Chapter 8
Transcriptional Response of Golden Pompano *Trachinotus ovatus* Larvae to Temperature

Mingyang Han, Zhengyi Fu, Zhenhua Ma, and Gang Yu

Abstract The molecular response pattern of golden pompano *Trachinotus ovatus* larvae under temperature stress is reviewed in this chapter. Gene ontology (GO) analysis and Kyoto Encyclopedia of Genes and Genomes (KEGG) analysis showed that a large number of differentially expressed genes (DEGs) were related to metabolic processes, protein synthesis, and nutrient digestion and absorption. The differentially expressed genes were most highly enriched into the pathways, including protein digestion and absorption, fat digestion and absorption, starch and sucrose metabolism, vitamin digestion and absorption, and glutathione metabolism. High temperature may inhibit the secretion of type II collagen by downregulating the expression of Shh and Sox9a genes. This chapter advances our understanding of the response mechanism to high temperature in *Trachinotus ovatus* and guides relevant production practices in hatcheries.

Keywords Transcriptional response · Temperature stress · Skeletal development · *Trachinotus ovatus*

8.1 Introduction

Environmental factors are essential to the success of aquatic animal breeding. Temperature is one of the most vital environmental factors in fish since it plays a profound and controlling role in the growth, reproduction, metabolism, feeding behavior, and all metabolic processes of fish (Katersky and Carter 2005; Ma 2014; Somero 2010; Yang 2016). Although fish can deal with temperature changes by extensive biochemical, metabolic, and physiological acclimations within a suitable range (Xu et al. 2018), the inappropriate temperature can still have an adverse

M. Han · Z. Fu · Z. Ma · G. Yu (✉)
Sanya Tropical Fisheries Research Institute, Sanya, China

Tropical Aquaculture Research and Development Center, South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Sanya, China
e-mail: yugang@scsfri.ac.cn

Z. Ma et al. (eds.), *Ontogenetic development of pompano Trachinotus ovatus*,
https://doi.org/10.1007/978-981-19-1712-7_8

impact. Low temperature may significantly reduce the growth rate and the activity of digestive enzymes in fish (Tang et al. 2018). A high or low temperature may lead to a high mortality rate for fish, whose physiological process is severely disrupted (Griffiths and Harrod 2007; Ibarz et al. 2010). Besides, the inappropriate temperature may also cause disease outbreaks because the immune functions of fish are affected by temperature (Chen et al. 2002; Ndong et al. 2007). Previous studies have revealed that the outbreaks of disease in aquaculture caused by bacteria are linked to rising ambient temperatures (Matanza and Osorio 2018). During the early development of fish larvae, temperature plays a vital role because fish larvae are more sensitive to the environment. The change of water temperature may lead to abnormal growth rate, low survival rate, and high deformity rate of fish larvae (Ornsrud et al. 2004a, b; Yang et al. 2016). With the vigorous development of industries and human activities, the frequency of abnormal changes in the environment caused by human intervention increases. The intensification of global warming makes the aquaculture industry face significant challenges. Some reports have shown that commercial farming of fish such as tilapia (*Oreochromis niloticus*) (Zerai et al. 2010), common carp (*Cyprinus carpio* L.) (Sun et al. 2019), and red seabream (*Pagrus major*) (Hwang et al. 2012) is adversely affected by temperature stress. The temperature-orientated stress has brought substantial economic losses to the aquaculture industry.

The golden pompano (*Trachinotus ovatus*) belongs to the family of Carangidae and is widely distributed in Asia-Pacific regions. The golden pompano is a popular and commercially valuable fish, which is broadly cultured in the coastal area of South China in recent years owing to fast growth and suitability for cage culture (Lin et al. 2012; Ma et al. 2014; Tan et al. 2016). The fry cultivation of golden pompano is usually carried out in spring and summer. There is a peak period of death between 3 and 7 days post-hatch (DPH) of golden pompano, especially during the first few days after initial feeding, but the mortality rate is generally less than 20% (Ou and Li 2017). It has been reported that the increase in water temperature results in an increase in mortality of the larvae at this stage (Wang et al. 2011). Furthermore, the experience of environmental adaptation in the early life of fish can subsequently alter their phenotypes and physiological responses to future environmental change (Scott and Johnston 2012). Due to climate change caused by global warming, water temperature and salinity in the shallow coastal water and intertidal zones are liable to fluctuate. In Hainan Province, the fry cultivation is mostly carried out in outdoor ponds, which was more susceptible to climate change, especially after several days of continuous high temperature. However, little is known about the responding mechanism of golden pompano larvae to the temperature change at this stage. As a species of warm-water fish, the growth and survival of golden pompano larvae are strongly dependent on water temperature, but the biochemical and molecular studies on the response to temperature stress are limited to a few proteins or genes (Allais et al. 2019; Ma et al. 2016a, b, c, 2017a, b).

Transcriptomics refers to the study of all transcripts of a particular cell, tissue, or organism at a particular stage of growth or development, or under a certain physiological condition (Wang et al. 2009). RNA-Seq is a method of transcriptome analysis using deep sequencing technology, allowing for a more efficient and clear

understanding of the entire transcriptome, including non-model organisms that lack complete genome sequencing (Ekblom and Galindo 2011; Qian et al. 2014). With the rapid development of the transcriptome technology, the emergence of RNA-Seq technology based on high-throughput sequencing provides a new and convenient method with a lower cost to understand various biological processes in fish and is now increasingly used in different areas of aquatic biology (Eissa and Wang 2016; Mu et al. 2014; Qian et al. 2014). A growing number of studies have used this technique to analyze the temperature stress response of fish, such as *Cyprinus carpio* (Sun et al. 2019), *Oreochromis niloticus* (Zhou et al. 2019), *Pagothenia borchgrevinki* (Bilyk and Cheng 2014), *Lates calcarifer* (Newton et al. 2013), *Acanthochromis polyacanthus* (Veilleux et al. 2015), and *Melanotaenia duboulayi* (Smith et al. 2013). The responses of extreme eurythermal and stenothermal fish species to acute and long-term exposure to temperature are gradually revealed (Logan and Buckley 2015). A large number of differentially expressed genes related to metabolism, development, and immunity under temperature stress are obtained. However, at the same time, the results also show that the mechanism by which fish respond to temperature stress is complex. Therefore, it is imperative to explore the response mechanism of different fish to temperature stress.

At present, the transcriptome responses of *T. ovatus* juveniles to different nutritional conditions have been studied (Lei et al. 2020; Liu et al. 2019), but the transcriptome responses of *T. ovatus* larvae to temperature have not been reported. This chapter addresses temperature stress on transcriptome responses in *T. ovatus* larvae by using RNA sequencing technology. The results will help improve the understanding of the molecular mechanism and biological basis of fish adaptation to temperature variation.

8.2 The GO and KEGG Analysis of Differentially Expressed Genes (DEGs) at Different Temperatures

This chapter discusses the transcriptome responses of *T. ovatus* to temperature based on our previous studies. The GO and KEGG analyses were conducted to determine the biological functions and pathways that are significantly correlated with DEGs at different water temperatures. DEGs were significantly enriched with 147 GO terms between the low temperature (LT) group and the medium temperature (MT) group, including 88 terms for biological processes, 30 terms for molecular functions, and 29 terms for cellular components. “Cellular component biogenesis” was the most significantly enriched terms in the biological process. “Organelle,” “intracellular organelle,” and “cytoplasm” were the predominant GO terms in the cellular component. The top three significantly enriched GO terms in the molecular function were “hydrolase activity,” “cation binding,” and “metal ion binding” (Fig. 8.1a).

Between the HT group and MT group, there were 152 significantly enriched GO terms, including 105 terms in biological process, 43 terms of molecular functions, and 4 terms in the cell components. In the biological process, “metabolic process,”

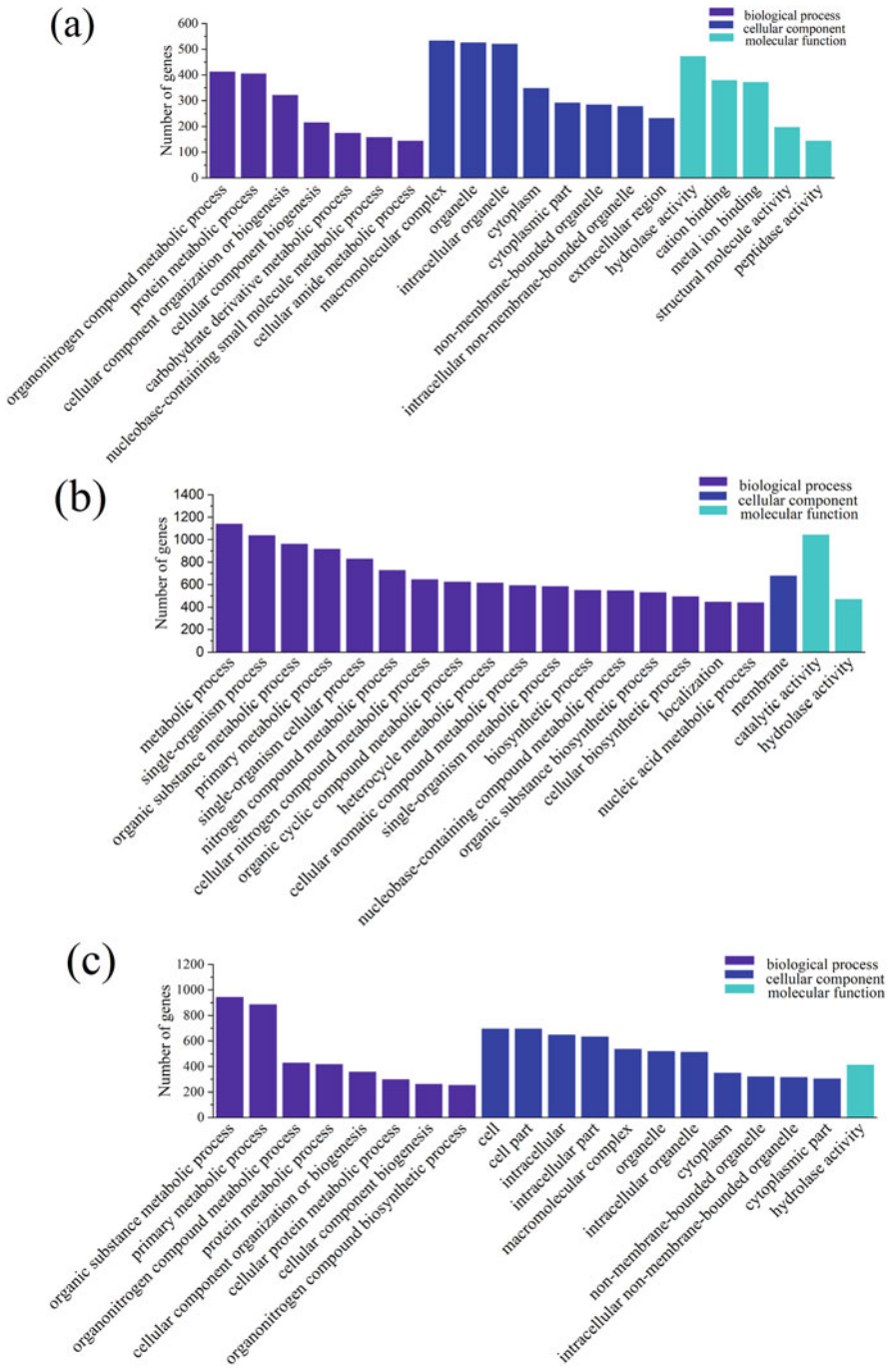

Fig. 8.1 GO classification of the DEGs. *BP* biological process, *CC* cellular component, *MF* molecular function. (**a**) LT group versus MT group; (**b**) HT group versus MT group; (**c**) LT group versus HT group

"single-organism process," "organic substance metabolic process," and "primary metabolic process" were the predominant terms. In the cellular component, "membrane" was the most significant terms. In the molecular function, "catalytic activity," "hydrolase activity," and "oxidoreductase activity" were dominant (Fig. 8.1b).

In comparing the LT group and the high temperature (HT) group, there were 164 significantly enriched GO terms, while 103 terms were enriched significantly in the biological process, 33 terms in the cell components, and 28 terms in the molecular functions. The GO terms of the "organonitrogen compound biosynthetic process," "protein metabolic process," and "cellular component organization or biogenesis" were the predominant terms in the biological process. "Macromolecular complex," "organelle," and "intracellular organelle" were the predominant GO terms in the cellular component. "Hydrolase activity" was the most significantly enriched terms in molecular function (Fig. 8.1c).

As for the KEGG pathway analysis, the top 20 pathways with the most significant enrichment were selected and displayed in Fig. 8.2. In the comparison between HT group and MT group, DEGs were enriched into 245 metabolic pathways. The significantly enriched pathways included protein digestion and absorption, chemical carcinogenesis, *Staphylococcus aureus* infection, metabolism of xenobiotics by cytochrome P450, drug metabolism–cytochrome P450, fat digestion and absorption, drug metabolism and other enzymes, starch and sucrose metabolism, retinol metabolism, vitamin digestion and absorption, and glutathione metabolism. Between the LT group and HT group, DEGs were enriched into 256 metabolic pathways, and 4 pathways were enriched significantly in the ribosome, phototransduction, cardiac muscle contraction, and protein digestion and absorption. Between the LT and MT groups, DEGs were enriched into 261 metabolic pathways, including significantly enriched pathways of the ribosome, phototransduction, cardiac muscle contraction, and protein digestion and absorption.

8.3 Effects of Water Temperature on Transcription, Translation, Protein Folding, and Degradation-Related Genes

Understanding the response of organisms to environmental changes in different ontogenetic periods is of great significance for ecological protection and sustainable development of related industries. Existing research points out that the potential threat of global warming to tropical species or warm-adapted species may be more prominent because their living water is close to the upper limit of the thermal tolerance (Pérez-Portela et al. 2020; Tomanek 2010). The aggravation of global warming and high temperature in summer will pose a potential threat to the farming regions of *T. ovatus*.

All organisms must respond to environmental stress (Buckley and Huey 2016; Logan and Buckley 2015). Under a stress condition, heat shock proteins (HSPs) play a vital role in maintaining cellular homeostasis (Deane and Woo 2011; Kayhan and

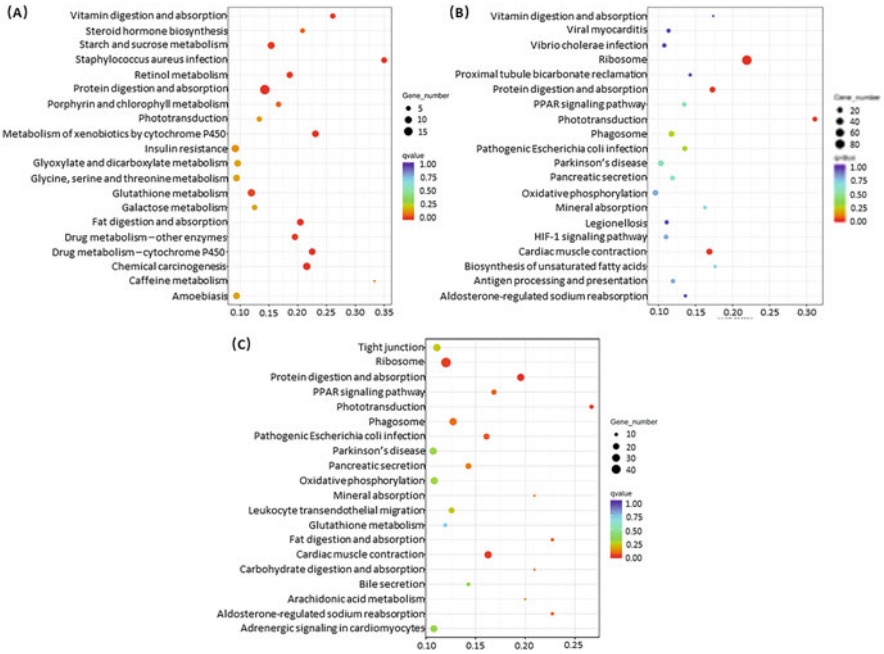

Fig. 8.2 KEGG pathways of DEGs. (**a**) HT group versus MT group; (**b**) LT group versus HT group; (**c**) LT group versus MT group

Duman 2010). For instance, HSP70 proteins are one of the most ubiquitous classes of chaperones, which have crucial functions in protein folding, maintenance of protein homeostasis, and enhancement of cell survival following a multitude of stresses (Murphy 2013). HSP90α is involved in the activation and maintenance of a wide range of regulatory and signaling proteins of cell proliferation, which is vitally important for maturation and activation of proteins (Neckers 2007). Many studies have indicated that thermal stress can increase in the expression level of HSPs in fish (Deane and Woo 2011; Ojima et al. 2005). The transcription level of *HSP70* was the highest in the MT group, and the lowest expression was observed in the HT group. Meanwhile, the transcription levels of *HSP90α* were downregulated with the increase of temperature (Fig. 8.3). This may indicate that when water temperature exceeds a certain range, the refolding efficiency of HSPs may not be high enough, or the ability of a larva to prevent protein damage and misfold through molecular chaperones such as HSPs may be inhibited (Parsell and Lindquist 1993). Another explanation may be that the increase in the synthesis of HSPs is completed, as the turnover of mRNA for HSPs is relatively rapid compared to the protein itself (Buckley et al. 2006; Logan and Buckley 2015).

In thermal stress, activation of other mechanisms, such as ubiquitin-mediated proteolysis, is often required to promote the degradation of damaged proteins and thus maintain cell homeostasis (Hatakeyama and Nakayama 2003; Kultz 2005;

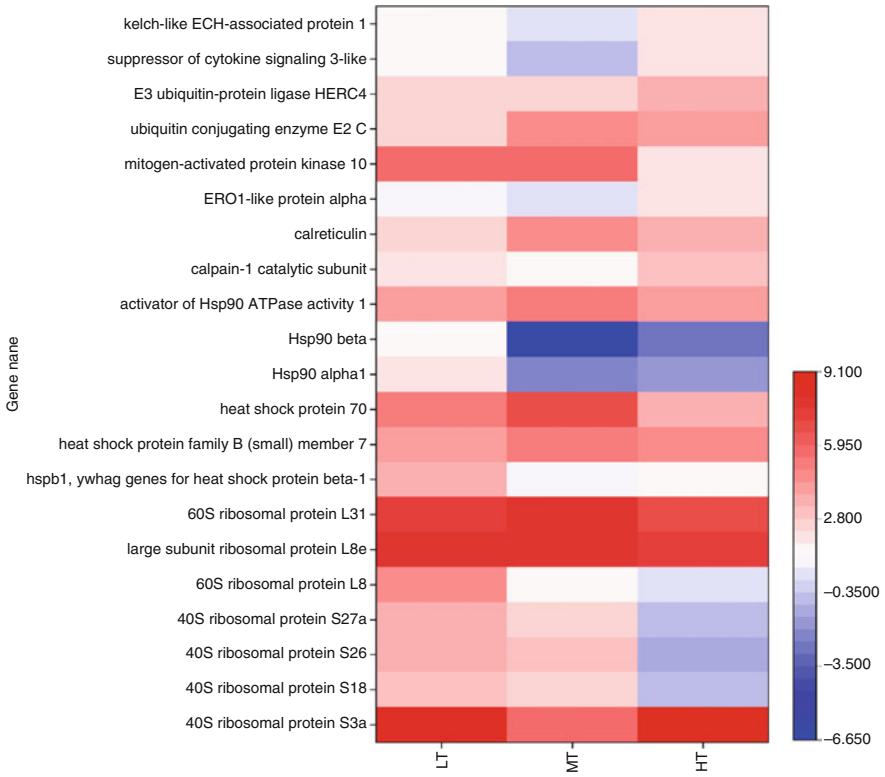

Fig. 8.3 Heat map of the DEGs related to transcription, translation, protein folding, and degradation of *T. ovatus* larvae at different temperatures. Log_2(RPKM) value for each gene has been taken the average of three values and is shown using a color scale

Pickart and Eddins 2004). Some genes belonging to the ubiquitin-mediated proteolysis pathway are upregulated in the MT group and the HT group, including ubiquitin-conjugating enzyme E2C, ubiquitin-protein ligase E3, suppressor of cytokine signaling 3-like, and kelch-like ECH-associated protein 1 (Fig. 8.3). At the same time, with the increase of temperature, many DEGs were enriched in the GO terms related to peptidase activity and hydrolase activity. This also indicates that the water temperature of 32 °C may harm *T. ovatus* larvae.

Compared with the LT group, DEDs enriched into the ribosome pathway were downregulated in the MT and HT groups (Fig. 8.3). The ribosome is the site of protein synthesis, and its primary function is to promote the mutual recognition of mRNA and rRNA and translate the nucleotide sequence on mRNA into the amino acid sequence on the polypeptide chain (Derenzini et al. 2017). Ribosomal protein is an essential component of ribosomes and plays a crucial role in the synthesis of proteins in cells. The results of this study are similar to those of Liu et al. (2013) who show that the ribosomal protein gene in gills of catfish treated with high temperature

was significantly inhibited. These results suggest that the general protein synthesis of the larvae may be inhibited under a too high temperature (Buckley et al. 2006). The study of Cai et al. for *Lateolabrax maculatus* similarly suggests that high temperature may decrease anabolism of protein (Cai et al. 2020).

8.4 Effect of Water Temperature on Metabolism-Related Genes

The metabolic response of *T. ovatus* larvae was significantly affected by high temperature. As a fundamental property of all organisms, metabolism is considered to be highly dependent on temperature and determine the rates of resource uptake or allocation to growth and reproduction (Ohlberger et al. 2012), and the effect of temperature on organism metabolism is species-specific. According to the research of Zheng et al. (2019), heat stress could lead to downregulation of transcription levels of some key enzymes in the glucose metabolism pathway and upregulation of enzymes related to fat metabolism in *Marsupenaeus japonicus*. In the heat stress study of zebra fish, the metabolic rate also increases with temperature (Vergauwen et al. 2010). The GO enrichment analysis showed that a large number of DEGs were enriched into metabolism-related items, including "metabolic process," "organic substance metabolic process," "primary metabolic process," "heterocycle metabolic process," "organic cyclic compound metabolic process," "organonitrogen compound metabolic process," "ATP metabolic process," "protein metabolic process," and "small molecule metabolic process." KEGG analysis showed that the pathways of starch and sucrose metabolism were significantly influenced at high temperature. In the HT group, the transcriptional levels of alpha-glucosidase, maltase-glucoamylase, and UTP-glucose-1-phosphate uridylyltransferase were significantly upregulated (Fig. 8.4). These results indicate that the metabolic activity of the larva under a high-temperature environment would be significantly enhanced. Compared with MT group, the "metabolism of xenobiotics by cytochrome P450," "drug metabolism–cytochrome P450," "drug metabolism and other enzymes," and "glutathione metabolism" pathway were significantly affected. The DEGs enriched to the glutathione metabolic pathway were all formed by upregulated genes (Fig. 8.4). Activation of the glutathione metabolic pathway can protect cells from oxidative damage and provide reducing substances for maintaining the internal environment of cells to resist high-temperature stress (Tate and Meister 1981). These results indicate that the larvae in the 32 °C water are more susceptible to stress from external substances.

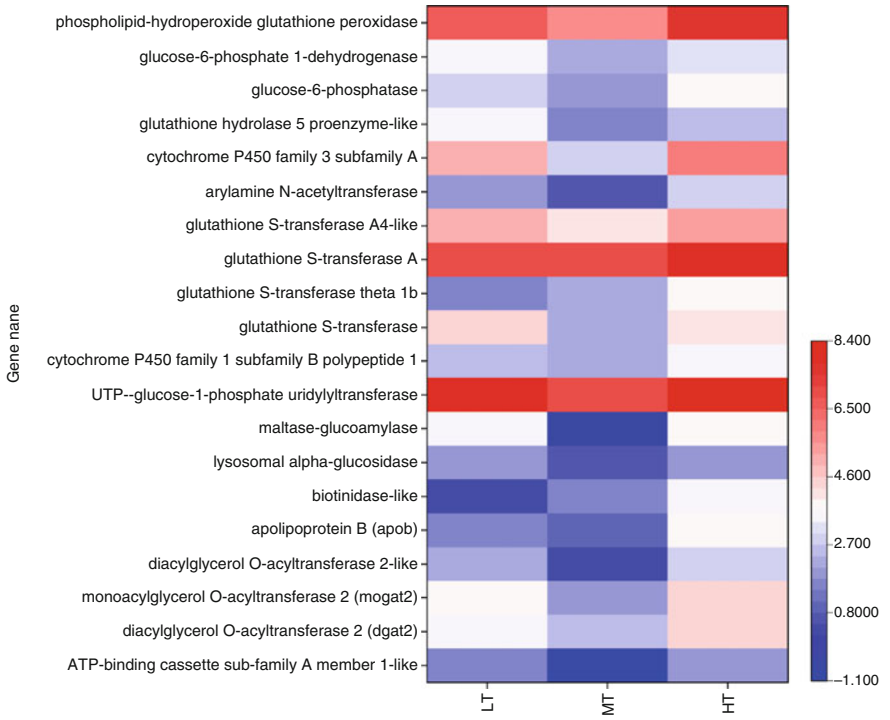

Fig. 8.4 Heat map of the DEGs related to the metabolism of *T. ovatus* larvae at different temperatures. Log_2(RPKM) value for each gene has been taken the average of three values and is shown using a color scale

8.5 Effects of Water Temperature on Genes Related to Digestion and Absorption

The first exogenous feeding *T. ovatus* usually starts at 3DPH, and the oil balls disappear completely at 7DPH (Ou and Li 2017). The larvae then transform from endogenous nutrition to exogenous nutrition. At this stage, adequate nutrition and energy are essential for the growth and survival of fish larvae. Temperature can affect the activity of digestive enzymes and the digestion efficiency of nutrient in fish (Yufera et al. 2019). With the increase of temperature, a large number of DEGs were enriched in pathways related to the digestion and absorption of nutrients, such as protein digestion and absorption pathway, fat digestion and absorption pathway, and vitamin digestion and absorption pathway. With the increase of temperature, the transcriptional levels of the trypsin (*PRSS*), chymotrypsin-like protease (*CTRL*), and carboxypeptidase (*CPA*, *CPB*) genes in this pathway were significantly downregulated, while the pepsin A (PGA) genes were significantly upregulated (Fig. 8.5). This may indicate that the increase in temperature enhanced the digestion of protein in the stomach of fish larvae. The DEGs enriched to the fat digestion and

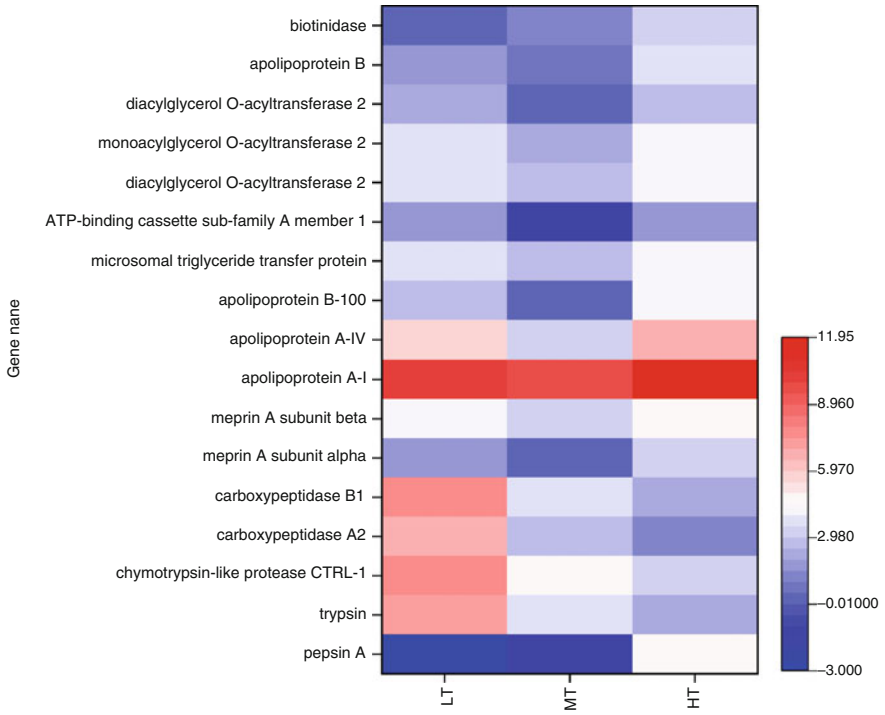

Fig. 8.5 Heat map of the DEGs related to digestion and absorption of *T. ovatus* larvae at different temperatures. Log_2(RPKM) value for each gene has been taken the average of three values and is shown using a color scale

absorption pathway were all formed by upregulated genes (Fig. 8.5). This may indicate that high temperature promotes the fat utilization of the larva to meet the higher energy requirement at high temperature. Notably, vitamin digestion and absorption pathway and retinol metabolism pathway were also significantly affected, indicating higher vitamin requirements at this high temperature. The results demonstrate at the molecular level that high temperatures may cause a significant increase in the nutritional need of *T. ovatus* larvae, which is consistent with the view of Cahu et al. (2003).

8.6 Effects of Water Temperature on Bone Development-Related Genes

The temperature can affect the bone development of the larva and even lead to bone malformation by promoting or inhibiting the expression of some genes related to bone development. Bone morphogenetic proteins (BMPs), the vital growth factors in transforming growth factor beta (TGF-β) superfamily, regulate the growth and

differentiation of osteoblasts and chondrocytes (Bragdon et al. 2011; Marques et al. 2016). For instance, BMP2 and BMP4 are involved in differentiation of chondrocytes to form cartilage (Mei and Xu 2005). Previous studies have shown that the expression of BMP2 and BMP4 in fish is upregulated due to the increase in temperature (Ma et al. 2016a, b, c). However, in the study of Han et al. (2020), although the expressions of BMP2 and BMP4 showed an upregulated trend, the differences in their expressions under different temperature treatments were not significant, which may be due to the single sampling event only at 8DPH (Fig. 8.6). The Sox gene family is a group of transcription factors that exhibit extensive spatiotemporal expression patterns during early development in vertebrates, involving many developmental processes and gender determination (Russell et al. 1996). Sox9 is the main gene that regulates chondrogenic differentiation and is found in all chondrogenic progenitor cells and chondrocytes except hypertrophic chondrocytes in mouse embryos (Akiyama 2008). Ytteborg et al. (2010) reported that the increase of temperature would result in the downregulation of sox9 gene in Atlantic salmon, thus inducing vertebral deformity. The study of Ma et al. (2017a, b) on *T. ovatus* also found that sox9 expression was downregulated at high temperature. In the study of Han et al. (2020) at 32 °C, the expression of sox9a was significantly lower than at 24 °C and 28 °C, which is in line with previous studies (Fig. 8.6).

Proteins in the Hedgehog (Hh) gene family of vertebrates act in a signaling pathway to transmit information for cell differentiation in embryogenesis and development (Bijlsma et al. 2004). Sonic Hedgehog (Shh) is a subgroup of Hh genes, the most widely expressed Hh protein in mammals and plays a key role in the induction of early chondrocyte differentiation (Bijlsma et al. 2004; Pusapati et al. 2018). The results of Han et al. (2020) showed that Shh expression in *T. ovatus* larvae was significantly downregulated at 32 °C (Fig. 8.6). This indicates that temperature teratogenicity of fish may be related to high temperature inhibiting the expression of Shh gene. However, some studies have shown that the increased temperature does not affect Shh expression in Atlantic salmon (Ornsrud et al. 2004a, b). Therefore, the

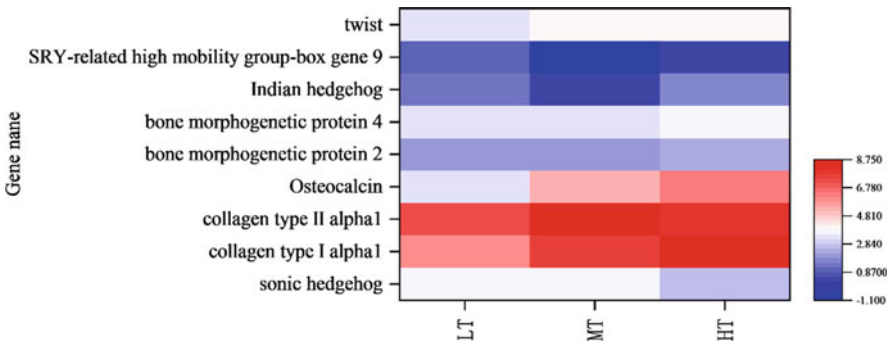

Fig. 8.6 Heat map of the DEGs related to bone development of *T. ovatus* larvae at different temperatures. Log_2(RPKM) value for each gene has been taken the average of three values and is shown using a color scale

regulation mechanism of temperature on Shh needs to be further studied. Shh can regulate the expression of col2a1 and runx genes, and Sox9 is the direct upstream gene of col2a1 (Lefebvre 2019; Lefebvre et al. 1997). In zebra fish, Sox9a can upregulate the expression of chondrogenic genes such as Col2a1, Runx3, and Runx2b (Dalcq et al. 2012). The study in *T. ovatus* indicates that the expression of col2a1 gene is significantly downregulated at high temperatures, while runx2 is not significantly different and has low expression levels under different temperature treatments (Fig. 8.6).

Therefore, we consider that high temperature can affect the nutrient metabolism and hedgehog signaling pathways of *T. ovatus* larvae and inhibit the secretion of type II collagen by downregulating the expression of Shh and Sox9a genes, which may lead to abnormal bone development. In addition, ocn is associated with bone mineralization (Riera-Heredia et al. 2018), and we found the expression of ocn gene is significantly upregulated when the temperature went up (Fig. 8.6). Some studies (Balbuena-Pecino et al. 2019) also show that increasing temperature could induce an upregulating response on ocn genes in the cultured bone-derived cells. However, more experiments are needed to verify the effect of temperature on ocn gene expression and explore the regulatory mechanism.

8.7 Conclusion

We believe that high temperature may lead to increased metabolism and nutritional requirements of golden pomfret larvae and affect the expression of genes related to bone development. RNA-seq based on high-throughput sequencing can reveal gene expression, pathway information, and regulatory mechanism involved in *T. ovatus* larvae under temperature stress. This study provides clues for understanding the response to high temperature in fish and guiding production practices.

References

Akiyama H (2008) Control of chondrogenesis by the transcription factor Sox9. Mod Rheumatol 18(3):213–219

Allais L, Zhao C, Fu M, Hu J, Qin JG, Qiu L, Ma Z (2019) Nutrition and water temperature regulate the expression of heat-shock proteins in golden pompano larvae (*Trachinotus ovata*, Limmaeus 1758). Fish Physiol Biochem 45(2):485–497

Balbuena-Pecino S, Riera-Heredia N, Velez EJ, Gutierrez J, Navarro I, Riera-Codina M, Capilla E (2019) Temperature affects musculoskeletal development and muscle lipid metabolism of gilthead sea bream (*Sparus aurata*). Front Endocrinol 10:15

Bijlsma MF, Spek CA, Peppelenbosch MP (2004) Hedgehog: an unusual signal transducer. BioEssays 26(4):387–394

Bilyk KT, Cheng CHC (2014) RNA-seq analyses of cellular responses to elevated body temperature in the high Antarctic cryopelagic nototheniid fish *Pagothenia borchgrevinki*. Mar Genom 18:163–171

Bragdon B, Moseychuk O, Saldanha S, King D, Julian J, Nohe A (2011) Bone morphogenetic proteins: a critical review. Cell Signal 23(4):609–620

Buckley LB, Huey RB (2016) How extreme temperatures impact organisms and the evolution of their thermal tolerance. Integr Comp Biol 56(1):98–109

Buckley BA, Gracey AY, Somero GN (2006) The cellular response to heat stress in the goby *Gillichthys mirabilis*: a cDNA microarray and protein-level analysis. J Exp Biol 209(14): 2660–2677

Cahu C, Zambonino Infante J, Takeuchi T (2003) Nutritional components affecting skeletal development in fish larvae. Aquaculture 227(1–4):245–258

Cai L, Wang L, Song K, Lu K, Zhang C, Rahimnejad S (2020) Evaluation of protein requirement of spotted seabass (*Lateolabrax maculatus*) under two temperatures, and the liver transcriptome response to thermal stress. Aquaculture 516:1–9

Chen W, Sun L, Tsai C, Song Y, Chang C (2002) Cold-stress induced the modulation of catecholamines, cortisol, immunoglobulin M, and leukocyte phagocytosis in tilapia. Gen Comp Endocrinol 126(1):90–100

Dalcq J, Pasque V, Ghaye A, Larbuisson A, Motte P, Martial JA, Muller M (2012) RUNX3, EGR1 and SOX9B form a regulatory cascade required to modulate BMP-signaling during cranial cartilage development in zebrafish. PLoS One 7(11):1–17

Deane EE, Woo NYS (2011) Advances and perspectives on the regulation and expression of piscine heat shock proteins. Rev Fish Biol Fish 21(2):153–185

Derenzini M, Montanaro L, Trere D (2017) Ribosome biogenesis and cancer. Acta Histochem 119(3):190–197

Eissa N, Wang HP (2016) Transcriptional stress responses to environmental and husbandry stressors in aquaculture species. Rev Aquac 8(1):61–88

Ekblom R, Galindo J (2011) Applications of next generation sequencing in molecular ecology of non-model organisms. Heredity 107(1):1–15

Griffiths D, Harrod C (2007) Natural mortality, growth parameters, and environmental temperature in fishes revisited. Can J Fish Aquat Sci 64(2):249–255

Han M, Luo M, Yang R, Qin JG, Ma Z (2020) Impact of temperature on survival and spinal development of golden pompano *Trachinotus ovatus* (Linnaeus 1758). Aquac Rep 18:1–7

Hatakeyama S, Nakayama KI (2003) Ubiquitylation as a quality control system for intracellular proteins. J Biochem 134(1):1–8

Hwang HK, Park KI, Park SW, Choi MS, Kim EO, Do JW, Oh BS (2012) Physiological response of juvenile red sea bream Pagrus major exposed to low temperature shock. Bull Eur Assoc Fish Pathol 32(1):34–40

Ibarz A, Padros F, Gallardo MA, Fernandez-Borras J, Blasco J, Tort L (2010) Low-temperature challenges to gilthead sea bream culture: review of cold-induced alterations and 'Winter Syndrome'. Rev Fish Biol Fish 20(4):539–556

Katersky RS, Carter CG (2005) Growth efficiency of juvenile barramundi, Lates calcarifer, at high temperatures. Aquaculture 250(3–4):775–780

Kayhan FE, Duman BS (2010) Heat shock protein genes in fish. Turk J Fish Aquat Sci 10(2): 287–293

Kultz D (2005) Molecular and evolutionary basis of the cellular stress response. Annu Rev Physiol 67:225–257

Lefebvre V (2019) Roles and regulation of SOX transcription factors in skeletogenesis. In: Olsen BR (ed) Vertebrate skeletal development. Elsevier Academic Press Inc., San Diego

Lefebvre V, Huang WD, Harley VR, Goodfellow PN, de Crombrugghe B (1997) SOX9 is a potent activator of the chondrocyte-specific enhancer of the pro alpha 1(II) collagen gene. Mol Cell Biol 17(4):2336–2346

Lei C, Li M, Tian J, Wen J, Li Y (2020) Transcriptome analysis of golden pompano (*Trachinotus ovatus*) liver indicates a potential regulatory target involved in HUFA uptake and deposition. Comp Biochem Physiol D 33:1–8

Lin H, Chen X, Chen S, Li Z, Huang Z, Niu J, Wu K, Lu X (2012) Replacement of fish meal with fermented soybean meal in practical diets for pompano *Trachinotus ovatus*. Aquac Res 44(1): 151–156

Liu S, Wang X, Sun F, Zhang J, Feng J, Liu H, Rajendran KV, Sun L, Zhang Y, Jiang Y, Peatman E, Kaltenboeck L, Kucuktas H, Liu Z (2013) RNA-Seq reveals expression signatures of genes involved in oxygen transport, protein synthesis, folding, and degradation in response to heat stress in catfish. Physiol Genomics 45(12):462–476

Liu K, Tan B, Zhang W, Liu H, Dong X, Yang Q, Chi S, Zhang S, Zhang H (2019) Transcriptome, enzyme activity and histopathology analysis reveal the effects of high level of dietary carbohydrate on glycometabolism in juvenile golden pompano, *Trachinotus ovatus*. Aquac Res 50(8): 2155–2169

Logan CA, Buckley BA (2015) Transcriptomic responses to environmental temperature in eurythermal and stenothermal fishes. J Exp Biol 218(12):1915–1924

Ma Z (2014) Food ingestion, prey selectivity, feeding incidence, and performance of yellowtail kingfish *Seriola lalandi* larvae under constant and varying temperatures. Aquac Int 22(4): 1317–1330

Ma Z, Guo H, Zheng P, Wang L, Jiang S, Qin JG, Zhang D (2014) Ontogenetic development of digestive functionality in golden pompano Trachinotus ovatus (Linnaeus 1758). Fish Physiol Biochem 40(4):1157–1167

Ma Z, Hu J, Liu Y, Yang R, Qin JG, Sun D (2016a) Molecular cloning and response to water temperature and nutrient manipulation of insulin-like growth factor (IGF) genes in golden pompano *Trachinotus ovatus* (Linnaeus 1758) larvae. Isr J Aquacult Bamidgeh 68:1–14

Ma Z, Yang Q, Wen W, Jiang S, Qin JG (2016b) The ontogenic expressions of BMP and IGF genes in golden pompano *Trachinotus ovatus* (Linnaeus 1758) larvae. Indian J Anim Res 50(5): 637–645

Ma Z, Zhang N, Qin JG, Fu M, Jiang S (2016c) Water temperature induces jaw deformity and bone morphogenetic proteins (BMPs) gene expression in golden pompano *Trachinotus ovatus* larvae. Springerplus 5(1):1475

Ma Z, Fu M, Hu J, Yang R, Wei C, Qin JG, Yu G (2017a) Molecular cloning of Indian hedgehog gene and its expression in golden pompano Trachinotus ovatus (Linnaeus 1758) larvae at different water temperatures. Isr J Aquacult Bamidgeh 69:1–13

Ma Z, Fu M, Peng X, Qin J (2017b) Expression of Sox5, Sox8 and Sox9 genes in golden pompano *Trachinotus ovatus* (Linnaeus 1758) larvae during ontogeny and in response to water temperature. Isr J Aquacult Bamidgeh 69:1–10

Marques CL, Fernandez I, Viegas MN, Cox CJ, Martel P, Rosa J, Cancela ML, Laize V (2016) Comparative analysis of zebrafish bone morphogenetic proteins 2, 4 and 16: molecular and evolutionary perspectives. Cell Mol Life Sci 73(4):841–857

Matanza XM, Osorio CR (2018) Transcriptome changes in response to temperature in the fish pathogen *Photobacterium damselae subsp. damselae*: clues to understand the emergence of disease outbreaks at increased seawater temperatures. PLoS One 13(12):1–23

Mei W, Xu C (2005) BMP signaling in skeletal development. Biochem Biophys Res Commun 328(3):651–657

Mu Y, Li M, Ding F, Ding Y, Ao J, Hu S, Chen X (2014) De novo characterization of the spleen transcriptome of the large yellow croaker (*Pseudosciaena crocea*) and analysis of the immune relevant genes and pathways involved in the antiviral response. PLoS One 9(5):12

Murphy ME (2013) The HSP70 family and cancer. Carcinogenesis 34(6):1181–1188

Ndong D, Chen Y, Lin Y, Vaseeharan B, Chen J (2007) The immune response of tilapia *Oreochromis mossambicus* and its susceptibility to Streptococcus iniae under stress in low and high temperatures. Fish Shellfish Immun 22(6):686–694

Neckers L (2007) Heat shock protein 90: the cancer chaperone. J Biosci 32(3):517–530

Newton JR, Zenger KR, Jerry DR (2013) Next-generation transcriptome profiling reveals insights into genetic factors contributing to growth differences and temperature adaptation in Australian populations of barramundi (*Lates calcarifer*). Mar Genom 11:45–52

Ohlberger J, Mehner T, Staaks G, Holker F (2012) Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishes and its ecological implications. Oikos 121(2): 245–251

Ojima N, Yamashita M, Watabe S (2005) Quantitative mRNA expression profiling of heat-shock protein families in rainbow trout cells. Biochem Biophys Res Commun 329(1):51–57

Ornsrud R, Gil L, Waagbo R (2004a) Teratogenicity of elevated egg incubation temperature and egg vitamin A status in Atlantic salmon, *Salmo salar* L. J Fish Dis 27(4):213–223

Ornsrud R, Wargelius A, Saele O, Pittman K, Waagbo R (2004b) Influence of egg vitamin A status and egg incubation temperature on subsequent development of the early vertebral column in Atlantic salmon fry. J Fish Biol 64(2):399–417

Ou Y, Li J (2017) Biology and culture of ovate pompano. China Ocean Press, Beijing

Parsell DA, Lindquist S (1993) The function of heat-shock proteins in stress tolerance: degradation and reactivation of damaged proteins. Annu Rev Genet 27:437–496

Pérez-Portela R, Riesgo A, Wangensteen OS, Palacin C, Turon X (2020) Enjoying the warming Mediterranean: transcriptomic responses to temperature changes of a thermophilous keystone species in benthic communities. Mol Ecol 29(17):3299–3315

Pickart CM, Eddins MJ (2004) Ubiquitin: structures, functions, mechanisms. BBA-Mol Cell Res 1695(1–3):55–72

Pusapati GV, Kong JH, Patel BB, Gouti M, Sagner A, Sircar R, Luchetti G, Ingham PW, Briscoe J, Rohatgi R (2018) G protein-coupled receptors control the sensitivity of cells to the morphogen Sonic Hedgehog. Sci Signal 11(516):1–15

Qian X, Ba Y, Zhuang Q, Zhong G (2014) RNA-Seq technology and its application in fish transcriptomics. OMICS 18(2):98–110

Riera-Heredia N, Martins R, Mateus AP, Costa RA, Gisbert E, Navarro I, Gutierrez J, Power DM, Capilla E (2018) Temperature responsiveness of gilthead sea bream bone; an in vitro and in vivo approach. Sci Rep 8:14

Russell SR, SanchezSoriano N, Wright CR, Ashburner M (1996) The Dichaete gene of Drosophila melanogaster encodes a SOX-domain protein required for embryonic segmentation. Development 122(11):3669–3676

Scott GR, Johnston IA (2012) Temperature during embryonic development has persistent effects on thermal acclimation capacity in zebrafish. Proc Natl Acad Sci U S A 109(35):14247–14252

Smith S, Bernatchez L, Beheregaray LB (2013) RNA-seq analysis reveals extensive transcriptional plasticity to temperature stress in a freshwater fish species. BMC Genomics 14:12

Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. J Exp Biol 213(6):912–920

Sun J, Zhao L, Wu H, Lian W, Cui C, Du Z, Luo W, Li M, Yang S (2019) Analysis of miRNA-seq in the liver of common carp (*Cyprinus carpio L.*) in response to different environmental temperatures. Funct Integr Genomics 19(2):265–280

Tan X, Lin H, Huang Z, Zhou C, Wang A, Qi C, Zhao S (2016) Effects of dietary leucine on growth performance, feed utilization, non-specific immune responses and gut morphology of juvenile golden pompano Trachinotus ovatus. Aquaculture 465:100–107

Tang X, Liu Y, Wu X, Cheng F, Hu J, Meng X, Ma Z (2018) Response of antioxidant enzymes and digestive enzymes to temperature stress in *Lates calcarifer* larvae. Isr J Aquacult Bamidgeh 70: 12

Tate SS, Meister A (1981) gamma-Glutamyl transpeptidase: catalytic, structural and functional aspects. Mol Cell Biochem 39:357–368

Tomanek L (2010) Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. J Exp Biol 213(6):971–979

Veilleux HD, Ryu T, Donelson JM, van Herwerden L, Seridi L, Ghosheh Y, Berumen ML, Leggat W, Ravasi T, Munday PL (2015) Molecular processes of transgenerational acclimation to a warming ocean. Nat Clim Chang 5(12):1074–1078

Vergauwen L, Benoot D, Blust R, Knapen D (2010) Long-term warm or cold acclimation elicits a specific transcriptional response and affects energy metabolism in zebrafish. Comp Biochem Physiol A 157(2):149–157

Wang Z, Gerstein M, Snyder M (2009) RNA-Seq: a revolutionary tool for transcriptomics. Nat Rev Genet 10(1):57–63

Wang G, Li B, Lou L, Zhong Y, Huang X, Lv W (2011) The effects of temperature and salinity on survival and development of larvae *Trachinotus ovatus*. J Shanghai Ocean Univ 20(06): 831–837

Xu D, You Q, Chi C, Luo S, Song H, Lou B, Takeuchi Y (2018) Transcriptional response to low temperature in the yellow drum (*Nibea albiflora*) and identification of genes related to cold stress. Comp Biochem Physiol D 28:80–89

Yang Q (2016) Effect of temperature on growth, survival and occurrence of skeletal deformity in the golden pompano *Trachinotus ovatus* larvae. Indian J Fish 63(1)

Yang Q, Ma Z, Zheng P, Jiang S, Qin JG, Zhang Q (2016) Effect of temperature on growth, survival and occurrence of skeletal deformity in the golden pompano *Trachinotus ovatus* larvae. Indian J Fish 63(1):74–82

Ytteborg E, Torgersen J, Baeverfjord G, Takle H (2010) Morphological and molecular characterization of developing vertebral fusions using a teleost model. BMC Physiol 10:13

Yufera M, Nguyen MV, Navarro-Guillen C, Moyano FJ, Jordal AEO, Espe M, Conceicao LEC, Engrola S, Le MH, Ronnestad I (2019) Effect of increased rearing temperature on digestive function in cobia early juvenile. Comp Biochem Physiol A 230:71–80

Zerai DB, Fitzsimmons KM, Collier RJ (2010) Transcriptional response of delta-9-desaturase gene to acute and chronic cold stress in Nile tilapia, *Oreochromis niloticus*. J World Aquacult Soc 41(5):800–806

Zheng JB, Cao JW, Mao Y, Su YQ, Wang J (2019) Comparative transcriptome analysis provides comprehensive insights into the heat stress response of *Marsupenaeus japonicus*. Aquaculture 502:338–346

Zhou T, Gui L, Liu ML, Li WH, Hu P, Duarte DFC, Niu HB, Chen LB (2019) Transcriptomic responses to low temperature stress in the Nile tilapia, *Oreochromis niloticus*. Fish Shellfish Immun 84:1145–1156