

Combined effects of a simulated marine heatwave and an algal toxin on a tropical marine aquaculture fish cobia (*Rachycentron canadum*)

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Abstract

Ongoing global warming is one of the major challenges for the development of aquaculture in the tropical regions where species are already cultured in the water temperature close to their upper physiological thresholds. Furthermore, warming can trigger blooms of toxic algae, yet we do not know how extreme warming such as a marine heatwave (MHW) and algal toxins may affect marine aquaculture species. To address this issue, we investigated the effects of a simulated MHW in combination with exposure to *trans*-4-*trans*-decadienal (PUA), a diatom-derived toxin, on survival, growth, development and biochemical composition of cobia larvae and juveniles. Cobia larvae were exposed for 48 hr to one of two temperatures (29 vs. 34°C) and two PUA treatments (0 vs. 0.5 µM). Surviving larvae from each treatment were divided into two subsets: three replicates were used for the feeding test and five replicates were used for the recovery test in a non-contaminated environment at the respective temperatures of 29 or 34°C. Survival of cobia larvae was reduced by 16% in either MHW or PUA, but it dropped by 60% when both stressors were present, indicating a synergistic effect. MHW, but not PUA, reduced the feeding of cobia larvae. PUA had no delayed effects on growth rate and biochemical composition of the fish. MHW strongly reduced specific growth rate, body protein and lipid contents in cobia. Our results provide the first empirical evidence of how MHW and toxic algae may interact and challenge cobia and marine aquaculture production in tropical countries.

KEYWORDS

climate change, cobia, heatwaves, interactive effect, toxic algae, tropical marine aquaculture

1 | INTRODUCTION

Countries around the South China Sea are the largest aquaculture producers in the world, accounting for more than 70% of

the world's aquaculture production (FAO, 2018). However, this region is highly vulnerable to climate change (Germanwatch, 2018; Vietnamese Ministry of Natural Resources & Environment, 2009), particularly the phenomenon of marine heatwaves (MHW)

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(Frölicher & Laufkotter, 2018; Oliver et al., 2018). MHWs are events of anomalously high temperatures lasting for durations from at least five consecutive days to several months (Hobday et al., 2016). The frequency and severity of MHWs have increased in the tropical and sub-tropical marine ecosystems worldwide (Frölicher & Laufkotter, 2018; Oliver et al., 2018). Between 1982 and 2016, the number of MHW days was doubled (Frölicher, Fischer, & Gruber, 2018). MHWs cause serious changes in structure, function and ecological services of marine communities (Smale et al., 2019; Wernberg et al., 2013). However, we know little about the impact of MHWs on tropical marine organisms (Doan et al., 2019; Frölicher & Laufkotter, 2018; Smale et al., 2019), particularly tropical aquaculture species (Doan et al., 2018).

Few studies have investigated the impact of MHWs on marine aquaculture. Caged Atlantic salmon (*Salmon salar*) (Wade et al., 2019) and tropical copepods (Doan et al., 2018) strongly decreased their feeding rate under a simulated MHW temperature. The pink flesh colour of salmon may be lost under extreme temperatures of MHWs (Wade et al., 2019). The MHW has been also predicted as a major climate change impact on the marine aquaculture of the Mediterranean Sea (Rosa, Marques, & Nunes, 2012). In the Southeast Asian countries, aquaculture species are cultured at the water temperature near their upper physiological thresholds (Comte & Olden, 2017; Doan et al., 2018, 2019; Sun & Chen, 2014); an increase of temperature is therefore expected to result in a huge challenge for culturing marine species.

Climate change can also trigger harmful algal blooms (HABs) (Brown et al., 2020; Cavole et al., 2016; Dam, 2013; Johnk et al., 2008; Lopez-Cortes et al., 2015; Moore et al., 2008; Wells et al., 2015). HABs have recently identified as one of the most critical threats to aquaculture production due to the potentials of rapid and mass mortalities of cultured species (Brown et al., 2020). In HABs, diatom species such as *Pseudo-nitzschia* spp., *Thalassiosira* spp. and *Chaetoceros* spp. can produce and release to the environment a variety of toxins, particularly domoic acids (DAs), oxylipins, saxitoxin, okadaic acid, dinophysistoxins and *trans-4-trans*-decadienal (PUA) (Lopez-Cortes et al., 2015; Villac, Doucette, & Kaczmarek, 2010). While approximately one-third of diatom species produce PUA (Wichard et al., 2005), the effect of PUA on marine species has mainly focused on the effects of DAs from *Pseudo-nitzschia* (Bacillariophyceae) (Mincarelli, Paula, Pousao-Ferreira, Rosa, & Costa, 2018) and on grazer species such as copepods (Caldwell, 2009; Dhanker et al., 2015; Miralto et al., 1999). Much less is known about the impact of PUA and especially its interaction with increasing temperatures on marine fish.

In general, the toxicity of a range of substances such as metals (Dinh et al., 2013; Janssens, Dinh, Debecker, Bervoets, & Stoks, 2014; Sokolova & Lannig, 2008) and pesticides (Dinh, Janssens, Debecker, & Stoks, 2014a; Dinh, Janssens, & Stoks, 2016; Holmstrup et al., 2010) increases under elevated temperatures, causing synergistic effects of the stressors (Crain, Kroeker, & Halpern, 2008; Dinh et al., 2013, 2014a, 2016; Sokolova & Lannig, 2008). However, it is relatively unknown how the harmful effects

of algal toxins may change under extreme temperatures (Lamb, Kimmel, & Field, 2019). This is highly relevant for two reasons. Firstly, the co-occurrence of warmer waters and HABs suggests that species may have to cope with both elevated temperatures and algal toxins simultaneously (Dam, 2013; Lamb et al., 2019). Secondly, the occurrence of MHW (Doan et al., 2018) and toxic algal blooms (Quang, Hai, & Lam, 2016) often coincides with the period of fish production. Therefore, knowledge of how and to what extent aquaculture species will be affected by MHW and toxic algae is of crucial importance for production.

In this study, we aimed to test for the combined effects of a simulated MHW and PUA on cobia (*Rachycentron canadum*) larvae and juveniles, one of the major marine aquaculture species (Estrada, Yasumaru, Tacon, & Lemos, 2016; Klinger, Levin, & Watson, 2017; Liao et al., 2004; Nhu et al., 2011), especially in countries around the South China Sea (Liao et al., 2004). More importantly, we tested whether both stressors interact to modulate each other's effects (Crain et al., 2008; Darling & Côté, 2008; Folt, Chen, Moore, & Burnaford, 1999). Finally, we tested to what extent the exposed larvae may recover from effects of PUA exposure under the extreme temperature of a MHW. We quantified key parameters for cobia larval and juvenile production including survival, feeding and specific growth rate. We also measured the changes in the proximate biochemical composition of fish muscle as an indicator of fish quality.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Based on the National Regulations for the Use of Animals in Research in Vietnam, cobia is not listed in two groups IB (endangered and critically endangered species) and IIB (threatened and rare species) (Decree32/2006/ND-CP, 2006). Therefore, this study does not require a permit or ethical approval. However, the authors have implemented their best practice of using animals in research.

2.2 | Study species

Cobia larvae (500 larvae; body weight - BW of 0.35 ± 0.12 g) were purchased from a local hatchery in Ninh Thuan province, Vietnam. They were transported to the Cam Ranh Centre for Tropical Marine Research and Aquaculture (Cam Ranh), Institute of Aquaculture, Nha Trang University, Vietnam. Here, they were acclimatized for 1 week at room temperature ($\sim 28^\circ\text{C}$) in two indoor fibreglass tanks ($V = 2 \text{ m}^3$). Thereafter, they were thermally acclimated to the experimental temperatures of 29 and 34°C by gradually increasing the water temperature in tanks to the set temperatures in 5 days. During the acclimation periods, fish larvae were fed on copepod *Pseudodiaptomus annandalei*. The photoperiod, salinity and dissolved oxygen (DO) were kept at 12L:12D (light:dark cycle), 29 ± 3.1 ppt and >6 mg/L respectively.

2.3 | Pilot experiments

A range-finding experiment was conducted in which cobia larvae were randomly assigned to one of six series *trans-4-trans*-decadienal (PUA) treatments (0, 0.1, 0.3, 0.5, 0.7, 1.0 μM) at room temperature ($\sim 28^\circ\text{C}$). Each treatment had three replicates. The experimental units were glass tanks ($V = 7\text{ L}$), each containing 10 individuals. The body weight and total length (the distance from the tip of the snout to the distal end of the hypural bone) of cobia were $0.35 \pm 0.12\text{ g}$ and $4.42 \pm 0.68\text{ cm}$ respectively. DO was maintained above 6 mg/L by gentle aeration. The copepod *P. annandalei* was used as food for cobia larvae during the exposure period. The exposure duration lasted 72 hr. The survival of larvae was observed every 24 hr. Based on the results of the experiment, the algal toxin concentration of 0.5 μM , which caused 40% mortality, was used for the main experiment (Figure S1).

To also test whether exposure to PUA may reduce survival of the copepod *P. annandalei* as food for cobia larvae, we conducted an experiment in which *P. annandalei* were exposed to one of six PUA exposure solutions: 0, 1, 2, 3, 4 and 6 μM PUA for 24 hr. The survival did not statistically differ between the control (0) and the PUA concentrations of 1–3 μM , but was lower at the PUA concentrations of 4–6 μM . The detailed results are provided in Figure S2.

2.4 | Experimental design and setup

To test for the effect of a simulated MHW, PUA and their interactions on the larvae of marine fish, we conducted a factorial experiment in which cobia larvae (18 days after hatching) were exposed to one of the four treatment combinations of 2 temperatures (29 and 34°C) and two PUA concentrations (0 and 0.5 μM) for 48 hr. Each treatment had 8 replicates (a total of 32 experimental units, 7-L glass tanks, each contained 10 fish larvae, Figure 1). Temperatures of 29 and 34°C are the mean (control) and extreme water temperature (heatwave) in the outdoor aquaculture pond where cobia larvae are reared (Doan et al., 2018; Nhu et al., 2011). The heatwave period is relevant to the number of heatwave days observed in the region (K.V. Dinh, X.N. Doan, M.H. Le, unpublished data) and this is also relevant to a production cycle of cobia larvae and juveniles (Nhu et al., 2011). The exposure concentration of 0.5 μM PUA is equivalent to the density of several hundred thousands to approximately a million cells of diatoms/L (Pohnert, 2000). During blooms, the density of diatoms may reach several million cells/L (Miralto et al., 2003; Scholin et al., 2000; Simon, Lipsewers, Giebel, Wiltshire, & Simon, 2014). During the exposure period, cobia larvae were fed ad libitum with copepod *P. annandalei*. We frequently checked the availability of copepods in the experimental tanks to ensure there was always an abundance of food items for the larvae. Other environmental parameters such as light cycles, salinity and DO were maintained similar to the acclimation periods. At the end of the PUA exposure period, survival was assessed.

Subsequently, three replicates of each treatment were used for the feeding trial (see below) and the remaining five replicates were transferred to clean water (200-L tanks) to test for the recovery

from PUA exposure at 29 or 34°C (Figure 1). They were fed at 3% body weight/day with commercial food pellets including NRD 3/5 (300–500 μm); NRD 5/8 (500–800 μm); NRD G8 (800 μm); NRD G12 (1,200 μm); NRD P16S (1,600 μm) (INVE, Belgium). The DO, salinity and photoperiod were kept similar to the PUA exposure period. The recovery experiment was terminated after 21 days when the fish reached a total length of approximately 10 cm, a typical commercial fingerling size (Nhu et al., 2011).

2.5 | Response variables

Survival and feeding rates were assessed at the end of the PUA exposure periods. The survival was the percentage of fish alive at the end of the PUA exposure and recovery period.

To test for the feeding rate, fish larvae were collected and reared in clean seawater (no PUA) for 12 hr to empty the gut. During this period, fish larvae were maintained at the same temperatures as during the exposure period. Subsequently, *P. annandalei* copepods ($\sim 1,000$ individuals/L) were added to each of the experimental tanks. Three fish larvae were collected from each tank after 15 and 45 min of feeding respectively. They were immediately fixed in alcohol (99%). We visually checked and confirmed that copepods were still available in the experimental tanks at the end of the feeding test, indicating that no food limitation during the test. To determine the number of eaten copepods, the digestive tract of the fish larva was opened and the number of copepods was counted using a stereomicroscope (SZ40, Olympus). The average number of copepods eaten by a larva of each experimental tank was used for statistical analyses.

We also assessed the survival, specific growth rate (SGR) and proximate composition of fish during the PUA recovery period. The SGR was calculated as the per cent daily growth increase: $\text{SGR} (\%/\text{day}) = (\ln W_2 - \ln W_1) \times \text{days of experimental duration} \times 100$; where W_1 and W_2 were the initial and the final body weights (g) respectively.

The proximate composition includes the body protein content was analysed using Kjeltac Auto 1030 analyzer (Foss Tecator, Höganäs); the lipid content was analysed its extractions were undertaken by petroleum ether extraction in a Soxhlet extraction system; the moisture was determined by drying at 105°C in an oven (Thermotec 2000, Contherm Scientific) and the ash was determined by combustion at 550°C for 24 hr in an electric furnace (Carbolite).

2.6 | Statistical analyses

To test for the direct effects of MHW and PUA on the survival and feeding rate at the end of the PUA exposure period, the growth rate and the proximate biochemical composition at the end of the PUA recovery period, we ran general linear models with MHW and PUA as two fixed factors. For the feeding, we also tested for the number of copepod *P. annandalei* eaten by a larva over time (15 and 45 min); therefore, we included Time as the repeat factor in the model. For all GLMs,

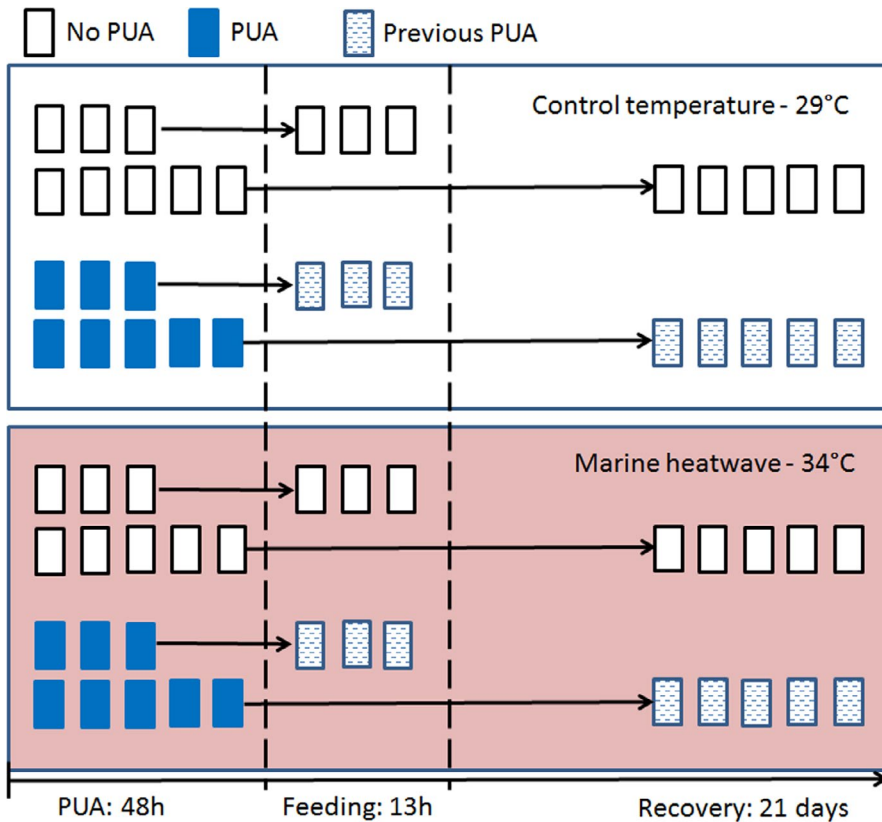


FIGURE 1 Schematic of the experimental design testing for the direct and delayed effects of *trans-4-trans-decadienal* (PUA) exposure on cobia under a simulated marine heatwave [Colour figure can be viewed at wileyonlinelibrary.com]

we tested the assumption of normality of the error distributions with Shapiro–Wilk tests and the homogeneity of variances with Levene's tests (Krause, Dinh, & Nielsen, 2017). Statistical differences were considered significant if $p < .05$. All statistical analyses were performed in Statistica 12 (StatSoft Inc.). Data are presented as mean + SE.

3 | RESULTS

3.1 | The exposure period

Overall, the survival of cobia larvae was reduced 28% in MHW (main effect of MHW; $F_{1,16} = 12.76$, $p = .0026$). Exposure to PUA reduced survival and this effect was stronger MHW than in the control (main effect of PUA, $F_{1,16} = 13.12$, $p = .0022$, and MHW \times PUA interaction, $F_{1,16} = 5.18$, $p = .037$, Figure 2). Specifically, the survival of PUA-exposed larvae dropped by 12% in the control and by 44% in MHW.

The number of copepods eaten per larva was highly variable as indicated by high standard errors. The feeding of cobia larvae was reduced 52% in MHW (main effect of MHW, $F_{1,23} = 11.95$, $p = .0021$, Figure 3). This effect was independent of PUA exposure and feeding time (p -Values > 0.05). There was no overall effect of PUA on the feeding of cobia larvae ($F_{1,23} = 1.68$, $p = .21$). However, Duncan Posthoc test showed that PUA-exposed cobia larvae increased their feeding rate in two specific conditions: at 15 min in the control (Figure 3a), and at 45 min in MHW (Figure 3b). There were no interactions of PUA and MHW (PUA \times MHW, $F_{1,23} = 0.03$, $p = .87$) or feeding time (PUA \times Feeding time, $F_{1,23} = 0.66$, $p = .43$).

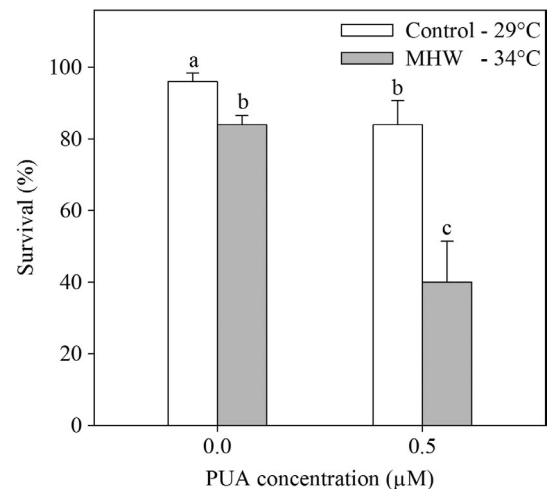


FIGURE 2 Survival of cobia larvae (*Rachycentron canadum*) as a function of a marine heatwave (MHW) and PUA exposure. Data are means + 1 SE. Statistical differences ($p < .05$) are indicated in small letters above the bars

3.2 | The PUA recovery period

MHW and the previous exposure to PUA had neither effect nor interactions on survival during the PUA recovery period (p -Values $> .05$, Figure 4a). MHW reduced the specific growth rate of cobia juveniles with 10% (main effect of MHW, $F_{1,15} = 18.30$, $p < .001$ Figure 4b). PUA had no delayed effect on the specific growth rate of cobia juveniles (p -Value $> .05$).

FIGURE 3 Feeding of cobia larvae (*Rachycentron canadum*) after 15 min (a) and 45 min (b) as a function of a marine heatwave (MHW) and PUA exposure. Data are means + 1 SE. Statistical differences ($p < .05$) are indicated in small letters above the bars

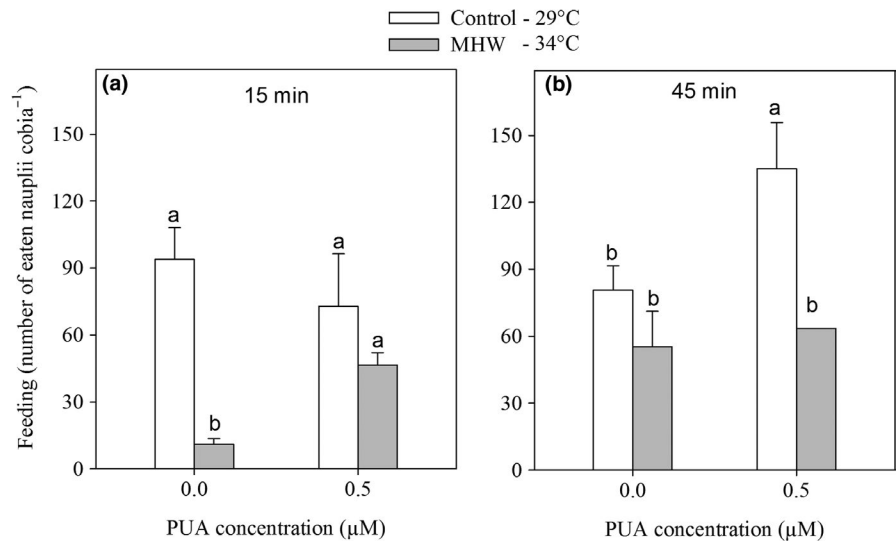
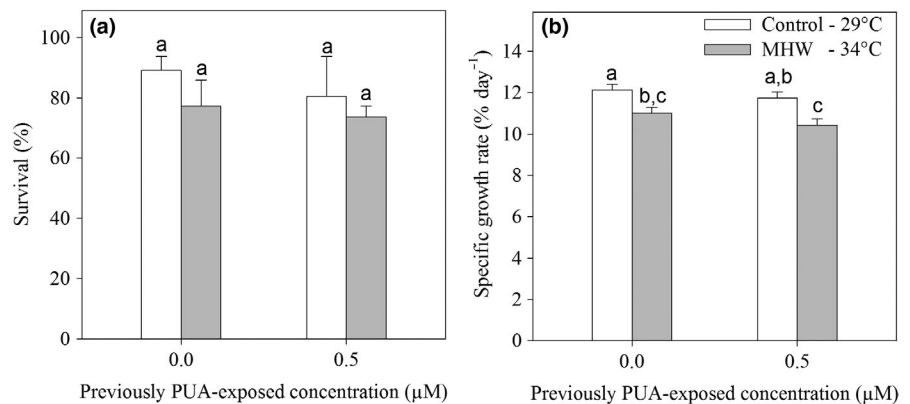


FIGURE 4 Effects of a marine heatwave (MHW) and delayed effects of PUA on the survival (a) and specific growth rate (b) of cobia juveniles (*Rachycentron canadum*). Data are means + 1 SE. Statistical differences ($p < .05$) are indicated in small letters above the bars



Under MHW, body protein and lipid contents were lower compared with controls by 13% and 17% respectively (main effect of MHW, Table 1, Figure 5a,b). At 29°C, body protein levels were not affected by previous exposure to PUA, but it was lower under MHW (main effect of MHW), especially in previously PUA-exposed cobia (interaction of MHW × PUA, Table 1, Figure 5a). Specifically, body protein levels were 8% lower under MHW, and 18% lower in cobia that were also exposed to PUA compared with the control. PUA had no delayed effect on the relative lipid content, and this was consistent across the two temperatures (p -Values > .05, Figure 5b).

Under MHW ash content was 36% higher while the moisture was 4% lower than in the control temperature (main effects of MHW, Table 1, Figure 5c,d). PUA had no delayed effect on the ash and moisture content, and these effects were not dependent on temperature (Table 1, Figure 5c,d).

4 | DISCUSSION

This is, based on our knowledge, the first laboratory study investigating the combined effects of MHW and algal toxin on a marine aquaculture species. We found strong single and interactive effects of MHW and PUA on cobia larvae and juveniles. To structure the

discussion, we will first focus on the direct effects of MHW, PUA and their interactions, and then discuss mainly the effects of MHW and the absence of the delayed effect of PUA on cobia juveniles; all are relevant to cobia and more generally, to finfish production in the tropical condition.

4.1 | Direct effects of MHW and PUA and their interactions

The survival of cobia larvae (ca. 0.35 ± 0.12 g/individual) was lower in MHW, indicating that 34°C is close to the upper lethal temperature (T_{L50}) for this size of cobia. However, for larger cobia no mortality occurred during the PUA recovery period indicating that 34°C is below the T_{L50} for juvenile cobia. The high thermal tolerance of cobia juveniles was in agreement with the finding of our previous study that no mortality of cobia (3.8 ± 0.4 g/individual) was observed at 34°C (Nguyen et al., 2019). In this study, cobia larvae showed mortality at a water temperature that has been considered optimal for the growth of cobia juveniles (Sun & Chen, 2014), suggesting that cobia larvae may be more vulnerable to MHW than the later stages. This finding has an important implication for the rearing protocols for cobia larvae in commercial hatcheries. Lethal effects of heatwaves

TABLE 1 The result of general linear models testing for the effects of the marine heatwave (MHW) and delayed effects of PUA on the body protein, lipid, ash and moisture of cobia fingerling *Rachycentron canadum* during the PUA recovery period. *df*1 and *df*2 are the degrees of freedom for the numerator (*df*1) and for the denominator (*df*2) of the *F* test (*F*)

Effects	Protein			Lipid			Ash			Moisture		
	<i>df</i> 1, <i>df</i> 2	<i>F</i>	<i>p</i>	<i>df</i> 1, <i>df</i> 2	<i>F</i>	<i>p</i>	<i>df</i> 1, <i>df</i> 2	<i>F</i>	<i>p</i>	<i>df</i> 1, <i>df</i> 2	<i>F</i>	<i>p</i>
MHW	1, 15	53.71	<.001	1, 15	41.72	<.001	1, 15	87.45	<.001	1, 15	88.16	<.001
PUA	1, 15	6.71	.020	1, 15	0.19	.67	1, 15	0.030	.86	1, 15	0.25	.63
MHW × PUA	1, 15	7.94	.013	1, 15	0.83	.38	1, 15	0.023	.88	1, 15	0.0029	.96

Note: Significant *p* Values (*p* < .05) are indicated in bold.

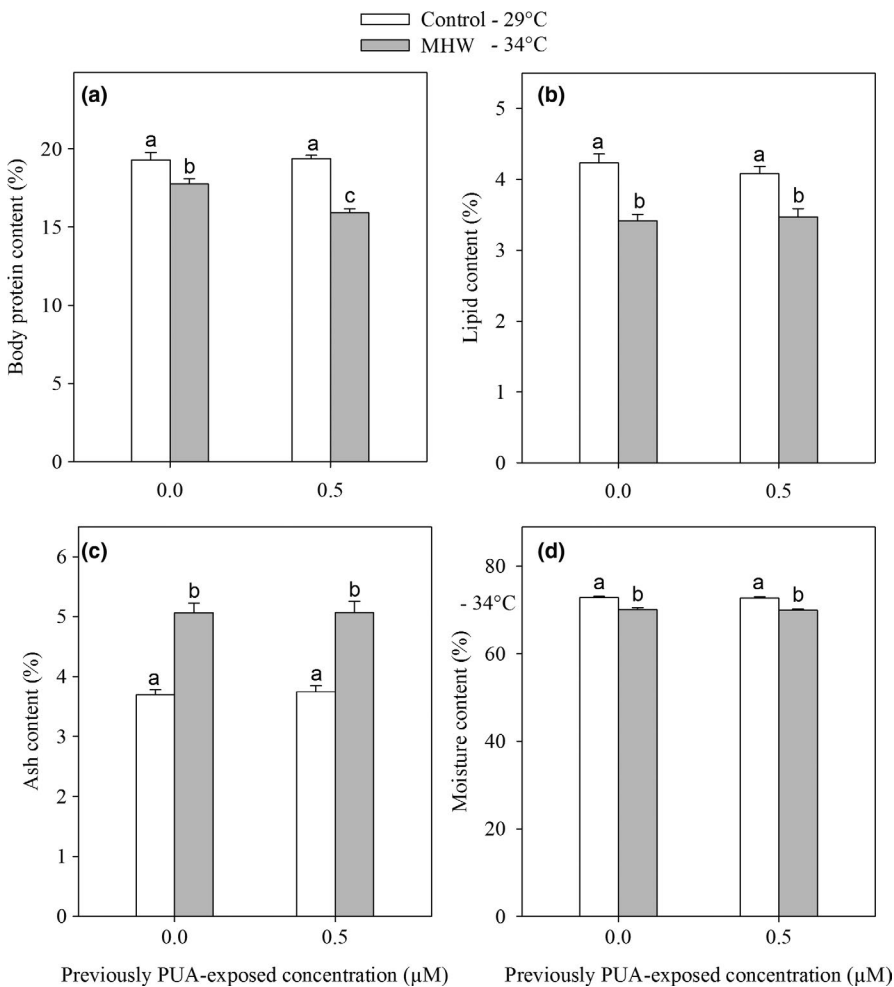


FIGURE 5 Effects of a marine heatwave (MHW) and delayed effects of PUA on the body protein (a), lipid (b), ash (c) and moisture (d) of cobia juveniles (*Rachycentron canadum*). Data are means + 1 SE. Statistical differences (*p* < .05) are indicated in small letters above the bars

on aquatic species have been observed in previous studies (Dinh et al., 2016; Garrabou et al., 2009; Mislán & Wethey, 2015). Extreme temperature-induced mortality has been explained by physiological impairments (Dinh et al., 2016; Garrabou et al., 2009; Harada, Healy, & Burton, 2019; Mislán & Wethey, 2015). Specifically, respiration may be depressed (Dinh et al., 2016), thereby oxygen demand at higher temperatures may not be met due to the inefficiency of the oxygen delivery (Pörtner, Bock, & Mark, 2017; Pörtner & Farrell, 2008). Furthermore, extreme temperatures may result in a reduction or collapse of ATP synthesis (Harada et al., 2019). The capacity of ATP synthesis under extreme temperatures shows a positive correlation to thermal tolerance (Harada et al., 2019). A depression of heat

shock protein syntheses may reduce the ability to deal with extreme temperatures (Dinh et al., 2016). Finally, extreme temperatures may cause membrane and protein structure instability (Somero, 1995).

In line with previous findings (e.g. Caldwell, Lewis, Olive, & Bentley, 2005; Dhanker et al., 2015), exposure to PUA strongly reduced survival. It has been shown that survival of polychaetes (*Arenicola marina* and *Nereis virens*), echinoderms (*Asterias rubens* and *Psammochinus miliaris*) was reduced when exposed to PUA concentrations of 6.5 and 32.8 nM and 65.7 and 656.9 nM respectively (Caldwell et al., 2005). PUA can induce apoptosis in copepods and sea urchins (Romano, Russo, Buttino, Ianora, & Miralto, 2003). More generally, toxic diatoms such as *Skeletonema costatum*, *Thalassiosira aestivalis*, *T. rotula* and

Chaetoceros wighami have been known to cause respiratory distress, severe necrosis of gills, livers and guts of farmed Atlantic salmon (*Salmo salar*) (Kent, Whyte, & Latrace, 1995; Treasurer, Hannah, & Cox, 2003).

There is mixed evidence of the effects of the diatom toxins on the feeding rate of marine species. The toxic effect of diatoms may reduce appetite of fish, hence reduced feeding rate (Treasurer et al., 2003). The bloom of *Chaetoceros wighami* caused 20%–90% reduction in feed intake of Atlantic salmon (Treasurer et al., 2003). Another study showed a reverse pattern that PUA exposure resulted in a higher ingestion rate in copepod *Temora stylifera* (Ka et al., 2014). Ka et al. (2014) suggested that PUAs may be a food-finding cue or feeding stimulant for some planktonic copepods. In our study, the effect of PUA on the feeding of cobia larvae was unclear. Specifically, there was a weak indication that PUA-exposed cobia had a higher feeding rate than those in the control (Figure 3a,b). Potentially, any reduction in appetite was no longer present when fish larvae were transferred to the clean water for the feeding trial. While we do not exclude the possibility that PUAs may also be a signal for cobia larvae to find their planktonic copepod prey, the higher feeding rate of cobia in some specific conditions of PUA, temperature and feeding time combinations may be a random factor as it was inconsistent and highly variable among treatments without any clear trend.

An important finding is that the mortality of cobia increased by 16% in both MHW as well as PUA, and increased to 60% in the presence of both MHW and PUA. It is well known that the mortality of a range of aquatic species was substantially higher when they were exposed to contaminants such as metals (Dinh et al., 2013; Sokolova & Lannig, 2008) and pesticides (Dinh et al., 2014a; Dinh, Janssens, Debecker, & Stoks, 2014b) under elevated temperature, but the interaction of algal toxins with temperature is poorly documented. The mechanisms for the increasing toxicity of PUA under elevated temperatures are not known due to the complex mode of actions of this toxin (Ka et al., 2014; Michalec et al., 2013) and need further investigations. Irrespective of the mechanisms, our result suggests that the larval and juvenile production of cobia, important marine aquaculture species, may face great challenge under ongoing climate change with increasing frequency, severity and duration of MHWs and it furthermore induces the outbreak of algal blooming (Brown et al., 2020; Dam, 2013; Gobler et al., 2017), exaggerating the negative effects on marine aquaculture species.

4.2 | The recovery period

There was no effect of MHW on the survival of cobia juveniles, but the specific growth rate was lower at 34°C. This result is in contrast to the previous observations of a higher growth rate of cobia juvenile reared at 32°C compared to 27°C (Bignami, Sponaugle, Hauff, & Cowen, 2017; Sun & Chen, 2014), but in agreement with the result of our recent study (Nguyen et al., 2019). A lower growth rate of tropical fish under MHW has been observed before in coral fish (Donelson, Munday, McCormick, Pankhurst, & Pankhurst, 2010). While the food conversion efficiency of cobia did not differ between

27 and 33°C (Sun & Chen, 2014), cobia larvae had a lower feeding rate in MHW treatment. Additionally, cobia juveniles may have to invest more energy on costly physiological responses such as the up-regulation of heat shock proteins, a general physiological mechanism of organisms to cope with thermal stress (Hofmann, 1999; Sørensen, Kristensen, & Loeschcke, 2003) and an upregulation of heat shock proteins has been observed previously in other fish species such as in medaka *Oryzias melastigma* (Li, Leung, Bao, Lui, & Leung, 2015).

We observed a strong effect of MHW on the proximate biochemical composition of fish larvae. Indeed, the body protein and lipid contents were lower in fish reared in MHW while ash increased. These results were in agreement with the findings of Sun and Chen (2014). Surprisingly, while PUA caused strong mortality during the exposure period, the negative effects of PUA and its interactions with MHW were no longer present during the recovery period. We tentatively suggest that the acute and lethal effects of PUA on cobia larvae occur rapidly and also disappear rapidly.

4.3 | Implications and perspectives

The lethal and sublethal effects of MHW on cobia larvae and juveniles suggest that ambient conditions in areas with commercial aquaculture in tropical countries may often not be optimal for cobia and marine fish production. Indeed, temperatures >34°C often occur in the coastal aquaculture ponds (Doan et al., 2018) where cobia larvae and juveniles are reared. Such extreme temperatures are projected to occur more often in the near future as the result of the ongoing global warming (Frölicher et al., 2018; IPCC, 2013; Meehl & Tebaldi, 2004; Oliver et al., 2018). These results support the prediction that global fish production may decline in tropical regions (Brander, 2007), especially in the Southeast Asian countries where more than 30% of aquaculture areas are predicted to become unsuitable for production by 2050–2070 (Froehlich, Gentry, & Halpern, 2018). The aquaculture production of Southeast Asian countries is predicted to reduce 10%–20% by 2050–2070 due to climate change (Froehlich et al., 2018). Furthermore, the impacts of harmful algal blooms on aquaculture may amount to approximately \$8 billion per year, globally (Brown et al., 2020) that may further challenge the aquaculture production and food security (Brown et al., 2020; Quang et al., 2016). Negative effects of MHWs and harmful algal blooms on aquaculture species have been observed in a range of taxa such as copepods (Doan et al., 2018, 2019), shrimps, fish and shellfish (Brown et al., 2020). Our results add to this by showing that the production of cobia, one of the keys aquaculture species (Estrada et al., 2016; Klinger et al., 2017; Liao et al., 2004; Nhu et al., 2011) may be highly vulnerable to both MHWs and diatom toxins. Furthermore, this is also the first laboratory study showing that MHWs and harmful algal blooms may interact synergistically to increase the lethal effects on fish at the larval stage. Altogether, aquaculture production in tropical countries in Southeast Asia may face great challenges under the increasing frequency and severity of MHWs

and harmful algal blooms that may threaten the local and global food security (Brown et al., 2020; FAO, 2018).

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CONFLICT OF INTEREST

Authors declare no conflict of interest exists.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are deposited on the server of Nha Trang University. Data are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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