

## Critical Thermal Maximum, Temperature Acclimation and Climate Effects on Thai Freshwater Fishes

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### Abstract

Critical thermal maximum (CT<sub>max</sub>) related positively with acclimation temperature between 20.0°C and a maximum that varied with the four species; *Devario acrostomus*, *Mystacoleucus chilopectus*, *Barbodes binotatus* and *Rasbora caudimaculata*, between 30.0 and 35.0°C. Highest and lowest CT<sub>max</sub> were 39.0±1.0°C at 35.0°C acclimation for *B. binotatus* and 34.6±0.5°C at 20.0°C for *D. acrostomus*, respectively. Thermal scope at 25.0°C acclimation was lowest at 26.8°C for *D. acrostomus* and, higher at 29.6, 29.7 and 30.1°C for *M. chilopectus*, *R. caudimaculata* and *B. binotatus*, respectively. Interestingly, the majority of tropical Thai fish and temperate species examined to date showed a similar maximum thermal tolerance from the mid to high 30s that almost certainly relates to temperature induction of HSP and their production. Global temperature increases predicted for Thai rivers and others in Southeast Asia during the latter portion of the current century are likely to exceed the thermal tolerance of many indigenous fishes with important losses in species diversity.

**Keywords:** critical thermal maximum; thermal tolerance; thermal scope; climate change

### 1. Introduction

Fish are confined largely to habitats with specific environmental signatures, which temperature is one of the important factors (Winterhalder, 1980; Kitano, 2002; Penczak, 2015). The concept of adaptation has wide application in understanding fish distribution and refers to the development of physiological, behavioral or genetic characteristics that enable organisms to cope with environmental conditions and changes (Wood and McDonald, 2008; Nithirojapakdee *et al.*, 2014). Acclimation, a component of adaptation is a short-term reversibly physiological extension to some environmental changes such as temperature and depends to a considerable extent on previous experience (Brett, 1970; Fry, 1971).

Determination of maximum or minimum temperature that fish can tolerate is without a single methodological standard but three experimental approaches are in general use (Beitinger *et al.*, 2000); incipient lethal temperature (Fry, 1947), critical temperature (Huntsman and Sparks, 1924; Sumner and Doudoroff, 1938; Cowles and Bogert, 1944; Becker and Genoway, 1979) and chronic temperature (Hickman and Dewey, 1973). Critical and chronic temperatures differ in their respective endpoints, lethal and sub-lethal and in the magnitude and time period between changes in temperature.

Acute lethal temperatures impose their effects at low and high temperatures and are generally determined by either of two procedures. Critical thermal maximum (CT<sub>max</sub>) and minimum (CT<sub>min</sub>) following acclimation to a specified temperature are determined by heating or cooling water at a rate that continues to a defined end point such as a loss in equilibrium or respiratory movement that approximates an eminent death. Rate of temperature change can influence CT<sub>max</sub> but the pattern among species has not been shown to follow a consistent pattern (e.g. Cox, 1974; Cheetham *et al.*, 1976; Bennett *et al.*, 1998; Currie *et al.*, 1998). The second common procedure, incipient upper or lower lethal temperatures, exposes fish to an abrupt change in a static temperature, upward or downward from acclimation that is continued until death occurs (Brett, 1944; Fry, 1947; Hart, 1952).

Fishes found between latitudes of 23° 26' N (Tropic of Cancer) and 23° 26' S (Tropic of Capricorn) are known as tropical fishes, and those that occur at higher latitudes to 60° as temperate fishes. Freshwater fishes are numerous in tropical Thailand with over 600 species described (Smith, 1945; Vidthayanon *et al.*, 1997) and perhaps as many as 1100 or 1200 including those yet to be described (Khachonpisitsak, 2012). Global ambient temperatures are increasing (IPCC, 2014) and, in Thailand, daily maxima occasionally reach >38°C during the typically warm

month of April (Manton *et al.*, 2001; Sharma and Babel, 2014). Such high temperatures are at or above lethal temperatures recorded for most temperate freshwater fishes (Beitinger *et al.*, 2000). Recent measurements of CTmax for a number of Thai freshwater fishes acclimated to 25.0°C indicated current seasonal maximal temperatures in some rivers to be close to their respective critical thermal maxima. The potential of further global temperature increases with being dependent on subsequent anthropogenic activities is certain to further endanger fish habitats in Thailand. Beaufort (1951) suggests fishes from relatively stable environments such as the tropics may be deficient in thermal adaptations for broad temperature ranges and quite sensitive to changes in environmental temperature outside those seasonally encountered. The present study was undertaken to provide additional perspective on the potential influence of temperature acclimation on critical thermal maxima and, to a limited extent, minima of Thai fishes and relative to predicted regional temperature increases attributable to global warming (IPCC, 2014).

## 2. Materials and Methods

Fish were collected by electro-fishing (Smith Root, Model LR 24, USA) in riffle areas of small rivers (23.0-25.0°C) in western Thailand, Kanchanaburi Province (24.9±1.5°C). Electro-shocker capture settings were: output, 300 volts; wave width, 25 Hz, pulse width, and frequency, 100 ms. Settings were made, based on experience, to avoid damage to fish. Previous studies using the same capture technique failed to exhibit any deleterious effects from electro-fishing on fishes returned to the laboratory and held in aquaria over periods of up to two years (Beamish *et al.*, 2005). Species selected for this study are typical of the fish fauna found in river riffle habitats in western Thailand and consisted of *Barbodes binotatus*, *Devario acrostomus*, *Mystacoleucus chilopterus* and *Rasbora caudimaculata*.

Fish were transferred to our laboratory (25.0°C) in insulated tanks within a few hours of capture and held in circular tanks (200 L) containing strongly aerated water (dissolved oxygen >75% of air saturation). Water was changed once daily and dissolved oxygen, total ammonia and pH measured twice daily. Food was withheld for two days after fish were placed in holding tanks. Once fish fed well on dry commercial fish food they were transferred to pre-experimental tanks (25.0°C, 15L) and thermal acclimation to an experimental temperature was begun. Tanks were vigorously aerated and temperature controlled to ±0.1°C. Each species was represented by 10 individuals of similar weight in each of two replicate tanks. In all tanks throughout the study

dissolved oxygen was >75% of air saturation; total ammonia, <0.001 mg NH<sub>3</sub> L<sup>-1</sup> and pH 7.5±0.2.

Temperature was increased 1.0°C day<sup>-1</sup> upwards for acclimation temperatures >25.0°C or 1.0°C 2 days<sup>-1</sup> downward for acclimation temperatures <25.0°C in accord with the traditional protocol (Fry, 1947). Fish were fed to satiation for 10 minutes twice daily throughout each acclimation procedure in the pre-experimental tanks.

After reaching the target acclimation temperature, fish were held initially for one of three additional time periods that were examined from the perspective of stability. Fry (1947) considered acclimation complete when a pre-set response was stable; for the present study CTmax was applied as the criteria for stability. A change in tank temperature of 1.0 or 2.0°C required approximately 10-12 minutes to complete. In our first study, conducted at 25.0°C, we measured stability of CTmax following thermal acclimation to 25.0°C and one of 4, 10 or 20 additional days during which fish were fed to satiation twice daily. Following each additional time period fish were moved to experimental tanks and, subsequently CTmax was measured. The shortest time period that provided a stable CTmax was applied in further studies.

CTmax was measured for the four species in a second study in relation to acclimation temperatures of 20.0, 22.5, 25.0, 27.5, 30.0, 32.5 and 35.0°C. This range was within 3.0°C of seasonal ambient minima and maxima temperatures in the species' natal rivers. Once an acclimation temperature was reached fish were held at that temperature for an additional time period (four days) based on our initial study (above). CTmin was measured at 25.0°C acclimation for the four species. Thermal scope was measured at 25.0°C acclimation as the difference between CTmax and CTmin. Again, fish were fed to satiation for 10 minutes twice daily throughout each acclimation procedure in the pre-experimental tanks.

CTmax and CTmin were taken as the respective calculated highest and lowest temperatures fish tolerated for 1 hour following increases or decreases of 1.0°C h<sup>-1</sup> above or below their acclimation temperature. The experimental end point was the cessation of respiratory movements as applied earlier by Sumner and Doudoroff (1938). Fish were deprived of food for 24 hours following the final feeding on the fourth day in the pre-experimental acclimation tank. Thereafter fish were transferred to an experimental tank (15 L) at their acclimation temperature and food withheld for an additional 12 hours. An earlier study found the total of 36 hours of food deprivation was sufficient for complete gastric evacuation, minimizing metabolic stress.

CTmax measurements began by increasing temperature 1.0°C above acclimation which was held for 1 hour. Stepwise hourly increases of 1.0°C were continued until individual fish sequentially exhibited a visible absence of opercular movements when death was assumed. It is noted that this endpoint may not always represent fish death (Sumner and Doudoroff, 1938), but a qualitative assessment in the present study suggested it did for the majority of fish and it is less subjective than behavioral irregularities sometimes applied in these studies (Beitinger *et al.*, 2000). CTmin measurements began by decreasing temperature 1.0°C from the 25.0°C acclimation temperature. Stepwise hourly decreases of 1.0°C were continued until the absence of opercular movements. For both CTmax and CTmin measurements, when opercular movements ceased fish were removed, blotted on tissue to remove excess water and weighed (0.01 g). CTmax was calculated as the highest temperature at which an individual survived for a full hour plus the time fraction of the unit temperature during which opercular movements ceased. Chemical measurements were made in each tank at the beginning and end of each experiment; dissolved oxygen with a calibrated probe ( $\pm 0.01$  mg O<sub>2</sub> L<sup>-1</sup>; Hanna, models HI9147), pH ( $\pm 0.1$  units; Hanna, models HI98127) and total ammonia ( $\pm 0.01$  mg NH<sub>3</sub> L<sup>-1</sup>; Merck-NOVA 60 model).

Paired replications of CTmax measurements at each acclimation temperature for each species were tested for differences by *t*-test;  $p < 0.05$ . Comparison of CTmax measurements for each species following additional periods of 4, 10 and 20 days at 25.0°C was tested by ANOVA with LSD multiple comparisons. The relationship between CTmax and acclimation temperature for each of the four species was examined by linear regression analysis with significance accepted at  $p < 0.05$ .

### 3. Results and Discussion

CTmax values and fish body weights in paired replicate tanks at 25.0°C for time periods of 4, 10 or 20 days did not differ significantly and were combined. CTmax values for each species did not differ significantly with 4, 10 or 20 additional days in the pre-experimental acclimation tanks providing support for the acclimation procedure applied in this study (Table 1).

All species acclimated to temperatures between 20.0 and 30.0°C fed quite well during each 4-day interval preceding the measurement of CTmax (Table 2). *D. acrostomus*, *R. caudimaculata* and *B. binotatus* were similar in body weight and less than that for *M. chiloferus*. Body weight and CTmax values for each species did not differ significantly between replicate tanks at each acclimation temperature and were combined for CTmax calculation. CTmax and food consumption in the preexperimental tanks, the latter arithmetically adjusted to a weight of 1 g body weight, increased between 20.0 and 30.0°C. Food consumption at the lowest acclimation temperature, 20.0°C, was highest for *D. acrostomus*, at 1.6% body weight of fish/day and, for the other species, similar at approximately 0.7% body weight of fish/day. With 2.5°C increments in temperature food consumption increased for all species. Increases did not exhibit an obvious pattern but daily averages were higher at approximately 33% for *M. chiloferus* and *R. caudimaculata* and about 12% for each of *D. acrostomus* and *B. binotatus*. Food intake by *B. binotatus* continued to increase to 32.5°C. *D. acrostomus* did not feed above 30.0°C and all remaining fish in both acclimation tanks died within 24 hours at 31.0°C. *R. caudimaculata* reduced their food intake at 32.5°C and did not feed at 35.0°C. CTmax for *M. chiloferus* acclimated to 32.5°C was

Table 1. CTmax for fish acclimated to 25.0°C for extended time periods. Values for CTmax and body weight are means  $\pm$ SD for 20 fish.

Species	N	Extended time (days)	Body weight (g)	CTmax (°C)
<i>D. acrostomus</i>	20	4	2.3 $\pm$ 0.3	35.8 $\pm$ 0.7
	20	10	2.1 $\pm$ 0.5	35.8 $\pm$ 0.3
	20	20	2.2 $\pm$ 0.5	35.8 $\pm$ 0.5
<i>R. caudimaculata</i>	20	4	2.0 $\pm$ 1.3	37.5 $\pm$ 0.4
	20	10	1.7 $\pm$ 1.3	37.5 $\pm$ 0.3
	20	20	1.4 $\pm$ 1.1	37.5 $\pm$ 0.5
<i>M. chiloferus</i>	20	4	9.7 $\pm$ 1.3	38.1 $\pm$ 0.6
	20	10	9.2 $\pm$ 1.2	38.3 $\pm$ 0.5
	20	20	8.5 $\pm$ 1.1	38.0 $\pm$ 0.6
<i>B. binotatus</i>	20	4	4.3 $\pm$ 1.7	38.6 $\pm$ 0.7
	20	10	2.1 $\pm$ 0.5	38.6 $\pm$ 0.3
	20	20	2.2 $\pm$ 0.5	38.5 $\pm$ 0.5

higher than those at lower temperatures but food consumption fell below measurable quantities at 32.5°C. All remaining *M. chilopterus* in both acclimation tanks died within 6 h at 33.0°C. Increases in CTmax for *B. binotatus* and *R. caudimaculata* continued at 32.5 and 35.0°C. Highest and lowest measured CTmax values among the four species were found for *B. binotatus*, 39.0±1.0°C at 35.0°C and for *D. acrostomus*, 34.6±0.5°C at 20.0°C acclimation (Table 2).

The relationship between CTmax values and acclimation temperature is described for each species by a statistically significant linear regression:

*D. acrostomus* (20.0-30.0°C):  
 $CT_{max} = 29.280 + 0.264 At$ , (df 1, 4;  $F = 26.561$ ,  $p < 0.05$ ,  $R^2 = 0.891$ )  
*R. caudimaculata* (20.0-35.0°C):  
 $CT_{max} = 35.275 + 0.087 At$ , (df 1, 6;  $F = 63.068$ ,  $p < 0.05$ ,  $R^2 = 0.927$ )  
*M. chilopterus* (20.0-32.5°C):  
 $CT_{max} = 32.353 + 0.207 At$ , (df 1, 5;  $F = 30.781$ ;  $p < 0.05$ ;  $R^2 = 0.885$ )  
*B. binotatus* (20.0-35.0°C):  
 $CT_{max} = 37.204 + 0.053 At$ , (df 1, 6;  $F = 50.704$ ;  $p < 0.05$ ;  $R^2 = 0.910$ )

Table 2. Relationship between acclimation temperature and mean measured CTmax for four fishes. N represents the number of fish in pooled replicate samples. Mean body weight and mean daily food consumption (4 days) as mg of food consumed were arithmetically adjusted to a fish weight of 1 g.

Species	Acclimation temperature (°C)	N	Mean body weight, g (SD)	Mean daily food consumption (mg/g fish/day±SD)	Mean CTmax (°C±SD)
<i>D. acrostomus</i>	20.0	20	2.8±1.4	15.7±2.4	34.6±0.5
	22.5	20	2.8±1.1	16.7±1.8	35.4±0.3
	25.0	20	2.0±1.3	18.8±1.0	35.8±0.2
	27.5	20	3.8±1.7	19.6±4.9	36.0±0.2
	30.0	20	4.9±2.3	23.5±1.6	37.6±0.1
<i>R. caudimaculata</i>	20.0	20	2.0±1.4	7.1±2.0	37.0±0.6
	22.5	20	1.3±1.1	7.3±2.7	37.2±0.2
	25.0	20	1.9±1.3	15.2±2.5	37.3±0.2
	27.5	20	1.9±1.3	16.2±4.1	38.0±0.1
	30.0	20	2.0±1.3	18.4±6.5	38.0±0.1
	32.5	20	1.9±1.3	10.1±3.3	38.1±0.2
	35.0	20	1.1±1.3		38.2±0.2
<i>M. chilopterus</i>	20.0	20	10.1±1.1	3.7±1.7	36.3±0.7
	22.5	20	9.4±1.5	4.6±1.9	36.7±0.7
	25.0	20	8.2±1.2	5.8±1.0	38.1±0.3
	27.5	20	9.5±1.5	10.0±1.6	38.3±0.5
	30.0	20	12.1±1.	11.1±3.7	38.5±0.4
	32.5	20	9.7±1.3		38.8±0.1
<i>B. binotatus</i>	20.0	20	2.2±1.4	8.4±2.9	38.1±0.3
	22.5	20	2.4±1.6	8.8±2.4	38.5±0.2
	25.0	20	1.3±1.2	11.2±7.0	38.6±0.1
	27.5	20	2.5±1.2	12.6±3.6	38.7±0.1
	30.0	20	2.5±1.3	14.2±4.4	38.8±1.4
	32.5	20	2.2±1.2	17.7±4.1	38.9±0.1
	35.0	20	2.5±1.4		39.0±1.0

SD refers to standard deviation.

where: At represents acclimation temperature and acclimation temperature range is in parentheses.

Thus, with an increase in acclimation temperature from 20.0 to 30.0°C, measured and calculated CTmax values increased for *D. acrostomus*, *R. caudimaculata*, *M. chiloferus* and *B. binotatus* by 3.0°C (2.64°C), 1.0°C (0.87°C), 2.2°C (2.07°C) and 0.9°C (0.53°C), respectively. Over the full acclimation range (20.0-35.0°C) measured and calculated increases in CTmax for *R. caudimaculata* and *B. binotatus* were 1.2°C (0.2°C) and 0.7°C (0.1°C), respectively.

CTmin at 25.0°C acclimation varied among the four species from 7.6°C (*R. caudimaculata*) to 9.0°C (*D. acrostomus*; Table 3). CTmax and CTmin and their respective body weights did not differ significantly between replicate tanks for any of the species and their values were pooled. Thermal scopes at 25.0°C differed significantly among species ( $p < 0.05$ ; Table 3). Thermal scope for *D. acrostomus* was lowest at 26.8°C while those for *M. chiloferus*, *R. caudimaculata* and *B. binotatus* were slightly higher at 29.6°C, 29.7°C and 30.1°C, respectively.

Freshwater fishes have established a wide range of habitats in which ambient temperatures vary temporally from near zero to >40.0°C. Implicit by the terms ‘tropical’ and ‘temperate’ fishes is that the former occur in warmer water than the latter and some sense that this relates to physiological differences in heat tolerance. Many, if not most temperate species commonly experience seasonal ambient temperatures that range from 0 to >30.0°C whereas the general range for Thai tropical fishes is less at a few degrees below 20.0 to a few above 30.0°C. Temperatures of most rivers are comparatively homothermous at least within modest reaches and periods of time but, both temperate and tropical rivers undergo diel and seasonal variations with those for the former generally the greater. Tropical fish hobbyists are instinctively aware that tropical species seldom survive in winter when introduced accidentally or intentionally into temperate rivers. Temperate species are likely better

suitable to survive tropical temperatures but unlikely to withstand ecological pressures from their indigenous competitors. Interestingly, the majority of tropical and temperate species examined to date show a similar maximum thermal tolerance from the mid to high 30s with only a few species exceeding 40.0°C (Beitinger et al., 2000; Prodocimo and Freire, 2001; Chatterjee et al., 2004; Dalvi et al., 2009). CTmax values for South American and the Southeast Asian species in the present study, while similar, are mostly slightly lower for the latter species at the same acclimation temperatures (Rantin and Petersen, 1985; Barrionuevo and Fernandes, 1995; Prodocimo and Freire, 2001; López-Olmeda and Sánchez-Vázquez, 2011; Das et al., 2005; Brahmane et al., 2014). This difference, however, may simply reflect a lower rate of temperature increase in the determination of CTmax for Southeast Asian fishes rather than physiological or other differences under similar experimental conditions (e.g. Rantin and Petersen, 1985; Barrionuevo and Fernandes, 1995; Prodocimo and Freire, 2001). Clearly temperate species have greater tolerance of cold temperatures than tropical species that has been corroborated by lower CTmin values at comparable acclimation temperatures (Rantin and Petersen, 1985; Barrionuevo and Fernandes, 1995; Beitinger et al., 2000; Brahmane et al., 2014). There is, however, a large variation in the full range of ambient temperatures tolerated by fishes. Temperate species tend to occur within a wider range of temperatures than tropical species but there are notable exceptions. Thus, salmonids occur mostly within a more narrow range of temperatures than many other temperate species, being found mostly in habitats where temperatures range from near zero to the low 20s°C with CTmax values in the high 20s (McLeay et al., 1983; Elliott and Elliott, 1995; Currie et al., 1998). Some species of the subtropical *Cyprinodon* genus occur where ambient temperatures are mostly between 15.0 and 35.0°C with CTmax values between 40.0 and 45.0°C (Feldmeth et al., 1974; Bennett et al., 1997).

Table 3. Mean measured CTmax and CTmin values following 25.0°C acclimation. Thermal scope represents the difference between CTmax and CTmin. Body weights are means. Sample size was 20 fish for each of CTmax and CTmin.

Species	Body weight g (±SD)	CTmax (°C±SD)	Body weight g(±SD)	CTmin (°C±SD)	Thermal scope (°C)
<i>D. acrostomus</i>	2.0±1.4	35.8±0.2	1.8±1.2	9.0±0.4	26.8
<i>R. caudimaculata</i>	1.9±1.3	37.3±0.2	1.7±1.3	7.6±0.2	29.7
<i>M. chiloferus</i>	8.2±1.2	38.1±0.3	9.2±1.2	8.5±0.3	29.6
<i>B. binotatus</i>	1.3±1.2	38.6±0.1	1.9±0.4	8.5±0.2	30.1

SD represents standard deviation.

Few fishes, temperate or tropical are able to survive for long at temperatures at or above 40.0°C (Beitinger *et al.*, 2000). Most species, temperate and tropical, exhibit CTmax in the range of 34.0 to 38.0°C. Generally food intake by ectothermic fishes, temperate and tropical increases with temperature to a maximum but declines with further temperature increases reflecting declines in physiological function and, likely, swimming performance (LeBreton and Beamish, 2004). In the present study food intake tended to decline above 30.0°C to suggest that while these species may not die in the short term at or above these temperatures it is likely a sustainable and vigorous life would be difficult. Generally tropical species appear intolerant of temperatures much below 8.0°C (Rantin and Petersen, 1985; Barrionuevo and Fernandes, 1995; Brahmane *et al.*, 2014). In central Thailand seasonally low river temperatures commonly fluctuate from 17.0 to 20.0°C, certainly well above the minima of many if not most temperate rivers. Relatively few CTmin have been measured for tropical species but those for which information is available indicate a range from about 6.0 to 15.0°C depending on acclimation temperature (Rantin and Petersen, 1985; Barrionuevo and Fernandes, 1995; Prodocimo and Freire, 2001; López-Olmeda and Sánchez-Vázquez, 2011; Brahmane *et al.*, 2014). These contrast from CTmin for temperate species that range mostly from 0 to <10.0°C, again dependent on acclimation temperature (Becker *et al.*, 1977; Hockett and Mundahl, 1988; Currie *et al.*, 1998).

The concept of temperature adaptation and acclimation has wide application in regards habitat (Holling, 2001; Folke, 2006) and broadly refers to the long and short-term development of physiological, behavioral or genetic characteristics that enable an organism to cope with environmental change thereby facilitating survival and reproduction. A family of genetically conservative proteins called 'heat-shock proteins' (HSP) in fish and other animals serve as protective adaptations against temperature and, importantly temperature change (Healy and Schulte, 2012; Tomanek, 2010; Schulte, 2014). Temperature necessary to induce HSP synthesis varies among species (Lindquist and Craig, 1988; Fangue *et al.*, 2011; Sørensen *et al.*, 2003). Measured HSPs in tropical and temperate species as well as the broad similarity in CTmax values suggests both groups of fishes probably depend to varying degrees on physiological support from HSPs or analogous substances for temperature protection (Fader *et al.*, 1994; Norris and Hightower, 2000).

Temperature acclimation provided considerably greater benefits to thermal tolerance for species in the present study at low acclimation temperatures. The

upper thermal scope of Thai fishes in the present study as the difference between CTmax and acclimation temperature, varied inversely with the latter, in accord with the pattern found for other species of freshwater fishes (Beitinger *et al.*, 2000). Thus at the lowest acclimation temperature in the present study, 20.0°C, CTmax for the four species was higher by 14.6 to 18.1°C but only 7.6 to 8.8°C higher at 30.0°C. The tolerance pattern for the species in this study was similar to that for temperate species but with values for temperate species about twice that for tropical freshwater fishes at the same acclimation temperature. The induction temperature for the HSP response appears not fixed among species (Lund *et al.*, 2006; López-Olmeda and Sánchez-Vázquez, 2011). HSP production increases directly with temperature and season (Fader *et al.*, 1994), an apparent adaptation for protection against increases in metabolism and cellular proteins induced by high temperatures. Presumably the relative decline in CTmax at high acclimation is a reflection of physiological constraints on HSP production capacity.

Less information is available on the protective mechanisms of either temperate or tropical fishes in cold water, however, some studies on temperate and the tropical *Channa striatus*, have found an increase, although smaller, in one HSP (HSP70) when exposed to cold water (Hallare *et al.*, 2005; Eid *et al.*, 2016). The higher CTmin for tropical species might suggest HSP have not developed or are unable to activate an analogous complement of HSPs capable of providing physiological support in cold water thus accounting for the higher CTmin values (Airaksinen *et al.*, 2003; Hallare *et al.*, 2005; Eid *et al.*, 2016). Eid *et al.* (2016) suggest that survival of tropical *C. striatus* in cold water supports ongoing natural selection on the HSP70 gene.

The climate change report (IPCC, 2014) predicts changes in global temperatures as well as in precipitation and storms, the extent based on anthropogenic emission models for various levels of economic and industrial activity. Models predict that during the latter part of the present century surface temperatures will increase approximately 3.0 to 5.0°C relative to current temperatures in Southeast Asia. They suggest also that in low latitude tropical wet regions heat waves and extreme precipitation events will become more intense and last longer. The potential of such temperature increases acting in concert with other stressors such as habitat modifications, fish behavior, overexploitation of fish and invasions by non indigenous fishes are certain to impact freshwater fishes (Freitas *et al.*, 2016). Earlier studies in Thailand have demonstrated clear

and significant associations between ambient temperature and distribution of fishes in rivers where minimum and maximum of water temperature commonly range from 17.3 to 32.6°C (Tongnunui and Beamish, 2009; Tongnunui et al., 2016; Suvarnaraksha et al., 2012; Beamish and Plongsesthee, 2015). Ambient river temperatures are rising. Maximum monthly water temperatures of >38.0°C have already been recorded in some Thai rivers (Thailand Meteorological Department, 1994; Sharma and Babel, 2014). These are equal to or exceed the CTmax values found in this study for *D. acrostomus* and *R. caudimaculata* and within a degree of those for *M. chilopterus* and *B. binotatus*. Further increases are predicted so that at a minimum, fish distributions will undergo major changes. More likely, without stringent efforts to reduce global greenhouse gas emissions, temperature increases in Thai rivers (Sarajit et al., 2015) and, indeed in all of Southeast Asia (Giang et al., 2014; Limsakul et al., 2014) will rise beyond the adaptive behavioral or physiological capacity and thermal tolerance of many fishes. This, in concert with habitat modifications, is likely to impose severe losses in species diversity, abundance and, indeed on entire ecosystems.

#### 4. Conclusions

CTmax was positively related to acclimation temperature for four freshwater fishes from tropical rivers of Thailand. CTmax values varied among species and acclimation temperature from 34.6 to 39.0°C. Maximum monthly water temperatures of >38.0°C have already been recorded in some Thai rivers (Thailand Meteorological Department, 1994; Sharma and Babel, 2014). Global climate models predict further increases in ambient river temperatures, the extent dependent on economic and industrial activities. This research highlights the potential of severe disturbance to riverine fish communities in Thai rivers including temporal losses in biodiversity and species' extinction.

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