calcium ($Ca2+$) and dissolved carbon compounds in the form of bicarbonate ($HCO3^-$) absorbed from the seawater (Marin et al., 2012; Song et al., 2019). The interaction between inorganic ions and the organic matrix drives crystal nucleation, growth, orientation and $CaCO_3$ precipitation (Pokroy et al., 2007; Nudelman, 2015). The result is a complex $CaCO_3$ micro-laminate that is present in nature in different forms known as 'polymorphs'. Nacre is perhaps the best studied polymorph in mollusks, yet aragonite (located in the inner nacre layer as orthorhombic crystals), calcite (present in the prismatic layer as rhombohedral crystals), and more rarely vaterite, are also important (Marin et al., 2012; Checa, 2018). These polymorphs may be different in each mollusk species, but act together to give the shell its mechanical properties of hardness and strength (Pokroy et al., 2007; Dauphin et al., 2008).

In pearl oysters of the genus *Pinctada*, the arrangement of calcite and aragonite crystals follows the typical 'brick and wall model', which means that each tablet of growing nacre is horizontally deposited on top of another growing layer to build a staggered structure (Levi et al., 1998; Checa, 2018). The mineralogical and crystallographic properties of these structures, organized at the nanometer scale, are regulated by specific genes that give the nacreous layer its unique luster and color; both nacre characteristics are aragonite-dependent (Dauphin et al., 2008). These structures are also under the control of large, structural biomolecules named Shell Matrix Proteins (SMPs) (Falini et al., 1996; Song et al., 2019). SMPs are located in the outer mantle epithelium that covers the extrapallial space, are insoluble in water and create acid microenvironments favorable for the formation of $CaCO_3$ and nacre (Müller, 2011; Marin et al., 2012). To date, about 15 SMPs have been reported to form crystal-biomineralizing proteins and Ca2 + binding sites to both regulate $CaCO_3$ growth inhibition and nucleate calcite and aragonite polymorphs in the main *Pinctada* species. These include Nacreine, Perlin, Pearlin, Prismalin-14, Aspein, N66, MS17, MSI60, MSI31, N16, N19, Pif177, Pif80, Pif97 and N14 (Marin and Luquet, 2004; Simkiss and Wilbur, 2012; Song et al., 2019).

The general structure of nacre in gastropods is similar to that of bivalves, but differs in the arrangement and orientation of calcite and aragonite crystals (Müller, 2011; Marin et al., 2012). In abalone, crystals are not staggered horizontally, but stacked vertically in the form of tablets that are deposited one on top of the other following a 'coin stack model' (Dauphin et al., 2008; Heinemann et al., 2011; Nudelman, 2015). Since this arrangement determines the mechanical properties of nacre as biomineral, at least 13 SMPs with calcium-binding sites and key roles in $CaCO_3$ precipitation have been described for different abalone species, including Lustrin-A, Perlucin, Perlustrin, Perlwapin, Perlinhibin, AP7, AP8, AP24, ML1A2, htCA1, htCA2 and hf15 (Marin and Luquet, 2004; Simkiss and Wilbur, 2012; Song et al., 2019).

In conclusion, there are key differences between the Haliotidae and Pteriidae regarding the structural and crystallographic properties of nacre, which are the result of distinctive mechanisms of shell growth during biomineralization in each mollusk group. Thus, studies aimed to characterize new SMPs and genes modulating nacre deposition during pearl sac and pearl formation are recommended for *H. rufescens*, given its potential value for pearl culture.

4. Development of pearl culture technology for the red abalone *H. rufescens* in Chile

4.1. Fundamentals of the seeding technique

The technology used to produce cultured abalone pearls was developed from the pearl oyster model and relies on the same microsurgery in which an inert nucleus (bead) and a piece of nacre-secreting mantle tissue (saibo) from the donor are inserted into the soft tissue of the host (Taylor and Strack, 2008). This surgery is called 'seeding or nucleation'. In members of the genus *Pinctada* (*P. fucata*, *P. margaritifera*, *P. maxima*), the oyster is placed on a shell stand and a small incision is made at the base of the gonad to ventrally open a pathway towards the intestinal loop (or pearl pocket); the bead and saibo are inserted here (Southgate, 2021; Zhu et al., 2019). In members of the genus *Pteria* (*Pt. sterna*), however, the intestinal loop is either absent, too small or too thin; in this case, the pathway is made from the base of the foot to a more proximal area in the gonad, which is closer to its base and as far as possible from the intestinal loop (Nava et al., 2000; Saucedo et al., 2023).

The scenario is very different in abalone, since the seeding surgery for the production of bead-seeded cultured pearls has been particularly difficult to adapt in this mollusk species due to four clear anatomical differences with pearl oysters (Saucedo et al., 2015; Araya et al., 2016; Sáez-Saavedra, 2024). The differences are: (1) Abalone, unlike pearl oysters, lack an intestinal loop to place the bead and saibo (Fig. 2), which made it necessary to seed in a different position in the soft body to reduce the high bead rejection rates (see details in subsection below); (2) Abalone continually move in search for food and their large-central foot exerts constant pressure over the seeded area, resulting in many cases, in the separation of the bead and saibo that remain together by simple adherence. When separation occurs, the pearl either fails to form or develops into a non-seeded, baroque pearl named 'keshi'. This problem is far less common in pearl oysters that are sessile and lack mobility (Gervis and Sims, 1992); (3) Only two of the three mantle lobes present in pearl oysters appear to be functional in abalone (Figs. 1A, 1B), which has some implications for saibo preparation prior to the surgery, specifically to keep the usable, nacre-secreting portion of the tissue and discard the unusable portion (Saucedo et al., 2015; Sáez-Saavedra, 2024); and (4) In abalone, mantle tissue is at least half as thin as in pearl oysters, and thus, handling before and during the seeding surgery is more difficult.

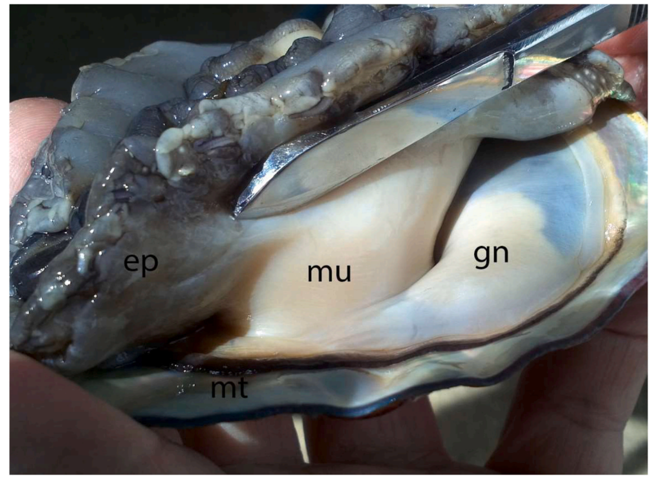

Fig. 2. Anesthetized abalone (*Haliotis discus hannai*) showing the muscle (mu), epipod (ep) and mantle tissue (mt) fully distended and exposing the area near the gonad (gn) where the seeding surgery will be performed to produce bead-seeded pearls. Photo by Pedro E. Saucedo.

For the seeding surgery, abalone are anesthetized to reduce their stress, fully relax their soft body tissues (mantle, epipod, muscle) and facilitate their handling (Rojas-Figueroa et al., 2023). Each animal is then placed on its back to expose the area where the surgery will be performed (Fig. 2) and the bead and saibo are seeded in the visceral mass, near the gonad (Saucedo et al., 2015; Araya et al., 2016). Following seeding, as with pearl oysters, the outer epithelial cells from the donated saibo proliferate around the bead and enclose it within a continuous epithelial layer forming the pearl-sac (Fougerouse et al., 2008; Awaji and Machii, 2011). The exact time for this process to occur has not yet been determined for any abalone species. Subsequent secretion of a nacre coating from the pearl sac onto the bead results in cultured pearl formation after 18 to 24 months, depending on the species, operator skills and external culturing conditions (Saucedo et al., 2015).

4.2. Fundamentals of the half-pearl (mabé) technique

Different to the complexity of the seeding surgery, the method to produce composite, cultured pearls (or mabé pearls), is relatively simple and widely used today in both pearl oysters (Ruíz-Rubio et al., 2006; Kishore et al., 2013; Freites et al., 2020; Jara et al., 2021) and abalone (Fankboner, 1995; Wentzell, 1998; Victor et al., 2001; Hutchins, 2005; Rojas-Figueroa et al., 2019). With this method, a different number of nuclei are cemented (or implanted) on the inner nacreous face of the shell using a cyanoacrylate-type glue (Fig. 3). In general, nuclei are plastic-made and have hemispherical shape, but ovals and drops may also be considered. In both pearl oysters and abalone, the number, size and position of nuclei to implant are important criteria to consider, as they exert a significant influence on the quality of formed mabé . Of these, the position on the shell is perhaps the most important criterion, as not all mantle regions support the same nacre deposition rate and color (Kishore et al., 2013; Rojas-Figueroa et al., 2019). In the winged pearl oyster *Pt. sterna*, nuclei placed on the anterior and posterior shell positions, rather than on the central position, produce higher-quality mabé (Ruíz-Rubio et al., 2006; Jara et al., 2021). Also in this species, mabé pearls can result dull, thin and of poor quality when the nuclei are implanted either in young, fast-growing oysters (and are overgrown by adductor muscle) or too close to the shell edge (and are partially covered with periostracum) (Ruíz-Rubio et al., 2006; Jara et al., 2021). In abalone, the dorsal position is optimal for higher mabé quality, whereas the ventral position is not recommended for implantation, mainly

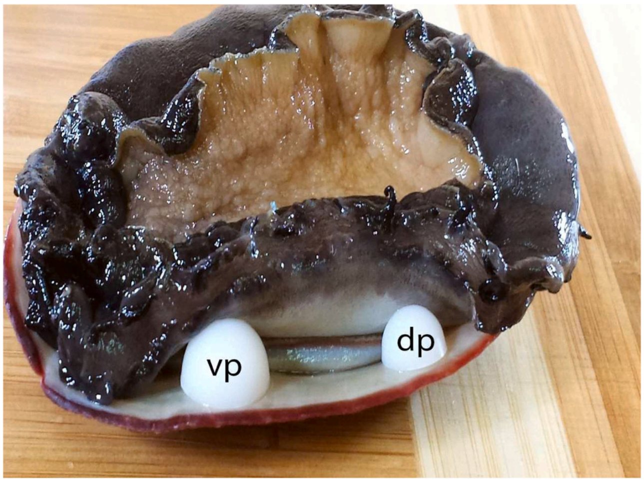

Fig. 3. Anesthetized abalone (*Haliotis rufescens*) showing two hemispherical plastic nuclei (7 and 9 mm in diameter) implanted in the dorsal position (dp) and ventral position (vp) of the inner side of the shell to produce cultured mabé pearls. Photo by Pedro E. Saucedo.

because mantle tissue tends to fold here and does not completely cover the nucleus, resulting thin mabé pearls with low nacre coverage (Rojas-Figueroa et al., 2019) (Fig. 4).

Implanted abalone are observed for a short period of convalescence (24 to 36 h) and then transferred to the final culture stage for additional 12 to 18 months until harvesting the mabé pearls. Both types of cultured pearls (bead-seeded and mabé) can be graded using the same criteria (luster, size, shape, color, surface, and thickness of the nacre coating) and classified according to the alphabetic-type scheme available for pearl oysters (Freites et al., 2020; Saucedo et al., 2023). However, grading the shape of bead-seeded pearls is far more difficult in abalone than in pearl oysters, due to the conspicuous forms these gems may adopt (Saucedo et al., 2015; Araya et al., 2016; see details in subsection below).

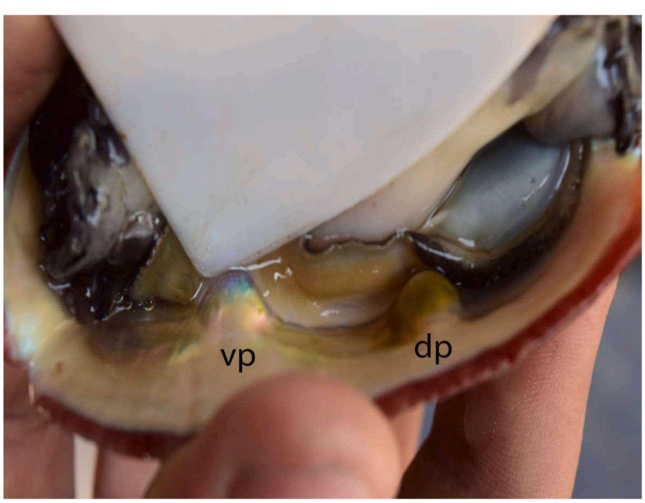

Fig. 4. Composite, blister-type (mabé) pearls produced in Chile from the red abalone (*Haliotis rufescens*). The pearl displays a combination of two colors, golden-pink near the dorsal position (dp) and turquoise blue towards the ventral position (vp). The mabé formed in the dp is of higher quality than the pearl from the vp, mostly because mantle tissue tends to fold ventrally and does not completely cover the nucleus, resulting in some cases in dull, thin pearls with low nacre coverage. Photo by Pedro E. Saucedo.

4.3. Current status of abalone pearl culture in Chile

To date, Chile is the only country in Latin America –and likely in the entire Western Hemisphere– that has made considerable progress in optimizing the seeding technique to produce bead-seeded pearls on a commercial scale using the red abalone *H. rufescens*. For the pre-operatory stage (anesthesia), several natural and artificial substances have been evaluated in this abalone species, including benzocaine, clove oil, phenoxy ethanol, phenoxy propanol and CO_2 (Rojas-Figueroa et al., 2023). From these, the injection of saturated CO_2 in seawater has proven to be the best treatment for a fast relaxation of body tissues and full recovery of the animals with minimum deleterious effects, such as mucus production, oxidative stress, oxidative damage and mortality. In contrast, the use of clove oil as anesthetic is not recommended for *H. rufescens*, due to its various side effects, particularly death of the animals. Interestingly, the response to anesthesia reports contrasting results in pearl oysters (Acosta-Salmon et al., 2005; Mamangkey et al., 2009; Kishore et al., 2013) and abalone (White et al., 1996; Burke et al., 2001; Bilbao et al., 2010; Soza-Chinchilla, 2014). This indicates that tolerance to anesthesia is species-dependent, and likely, substance-, dose- and time-dependent.

The operatory stage (seeding) has been the most difficult to adapt in *H. rufescens*, particularly to identify the optimal site in the body tissue to place the bead and saibo. This is due to the already-mentioned anatomical differences with pearl oysters. Despite this, three main outcomes or achievements summarize the work made with this species in the last ten years. These outcomes, which are entirely based on reports by Saucedo et al. (2015), Araya et al. (2016) and personal observations by the staff of *Unidad de Cultivo de Abalón* (*UCA*) of Universidad de Antofagasta, in Chile, are: (1) Identification of a space in the distal part of the gonad (Fig. 5 A) and the abdominal cavity between the base of the gonad and the foot (Fig. 5B) to execute the seeding surgery; both spaces, particularly the latter, have proved to be the most appropriate for *H. rufescens* in terms of lower bead rejection rates; (2) Seeding of abalone without a shell stand or special operating tools, such as the shell opener and side knife that are routinely used with pearl oysters; a sterilized wooden board, curved scalpel and nucleators of different sizes are enough to complete the surgery; and (3) Use of surgical suture to close the wound and minimize the risk of bead rejection (Fig. 5 C).

With the adoption of these strategies, the production data of *H. rufescens* bead-seeded pearls at *UCA* of Universidad de Antofagasta, in Chile, substantially improved between 2013 and 2022. First, the number of abalone that survived the seeding surgery, successfully retained the bead and were in conditions to produce a bead-seeded pearl increased from about 100 animals (in 2013) to nearly 8000 animals (in 2022). These animals are farmed in land-based facilities, consisting of $5 m^3$ raceway units supplied with continuous flow-through of recirculated ($5000\ L\ h^{-1}$; $1\ L\ h^{-1}$ exchange; $16 \pm 1\ °C$) and aerated seawater for a minimum of 24 months. This time period is relatively longer than the 9- to 24-month period reported for pearl oysters (Haws, 2002; Taylor and Strack, 2008), basically because the rate of nacre deposition is lower in abalone (Lin et al., 2008). Second, post-seeding bead rejection rates were reduced from 80% to ~35% between 2013 and 2022, as well as mortality rates from 8% to $<$ 1%. Finally, the success rate of fully formed pearls (7 to 10 mm in diameter; 0.8 to 1.2 mm of nacre coating) was increased from 0.4% to 7% between 2014 and 2022, with an estimated increase to ~10% in 2024. These values can considerably vary in pearl oysters used for commercial pearl production in Southeast Asian and South Pacific nations, but on average, they indicate that 20% to 30% of oysters will die or reject the bead within 30 days; they also report that marketable pearls will be obtained from at least 45% of the oysters that retained the bead one month after the seeding (Haws, 2002).

In terms of quality, *H. rufescens* bead-seeded pearls produced at *UCA* in Chile display a combined pattern of intense luster and vibrant metallic colors with dominant turquoise tones and violet, green, pink, and golden overtones (Homkrajae et al., 2023) (Fig. 6). These abalone pearls also

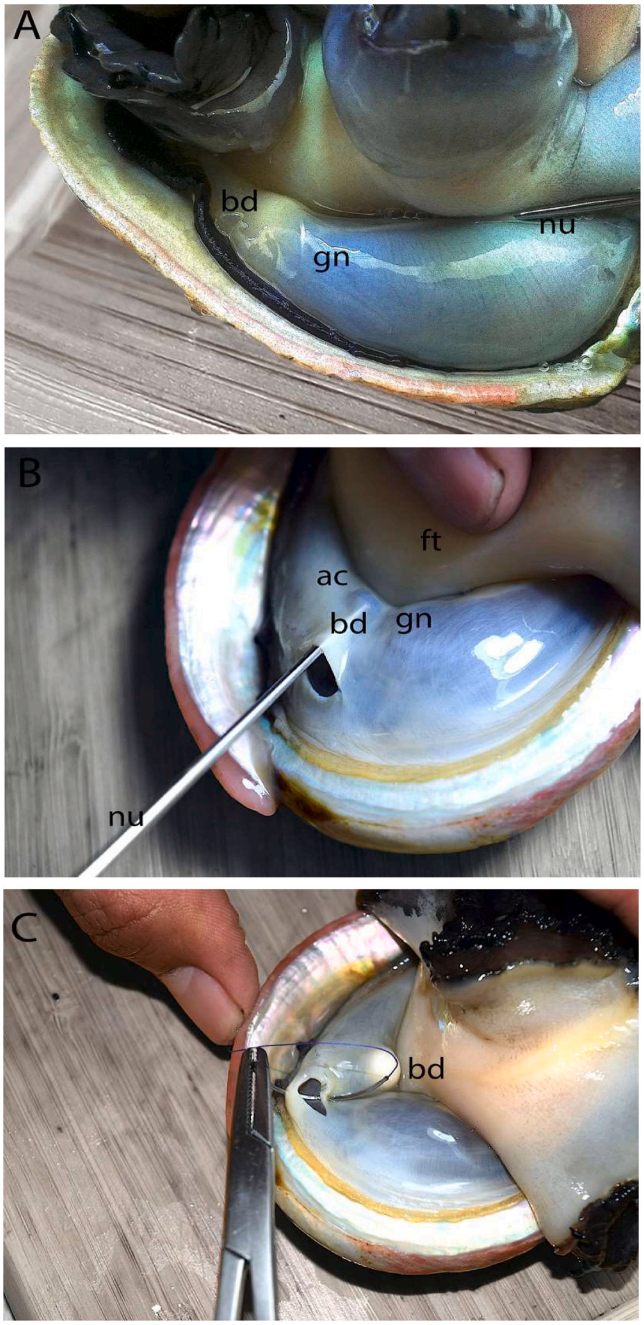

Fig. 5. Anesthetized abalone (*Haliotis rufescens*) showing details of the seeding technique used to produce bead-seeded cultured pearls in Chile. (A) Seeding of a 9 mm diameter bead (bd) into the more distal part of the gonad (gn) using a nucleator (nu); (B) Seeding of the bd into the abdominal cavity (ac) between the base of the gn and the central foot (ft) using a nu; and (C) closure of the wound with surgical suturing to help reduce bead rejection rates. The photos show that, unlike pearl oysters, no shell stand is required to seed an abalone, just a sterilized wooden board, curved scalpel and nu of different sizes. Photos by Pedro E. Saucedo.

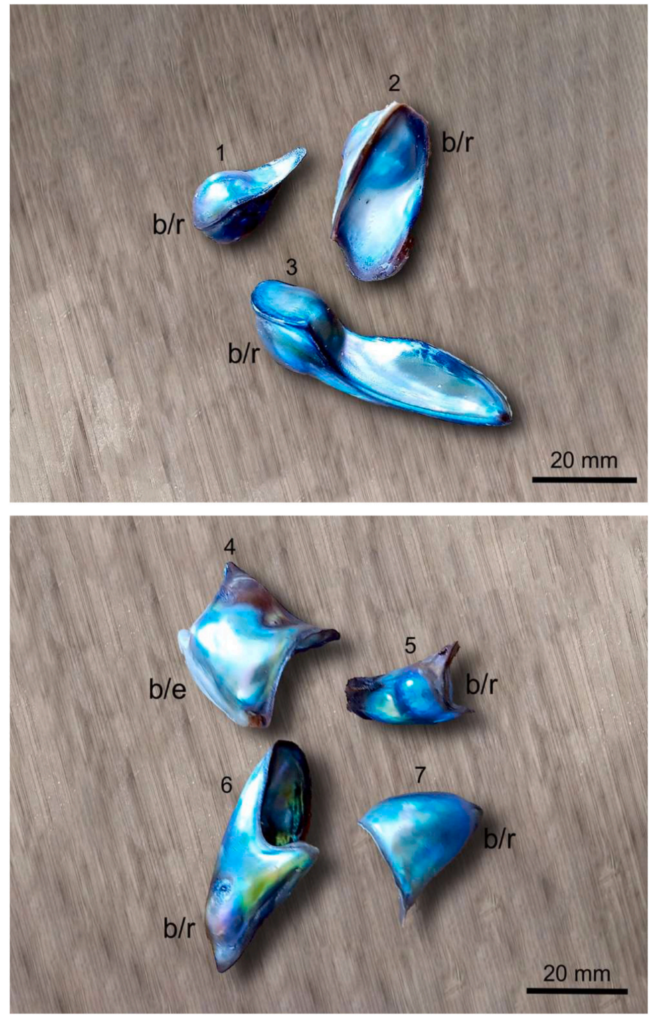

Fig. 6. Commercial bead-seeded pearls produced in Chile from the red abalone (*Haliotis rufescens*). The photos show beads that were retained (b/r) in six of the pearls due to the use of surgical sutures (1–3, 5–7) and only one bead that was expelled (b/e) in pearl (4) to form a keshi. The photos also reveal pearls of conspicuous and very varied shapes that mostly include fireballs (1–3) and baroques (4–6), and to a lesser extent, a tooth (7) and a near-round (also 1). These cultured abalone pearls of baroque shapes, which resemble the most the baroque shapes of natural abalone pearls, display vibrant metallic colors with dominant turquoise tones and violet overtones. The technology to produce these abalone pearls is patented in Chile and also licensed to the company '*Atacama Pearls*'. Photos by Ruben Araya.

adopt very conspicuous shapes that mostly include baroques, and to a lesser extent, tusks, teeth and fireballs with tails or horns; round and near-round pearls are rare (Rubén Araya, *pers. obs.*) (Fig. 6). This does not occur much in pearl oysters that produce higher proportions of bead-seeded pearls with spherical shapes. In the pearl oyster *P. margaritifera*, tails are suspected to originate from bacterial infections caused by hemolymph and inflammatory cells accumulated in the dead space that the incision channel created during the seeding surgery (Norton et al., 2000). The authors believe that these inflammatory cells collected around the bead during pearl sac formation develop into a calcified tail that grows together with the pearl.

For the culture of mabé pearls, relaxed *H. rufescens* (7 to 12 cm in shell length) are regularly implanted with a single, 6 to 10 mm in diameter hemispherical nucleus on the dorsal position of the shell (Rojas-Figueroa et al., 2019). A maximum of two nuclei implanted on the dorsal and central positions is recommended (Fig. 4). This considering that each individual has a threshold for the production of a maximum number of high-quality mabé pearls before their average quality decreases. This is the case with the pearl oysters *Pt. sterna* (Ruíz-Rubio et al., 2006; Freites et al., 2020; Jara et al., 2021) and *P. margaritifera* (Kishore et al., 2013), as well as with the abalone *H. rufescens* (Rojas-Figueroa et al., 2019). In this abalone species in particular, color display usually maintains a relationship with the implanting position, and the same individual can produce mabé pearls of two different colors at the same time. For instance, the animal can display a golden-pink color in the dorsal position and a turquoise blue color in the ventral position (Fig. 4). Currently, commercial production of *H. rufescens* mabé pearls is secondary in Chile and comprises only ~10% of total production; the remaining 90% is covered by bead-seeded pearls.

5. Challenges and future prospects for abalone pearl culture

Between 1989 and 2019, worldwide landings of abalone drastically fell by 70% due to overfishing and illegal fishing (Morales-Bojórquez et al., 2008; Cook, 2016; Nguyen et al., 2022). Additionally, many abalone species are considered endangered or critically endangered by the IUCN Red List, including all the seven abalone species inhabiting the US Pacific Coast (https://www.vetmed.ucdavis.edu/news/all-west-coast-abalones-risk-extinction-iucn-red-list). Despite this, abalone global farming and production continues to grow, coupled with constant demand and high and stable prices (FAO Aquaculture News, 2021). This has made it necessary to focus aquaculture towards sustainable management models (e.g. the Blue Transformation), particularly in many Latin American countries that had historically suffered from overfishing, lack of regulation and severe decline in abalone wild stocks (FAO, 2022; Wurmann et al., 2022). Other problems such as global climate change, spread of resistant infectious diseases and water pollution and acidification have increased the pressure on natural populations, and with this, the relevance of aquaculture (Shor, 2007; Cheung et al., 2010). Finally, the recent COVID-19 pandemic limited access to aquatic goods and services and impacted local sales in many countries across the globe, although these impacts remain unquantified to date (Freitas-Souza and Carvalho-Viana, 2020).

In some Latin American countries, where abalone farming is commercially important, pearl culture from this mollusk group is slowly emerging as a promising activity that may help improve livelihood opportunities and promote socioeconomic growth in local communities. In Mexico and Chile, for instance, the culture of beaded and mabé pearls using the red abalone *H. rufescens* now offers an innovative, added-value alternative to meat production (Saucedo et al., 2015). The nacre coating in this –and other abalone species– is iridescent and displays a wide range of metallic tones and overtones, which is appealing to jewelers and gemmologists (Homkrajae et al., 2023) and could offer a marketing edge compared to other pearl-producing species that currently dominate the pearl sector, such as marine pearl oysters (Southgate, 2021; Zhu et al., 2019) and freshwater mussels (Saucedo et al., 2021).

Abalone pearl culture started in Mexico in 2007 (Monteforte and Bervera, 2010) and in Chile in 2012 (Saucedo et al., 2015), covering both the areas of basic science and technological development. In Chile in particular, this activity has been funded by several national and regional grants and is now spearheaded by Universidad de Antofagasta. From these projects, basic research tied to *H. rufescens* pearl farming has covered the aspects of anesthesia as pre-operatory stage (Soza-Chinchilla, 2014; Rojas-Figueroa et al., 2023); definition of criteria for mabé pearl implants (number, size and position of nuclei to implant) (Rojas-Figueroa et al., 2019); characterization of the microanatomy of mantle tissue using histological, histochemical, and molecular tools (Sáez-Saavedra, 2024); identification of the optimal site of the abalone body to seed the bead and saibo and post-operatory care of seeded animals prior to their final grow-out and harvest of cultured pearls (Saucedo et al., 2015). However, to broaden the understanding of pearl formation in the species, particularly to reduce the proportion of baroque pearls and increase that of round and near-round pearls, future studies to characterize pearl sac formation and its influence on pearl quality are recommended.

The technological development of abalone pearl farming also shows a positive progress in Latin America. In Mexico, a collaborative agreement between a research institution and a cooperative society supported the creation in 2009 of the private venture *Baja Pearls* in Baja California, aimed to commercially produce mabé pearls using the red abalone *H. rufescens* (Monteforte and Bervera, 2010). Baja Pearls seeks to create abalone pearl jewelry designs oriented to the exclusive gemstone sector, where niche markets and marketing strategies are unique to this Mexican region. In Chile, mabé pearls from *H. rufescens* are also produced at a pre-commercial scale since 2012. Although adapting the technology for culturing bead-seeded pearls has been challenging in *H. rufescens*, important advancements have been made in recent years. These include reducing post-seeding mortality and rejection rates with the use of surgical suturing, increasing the quantity and quality of pearls fully covered by nacre and improving individual and group learning curves of seeding technicians. As a result, bead-seeded pearls from *H. rufescens* are now produced using a technology that was patented in 2016 in Chile and other pearling countries such as Australia and Hong Kong (Araya et al., 2016). Additionally, this technology has recently undergo two important processes: (1) The creation in 2021 of the spin-off *'Abalone Pearl Technology'* (APT-SpA) at Universidad de Antofagasta for the commercialization of abalone bead-seeded cultured pearls; and (2) The licensing in 2023 of the trademark '*Atacama Pearls*' (www.atacamapearls.com) that looks to maximize the value of these unique pearls through the manufacture and selling of fine jewelry in international markets, as well as for marketing strategies and transferring of the technology to the productive sectors.

Despite the progress achieved in abalone pearl farming in Mexico and Chile, Latin America has not been able to develop a consolidated and profitable pearl sector, as is the case in Asia and the South Pacific (Saucedo et al., 2023). As a competitive advantage, there is a small trade in natural abalone pearls that remain exceedingly rare (approximately one in one hundred thousand abalone form a natural pearl). Additionally, the technology to produce bead-seeded pearls from *H. rufescens* has gradually generated more acceptance among specialists within the pearl sector, including pearl sellers, influencers, collectors, jewelers, and specialized press. An example of this acceptance was the exhibition of *H. rufescens* pearls to the attendees of the annual forum organized in 2022 by the Pearl Guide entitled '*Pearls by the Bay*' in Sausalito, California (USA) (Rubén Araya, *pers. obs.*). During this event, a mean price of US$200 per carat of nacre was estimated for *H. rufescens* bead-seeded pearls, considering not only the current value per carat of natural abalone pearls, but a series of sustainability criteria that these abalone pearls have for their formation at *UCA* in Chile (e.g. use of recirculation systems, disposal of solid wastes, management of kelp forests, and incorporation of animal welfare programs). These criteria are consistent with environmental requirements proposed by Burke et al. (2001) for farmed abalone.

As a complement to the *Pearls by the Bay* forum, separate samples of *H. rufescens* bead-seeded pearls were donated to the *Gemological Institute of America (GIA)* museum and also used for specific scientific analyses. The results of the analyses indicated that, structurally, spectroscopically and chemically, these cultured abalone pearls (of baroque shapes) are similar to natural abalone pearls (also baroque), which are very rare (Homkrajae et al., 2023). This confirms the commercial value of *H. rufescens* cultured pearls. Undoubtedly, these unique pearls represent the first of their kind in the Western hemisphere and their production may be a positive addition to the gem and jewelry sectors. Because of this, the company *Atacama Pearls* recently started marketing strategies for their commercialization in jewelry, highlighting their origin in north Chile through the patented technology (Araya et al., 2016).

Unlike pearl oysters, whose economic value is well established for most of the South Eastern and South Pacific nations, there is no market study to date that estimates the exclusive commercial potential of abalone pearls in any region of the planet. Despite this, the potential of these cultured pearls is estimated to be high, particularly in the west coast of the United States (California), where the demand for marine pearls is expected to increase by 13% from 2021 to 2025, according to Forbes 2018 (Danziger, 2018). Two arguments support this estimate: First, the valuation of the renewable origin of marine pearls, compared to other gems and gemstones of non-renewable mineral origin. Second, the recognition by jewelers, gemologists and pearl lovers that cultured abalone pearls represent a unique type of baroque pearl with colors and shades different from pearls commonly produced by pearl oysters and freshwater mussels. This feature turns abalone pearls into rare and exotic gems with an interesting future within the global pearl sector; in Chile, this is being evaluated by the scientific and technological area of APT-SpA and *Atacama Pearls*.

In conclusion, the dual-crop farming of *H. rufescens* to produce canned medallion and pearls represents an aquaculture activity with considerable potential for growth and technological development in Latin America. To date, the evidence indicates that pear culture does not affect meat culture at all. To achieve the proposed goal, it is necessary to identify key bottlenecks that prevent this sector to achieve its full potential in the region. One of the main challenges for the near future is the improvement of very specific steps of the seeding surgery, particularly with regard to pearl sac formation. For this, we recommend using histological, histochemical and molecular tools to characterize the functional anatomy of mantle tissue and describe the cellular changes occurring during pearl sac development. Identifying the genes encoding for nacre deposition and color during this process may also help producing pearls in tones and overtones more attractive to the global pearl sector. Scaling-up abalone pearl production is also considered as part of the activities of the *Atacama Pearls* project in Chile.

Funding statement

Part of the data generated in this review received funding from National Research Agency (ANID), Corporación de Fomento Productivo (CORFO) and Fondo de Innovación de la Competitividad del Gobierno Regional de Antofagasta.

CRediT authorship contribution statement

Araya Rubén: Conceptualization, Formal analysis, Funding acquisition, Investigation, Project administration, Validation, Writing – original draft, Writing – review & editing. **Sáez-Saavedra Camila:** Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Acosta-Salmon Hector:** Investigation, Validation, Writing – review & editing. **Saucedo Pedro E.:** Conceptualization, Formal analysis, Investigation, Supervision, Validation, Writing – original draft, Writing – review & editing. **Tanguy Arnaud:** Formal analysis, Investigation, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that influenced the work reported in this review.

Data Availability

Data will be made available on request.

Acknowledgements

This review reports part of the results of the doctoral thesis prepared by C.S.S. at Universidad de Antofagasta, Chile (fellowship from the *Comisión Nacional de Investigación Científica y Tecnológica* RE-2736). Other data presented here originated from projects funded in Chile by the *National Research Agency* (ANID, MEC #80110045), *Corporación de Fomento Productivo* (CORFO #12IDL2–16176 and #15VEIID-45595) and *Fondo de Innovación a la Competitividad del Gobierno Regional de Antofagasta* (FIC BID #30488446–0). We thank the staff involved in the start-up and development of *Unidad de Cultivo de Abalón* of Facultad de Ciencias del Mar y Recursos Biológicos, Universidad de Antofagasta: Alejandro Rojas-Figueroa, Sebastian Gallardo, Felipe Chávez, Roberto Pizarro, Fabián Castillo, Andrea Moreno and Jimmy Villanueva. Some entrepreneurs who also participated in this process are Alex Abumohor and Alex Poblete (*Cultivos Live Sea Food and Chilesan*), Joaquín Prieto and Rafael Crisostomo (*Aquaoceana S.A.*) and the staff from the *Office of Transfer and Licensing (OTL)* of Universidad de Antofagasta. Special thanks to Jaime Maturna (Abalone Pearl Technology APT-SpA) for providing information on the market study that estimates the commercial potential of cultured *H. rufescens* pearls. We finally thank Alejandro Rojas-Figueroa (doctoral student at Centro de Investigaciones Biológicas del Noroeste: CIBNOR, Mexico) for donating mantle tissue microphotographs, Diego A. Saucedo for editing some of the images of bead-seeded pearls, and Chris Harrod (Universidad de Antofagasta) for editing the English of this manuscript.

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