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Lipid modification to improve cryotolerance of gametes, embryos and larvae and its potential application in aquaculture species: a review

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Cryopreservation is a technique to maintain biological materials' physiological and genetic stability at an ultralow temperature. For commercially important livestock or aquatic species, gamete and embryo cryopreservation could play a significant role in breeding programs and commercial production. For example, it could help overcome key problems such as asynchronous maturation and an unbalanced sex ratio. However, the physiochemical stresses imposed by cryopreservation can negatively affect gametes and embryos, leading to a poor survival rate. Recent studies on cryoinjury have demonstrated that the cryosensitivity of lipids is one of the key causes of cryodamage in mammalians, as lipid compositions in membranes of gametes and embryos are closely related to their cryoresistance. In addition, the cryotolerance of gametes and embryos in some mammalian species has been improved by lipid modification. However, studies on the role of lipids in the cryopreservation of gametes, embryos, and larvae are rare in fish and shellfish. Therefore, this review focuses on recent methodological advances to improve cryotolerance by lipid modification, including lipid application or manipulation in human and livestock sperm, oocytes, and embryos, and how these novel approaches could improve cryopreservation techniques in aquatic species, especially for oocytes and embryos.

KEYWORDS

cryopreservation, lipid application, sperm, oocyte, embryo, larva, aquaculture

1 Introduction

Cryopreservation is a technique to store living materials (such as gametes, embryos, larvae, cells, and tissues) at an ultralow temperature to maintain their long-term physiological and genetic stability (Kopeika et al., 2015; Dhali et al., 2019). Cryopreservation of gametes, embryos and larvae (fish and shellfish) could play a significant role in reproductive and genetic improvement programs for commercially important livestock or aquatic species. It could also reduce the costs of transporting live animals for breeding and manage issues related to asynchronous maturation and unbalanced sex ratios (Huang et al., 2019; Díaz et al., 2021). The development of gamete and embryo cryopreservation protocols has been an integral step in advancing assisted reproductive technology (ART). From the first human infant derived from frozen sperm in 1953 (Bunge and Sherman, 1953) to the first human live birth after embryo cryopreservation in 1984 (Zeilmaker et al., 1984), ART in humans has become a mature technique. Cryopreservation techniques have also been greatly improved in livestock and pet animals (Galiguis et al., 2014; Mandal et al., 2014; Nagashima et al., 2015). In addition, the technical details of the governing factors and mechanisms contributing to cryoinjury have been gradually revealed (Kopeika et al., 2015; Dhali et al., 2019).

Several physical and chemical factors causing severe cryoinjuries have been reported in previous reviews in mammalian species (Amstislavsky et al., 2019; Dhali et al., 2019). Among them, intracellular ice crystal formation, osmotic shock, free radicals such as reactive oxygen and nitrogen species (ROS and RNS), and lipid phase transition (LPT; a transition from a liquid phase to a crystalline-gel phase) are the primary factors causing cryoinjuries (Figueroa et al., 2019). Additionally, many adverse impacts of cryopreservation have been identified. For example, frozen-thawed sperm are characterized by lower motility, acrosome integrity, and mitochondrial membrane potential, resulting in low fertilization capacity (O'Connell et al., 2002; Ozkavukcu et al., 2008; Ugur et al., 2019). Fracture and membrane damage, mitochondrial dysfunction, and rupture and disruption of the cytoskeleton structure can negatively impact the further development of cryopreserved oocytes and embryos (Saunders and Parks, 1999; Kasai, 2002; Iussig et al., 2019; Gualtieri et al., 2021). At the molecular level, genomic DNA lesions and mitochondrial DNA damage have been detected in cryopreserved mammalian gametes and embryos (Lin and Tsai, 2012; Valcarce et al., 2013; Liu et al., 2016). Additionally, epigenetic and transcriptomic profiles are also susceptive to the stress caused by cryopreservation (Chatterjee et al., 2017; Barberet et al., 2020).

Lipids are hydrophobic or amphiphilic molecules, including fatty acids (FAs), sterols, phospholipids (PLs) and triglycerides, and function as energy, signaling transduction, and cell membrane components (Fahy et al., 2009; Subramaniam et al., 2011). Lipid droplets (LDs) are also a significant component of oocytes, embryos and early-stage larvae in aquatic species. In gamete and embryo cryopreservation in mammalian species, among all chemical constituents, lipids such as the PLs - the main component of the plasma membrane, are the most susceptible to freezing damage (Quinn, 1985; Sieme et al., 2015). During the freezing process, LPT occurs, which is accompanied by the alteration in PLs structure and composition (Jung et al., 2014; Fang et al., 2016; Jung et al., 2021). The membrane then loses its high elasticity and becomes rigid, resulting in poor membrane permeability and hydrophobic molecule diffusion (Amstislavsky et al., 2019). Ultimately, this process leads to the loss of cellular functionality (Hinkovska-Galcheva et al., 1989; Schuffner et al., 2001; Fang et al., 2016). Therefore, LPT at the nonphysiological temperature is considered one of the major causes of freezing damage. In general, mammalian gametes or embryos with lower LPT temperatures are likely to have better cryotolerance (Drobnis et al., 1993; Ghetler et al., 2005). Given that the LPT temperature is greatly dependent on lipid composition, features of the lipid profile are related to the cryoresistance of gametes and embryos. For example, the ratio between cholesterol and PL, and unsaturation rates are related to cryotolerance of spermatozoa (Waterhouse et al., 2006; Oldenhof et al., 2012), and lipid-rich oocytes or embryos usually exhibit high cryosensitivity. Therefore, lipid modification has become one of the key approaches to further improve post-thaw performances in mammalian gamete and embryo cryopreservation. For example, cryotolerance has been enhanced significantly by delipidation in lipid-rich oocytes and embryos (Amstislavsky et al., 2019) and membrane lipid replacement (MLR) in sperm (Vireque et al., 2016).

In aquatic animals, cryopreservation of oocytes, embryos and larvae is more challenging than sperm. Apart from their larger size and complex structure, the higher lipid content is another key factor that contributes to the chanlleges. For example, the egg lipid content is 32.4% on a wet weight basis in the whitefish *Coregonus albula* (V'uorela et al., 1979) and 38% on a dry weight basis in the Pacific oyster *Magallana gigas* (Massapina, 1999). These lipids serve as a vital energy reservoir for the early development of aquatic species as their digestive system has not fully evolved. Since lipid content and composition can affect cryotolerance, it is anticipated that lipid modification could play a similar role as in mammalians and improve the cryopreservation techniques in aquatic animals. Indeed, a few studies have demonstrated the potential of lipid modification in cryopreservation of gametes and larvae in aquatic animals. For instance, embryos produced from broodstock fed with diet supplemented with a fish oil showed a better permeability to cryoprotectants in *Prochilodus lineatus* (Costa et al., 2018). The supplement of exogenous lipids in cryoprotectants resulted in the improved performances in post-thaw fish sperm, and coral and oyster larvae (Cirino et al., 2021; Díaz et al., 2021; Zhu et al., 2023).

This review aims to update the recent development in lipid manipulation in the cryopreservation of sperm (both mammalian and aquatic species), oocytes (mammalian species), embryos (mammalian species), and larvae (aquatic species) and explore their applications to overcome some key challenges in aquatic species. In this review, we first discuss the effect and modification of lipids in the sperm, oocyte and embryo cryopreservation in mammalian species. We then present the recent development of lipid manipulation in cryopreservation of aquatic species. Finally we draw conclusions and propose future studies in aquatic species.

2 The effect of lipids on sperm cryopreservation in mammalian species

2.1 Current status of sperm cryopreservation

The cryopreservation of sperm is a reliable technique and has been extensively used in human ART and genetic germplasm conservation in livestock, and pet animals (Mandal et al., 2014).

This technique, however, has also showed several adverse effects on post-thaw spermatozoa, such as a decrease in motility and viability, the increase of single-strand DNA lesions, and the elevation of abnormal morphological characteristics (O'Connell et al., 2002; Ozkavukcu et al., 2008; Figueroa et al., 2019). It has been found that fluidity and permeability of the membrane serve a significant part in sperm cryoresistance and are related to the nature and percentage of PLs, polyunsaturated fatty acids (PUFAs), and cholesterol (Waterhouse et al., 2006; Oldenhof et al., 2012).

2.2 Plasma membrane lipid composition and sperm quality

Membrane lipid composition is diverse among organisms, cell type, organelle, membrane, bilayer-leaflet, and membrane subdomain levels (Harayama and Riezman, 2018). Compared with other tissues, spermatozoa membrane lipid is characterized by high PUFAs, especially dipolyunsaturated fatty acid (Bell et al., 1997; Fang et al., 2016). Given the low LPT temperature of PUFAs and the kinks of double bonds in PUFAs hindering the acyl chains from packing, PUFAs increase overall membrane fluidity (Israelachvili et al., 1980; Sieme et al., 2015). In addition to the small size of spermatozoa, the high quantity of PUFAs also contributes to better cryoresistance in spermatozoa than in oocytes and embryos.

Spermatozoa membrane lipid composition varies between individuals, ages, and seasons (Kelso et al., 1996; Cerolini et al., 1997; Argov-Argaman et al., 2013aArgov-Argaman et al., 2013b). These variations contribute to the difference in fresh sperm quality including motility and viability. In boar semen, for example, several lipid parameters such as the total lipid content, cholesterol, PL, n-3 PUFAs and Docosahexaenoic acid (DHA) are positively associated with sperm quality. On the other hand, saturated fatty acids (SFAs) and the ratio of n-6 to n-3 PUFAs are negatively correlated with sperm quality (Am-in et al., 2011). Similarly, in humans, PUFAs (especially DHA) play a significant role in normal sperm motility, concentration, and morphology, whereas monounsaturated fatty acids (MUFAs) adversely influence the quality parameters (Aksoy et al., 2006; Andersen et al., 2016).

2.3 Effect of cryopreservation on sperm lipid composition

The alteration of lipid composition in sperm can result in irreversible damage to the cellular membrane and the shift of cell homeostasis after cryopreservation (Schiller et al., 2000; Maldjian et al., 2005). In general, the changes can be summarized as follows: First, PUFAs and SFAs are commonly decreased and increased respectively as the result of lipid peroxidation after sperm cryopreservation in humans and domestic mammalians (Alvarez and Storey, 1992; Schiller et al., 2000; Maldjian et al., 2005). Second, cryopreservation can reduce cholesterol levels (Cerolini et al., 2001). Cholesterol plays a vital role in the structure and function of cell membranes, including the stability, permeability and fluidity of the cell membrane and the microenvironment of membrane proteins (Crockett, 1998; Partyka et al., 2016; Zhang et al., 2019). The loss of cholesterol can trigger the degeneration of the plasma membrane and apoptosis (Aitken, 2011). Third, the alteration of PLs composition and the translocation of membrane PLs have been found in frozen-thawed sperm (Schuffner et al., 2001; Fang et al., 2016). Normally, the distribution of PLs on the bilayer of the cellular membrane is asymmetric. For example, phosphatidylserine (PS), phosphatidylinositol (PI), and phosphatidylethanolamine (PE) are primarily distributed on the cytoplasmic leaflet, while Phosphatidylcholine (PC) and sphingomyelin (SM) are mainly located on the outer leaflet (Quinn, 2004; Fadeel and Xue, 2009).

The asymmetric distribution of PLs plays an important role in maintaining the physiological function of cells. Some specific proteins (e.g. protein kinase C, annexin, membrane skeletal proteins) are distributed on the cytoplasmic side by binding with PS (Manno et al., 2002). In the frozen-thawed sperm of ram, a significant reduction of PLs (PS, PI, PE, PG), an increase of diphosphatidylglycerol (DPG), and translocation of PLs between the cytoplasmic and outer layers were observed (Fang et al., 2016). Additionally, externalizations of PS and DPG were detected in cryopreserved ram sperm (Hinkovska-Galcheva et al., 1989; Schuffner et al., 2001). Hinkovska-Galcheva et al. (1989) suggested that the externalization of DPG inhibited the subsequent acrosome reaction and eventually impaired the fertilization capacity of sperm.

2.4 Lipid manipulation and sperm cryopreservation

Maintaining the lipid composition (PUFAs, cholesterol, PLs) and the physiological function of the membrane has been one of the key methods to improve the success rate of spermatozoa cryopreservation in many investigations (Ferreira et al., 2018). Egg yolk has become a common ingredient in the sperm extender in many mammalian species due to its protective influence (Anzar et al., 2019), which was first identified in bull semen (Phillips and Lardy, 1940). Despite the complex composition of egg yolks, low-density lipoprotein (LDL) plays a significant role in protecting spermatozoa in cryopreservation (Prapaiwan et al., 2015). In addition to egg yolk and LDL, other lipids, such as FAs and cholesterol, can also protect sperm during cryopreservation (Purdy and Graham, 2004; Moore et al., 2005; Hossain et al., 2007).

Three main strategies are currently used to modify the lipid compositions to counteract the cryopreservation stress in mammalian sperm. The first is the supplementation of PUFAs in

diet, which has enhanced the performance of post-thaw sperm in a few species, such as water buffalo, and goat (Souza et al., 2019; Silva et al., 2020). The second is the *in vitro* sperm incubation with exogenous lipids to improve sperm cryotolerance in humans, bovine, and swine (He et al., 2001; Röpke et al., 2011; Ferreira et al., 2018). The third and most common strategy is the supplementation of exogenous lipids in the cryopreservation extender, which can provide almost instantaneous protection from cold shock and freezing to increase the sperm cryoresistance (Quinn et al., 1980; He et al., 2001; Vireque et al., 2016).

While the mechanism of freezing protection of sperm by exogenous lipids is not fully understood, some theories have been proposed. First, a "loose interaction" between PL and membrane bilayers was inferred by Quinn et al. (1980) and Simpson et al. (1987) in ram and boar sperm, where the protection of PC against the cold shock was instantaneous and could be readily disrupted by a gentle wash. Second, the adhesion of PL micelles to and possible formation of PL protective film on the membrane surface have been suggested for the improvement of sperm cryotolerance in many studies (Ricker et al., 2006; Zhang et al., 2009; Vireque et al., 2016). Third, the monomeric transfer and the fusion between the liposome and sperm membrane bilayers were detected by Gadella et al. (1999) using 6-(7-nitrobenz-2-oxa-1,3-diazol-4-yl) amino-caproyl (C6NBD) labeled PLs in boar. The incorporation of exogenous lipids into the sperm has also been confirmed by ^{14}C-labeled FAs and octadecyl rhodamine B (Neill and Masters, 1972; Vasquez and Roldan, 1997). Therefore, the properties of the sperm membrane can be modified by manipulating exogenous lipids, which could improve sperm cryotolerance.

It is worth noting that the application of antioxidants in combination with exogenous lipids could enhance sperm cryoresistance by neutralizing the ROS produced during cryopreservation as lipids (especially PUFAs) are highly susceptible to this chemical (Ortega Ferrusola et al., 2009; Towhidi and Parks, 2012; Towhidi et al., 2013).

3 The impact of lipids on oocyte and embryo cryopreservation in mammalian species

3.1 Current status of oocyte and embryo cryopreservation

Aside from maternal genetic material, oocytes provide essential nutrients, energy, and mitochondria for subsequent development after fertilization (Kopeika et al., 2015). On the other hand, the embryo contain genetic material from both maternal and paternal sides. Compared to sperm, the larger size of oocytes and embryos reduces their cryotolerance (Pai et al., 2021). As oocytes and embryos share similarities in freezing sensitivity, the methods to modify their lipid compositions are discussed together.

After decades of effort, the viability of post-thaw oocytes and embryos in mammalians has improved substantially (Tharasanit and Thuwanut, 2021). In human, for example, the live birth rates of cryopreserved embryos and oocytes reach 41% and 32%, respectively (Fraison et al., 2023). In bovine, this rate has been improved to the fresh control level of 53% (Gómez et al., 2020). Compared with sperm, the substantially lower surface-to-volume ratio and higher cytoplasmic lipid content in oocytes and embryos also contribute to their higher cryosensitivity in mammalians (Amstislavsky et al., 2019). In oocytes and embryors, lipids also aggregate into LDs, which are often structurally bound to key cellular organelles, such as mitochondrion and endoplasmic reticulum (ER), cytoskeleton (microfilaments and microtubules), and cellular membrane (Guo et al., 2009; Zhou and Li, 2009). While this structural association has yet to be fully understood, the cluster of LDs, ER, and mitochondrion facilitate lipid metabolism (Guo et al., 2009). LDs normally contain triglycerides, PLs, sterols, and FAs (Dunning et al., 2014) and serve as an energy resource during the development of oocytes and embryos (Romek et al., 2011; Amstislavsky et al., 2019). The phase separation and further consolidation of LDs during cryopreservation could reduce the chance of successful cryopreservation of oocytes and embryos (Amstislavsky et al., 2019).

3.2 Lipid composition and cryopreservation of oocytes and embryos

Similar to sperm, the occurrence of LTP during cryopreservation is the primary source of cryodamage of oocytes and embryos (Arav et al., 1996; Amstislavsky et al., 2019), which can change the properties of cellular membrane and disrupt its function (Quinn, 1985; Van Meer et al., 2008). Changes in lipid composition have also been observed in post-thaw oocytes and embryos. For instance, in comparison with the fresh controls, the levels of certain PLs were significantly lower in post-thaw bovine embryos (three lysophosphatidylcholines; Janati Idrissi et al., 2021) and mouse oocytes [phosphatidic acid (PA), lysophosphatidic acid (LPA), lysophosphatidylglycerol (LPG); Jung et al., 2021].

Lipid content and composition in oocytes and embryos are species-specific and important for assessing their quality and potential cryotolerance (Pereira and Marques, 2008). Empirically, those species with lipid-rich oocytes and embryos (e.g. pig and domestic cat) have poor cryoresistance (Nagashima et al., 1999; Pereira and Marques, 2008; Galiguis et al., 2014). However, a higher proportion of unsaturated lipids can also produce a better cryosurvival rate due to lower LPT temperatures (Amstislavsky et al., 2019). For example, in comparison with bovine or ovine, the higher survival rate of cryopreserved embryos of domestic cats is attributed to being richer in unsaturated lipids (Pope, 2014; Amstislavsky et al., 2019). Lipid compositions also vary among breeding strains, individuals and seasons (Zeron et al., 2001; Sudano et al., 2012). For example, by using the MALDI-MS/MS laser-induced fragmentation technique (LIFT), Sudano et al. (2012) revealed that embryos of Simmental subspecies showed a better cryosurvival rate than Nellore subspecies due to significant differences in particular PCs [e.g. PC(32:0), PC (34:1), PC (34:2) and PC (36:5)], and suggested these PCs be used as biomarkers to predict the outcome of cryopreservation.

3.3 Lipid modification and oocyte and embryo cryopreservation

The modification of lipid composition is an important strategy to further improve the cryopreservation technique in mammalian oocytes and embryos in recent years. The main strategies include: 1) nutritional management; 2) delipidation using mechanical methods; 3) delipidation using chemical methods; and 4) cholesterol level modification. They are summerized in Table 1.

3.3.1 Nutritional management

The lipid composition of a female diet can affect the quality of oocytes and embryos (Childs et al., 2008a; Childs et al., 2008b; Wonnacott et al., 2010), which can affect their resistance to freezing. For instance, a diet with the addition of PUFAs can increase the quality of oocytes in ewes (Zeron et al., 2002). The increase of long-chain PUFA content in the follicle component could lower the midpoint of the LPT temperature of sheep oocytes and result in a better membrane integrity rate after chilling (Zeron et al., 2002).

As lipid is the primary energy resource for oocytes and embryos, the lipid content can be reduced if the nutrient restriction is applied *in vitro* (Abe et al., 2002). Sudano et al. (2011) also found that when a high fetal calf serum (FCS) concentration was used in the culture medium, LDs accumulated in both fresh and post-thaw bovine embryos, leading to a lower re-expansion rate after vitrification. Compared to the whole sheep serum, delipidated sheep serum in the culture medium could reduce the LDs content of ovine cumulus-oocyte complexes (Barrera et al., 2018). The application of serum-free culture medium has improved the survival rates of post-thaw bovine and domestic cat embryos (Abe et al., 2002; Murakami et al., 2011).

Some FAs have also been supplemented in the *in vitro* culture medium to improve the cryosurvival of mammalian oocytes and embryos by altering their lipid compositions (Al Darwich et al., 2010; Leão et al., 2015; Aardema et al., 2022). For example, conjugated linoleic acid (CLA) could reduce the accumulation of lipids to large- and medium-size LDs by inhibiting the expression and activities of stearoyl–CoA desaturase and lipoprotein lipase

TABLE 1 Lipid modification for improving the cryopreservation of oocytes and embryos in mammalian species.

Lipid modification strategy	Method	Material	Post-thaw parameter improved	Reference
Nutritional management	Application of serum-free culture medium	Bovine embryos	Survival rate Hatching rate	Aardema et al., 2022
	Application of serum-free culture medium	Domestic cat embryos	Hatching rate	Murakami et al., 2011
	Conjugated linoleic acid treatment	Bovine embryos	Intact embryos rate Re-expanded embryos rate	Pereira et al., 2007
		Bovine embryos	Re-expansion rate	Leão et al., 2015
		Bovine oocytes	Survival rate Cleavage rate	Matos et al., 2015
	Docosahexaenoic acid or linolenic acid treatment	Bovine embryos	Survival rate	Al Darwich et al., 2010
	Oleic acid treatment	Bovine embryos	Survival rate	Aardema et al., 2022
Delipidation using mechanical method	Centrifugation and micromanipulation	Porcine oocytes	Survival rate Germinal vesicle breakdown rate Metaphase II rate	Hara et al., 2005
		Porcine embryos	Blastocyst rate	Nagashima et al., 1999
		Bovine zygotes	Survival rate Hatching rate	Diez et al., 2001
	Centrifugation	Domestic cat oocytes	Degeneration rate (reduced)	Galiguis et al., 2014
Delipidation using chemical method	Forskolin treatment	Swamp buffalo embryos	Morula rate Blastocyst rate Hatched blastocyst rate Cell numbers of blastocyst	Panyaboriban et al., 2018
		Bovine embryos	Blastocyst rate Hatched blastocyst rate Cell numbers of blastocyst	Panyaboriban et al., 2018
		Porcine oocytes	Survival rate	Fu et al., 2011

(Continued)

TABLE 1 Continued

Lipid modification strategy	Method	Material	Post-thaw parameter improved	Reference
		Bovine embryos	Re-expansion rates	Meneghel et al., 2017
	L-Carnitine treatment	Bovine embryos	Survival rate	Takahashi et al., 2013
		Bovine embryos	Recovery rate Hatching rate	Ghanem et al., 2014
	Acetyl-L-carnitine treatment	Buffalo oocytes	Cleavage rate Morula rate Blastocyst rate Mitochondrial membrane potential	Xu et al., 2019
	Phenazine ethosulfate treatment	Bovine embryos	Recovery rate Hatching rate	Ghanem et al., 2014
		Porcine embryos	Blastocyst rate	Gajda et al., 2008
Cholesterol level modification	Cholesterol-loaded methyl-β-cyclodextrin treatment	Bovine oocytes	Cleavage rate Eight-cell rate	Horvath and Seidel, 2006
	Cholesterol-loaded methyl-β-cyclodextrin treatment before vitrification Methyl-β-cyclodextrin treatment after thawing	Bovine oocytes	Sperm binding capacity Two-pronuclear rate Cleavage rate Blastocyst rate Cell numbers of blastocyst	Hao et al., 2021

(Pariza et al., 2001). CLA could also improve membrane fluidity by incorporation between CLA fatty acyl residues and SM or PC (Leão et al., 2015), and it has a better free radical scavenging property than linoleic acid or methyl linoleate (Fagali and Catalá, 2008). Due to these three functions, CLA-treated bovine embryos showed a higher survival rate after cryopreservation than the untreated control (Pereira et al., 2007; Leão et al., 2015). In addition to CLA, the supplementation of linolenic acid, docosahexaenoic acid (DHA), and oleic acid in the *in vitro* medium could also improve the cryosurvival of bovine embryos (Al Darwich et al., 2010; Karaşahin, 2019; Aardema et al., 2022).

3.3.2 Delipidation using mechanical methods

The mechanical approach is an option to remove lipids in lipid-rich oocytes and embryos (Nagashima et al., 1994; Nagashima et al., 1999). LDs can be extruded by centrifugation under a hypertonic condition or removed by micromanipulation after polarization by centrifugation. Both methods have significantly improved the post-thaw survival rate and further developmental capacity of porcine oocytes, embryos, and domestic cat zygotes (Hara et al., 2005; Karja et al., 2006; Nagashima et al., 1994). Furthermore, when the lipid polarization method was used in domestic cat oocytes, the cryosurvival rate was improved in partially polarized cat oocytes (Galiguis et al., 2014). In contrast, the developmental competence was compromised in fully polarized oocytes, probably due to the adverse effect of lipid redistribution (Galiguis et al., 2014).

3.3.3 Delipidation using chemical methods

In comparison with mechanical delipidation, the *in vitro* chemical treatment is a more prevalent lipid modification method in cryopreservation of oocytes and embryos. Forsklin, L-carnitine, and Phenazine ethosulfate are the main chemicals used in the culture medium to enhance lipolysis (Borges and Vireque, 2019).

Forskolin

Forskolin triggers adenylate cyclase, which can raise the cyclic adenosine monophosphate (cAMP) level and induce lipolysis (Paschoal et al., 2016). When 10 μM forskolin was applied in the medium for *in vitro* maturation, the development competence of porcine oocytes was not impaired and showed higher resistance against cryopreservation (Fu et al., 2011). Likewise, after incubation with 5.0 μM forskolin for 24 hours, bovine embryos had less lipid and greater cryotolerance (Meneghel et al., 2017). Besides diminishing lipid content, forskolin could also attenuate cytoskeleton actin filament damages caused by vitrification in bovine oocytes (Meneghel et al., 2017).

L-carnitine

In animal cells, the primary role of L-carnitine is to transfer long-chain FAs across the inner mitochondrial membrane for the subsequent β-oxidation. It is, therefore, an enhancer of lipid metabolism (Longo et al., 2016; Borges and Vireque, 2019). L-carnitine supplementation could increase the rate of zygote development to the blastocyst stage and improve the survival rate after cryopreservation in bovine (Takahashi et al., 2013). L-carnitine could also reduce ROS formation during vitrification (Sprícigo et al., 2017). Thus, the supplementation of L-carnitine could not only lower the density of LDs and modify the PL composition, but it could also enhance the physiological function of mitochondria (Somfai et al., 2011; Xu et al., 2019).

Phenazine ethosulfate

Phenazine ethosulfate (PES) can oxidize nicotinamide adenine dinucleotide phosphate hydrogen to nicotinamide adenine dinucleotide phosphate and arouse the pentose-phosphate pathway to generate more Adenosine triphosphate (ATP) through glucose metabolism (De La Torre-Sanchez et al., 2006; Barceló-Fimbres and Seidel, 2007). The lipid accumulation in bovine and porcine embryos could be inhibited when incubated with PES (De La Torre-Sanchez et al., 2006; Gajda et al., 2011). Ghanem et al. (2014) found that PES-treated bovine embryos showed enhanced cryotolerance.

3.3.4 Cholesterol level modification

A high ratio between cholesterol and PL in the cytoplasm membrane is usually associated with higher membrane fluidity, especially at low temperatures, meaning that cholesterol content in the membrane bilayer can affect the cryotolerance of oocytes (Horvath and Seidel, 2006). Methyl-β-cyclodextrin (MBC) is a water-soluble cyclic heptasaccharide that can be used to deliver hydrophobic substances, such as cholesterol or FAs, through its hydrophobic cylindrical cavity (Brewster and Loftsson, 2007). Horvath and Seidel (2006) showed that Cholesterol-loaded Methyl-β-cyclodextrin (CLC) treated oocytes had a better cleavage and 8-cells rate compared to untreated oocytes in bovine vitrification, although the advantage was not apparent in subsequent development. Conversely, Arcarons et al. (2017) found that CLC treatment did not significantly affect the cleavage and blastocyst rate in the same species. Nevertheless, the expression of some development-related genes (e.g. *DNMT3A* and *BAX*) indicates that oocytes treated by CLC could have a better quality, especially when they are vitrified at the germinal vesicle stage (Arcarons et al., 2017).

4 Lipid manipulation in cryopreservation of aquatic species

4.1 Current status of cryopreservation of gametes, embryos and larvae

The first successful fish sperm cryopreservation in aquatic species was reported in 1953 (Blaxter, 1953), almost at the same time as that of domestic mammalians. However, despite sperm cryopreservation having become a lucrative global industry in the livestock sector, it has not been widely applied to commercially important aquatic species (Tiersch et al., 2007; Migaud et al., 2013). The development of cryopreservation technique in oocytes, embryos, and larvae in aquatic species is still in its early stages, and has focused on the selection of cryoprotectant, optimization of freezing rate, and assessment of developmental stages suitable for freezing (Martínez-Páramo et al., 2017). The potential application of cryopreservation in the aquaculture industry is significant, as it could resolve key issues during seed production, such as the unbalanced sex ratio of broodstock, asynchronous sexual maturation, long-distance broodstock transportation, and seasonal constraints. This technique could also play an essential role in germplasm resource protection of rare breeding varieties and endangered species, especially in the face of natural disasters, environmental pollution, and disease outbreak (Liu et al., 2020a; Díaz et al., 2021).

To date, hundreds of fish sperm cryopreservation protocols have been reported and comprehensively reviewed by Cabrita et al. (2010), Tsai and Lin (2012), and Martínez-Páramo et al. (2017). Sperm cryopreservation techniques have also been developed for most farmed and some ecologically important aquatic invertebrates (Diwan et al., 2020). The freezing of oocytes, embryos, and larvae in aquatic organisms is more challenging than that of spermatozoa. In comparison with sperm, the additional challenges are their poor membrane permeability, large size, high lipid content, and high sensitivity to temperature shock (Martínez-Páramo et al., 2017; Diwan et al., 2020). Although studies on cryopreservation of early-stage oocytes (Tsai et al., 2009), ovarian tissue fragments (Anil et al., 2011), and primordial germ cells or a genital ridge (Kobayashi et al., 2007; Higaki et al., 2010; Inoue et al., 2012) have occurred in some fish species, these methods are subject to the success of subsequent *in vitro* maturation or transplantation. Compared with fish, the cryopreservation of oocytes, embryos and larvae of aquatic invertebrates is more promising due to their holoblastic cleavage, relatively less egg lipid content, and smaller size (Martínez-Páramo et al., 2017). To date, studies on larval cryopreservation have been reported in crustaceans (Subramoniam and Newton, 1993; Huang et al., 2017; Diwan et al., 2020) and echinoderms (Paredes, 2016; Dupré and Carvajal, 2019), and successful cryopreservation of oocytes, embryos and/or larvae has been published in mollusks (Tervit et al., 2005; Liu and Li, 2015; Liu et al., 2020b; Heres et al., 2021) and corals (Daly et al., 2018), although the post-thaw oocyte survival rates were low (Tervit et al., 2005; Liu and Li, 2015). Progresses of molluscan larval cryopreservation have been summarized recently by Yang and Huo (2022).

4.2 Lipid modification and cryopreservation

As with livestock, the relationship between gamete or embryo quality and lipid composition has been established in many aquatic species, especially those of commercial importance (Mansour et al., 2011; Beirão et al., 2012; Glandon et al., 2016; Díaz et al., 2018). However, studies on lipid composition and cryopreservation are limited in aquatic species. Based on mammalian studies, it can be assumed that membrane fluidity, permeability, and lipid composition can play a similar role in the cryosurvival of gametes, embryos and larvae in aquatic animals, which has been demonstrated recently in Pacific oysters (Zhu et al., 2023). Therefore, lipid manipulations could enhance cryotolerance in aquatic species.

4.2.1 Lipid modification through nutritional management

To improve gamete quality, gamete lipid modification through dietary manipulation during broodstock conditioning is common in

aquatic species (Helm et al., 1973; Fernández-Palacios et al., 1997; Asturiano et al., 2001; Ehteshami et al., 2011; Diogo et al., 2015; Valdebenito et al., 2015). Promising results have been reported in a few studies related to sperm or oocyte cryotolerance. For instance, a fish oil-supplement diet for broodstocks of *Prochilodus lineatus* led to a higher amount of total PUFAs, n-6 PUFAs, and long-chain PUFAs, and a lower amount of total MUFAs in the embryos. Those embryos also presented better permeability to cryoprotectants (1,2-Propanediol; Costa et al., 2018). Bivalves usually do not have sufficient capability to elongate and desaturate short-chain saturated FAs to long-chain PUFAs (de Moreno et al., 1976; de Moreno et al., 1977; Helm et al., 1991). Hence dietary lipid profiles can significantly affect the composition of FAs in bivalves (Langdon and Waldock, 1981; Dudognon et al., 2014). In Pacific oysters, when the broodstock was fed with microalgae containing a high fraction of PUFAs during cold preconditioning at 9 °C, the fertilization rate of post-thaw oocytes was significantly increased in comparison with the control (Adams et al., 2013). These authors have proposed that the absolute content of PUFAs, rather than the ratios between PUFAs and MUFAs or SFAs, plays a vital role in cryotolerance of post-thaw oocytes.

4.2.2 Lipid modification and sperm cryopreservation

In addition to lipid modification through diet, there have been a few examples of improving sperm tolerance by supplementary FAs, cholesterol, and LDLs in fish sperm extenders (Table 2). According to Lahnsteiner et al. (2009), when FAs (including palmitic acid, arachidonic acid, linoleic acid, and arachidic acid) were added to the rainbow trout (*Oncorhynchus mykiss*) sperm motility-inhibiting extenders, the motility rate and the average path velocity were improved after 72 h storage at 4°C. However, their cryotolerance was not enhanced in the same study. On the contrary, when the arachidonic acids were used in the freezing medium of Atlantic salmon (*Salmo salar*), the membrane integrity and fertility rate of post-thaw sperm were significantly increased (Díaz et al., 2021). It is worth mentioning that the protective effect of egg yolk in the extender in the study by Lahnsteiner et al. (2009) was likely to be veiled by its LDL component (Pérez-Cerezales et al., 2010). The impact of cholesterol in sperm cryopreservation is species-specific. Its addition had no positive effect on the viability of cryopreserved sperm in *S. Salar* (Díaz et al., 2021), whereas showed significant improvement in cryoresistence in the common carp (*Cyprinus carpio*) when was used at a dose of 1.5 mg cholesterol per 120 × 10^6 spermatozoa (Yildiz et al., 2015).

4.2.3 Lipid modification and oocyte and larval cryopreservation

Total lipid extracts from aquatic invertebrates present cryoprotective abilities when they were added into the medium to cryopreserve molluscan primary larval cells (Odintsova et al., 2001; Odintsova et al., 2006; Kostetsky et al., 2008). For example, the post-thaw survival rate of *Mytilus trossulus* trochophore larval cells was increased from 5% to 13% by the addition of lipid extract of *Crenomytilus grayanus*, which was further improved to 35% when antioxidants (vitamin C and vitamin E) were supplemented (Kostetsky et al., 2008). The lipid profile analysis revealed that the addition of lipid extracts and antioxidants effectively increased percentages of MUFAs, PUFAs, n-3 PUFAs, n-6 PUFAs, and the unsaturation index and reduced the percentage of SFAs in the post-thaw larval cells (Kostetsky et al., 2008).

Attempts have also been made to alter the lipid composition of oocytes and larvae to improve cryoresistance. For example, Salinas-Flores et al. (2008) cultured the oocytes of *M. gigas* with CLC and MBC to increase and decrease the cholesterol level in the oocyte, respectively. Although the incorporation of cholesterol in oocytes was confirmed by fluorescence assessment, the treated and untreated oocytes showed similar post-thaw fertilization rates. In corals, Cirino et al. (2021) reported a methodology to improve the cryoresistance of coral larvae by adding exogenous lipids and gold nanoparticles to the vitrification solution. The vitality rate of vitrified *Seriatopora caliendrum* larvae was increased by erucic acid liposomes, whereas the settlement rate of vitrified *Pocillopora verrucosa* larvae was enhanced by PE liposomes. In addition, the survival rate of post-thaw *M. gigas* larvae was significantly improved by including 1-palmitoyl-2-oleoyl-sn-glycero-3-phosphocholine (POPC) and α-tocopherol in the cryopreservation medium (Zhu et al., 2023).

5 Conclusions and future research in aquatic species

The development of oocyte, embryo and larvae cryopreservation techniques is still in its early stages in aquatic organisms, although progresses have been made in some species, especially in bivalves. In comparison with mammalians, aquatic species possess even higher intracellular lipid content in oocytes, embryos and early-stage larvae (prior to feeding), which means that the cryopreservation of these materials might be more challenging. Therefore, the introduction of lipid modification might be a cornerstone in the development of cryopreservation techniques in aquatic species. The following will be the primary aspects the future studies should focus on.

While the relationship between lipid composition and gamete quality and/or development capability has been investigated in some species, most of these studies have not been focused on cryopreservation. Therefore, investigations on the relationship between specific lipid composition and cryotolerance would be a key research priority, which could be achieved by manipulating nutritional ingredients. Theoretically, when broodstock are fed with a diet rich in PUFAs during gametogenesis, they are likely to yield gametes with lower LPT, thus enhancing the cryoresistance of both gametes produced and the resulting embryos and larvae.

Given its effectiveness in larvae cryopreservation in some bivalve and coral species, the application of exogenous lipids (e.g. PLs, and lipid extract from hydrobiontes) in the cryoprotectant is likely to offer a new strategy to optimize existing or develop new larvae cryopreservation techniques. Due to the hydrophobic nature of exogenous lipids, they usually present in the form of liposomes in

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TABLE 2 Positive effects of exogenous lipid supplements in cryopreservation in aquatic animals.

Material cryopreserved	Species	Supplements - exogenous lipids and other chemicals	Base extenders/ Cryoprotectants	Post-thaw parameters improved	Reference
Sperm	*Prochilodus brevis*	Egg yolk	5% glucose 10% dimethyl sulfoxide	Membrane integrity	Torres et al., 2022
	Rasbora tawarensis	Egg yolk	Ringer's solution /5% dimethyl sulfoxide	Mortility Fertilization rate Hatching rate	Muchlisin et al., 2020
	Salmo salar	Arachidonic acid	Cortland® medium	Mortility Membrane integrity Mitochondrial membrane potential Fertility	Díaz et al., 2021
	Oncorhynchus mykiss	Low density lipoprotein	Erdahl & Graham's /7% dimethyl sulfoxide	Membrane integrity DNA integrity Eyed embryo survival rate	Pérez-Cerezales et al., 2010
	Cyprinus carpio	Cholesterol-loaded cyclodextrin	300 mM glucose, 10% dimethyl sulfoxide	Motility Duration of motility Vitality rate Fertilization rate	Yildiz et al., 2015
Larval cells	*Mytilus trossulus*	Lipid extract from *Crenomytilus grayanus*, vitamine C and vitamine E	10% dimethyl sulfoxide 1.5% trehalose	Vitality rate Unsaturation index	Kostetsky et al., 2008
Larval cells	*Strongylocentrotus intermedius*	Lipid extract from *Crenomytilus grayanus*, echinochrome	6% dimethyl sulfoxide 4 mM trehalose	Survival rate RNA synthesis level	Odintsova et al., 2009
Larvae	*Seriatopora caliendrum*	Erucic acid	2 M ethylene glycol (EG), 1 M propylene glycol (PG), 40% (w/v) Ficoll, 10% gold nanoparticles	Survival rate	Cirino et al., 2021
Larvae	*Pocillopora verrucosa*	Phosphatidylethanolamine	2 M ethylene glycol (EG), 1 M propylene glycol (PG), 40% (w/v) Ficoll, 10% gold nanoparticles	Settlement rate	Cirino et al., 2021
Trochophore larvae	*Magallana gigas*	1-palmitoyl-2-oleoyl-sn-glycero-3-phosphocholine, α-tocopherol	10% (v/v) ethylene glycol (EG) 5% (w/v) Ficoll (FIC) 0.2% (w/v) polyvinylpyrrolidone	D-stage larvae survival rate Spat yield	Zhu et al., 2023

extenders or cryoprotectants. Their particle size and other properties could affect their interaction with plasma membrane and subsequently the cryopreservation outcomes. For example, sonicating the extender containing egg yolk has resulted in smaller liposomes and better post-thaw motility in donkey sperm compared to that without the treatment (Zhang et al., 2018). In the study by Cirino et al. (2021), the application of gold nanoparticles played a significant role in the success of coral larval cryopreservation because gold nanoparticles can change the biophysic features of liposomes such as zeta potential, temperature of LPT (Mady et al., 2012). Therefore, understanding the biophysical characteristics of liposomes and their effects on the cryopreserved materials will be beneficial for the further improvement of cryopreservation techniques.

Furthermore, partial removal of yolk through micromanipulation would be worth trying to improve the cryosurvival of oocytes, embryos, and larvae in aquatic animals when their cryopreservation has been investigated by optimizing other parameters. This method may not only hold significance academically but could also be critical to establish cryopreservation techniques, although the application of this technique might be limited to specific requirements such as gene banking and difficult to meet the quantity demands for commercial hatchery production. With the development of extended *in vitro* oocyte culture techniques in aquatic species, chemical delipidation and in virto lipid modulation could become practicable. This method would have broader applications than micromanipulation, since it could manipulate a larger quantity of materials.

As the vitrification method has been routinely used in the cryopreservation of oocyts and embryos in some mammalian species, including lipid-rich materials (Amstislavsky et al., 2019; Du et al., 2021; Tharasanit and Thuwanut, 2021), and has also been successfully applied in a couple of coral species (Daly et al., 2018; Narida et al., 2023), the integratation of lipid modification and vitrification is likely to become a novel technological pathway for

the cryopreservation of oocytes, embryos, and larvae in aquatic organisms.

Author contributions

XZ conceived and developed the idea and prepared the draft of the manuscript. YZ, YL, and YT helped for the collection of references and provided comments and suggestions to improve the manuscript. PM-E, JQ, and XL have critically gone through the draft and finalized the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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