Characterization and expression of the gene glucose transporter 2 (GLUT2) in embryonic, larval and adult Bay snook *Petenia splendida* (Cichliformes: Cichlidae)

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Bay snook (*Petenia splendida*) is a carnivorous cichlid species with excellent economic value in Southeast Mexico. Although this species presents an excellent potential for commercial aquaculture, the information about its nutritional, physiological, and reproductive metabolic pathways is meager. The current study focuses on the expression of glucose transporter 2 (*glut2*) in embryos and larvae at 5, 10, 15-, 20-, 25-, and 30-days post-hatch (dph) and in the liver, intestine, kidney, muscle, heart, testicle, gill, stomach, pancreas, and brain of adult fish. The partial sequence of *glut2* was obtained, and specific qPCR primers were designed. In embryos, the expression was lower compared to larvae at 5, 15, and 20 dph. The highest expression in larvae occurred at 20 dph and the lowest at 25 and 30 dph. Maximum expression levels in adults occurred in the liver and intestine. Our results show that *glut2* is expressed differentially across tissues of adult bay snook, and it fluctuates during larval development.

Keywords: Adult fish, Early ontogeny, Gene expression, Glucose transporter, *Petenia splendida*.

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La mojarra tenguayaca (*Petenia splendida*) es una especie de cíclido carnívoro con excelente valor comercial en el sureste de México. A pesar de su potencial para la acuicultura, existe muy poca información sobre sus rutas metabólicas relacionadas con su nutrición, fisiología y reproducción. El presente estudio se enfoca en la expresión del transportador de glucosa (*glut2*) en embriones y larvas de 5, 10, 15, 20, 25 y 30 días post eclosión (dph) y en el hígado, intestino, riñón, músculo, corazón, testículo, branquias, estómago, páncreas y cerebro en peces adultos. Se diseñaron cebadores de qPCR específicos para *glut2*. La expresión en los embriones fue menor que en larvas a los 5, 15 y 20 dph. La expresión máxima en larvas se observó a los 20 dph y la mínima a los 25 y 30 dph. La expresión más alta en los adultos ocurrió en el hígado y el intestino. Nuestros resultados muestran que el gen *glut2* se expresa de manera diferencial en los tejidos de adultos de la mojarra tenguayaca y su expresión fluctúa durante el desarrollo larvario.

Palabras clave: Expresión genómica, Ontogenia inicial, Peces adultos, *Petenia splendida*, Transportador de glucosa.

INTRODUCTION

The Bay snook *Petenia splendida* Günther, 1862 is a carnivorous freshwater cichlid species distributed from Southeast Mexico to Central America (Álvarez-González *et al*., 2008). This species possesses an excellent economical value and is widely accepted in local markets (Pérez-Sánchez, Páramo-Delgadillo, 2008). Additionally, it presents suitable characteristics for aquaculture, including high growth rate, tolerance to overcrowding, relative low time of production (~1 year) and its meat has high nutrimental content (Uscanga-Martínez *et al*., 2011). Various studies have described different aspects of *P. splendida*, such as its biology and physiology (Álvarez-González *et al*., 2008; Jiménez-Martinez *et al*., 2019), taxonomy and ecology (Méndez *et al*., 2011), aquaculture technology (Pérez-Sánchez, Páramo-Delgadillo, 2008; Vidal-López *et al*., 2009; Treviño *et al*., 2011, Jiménez-Martínez *et al*., 2019), nutrition and digestive physiology (Álvarez-González *et al*., 2008; Uscanga-Martínez *et al*., 2011; Rodríguez-Estrada *et al*., 2020), and cytogenetics (Arias-Rodriguez *et al*., 2008). However, there is gap in the understanding of nutritional metabolic pathways, especially for glucose. Glucose is a primordial energy source for most physiological processes and the correct functioning of various tissues such as the brain, liver, gonads, and muscle (Hemre *et al*., 2002; Deng *et al*., 2020). This molecule is absorbed in the gut by enterocytes through specific glucose transporters (Blanco *et al*., 2017). Two types of transporters for glucose and other monosaccharides have been described: 1) sodium-glucose transporters (*sglt*) mainly related to renal glucose reabsorption, and 2) glucose transporters (*glut*) which facilitates the transport of glucose across the plasma membrane via facilitated diffusion (Thorens, 2015; Bertrand *et al*., 2020). In mammals, 14 glucose transporters (*glut1-14*) have been described (Wood, Trayhurn, 2003; Scheepers *et al*., 2004; Mueckler, Thorens, 2013; Thorens, 2015; Holman, 2020) and each GLUT isoform plays a specific role in glucose metabolism depending on tissue expression patterns, substrate specificity, and the regulation of the expression under different physiological conditions (Wright Jr. *et al*., 1998; Castillo *et al*., 2009; Gómez-Zorita, Urdampilleta, 2012). In teleost fish, *glut1* has been characterized in common carp (*Cyprinus carpio*) (Teerijoki *et al*., 2001b), grass carp (*Ctenopharyngodon idella*) (Li *et al*., 2018), rainbow trout (*Oncorhynchus mykiss*) (Teerijoki *et al*., 2000, 2001a) and Atlantic cod (*Gadus morhua*) (Hall *et al*., 2004); *glut3* in grass carp, (*C. idella*) (Zhang *et al*., 2003) and Atlantic cod (*G. morhua*) (Hall *et al*., 2005); and *glut2* and *glut4* in Atlantic salmon (*Salmo salar*) (Menoyo *et al*., 2006) and Atlantic cod (*G. morhua*) (Hall *et al*., 2006, 2014). In the case of *glut1-6*, *glut8-13* and *glut15* are reported in the spotted sea bass (*Lateolabrax maculatus*) (Fan *et al*., 2019).

GLUT2 is considered the main isoform of glucose transporters in the liver, plays a role in regulating insulin, and removes excess glucose from the blood (Mueckler, Thorens, 2013). This molecule is involved in different processes, including intestinal and renal glucose absorption, stimulation of insulin secretion in pancreatic cells, and the glucose detection capacity in specific brain regions involved in the regulation of glucose and food metabolism (Castillo *et al*., 2009; Yan, 2017; Zhao *et al*., 2020). In fish, *glut2* has been detected in different tissues (pancreatic cells, hypothalamus, pancreas, kidney, and liver), and its expression is related to feeding habits and nutrition in species such as zebrafish (*Danio rerio*), common carp (*C. carpio*), rainbow trout (*Oncorhynchus mykiss*), Nile tilapia (*O. niloticus*), blunt snout bream (*M. amblycephala*), grass carp (*C. idella*), and cobia (*Rachycentron canadum*) (Krasnov *et al*., 2001; Panserat *et al*., 2001; Castillo *et al*., 2009; Polakof *et al*., 2010; Liu *et al*., 2014; Liang *et al*., 2018; Deng *et al*., 2020; Zhao *et al*., 2020; Ye *et al*., 2020). In Atlantic cod (*G. morhua*), the expression of *glut2* during larval development decreased with starvation because of changes in blood glucose (Hall *et al*., 2006). However, there is no available information regarding *glut2* regulation during the larval development of the *P. splendida*. For this reason, this study examined the expression of *glut2* in various organs of *P. splendida* adults and contributed to understanding the gene's regulation and dynamics during the early ontogeny of this species.

MATERIAL AND METHODS

Fish acquisition. Twenty male individuals of *P. splendida* (450–490 g and 20–25 cm) were obtained from the Tropical Aquaculture Laboratory, División Académica de Ciencias Biológicas, Universidad Júarez Autónoma de Tabasco, Southeast Mexico. Fish were kept in circular 2000-L polyethylene tanks and were fed the rainbow trout diet (45% protein and 16% fat, El Pedregal® Silver Cup, Toluca, Mexico) with particle diameters ranging between 5.5- and 9.0-mm. Embryos and larvae were obtained from simultaneous spawning from the broodstock kept in the same facility. Six females and three males were transferred from holding tanks to a 2000-L breeding tank. Six acrylic sheets (one side smooth, one side rough) were placed in each tank to provide shelter and egg-laying surfaces (rough side). Right after hatching, larvae were separated from the adults. After 3 days 150 larvae per tank were placed in three 70-L oval tanks with constant aeration (~95% air saturation), pH ~8.0, connected to an open system, at 28°C, with water changes (80%) every two or three days. Larvae were fed satiety with brine shrimp (*Artemia* sp.) nauplii five times per day (at 8:00, 11:00, 13:00, 15:00, and 18:00 h) for 7 days (until 10 days post-hatching, dph). From 11 to 13 dph, larvae were provided with a co-feeding of *Artemia* nauplii and trout feed (Silver Cup; Nelson and Sons, Inc; proximate composition: 45% proteins, 16% lipids, 21% carbohydrates, 9–12% ashes) and from day 14 dph, larvae were only provided with trout feed until 30 dph. Food was provided at apparent satiation, and particle size was adjusted according to larval growth (250–500, 500–750, and > 750 m). Temperature (28.0 ± 0.7°C), dissolved oxygen (5.9 ± 0.6 mg/L), and pH (7.1 ± 0.3) Water parameters were constantly assessed with a YSI 85® Meter, YSI Inc., Yellow Springs, OH (temperature (28.0 ± 0.7°C), dissolved oxygen (5.9 ± 0.6 mg/L), and pH (7.1 ± 0.3).

Sampling. After males were euthanized by cold thermal shock (at -4°C) after 24 h of fasting. Fish were dissected in ice to obtain the liver, intestine, kidney, muscle, heart, testicles, gills, stomach, pancreas, and brain. Larvae were sampled on different days after hatching (10 larvae per tank): before first feeding, starting from the embryo (considered as 0 dph), and 5, 10, 15, 20, 25, and 30 dph. Larvae were removed from each tank, rinsed in distilled water, and transferred to Eppendorf tubes with 1.5 mL of RNA Later and stored at -80°C.

RNA extraction and cDNA synthesis. The RNA *e*xtraction was performed from tissues and pooled larvae (10) using the Trizol Reagent (Invitrogen, Carlsbad, CA) method under the manufacturer's indications. One microgram of RNA was used for reverse transcription with iScript TM Select cDNA Synthesis Kit 170 – 8,896 (BioRad, Hercules, CA). Subsequently, 1 µL of cDNA was used for the end-point Polymerase Chain Reaction (PCR). To obtain the partial sequence of *glut2*, samples were run in a 96-well thermocycler using the Platinum Taq DNA Polymerase (Invitrogen, Carlsbad, CA). Amplification was conducted under the following conditions: 10 min at 95°C, followed by 35 cycles at 95°C for 30 s, 58°C for 30 s, and 72°C for 50 s with a 5 min extension at 72°C using specific oligonucleotides previously obtained from alignment (using Clustal-W software, Infobiogen) of corresponding sequences available in the library from different species of cichlids including Nile tilapia (*O. niloticus* ACZ73587.1), Burton's mouthbrooder (*Astatotilapia burtoni* XP_005926097) and zebra mbuna (*M. zebra* XP_004540234.1) (Tab. 1). The amplification products were separated in 1.5% agarose gel stained with ethidium bromide. Observed bands under UV light (Biorad® Model Universal Hood II, Hercules, CA) were cut from the gel and purified using the PureLink® PCR Purification Kit (Invitrogen). The purified bands were sent to the Synthesis and Sequencing Unit of the Institute of Biotechnology of the Universidad Nacional Autónoma de México (UNAM) to be sequenced.

Sequence analysis. Obtained partial sequences were edited and analyzed using ExPASy translation software to search for the open reading frame (ORF). Once the ORF was identified, it was translated to amino acid (AA) sequences using standard genetic codes. The nucleotide sequence was compared with DNA sequences from other fish available in the GenBank database network service at NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Protein sequence alignments were performed by the multiple sequence alignment software BioEdit 7.2 (www.mbio.ncsu.edu/bioedit/bioedit.html). A phylogenetic tree was generated using neighbor-joining (NJ) methods based on the AA sequence using MEGA 7.0 software.

TABLE 1 | Oligonucleotides used for *glut2* gene sequencing and q-PCRs in *Petenia splendida*.

Primer name	Forward primer (5'-3')	Reverse primer (5'-3')	Size, pb	Step
GLUT2	ATCATGTACTGGTCGTTGT GGGCCGCATGATCCAACTAT	GTAATTTGAGGCCCACTGTCA TGCATCATGAGGGCAACAAC	889 139	RT-PCR qPCR
18S rRNA	GGACACGGAAAGGATTGACAG	GTTCGTTATCGGAATTAACCAGAC	111	qPCR

Real-time polymerase chain reaction (q-PCR). The resulting cDNA from adult tissues, embryos, and larvae were diluted in 200 µL of distilled water. The quantitative polymerase chain reactions (qPCRs) were performed in a 96-well thermocycler CFX96 Real-Time System Thermal Cycle (Model C1000, CA). The reaction mixture included 10 µL of Eva Green, 2 µL cDNA, and 0.2 µL of each primer (shown in Tab. 1). The thermal program included 2 min at 95°C, followed by 38 cycles at 95°C for 10 s, 60°C for 30 s, and extension at 70°C for 5 s. All reactions were performed by duplicates. The normalization of cDNA 18S rRNA was used as a constitutive gene and carried out in parallel with all samples, according to Wang *et al*. (2015) and Yang *et al*. (2013). A standard curve for each pair of primers was generated to estimate amplification efficiencies based on known amounts of cDNA (four serial dilutions corresponding to cDNA transcribed from 100 to 0.1 ng of total RNA). Relative gene expression of tissues and larval growth stages was calculated by the delta-delta copy threshold (CT) method (Pfaffl, 2001).

Statistical analysis. The relative expression of *glut2* between the different tissues of adult *P. splendida* and the comparison between embryos and the different dph of larvae were analyzed using the Kruskal-Wallis test. A posteriori Nemenyi test was performed to determine significant differences between tissues (adults) and developmental time (embryos and larvae) ($P \leq 0.05$). All statistical analyses were performed using the software STATISTICA TM v. 7.0 (StatSoft, Inc., Tulsa, OK.).

RESULTS

PCR amplification and sequencing analysis. A partial sequence for *glut2* of 889 bp encodes 296 AA was obtained and registered in the GenBank (accession number QKG31965.1, MN792759.1; Fig. 1). The alignment of *P. splendida* AA concerning other fishes exhibited conserved regions of *glut2.* Identity values were shown as 98.5 % for Nile tilapia (*Oreochromis niloticus*), 97.97% for zebra mbuna (*Maylandia zebra*), 93.24% for Burton's mouthbrooder (*Astatotilapia burtoni*), 88.85% for Turquoise killifish (*Nothobranchius furzeri*), 93.58% for flameback (*Pundamilia nyererei*), 92.57% for princess cichlid (*Neolamprologus pulcher*), 90.20% for flier cichlid (*Archocentrus centrarchus*), 88.51% for yellow perch (*Perca flavescens*), 43.7% for zebrafish (*Danio rerio*), 43.6% for common carp (*Cyprinus carpio*) 43.5 % for blunt snout bream (*Megalobrama amblycephala*), 43.2 % for grass carp (*Ctenopharyngodon idella*) and 29.5% for rainbow trout (*Oncorhynchus* *mykiss*) (Fig. 2). According to the AA sequence of *glut2,* the phylogenetic three clusters *P. splendida* (bootstrap value of 74%) with the Nile tilapia (*O. niloticus*), blue tilapia, zebra mbuna (*M. zebra*), Burton's mouthbrooder (*A. burtoni*), flameback (*P. nyererei*) and princess cichlid (*N. pulcher*) (Fig. 3).

ACCESSION: QKG31965 glucose transporter 2 (GLUT2), partial *Petenia splendida*

atc atg tac tgg tct ctg tct gtg tca atc ttc tcc atc ggt ggc gtg gta tcc tcc ttc 60
I M Y W S L S V S I F S I G G V V S S F 20

ttg gtt gga ttt gtg gga gat ctg aaa ggg agg gta aaa ggg atg tta atg gtc aat gtt 120
L V G F V G D L K G R V K G M L M V N V 40

ctg gct gta gca gct gga ctg ctg atg ggt ctt tgt aag atg tgg aag cca cac atc atg 180
L A V A A G L L M G L C K M W K P H I M 60

gtc atc tca ggc cgc gct gtt atg ggt ttc tat tgt ggt ctg acg tct ggg cta gtg cct 240
V I S G R A V M G F Y C G L T S G L V P 80

atg tac att ggg gag act gca cca aaa gct tac aga ggg gct ctg gga aca tta cac cag 300
M Y I G E T A P K A Y R G A L G T L H Q 100

ctc gct gtt gtc att ggc att cta atc agc cag ata ata ggt ttg gat ttt gtg ctt ggt 360
L A V V I G I L I S Q I I G L D F V L G 120

aat gac caa atg tgg ccc ctg ttg ctc ggt ctg tct gga gct cca gca ata tta caa tcc 420
N D Q M W P L L L G L S G A P A I L Q S 140

ctt ctg ctg cct ctt tgt cct gag agt cca cga cac ctt tac atc cta ttg ggc aag gaa 480
L L L P L C P E S P R H L Y I L L G K E 160

PRIMER 5'

caa gag gct cga aaa agt ctg tat cgt cta aag **ggg ccg cat gat cca act at**t gat ctg 540
Q E A R K S L Y R L K G P H D P T I D L 180

gaa gag atg aga agg gaa aaa gaa gag gca aac aaa gag gac aaa gtc tct atc ttt tct 600
E E M R R E K E E A N K E D K V S I F S 200

PRIMER 3'

ttg atc tcc tct tct gta tac aga aaa cag ctg **gtt gtt gcc ctc atg atg ca**c ctt tcc 660
L I S S S V Y R K Q L V V A L M M H L S 220

cag cag ttg tct ggc att aat gct atc ttt tac tac tct acg gct atc ttc tct cga gct 720
Q Q L S G I N A I F Y Y S T A I F S R A 240

ggt gtg agt cat cca gtt tat gcc act ata gga gtc ggg gtc att aac acg atc ttc act 780
G V S H P V Y A T I G V G V I N T I F T 260

ctg atg tct gtg gca ctt gtg gac agg gct ggc aga cgc act cta act ctg gtt ggt ctt 840
L M S V A L V D R A G R R T L T L V G L 280

ggg gga atg tgt tgc tgt gct gtt gcc atg aca gtg ggc ctc aaa tta c 889
G G M C C C A V A M T V G L K L 296

FIGURE 1 | Partial sequence of nucleotides and amino acids (AA) encoding *glut2* (glucose transporter 2) from *Petenia splendida* taken from Gen Bank to design specific oligonucleotides for qPCR.

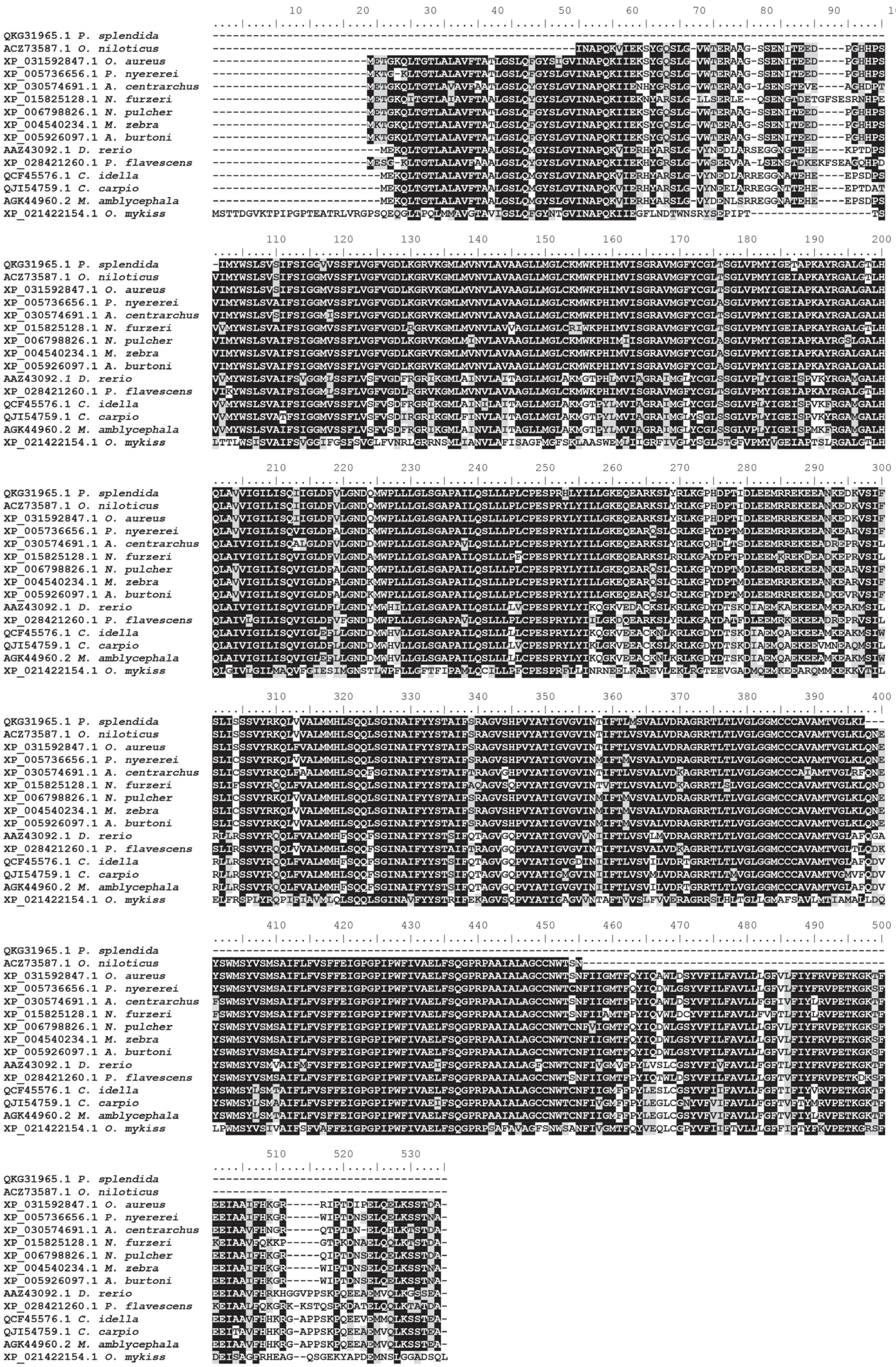

FIGURE 2 | Amino acid sequence of *glut2* in *Petenia splendida* aligned with other species other species of teleost fish. Identical amino acids are presented in black, and the high and less conserved amino acids are presented in gray and period, respectively.

Relative expression of *glut2* in *P. splendida* adults and larvae. The highest expression of *glut2* occurred in the liver, followed by the intestine, kidney, and muscle, while the lowest was in the pancreas, gill, heart, brain, testicle, and stomach, respectively ($P \leq 0.05$) (Fig. 4). On the other hand, *glut2* expression in embryos and larvae as a function of developmental time showed high variation (Fig. 5). Embryos had higher expression than larvae at 10, 25, and 30 dph and lower expression when compared to larvae at 5, 15, and 20 dph ($P \leq 0.05$). The highest expression of *glut2* occurred in 20 dph larvae and the lowest in 25 and 30 dph larvae (Fig. 5).

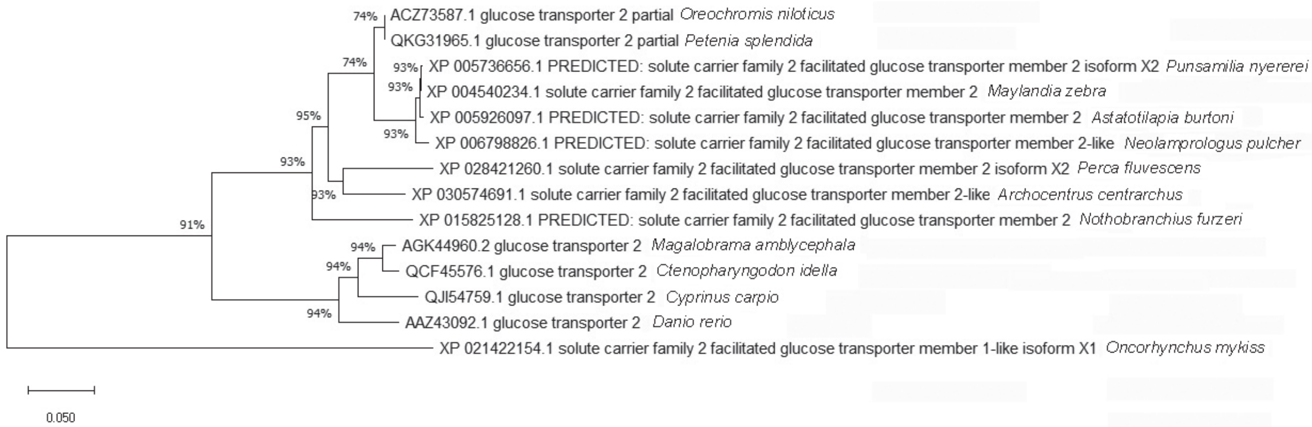

FIGURE 3 | Phylogenetic tree based on the sequence of *glut2* (glucose transporter 2) from *Petenia splendida* and other teleosts using the neighbor-joining (NJ) method. Values at branch points represent percentage frequencies for tree topology after 1,000 interations.

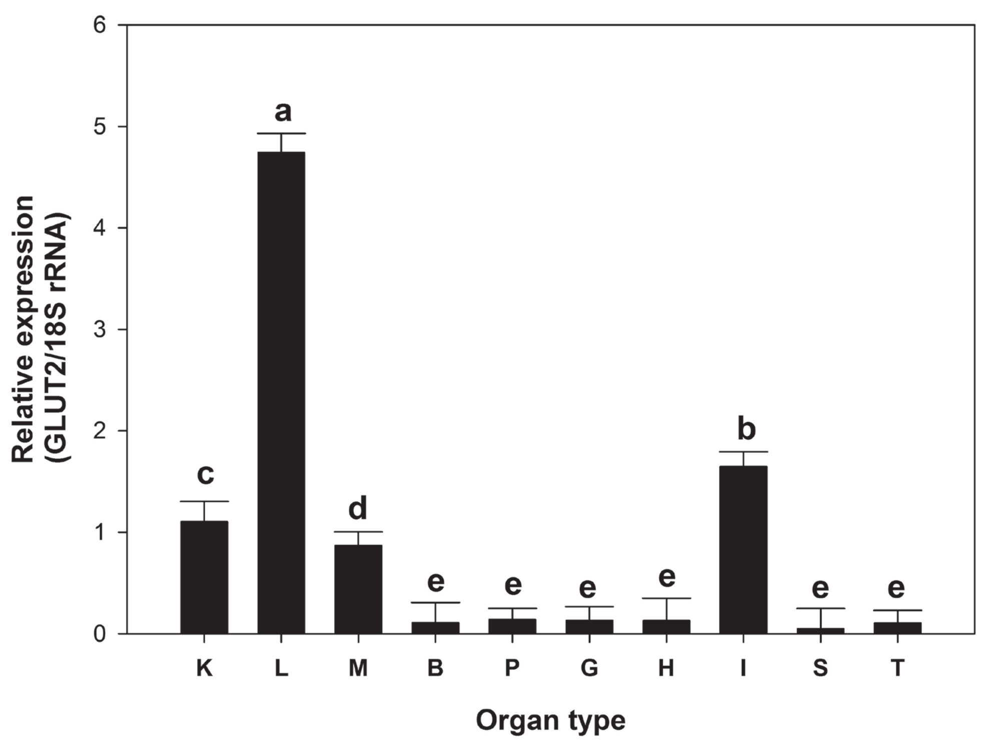

FIGURE 4 | Relative expression of *glut2* in kidney (K), liver (L), muscle (M), brain (B), pancreas (P), gill (G), heart (H), intestine (I), stomach (S) and testis (T) of adult *Petenia splendida* (mean ± SEM; n = 3). Lowercase letters indicate significant differences between the expression level in the tissues ($p < 0.05$).

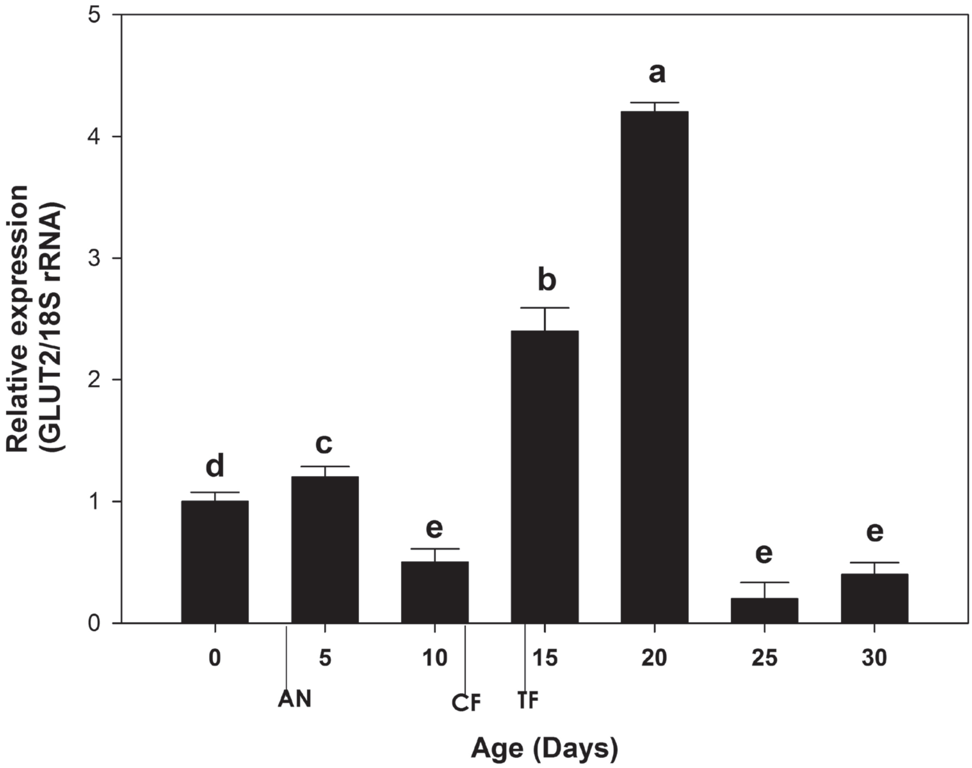

FIGURE 5 | Relative expression of *glut2* during the early ontogeny of *Petenia splendida*. Lowercase letters indicate significant differences in the expression of *glut2* as a function of developmental time ($p < 0.05$). AN: Artemia nauplii (3–10 dph), CF: cofeeding (Artemia nauplii and tilapia feed) (11–13 dph), TF: trout feed (14–30 dph) (mean ± SEM; n = 3).

DISCUSSION

Characterization and expression of *glut2* in tissues from *P. splendida* adults. In the current study, the partial sequence of *glut2* was isolated and identified from the liver of *P. splendida*. Amino acid alignment of *glut2* showed a great identity and highly conserved regions among cichlids and other teleosts. These results are consistent with *O. niloticus*, *M. amblycephala*, and *C. carpio*, where *glut2* contains 12 transmembrane domains (Liu *et al*., 2014; Liang *et al*., 2018; Deng *et al*., 2020). Moreover, the exact phylogenetic trend, including high values of convergence, is undeviating with results from Liu *et al*. (2014).

Furthermore, expression of *glut2* was observed in all the analyzed tissues from *P. splendida* (liver, intestine, kidney, muscle, heart, testicle, gill, stomach, pancreas, and brain). The highest mRNA expression occurred in the liver, followed by the intestine and kidney. These results agree with studies in other teleosts, including *O. niloticus* (Liu *et al.,* 2014), *C. carpio* (Deng *et al*., 2020), *M. amblycephala* (Liang *et al*., 2018), *O. mykiss* (Panserat *et al*., 2001; Krasnov *et al*., 2001), *G. morhua* (Hall *et al*., 2006) and European sea bass *Dicentrarchus labrax* (Terova *et al*., 2009). In addition, studies in mammals show that the highest expression of *glut2* occurs in the liver, pancreas, intestine, and kidney (Karim *et al*., 2012; Thorens, 2015), which suggests that the patterns of *glut2* expression are highly conserved within vertebrates. One possible explanation could be the similarity between the aminoacid sequences in fish and mammals, including humans (Krasnov *et al*., 2001; Castillo *et al*., 2009).

The increased expression of *glut2* in the liver may occur since this organ is responsible for the synthesis, storage, and redistribution of glucose in the form of glycogen (Polakof *et al*., 2010; Karim *et al*., 2012; Liang *et al*., 2018). Furthermore, the intestine is a vital organ for glucose absorption, and its dynamics and mechanisms are critical endpoints in elaborating specific diets for cultured fish species (Thorens, Mueckler, 2010; Blanco *et al*., 2017; Zhao *et al*., 2020). In zebrafish, *glut2* expresses in the brush border and basolateral membranes of the intestines. However, metabolic and endocrine factors regulate mRNA levels and the distribution of molecules of this gene to the apical membrane (Cheeseman, 2002; Castillo *et al*., 2009). In contrast, the expression of *glut2* in the kidney has been detected in other species such as *O. mykiss*, *D. rerio*, and *G. morhua* (Krasnov *et al*., 2001; Panserat *et al*., 2001; Castillo *et al*., 2009; Hall *et al*., 2014), where they mention that the kidney is involved in the regulation of glucose homeostasis through 3 primary mechanisms: 1) the release of glucose into the bloodstream through gluconeogenesis, 2) the consumption of glucose to meet the renal energy needs, and 3) glucose reabsorption in the proximal tubule (Segura, Ruilope, 2013).

Expression of *glut2* in embryos and larvae of *P. splendida*. In our study, *glut2* expression was observed from the embryonic period. Expression in embryos could be attributed to zygotic gene activation during early development or maternal mRNA transference; however, details about gene activation in *P. splendida* zygotes are unknown. Fish energy reserves such as proteins, carbohydrates, and lipids are found in yolk and oil droplets in larvae, and their functions are namely structural and for the maintenance of metabolic pathways, which depend on both genetic and epigenetic factors (Burggren, Blank, 2009; Treviño *et al*., 2011; Lubzens *et al*., 2017). The low expression of *glut2* in 5 dph larvae may be related to the poor differentiation of the digestive system, where the intestine is a straight tube (dorsally to the liver) connected directly to the esophagus (Treviño *et al*., 2011). Our results are consistent with previous reports in zebrafish, where *glut2* expression is detected in 5 dph by foregut development anterior intestine (intestinal bulb), which plays an essential role in the absorption of glucose via facilitated diffusion occur, especially in the enterocytes of the luminal and basolateral membrane (Castillo *et al*., 2009; Polakof *et al*., 2010; Blanco *et al*., 2017). Therefore, Holmberg *et al*. (2004) mention that the efficiency of carbohydrate utilization in fish larvae depends on an adequate development of the digestive system and the concentration of this nutrient in live prey, which in the case of *Artemia* nauplii, ranges from 11 to 17% (Guevara, Lodeiros, 2003). For *P. splendida* larvae, the intestine is fully functional on day 5 dph when a regular movement pattern marks exogenous feeding is visible, being the moment where *glut2* expression increases when the *Artemia* nauplii are provided. Similarly, to the results obtained with the cobia *Rachycentron canadum* larvae when they were fed with a diet rich in carbohydrates by the addition of rotifers and *Artemia* (Hall, 2006). In this sense, the regulation of several genes for carbohydrate metabolism in fish larvae is related to innate genomic expression and the external stimuli when the live prey is offered (Darias *et al*., 2006).

Expression of *glut2* in *P. splendida* decreased at 10 dph and subsequently increased at 15 dph. The increment in glut2 expression could be related to the change in the diet (co-feeding). By 15 dph, larvae were fed with a balanced commercial diet, increasing the glucose intake using carbohydrates in the formulation. For example, wheat, soy, sorghum meals, and starch are used as binders (Kamalam *et al*., 2017). Uscanga-Martínez *et al.* (2011) mentioned that 15 dph *P. splendida* larvae present a digestive system formed with three well-differentiated segments in the intestine (anterior, middle, and posterior). The liver occupies the liver most of the anterior part of the abdominal cavity. In this regard, the maximum glut2 expression was registered at 20 dph, where *P. splendida* can be considered a juvenile with all its organs fully formed and functional, especially the liver, intestine, and endocrine pancreas, where pancreatic hormones including insulin, glucagon, and somatostatin are expressed (Treviño *et al*., 2011; Liu *et al*., 2014; Liang *et al*., 2018; Deng *et al*., 2020). The maximum *glut2* expression was detected in *P. splendida* larvae at 20 dph. It can be attributed to the use of balanced feeds because their composition contains high concentrations of vegetable ingredients (up to 21% carbohydrate content), resulting in a considerable accumulation of glycogen in the liver. Although, high carbohydrate accumulation did not show histological damage (Treviño *et al*., 2011). Additionally, the high content of carbohydrates in diets for *O. niloticus* larvae is frequent since many cichlids are omnivorous species and can quickly assimilate these molecules (El-Sayed, 2006; Stickney, 2006). In contrast, *P. splendida* is a carnivorous fish and cannot tolerate a carbohydrate-rich diet such as other freshwater or marine carnivorous teleosts (Polakof *et al*., 2012; Thorens, 2015; Marandel *et al*., 2016).

In summary, the maximum *glut2* expression in bay snook larvae occurred when organogenesis was completed (20 dph), especially in the liver and intestine. Similarly, *glut2* expression in adults of *P. splendida* is mainly expressed in the liver and intestines to facilitate glucose absorption. Moreover, the decrease in glucose generated by gluconeogenesis and *glut2* expression can be influenced by diet composition.

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Gil Martínez-Bautista: Data curation, Formal analysis, Investigation, Methodology, Software, Supervision, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

Animals were handled in compliance with the Norma Oficial Mexicana NOM-062-ZOO-1999 from Secretaria de Agricultura, Ganaderia, Desarrollo Rural, Pesca y Alimentación, the Mexican standards for good welfare practices of laboratory animals.

COMPETING INTERESTS

The authors declare no competing interests.

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