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Water temperature induces jaw deformity and bone morphogenetic proteins (BMPs) gene expression in golden pompano *Trachinotus ovatus* larvae

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Abstract

Golden pompano *Trachinotus ovatus* larvae were kept at 26, 29 and 33 °C for 15 days from 3-day post hatching (DPH) to 18 DPH to test temperature-dependent growth and jaw malformation. The growth, survival, jaw deformity and the gene expressions of bone morphogenetic proteins (BMPs) were used as criteria to examine the fish response to temperature manipulation. The growth rate of fish at 29 or 33 °C was significantly faster than fish at 26 °C, while fish survival at 29 °C was significantly higher than fish at 33 °C. Jaw deformity was significantly affected by water temperature. The highest jaw deformity occurred on fish at 33 °C, and the lowest jaw deformity was at 26 °C. The expressions of all BMP genes except BMP10 were significantly affected by water temperature. The highest gene expression of BMP2 was on fish at 29 °C, and the lowest expression was at 33 °C. For the BMP4 gene, the highest and lowest expressions were found on fish at 33 and 26 °C, respectively. The present study indicates that jaw deformity of golden pompano larvae increases with increasing temperature, and the gene expression of BMP4 proteins coincides with high jaw deformity and water temperature elevation.

Keywords: Temperature, Jaw deformity, Bone morphogenetic proteins, Golden pompano *Trachinotus ovatus*

Background

Temperature is a primary factor affecting early development of fish larvae and can regulate fish metabolism and feeding behavior during fish ontogeny (Kestemont and Baras 2001; Ma 2014). Furthermore, studies have demonstrated that the inappropriate range of temperature can lead to high mortality and body malformation on fish larvae (Lein et al. 1997; Ørnsrud et al. 2004; Ludwig and Lochmann 2009).

Jaw and skeletal malformations are often associated with poor growth and low survival of fish larvae and are a major bottleneck for efficient production of marine fish juveniles for aquaculture (Koumoundouros 2010; Bogliione et al. 2013a, b). Jaw malformation can reduce

fish survival and devalue fish quality on market (Barahona-Fernandes 1982; Cobcroft et al. 2004; Ma et al. 2014c). Jaw and skeletal malformations have been frequently observed on fish species in aquaculture such as striped trumpeter *Latris lineata* (Cobcroft et al. 2012), gilthead sea bream *Sparus aurata* (Andrades et al. 1996; Prestinicola et al. 2013), and yellowtail kingfish *Seriola lalandi* (Cobcroft et al. 2004). Lein et al. (1997) demonstrated that the increase of water temperature can induce jaw deformities. Under suboptimal temperatures, significant deformities of gill-cover and skeleton occur on gilthead seabream *Sparus aurata* (Georgakopoulou et al. 2010) and cranial deformities on European sea bass *Dicentrarchus labrax* (Georgakopoulou et al. 2007). In golden pompano *Trachinotus ovatus*, over 33 % of fish population exhibited at least one type of malformation during the larval period (Ma et al. 2014c; Zheng et al. 2014), but it is unclear if temperature leads to jaw deformities in this species. Therefore, it is necessary to

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explore the relationship between temperature and jaw deformity during early ontogeny of golden pompano larvae.

Skeletogenesis is a process of cell differentiation and proliferation in chondrocytes, osteoblasts, osteocytes and osteoclasts, and these cells determine the size, shape and mineral composition of bone structure (Nijweide et al. 1986; Karsenty and Wagner 2002; Phan et al. 2004). The gene expression during skeletogenesis is affected by both genetic and abiotic factors (Bogliione et al. 2013a, b). Therefore, unveiling gene networks may provide insights into the potential mechanisms of skeletal malformations. The abiotic and biotic factors could induce skeleton deformity, while the gene expression drives the functional change of organs mediated by environmental factors.

In vertebrates, bone morphogenetic proteins (BMPs) control bone formation at different cell developmental states (e.g., stem cells, proliferative and hypertrophic chondrocytes, maturing osteoblast) (Hogan 1996a, b; Alaei et al. 2014; Windhausen et al. 2015). BMPs are genetically conserved in the animal kingdom, and their biological importance is reflected through functional and structural redundancy of different BMPs in a single species (Razdorov and Vukicevic 2012). For instance, BMPs 1, 2 and 3 can stimulate osteoblast, and play an important role in bone fracture healing (Grgurevic et al. 2011). BMPs 2, 4 and 6 are involved in skeletogenesis, especially in differentiation of chondrocytes to form cartilage, and both differentiation and maturation of the chondrocytes in the osteoblastic lineage will give a rise to bone formation (Rickard et al. 1994; Minina et al. 2001; Canalis et al. 2003; Wan and Cao 2005). Although the expression of BMP genes have been studied in several fish species, our understanding on these genes are limited to their discrepant expression at different developmental stage but not on the change body structure and function (Myers et al. 2002; Marques et al. 2014; Palomino et al. 2014; Tiago et al. 2014; Marques et al. 2015). In marine fish, the expression of BMP genes has been studied when fish larvae are under different supply of nutrients such as vitamins and lipids (Villeneuve et al. 2005a, b, 2006). Recently, BMP genes have been used to evaluate the hyperthermic effects on the skeletal malformation of fish larvae (Ytteborg et al. 2010). Up to present, information on the expression of BMPs in golden pompano is rare despite a high frequency of jaw deformation during the period of larval fish development. Investigation on the expression of BMPs in the ontogeny of golden pompano may provide a hint on the reason associated with jaw malformation in fish larvae during osteogenesis.

Golden pompano belongs to the Carangidae family and is a potential species for aquaculture diversification (Guo et al. 2014). Although the early ontogenetic development

of digestive functionality (Ma et al. 2014a, b) and weaning strategies have been studied on golden pompano (Ma et al. 2014d), high jaw malformation during the early developmental stages has severely compromised production efficiency of this fish species in hatcheries. Our previous studies have identified the type, position, and frequency of jaw and skeletal malformations in golden pompano larvae (Ma et al. 2014c; Zheng et al. 2014), but factors causing skeletal malformation on this fish have never been evaluated. This paper aims to understand the impact of water temperature on jaw malformation of golden pompano larvae from the perspective of BMP expression on 18 DPH when jaw deformity starts to occur when weaning starts. The results of this study may contribute to improvement of fish quality and production efficiency in farming golden pompano and other marine fish larvae.

Methods

Fertilized eggs from the same brood cohort were obtained from a fish farm in Lingshui, Hainan Province, and transported to the Tropical Fisheries Research and Development Center, South China Sea Fisheries Research Institute, Chinese Academy of Fishery Science, Xincun Town. Upon arrival, all eggs were transferred into 500-L incubators until hatching. The water temperature was maintained at 26 °C in the incubators. The experimental design included three constant temperatures 26, 29, and 33 °C with three replicates each. On 2 days post hatch (DPH), yolk sac larvae were acclimatized at each desired temperature for 5 h, and then stocked in 500-L fiberglass tanks at a density of 60 fish L⁻¹. All rearing tanks were supplied with filtered seawater with a 5- μ m filter from the bottom of each tank through upwelling with a daily water exchange rate of 200 % tank volume. One air stone was used in each tank to maintain dissolved oxygen close to saturation (6.72 ± 0.21 mg L⁻¹) and also to promote even distribution of microalgae, rotifers and *Artemia* nauplii. Light intensity was maintained at 2300 lux (measured at the surface) at the light phase under a photoperiod of 13L:11D. Salinity was maintained at 33 ‰ throughout the experiment. For each temperature treatment, there were three biological replicates, and nine tanks were used. The experiments were conducted in accordance with the guideline and approved by the Ethics Committee of South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences (2014YJ01).

Feeding protocol

Rotifers (*Brachionus rotundiformis*) were provided to fish larvae from 2 DPH until 13 DPH three times a day at a density of 10 rotifers mL⁻¹. Rotifers were cultured at 25.5 °C. The rotifers fed microalgae (*Nannochloropsis*

Table 1 Summary of genes cloning primers used in this study

Primers	Sequence (5'-3')	Amplicon sizes (bp)
BMP2-F	CGTGCTGACCAAGACCTAAC	
BMP2-R	AACCGGGTGTCCATAATAAC	1549
BMP4-F	GACACCTTCCCTTTACAT	
BMP4-R	CAAGTCCAAGTTCTAGTTAGTTT	1425
BMP5-F	CCAACGAAGACACTACAAGG	
BMP5-R	TTAAAGTTAGCCAGCCACT	871
BMP10-F	GAAGGACAGTCCCTCCCTCAA	
BMP10-R	TGCAGCATTGCTTTGCTTTA	1854
EF-1 α -F	TGTTACCTGGCTAGGGG	
EF-1 α -R	GAGAAGAGGCCACCGTCA	1662

Note for BMP names: *F* forward primer, *R* reverse primer

sp.) were enriched with DHA Protein Selco (INVE Aquaculture, Salt Lake City, UT, USA) before the rotifers were added into larval rearing tanks. The enrichment process was followed by the manufacturer's instruction. Instant microalgae paste (*Nannochloropsis* sp., Qingdao Hong Bang Biological Technology Co., Ltd, Qingdao, China) was also added into larval fish tanks to feed rotifers and also create a green water background for fish larvae. *Artemia* nauplii enriched with DHA Protein Selco (INVE Aquaculture) were introduced to the fish tank from 9 to 18 DPH at 5 nauplii mL⁻¹.

Growth and survival measurement

In each tank, 10 fish were sampled for size measurements during 1, 3, 5, 9, 12 and 18 DPH. Fish were anaesthetized with AQU-I-S (New Zealand Ltd., Lower Hutt, New Zealand) and were measured on a stereo microscope (Phoenix Optical Instrument Group Co., LTD, China) with an eyepiece micrometer at 10 \times magnification to the nearest 0.01 mm. Growth was determined by the specific growth rate (SGR) as %/day using the following equation (Hopkins 1992): $SGR = 100 (LnSL_f - LnSL_i) / \Delta t$, where SL_f and SL_i were the final and initial fish standard lengths (mm), respectively, and Δt was the time between sampling intervals. At the end of this experiment, fish from each rearing tanks were harvested and counted for the final survival. Degree-days (D $^\circ$) was calculated using following equation: $D^\circ = \Delta t \times T$, where T was the rearing temperature ($^\circ$ C) and Δt is the period of time in days.

Jaw malformation

At the end of this experiment, 100 fish larvae were randomly collected from each rearing tank to examine the incidence of malformation. Fish were anaesthetized with overdosed Aqu-i-S (AQU-I-S New Zealand Ltd., Lower Hutt, New Zealand) and fixed in 10 % neutrally buffered

formalin. Jaw deformity was directly assessed on a stereo microscope (Olympus SZ40, Tokyo, Japan) using the criteria described by Ma et al. (2014c). Jaw malformation (%) was calculated by the following equation: $Jaw\ malformation = (malformed\ larvae / total\ larvae) \times 100$.

Total RNA extraction and reverse transcription

Approximately 50 individuals were collected from each rearing tank on 18 DPH. Total RNA was extracted using TRIzol Reagent (Invitrogen, USA) according to the manufacture protocol. RNA integrity was verified by electrophoresis on a formaldehyde-agarose gel (1.2 %). The RNA concentration was measured by absorbance at 260 nm and the purity was determined at the OD 260/280 ratio ($1.7 < OD260/OD280 < 2.0$), OD 260/230 ratio ($2.0 < OD260/OD230 < 2.5$) and agarose gel electrophoresis. RNA was reverse-transcribed to cDNA with oligo (dT) primers using a PrimeScript 1st strand cDNA synthesis kit (TaKaRa Biotechnology, Dalian Co., Ltd). The cDNA was used as a template in subsequent PCR. The cDNAs for quantitative real-time PCR were synthesized from one microgram of the total RNA of each sample using the PrimeScriptTM RT reagent kit with gDNA Eraser (TaKaRa).

Gene cloning

Based on unpublished golden pompano transcriptome sequences (Illumina HiSeq 2000, annotated by NR, KOG, kegg, and Swissprot), the genes cloning primers were designed (shown in Table 1). The reagents for PCR reaction included 1 μ L of golden pompano larval cDNA, 1 μ L of gene-specific forward primer (F, 10 μ mol L⁻¹), 1 μ L of gene-specific reverse primer (R, 10 μ mol L⁻¹), 0.5 μ L of ExTaq, 5 μ L of PCR buffer and 4 μ L of dNTP mixture (2.5 μ M), 37.5 μ L of ddH₂O in a total volume of 50 μ L. The PCR conditions were as follows: denaturation at 94 $^\circ$ C for 1 min, 35-cycles of 94 $^\circ$ C for 30 s, annealing temperature of each genes for 30 s, 72 $^\circ$ C for 4 min, followed by a 10 min extension at 72 $^\circ$ C. The PCR products were cloned into the PMD-19T vector (TaKaRa Biotechnology, Dalian Co., Ltd), and then were sequenced.

Gene expression analysis by quantitative real-time PCR

Quantitative real-time PCR (qPCR) was used to analyze the expression levels of BMP genes in golden pompano larvae. Gene specific primer pairs for BMP genes (Table 2) were amplified in LightCycler480 II (Roche, Switzerland). The EF-1 α (GenBank Accession NO. KT727924) was used as the reference and amplified. The cycling conditions for the BMP genes and EF1 α were as follows: 1 min at 95 $^\circ$ C, followed by 40 cycles at 95 $^\circ$ C for 15 s, and 60 $^\circ$ C for 1 min. Dissociation curves were employed to ensure that only one single PCR product was amplified in each gene reaction. For each test,

Table 2 Summary of quantitative real-time PCR primers used in this study

Primers	Sequence (5'-3')	Amplicon sizes (bp)
BMP2-qF	CAGGCAGCACTCCGCAAAC	146
BMP2-qR	TCCCCGTGGCAGTAAAAGG	
BMP4-qF	GTGAACAACAACATTTCCCAAGG	126
BMP4-qR	GCAGCCCTCCACTACCATTT	
BMP5-qF	GTGGAGACTGTAGACGGACGAA	100
BMP5-qR	TGAAGAAAGCAACCAGGAAGG	
BMP10-qF	CCGCTTCAGTCTTCTCCAACC	149
BMP10-qR	CGGATTATCACCCACATCCCTA	
EF-1 α -qF	CCCCTTGGTCGTTTTTGCC	101
EF-1 α -qR	GCCTTGGTTGTCTTTCCGCTA	

Note for BMP names: qF forward primer for real-time PCR, qR reverse primer for real time PCR

Table 3 Specific growth rate, survival, and jaw deformity rate of golden pompano larvae cultured at 26, 29, and 33 °C

	26 °C	29 °C	33 °C
Specific growth rate (%/day)	2.70 ± 0.42 ^a	3.64 ± 0.20 ^b	4.31 ± 0.74 ^b
Survival (%)	10.30 ± 0.41 ^{a,b}	11.36 ± 1.08 ^b	9.57 ± 0.23 ^a
Jaw deformity rate (%)	5.00 ± 0.64 ^a	10 ± 2.65 ^b	20.00 ± 3.54 ^c

Different lowercase letters (i.e., a, b and c) indicate statistically significant differences ($P < 0.05$)

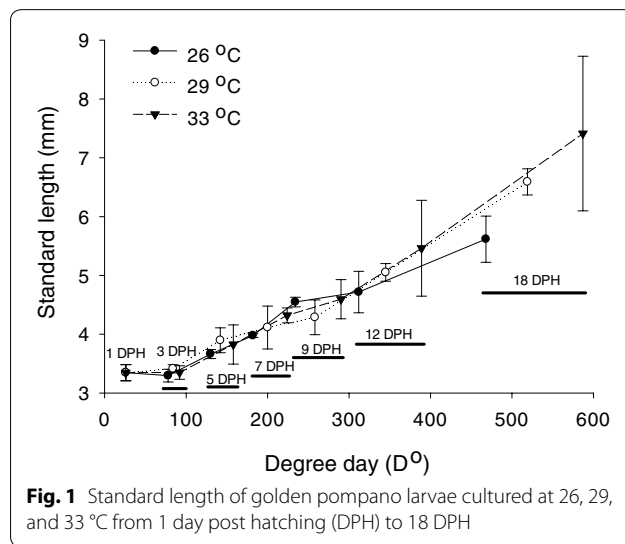


Fig. 1 Standard length of golden pompano larvae cultured at 26, 29, and 33 °C from 1 day post hatching (DPH) to 18 DPH

three replicates were performed. The relative quantification (RQ) was calculated using the $\Delta\Delta CT$ (comparative threshold cycle) method ($\Delta\Delta CT = CT$ of target gene - CT of EF-1 α , $\Delta\Delta CT = \Delta CT$ of any sample - ΔCT of calibrator sample). The efficiencies of the primers (E) were $E_{BMP2} = 0.998$, $E_{BMP4} = 1.004$, $E_{BMP5} = 0.923$, $E_{BMP10} = 1.004$.

Statistical analysis

All percentage data were arcsine-transformed prior to statistical analysis. However, the data were presented as untransformed values in figures. The data were all expressed as mean ± SD, and compared with one way ANOVA (PASW Statistics 18.0, Chicago, SPSS Inc.). When a significant treatment effect was found, Tukey's test was performed for multiple range comparisons with the level of significant difference set at $P < 0.05$. All data were tested for normality, homogeneity and independence to satisfy the assumptions of ANOVA.

Results

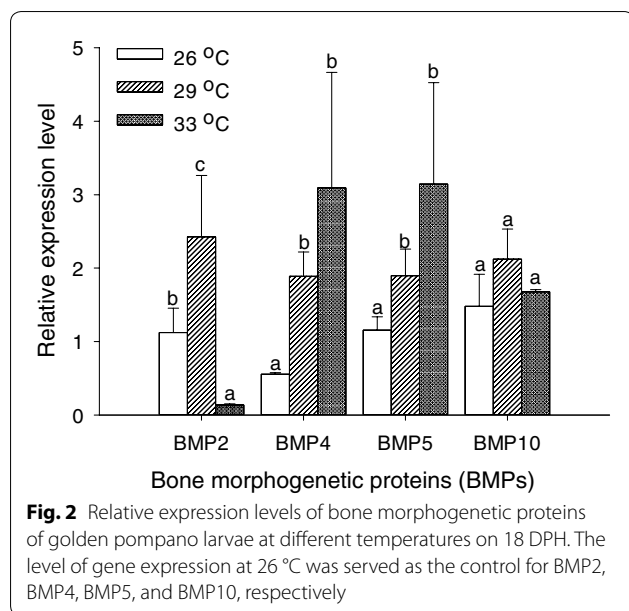
Growth performance, survival and jaw deformities

At the end of this experiment, the standard length of fish larvae at 26, 29, and 33 °C were 5.62 ± 0.39 , 6.59 ± 0.22 , and 7.41 ± 1.31 mm, respectively. Temperature significantly affected the growth of golden pompano larvae ($P < 0.05$, Table 3). The SGRs of fish at 29 and 33 °C were 3.64 ± 0.20 and 4.31 ± 0.74 %/day, respectively, which were significantly higher than those reared at 26 °C ($P < 0.05$). The SGR of fish was not significantly different between fish at 29 and 33 °C ($P > 0.05$). During the ontogenetic development, the variation of fish length on each sampling day increased with the increase of degree-days (Fig. 1). In this study, the growth of newly hatched golden pompano was slow before 234 degree-day (D°) on 9 DPH. When the number of degree-days reached 312–389 D° (12 DPH), the size of fish larvae gradually became different between temperature treatments. When the degree-days reached 468–587 D° (18 DPH), fish growth was clearly affected by water temperature, and fish growth was accelerated when temperature increased from 29 to 33 °C.

Rearing temperature significantly affected the survival of golden pompano larvae ($P < 0.05$, Table 3). The highest survival was achieved in fish at 29 °C, and the lowest survival was observed in fish at 33 °C. In this study, water temperature significantly affected fish jaw deformities ($P < 0.05$, Table 3). Jaw deformity of fish at 33 °C was 20.00 ± 3.54 %, which was significantly higher than the deformity rates of fish at 26 and 29 °C ($P < 0.05$). The lowest jaw deformity rate was observed in fish reared at 26 °C.

Expression of BMPs in fish at different temperatures

Partial sequences of BMP2 (GenBank Accession NO. KT727918), BMP4 (GenBank Accession NO. KT727919), BMP5 (GenBank Accession NO. KT727921), and BMP10 (GenBank Accession NO. KT727920) genes were obtained after sequencing analysis (Appendices 1–4). Water temperature significantly affected the expressions of BMP2, BMP4 and BMP5 genes in golden pompano



larvae ($P < 0.05$, Fig. 2). In the gene expression of BMP2, the highest expression was found in fish at 29 °C, and the lowest expression was in fish at 33 °C. In the gene expressions of BMP4 and BMP5, the expression levels were not significantly different between fish at 29 and 33 °C ($P > 0.05$), but were significantly higher than fish reared at 26 °C ($P < 0.05$, Fig. 2). On 18 DPH, the expression of BMP10 in golden pompano larvae was not significantly affected by the rearing temperature ($P > 0.05$).

Discussion

Growth and survival of fish larvae

Water temperature is a critical factor for the success of fish hatchery production, and it has significant implication on the growth performance of fish larvae (Boglione et al. 2013b). Temperature can regulate fish metabolism, food intake and growth (Jobling 1994; Ma 2014), and the effects of temperature on fish growth have been well documented in the larvae of commercially important fish species including haddock *Melanogrammus aeglefinus* L. (Martell et al. 2005), nase *Chondrostoma nasus* L. (Keckeis et al. 2001), Australian snapper *Pagrus auratus* (Fielder et al. 2005), striped trumpeter *Latris lineata* (Choa et al. 2010), and yellowtail kingfish *Seriola lalandi* (Ma 2014). In golden pompano, the fast growth at high temperature may be attributed to the improved food ingestion and digestive function of fish larvae after 15 DPH as Ma et al. (2014b) reported that the goblet cells and gastric glands appeared in the gut of golden pompano larvae after 15 DPH at 27–29 °C. The growth of fish larvae tended to be accelerated when fish were weaned from rotifers to *Artemia* nauplii. Similar to the Florida pompano *Trachinotus carolinus* (Riley et al. 2009), the

length of mouth gape close to 1.05 mm should allow golden pompano larvae to ingest *Artemia* nauplii and other similar size of food particles by 12 DPH. Therefore, the significant difference in fish size between thermal treatments at 18 DPH may be also related to the use of high energy food from 9 DPH onwards.

In both wild and artificial environments, fish mortality is often observed at the critical period of nutritional transition from endogenous to exogenous feeding (Otterlei et al. 1999; Ma et al. 2012). During the period of food transition, when the food supply and light condition are optimal, temperature can be a key determinant for fish survival (McGurk 1984; Kamler 1992; Gardeur et al. 2007; Ma 2014). Previous studies have demonstrated that mortality is strongly temperature-dependent in the larvae and juveniles of *Seriola lalandi* (Ma 2014), *Pangasianodon hypophthalmus* (Baras et al. 2011), *Inimicus japonicas* (Wen et al. 2013), and *Glyptocephalus cynoglossus* (Bidwell and Howell 2001). Ma (2014) suggests that there is a temperature-sensitive period during early ontogeny where mortality is likely to occur in fish larvae. In the present study, lower survival was observed when fish were reared at 33 °C than at other temperatures, suggesting the importance of temperature for golden pompano larval rearing. In the present study, the fish density was reduced at high temperatures due to high mortality, which may contribute to temperature-dependent fish growth in this study.

Temperature effect on jaw malformation

Jaw malformation is a major concern in fish culture because it affects fish morphology and quality at the growout stage (Von Westernhagen 1988). In the present study, the proportion of fish larvae exhibiting jaw deformities increased with the increase of water temperature, and peaked at 33 °C. Similar results have also been found in other fish species such as Atlantic halibut *Hippoglossus hippoglossus* (Lein et al. 1997) and Pacific herring *Clupea pallasii* (Alderdice and Velsen 1971). Such a temperature-dependent developmental pattern is generally attributed to high oxygen (Rombough 1997) and high nutritional requirements at high temperatures, which may not be fulfilled unless the feed with high energy or protein contents is provided (Cahu et al. 2003a, b; Ma 2014). Furthermore, temperature fluctuation might also interfere with the harmonic development of functional organs such as the digestive tract and skeleton, leading to skeletal deformities at high temperature. In the present study, fertilized fish eggs hatched at 26 °C, and yolk sac larvae were acclimatized at each desired temperature for 5 h on 2 DPH. The quick increase of rearing temperature from 26 to 29 or 33 °C may affect skeletogenesis and induce jaw deformity.

BMP gene expression at different temperatures

The present study was design to evaluate the effects of temperature appear to be specific to certain BMP family members impacting bone formation. The growth of skeleton relies on the dynamic equilibrium between cartilage production and bone apposition rate (Breur et al. 1991). The BMP2 and BMP4 proteins are involved in processes of dorsal–ventral axis specification (Graff 1997), epithelio-mesenchymal interactions (Vainio et al. 1993), and apoptosis (Graham et al. 1994; Glozak and Rogers 1996; Zou and Niswander 1996). The BMP2 gene in zebrafish is related to the induction and maintenance of ventro-lateral cell fate during early development, while a missense mutation in the BMP2b gene can lead to the early dorsalized phenotype of the zebrafish *swirl* mutant which lacks the cardiogenic mesoderm (Kishimoto et al. 1997). Ytteborg et al. (2010) found that the expression of BMP2 was up-regulated when fish was under a hyperthermic condition. In the present study, the expression of BMP2 in fish reared at 29 °C showed a up-regulating trend comparing to the expresion of BMP2 in fish reared at 26 °C, which is consistent with the results reported by Ytteborg et al. (2010). However, the reason for low expression of BMP2 in fish at 33 °C is unclear.

BMP4 plays a diverse role during vertebrate development (Hogan 1996b; Mehler et al. 1997; Whitman 1998; Dale and Johns 1999; Shi and Massague 2003), and has been used to evaluate if the BMP metabolic pathway is related to skeletal deformities under an unbalanced nutritional supply (Villeneuve et al. 2005a, b, 2006) (Ytteborg et al. 2010). Villeneuve et al. (2006) suggested that the increase of BMP4 and RAR γ expression can reduce the number of osteoblasts available for bone formation and that the loss of bone cells is counterbalanced by the cooperation between retinoic acid and BMP4. In the present study, the expression of BMP4 in fish at 29 and 33 °C increased significantly, and jaw deformities at these two temperatures were significantly higher than fish at 26 °C. This result supports to the notion that the expression of BMP4 tends to increase when fish are reared at a high temperature (Ytteborg et al. 2010), and the proportion of jaw deformities in fish larvae increases when the expression of BMP4 in fish shows a trend of up-regulation (Villeneuve et al. 2006). However, to confirm this result, future research should evaluate the gene expression in the jaw and conduct in situ hybridization analysis and mineralization analysis.

Previous studies indicate that the 60A subgroup (BMPs5, 6 and 7) is functionally redundant and that the collective expression of the 60A subgroup determines developmental function (Solloway and Robertson 1999; Kim et al. 2001). Specifically, BMP5 can be expressed during endochondral ossification, inducing condensation

of mesenchymal cells to chondrocytes (King et al. 1994; Bailon-Plaza et al. 1999). Furthermore, the mutated BMP5 gene can lead to skeletal and bone abnormalities, suggesting the importance of BMP5 in skeletal development (Kingsley et al. 1992; Storm et al. 1994; Wolfman et al. 2003). In the present study, the expression pattern of BMP5 was similar to that observed in BMP4. The expression level of BMP5 in fish at 29 or 33 °C was significantly higher than that at 26 °C. Although the expression of BMP5 increased with increasing temperatures and the occurrence of jaw deformity, it is unclear if deformity and high temperature are concomitant events in fish.

Existing literature indicates that the BMP10 gene plays little role in craniofacial or bone development. The BMP10 gene is expressed predominantly in the adult heart and to a lesser extent in the liver and lung (Neuhaus et al. 1999). During heart development, BMP10 is expressed in the trabeculae of the *bulbus cordis*, the common ventricular chamber, and of the atrium (Neuhaus et al. 1999). In zebrafish, relatively high BMP10 expression occurs in the heart and liver, but low expression is detected in the brain, and kidney (Bland 2001). In the present study, the expression of BMP10 was not significantly affected by the rearing temperature. This may suggest that the expression of BMP10 in golden pompano larvae is not sensitive to temperature by 18 DPH.

Conclusion

In summary, the present study examined the effect of temperature on the jaw deformity in golden pompano larvae. Jaw deformity in fish larvae increased with the increase of water temperature, and peaked at 33 °C. This study suggests that the rearing temperature of golden pompano larvae should be controlled at 26–29 °C and the expression levels of BMP4 and BMP5 genes are positively synchronized with the occurrence of jaw deformities.

Authors' contributions

ZM, NZ, MF, SJ, and JG designed and run the experiment, ZM, MF, and JGQ analysis the sample and finalized the manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Appendix 1: Partial sequences of BMP2

1 CGTGCTGACCAAGACCTAACCCGAAGTGCAGCTGGTGAGAATATGTGCGAGAGGCGATCG 60
 61 GCGAAGGGCATGGGCTGTCTCTGGTCCCCAAGGAGAAGCAGCGTGGATTAACACGAAT 120
 121 TAATGTGGAATTTATCGGAGCCAAAGGTGGAACGACGACCGGACACAGCGCTTCCTCGT 180
 181 CAGGGACTGACTGATCAtggtcgccgtggctccgctctctcatggtactgctgctcgctca 240
 1 M V A V V R S L M V L L L A Q 15
 241 ggtgttgcctggaaggtgctacgggactaatccccgaggtcggccggaggaaatatagcga 300
 16 V L L E G A T G L I P E V G R R K Y S E 35
 301 atccgggaagcagacccccggagcagtcggagagcttctcaacgagtttgagcttcggct 360
 36 S G K Q T P E Q S E S F L N E F E L R L 55
 361 tctcaatatgtttggactgagcgcagccgacccccgagcaagcaagccgtggtgccgca 420
 56 L N M F G L R R R P T P S K Q A V V P Q 75
 421 gtacatggtggacctttaccgcatgcaactcagcgaacggagaccacagcactaaacgacc 480
 76 Y M V D L Y R M H S A N G D H S T K R P 95
 481 caagagcatggggaacacgcagatagagccgccagcaaggccaacacgattagaagctt 540
 96 K S M G K H A D R A A S K A N T I R S F 115
 541 tcaccatgaagagtccatggaggccttggccagcctgaaaggcaaacgaccagcagtt 600
 116 H H E E S M E A L A S L K G K T T Q Q F 135
 601 ctacttcaacctcacttctatccctgatgaggagctcatcacctctgcagagctacgtat 660
 136 Y F N L T S I P D E E L I T S A E L R I 155
 661 ctacagggatcaggtcctgggagctgcaaccctagcaacagctccagaaacagcagcac 720
 156 Y R D Q V L G A A T P S N S S R N S S T 175
 721 cagtgatagtggctcctgctgctgggtttccatcgtatcaacattatgagatatcggagt 780
 176 S D S G P A A G F H R I N I Y E I F G V 195
 781 tcttccactgatggtgggaacctctggcacgtctgctggacactcggctagtgcagga 840
 196 P S T D G G E P L A R L L D T R L V Q D 215
 841 ctctttaagccgctgggagagctttgacgtcagcccagctgtatctcagtggacctccgg 900
 216 S L S R W E S F D V S P A V S Q W T S G 235
 901 caaaggccacaaccatggttctcatggtggaggtacttccaccagaggaaggggagatgga 960
 236 K G H N H G F M V E V L H P E E G E M D 255
 961 tggagagcatgcccagagacgtatgtaggcatgtcagggtgagccggctccctgcaccagga 1020
 256 G E H A Q R R S R H V R V S R S L H Q D 275
 1021 ccaggactcatggcctcaggtcggcccttgtgtggtgacgtacggtcacgacggcctgg 1080
 276 Q D S W P Q A R P L L V T Y G H D G R G 295
 1081 ggactcagtactccacacagagaaaaacgtcaggcagcactccgcaaacacgcagaaa 1140
 296 D S V L H T R E K R Q A A L R K Q R R K 315
 1141 gcaacagcacaaggcaagctgcaagagcagcctgtatgtggacttcagtgatgtggg 1200
 316 Q Q H K A S C K R H A L Y V D F S D V G 335
 1201 gtggaacgagtgatggtgacccccctggttaccacgccttttactgccacggggaatg 1260
 336 W N E W I V A P P G Y H A F Y C H G E C 355
 1261 tccgttccccctagcagaccacctcaattctaccaatcatgccattgtgcagacgctggt 1320
 356 P F P L A D H L N S T N H A I V Q T L V 375
 1321 caactcagtcactcaaacatccccagagcctgttgtgtccctactgacctcagcccat 1380
 376 N S V N S N I P R A C C V P T D L S P I 395
 1381 ctccctgctctacttggatgaatatgagaaggtcatcctgaaaaactaccaggacatggt 1440
 396 S L L Y L D E Y E K V I L K N Y Q D M V 415
 1441 ggtggagggatgtggtgcccgtgaGCAACTGACAGTGGTATGGATAGAAAGAAAGAGTG 1500
 416 V E G C G C R * 422
 1501 GGCAAGAAAGACTGAGAGGGCATCAGAGGTTATTATGGACACCCGGTT 1549

Appendix 2: Partial sequences of BMP4

1 GACACCTTCCCTTTCACATTCACCTCCATTTCGAGGATACCTGTACCTCTACTGATGGAACA 60
 61 GGGTCACTCCAACGTTCTCTGCAGCCGCCAACACCACCTAACATTTCCCTGGAAAAACG 120
 121 TGTCCATTGCCTCCTCCCAACAAACATGGACTGTTTTCCCATGCTTATTTTCTGTCGAG 180
 181 ACATCatgattcctgtaaatcgaatgctgatggcatttttaatatgccaagtcctgctgg 240
 1 M I P G N R M L M V I L I C Q V L L G 19
 241 gagagagtaaccatgctagtctgataacctgaagaagggaagaaagtaaccgggctgc 300
 20 E S N H A S L I P E E G K K K V P G L Q 39
 301 agggctcgttcggccgctcagagccatgaactgctcgggacttcgaggccacgctgctgc 360
 40 G R S A A Q S H E L L R D F E A T L L H 59
 361 acatgttcggcctcaagaggcggccgcccagccgctccaccacgctgccccgctacc 420
 60 M F G L K R R P R P S R S T T V P R Y L 79
 421 tgctggacctctatcgctacagtcggggaggctgaggaggctggaggctcatgacattg 480
 80 L D L Y R L Q S G E A E E A G G H D I A 99
 481 cttttgagtaccagagaggtcagccagccgagcgaacctgtgaggggcttccaccatg 540
 100 F E Y P E R S A S R A N T V R G F H H E 119
 541 aagagcacatggagagggctgcatgagctggaggatggagagaccatgccccctcgttcc 600
 120 E H M E R V H E L E D G E T M P L R F L 139
 601 tgttcaacctcagcagcatcccagaggacgagctgctctcttcgccgaacttaggctct 660
 140 F N L S S I P E D E L L S S A E L R L Y 159
 661 accgtcatcagatcgacaggccattgctgactcctctcagggtgacagggacttcacc 720
 160 R H Q I D E A I A D S L S G E Q G L H R 179
 721 ggataaacgtgtatgaggtgttgaagcccccgggcccgggcagctgatacagcagctct 780
 180 I N V Y E V L K P P R P G Q L I T Q L L 199
 781 tggatacgggctcgtgcgccacaatacgtcgcgctgggagagcttcgacgtcagccctg 840
 200 D T R L V R H N T S R W E S F D V S P A 219
 841 ccgtgctgcgctggactcgagagcgcctcccgaattatgggctggctgtggagttctgc 900
 220 V L R W T R E R L P N Y G L A V E V L H 239
 901 accttaaccagacgcccgcgtcaccaggccgacacgtccgcatcagtcgcttactacacc 960
 240 L N Q T P R H Q G R H V R I S R S L H Q 259
 961 aggagcctgggtgaggactgggaacagctacgccccctcctggttacctttggccatgacg 1020
 260 E P G E D W E Q L R P L L V T F G H D G 279
 1021 gaaagggtcaccgctgaccgcccggaccaagcgcagcccaagcaacggggccgtaaac 1080
 280 K G H P L T R R T K R S P K Q R G R K R 299
 1081 gcaaccgcaactgccggcgcacgcactgtacgtagacttcagtgatgtaggctggaatg 1140
 300 N R N C R R H A L Y V D F S D V G W N D 319
 1141 actggatagtgggccccctggttaccaggcttattactgccacggggaatgcccccttc 1200
 320 W I V A P P G Y Q A Y Y C H G E C P F P 339
 1201 ctctggcggatcatctgaattcaaccaaccatgccattggtcagacactggtgaactctg 1260
 340 L A D H L N S T N H A I V Q T L V N S V 359
 1261 tgaacaacaacattcccgaagcctgctgcgtgccaacagagctcagcgcctctccatgc 1320
 360 N N N I P K A C C V P T E L S A I S M L 379
 1321 tctacctagacgaacatgacaaggtggctcctaaaaaactaccaggaaatggtagtgagg 1380
 380 Y L D E H D K V V L K N Y Q E M V V E G 399
 1381 gctgcggctgccgctaaCACACAACTAACTAGAACTTGGACTTG 1425
 400 C G C R * 403

Appendix 3: Partial sequences of BMP5

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1  gggactcccgtgtggcacagccttaccgagcggcccctctgttaggccacagccccgca 60
1  G Y S R V A Q P Y R A A P L L G H S P A 20
61  ctcaccacagcgcacacaccaacttctcaatgacccgacatggtgatgagttttgtc 120
21  L T T A H D T N F L N D A D M V M S F V 40
121 aatthagtgagaaaagataaagatTTTTCCCAACGAAGACACTACAAGGAGTTCGCT 180
41  N L V E K D K D F S H Q R R H Y K E F R 60
181 tttgatctgactcagatcccagatggagaggcggtagcggctgcagagtttcggatctat 240
61  F D L T Q I P D G E A V T A A E F R I Y 80
241 aaggaccgcagccatgcccgtacgacaatattactctcaagtttccatatatcaagtt 300
81  K D R S H A R Y D N I T L K V S I Y Q V 100
301 atcaaggaatatcaaaacaaagatgcagagacattcttgctcgactccaaaagggtccag 360
101 I K E Y Q N K D A E T F L L D S K K V Q 120
361 gcgtccgatggggctggctggtgtttgacatcacggccaccagtaaccactgggtgatg 420
121 A S D G G W L V F D I T A T S N H W V M 140
421 aaccacagcagaacttgggctgcagctctgtgtggagactgtagacggacgaagtatc 480
141 N P Q Q N L G L Q L C V E T V D G R S I 160
481 aacataaaatctgctggaatcattgggaggaatgggccccagtccaaacagcccttctc 540
161 N I K S A G I I G R N G P Q S K Q P F L 180
541 gttgctttcttcaagccagcgggggtgttacttegetctgtcagagctgctgggtggaag 600
181 V A F F K A S G V L L R S V R A A G G K 200
601 aaaaagaaccacaatcgcaataaatctactaatcagcaagaatcatcgagggcgccaaa 660
201 K K N H N R N K S T N Q Q E S S R A P K 220
661 actggagattacaacaccagtgaacagaagcaagcctgtaagaagcatgaactttatgtc 720
221 T G D Y N T S E Q K Q A C K K H E L Y V 240
721 agctttcagatTTGGGCTGGCAGGATTGGATCATTGCACCTGAGGGCTACGCTGCTTTT 780
241 S F R D L G W Q D W I I A P E G Y A A F 260
781 tactgtgatggtgaatgctcgttcccactcaacgcacacatgaacgcaacaaatcatgca 840
261 Y C D G E C S F P L N A H M N A T N H A 280
841 attgtgcaaacctgggtccatttaattgTTTCTGAAAATGTGCCAAAGCCGTGCTGTGCC 900
281 I V Q T L V H L M F P E N V P K P C C A 300
901 ccaaccaagctcaacgcaatatcagtactttactttgatgacagctcaaacgttatcctc 960
301 P T K L N A I S V L Y F D D S S N V I L 320
961 aagaaatacagaaatatggttagtcaggtcttgtggetgccattagTGGCTGGGCTAACTT 1020
321 K K Y R N M V V R S C G C H * 334
1021 T 1021

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Appendix 4: Partial sequences of BMP10

1 GAAGGACAGTCTCCCTCAAAACATTGAACTGTTTGAAGTATCCTCTACAAAGGATCCA 60
 61 TCACATCTTCTCATCTGATACTCTAAGCTTTGGATCTAAGCTTTTCTCCACTCAGCCa 120
 1 M 1
 121 tgaccgcttcagttcttccaacctcggtttatccgctctctgaatgtcctacttctgg 180
 2 T A S V F S N L G F I R S L N V L L L V 21
 181 tgttgactgctgactttgagcttgagcagtccecatcaagtctcctgagaacctcacaggg 240
 22 L T A D L S L S S P I K S P E N H H R A 41
 241 catcagtcggttaggatgtgggtgataatccgcttcttgatgcacaggactttctgagcc 300
 42 S V G R D V G D N P L L D A Q D F L S Q 61
 301 agtttctgtccactgaacctcacagagctgaggccccagccagggccccctgctgccc 360
 62 F L S T L N L T E L R P Q P R P L A A L 81
 361 ttaaggagccaccagagtacatgttggagctgtacaaccgatttccaatgaccgcactt 420
 82 K E P P E Y M L E L Y N R F A N D R T S 101
 421 ctgtgcctcagccaacttctgctcagtttcaagaatgaagattcctccccctacagtt 480
 102 V P S A N I V R S F K N E D S S P Y S L 121
 481 tatctgccaggggtgtaaggataccccctgctgttcaacatctccatgccccaccatg 540
 122 S A R G V R I H P L L F N I S M P H H E 141
 541 agcacataacaatagctgagcttgcattttccccctgttgggaagggccgaaggccat 600
 142 H I T I A E L R I F P L L R K A R R P Y 161
 601 attctggcattgactgcaaggtgaccatttacaatatacatgaggcgcttgtttggaaa 660
 162 S G I D C K V T I Y N I H E G V V W T K 181
 661 aagagtggtgggaagaagggaaggaggatagagagggtggtggagatgagggtt 720
 182 E V G K E G R R R D R E E V V E M R D L 201
 721 tggaggaactggtgacaagcatattcgtgccaagataacagctgggtgtcgtttgacc 780
 202 E E L V T K H I R A K D N S W V S F D L 221
 781 tgactcatgtggttactctggtggaaatctgggtgtgcaactcacagactggaggttc 840
 222 T H V V T L W R K S G C A T H R L E V H 241
 841 acattgcaagtctgggtcagaggaggaagggccacacaagaggtcacagaggagggtg 900
 242 I A S L G S E E E G A T Q E V T E E G E 261
 901 aagatttggtagagattgatatcgacaggagcttggagggaaaacacaatgcagtgatta 960
 262 D L V E I D I D R S L E G K H N A V I I 281
 961 tagtattctcagatgatcagagaagagagcacaacaggatcaacaagagctcaaccaga 1020
 282 V F S D D Q R R E H K Q D Q Q E L N Q M 301
 1021 tgattgaacatgagaatgaccttccagaaaacatggcggagccaacaagcttcttggg 1080
 302 I E H E N D L P E N M G R S Q Q A F W G 321
 1081 ggcaacttgatcacaactgcccacgctaaccaggacgagctggacaacagtcctca 1140
 322 H V D H N T G H A N Q D E L D K Q S L M 341
 1141 tgcaactgcaactgcaactgctatgatgacacacctccccgaatccgtcgcaatgtaaga 1200
 342 Q L Q S N V I Y D T P P R I R R N V K S 361
 1201 gcgagccatgcaagagaccacctcttctgtgattttaagacattggtctgggttctgt 1260
 362 E P C K R T P L F V D F K D I G W D S W 381
 1261 ggatcatccagcctctgggtcagagcgtatgagtgcaacggtgtgtgcaaccaccta 1320
 382 I I Q P L G Y E A Y E C N G V C N P P M 401
 1321 tgacctccgaggtctcgcctaccaaacagccatagtgacagctctgctgagtgtaaga 1380
 402 T S E V S P T K H A I V Q T L L S V K S 421
 1381 gtccagagagagcagctcgcctgctgtgtaccactaagttggagccgatctcactcc 1440
 422 P E R A S R A C C V P T K L E P I S L L 441
 1441 tttatcatgataatgggtgatcactttcaaccacaagtatgaggggatggtggtggcag 1500
 442 Y H D N G V I T F N H K Y E G M V V A E 461
 1501 agtgtggatgcagatagTCCTGAAAGTGATGCTATTACACAGAGATAGAGACTGCACATC 1560
 462 C G C R * 465
 1561 GCACACATCTCTCATGTGCTTCTTCCACAATATCTAAGATCTCATACAGTGGCGTGTA 1620
 1621 AAAACACAAGTCTGGACTTAGTTGTAATAATTAGTGACACAAAATCTGTGCTACATGATGTA 1680
 1681 AATTTGCAATTGTATAAAGGTAATCAGTTATTATATTAATGTAGAATATAAAGCAAAGC 1740
 1741 AATGCTGCA 1749

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References

- Alaee F, Hong SH, Dukas AG, Pensak MJ, Rowe DW, Lieberman JR (2014) Evaluation of osteogenic cell differentiation in response to bone morphogenetic protein or demineralized bone matrix in a critical size defect model using GFP reporter mice. *J Orthop Res* 32:1120–1128
- Alderdice DF, Velsen FPJ (1971) Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasii*). *J Fish Res Board Can* 28:1545–1562
- Andrades JA, Becerra J, Fernández-Llebrez P (1996) Skeletal deformities in larval, juvenile and adult stages of cultured gilthead sea bream (*Sparus aurata* L.). *Aquaculture* 141:1–11
- Bailon-Plaza A, Lee AO, Veson EC, Farnum CE, van der Meulen MC (1999) Bmp-5 deficiency alters chondrocytic activity in the mouse proximal tibial growth plate. *Bone* 24:211–216
- Barahona-Fernandes MH (1982) Body deformation in hatchery reared European sea bass *Dicentrarchus labrax* (L.). Types, prevalence and effect on fish survival. *J Fish Biol* 21:239–249
- Baras E, Raynaud T, Slembrouck J, Caruso D, Cochet C, Legendre M (2011) Interactions between temperature and size on the growth, size heterogeneity, mortality and cannibalism in cultured larvae and juveniles of the Asian catfish, *Pangasianodon hypophthalmus* (Sauvage). *Aquacult Res* 42:260–276
- Bidwell DA, Howell WH (2001) The effect of temperature on first feeding, growth, and survival of larval witch flounder *Glyptocephalus cynoglossus*. *J World Aquac Soc* 32:373–384
- Bland RJ (2001) Isolation, characterisation and evolution of zebrafish (*Danio rerio*) *bmp9*, *bmp10*, and *gdf11*. University of Auckland, New Zealand, p 334
- Boglione C, Gavaia P, Koumoundouros G, Gisbert E, Moren M, Fontagne S, Witten PE (2013a) Skeletal anomalies in reared European fish larvae and juveniles. Part 1: normal and anomalous skeletogenic processes. *Rev Aquac.* 5:S99–S120
- Boglione C, Gisbert E, Gavaia P, Witten PE, Moren M, Fontagne S, Koumoundouros G (2013b) Skeletal anomalies in reared European fish larvae and juveniles. Part 2: main typologies, occurrences and causative factors. *Rev Aquacult* 5:S121–S167
- Breuer GJ, Vanenkervort BA, Farnum CE, Wilsman NJ (1991) Linear relationship between the volume of hypertrophic chondrocytes and the rate of longitudinal bone-growth plates. *Journal of Orthopaedic Research* 9:348–359
- Cahu C, Zambonino Infante J, Takeuchi T (2003a) Nutritional components affecting skeletal development in fish larvae. *Aquaculture* 227:245–258
- Cahu CL, Infante JLZ, Barbosa V (2003b) Effect of dietary phospholipid level and phospholipid: neutral lipid value on the development of sea bass (*Dicentrarchus labrax*) larvae fed a compound diet. *British J. Nutr.* 90:21–28
- Canalis E, Economides AN, Gazzerro E (2003) Bone morphogenetic proteins, their antagonists, and the skeleton. *Endocr Rev* 24:218–235
- Choa BY, Carter CG, Battaglene SC (2010) Effects of temperature regime on growth and development of post-larval striped trumpeter (*Latris lineata*). *Aquaculture* 305:95–101
- Cobcroft JM, Pankhurst PM, Poortenaar C, Hickman B, Tait M (2004) Jaw malformation in cultured yellowtail kingfish (*Seriola lalandi*) larvae. *NZ J Mar Freshw Res* 38:67–71
- Cobcroft J, Shu-chien A, Kuah M, Jaya-Ram A, Battaglene S (2012) The effects of tank colour, live food enrichment and greenwater on the early onset of jaw malformation in striped trumpeter larvae. *Aquaculture* 356–357:61–72
- Dale L, Johns CM (1999) BMP signaling in early *Xenopus* development. *BioEssays* 21:751–760
- Fielder DS, Bardsley WJ, Allan GL, Pankhurst PM (2005) The effects of salinity and temperature on growth and survival of Australian snapper, *Pagrus auratus* larvae. *Aquaculture* 250:201–214
- Gardeur JN, Mathis N, Kobilinsky A, Brun-Bellut J (2007) Simultaneous effects of nutritional and environmental factors on growth and flesh quality of *Perca fluviatilis* using a fractional factorial design study. *Aquaculture* 273:50–63
- Georgakopoulou E, Angelopoulou A, Kaspiris P, Divanach P, Koumoundouros G (2007) Temperature effects on cranial deformities in European sea bass, *Dicentrarchus labrax* (L.). *J Appl Ichthyol* 23:99–103
- Glozak MA, Rogers MB (1996) Specific induction of apoptosis in P19 embryonal carcinoma cells by retinoic acid and BMP2 or BMP4. *Dev Biol* 179:458–470
- Graff JM (1997) Embryonic patterning: to BMP or not to BMP, that is the question. *Cell* 89:171–174
- Graham CA, Francis-West P, Brickell P, Lumsden A (1994) The signalling molecule BMP4 mediates apoptosis in the rhombencephalic neural crest. *Nature* 372:684–686
- Grgurevic L, Macek B, Mercep M, Jelic M, Smoljanovic T, Erjavec I, Dumic-Cule I, Prgommet S, Durdevic D, Vnuk D, Lipar M, Stejskal M, Kufner V, Brkljacic J, Maticic D, Vukicevic S (2011) Bone morphogenetic protein (BMP)1-3 enhances bone repair. *Biochem Biophys Res Commun* 408:25–31
- Guo H, Ma Z, Jiang S, Zhang D, Zhang N, Li Y (2014) Length-weight relationship of oval pompano, *Trachinotus ovatus* (Linnaeus 1758) (Pisces; Carangidae) cultured in open sea floating sea cages in South China Sea. *Indian J Fish* 61:93–95
- Hogan BLM (1996a) Bone morphogenetic proteins in development. *Curr Opin Genet Dev* 6:432–438
- Hogan BLM (1996b) Bone morphogenetic proteins: multifunctional regulators of vertebrate development. *Genes Development* 10:1580–1594
- Hopkins KD (1992) Reporting fish growth: a review of the basics. *J World Aquacult Soc* 23:173–179
- Jobling M (1994) Fish bioenergetic. Chapman and Hall, London
- Kamler E (1992) Early life history of fish: An energetics approach. Chapman and Hall, London
- Karsenty G, Wagner EF (2002) Reaching a genetic and molecular understanding of skeletal development. *Dev Cell* 2:389–406
- Keckeis H, Kamler E, Bauer-Nemeschkal E, Schneeeweiss K (2001) Survival, development and food energy partitioning of nase larvae and early juveniles at different temperatures. *J Fish Biol* 59:45–61
- Kestemont P, Baras E (2001) Environmental Factors and Feed Intake: Mechanisms and Interactions. In: Houlihan D, Boujard T, Jobling M (eds) Food intake in fish. Blackwell Science, Cornwall, pp 131–156
- Kim RY, Robertson EJ, Solloway MJ (2001) Bmp6 and Bmp7 are required for cushion formation and septation in the developing mouse heart. *Dev Biol* 235:449–466
- King JA, Marker PC, Seung KJ, Kingsley DM (1994) Bmp5 and the molecular, skeletal, and soft-tissue alterations in short ear mice. *Dev Biol* 166:112–122
- Kingsley DM, Bland AE, Grubber JM, Marker PC, Russell LB, Copeland NG, Jenkins NA (1992) The mouse short ear skeletal morphogenesis locus is associated with defects in a bone morphogenetic member of the tgfbeta superfamily. *Cell* 71:399–410
- Kishimoto Y, Lee K, Zon L, Hammerschmidt M, Schulte-Merker S (1997) The molecular nature of zebrafish swirl: BMP2 function is essential during early dorsoventral patterning. *Development* 124:4457–4466
- Koumoundouros G (2010) Morpho-anatomical abnormalities in Mediterranean marine aquaculture. In: Koumoundouros G (ed) Recent advances in aquaculture research. Transworld Research Network, Kerala, India, pp 125–148
- Lein I, Holmefjord I, Rye M (1997) Effects of temperature on yolk sac larvae of Atlantic halibut (*Hippoglossus hippoglossus* L.). *Aquaculture* 157:123–135
- Ludwig GM, Lochmann SE (2009) Effect of temperature on larval sunshine bass growth and survival to the fingerling stage. *N Am J Aquacult* 71:260–266
- Ma Z (2014) Food ingestion, prey selectivity, feeding incidence, and performance of yellowtail kingfish *Seriola lalandi* larvae under constant and varying temperatures. *Aquacult Int* 22:1317–1330
- Ma Z, Qin JG, Nie Z (2012) Morphological changes of marine fish larvae and their nutrition need. In: Pourali K, Raad VN (eds) Larvae: morphology, biology and life cycle. Nova Science Publishers Inc., New York, pp 1–20
- Ma Z, Guo H, Zhang D, Hu CQ, Jiang S (2014a) Food ingestion, consumption, and selectivity of pompano, *Trachinotus ovatus* (Linnaeus 1758) under different rotifer densities. *Aquacult Res*. doi:10.1111/are.12413
- Ma Z, Guo H, Zheng P, Wang L, Jiang S, Qin JG, Zhang D (2014b) Ontogenetic development of digestive functionality in golden pompano *Trachinotus ovatus* (Linnaeus 1758). *Fish Physiol Biochem* 40:1157–1167

- Ma Z, Zheng P, Guo H, Zhang N, Jiang S, Zhang D, Qin JG (2014c) Jaw malformation of hatchery reared golden pompano *Trachinotus ovatus* (Linnaeus 1758) larvae. *Aquacult Res*. doi:10.1111/are.12569
- Ma Z, Zheng P, Guo H, Zhang N, Wang L, Jiang S, Qin JG, Zhang D (2014d) Effect of weaning time on the performance of *Trachinotus ovatus* (Linnaeus 1758) larvae. *Aquac Nutr*. doi:10.1111/anu.12183
- Marques CL, Fernandez I, Rosa J, Viegas MN, Cancela ML, Laize V (2014) Spatiotemporal expression and retinoic acid regulation of bone morphogenetic proteins 2, 4 and 16 in Senegalese sole. *J Appl Ichthyol* 30:713–720
- Marques CL, Fernández I, Viegas MN, Cox CJ, Martel P, Rosa J, Cancela ML, Laize V (2015) Comparative analysis of zebrafish bone morphogenetic proteins 2, 4 and 16: molecular and evolutionary perspectives. *Cell Mol Life Sci*. doi:10.1007/s00018-015-2024-x
- Martell DJ, Kieffer JD, Trippel EA (2005) Effect of temperature during early life history on embryonic and larval development and growth in haddock. *J Fish Biol* 66:1558–1575
- McGurk MD (1984) Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. *Mar Biol* 84:13–26
- Mehler MF, Mabie PC, Zhang D, Kessler JA (1997) Bone morphogenetic proteins. *Trends Neurosci* 20:309–317
- Minina E, Wenzel HM, Karp S, Gaffield W, McMahon AP, Vortkamp A (2001) BMP and Ihh/PTHrP signaling interact to coordinate chondrocyte proliferation and differentiation. *Development* 128:4523–4534
- Myers DC, Sepich DS, Solnica-Krezel L (2002) Bmp Activity Gradient Regulates Convergent Extension during Zebrafish Gastrulation. *Dev Biol* 243:81–98
- Neuhaus H, Rosen V, Thies RS (1999) Heart specific expression of mouse BMP-10 a novel member of the TGF- β superfamily. *Mech Dev* 80:181–184
- Nijweide PJ, Burger EH, Feyen JH (1986) Cells of bone: proliferation, differentiation, and hormonal regulation. *Physiol Rev* 66:855–886
- Ørnsrud R, Gil L, Waagbø R (2004) Teratogenicity of elevated egg incubation temperature and egg vitamin A status in Atlantic salmon. *Salmo salar* L. *J Fish Dis*. 27:213–223
- Otterlei E, Nyhammer G, Folkvord A, Stefansson SO (1999) Temperature- and size- dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. *Can J Fish. Aquacult Sci* 56:2099–2111
- Palomino J, Herrera G, Dettliff P, Martinez V (2014) Growth differentiation factor 9 and bone morphogenetic protein 15 expression in previtellogenic oocytes and during early embryonic development of Yellow-tail Kingfish *Seriola lalandi*. *Biol Res* 47:1–7
- Phan TCA, Xu J, Zheng MH (2004) Interaction between osteoblast and osteoclast: impact in bone disease. *Histol Histopathol* 19:1325–1344
- Prestinicola L, Boglione C, Makridis P, Spano A, Rimatori V, Palamara E, Scardi M, Cataudella S (2013) Environmental conditioning of skeletal anomalies typology and frequency in gilthead seabream (*Sparus aurata* L., 1758) juveniles. *PLoS One* 8:1–22
- Razdorov G, Vukicevic S (2012) The Use of Mass Spectrometry in Characterization of Bone Morphogenetic Protein from Biological Samples. In: Prasain JK (ed) *Trandem mass spectrometry—applications and principles*. InTech, Rijeka, Croatia, pp 259–284
- Rickard DJ, Sullivan TA, Shenker BJ, Leboy PS, Kazhdan I (1994) Induction of rapid osteoblast differentiation in rat bone marrow stromal cell cultures by dexamethasone and BMP-2. *Dev Biol* 161:218–228
- Riley KL, Weirich CR, Cerino D (2009) Development and growth of hatchery-reared larval Florida pompano (*Trachinotus carolinus*). *Fish Bull* 107:318–328
- Rombough PJ (1997) The effects of temperature on embryonic and larval development. In: Wood CM, McDonald DG (eds) *Global Warming*. Cambridge University Press, Cambridge, Implications for Freshwater and Marine Fish, pp 177–223
- Shi Y, Massague J (2003) Mechanisms of TGF- β signaling from cell membrane to the nucleus. *Cell* 113:695–700
- Solloway MJ, Robertson EJ (1999) Early embryonic lethality in Bmp5; Bmp7 double mutant mice suggests functional redundancy within the 60A subgroup. *Development* 126:1753–1768
- Storm EE, Huynh TV, Copeland NG, Jenkins NA, Kingsley DM, Lee SJ (1994) Limb alterations in brachypodism mice due to mutations in a new member of the tgfbeta-superfamily. *Nature* 368:639–643
- Tiago DM, Marques CL, Roberto VP, Cancela ML, Laize V (2014) Mir-20a regulates in vitro mineralization and BMP signaling pathway by targeting BMP-2 transcript in fish. *Arch Biochem Biophys* 543:23–30
- Vainio S, Karavanova I, Jowett A, Thesleff I (1993) Identification of BMP-4 as a signal mediating secondary induction between epithelial and mesenchymal tissues during early tooth development. *Cell* 75:45–58
- Villeneuve L, Gisbert E, Delliou HL, Cahu CL, Zambonino-Infante JL (2005a) Dietary levels of all-trans retinol affect retinoid nuclear receptor expression and skeletal development in European sea bass larvae. *Br J Nutr* 93:791–801
- Villeneuve L, Gisbert E, Zambonino-Infante JL, Quazuguel P, Cahu CL (2005b) Effect of nature of dietary lipids on European sea bass morphogenesis: implication of retinoid receptors. *Br J Nutr* 94:877–884
- Villeneuve LAN, Gisbert E, Moriceau J, Cahu CL, Zambonino JL (2006) Intake of high levels of vitamin A and polyunsaturated fatty acids during different developmental periods modifies the expression of morphogenesis genes in European sea bass (*Dicentrarchus labrax*). *Br J Nutr* 95:677–687
- Von Westernhagen H (1988) Sublethal effects of pollutants on fish eggs and larvae. In: Hoar WS, Randall DJ (eds) *Fish physiology*. Academic Press INC, San Diego
- Wan M, Cao X (2005) BMP signaling in skeletal development. *Biochem. Biophys. Res. Commun.* 328:651–657
- Wen W, Huang X, Chen Q, Feng L, Wei L (2013) Temperature effects on early development and biochemical dynamics of a marine fish, *Inimicus japonicus*. *J Exp Mar Biol Ecol* 442:22–29
- Whitman M (1998) Smads and early developmental signaling by the TGF- β superfamily. *Genes Dev* 12:2445–2462
- Windhausen T, Squifflet S, Renn J, Muller M (2015) BMP signaling regulates bone morphogenesis in zebrafish through promoting osteoblast function as assessed by their nitric oxide production. *Molecules* 20:7586–7601
- Wolfman NM, McPherron AC, Pappano WN, Davies MV, Song K, Tomkinson KN, Wright JF, Zhao L, Sebald SM, Greenspan DS, Lee SJ (2003) Activation of latent myostatin by the bmp-1/tolloid family of metalloproteinases. *Proc Natl Acad Sci USA* 100:15842–15846
- Ytteborg E, Baeverfjord G, Torgersen J, Hjelde K, Takle H (2010) Molecular pathology of vertebral deformities in hyperthermic Atlantic salmon (*Salmo salar*). *BMC Phy* 10:1–16
- Zheng P, Ma Z, Guo H, Zhang D, Fu M, Zhang N, Jiang S (2014) Osteological ontogeny and malformations in larval and juvenile golden pompano *Trachinotus ovatus* (Linnaeus 1758). *Aquacult Res*. doi:10.1111/are.12600
- Zou H, Niswander L (1996) Requirement for BMP signaling in interdigital apoptosis and scale formation. *Science* 272:738–741

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