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Chorion in fish: Synthesis, functions and factors associated with its malformations

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ABSTRACT

The chorion is an acellular envelope surrounding the oocyte. In fish, this envelope plays a pivotal role during fertilization and protects the developing embryo against environmental and mechanical factors until the moment of hatching. The chorion comprises a diverse number of glycoproteins called choriogenins, for which synthesis is mediated by the plasma concentrations of estradiol-17β hormone. In fish, its synthesis can occur in the liver, the oocyte or both, depending on the species. The quality of this envelope, as well as other intrinsic characteristics of the egg (its genes, its maternal mRNA transcripts, and the composition of the yolk) can be affected by environmental and/or nutritional factors and, therefore, the quality and/or embryo survival. The analysis of the studies carried out on the chorion and the factors associated with its quality are required in identifying practical solutions for the aquaculture industry, especially for those dedicated to producing and selling embryos, considering that the presence of these malformations can lead to economic losses. Thus, this review analyzed some reports on fish chorion malformations and highlights the need for specific studies on the factors that influence these alterations, especially those related to the diets and nutritional status of reproductive females. Although there are studies that allow us to infer how environmental or nutritional factors can affect the biology of the chorion, there is an evident need for other studies that directly relate the molecular machinery of choriogenesis with the occurrence of malformations. This review summarizes the knowledge of the genesis of the chorion and gives an approach to the effect of environmental and/or nutritional factors on its quality and embryo survival to establish perspectives for future studies.

1. Introduction

In the food industry, aquaculture is considered the fastest developing sector (Gephart et al., 2020). This provides more than 50% of the production of aquatic organisms for human consumption, whose apparent consumption, not including algae, has increased at an average annual rate (3% between 1991 and 2019) greater than the human population (1.6%, in the same period) (Peñalosa-Martinell et al., 2020; FAO, 2022). In fish, one of the biggest challenges is to guarantee the good quality of the eggs, that is, eggs that present high fertilization rate, high survivability at the different critical stage (eyeing, hatching and first feeding) and that generate viable offspring (Callet et al., 2022). An acellular layer surrounds fish eggs with multiple functions, including the embryo's protection against sudden changes in the physical-chemical incubation conditions (Bonsignorio et al., 1996; Kholodnyy et al., 2020; Yanagimachi, 2020; Valdebenito et al., 2021).

This acellular layer receives several names,(Litscher and Wassarman, 2018) and for this review, it will be named chorion. Fish's chorion has one or more layers (Sugiyama et al., 1999; Modig et al., 2007; Murata et al., 2014), from proteins synthesized in organs such as the liver, the oocyte or both, depending on the species (Modig et al., 2006; McMillan, 2007; Litscher and Wassarman, 2018). The estradiol-17β hormone (E2) regulates the synthesis of these proteins (Sugiyama et al., 1999; Montserrat et al., 2004; King et al., 2007; Miller, 2007; Modig et al.,

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2007; Ramezani-Fard et al., 2013). The fish chorion helps prevent polyspermy by breaking the cortical alveoli and subsequent release of their contents, creating the perivitelline space (Hyllner et al., 2001; Valdebenito et al., 2013; Rojas et al., 2021). In addition, it provides further protection to the embryo during its development (Bonsignorio et al., 1996; Vijay and Sehgal, 2020). Chorion function ends with hatching (Babin et al., 2007). For the first case, the chorion is considered impenetrable to spermatozoa. It allows the oocyte to be fertilized by a single spermatozoon through of one micropyle (as in salmonids) or more (in Acipenseridae or sturgeons) (Siddique et al., 2014; Valdebenito et al., 2013). Micropyle is formed by follicular cells modified and differentiated as specialized micropylar cell (McMillan, 2007).

Therefore, maintaining the quality of the chorion is a crucial point to guarantee not only the egg fertilization but also the survival of the embryo and the ability to deliver a viable larva (Bobe and Labbé, 2010). In a recent study, increased malformations of this envelope (described as soft egg, perforated egg, white-spotted egg and dark egg) were reported for salmonids produced in Chile (Valdebenito et al., 2021). Furthermore, problems in the embryos' hatching time and hatchability were evaluated by analyzing the chorion ultrastructural morphology and the SDS-PAGE electrophoretic characterization of its proteins [choriogenins (Jaramillo et al., 2009, 2012)].

A total infection rate of approximately 10% has been estimated for salmonid eggs with some kind of chorion malformations (Bruno et al., 2011). These infections may be due to opportunistic pathogens related to soft-egg malformation. This malformation represents between 3% and 5% for Lake Oahe salmon (Barnes et al., 2003), 0.5–35% for *Salmo salar*, 7.4–10% for *Oncorhynchus kisutch* and 0.6–5.7% for *Oncorhynchus mykiss* in eyed-eggs (Valdebenito et al., 2021).

Some studies infer that factors such as water temperature (Cousins and Jensen, 1994; Pankhurst et al., 1996; Korwin-Kossakowski, 2008), water pH (Haya and Waiwood, 1981; Marimuthu et al., 2019; dos Santos et al., 2020), water hardness (Barnes et al., 2003) or the presence of opportunistic pathogens (Songe et al., 2016a, 2016b) could be associated with malformations in the conformation of the chorion. Another factor that possibly influences its quality is broodstock nutrition (Xu et al., 2019; Król et al., 2021). For example, the dietary content of marine ingredients replacement by plant-origin raw materials. In a study carried out with olive flounder (*Paralichthys olivaceus*) on the maturation process, it was shown that the replacement of 30% fishmeal by plant ingredients resulted in a low hepatic expression of estrogen receptor (ER)α, ERβ and follicle-stimulating hormone (FSH)β (Park et al., 2021), which are biological markers associated with the biosynthesis of chorion proteins. However, little information is associated with the effects of plant ingredients on chorion conformation or structure development. Thus, this review aims to analyze the studies on fish chorion malformations and the factors associated with their occurrence, conformation process and importance during fertilization, embryonic development and survival, with a final focus on nutritional aspects.

2. Fish chorion

A fibrillar and elastic acellular layer surrounds all fish eggs with a species-dependent thickness (Eddy et al., 1990), and which width can vary ranging from 1.3 μm in *Danio rerio*, 30–60 μm in *Salmo salar* or up to 100 μm in *Acipenser transmontanus* (Litscher and Wassarman, 2018). Before ovulation, the fish chorion is a structure that is synthesized, produced, and developed by exocytosis between the oolemma and the granulosa cells, through which microvilli protrude (Lubzens et al., 2010). The different names it receives, such as zona pellucida (ZP) or egg envelope (Litscher and Wassarman, 2018), are probably associated with the oocyte development stage before ovulation or if it corresponds to a fertilized egg. For example, some authors call it zona radiata (ZR) even after the oocyte fertilization in coho salmon [*O. kisutch* (Cousins and Jensen, 1994)]. On the other hand, for carp (*Cyprinus carpio*), the envelope that protects the embryos has been defined as the fertilization envelope (FE), that is because the eggs of some fish species, such as the carp, are adhesive. In this case, after oocyte fertilization, new components are added to the chorion from the cortical alveoli egg surface (Chang et al., 2002; Wang et al., 2021), and it was shown that the number of layers that make up the chorion in *C. carpio* could be reduced during hardening (Luchi et al., 1991). A diverse number of glycoproteins make up the structure of the chorion (Mold et al., 2001), and this set of proteins is called by various names such as zona radiata proteins [Zrp (Arukwe and Goksøyr, 2003)], zona pellucida proteins [ZPs (Giacomini et al., 2011; Litscher and Wassarman, 2018; Betsy and Kumar, 2020)], vitelline envelope proteins [VEP (Modig et al., 2007)] or choriogenins [Chg (Yamagami, 1996; Hara et al., 2016), name that will be used for this document.

Choriogenins synthesis can occur in the liver [e.g. *Gadus morhua, Hippoglossus hippoglossus* (Oppen-Berntsen et al., 1992b; Litscher and Wassarman, 2018), in the oocyte [e.g. *D. rerio* (Modig et al., 2007; Litscher and Wassarman, 2018)] or in both [e.g. *Oryzias latipes, Sparus aurata, O. mykiss* (Hyllner et al., 2001; Litscher and Wassarman, 2018; Modig et al., 2007, 2006)], additionally, a possible triple origin (liver, oocyte and follicular cells) was reported for white sturgeon [*Acipenser transmontanus* (Murata et al., 2014)]. Choriogenins synthesis (summarized in Fig. 1) depends of the novo synthesis of cholesterol, a precursor of the hormone estradiol-17β (E2), E2 receptors (ER) and other endocrine processes in female fish (Miller, 2007). This synthesis has already been previously described by other authors (Sugiyama et al., 1999; Le Menn et al., 2007; Berois et al., 2011; Murata et al., 2014; Hara et al., 2016;). Chorion fish can be made up of 2–4 glycoprotein layers; the number of Chg will depend on the state of maturation of the oocyte during oogenesis (Murata et al., 2014), the embryonic development (Jaramillo et al., 2015), and the species (Modig et al., 2007) (Table 1). Inconsistencies and a lack of standardization were observed in the nomenclatures used for the chorion layers and Chg proteins in fish, which can lead to misinterpretations. The previous makes clear the need for other studies that allow for more concise information in this regard.

2.1. Chorion functions

The chorion fulfils mechanical, physical, chemical and biological functions that seem generally conserved between different fish species. The main function of the chorion is to form an elastic and protective barrier to the embryo in interaction with the perivitelline fluid (Eddy and Talbot, 1985; Bonsignorio et al., 1996; Shibata et al., 2000). After fertilization or egg activation, the yolk, bounded by the vitelline membrane and the embryo, are contained in the perivitelline fluid encased by the chorion (Eddy and Talbot, 1985). Thus, the chorion protects the embryo against mechanical actions, drying, and abrupt changes in the physicochemical conditions of the milieu. In addition, it also involves nutrients uptake, fertilization, and control of pathogen agents until hatching (Valdebenito et al., 2021). The above-mentioned is summarized in that the chorion fulfils vital functions for embryonic and larval survival since it promotes protection from environmental conditions and allows the diffusion of gases (Chang et al., 1996, 1997; Fan et al., 2001; Mold et al., 2001) and metabolic waste products, in addition to providing mechanical protection and thermal insulation to the embryo (Iconomidou et al., 2000).

Fish chorion has one (e.g. salmonids) or several (e.g. sturgeons) orifices called micropyles, through which the spermatozoa penetrate during fertilization (Berois et al., 2011; Valdebenito et al., 2013; Murata et al., 2014; Siddique et al., 2014). Fish chorion playing a vital role in sperm-egg interaction (Kholodnyy et al., 2020) and preventing polyspermy (Foltz, 1995; Siddique et al., 2014). In some fish species (e.g. flounder, herring, salmon, medaka), fertilization occurs due to the signalling of specific glycoproteins on the surface of the chorion, which acts as signalling or by activating areas of the sperm, as a species-specific mechanism (Yanagimachi et al., 2013). Among the glycoproteins are the sperm motility initiation factor (SMIF, e.g. in herring), and the

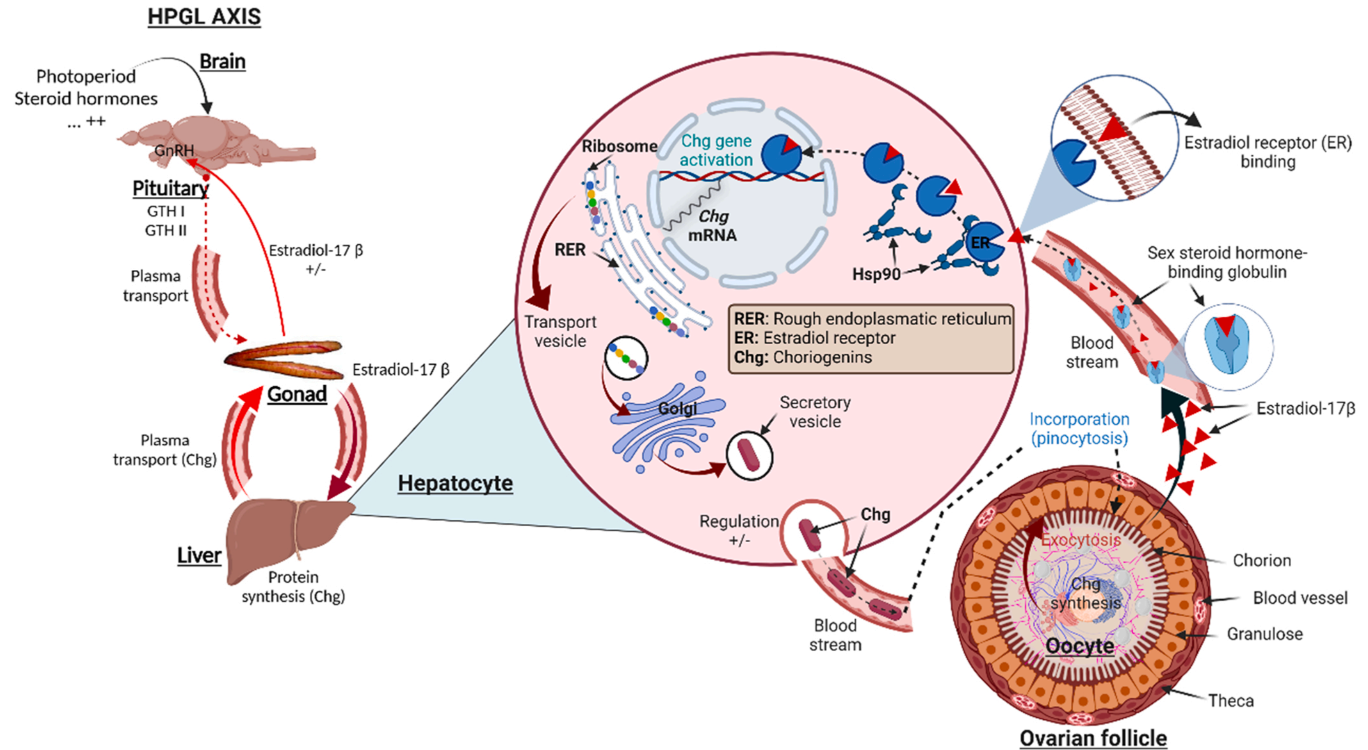

Fig. 1. Model of hepatic choriogenesis regulated by estradiol-17β hormone (E2) in fish. In brief, Chg synthesis are regulated by the E2 hormone, which is released by follicular cells and transported by sex steroid hormone-binding globulin through blood plasma to the hepatocyte. After E2 reaches the hepatocyte, it binds to a specific ER which binds to a heat shock protein 90 (Hsp90) from which it is it dissociates during the ligand-binding process, undergoing dimerization before entering the nucleus. Subsequently, Chg are extensively synthesized and modified in the RER with oligosaccharides, secreting and assembling in a cross-linked filament with structural repetition. The modified Chg is secreted and transported into the ovary via the bloodstream for pinocytosis and finally to the space between the granulose cells and the basement membrane of the oocyte by exocytosis. The E2, added to testosterone, exert regulatory mechanisms on gonadotropins GTH I and GTH II, necessary in the functioning of the HPGL axis. HPGL axis: Hypothalamic-pituitary-gonad-liver axis. Chg: Choriogenin. GTH I/II corresponds to FSH and LH in mammals, E2 receptor (ER), rough endoplasmic reticulum (RER). Created with BioRender.com.
Adapted from Arukwe and Goksøyr,(Arukwe and Goksøyr, 2003) Modig et al.,(Modig et al., 2007) and Hara et al.(Hara et al., 2016).

Table 1
Nomenclatures used for some fish species for the layers and proteins (choriogenins) that make up the chorion in different stages of maturation and tissues for identification of the synthesis site. Al: adhesive layer; Zri: zona radiata interna; O, outer layer of the egg envelope; ZI-(1,2), ZI-3; L1, L2, L3, Z1, Z2 and Z3 are the layers of chorion. Chg H, Chg L, ZP, VEP; these are the nomenclatures given for the chorion proteins for different species of fish.

Species	Identification site	Chorion layer (macromolecuar composition)	Choriogenins proteins	
Oryzias latipes	Unfertil ized egg envelopes	ZI-1,2 and ZI-3	Choriogenin H (Chg H) and L (Chg L)	(Sugiyama et al., 1999)
Sparus auratus	Chorion (eggshell) – Ovarium tissue	-	ZP1a (77 kDa), ZP1b (55 kDa), ZP3 (49 kDa) and ZPx (86 kDa)	(Modig et al., 2006)
Acipenser transmontanus	Stagio III ovary Ovulated egg	L2 and L3 Zri (L1, L2 and L3 - Inner to outer layer); Zre (O)	ChG1 and ChG2 (86–100 kDa) and ChG4 (47 kDa) - Tree chorion proteins inmunolocalizadas in the liver and ovary for Western blot analysis	(Murata et al., 2014)
Oncorhynchus mykiss	Liver tissue	-	VEPα, VEPβ and VEPϒ - Transcription site of the VEP RNAm determined from the total RNA extracted from the liver	(Hyllner et al., 2001)
	Gonads	-	VEPϒ - Transcription site of the VEP RNAm determined from the total RNA extracted from the female gonads	
	Hepatocytes	-	zrα (60 kDa), zrβ (55 kDa) and zrϒ (50 kDa)	(Oppen-Berntsen et al., 1992a)
Danio rerio	Mature oocyte	Z1, Z2 and Z3 (Outer to inner layer)	116 kDa, 97 kDa, 50 kDa and 43 kDa	(Bonsignorio et al., 1996)
Gadus morhua	Mature oocyte	-	α (74 kDa), β (54 kDa) and ϒ (47 kDa).	(Oppen-Berntsen et al., 1990)
Salmo salar	Chorion samples after hatching	-	179 kDa, 157 kDa, 54 kDa and 55 kDa - Molecular weight of four chorion protein extracts from normally hatched embryos (obtained with SDS-PAGE)	(Jaramillo et al., 2012)

micropylar sperm attractant (MISA, e.g. in salmonids) and its absence could make fertilization inefficient (Yanagimachi et al., 2017).

The chorion also has the function of guiding the sperm, for some fish species, due to the presence of grooves through the micropyle. These grooves allow sperm to travel preferentially towards the invagination forming the micropyle or micropylar pit on the surface of the chorion at the animal pole (Kinsey et al., 2007; Modig et al., 2007). In addition, it is considered that micropyle size may contribute to the expulsion of sperm from heterologous species sperm (Kinsey et al., 2007) since those characteristics such as the number, diameter, and surface structure of the micropyle are species-specific (Kim and Park, 2021).

The FE is many fish species, mainly freshwater such as cyprinids, Coregonus, or some percids is the external part of chorion made up mainly of neutral or acidic mucopolysaccharides and is responsible for the eggs adhering to the substrate allowing appropriate incubation conditions (Kudo and Teshima, 1991; Linhart et al., 1995; Murray et al., 2013; Zarski et al., 2015). There is evidence that the chorion has bactericidal properties and is effective against Gram-positive and Gram-negative bacteria (Modig et al., 2007). However, this bactericidal effect only occurs from the activation or fertilization of the oocyte due to the production of enzymes such as phospholipase D, lysozyme, proteinases, and DNases present in the FE, as is the carp's case (Kudo and Teshima, 1991). Protection against pathogens (bacteria, viruses, water moulds, fungi, metazoans, and protozoan parasites) that cause infectious diseases in aquaculture fishes, crustaceans, and molluscs (Sakaguchi et al., 2022) is preceded by the hardening of the chorion (Wang et al., 2021). The hardness of the chorion also makes it resistant to other factors such as drugs, enzymes (Modig et al., 2007), water temperature, pH, and oxygen, allowing these factors not to affect the embryo immediately but after continuous and prolonged exposure to them.

3. Chorion malformations

Chorion malformations (Fig. 2) are recurrent in fish farms during embryo development; however, their incidences and features have rarely been reported. A recent retrospective study with salmonid embryos in the eyed-staged identified and described five chorion malformations [soft (Fig. 2 A(a,b) and B), bubbles Fig. 2 A(c), white-spotted (Fig. 2 C), perforated (Fig. 2D), and dark (Valdebenito et al., 2021)]. Another malformation has been reported under the name of hard chorion (Jaramillo et al., 2012). Other studies carried out with fish also reported the presence of soft (Cousins and Jensen, 1994; Barnes et al., 2003; Valdebenito et al., 2021) or hard chorion (Masuda et al., 1991; Jaramillo et al., 2012, 2015; Wang et al., 2021), however, no other studies were found reporting the presence of perforated, white-spotted or dark embryos. The chorion with a disc has been another of the malformations identified for embryos of *S. salar*, however, no reports or studies on it were found (Fig. 2E and F).

Mais Thus, alterations in this structure could compromise the quality of the eggs. Egg quality can be defined as the ability to produce a normal embryo (Ubilla et al., 2016), but it also refers to the ability of the gametes to present high embryonic survival (Valdebenito et al., 2013). Embryo survival in pikeperch (*Sander lucioperca*) was positively correlated with chorion malformation (flaccid and collapsed structural appearance of the chorion on the egg plasma membrane) within the first 3–5 min after egg activation. This appearance begins to recede after 5 min after activation (Zarski et al., 2012). This occurs thanks to the hydration capacity of the egg and the action of the cortical granules that form the previtelline space (Lahnsteiner et al., 2001; Lahnsteiner and Patzner, 2002). The endocrine status of the female during oogenesis, the broodstock diet, nutrients deposited into the oocyte, and the physiochemical and pathogenic conditions of the water in which the eggs are subsequently incubated are some components that affect egg quality (Brooks et al., 1997).

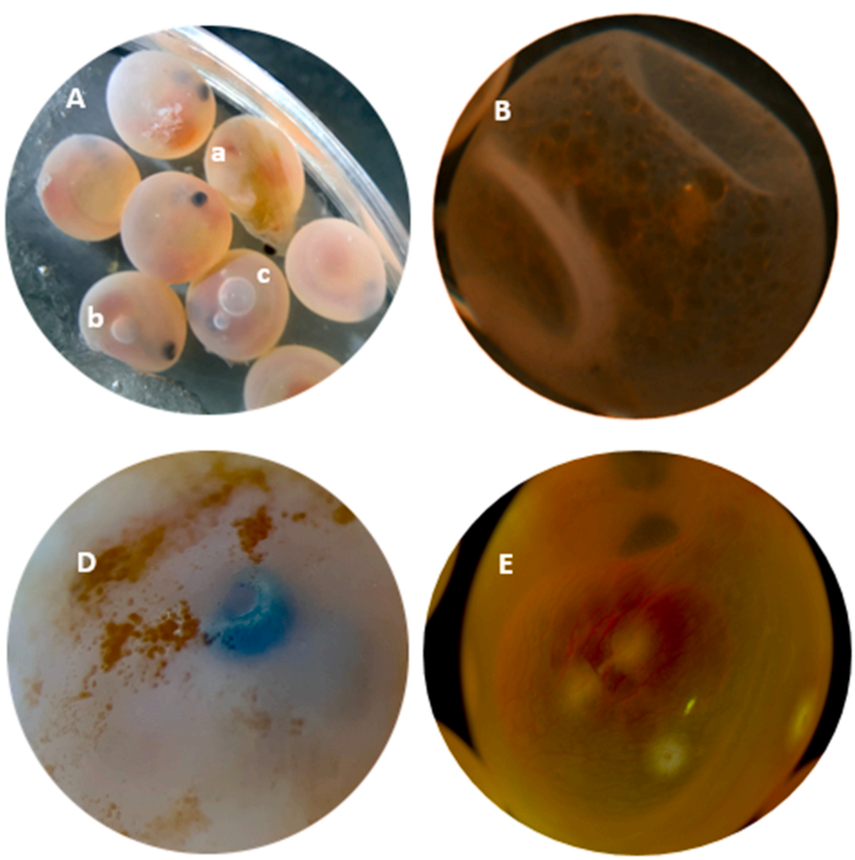

Fig. 2. Some malformations identified in the chorion of Atlantic salmon (*Salmo salar*) embryos. A(a). A type of soft chorion where the embryo hatches prematurely; A (b). Another type of soft chorion where full turgor (elevation) of the chorion is not achieved and presence of bubbles; A(c). Embryo with presence of bubbles; B. Soft chorion, without complete turgor of the embryo or elevation of the chorion; C. Spotted chorion (presence of white spots); D. Perforated chorion; E. Chorion with discs; F. Chorion presenting discs and some perforations in the center of the disc.

3.1. Soft chorion

Soft chorion (Fig. 2 A(a,b) and B, also known as soft shell disease or soft egg disease, is an abnormality often noted during the incubation of fish eggs, induced by the loss of their hydrostatic pressure causing the shell of this egg to sink around the embryo; this can generate early hatching that is followed for the embryo death (Cousins and Jensen, 1994). This is a malformation frequent in salmonids, as shown in studies carried out with chinook salmon (*Oncorhynchus tshawytscha*), *O. kisutch* and *S. salar* (Cousins and Jensen, 1994; Barnes et al., 2003; Valdebenito et al., 2021). The presence of soft chorion could be associated with mutations in the breeders. A study showed that *larp6α D. rerio* mutant females presented defective chorion in developing oocytes; moreover, the envelope of their eggs presented a defective layer structure, reduced elevation or turgidity, fragility and altered protein composition (Hau et al., 2020). The chorion thickness is associated with the vulnerability of the egg to infectious agents such as *Saprolegnia* (Songe et al., 2016a). In particular, infectious diseases that frequently occur in farms, and their treatments, lead to the presence of soft chorion. These infections are caused by oomycetes (*S. Aphanomyces, Achlya and Pythium*), bacteria or amoebas that cause dissolution and rupture of the chorion (Sakaguchi et al., 2022).

3.2. Hard chorion

Before ovulation, the chorion appears as a soft envelope, and its hardening increases and continues after ovulation occurs, generally preceded by fertilization (Jaramillo et al., 2012). This envelope is permeable to water and the molecules contained in it even after it has hardened, as shown in *O. latipes* (González-Doncel et al., 2003), but the permeability decreases and is limited to the external part of the chorion as previously reported for *S. salar* (Potts and Rudy, 1969). During chorion hardening, the elastic fibres of this envelope expand with increasing osmotic pressure (McMillan, 2007) and the cortical granule exocytosis creating the perivitelline space (Valdebenito et al., 2013). The cortical granule exocytosis is a Ca^{2+} dependent process. The interaction of Ca^{2+} with other ions such as Zn^{2+} and Mg^{2+} promote the prevention of polyspermy in addition to chorion hardening (Converse and Thomas, 2020; Rojas et al., 2021).

In the case of fertilized oocytes, embryonic development begins on the protection of the hardened chorion (Shibata et al., 2000). Chorion hardness occurs after oocyte activation, hydration and/or fertilization (Cotelli et al., 1988; Luchi et al., 1991; Masuda et al., 1991; Shibata et al., 2000). According to Wang et al. (2021) the post-fertilization hardening of the chorion is an evolutionarily conserved phenomenon across species and can be summarized in two steps. First, a metalloprotease (alveolin) hydrolyzes the N-terminal region of proline-glutamine (Pro-Gln) of the ZP1 (Chg1), which leads to a second moment where intermolecular cross-linking to ZP3 (Chg3) catalyzed by transglutaminase (TGase) is triggered. Therefore, the biochemical function and the interaction of the metalloprotease, TGase, peroxidase/ovoperoxidase, and other factors (carbohydrate moieties, zinc and its transporter ZIP9, and Larp6 proteins), among others, are essential to egg chorion hardening in mammalian and nonmammalian species, including fish (Converse and Thomas, 2020; Hau et al., 2020; Rojas et al., 2021; Wang et al., 2021).

Hard chorion malformation is associated with alterations in the structural organization of the protein fibres that make up the chorion of partially or incompletely hatched embryos (Jaramillo et al., 2009, 2012). A property that probably indicates an abnormal hardening of fish chorion and changes in its morphology is associated with reducing susceptibility to proteases, as shown in mice (Longo, 1981). Protein changes in the chorion structure that promote its hardness can lead to decreasing size of the internal layer pores (Jaramillo et al., 2009, 2012), limiting the function of the hatching enzyme, known as chorionase or choriolysin (proteolytic endoprotease). This initiates the degradation process of the internal wall of the chorion, producing the progressive thinning and weakening of this envelope, which facilitates hatching [rupture and subsequent exit of the fry with sack from inside the chorion (Yamagami, 1996, 1981)].

4. Environmental factors associated with chorion malformations

Chorion malformations can be caused by biotic and abiotic factors, promoting events such as embryo malformations or embryonic death (Barnes et al., 2003). Among these factors, physical and chemical parameters of the incubation water, age, over-maturation, and pathogens could be mentioned (Valdebenito et al., 2013). A recent review summarizes that the occurrence of shrimp diseases is directly related to environmental stress and physiological dysfunction, which can affect the immune system (Tong et al., 2022). In this sense, from the broodstock point of view; a depressed immune system could also be suggested to negatively affect their nutritional and reproductive physiology and probably affect both the ovarian and hepatic synthesis of Chg. Below are some examples of the environmental factors and how they might affect the conformation or functionality of the chorion, summarized in Table 2.

4.1. Physical factors

Temperature is considered to be one of the most important factors, if not the most important, affecting early ontogeny (Korwin-Kossakowski, 2008). Furthermore, exposure of female *O. mykiss* to high water temperatures inhibited reproduction in terms of ovulation and embryo survival (Pankhurst et al., 1996). A study carried out with salmon showed that increasing the water temperature to 13 °C led to soft chorion due to hydrostatic pressure rise, especially in the eyed-stage embryos (Cousins and Jensen, 1994). The increase in hydrostatic pressure increases as the incubation process progresses, and therefore, the tension of the chorion increases (Rombough, 1988). Cousin and Jensen (1994) associated the presence of soft chorion with alterations in the regulation of hydrostatic pressure due to opportunistic pathogens. The authors reported that tension is regulated by the upward bulging of pore channel plugs located on the surface of the chorion, which with high temperatures and accumulation of metabolic wastes, such as ammonia, could increase the hydrostatic pressure of the egg, causing the non-closing of the pores and, therefore, the entry of a type of opportunistic pathogens, such as proteolytic bacteria.

Oxygen availability is essential during embryonic development and its demand increases during hatching (Dumas et al., 2007). Restricted exchange of oxygen across the chorion affects the availability of oxygen to incubating embryos (Greig et al., 2005). This hypoxic environment can be created by the presence of organic particles (shown in *S. salar*) or certain concentrations of some heavy metals in the incubation water, for different species of fish such as *C. carpio*, accelerates or lengthens hatching time (Cornet et al., 2021; Jezierska et al., 2009). Hypoxia can also affect the proper functioning of the endocrine system (hypothalamic-pituitary-gonad-liver axis - HPGL) in females and cause transgenerational disorders and phenotypic changes (DNA methylation pattern and histone modification) (Servili et al., 2020). With the above, it could be inferred that hypoxic stress or the presence of metals in the extrinsic environment of the reproducers or embryos can affect the formation of the chorion or its function due to the possible presence of malformations such as soft or hard chorion. However, no studies were found to demonstrate this hypothesis. Therefore, future studies would be important in order to clarify this effect as possible predictors of chorion quality, both for species of commercial interest and for species that live in a natural environment.

4.2. Chemical factors

Egg quality (e.g. fertilization rate, hatching rate, embryonic survival)

Table 2
Some studies carried out on environmental factors and aging and their influence on chorion quality.

Factor		Effect	Mechanism of action	Species	Author
Physical	Fine particles (clay)	Restricting the transport of O_2 across the egg chorion	Clay particles block the pore channels of the chorion	*S.salar*	(Greig et al., 2005)
	Temperature	Increased hydrostatic pressure of eggs incubated at 13 °C	Entry of opportunistic pathogens. This could promote the presence of soft chorion	*O. kisutch*	(Cousins and Jensen, 1994)
Chemical	pH	Increased diffusion of H^+ ions to the perivitelline space (pH 5 and 6)	Reduced hydration of the perivitelline space	*P. mesopotámicus*	(dos Santos et al., 2020)
		Low pH (4.0–6.0 and 4.0–5.5)	Negative effect on hatching	*S.salar*	(Haya and Waiwood, 1981; Peterson et al., 1980)
	Antifungal agent	30 mg/L of sodium hypochlorite in incubation water for 60 min every third day	Egg softening	*O. mykiss*	(Kashiwagi et al., 2007)
Biological	Pathogen infections	Thicker chorion	A thicker chorion (42 µm) offers more protection from pathogen infections	*S. salar*	(Songe et al., 2016a)
	Saprolegnia spp.	*S. diclina:* Destruction of some areas of the chorion *S. parasitica*: Apparently intact chorion with hyphae growing within or below the chorion	Alteration of the conformation of the chorion affecting the protection of the embryo	*S. salar*	(Songe et al., 2016b)
	Ageing	Oocyte ageing	Production of reactive oxygen species (ROS) that could affect fertilization capacity or embryonic development	Review - Several fish (e.g *Carassius auratus, O. mykiss*	(Samarin et al., 2015)

can also be affected by high or low water pH, an effect that depends on the species (Marimuthu et al., 2019; dos Santos et al., 2020). For example, during incubation tests with different pH levels with *Astyanax lacustris* and *Piaractus mesopotamicus*, it was found that the pH did not result in chorion malformations or hatching problems for *A. lacustris*, unlike *P. mesopotamicos* where a low pH (5−6) resulted in malformations of the chorion (especially the division of the chorion into two parts). In addition, with pH< 9 the hatching percentage decreased (dos Santos et al., 2020). Hatching is carried out thanks to the action of an enzyme secreted by cells located in the head and oral cavity of fish larvae (chorionase), essential for hatching progress by degrading the inner layer of the chorion, ending with the mechanical action of the embryo with the breaking of the outer layer (Haya and Waiwood, 1981; Yamagami, 1996, 1981). Low water pH was also associated with the inhibition of the chorionase enzyme and the activity of the embryo, as shown in Atlantic salmon (*S. salar*) (Peterson et al., 1980; Haya and Waiwood, 1981).

In order to improve hatch rates, many chemical treatments are used for pathogen control, such as formalin, copper sulfate, potassium permanganate, hydrogen peroxide, trichlorfon, Bronopol, among others (Doan et al., 2020). Water treatment against bacterial or fungal pathogens is standard in salmon hatcheries. It was shown that a concentration of sodium hypochlorite of 30 mg/L for 60 min every third day as an antifungal agent resulted in soft chorion (Kashiwagi et al., 2007). With the above, it can be seen that the pH and some chemical components present in the incubation water are associated with the presence of chorion malformations. However, more studies with different focus on different fish species are needed in order to identify specific effects on chorion quality.

4.3. Biological factors

Over-ripeness or ageing of the oocyte refers to the time between ovulation and fertilization, which can occur inside or outside the fish's body. Is a term used in some fish species, for example salmonids, which fail to spawn naturally in fish farming systems, requiring manual extraction (Valdebenito et al., 2013; Samarin et al., 2015). Egg quality is influenced by the individual physiological conditions of fish and by over-ripeness (Mansour et al., 2008) which generate molecular modifications that are associated with limited fertilization rate, poor embryo development, larval malformation, ploidy anomalies and various other offspring abnormalities (Samarin et al., 2019).

Other deleterious effects may be due to the presence of pathogenic agents. *Saprolegnia* is responsible for significant infections of live and dead fish and eggs maintained in freshwater aquaculture facilities (Bruno et al., 2011). In salmon, it was estimated that 10% of the eggs could be infected, leading to the presence of malformations, which would represent millionaire losses for aquaculture industries (van West, 2006; Bruno et al., 2011).

It is suggested that a thicker chorion offers more efficient protection from pathogen infections. In *S. salar,* a chorion with a mean thickness of 42 µm was considered resistant to attack by *Saprolegnia* compared to those with a mean thickness of 35.71 µm (Songe et al., 2016a). One study showed that *Saprolegnia* has different colonization strategies and levels of chorion involvement, depending on the species. Thus, *S. salar* chorion infected with *S. parasitica* showed an intact structure with hyphae growing within or below the chorion, while with *S. dicline,* some areas were destroyed (Songe et al., 2016b). Probably, dead embryos not removed from incubators create an environment favourable to fungal infections capable of invading the egg chorion and degenerating it and, therefore, promote a softening of this envelope.

5. Breeding female nutrition and chorionic alterations

Broodstock nutrition is crucial for the formation of egg structures (Izquierdo et al., 2001; Tessaro et al., 2011; Xu et al., 2019; Hernandez de-Dios et al., 2022). The layers that make up the chorion are made up of different amino acids and carbohydrates (Iuchi and Yamagami, 1976; Cotelli et al., 1988). Its synthesis depends of a complex metabolic system involving cholesterol, hormone synthesis and receptor function, among others (Fig. 1). However, few studies show a direct relationship between the nutritional quality of food and the presence of chorion malformations, and other studies allowing to infer these effects (summarized in Table 3).

In marine or carnivorous fish, the substitution of vegetable meals and oils is limited and, like prolonged fasting, can result in nutritional stress of broodstock and affect, for example, the functioning of the HPGL axis or generate DNA methylation that could be transmitted multigenerationally (Tacon et al., 2006; Yamamoto et al., 2011; Hara et al., 2016; Labbé et al., 2017; Hodar et al., 2020; Weber et al., 2022). In the case of oils, the presence of anti-nutritional factors (ANFs) such as phytosterols, the low content of polyunsaturated fatty acids, especially omega-3, affecting, for example, cholesterol metabolism (Ulvund and Grahl-Nielsen, 1988; Lund et al., 2008; Foroutani et al., 2018; Sicuro,

Table 3
Some studies carried out on nutritional factors and their potential influence on chorion quality.

Species	Evaluated nutritional factor	Determined result	Possible effect on the chorion	Author
D. rerio	Inhibition the zinc transporter	Decreased exocytotic action of cortical granules during oocyte activation and after fertilization	Affects chorion hardening	(Converse and Thomas, 2020)
O. kisutch	Fasting	Reduced levels of plasmatic E2 and pituitary FSH and decreased enzyme P450 aromatase (cyp19a1a)	Poor quality of chorion conformation	(Yamamoto et al., 2011)
O. mykiss	Plant-based diet	Genes involved in cholesterol synthesis were upregulated when fed the vegetable oils diet	Decreased synthesis of Chg	(Zhu et al., 2018)
O. mykiss	Feeding level	A feed ration below 0.50% biomass can affect gonadal development and estrogen receptor expression	Decreased synthesis of Chg	(Weber et al., 2022)
P. Olivaceus	Replacing the content of fishmeal in the diet	Decreased expression of ERs and FSH-β with diets with a 30% reduction in fishmeal protein by plant proteins	Negative effects on chorion synthesis	(Park et al., 2021)
S. aurata	Fishmeal replacement by plant meal in broodstock diets	Reduced growth, feed efficiency, and liver function in offspring juveniles	Poor functioning of the liver in the juvenile stage could alter the future synthesis of Chg	(Xu et al., 2019)
-	Anti-nutritional factors (ANFs) - Phytates	Chelate Zn or other minerals or even form complexes with proteins	Negative effects on the chorion synthesis or its hardening after ovulation	(Bandara, 2018)

2018; Zhu et al., 2018). On the other hand, the substitution of 30% of fish meals by proteins of vegetable origin resulted in the decrease of the expression of the genes that produce the FSH-β and ERα and β proteins in *P. olivaceus* (Park et al., 2021). In *S. aurata*, substituting fish meals for vegetable meals in broodstock feed affected the progeny liver function (Xu et al., 2019).

Some vegetable ingredients, such as soybean meal, have ANFs that can chelate Zn or other minerals or even form complexes with proteins, as is the case with phytates (Bandara, 2018). Zinc is a cation incorporated during the oocyte's maturation into the interior of the cortical granules and contribute to the chorion hardening during the activation and/or hydration of the eggs due to the exocytosis of its granules (Rojas et al., 2021). In mutant *D. rerio* (*zip9* $^{-/-}$) was compared with a wild type (*zip* $^{+/+}$), resulting in low chorion elevation, low fertilization rates and a higher percentage of malformations during embryonic development and embryos of free life (Converse and Thomas, 2020).

Based on the need for substitution or a possible elimination in the future of fishmeal or fish oil, it is hypothesized that this substitution or some characteristics associated with these substitute raw materials, such as FANs, may affect the quality of the fish chorion or lead to the presence of malformations of this envelope in different species of fish, especially those of commercial interest. Likewise, the Chg proteins or genes related to their synthesis obtained from the blood of mature females, from the eggs or from their progeny, can be used as biomarkers of endocrine alterations caused by nutritional factors.

6. Future perspectives and studies challenges

The previous review summarized the main characteristics of the chorion, its importance and main information identified. It was possible to find that both nutrition and environmental factors are critical aspects, which require further studies to understand how soft, hard, or other chorion malformations can occur to a lesser or greater extent in different fish species, especially those of economic interest. The baseline for research in relation to the effect of the different factors that affect the synthesis of the chorion or its functioning after ovulation, fertilization or during embryonic development, is the standardization of nomenclatures and concepts associated with this envelope (layers of the chorion, choriogenin proteins), in order to obtain consistent information and avoid possible errors in the interpretation of the information, which would facilitate future studies.

Future studies that allow explaining, for example, how the presence of ANFs in aquafeeds, the substitution of marine origin ingredients, in addition to water temperature, pH, oxygen and/or their combined effect, can affect the expression of genes associated with the functioning of the HPGL axis and/or the chorion. In the case of genes associated with the HPGL axis, responsible for producing the FSH, LH, E2 or estradiol receptors (ER), among others, could be considered. There are also the *larp6* and *zip9* genes, where their downregulation affects the ability to elevate the chorion during hydration and/or after fertilization, an effect that could be associated with the presence of a soft chorion.

The conjugated use of techniques such as the structural characterization of the chorion with electron microscopy, electrophoresis for the separation of proteins by their molecular weights or the identification of specific proteins, ELISA, added to studies of proteomics, metabolomics, genomics, epigenomics, will be keys to study the phenological, physiological and molecular effects of nutrition and the environment on the synthesis, the quality of the chorion and the presence of malformations in this envelope.

As previously observed, both the nutritional quality and the water environment (e.g. temperature, pH) in which the broodstock are kept can affect the endocrine system. Therefore, the identification of choriogenins in the ovary or those transported from the liver to the blood and from there to the developing oocyte could be a potential biomarker of endocrine alterations, knowing that E2 is the inducer of these proteins. Additionally, it could also be used as a predictive biomarker of egg quality in fish depending on the type of stress (nutritional or environmental) to which the breeding female may be exposed during oogenesis.

All of the above requires synergistic work between the aquaculture industry, universities, development companies, among others, for the creation of, for example, portable technologies (e.g. that include protein profile analysis, identification of epigenetic modification markers, among others), which will facilitate direct work in the field (e.g. aquacultures), reducing the cumbersome task of storing and/or transporting samples to laboratories, seeking to have increasingly agile responses to problems associated with egg quality.

CRediT authorship contribution statement

Maritza Pérez Atehortúa: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision. **Adrián J. Hernández Arias:** Conceptualization, Methodology, Validation, Writing – review & editing. **Patricio Dantagnan:** Methodology, Validation, Writing – review & editing. **Mauricio Silva Jiménez:** Conceptualization, Methodology, Validation, Writing – review & editing. **Jennie Marianne Risopatrón González:** Methodology, Validation, Writing – review & editing. **Jorge G. Farías:** Methodology, Validation, Writing – review & editing. **Elías Gustavo Figuero Villalobos:** Conceptualization, Methodology, Validation, Writing – review & editing. **Iván Valdebenito Isler:** Conceptualization, Methodology, Investigation, Writing – original draft, Supervision, Resources, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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