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Temperature physiology in grouper (Epinephelinae: Serranidae) aquaculture: A brief review

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ABSTRACT

Grouper aquaculture has emerged as a promising food production sector on the basis of the belief that it can lessen the pressure on overfished populations, particularly in the Asia–Pacific. This review provides an outline of the temperature physiology of aquacultured groupers in tropical and sub-tropical regions as described in 34 research articles published between 1979 and 2018. A total of 24 grouper species (i.e., 23 *Epinephelus* spp. and 1 *Cromileptes* sp.) and 4 hybrids (*Epinephelus* spp.) were reported to be aquacultured for temperature physiology studies; among these species, five are considered threatened (three are vulnerable species, one is critically endangered, and one is endangered). More than half of the species ($n = 13$, 54 %) were categorized as “Least Concern,” while five species were considered “Data Deficient.” The overall test temperatures applied across the different life stages of the aquacultured groupers ranged from 13 °C to 35 °C, with a mean optimum rearing temperature of 26.32 °C ± 0.62 °C. The majority of the experimental studies demonstrated that a rearing temperature of 28 °C could be optimal for grouper hatcheries in the Asia–Pacific. Although comparative experimental studies on the mean daily growth of groupers showed higher increments in recirculating hatchery tanks compared with those in floating net cages in the tropics, temperature alone may not completely govern the grouper physiology. In-depth research is imperative for precise predictions of the future prospects of sustainable grouper aquaculture, especially in the tropics.

1. Introduction

Groupers (Epinephelinae: Serranidae) are a highly traded seafood commodity in the Asia–Pacific because of their desirable taste (Cheng et al., 2013; Sadovy et al., 2013). Unfortunately, increased fishing pressure on capture fisheries, habitat destruction, and targeting of spawning aggregations have depleted grouper populations in the wild (Sadovy et al., 2013). A study by Shapawi et al. (2018) highlighted the significance of large-scale sustainable grouper aquaculture as a potential solution to mitigate the impacts of biodiversity conservation impacts.

Grouper aquaculture has emerged as a promising food production sector on the basis of the belief that it can lessen the pressure on overfished populations, particularly in the Asia–Pacific (Shapawi et al., 2018). According to the FAO (2020), approximately 200,000 tons of groupers were produced in 2018.

The potential of groupers in sustainable aquaculture and fisheries, experimental trials to understand their environmental resilience and the use of inter–specific hybrids are some of the subjects of intensive research investigations. The effects of temperature and salinity on the physiological characteristics of groupers, including their survival, growth, and digestive enzyme activities, have been extensively studied to optimize their environmental and physical conditions. However, optimal conditions and practical limits have not been established for most grouper species (Rimmer and Glamuzina, 2017).

The impacts of climate change on biodiversity loss have been well documented (Cochrane et al., 2009). While the relevance of climate-resilient species to aquaculture is not immediately apparent, identifying such species is imperative (Shapawi et al., 2018). As is the

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case with many other tropical fishes, groupers are vulnerable to increases in temperature on account of their evolution in a relatively stable thermal environment (Munday et al., 2012). Changes in temperature can alter the physiological traits of these fishes associated with digestion, health, and, ultimately, growth performance (Bendiksen et al., 2002; Shapawi et al., 2018).

Any change in the surrounding environment beyond the threshold of ectothermic organisms, especially tropical species, can negatively affect their biochemical and physiological processes (Fu et al., 2018). Evidence indicates that tropical marine species are more vulnerable to fluctuations in water temperature and pH than sub-tropical or temperate marine species. Tropical species generally live in environmental temperatures at their upper tolerance limit; thus, changes in temperature beyond this limit could severely impact their life (Deutsch et al., 2008; Ehrlén and Morris, 2015; Sunday et al., 2012). Respiration and digestion are the primary metabolic processes commonly measured to understand the effects of environmental factors on fish growth and usually represented as aerobic scopes and metabolic curves (Cao et al., 2014). However, higher energy expenditures are required to achieve aerobic scope needs when fish are exposed to extremely high or low temperatures. Thus, fish must modify their physiological needs by either increasing their food intake to meet increased energy demands (Fernández-Montero et al., 2018; Liew et al., 2013) or limit energy for crucial metabolism needs. An increase in feed intake is a strategy used by many animals to compensate for high metabolic demands during thermal shift conditions. Thus, grouper production could be maximized by optimizing the physicochemical parameters, such as the temperature, salinity, and carbon dioxide level, of the rearing environment (Othman et al., 2015; Noor et al., 2018, 2019a; Noor and Das, 2019).

This review provides an outline of the temperature physiology in grouper aquaculture and summarizes the effects of temperature on the growth, digestion, and other physiological characteristics of aquacultured groupers from tropical and sub-tropical regions.

2. Species diversity of groupers

A total of 24 groupers (i.e., 23 *Epinephelus* spp. and 1 *Cromileptes* sp.) and 4 hybrids have been aquacultured for temperature physiology studies (Table 1), thereby indicating high species diversity in aquaculture (Rimmer and Glamuzina, 2017). *E. lanceolatus* and *E. fuscoguttatus* are involved in three of the four hybrids included in this review, namely, *E. coiodes* × *E. lanceolatus, E. fuscoguttatus* × *E. lanceolatus* (TGGG), *E. fuscoguttatus* × *E. polyphekadion*, and *E. marginatus* × *E. aeneus*. Although other inter-specific combinations have also been attempted in grouper aquaculture (Shapawi et al., 2018), these four crosses were specifically investigated to assess temperature-driven changes in their physiological characteristics (Glamuzina et al., 1999; James et al., 1999; Kiriyakit et al., 2011; De et al., 2016; Zhe et al., 2018; Table 2).

Among the 24 groupers species included in this review, five (21 % of the total grouper diversity) are considered threatened (three are vulnerable species, one is critically endangered, and on is endangered). Over half of the species ($n = 13$, 54 %) are categorized as “Least Concern,” and five species are considered “Data Deficient.”

3. Effects of temperature on growth in grouper aquaculture

The effects of temperature on grouper growth is an extensively investigated research topic because of the importance of this trait in aquaculture. Research articles and conference proceedings published between 1979 and 2018 and discussing grouper aquaculture in the tropics ($n = 34$) were considered in this review to evaluate the optimal rearing temperature of grouper (Table 2). While this list is certainly not exhaustive, it provides an outline of the species-specific optimum temperatures for experimental groupers. Most of the available research was conducted in the Asia–Pacific, and the earliest of these studies was conducted in Ecuador by Haschemeyer et al. (1979).

Table 1
Grouper species in aquaculture and their IUCN Conservation status.

Species	Common name	Conservation status
Epinephelus spp. (23)		
Epinephelus aeneus	White grouper	Near Threatened
E. akaara	Hong Kong grouper	Endangered
E. amblycephalus	Banded grouper	Least Concern
E. areolatus	Areolate grouper	Least Concern
E. bleekeri	Duskytail grouper	Data Deficient
E. bontoides	Palemargin grouper	Least concern
E. bruneus	Longtooth grouper	Data deficient
E. chlorostigma	Brown–spotted grouper	Least Concern
E. coiodes	Orange–spotted grouper	Least Concern
E. fasciatus	Blacktip grouper	Least concern
E. fuscoguttatus	Brown–marbled grouper	Vulnerable
E. labriformis	Starry grouper	Least Concern
E. lanceolatus	Giant grouper	Data deficient
E. maculatus	Highfin grouper	Least Concern
E. malabricus	Malabar grouper	Least Concern
E. marginatus	Dusky grouper	Vulnerable
E. ongus	White–streaked grouper	Least concern
E. polyphekadion	Camouflage grouper	Vulnerable
E. quoyanus	Longfin grouper	Least Concern
E. sexfasciatus	Sixbar grouper	Least Concern
E. striatus	Nassau grouper	Critically Endangered
E. tauvina	Greasy grouper	Data deficient
E. tukula	Potato grouper	Least Concern
Cromileptes sp. (01)		
Cromileptes altivelis	Humpback grouper	Data Deficient
Hybrids (♀ × ♂) (04)		
E. coiodes × *E. lanceolatus*	–	–
E. fuscoguttatus × *E. lanceolatus*	Pearl gentian grouper / TGGG	–
E. fuscoguttatus × *E. polyphekadion*	–	–
E. marginatus × *E. aeneus*	–	–

Most of the experiments used juvenile groupers to evaluate the optimal rearing temperature, and larvae were used in only five studies. Grouper larvae are more sensitive to environmental and physical conditions than more mature fish, and issues related to the optimization of environmental conditions for larvae were highlighted in Rimmer and Glamuzina (2017). The morphological development of both larval and juvenile blacktip grouper was studied by Kawabe and Kohno (2009) in Japan. In China, adult hybrids of TGGG, were studied by Zhe et al. (2018).

The overall test temperatures applied across the different life stages of the fish ranged from 13 °C to 35 °C. Discernible changes under optimal temperatures could be attributed to various reasons, such as species-specific thermal responses and differences in geographical location (e.g., the Americas, the Mediterranean, and the Indo–Pacific), as presented in Table 2. Table 2 illustrates that the single stressor temperature could affect grouper growth. The influence of temperature may be expected could exacerbate the physiology effects affecting growth. Experimental studies conducted in Indonesia, Japan, Saudi Arabia, and Taiwan have demonstrated that a rearing temperature of 28 °C may be optimal for grouper hatcheries in the Asia–Pacific (Hseu et al., 2004; Sugama et al., 2004; Yoseda et al., 2006; Mariskha and Abdulgani, 2012; Cheng et al., 2013).

The specific growth rate (SGR%) of groupers is generally higher at high water temperatures than at low ones, although the responses found appeared to be region and species-specific. Experimental studies have shown that the SGR% of Nassau grouper ranges from 1.95 to 2.07 at 22 °C – 28 °C (Ellis et al., 1997), those of *E. tauvina* and *E. fuscoguttatus* are 3 and 2.5, respectively, at 28–31 °C (Lim, 1993), and that of *E. coioides* ranges from 1.080 to 1.095 at 25 °C – 35 °C (Lin et al., 2008). A similar trend of optimal growth at higher water temperatures (26 °C) was observed in *E. marginatus* from Spain (López and Castelló, 2003).

Similarly, the feed conversion ratio (FCR) of groupers is higher at high water temperatures than at low ones. The FCR of *E. striatus*

Table 2
Test ranges and optimum temperature of aquacultured groupers (*Epinephelus* spp. and *Cromileptes* sp.).

Zone	Country	Life stage	Species	Temperature (°C) Test range	Temperature (°C) Optimum	Reference	Effects in Optimum Temperature
Sub-tropical	Israel	Juvenile	*E. aeneus*	19–27	15	Lupatsch et al., 2003	Higher metabolic body weight Higher protein efficiency Increase weight gain
Sub-tropical	Japan	Juvenile	*E. akaara*	22–28	23	Kayano and Oda, 1994	Increase feeding activity Higher relative growth rate
Sub-tropical	Japan	Juvenile	*E. amblycephalus*	16–26	24	Motomura et al., 2007	Higher relative growth rate
Sub-tropical	China	Juvenile	*E. areolatus*	15–30	25	Leung et al., 1999	Higher ammonia excretion Faster digestion Increase body weight
Sub-tropical	Japan	Juvenile	*E. bleekeri*	20–28	26	Ogawa, 2003	Increase feeding rate Higher growth rate
Tropical	Indonesia	Juvenile	*E. bontoides*	16–26	25	Prijono et al., 1998	Increase total length and body weight Increase gonadosomatic index (GSI) Higher reproduction rate
Sub-tropical	Korea	Larvae	*E. bruneus*	16–25	25	Song et al., 2005	Higher fertilization rate Increase total body length Low malformation rate
Tropical	UAE	Juvenile	*E. chlorostigma*	20–26	25	Agamy, 2013	Decrease in lamellar width Better health status
Sub-tropical	China	Juvenile	*E. coioides*	17–35	35	Lin et al., 2008	Higher food consumption Lower feed conversion efficiency Higher dry matter content Better growth
Sub-tropical	Taiwan	Juvenile	*E. coiodes*	19–35	28	Cheng et al., 2009	Lower total leucocyte count Lower respiratory burst Lower phagocytic activity Better immune system
Sub-tropical	Japan	Larvae & juvenile	*E. fasciatus*	24–29	25	Kawabe and Kohno, 2009	Increase body length Better growth
Tropical	Singapore	Larvae	*E. fuscoguttatus*	28–30	30	Lim, 1993	Better feeding performance Lower mortality
Sub-tropical	Taiwan	Juvenile	*E. fuscoguttatus*	22–29	28	Cheng et al., 2013	Higher survival rate
Tropical	Ecuador	Juvenile	*E. labriformis*	22–28	26	Haschemeyer et al., 1979	Higher protein synthesis Better growth
Sub-tropical	Taiwan	Juvenile	*E. lanceolatus*	22–30	28	Hseu et al., 2004	Higher total length Lower mortality Better growth
Tropical	Micronesia	Juvenile	*E. maculatus*	23–28	27	Rhodes et al., 2016	Higher body size Higher spawning behaviour
Sub-tropical	Japan	Juvenile	*E. malabricus*	24–30	28	Yoseda et al., 2006	Higher mean volume of yolk sac Facilitate initial feeding Better growth
Moderate	France	Juvenile	*E. marginatus*	13–25	19	Bouchereau et al., 1999	Higher total length Higher linear growth
Moderate	Spain	Juvenile	*E. marginatus*	20–26	26	López and Castelló, 2003	Higher mean weight gain Better feed conversion ratio
Sub-tropical	Japan	Juvenile	*E. ongus*	24–28	27	Craig, 2007	Higher body size Higher fecundity
Tropical	Micronesia	Juvenile	*E. polyphekadion*	24–28	27	Rhodes and Sadovy, 2002	Higher body size Better reproduction behaviour
Sub-tropical	Australia	Juvenile	*E. quoyanus*	24–28	27	Connell, 1998	Better predator abundance
Tropical	Indonesia	Juvenile	*E. sexfasciatus*	22–30	28	Mariskha and Abdulgani, 2012	Better reproduction behaviour
Tropical	Bahamas	Larvae	*E. striatus*	25–28	26	Watanabe et al., 1995	Higher mean body size Higher percentage of sexual maturity
		Juvenile	*E. striatus*	22–28	26	Ellis et al., 1997	Higher final weight Higher specific growth rate Better survival rate
Tropical	Kuwait	Larvae	*E. tauvina*	27–31	29	Akatsu et al., 1983	Higher survival rate Better growth
Sub-tropical	Taiwan	Larvae	*E. tukula*	23–30	27	Yeh et al., 2003	Higher percentage of sexual maturity
Tropical	Indonesia	Larvae	*C. altivelis*	26 –31	28	Sugama et al., 2004	Higher feeding activity Better growth
Tropical	Thailand	Juvenile	*E. coiodes* × *E. lanceolatus*	22–30	26	Kiriyakit et al., 2011	Higher fertilization rate
Tropical	Malaysia	Juvenile	*E. fuscoguttatus* × *E. lanceolatus*	22–34	30	De et al., 2016	Positive allometric growth

(*continued on next page*)

Table 2 (*continued*)

Zone	Country	Life stage	Species	Temperature (°C)		Reference	Effects in Optimum Temperature
				Test range	Optimum		
Sub-tropical	China	Adult		16–35	30	Zhe et al., 2018	Higher feeding rate Higher daily weight gain Lower food conversion ratio
Sub-tropical	Saudi Arabia	Juvenile	*E. fuscoguttatus* × *E. polyphekadion*	20–30	28	James et al., 1999	Higher body size Better growth
Sub-tropical	Croatia	Juvenile	*E. marginatus* × *E. aeneus*	15–25	18	Glamuzina et al., 1999	Higher hatching rate Higher embryonic development Higher survival rate

increased from 1.60 at 22 °C to 2.23 at 31 °C (Ellis et al., 1997). In *E. coioides*, the peak FCR is achieved at 35 °C (Lin et al., 2008). The mean FCR of *E. marginatus* was observed to be 1.23 at 24 °C ± 1.9 °C, and only small differences in this parameter were noted throughout the growth cycle of the fish (López and Castelló, 2003) at temperatures ranging from 20 °C to 26 °C.

Temperature, in combination with salinity and oxygen consumption, has been observed to influence the growth of groupers. Cheng et al. (2013) found that all individuals of *E. fuscoguttatus* survive gradual decreases in salinity until a salinity of 3 ‰ for 1 h but abruptly die when the salinity is suddenly changed to 0‰ within 1 h. The response of TGGG juveniles to salinity variations revealed high oxygen consumption rates under high salinity (Noor et al., 2019b). However, research findings that could be used to understand the complex interactions and factors influencing grouper aquaculture comprehensively are lacking. Studies pertaining to the combined influences of environmental parameters on groupers are limited, and all of the available research has indicated that although most groupers can acclimate to some extent, drastic changes in temperature and salinity could negatively impact their growth and survival rates and produce undesirable changes in their physiological responses (Gracia-López et al., 2004; Cheng et al., 2013; Choo et al., 2015).

Environmental changes across the different life stages of groupers appear to be species and location specific. Because the impacts of climate change on fish populations have been widely observed (Barange and Perry, 2009; Cochrane et al., 2009), improving the current scientific knowledge is necessary to achieve accurate estimations of the potential contributions of grouper aquaculture to climate change.

4. Effects of temperature on digestion

The critical role of enzymes in the digestive physiology of groupers is an important area of research from an aquaculture perspective. Few studies have yielded concrete experimental evidence of the impacts of temperature on digestive enzymes.

Yu et al. (2007) reported that the optimum temperature of a protease in the digestive tract of orange-spotted grouper across different growth periods is 30 °C. *Plectropomus leopardus* also showed maximum protease activity at 30 °C (Sun et al., 2015). However, this temperature may not be optimal for the different life stages of the fish. A decline in the activities of the digestive enzymes of fish beyond the optimum temperature levels has been reported, and this decline has been suggested to be due to changes in ion concentrations and pH (Solovyev et al., 2015).

De et al. (2014) found that TGGG requires approximately 13–17 h to pass and eliminate pellet food from its alimentary tract at different temperatures (range, 22 °C – 34 °C). The fastest elimination time (i.e., 13 h) was observed in fish acclimated at 30 °C, and the slowest elimination time (i.e., 17 h) was found at 22 °C. However, the gastric emptying time of TGGG is also much shorter than those of other carnivorous fishes.

Metabolic rates and the corresponding physical and chemical processes of groupers increase as water temperatures increase (Berens and Murie, 2008; De et al., 2014). Indeed, even small temperature variations could result in drastic changes in the growth efficiency of groupers. For example, drastic temperature changes exceeding the threshold value reduced the growth performance of *E. fuscoguttatus* (Cheng et al., 2013). Dramatic changes in temperature can have important consequences on the ability of groupers to continue vital biochemical processes. Tsuzuki et al. (2007) observed that the gastric juice output of *Centropomus parallelus* increases with increasing temperature and salinity. This effect may also be proposed in groupers because a reduction in digestion efficiency under the condition of a decrease in temperature has been reported for the species (Sun et al., 2015). This finding is suggestive of increased digestion rates with increasing temperature and salinity.

5. Effects of temperature on physiological status

Hematological studies are essential for analyzing the health status and understanding the relationship between the blood characteristics of fishes and their adaptability to their environment (Fazio et al., 2012; Mazumder et al., 2015). Hemoglobin (Hb) and hematocrit are two important hematological parameters used to understand the effects of temperature on fish physiology (Clark et al., 1979; Fazio et al., 2012; Mazumder et al., 2019a, 2019b). Decreasing Hb after cold-temperature exposure has been reported in several species (Staurnes et al., 1994; Chen et al., 1996). This pattern has also been observed in *E. morio*, the Hb levels of which increase at low temperatures (15 °C), indicating a stress response (Cho et al., 2015).

Thyroid hormones are involved in the control of osmoregulation, metabolism, somatic growth, and post-hatching metamorphosis (Power et al., 2001; Yamano, 2005; Schnitzler et al., 2012). Abbas et al. (2012) investigated the effect of seasonal changes in temperature on the thyroid structure and hormone secretion of *E. aeneus* and found low thyroid levels at low temperatures (21 °C) and high thyroid levels at high temperatures (25 °C). Lower grouper thyroid hormone cycles could be attributed to the decrease in food consumption of the fish at low temperatures (Abbas et al., 2012).

Some researchers have studied the effect of water temperature on the susceptibility and immune responses of groupers to some pathogens and diseases. For instance, the effects of temperature on the immune responses and susceptibility of groupers to vibriosis have been investigated in Taiwan (Cheng et al., 2009) and Malaysia (Albert and Ransangan, 2013). Temperatures beyond the optimum ranges were found to decrease leukocyte counts and the innate cellular and humoral immune responses of *E. coioides*, thereby increasing their susceptibility to vibriosis. Considerable increases or decreases in water temperatures (ca. 8 °C above or below the normal rearing temperature of 27 °C) could suppress the immunity of *E. coioides* (Cheng et al., 2009).

6. Temperature physiology of groupers in different production systems

Comparative studies on farmed groupers in different production systems (e.g., inland hatcheries using recirculating aquaculture systems [RAS] and sea cages) are limited. Experimental studies on the mean daily growth of some groupers (*E. itajara*, *E. tauvina*, and *E. salmoides*) have shown comparatively higher increments in RAS tanks compared with those in floating net sea cages (Chua and Teng, 1980; Gomez, 1983; Chou and Wong, 1985; Tacon, 1991). Temperatures usually range from 26.8 °C to 29.0 °C in recirculating hatchery tanks and from 32.0 °C to 33.5 °C in cages. The growth of groupers produced in RAS is similar to the best growth rates published in the literature because the temperature in this system could be adjusted; temperatures in open sea cages are close to the ambient sea temperature, which is generally higher than that in RAS (Tacon, 1991). The higher water exchange rate in RAS compared with that in sea cages has also been proposed to support the rapid growth of groupers (Chou and Wong, 1985).

The effects of water temperature on gonadal maturation and spawning have not been studied in detail (see Rimmer and Glamuzina, 2017). Sugama et al. (2012) noted a refractory phase in spawning activity at lower water temperatures (25 °C) in *E. fuscoguttatus* reared in RAS from Indonesia. However, a three-year experimental study in India involving the same species reared in RAS at higher temperatures (i.e., 27 °C) had indicated that temperature alone may not completely govern the physiology of *E. fuscoguttatus* and that its captive spawning activity may be inhibited at higher temperatures (Rimmer et al., 2013).

Inappropriate culture practices are known to activate the stress system of groupers, resulting in decreased body mass and increased corticotropin releasing factor expression under different water temperatures (Frisch and Anderson, 2005). Enhancement of these indicators has been reported in different fish species reared in sea cages (Seng, 1998; Baliao et al., 2000; Afero et al., 2010).

7. Conclusion

Temperature physiology must be carefully considered within the context of the normal environment of a species because thermal responses are generally a reflection of adaptation. Most predictions today regarding the biology and ecology of marine fish are obtained from captive indiscriminate models from temperate regions; however, the corresponding characteristics of tropical fish species, such as groupers, are incompletely understood. This review discusses findings for 24 groupers (i.e., 23 *Epinephelus* spp. and 1 *Cromileptes* sp.) and 4 hybrids (i.e., *Epinephelus* spp.) aquacultured for temperature physiology studies. The overall test temperatures applied over the different life stages of the aquacultured groupers ranged from 13 °C to 35 °C, with a mean optimum rearing temperature of 26.32 °C ± 0.62 °C. Experimental studies have demonstrated that a rearing temperature of 28 °C may be optimal for grouper hatcheries in the Asia–Pacific. Therefore, fish farmers may adopt this temperature to establish a healthy environment for groupers.

Although comparative experimental studies on the mean daily growth of groupers have shown higher increments in recirculating hatchery tanks compared with those in floating net cages in the tropics, temperature alone may not completely govern the grouper physiology. The physiology of groupers is known to improve under high temperatures, but extreme increases or decreases in water temperature could induce declines in the physiological activities of these fish.

While this review mainly focuses on the physiological aspects associated with grouper production, it also reflects the low availability of literature on this topic and the relative paucity of studies in other areas, especially those related to the temperature-based aspects of grouper aquaculture value chains. More in-depth research is imperative to achieve precise predictions of the future prospects of sustainable grouper aquaculture, particularly in the tropics.

Author statement

Simon Kumar Das: Conceptualization, project administration, Writing-original draft, review, editing and finalizing the manuscript, **Tou Wee Xiang:** drafted the manuscript, **Noorashikin Md Noor:** writing & editing, **Moumita De:** writing & editing, **Sabuj Kanti Mazumder:** writing, **M.P. Goutham-Bharathi:** Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

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