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Effects of Salinity and pH on the Expression of Sexually Selected Traits in the male Guppy (*Poecilia reticulata*)

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ABSTRACT

The ecological factors of aquatic environments are changing because of global climate change, which can directly or indirectly influence the expression of different phenotypic traits in many organisms. The present study was conducted under laboratory conditions to unveil the effects of salinity and pH on the expression of some selected traits in the male guppy (*Poecilia reticulata*)- a small freshwater live-bearing promiscuous fish species. The findings revealed that both salinity and pH had significant effects on courtship behaviors (e.g. sigmoid displays and gonopodial thrusts). The results also showed significant effects of salinity on body size (e.g. standard length and body area) and skin pigmentation (e.g. orange spot area). However, the study found that manipulations of these climate change parameters had no significant effect on other color spot numbers and areas. These findings elicit further information about the environmental condition dependent expression of reproductive traits of fishes, which would help to take necessary strategies for breeding, conservation and management of many fish species in a changing aquatic environment.

INTRODUCTION

Climate change influences the various parameters of many aquatic habitats, which concomitantly affect the existing organisms, particularly fishes **(Barbarossa *et al.*, 2021; Huang *et al.*, 2021)**. In the aquatic environment, most climate change impacts can be implicated by higher water salinity **(Bonte & Zwolsman, 2010)**, elevated temperature **(Kaushal *et al.*, 2010)**, increased acidification **(Koch *et al.*, 2013)**, changed patterns of dissolved oxygen **(Bello *et al.*, 2017)**, etc... The alterations of these water parameters may change fish abundance **(Barange *et al.*, 2018)** by affecting their different life-history traits, including growth, survival, behavior, etc... **(Crozier *et al.*, 2021; Huang *et al.*, 2021; O'Connor & Booth, 2021)**.

When fishes encounter a changing or new environment, they try to adapt to this environment through phenotypic plasticity by tuning their genotypes with their target phenotypes **(Schlichting & Pigliucci, 1998; Wrange *et al.*, 2014)**. Several studies have already documented plasticity in growth **(Hurst *et al.*, 2012)**, survival **(Reusch, 2014)**, appearance **(Ahas & Aasa, 2006)**, reproduction **(Spinks *et al.*, 2021)** in different fish species due to the contemporary changes in some climatic conditions. Thus, fishes need to modulate some phenotypes to adapt to changing conditions.

In fishes, particularly males' sexually selected traits are condition dependent, i.e. the expression of these traits is linked to resource availability **(Cotton *et al.*, 2006; Rahman *et al.*, 2013)**. They can invest the available resources to evolve the exaggerated traits, which assist them in achieving preferable mates for higher reproductive success (**Rahman *et al.*, 2014; Selz *et al.*, 2016; Scherer *et al.*, 2018)**. A vast number of literature has reported the modulation of phenotypic expression in different fishes due to changing climatic conditions **(Rijnsdorp *et al.*, 2009; Crozier & Hutchings, 2014; Reusch, 2014; Pilakouta & Ålund, 2021; Potts *et al.*, 2021;)**. This genre of work elicits mainly the ecology and evolutionary perspectives of different commercially important fish species, while a subtle ignorance about the modulations of sexually selected traits can be inferred. It is unquestionable that the global climate is changing, which ultimately affects different fishes in various ways. Considering the importance of this highly concerning issue, this study was carried out to investigate whether some important climate change variables (i.e. salinity and pH) can influence the expression of some sexually selected traits (e.g. courtship behavior, body size and color patterns) in a popular model species guppy (*Poecilia reticulate*).

Guppy is a small freshwater and/or slightly brackish water fish individual which is promiscuous in nature **(Houde, 1997)**. In this species, males are smaller than females and show complex color patterns, including orange iridescent, and black spots during mating **(Houde, 1997)**. Females prefer males which have relatively larger and brighter orange color spots **(Kodric-Brown, 1985)**. Numerous studies have shown that males mating behavior **(Evans *et al.*, 2015)**, color patterns **(Grether *et al.*, 2005)**, and female mate choices **(Gasparini *et al.*, 2013)** are strongly dependent on different ecological conditions which urged interest to use this popular model species in this present study.

MATERIALS AND METHODS

Fish collection and rearing

Around 500 juvenile guppies were collected from an aquarium shop in Khulna city, Bangladesh. Then they were transported in an oxygenated poly bag to the Wet Fish laboratory of Fisheries and Marine Resource Technology Discipline, Khulna University, Khulna where the experiments were carried out. Initially, they were kept in a large glass aquarium (50cm × 29cm × 30cm) and conditioned for two days before stocking them in the experimental aquariums. Then, all juvenile males were sorted out from the whole stock by observing the gonopodium. Finally, almost the same-sized juvenile males were selected for two different experiments, including 1) Experiemnt-1: salinity effect and 2) Experiemnt-2: pH effect. Before commencing these experiments, several trails were conducted to determine the lethal levels (the upper and lower limit) of these factors. Finally, three treatment groups were chosen (e.g. control, high and low) for each experiment based on the trial outcomes and the extreme water conditions. For example, the salinity experiment had control (0-0.5 ppt), low (14-15 ppt), and high (34-35 ppt) treatment groups, while pH experiment had low (4.5 -5.0), control (6.5-7.0) and high (8.5-9.0) treatment groups. Each treatment had three replications in which exactly 15 juvenile males were randomly assigned to each replication. Thus, 135 juvenile males were stocked separately in each experiment. For behavioral tests, 15 sexually mature females were kept in each replication of every experiment so that both males and females did not get any sudden stress of having a completely new environment. Every aquarium was covered with a net to stop the fish escape. The salinity was controlled by adding gradually diluted brine solution in experiment-1. In experiment-2, pH was regularly increased by adding diluted sodium hydroxide (NaOH) and decreased by adding diluted sulfuric acid (H_2SO_4) twice a day, following the method of previous studies **(Zahangir *et al.*, 2015; Maoxiao *et al.*, 2018)**.

Water quality management

Prior to stocking, every aquarium was cleaned up properly and fitted with continuous aeration. About half of the water was removed by siphoning once a week to clean the feces and uneaten food. Adhered dirt inside the aquarium walls were also cleaned once a week. During the experimental period, the temperature, salinity and pH of water were daily monitored. Temperature, salinity and pH records were taken with a celsius thermometer, a digital refractometer and a portable pH meter, respectively.

Feeding

The experimental fishes were fed 6 days per week (once a day) with commercial dry food (Wardley Total Tropical Gourmet Flake Blend^{TM}, The Hartz Mountain Corporation, Secaucus, NJ). Food was provided up to their satiation level throughout the experiments.

Mating behavior observation

First, a female (reared in a replication of an experiment) was transferred in a separate behavioral aquarium and allowed to settle for around 10 minutes. Then, a single experimental male of the same treatment was placed in the aquarium and allowed to settle for at least 5 minutes or until it showed sexual interest to the female (i.e. following the female or engaging in courtship). For each 10 minutes trial, the male mating behaviors were recorded as the number of sigmoid displays (males arch their body in a characteristic shaped posture and quiver), gonopodial thrusts (forced mating attempts in which males approach females from behind and attempt copulations without prior courtship or female solicitation) and the time (in seconds) spent by the male courting or chasing the female (a measure of the male's overall sexual interest in the female, hereafter "sexual interest") **(Houde, 1997)**. After the trial, each male was returned to its own tank and maintained for a further seven days before being used for the measurements of body size and color patterns.

Survival, body size and color patterns measurements

Fish was monitored every day, and thereby, survival was recorded. After one week of the behavioral tests, every male was narcotized for a while individually using MS222. Then, a clear photograph was taken under a standard lighting conditions by placing the fish on laminated graph paper. A digital camera (Canon DS126621) was ready with a stand to take a photograph from a fixed distance of 30cm. Each image included a unique code so that subsequent analyses of male traits were performed blind of treatment. The raw uncompressed images were imported into *ImageJ* software (v1.46) for the measurements of body size (standard length- the distance in mm from the fish snout to the tip of its caudal peduncle and body area- the area of the body excluding all fins and tail) and color patterns (orange, iridescent and black color spot number and area).

Statistical analyses

All analyses were performed using 'R' version 4.0.2 **(R Development Core Team, 2020)**. Descriptive statistics (means and SEs) were calculated using the 'pysch' package. The Shapiro-Wilk test of normality and the Levene's tests for homogeneity of variance were done with the 'onewaytests' package. An appropriate transformation method was applied for non-normal data.

The analyses of variance (ANOVA) model was selected using the 'car' package to explore the effects of experimental fixed effect (i.e. salinity/pH) on (i) fish body size (e.g. standard length and body area) and (ii) sexual color area (different color patches). The 'glmmADMB' package was used to create a generalized linear mixed models (GLMM) framework with negative binomial responses and zero-inflation ('TRUE' or 'FALSE' option). The experimental variables (e.g. salinity/pH) were entered as a fixed effect allowing or not allowing zero-inflation (based on having many zeros or not) in the models with negative binomial distribution. The negative binomial distribution was used to approximate over dispersion (**Lindén and Mäntyniemi, 2011)**. Thus, the count data (e.g. sigmoid displays, gonopodial thrusts, sexual interest, and sexual color spot number) were analyzed. The post-hoc (TukeyHSD) tests were performed using 'multcomp' package to find out multi-comparison among different treatments. To quantify the magnitude of treatment effects, we calculated the coefficient of determination R^2 (i.e. effect size) for each trait **(Nakagawa *et al.*, 2017)**. Finally, we calculated the Spearman's r to test for correlations between courtship displays (e.g. sigmoid displays, gonopodial thrusts and sexual interest) and other phenotypic traits (e.g. standard length, body area, orange and iridescent spot area) to explore any trade-off among traits. For these tests, we restricted our analysis to traits that were significantly affected by the treatments. The 'ggplot2' package was used to show all the significant variations among treatments graphically.

RESULTS

Experiment-1: salinity effect

98% fish survival was found in low salinity (14-15 ppt) treatment, while 89% and 84% fish survived in high (34-35 ppt) and control (0-0.5 ppt) groups, respectively.

Courtship behavior

At the end of the experiment, a significant effect of salinity was found on sigmoid displays (F=9.75, P<0.001 and R^2=0.34). The model disclosed that the high-treatment group fish performed a significantly lower number of sigmoid displays than the low (P<0.001) and control (p<0.001) group, whereas no significant variation was observed between the control and low-treatment group (P=0.39; Fig. 1A).

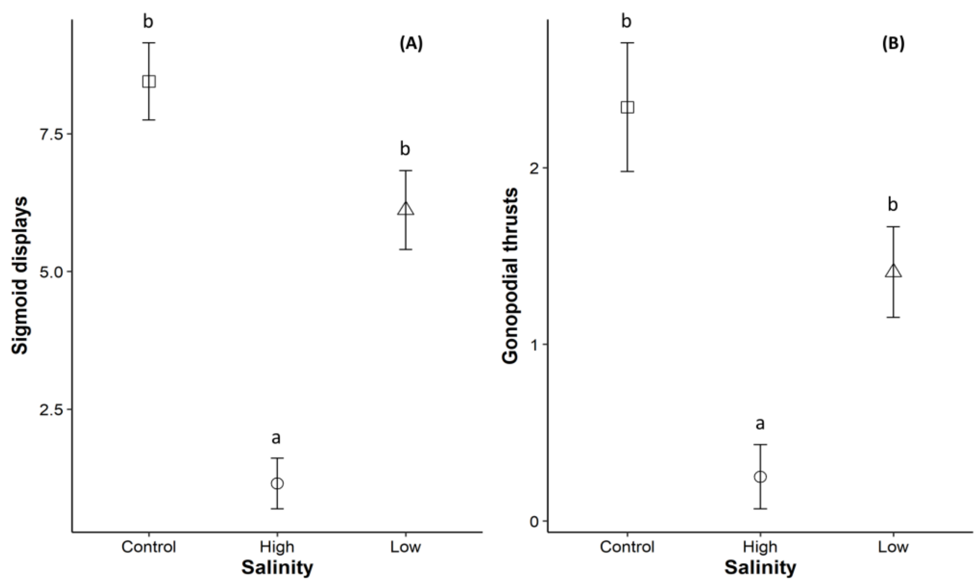

Fig. 1. Effects of salinity on (A) sigmoid displays and (B) gonopodial thrusts of experimental male guppy

Values are presented as mean ± standard error (SE). Differences in small letters at the top of each bar indicate significant variation between fish of different salinity treatments (P<0.05).

The analysis also exposed a significant influence of salinity on the number of gonopodial thrusts performed by experimental males (F=10.12; P<0.001, and R^2=0.23). The treatment-wise comparison showed that the high-treatment groups conducted a significantly lower number of gonopodial thrusts than the control group (P<0.001) and low group (P<0.01). No significant variation was found in gonopodial thrusts number between control and low treatment group (P=0.08; Fig. 1B).

The mixed model revealed no significant effect of salinity on the time that experimental males spent following the females (i.e. sexual interest) during the courtship behavioral test (F=2. 60, p=0.08 and R^2=0.05).

Body size

A significant effect of salinity was revealed on standard length (F=4.93; *P*<0.01, and R^2=0.11) and body area (F=4.16; *P*<0.05 & R^2=0.09). The treatment-wise comparison showed that the low salinity group possessed a significantly larger standard length than the high (*P*<0.05) and control group (*P*<0.05). No variation was found between control and high treatment group (p=0.99; Fig. 2A).

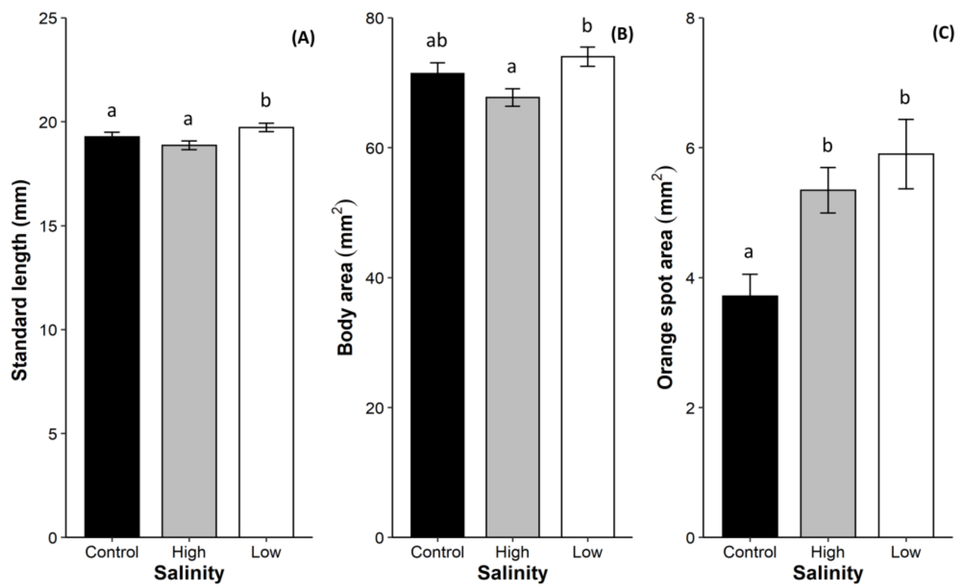

Fig. 2. Effects of salinity on (A) standard length and (B) body area and (C) orange spot area in experimental male guppy

Values are presented as mean ± standard error (SE). Differences in small letters at the top of each bar indicate significant variation between fish of different salinity treatments (*P*<0.05).

The analysis also revealed that the low salinity group had a significantly larger body area than the high salinity group (*P*<0.05), while no significant variation was found with the control group (*P*=0.07). No significant variation was found between control and high treatment group (*P*=0.99; Fig. 2B).

Color patterns

After analysis, the study disclosed a significant effect of salinity on the orange spot area (F=7.22; *P*<0.01 and R^2=0.15), while no significant effect was found on orange spot number (F=0.4 8; *P*=0.61 and R^2=0.02), black spot number (F=0.28; *P*=0.74 and R^2=0.01) and area (F=0.22; *P*=0.80 and R^2=0.005), and iridescent spot number (F=0.22, *P*=0.36 and R^2=0.02) and area (F=1.85; *P*=0.16 and R^2=0.04). The post-hoc (TukeyHSD) test showed that the control treatment fish had significantly less orange spot area than the high (*P*<0.05) and low (*P*<0.01) treatments, while no significant variation was found between the high and low groups (*P*=0.66; Fig. 2C).

Experiment-2: pH effect

96% of fish survived in the high pH (8.5-9.0) treatment, while 91% and 80% of fish survived in the control (6.5-7.0) and low (4.0-5.0) treatments, respectively.

Courtship behavior

The analysis revealed a significant effect of pH on sigmoid displays (F=3.15, *P*<0.05 and R^2=0.29). The high pH group performed a significantly higher number of sigmoid displays than the low (*P*<0.001) and control pH groups (*P*<0.05), while no significant variation was observed between the control and low pH groups (*P*=0.07; Fig. 3A).

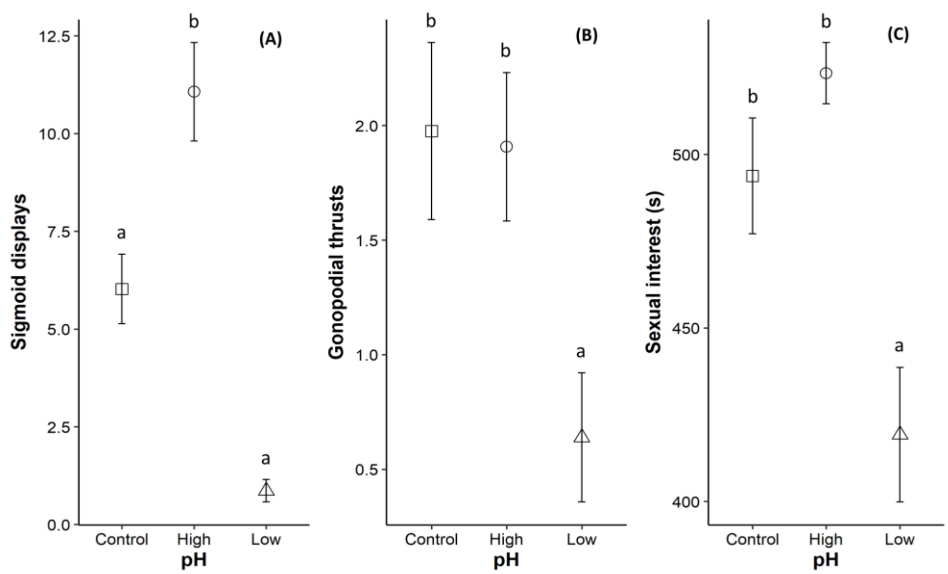

Fig. 3. Effects of pH on (A) sigmoid displays, (B) gonopodial thrusts and (C) sexual interest of experimental male guppy

Values are presented as mean ± standard error (SE). Differences in small letters at the top of each bar indicate significant variation between fish of different pH treatments (*P*<0.05).

A significant effect of pH was recorded on gonopodial thrusts number (F=5.81, *P*<0.01 and R^2=0.11). The post-hoc comparisons showed that the low treatment group conducted significantly lower performances, compared to high treatment (*P*<0.05) and control group (*P*<0.01), while no significant variation was observed between high & control groups (*P*=0.77; Fig. 3B).

A significant effect of pH was detected on sexual interest (F=5.23, *P*<0.01 and R^2=0.17) in this experiment. The analysis revealed that the low pH group invested significantly less amount of time to follow their mates than the control (*P*<0.01) and high pH groups (*P*<0.01). However, no significant difference was found in sexual interest between control and high pH groups (*P*=0.52; Fig. 3C).

Body size

The analysis unvealed no significant effect of water pH on standard length (F=1.57; *P*=0.21 and R^2=0.03) and body area (F=1.35; *P*=0.26 and R^2=0.02).

Color patterns

The selected models showed no significant effect of pH on black spot number (F=0.03; *P*=0.97 and R^2=0.003) and area (F=1.18; *P*=0.31 and R^2=0.02), orange spot number (F=2.04; *P*=0.13 and R^2=0.06) and area (F=1.14; *P*=0.32 and R^2=0.02), and iridescent spot number (F=0.64; *P*=0.53 and R^2=0.01) and area (F=0.34; *P*=0.71 and R^2=0.006).

DISCUSSION

The present study revealed that water salinity and pH profoundly affected some sexually selected traits in male guppies. Several research and predictions have confirmed that global climate change can alter pH levels **(McNeil and Matear, 2006; Sosdian *et al.*, 2018)** and the salinity **(Durack *et al.*, 2012; Gutchess *et al.*, 2018)** of aquatic ecosystems. These alterations may ultimately affect the living organisms, particularly many fish species, directly or indirectly **(Comte & Olden, 2017; Barange *et al.*, 2018; Giroux & Schlenk, 2021; Roy *et al.*, 2021)**. For instance, **Berasain *et al*. (2015)** have demonstrated that climate change reduced the total lake area (from 68.1 to 47.4 km2) and increased the salinity (from 18.9–41.5 g l^{-1}) in the Chasicó Lake of Argentina in which the overall production of *Odontesthes bonariensis* was significantly reduced due to the impaired reproduction and limited embryo and juvenile survival. In a long-term study, **Weiss *et al*. (2018)** have observed that pCO_2 was increased consistently along with pH level reduction in four freshwater reservoirs, which significantly decreased the predation perceptibility of *Daphnia* and also hampered their chemical communication affecting the inducible defense mechanism. Thus, evidences confirm that climate change is responsible for the alteration of many important variables, which ultimately affect the different life-history traits in many fish species.

Salinity effect

Water salinity is another important factor of global climate change, which can affect fish conversion efficiency **(Arunachalam & Reddy, 1979; Kang'ombe & Brown, 2008)**, metabolism **(Peterson-Curtis, 1997; Urbina & Glover, 2015)**, feed intake **(Wang *et al.*, 1997; Darwis *et al.*, 2009)**, growth **(Wang *et al.*, 1997; Bœuf & Payan, 2001)**, dissolved oxygen consumption **(Tsuzuki *et al.*, 2008; Ern *et al.*, 2014)** and hormones regulation **(Cooperman *et al.*, 2010; Peyghan *et al.*, 2013)**. Although guppies are well-known as freshwater species, they can tolerate a wide range of salinity up to 50 ppt **(Chervinski, 1984; Chiyokubo *et al.*, 1998)**. However, extreme salinity persuades them to cope with osmotic pressure **(Plaut, 1998; Sterzelecki *et al.*, 2013)** and make changes in their physiological activities **(Gonzalez, 2012; Komoroske *et al.*,**

2016). Thus, unfavorable extreme salinity costs lot of energy for maintenance **(Ern *et al.*, 2014; Urbina & Glover, 2015; Vaz *et al.*, 2015)**.

In the present study, guppies exposed to extremely high salinity (34-35 ppt) demonstrated significantly lower number of courtship displays than control and low salinity groups (Figs. 1A, B). The possible explanation of these findings might be that they allocated very high amount of energy to cope with osmotic pressure and physiological challenges that ultimately provoked them to reduce their body size **(Neves & Monteiro, 2003; Araújo *et al.*, 2014)**, color patterns **(Lawson & Alake, 2011; Küçük *et al.*, 2013)** and courtship behaviors **(Zakariah & Hassan, 2013; Lehtonen *et al.*, 2016; Sommers *et al.*, 2016)**.

Interestingly, low salinity (14-15 ppt) males grew significantly larger than control (0-0.5 ppt) and high salinity groups (34-35 ppt) (Figs. 2A, B) and possessed significantly more orange spot areas than control treatment (Fig. 2C). Although this finding predicts to have a trade-off between courtship displays and other phenotypes (e.g. body size and orange spot area), we did not find any trade-off after analysis (Table 1). In a study, **Araújo *et al*. (2014)** have found that different populations of *P. vivipara* in the coastal lagoons of Rio de Janeiro, Brazil showed a positive association between body size and salinity (i.e. specimens from freshwater lagoons were significantly smaller in size than the saline sites), which is also congruent with the findings of two previous studies **(Neves & Monteiro, 2003; Gomes & Monteiro, 2008)**. In the present study, the collected guppies are usually reared in slightly saline water (0.5 to 2 ppt), matching with their wild sources, which could afford them to adapt in low salinity treatment favorably along with low maintenance cost. In case of orange spot area, the favorable low saline environment and larger body size of the low treatment group could enable the orange patches to appear larger and prominent.

Table 1. Correlations between courtship displays and other phenotypic traits for salinity treatments

Salinity treatment	Traits	Standard length	Body area	Orange spot area
High	Sigmoid displays	-0.23 (0.13)	-0.04 (0.79)	0.13 (0.39)
	Gonopodial thrusts	-0.09 (0.54)	-0.08 (0.59)	**0.39 (0.01)**
Control	Sigmoid displays	**0.32 (0.04)**	0.25 (0.11)	**0.36 (0.02)**
	Gonopodial thrusts	0.11 (0.50)	0.18 (0.27)	-0.03 (0.82)
Low	Sigmoid displays	-0.19 (0.21)	-0.12 (0.43)	0.02 (0.86)
	Gonopodial thrusts	-0.17 (0.25)	-0.06 (0.67)	-0.06 (0.69)

Values shown are correlation coefficients and *P*-values (in brackets). Significant values are given in bold.

pH effect

Evidences show that global climate change may alter the water pH levels **(Caldeira & Wickett, 2003; McNeil & Matear, 2006; Sosdian *et al.*, 2018)** which enormously affect the living aquatic organisms, particularly fishes in various ways, such as affecting hormone regulation **(Brown *et al.*, 1989; Kwong *et al.*, 2014)**, reducing feed intake **(Lim, 1993; Maicá *et al.*, 2018)**, , impacting metabolism **(Teo & Chen, 1993; Laitinen *et al.*, 2009)**, hampering oxygen consumption **(Ellis & Morris, 1995; Miller *et al.*, 2016)**, influencing enzyme activities **(Kwong *et al.*, 2014; Maoxiao *et al.*, 2018)**, providing stresses **(Wu *et al.*, 2015; Zahangir *et al.*, 2015)**, etc... Thus, intolerable pH level can inhibit growth performance in many fishes **(Munday *et al.*, 2009; Reynalte-Tataje *et al.*, 2015; Maoxiao *et al.*, 2018)**, disrupt olfactory cues **(Dixson *et al.*, 2010; Ross & Behringer, 2019)**, affect behavioral approaches **(Leduc *et al.*, 2013; Kleinhappel *et al.*, 2019)** and reduce energy generation **(Leo *et al.*, 2018; Stiasny *et al.*, 2018)**.

In the present study, males exposed to low pH treatment (4.5 -5.0) performed significantly low number of courtship displays than control (6.5-7.0) and high (8.5-9.0) treatment groups (Figs. 3A, B & C). This finding corroborates the outcomes of other studies which have shown that acidic environment inhibits reproductive behavior **(Ikuta *et al.*, 2003)**, disrupts neural cues **(Leduc *et al.*, 2013)**, hampers swimming activity **(Taghizadeh *et al.*, 2013)** and induces behavioral abnormalities **(Mustapha & Mohammed, 2018)**, etc. As discussed above, the low pH in this present study could possibly create stress to the fish, hamper their required oxygen consumption, reduce feed intake and metabolism to produce enough energy for these physiologically costly courtship displays **(Seymour & Sozou, 2009; Clark, 2012; Mowles & Jepson, 2015)**. Contrary to the low treatment group, significantly high courtship performance of high pH group can be supported by the findings of previous studies in which they have found that fishes had either preferences or no avoidances of high pH environment **(Serafy & Harrell, 1993; West *et al.*, 1997; Scott *et al.*, 2005)**. They have discussed that their fishes adapted to the high pH because their habitats might have this alkaline water **(West *et al.*, 1997; Scott *et al.*, 2005)** or they would prefer this alkaline environment to avoid predators and better foraging **(Scott *et al.*, 2005)**. The males exposed to pH treatments in this study might have high pH in their previous rearing environment at the aquarium shop because of flexible maintenance (food, chemical treatments, etc…), which could enable them to adapt in the experimental high pH treatment comfortably. In a study, **Wilkie and Wood (1996)** discussed about how fishes can physiologically adapt in high pH containing lakes which could be another explanation about how our high pH group adapted and performed similarly like the control group. However, the low pH treatment group allocated enough energy under the extreme condition to express body size and color patterns normally, which could be a balance of energy to maintain these traits properly rather than the physiologically costly courtship traits.

CONCLUSION

People need to be highly aware that global climate is changing inconceivably by alarmingly increasing temperature (±2°C per decade), rising sea level (>3mm over the past two decades), rising carbon footprint of tourism (4.5Gt of CO_2 from 2009 to 2013), looming risk of extinction of 5% global species only from 2°C warming alone, which could be raised up to 16% at 4°C warming **(IPBES, 2019)**. Thus, we can reckon about how dangerously our normal aquatic environment is declining its natural qualities for the living organisms. These unprecedented changes can impose unbearable stresses to the living animals in various ways, and the impact on their life-history traits is one of them. Therefore, this study has tried to explore about how some of the important climate change variables (e.g. salinity and pH) can influence the expression of some phenotypic traits in a popular model fish species under laboratory conditions. Although there were lots of limitations to conduct this kind of study, it showed some significant effects on some important traits which may attract some attention of our researchers to carry out more effective research regarding this issue in future.

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