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Short Communication

Egg proteomic characterization of *Seriola rivoliana* in captivity

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ABSTRACT. Continuous and sustained production of good quality eggs and larvae is required to have economically viable and ecologically sustainable rearing of *Seriola rivoliana*. Nonetheless, the complete production cycle of these species has been challenging to achieve due to high mortality during embryonic and larval stages. The objective of the project was to study the expression of the proteins involved in the embryonic process of almaco jack. Proteomic characterization of fertilized eggs was performed using two-dimensional electrophoresis and mass spectrometry. Different vitellogenin proteins A, B, C and Ab, β-actin, peroxiredoxin, superoxide dismutase 1, alpha subunit proteasome, and keratin II were identified to their functions related to embryonic development, energy metabolism, protein synthesis, cell structure, cytoskeleton, and antioxidant proteins with defense enzymatic activity.

Keywords: *Seriola rivoliana*; fish eggs proteomics; two-dimensional electrophoresis; mass spectrophotometry; proteomic biomarkers; oxidative stress

The longfin yellowtail almaco jack (*Seriola rivoliana*, Carangidae) is a neritic and oceanic pelagic fish of wide distribution with significantly valuable fishery and aquaculture activities in Mexico. Artificial rearing of this species is required to become an economically viable and ecologically sustainable activity. Thus, constant and sustained production of good quality eggs and larvae should be performed under controlled conditions (Carnevali *et al*., 2001). Nevertheless, the complete reproduction cycle of almaco jack has been challenging to achieve due to the high mortality during embryonic and larval stages (Palomino *et al*., 2017) partly due to a lack of information on egg composition and physiology. The egg needs all the essential biochemical components to develop a viable embryo; these materials are obtained from the nutrients transferred by the females during oocyte growth within the ovary (Sullivan *et al*., 2015). The quality of fish eggs and larvae is variable; many of the factors that affect quality are still unknown, but spawning egg quality of animals in captivity is usually lower than that of organisms recently caught from the wild (Carnevali *et al*., 2001). In the aquaculture industry "good egg quality" has included some quantitative aspects, such as the fertilization capacity of the sperm and competence of the eggs to be fertilized, morphological characteristics, biochemical content, and hatching rates (Kjørsvik *et al*., 1990; Bromage *et al*., 1994). Various morphological and physiological characteristics have also been taken into account as quality indicators of fish gametes. Some authors have suggested that the shape of the egg, its transparency and distribution of the oil drops, and egg buoyancy are used as good quality markers in marine fish hatcheries (Kjørsvik *et al*., 1990; Carnevali *et al*., 2001). Spherical and highly ellipsoidal lipid droplets have been reported to be indicators of low embryonic survival and egg quality, while eggs with slightly ellipsoidal lipid droplets indicate high embryonic survival (Lahnsteiner *et al*., 2008). A series of parameters that directly or indirectly influence egg quality have been identified from induction mechanism to spawning; for example, physical and chemical factors, such as photothermal manipulation, oxygen concentration and salinity (Heming & Buddington, 1988), hormonal injection (Bromage *et al*., 2001). Important factors to consider are the broodstock nutri-

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tional quality, eggs incubation conditions, or breeders' physiological state, hatching rate, and survival at first artificial feeding (Sullivan *et al.*, 2015). Also, important would have a higher quality egg in species with controlled reproductive cycles already closed in captivity since the feeding of the parents guarantees good nutritional quality, and consequently, a better nutritional reserve would be expected in eggs (Lahnsteiner *et al*., 2008; Roo *et al*., 2014).

The different stages of fish oocyte development are associated with changes in protein composition necessary for their proper development; some of these proteins are stored to be used during fertilization and later in embryonic development (Cerdà *et al*., 2007). The production of good quality fish eggs depends on different molecular processes; many of them are still unknown, so their knowledge is essential. Inadequate reproductive confinement and nutritional conditions may induce changes in the oocyte proteome and affect egg quality (Cerdà *et al.*, 2007). For this reason, proteomic analyses of fertilized eggs can be instrumental in identifying proteins that are expressed or disappear during their development and could be used as quality biomarkers for fertilized eggs. The use of these technologies can discover new biological connections between proteins, genes, and metabolic pathways; thus, they can be potent tools for understanding the genetic and molecular basis of gamete (Cerdà *et al.*, 2007) and fertilized egg formation. Different studies have addressed the proteomic aspect of fish reproduction (Olin & Von Der Decken, 1990; Rime *et al*., 2004; Knoll-Gellida *et al.*, 2006; Link *et al*., 2006; Tay *et al*., 2006; Ziv *et al*., 2008; Palmblad *et al.*, 2013; Williams *et al*., 2014). However, very few have been available on proteomics and embryonic development of the genus *Seriola*. (Keyvanshokooh & Vaziri, 2008; Roo *et al*., 2014; Palomino *et al*., 2017; Pousis *et al*., 2018), which is important information required to support decision-making by aquaculture producers on their rearing.

The longfin yellowtail broodstock of *S. rivoliana* was collected in the locality of Cabo San Lucas, Baja California Sur (BCS), Mexico, using a fishing rod with a hook, which was transported in a 700 L container with supplemental oxygen, to avoid stress and suffering for the organisms. Broodstock was captured in the natural reproductive season, so that males and females were obtained at the same time as the capture, in the same courtship area; they were kept for two years in remaking through environmental stimulation. Breeders were maintained in captivity with a photoperiod of 12 h and 30 min/light and 11 h and 30 min/darkness, with closed flow and temperature of 25°C in 40 m^3 tanks with recirculation systems, 25% daily water exchange, and supplementary aeration for two years (Viader-Guerrero, 2019) until they had matured at Kampachi Farms at the Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, BCS, Mexico (24°08'N, 110°25'W). The organisms were fed with sardine (50%), mackerel (30%), and squid (20%) daily to satiety (Viader-Guerrero, 2019). *S. rivoliana* showed rapid growth, reaching a maximum standard length of 160 cm and a maximum weight of 59 kg in the wild, growing 1 kg in weight per year (Gopalakrishnan, 1985). The broodstock was sexed with a cannula inserted into the genital pore, where the presence of hydrated oocytes identified the females. The males underwent an abdominal massage to identify the presence of semen, which did not determine its quality or density and the volume of the semen. Once identified, the fish were marked according to sex (Viader-Guerrero, 2019). The fertilized eggs were obtained from spontaneous spawning from a batch of *S. rivoliana* breeders (seven females average weight = 7.5 ± 2.3 kg and length = 63.4 ± 5.3 cm; five males weight = 8.2 ± 3.2 kg and length = 75.3 ± 2.4 cm). The eggs used were obtained from the laying's timing, so it was not necessary to use hormones or carry out artificial fertilization. The fertilized eggs fell by gravity into a 500 L egg collector with a 500 µm retention mesh at the time of spawning. The egg's size and the lipid drop had a diameter of 1.0327 ± 0.00255 mm, showing a lipid drop of 0.2535 ± 0.0008 mm, at a spawning temperature of 25°C (Viader-Guerrero, 2019). The fertilized eggs were frozen at -80°C for subsequent proteomic analysis. Egg samples were evaluated following the methodology used by Serrano-Pinto *et al*. (2010) to perform proteomic characterization. Homogenized mixtures (100 µL) from samples of 100 eggs were run in five gels; the mixtures were prepared with phosphate saline buffer with 2-20 µg mL^{-1} protease cocktail inhibitors 0.1-0.5 mM serine and cysteine protease inhibitors (TLCK). Lysis buffer (8 M urea, 4% CHAPS, 2% formalin at pH 3-10) was added. For isoelectric focusing, an aliquot of 350 µg proteins was used with a rehydration buffer to provide a total volume of 250 µL for each aliquot of 200 µL rehydration buffers and supplied with 0.56 mg dithiothreitol (DTT) and 1 µL IPG buffer. The mixture was placed within the gel holder with the strip containing gel separators from pH 3-10 (Immobiline Dry Strip pH 3-10 NL, Amersham Biosciences (Buckinghamshire, UK). The first step was a 2 h rehydration time only with the rehydration buffer. The first dimension of the isoelectric focusing system was run for a rehydration time of 16 h with a continuous current of 50 mA for the strip with a program: 1-100 V h^{-2}, 2-500 V h^{-1}, 3-1,000 V h^{-1}, 4-8000 V $h^{-2.5}$, 5-8000 V $h^{-3.5}$. Two-dimensional electrophoresis (2-DE) was used to reveal soluble proteins in relatively high

abundance and a specific pH range (3-10), isoelectric point (Ip) from 4.5-8.5, and molecular weight (Mw) from 17.5-76 kDa (Biorad, CA, USA). The gels were balanced in a buffer (Merck KGaA, Darmstadt, DE) with 50 mg 5 mL^{-1} DTT and 125 mg 5 mL^{-1} iodoacetamide. Fish eggs were analyzed by 2-DE (OwlP9DS vertical gel system, Thermo Fisher Scientific, Waltham, MA) that separated proteins based on their molecular weight on 12% polyacrylamide gel SDS-PAGE at 100 V for eight hours. Gels were soaked for three hours, pre-incubated, and then dyed with 0.35 g L^{-1} Coomassie brilliant blue G-250 with gentle agitation at room temperature for five days. The gels were scanned with Imagescanner III (Amersham Biosciences, Buckinghamshire, UK), and a bioinformatics program (Image Master 2D Platinum v7.0, Amersham Biosciences, Buckinghamshire, UK) was used to detect the number of spots or protein stains in each gel. The spots selected based on their higher spot volume expression were excised, washed, and faded. The tandem time-of-flight (TOF/TOF) mass spectrometry analysis was performed on an AB Sciex 5800 proteomics analyzer equipped with TOF TOF ion optics (Ontario, CAN) and an OptiBeam™ on-axis laser irradiation with 1000 Hz repetition rate (Applied Biosystems, CA, USA). Two-protein databases were used, an updated compilation of the Swiss-Prot database (including 552,259 entries) with Metazoa as selected taxonomy and a database downloaded from NCBI using *Seriola* as the selected genus (including 41530 entries) (NCBI, 2017). Mascot data were then transferred to an in-house developed validation software for data filtering according to a significance threshold of <0.05 and the elimination of protein redundancy based on proteins evidenced by the same set or a subset of peptides. Each peptide sequence was checked manually to confirm or contradict the Mascot assignment.

This study analyzed the proteomics characterization of *S. rivoliana* eggs, describing proteins during the embryogenesis process in captivity. To our knowledge, it is the first proteomic evaluation performed in this fish genus. Using the Image Master 2D Platinum program, some proteins (spots) were obtained, which showed approximately 200 well-resolved Coomassie-stained spots (Fig. 1). The molecular weight of these spots varied from 5 to 140 kDa, and 3-10 of isoelectric point (pH) has been detected; 20 protein spots differentially expressed were identified (Fig. 1). The molecular weight of these spots varied from 15.8-131 kDa, with an Ip range from 3-8.

Table 1 shows the characteristics of each spot after the MS/TOF TOF analysis, previously indicated in Figure 1. The spots analyzed were identified as sequence fragments of four vitellogenin (Vtg): A, B, C,

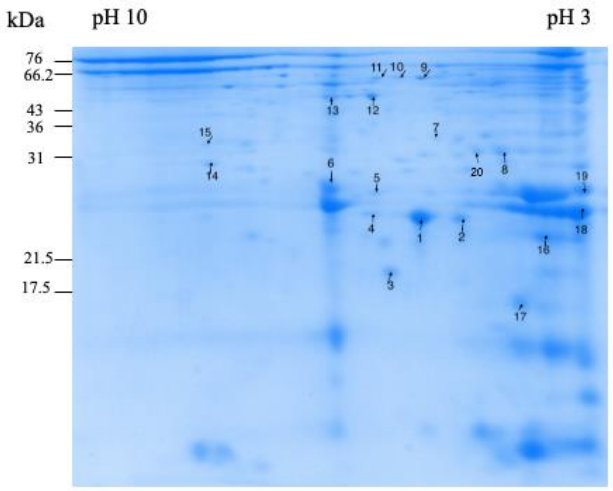

Figure 1. Display of two-dimensional electrophoresis of the full array of protein profile of *Seriola rivoliana* eggs.

and Ab. Five additional proteins were also identified as β-actin, peroxiredoxin, superoxide dismutase 1, proteasome sub-unit alpha, keratin II. According to their function, the proteins identified were related to embryonic development, enzymatic activity-proteolysis, enzymatic activity defense, cytoskeletal, and cell structure.

Among the proteins identified, five were expressed as multiple spots in different locations on the 2-DE map based on the peptide sequences, demonstrating that they were considered isoforms of the same protein (Table 1). These isoforms may be the result of post-translational modifications, such as phosphorylation or glycosylation (Jensen, 2004, 2006). Examples of these proteins are Vtg B, C, Ab, SOD1, and β-actin.

In aquatic organisms, synthesis and degradation processes of Vtg (glycolipophospho protein precursors to yolk in egg-laying oviparous organisms) (Byrne *et al*., 1989; Serrano-Pinto *et al*., 2003) are important in oogenesis and embryogenesis processes. They provide essential nutrients, such as amino acids, lipids, carbohydrates, phosphates, and metal ions to the embryo (Fagotto, 1995). The Vtg sequences found in this study had homology with those of *S. lalandi* (Palomino *et al.*, 2017) and *S. dumerili* (Pousis *et al*., 2018) (Table 1).

Another protein identified represented by three spots was a β-actin enzyme. Studies carried out on the *Danio rerio* embryo (Ziv *et al*., 2008) mentioned that the β-actin gene played a central role in structuring the cellular cytoskeleton. The embryo was subjected to a high cell proliferation rate; therefore, the β-actin gene was likely not to be expressed at the same level at different stages of embryo development. This protein had homology with the β actin of *S. quinqueradiata*

Table 1. List of the peptides obtained from *Seriola rivoliana* eggs by MS/ TOF TOF mass spectrophotometry. Ip: isoelectric point.

Spot N°	Ip	Protein name	Accession	Score	Mass	Coverage	Peptides	Molecular function
1	5.5-5.6	Vitellogenin C	AQV08209.1/ *Seriola lalandi*	183.47	123015.90	3.67	IKFPEYTVYR WGAECQSYEMSMR QEVSASVVAASADSVDVK FPEYTVYR	Embryonic development
2	5.2-5.3	Vitellogenin C	AQV08209.1/ *S. lalandi*	157.35	123015.90	3.31	IKFPEYTVYR AATAHLPGSKPTLK WGAECQSYEMSMR	Embryonic development
3	5.6-5.7	Superoxide dismutase 1	SODC_CALJA/ [Cu-Zn] OS=*Callithrix jacchus* GN=SOD1 PE=2 SV=3	109.90	15879.91	11.04	HVGDLGNVTAGKDGVAK	Enzymatic activity defense
3	5.6-5.7	Superoxide dismutase 1	SODC_CEREL/[Cu -Zn] OS=*Cervus elaphus* GN=SOD1 PE=2 SV=3	22.60	15818.94	11.18	HVGDLGNVTADKNGVAK	Enzymatic activity defense
4	5.7-5.8	Vitellogenin C	AQV08209.1/ *S. lalandi*	54.69	123015.90	0.89	IKFPEYTVYR	Embryonic development
5	5.7-5.8	Peroxiredoxin	PRDX_ASCSU/ OS=*Ascaris suum* PE=2 SV=1	63.88	21576.08	7.14	DYGVLKEDDGIAYR	Enzymatic activity defense
5	5.7-5.8	Peroxiredoxin	TDX_CYNPY/ OS=*Cynops pyrrhogaster* PE=2 SV=1	36.52	22325.44	5.45	QITINDLPVGR	Enzymatic activity defense
6	5.9-6.0	Vitellogenin Ab	AQV08208.1/ *S. lalandi*	123.00	131192.30	2.01	LQFLPVQGIDK FFGQEIAFANIDK	Embryonic development
7	5.4-5.5	Proteasome subunit alpha type-1	PSA1_BOVIN/ OS=*Bos taurus* GN=PSMA1 PE=1 SV=1	66.32	29566.87	5.60	NQYDNDVTVWSPQGR QHFSPFNVK	Enzymatic activity- proteolysis
8	5.0-5.1	Vitellogenin C	AQV08209.1/ *S. lalandi*	160.04	123015.90	3.22	QRGESVISTVR YVYTVKPTAEEGLITR	Embryonic development

continuation

Spot N°	Ip	Protein name	Accession	Score	Mass	Coverage	Peptides	Molecular function
9	5.5-5.57	Vitellogenin Ab	AQV08208.1/ *S. lalandi*	42.59	131192.30	1.09	FFGQEIAFANIDK LDINEGYFK	Embryonic development
10	5.6-5.65	Vitellogenin A, partial	AQM52318.1/ *Seriola dumerili*	369.94	81380.24	11.37	FFGQEIAFANIDK ATTTPTLPENFHIAHLLK AFIDQAIALATAPSVQAFGR IEALPVSVPEHIAAVHVETFAVAR LQFLPVQGIDK	Embryonic development
10	5.6-5.65	Vitellogenin B, partial	AQM52319.1/ *S. dumerili*	339.59	118923.74	6.11	FFGQEIAFANIDK AIVDQIIEVATGPAVYAQGR IASALVETFAIATNVEDLTAAK	Embryonic development
11	5.7-5.75	Vitellogenin Ab	AQV08208.1/ *S. lalandi*	37.46	131192.30	2.18	THYVISEDTKADR APVEPIRAEYLHR	Embryonic development
12	5.7-5.77	Vitellogenin Ab	AQV08208.1/ *S. lalandi*	37.46	131192.30	2.18	THYVISEDTKADR APVEPIRAEYLHR	Embryonic development
13	5.9-6.0	Beta-actin, partial	BAD20211.1/ *Seriola quinqueradiata*	427.38	41449.68	23.94	AGFAGDDAPR GYSFTTTAER AVFPSIVGRPR DSYVGDEAQSKR QEYDESGPSIVHR SYELPDGQVITIGNER VAPEEHPVLLTEAPLNPK	Cytoskeletal and cell structure
14	6.78-6.80	Beta-actin, partial	BAD20211.1/ *S. quinqueradiata*	188.29	41449.68	13.30	GYSFTTTAER AVFPSIVGRPR QEYDESGPSIVHR SYELPDGQVITIGNER AGFAGDDAPR	Cytoskeletal and cell structure
15	6.8-6.82	Beta-actin, partial	BAD20211.1/ *S. quinqueradiata*	201.15	41449.68	15.96	GYSFTTTAER AVFPSIVGRPR QEYDESGPSIVHR SYELPDGQVITIGNER	Cytoskeletal and cell structure

continuation

Spot N°	Ip	Protein name	Accession	Score	Mass	Coverage	Peptides	Molecular function
							IKFPEYTVYR	
							AATAHLPGSKPTLK	
			AQV08209.1/					
16	4.7-4.8	Vitellogenin C	*S. lalandi*	80.66	123015.90	3.31	WGAECQSYEMSMR	Embryonic development
			SODC_CALJA/[Cu-Zn] OS=*C. jacchus*					
		Superoxide	GN=SOD1 PE=2					
17	4.9-5.0	dismutase 1	SV=3	72.83	15879.91	11.81	HVGDLGNVTAGKDGVAK	Enzymatic activity defense
							IAWGIECK	
							LKVTWDKLPK	
							VQGYQIAAYFDK	
		Vitellogenin B,	AQM52319.1/					
18	4.5-4.6	partial	*S. dumerili*	218.77	118923.74	3.15	VQGYQIAAYFDKTTAR	Embryonic development
							IAWGIECK	
							LKVTWDKLPK	
							VQGYQIAAYFDK	
							LQVIFANLAENDHWR	
		Vitellogenin B,	AQM52319.1/					
19	4.5-4.6	partial	*S. dumerili*	314.04	118923.74	4.53	ADHKVQGYQIAAYFDK	Embryonic development
							SGGGFSSGSAGIINYQR	
							GGGGGGYGSGGSSYGSGG	
			K2C1_Human/				GSYGSGGGGGGR	
			OS=*Homo sapiens*				GSYGSGGSSYGSGGGGSYGS	
		Keratin, type II	GN=KRT1 PE=1					
20	5.1-5.2	cytoskeletal 1	SV=6	122.56	65999.00	14.52	GGGGGGHGSYGSGSSSGGYR	Cytoskeletal and cell structure

(Abe & Chiba, 2004) (Table 1). It was found in *Sparus aurata* oocytes (Ziv *et al*., 2008) and *Perca fluviatilis* eggs (Castets *et al*., 2012). Another protein identified in our study and represented by three spots was the antioxidant enzyme SOD1, which was the first to identify this enzyme in eggs of this fish group. Recently, the presence of some enzymes involved in energy metabolism have been identified as suitable biomarkers to define the quality of fish larvae (Lahnsteiner & Patarnello, 2004), and SOD1 is one of them. The study conducted by Valderrama-Díaz (2014) evaluating antioxidant enzymes SOD and catalase (CAT) in oocytes and embryos of *Brycon amazonicus* found that enzymatic antioxidant defense mechanisms increased their expression during embryonic development. Furthermore, they were the first line of defense against reactive oxygen species (ROS). The presence of oxidative stress in eggs or their parents caused by captivity could lead the fish to situations of anemia or opportunistic infections (Castillo-Hernández *et al*. (2020). Overexpression of this enzyme could be preventing damage by removing oxygen (O_2), hydrogen peroxide (H_2O_2), and some metal ions, such as iron (Fe), copper (Cu), and zinc (Zn), that can sequester and inhibit the uncontrolled action of O_2 (Halliwell & Gutteridge, 1999). The SOD1 protein was found in *Salmo iridaeus* (Aceto *et al*., 1994), *D. rerio*, and *S. aurata* oocytes (Ziv *et al*., 2008) and in *Oryzias melastigma* embryos (Dong *et al*., 2014) in the response of stress conditions.

Another kind of protein identified in this study and represented by two spots was peroxiredoxin, another protein associated with oxidative stress in fishes (Ziv *et al*., 2008; Castets *et al*., 2012; Yoshino *et al*., 2016). ROS, such as superoxide radicals, hydroxyl radicals, and H_2O_2 is formed during the reduction of dioxygen (O_2) in water. These species can damage proteins, lipids, and nucleic acids, so efficient antioxidant systems are required, including certain enzymes capable of degrading hydrogen peroxides, such as catalases, peroxidases, and peroxiredoxins (Díaz, 2003). The peroxidase and glutathione peroxidase (GPX) systems are the two main sets of oxidative stress response genes in chum salmon eggs (Yoshino *et al*., 2016). This same protein was also expressed in *D. rerio* and *S. aurata* oocytes (Ziv *et al*., 2008), and *Perca fluviatilis* eggs (Castets *et al*., 2012).

Another protein expressed in almaco jack eggs in this study was the proteasome subunit alpha type 1 -the proteins that make up the proteasome machinery (Baumeister *et al*., 1998). This machinery's function plays an essential role in the degradation of proteins in a wide range of cellular events. Eukaryotic cells have developed two mechanisms to perform many controlled proteolytic events - ubiquitination machinery and the proteasome. The collaborative action of these two machines is crucial for a variety of diverse processes that include cell cycle progression, development, apoptosis, signal transduction, antigen presentation, and gene expression regulation (Baumeister *et al*., 1998). This protein is a factor promoting fish oocyte maturation (Tokumoto, 1998; Chu *et al*., 2006) in response to situations of cellular stress, such as infections, sudden changes in temperature, or oxidative damage. Thus, these proteins are expressed to identify other poorly folded proteins and mark them for proteasomal degradation. This enzyme has also been identified in eggs of the species *P. fluviatilis* (Castets *et al*., 2012).

In conclusion, the results of this first experience of proteomic characterization of *S. rivoliana* fertilized eggs revealed some of the essential proteins required in forming an embryo and allowed us to identify antioxidant proteins associated with oxidative stress. This characterization will serve as a reference for future crops in captive conditions. The expression of these antioxidant proteins could represent early biomarkers of egg and larval quality in this species and the genus *Seriola* spp. These markers can be extremely important to avoid wasting efforts producing low-quality larvae in hatcheries.

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