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Effect of replacing darkness with dim light in the larviculture of red snapper, *Lutjanus campechanus*

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ABSTRACT

Progress towards the development of reliable hatchery technology for red snapper, *Lutjanus campechanus*, has been limited by inconsistent spawning and difficulties in larval rearing. We report on recent progress to improve this technology. A larval rearing trial assessing the effects of two different photoperiods was conducted at the University of Miami Experimental Hatchery (UMEH). Four 400-L tanks were subjected to a photoperiod of 16 h of full spectrum light, and four 400-L tanks were subjected to 16 h of full spectrum light and 8 h of dim light through 11 days post hatch (dph). S-strain rotifers, *Brachionus rotundiformis*, were used as the exclusive first feeding source and were maintained at a density of 25 ml^{-1} throughout the experimental period. Standard length, swim bladder inflation, and feed consumption were measured for each tank at 3, 6, 9 and 12 dph. Survival was quantified at 12 dph and at the completion of weaning onto dry feeds at 40 dph. No significant differences in growth, feed consumption, or survival rates were observed between treatments at the conclusion of the trial. However, tanks exposed to a treatment involving 8 h of dim light showed completion of swim bladder inflation in 92.5 ± 10.8 % of larvae sampled by 9 dph, while tanks maintained with 16 h of light and 8 h of darkness showed a significant reduction with only 60 ± 2.5 % swim bladder inflation at this sample date ($p = 0.0131$). By 12 dph, all larvae in all tanks showed >95 % swim bladder inflation success. Total survival across treatment groups through 13 dph was 66 ± 8.0 % and 4.6 ± 1.0 % at 40 dph when the larvae were fully weaned onto dry diets.

1. Introduction

Red snapper, *Lutjanus campechanus*, represents one of the most valuable fisheries in the United States with annual landings exceeding 16 million pounds in 2014 (SEDAR 52, 2018). For decades, regulators have attempted to balance the species' economic importance to fishing communities with the management needs surrounding the preservation of a suitable wild spawning stock (GMFMC, 2018a, b). Attempts at developing aquaculture technology for the species began in the late 1970's and received significant attention throughout the early 2000's (Blaylock et al., 2000). During this time, a number of milestones were achieved, including the first volitional and induced captive spawns (Arnold et al., 1978; Minton et al., 1983; Phelps et al., 2009), larval rearing and weaning (Miller et al., 2005; Ogle et al., 2005), and preliminary forays into the development of stock enhancement programs (Brennan et al., 2007). Watanabe et al. (2005) provided a thorough description of the status of developing an industry around species, along with two other Lutjanids; however, progress in expanding snapper aquaculture slowed in the following years. Most of these early attempts at expanding the production capacity of the species were hampered by inconsistent spawning and difficulties encountered during early developmental stages of the larvae (Bourque and Phelps, 2007). The present study aimed to build upon the success of past efforts while working to overcome many of the early challenges associated with reliable production of red snapper in aquaculture.

In the larval rearing of delicate marine fish species, the influence of light in the rearing tanks can have profound effects on overall endpoints such as growth, development, and survival. Light intensity, periodicity, and spectrum all have been shown to play essential roles in these subsequent endpoints (Barahona-Fernandes, 1979; Downing and Litvak, 1999; Honryo et al., 2018; Puvanendran and Brown, 1998; Villamizar et al., 2009). In particular, the ratio between periods of light and periods

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of darkness has been demonstrated to be one of the most significant parameters for larval growth and survival in a wide range of marine teleost species (Barlow et al., 1995; Boeuf and Le Bail, 1999; Fielder et al., 2002; Fuchs, 1978; Moustakas et al., 2004; Partridge et al., 2011; Villamizar et al., 2011; Stuart and Drawbridge, 2012). Principally, periodicity has been shown to significantly influence growth rates and overall survival due to the high reliance on visual cues to enable feeding in marine teleosts (Blaxter, 1986; Naas et al., 1996; Neave, 1984; Tandler and Helps, 1985; Utne-Palm and Stiansen, 2002). The most common hypothesis for this outcome has been that increased periods of light may allow larvae to consume higher total quantities of prey items in their earliest life stages, thereby allowing a more rapid progression through these sensitive times of ontogenetic development (Boeuf and Le Bail, 1999; Duray and Kohno, 1988; Villamizar et al., 2011). In some species, alternative outcomes have been observed, with slower growth rates potentially stemming from greater overall energy expenditures for which increased feeding success could not compensate during extended photoperiods (Barahona-Fernandes, 1979).

Additionally, different lighting regimes have been shown to affect larval ontogeny in marine teleosts, notably in terms of swim bladder development and inflation (Battaglene and Talbot, 1990; Hadley et al., 1987; Partridge et al., 2011; Stuart and Drawbridge, 2012; Trotter et al., 2003). Successful inflation of the swim bladder is an important predictor of larval survival and incomplete inflation has been shown to increase deformities in later life stages (Stuart and Drawbridge, 2012; Chatain, 1994; Iwasaki et al., 2017; Schwebel et al., 2018). While many species may achieve maximal swim bladder inflation when exposed to lengthened or continuous periods of light, some species require a period of darkness to cue proper swim bladder inflation (Cerqueira et al., 1991; Johnson and Katavic, 1984; Trotter et al., 2003; Villamizar et al., 2009, 2011; Woolley and Qin, 2010).

To our knowledge, no publications have been produced investigating swim bladder inflation in the Lutjanids. Furthermore, while multiple studies have shown the impacts of photoperiod manipulation in Lutjanid species during later life stages (Duncan et al., 2008; Guerrero-TorTolero et al., 2008), we believe the present study is the first to examine how different lighting regimes may impact the larvae of the family. In past work with red snapper larvae, behavioral changes associated with extended periods of light during the larval rearing period were observed anecdotally, including "shoaling" at the surface of the tank, disoriented swimming behavior, and eventual mortality. However, we found that these tendencies could be attenuated through use of darkness or dim light during nighttime hours. Because many marine fish hatcheries around the world extend periods of light as a means of improving feeding opportunities, growth, development, and survival (Divanach and Kentouri, 2000), the present study was conducted to determine if periods of low light during nighttime hours could confer advantages to larval growth and survival that were not observed in complete darkness during a diel light:dark cycle.

With eggs produced during the first volitional spawns of the reproductive season in the summer of 2019, we sought to assess the effect of implementing a 24 h light photoperiod for raising red snapper larvae in a controlled hatchery setting as a means to improve performance and survival through weaning in this species. Because previous studies have shown red snapper larvae can be raised utilizing a photoperiod involving 16 h of full spectrum light and 8 h of darkness, this strategy was compared against a treatment involving 16 h of full spectrum light and 8 h of dim light, hereafter referred to as the "16 + 8" treatment, to identify any advantages or disadvantages that prolonged exposure to light may impart. Larval performance was assessed based upon the endpoints of growth, feed consumption, swim bladder inflation, and survival. Identifying the effects of 24 h light for larval red snapper during this first attempt at rearing at UMEH is a critical step to develop a baseline hatchery protocol for the species.

2. Materials and methodology

2.1. Egg production

Wild-caught broodstock red snapper were kept in a 60 m^3 partially-recirculating system at the University of Miami Experimental Hatchery (UMEH), featuring mechanical and biological filtration, as well as ultraviolet light sterilization of seawater as described by Benetti et al. (2008) and Stieglitz et al. (2012, 2017). Fish were acclimated to captivity for one year prior to the spawning season that produced the embryos for this trial. Broodstock were fed a diet of diverse cut feeds (sardines, squid, mackerel, crustaceans, and polychaetes) and commercially-available supplemental vitamins containing high levels of DHA and DPA (MadMac-MS, Aquafauna Biomarine, Inc., Hawthorne, CA, US). A ~1:1 female to male sex ratio was maintained for the duration of the spawning season, during which a cohort of 13 adult fish ultimately produced over six million viable embryos through 29 volitional spawns from July through September of 2019. All eggs used for this experiment were collected from a single spawn from this brood cohort which likely involved a single spawning female.

2.2. Larval rearing

Floating, fertilized eggs were stocked into a cylindrical 400-L incubation tank, treated with 100 ppm Formalin (37 % Formaldehyde solution) for one hour during early embryonic development and hatched approximately 24 h after collection. A total of 114,000 larvae were then split evenly across eight 400-liter larval rearing tanks at a stocking density of 35 larvae L^{-1}. Each tank was fitted with a 300 μm mesh standpipe and aeration ring to allow for proper water exchange through the tank as well as proper circulation. Pure oxygen was also lightly diffused into the tank to ensure dissolved oxygen levels between 6.5–9.0 mg L^{-1}. Temperature, which has been shown to play an important role in the hatching and larval development in other Lutjanids, was maintained at 24.9 ± 0.08 °C for the duration of the trial (Peña et al., 2014). Daily water exchange began at 250 %, but increased throughout the trial to 1000 % per day as feeding rates increased and larvae became more apt swimmers.

Small, "S-strain" rotifers, *Brachionus rotundiformis*, were used as the exclusive first feeding source and were maintained at a density of 25 ml^{-1}. Residual rotifers were counted seven times daily by sampling 30 ml seawater from each tank and counting the number of prey items in three 1 ml aliquots. Each tank was also greened with algae paste (RotiGreen Nanno, Reed Mariculture, Campbell, CA) prior to each feeding in order to increase the opacity of the tank water and to maintain the enrichment of the rotifers within the tank (van der Meeren et al., 2007; Stuart and Drawbridge, 2011). *Artemia spp.* (SEP-Art, Inve Aquaculture Inc., Salt Lake City, UT) were introduced as a second feed source at 15 days post hatch (dph) and were co-fed with rotifers until larvae were completely weaned at 25 dph.

Because the tanks were maintained in a flow-through system with low density, nitrogenous compounds were not measured. Dissolved oxygen, and temperature were monitored twice daily.

2.3. Experimental design

165W marine full spectrum LED lights (460 nm–10,000 nm wavelength) were suspended approximately 1.0 m above each of the eight experimental tanks for illumination (NICREW Aquarium, USA). Two lighting treatments were tested: four tanks were subjected to a photoperiod of 16 h of light and 8 h of darkness ("16:8"), while the remaining four tanks were subjected to 16 h of light and 8 h of dim light ("16 + 8") with no dark period through 11 dph. An opaque plastic sheet was hung between each four tank array to prevent light intrusion from the 16 + 8 group into the 16:8 group. All larvae were divided randomly into these two treatments. Lux readings during periods of full spectrum light

ranged from 5100–5600 at the tank surface and 600–1000 at the tank bottom, while during periods of extended light in the 16 + 8 group, lux was maintained at the tank surface and tank bottom at 1300–1500 and 300–500, respectively. Beginning at 12 dph when swim bladder inflation had been completed successfully in >95 % across treatments, all tanks were maintained with a 16:8 photoperiod. Each tank remained separate until all larvae were fully metamorphosed into the juvenile stage and weaned onto artificial diets (Higashimaru Co., Ltd. Hioki, Japan) at 40 dph. At this stage, larvae were sampled, counted, and measured to elucidate any late developmental differences that might have occurred during the different photoperiods.

Swim bladder inflation and feed consumption were measured on subsamples of 10 larvae per replicate at 3, 6, 9, and 12 dph 3 h after first feeding. After 12 dph, the quantities of rotifer mastax found within the gut of each larva became too numerous to count. Similarly, once *Artemia* were introduced as a prey item, gut volume and varying levels of digestion made counting individual prey items unreliable. Notochord recordings were generated in the same manner but were also calculated at 16 and 25 dph. Before sampling, aeration was moderately increased in each tank to evenly distribute larvae throughout the water column. Larvae were euthanized with MS-222 (Syndel, Ferndale, WA, USA; 500 mg/L solution) prior to taking measurements. 10 larvae were placed on a clear watch glass, observed under a dissecting microscope, and notochord length was recorded. An assessment of swim bladder inflation was also conducted at this time by observing a separate group of 10 larvae under the same dissecting microscope. Another 10 larvae were then transferred to a standard microscope slide where a cover slip was placed over each larvae and depressed until the gut ruptured and the total number of rotifer mastax could be counted to obtain feed consumption data.

Survival was quantified at 12 dph and at the completion of weaning 40 dph. At 12 dph, while larvae were too sensitive to handle, 275 ml subsamples of tank water were collected in triplicate to estimate the total number of larvae in the tank. To accomplish this, aeration was increased as described above, a straight pipe with a valve was pushed vertically into the water, the valve was closed, and contents were transferred to a beaker. At this point, the contents of the beaker were poured over a 200 μm filter and the total number of larvae were counted.

2.4. Statistical analysis

Data for each treatment fit assumptions of normality and heteroscedasticity using Shapiro's test and a visual diagnosis of residual plots, respectively. Survival, standard length, total number of prey items consumed, and percentage of larvae with full swim bladder inflation were compared between treatments with t- tests. Swim bladder inflation rates were expressed as the number of larvae with inflated swim bladders out of 10 individuals per tank. All reported errors are standard errors around the mean values and statements of significance refer to the 0.05 level, unless otherwise stated. All data analysis was completed using Microsoft Excel and R.

3. Results

A flow-through filtered seawater system allowed maintenance of water quality parameters within adequate average and range for marine larval fish species such as the red snapper throughout the trial. Water temperature ranged from at 24.9 ± 0.08 °C for the duration of the trial. Dissolved oxygen was kept near saturation levels for the respective temperatures, ranging from 6.5 to 9.0 mg L^{-1}.

There was no significant difference in growth between the 16:8 lighting treatment and the 16 + 8 treatment at either 3 or 6 dph. At 9 dph, the mean larval size in the 16:8 photoperiod treatment (mean ± standard error; 3.315 ± 0.0319 mm) was significantly larger than the 16 + 8 treatment (3.235 ± 0.0293 mm; p = 0.0354); however, by 12 dph these differences had diminished. At 16 dph, larvae in the 16 + 8 treatment (4.554 ± 0.0734 mm) were significantly larger than the 16:8 (4.294.69 ± 0.0703 mm; p = 0.00597), however these differences did not persist through 25 dph (Fig. 1). Upon final measurements at 40 dph, there was no difference in standard length between the two treatments.

At 6 and 9 dph, the 16:8 photoperiod treatment contained a significantly higher number of rotifers per larvae than the 16 + 8 photoperiod treatment (respectively, 3.90 ± 0.290, 4.78 ± 0.458 and 2.83 ± 0.234, 3.675 ± 0.287; p = 0.00018, p = 0.001; Fig. 1). Larvae in the 16 + 8 photoperiod achieved swim bladder inflation significantly more rapidly than larvae in the 16:8 photoperiod (p = 0.0131; Fig. 1). There was no significant difference in survival between treatments at any sampling date (Fig. 1).

4. Discussion

Extending periods of light exposure has been shown to successfully improve survival and growth of larval stages across numerous marine teleost species. A wide range of studies have investigated these effects and have determined that increased photoperiods may improve these endpoints in marine fish (Partridge et al., 2011; Stuart and Drawbridge, 2012; Villamizar et al., 2011). The rationale behind this has stemmed from the increased time available to accomplish feeding, which is often an inhibiting parameter during the earliest life stages (Chen et al., 2007). Furthermore, it has been suggested that continuous light may increase survival by preventing positively phototactic larvae from sinking to the tank bottom (where there is a higher concentration of protozoans and bacteria) during periods of darkness (Attramadal et al., 2012). This may consequently subject susceptible larvae to a higher likelihood of encountering harmful pathogens during these dark periods. This problem may compound with incomplete or delayed inflation of the swim bladder due to the organ's importance in regulating buoyancy (Woolley and Qin, 2010; Partridge et al., 2011).

Results of this experimental trial demonstrate that growth was not enhanced by a continuous photoperiod. While larvae in the 16:8 photoperiod were larger at 9 dph, and larvae in the 16 + 8 photoperiod were larger at 16 dph, these differences were modest and did not persist by 25 dph and 40 dph, when no differences in size between the treatments were evident. In fact, the significantly higher average number of rotifer mastax observed in the 16:8 photoperiod at 6 and 9 dph suggests that larvae that experienced a period of darkness consumed a greater number of prey items during the shortened periods of light to which they were exposed. While there is no existing literature that describes this phenomenon, we suggest that this could occur in order to compensate for the inability to feed in the absence of light. Beginning at 12 dph when photoperiods were equilibrated, and continuing throughout the trial, average feed consumption between treatments showed no significant difference and growth between groups continued at effectively the same rate. These results contrast with the numerous species that have been shown to grow more rapidly during continuous light including the sole (*Solea solea)* (Fuchs, 1978), gilthead seabream (*Sparus auratus*) (Tandler and Helps, 1985), rabbitfish (*Siganus guttatus*) (Duray and Kohno, 1988), barramundi (*Lates calcarifer*) (Barlow et al., 1995), greenback flounder (*Rhombosolea tapirina)* (Hart et al., 1996), Australian snapper (*Pagurs auratus*) (Fielder et al., 2002), Atlantic cod (*Gadus morhua*) (Puvanendran and Brown, 1998), yellowfin tuna (*Thunnus albacares*) (Partridge et al., 2011), California yellowtail (*Seriola lalandi*) (Stuart and Drawbridge, 2012), and white seabass (*Atractoscion nobilis*) (Stuart and Drawbridge, 2012). The only other species that has been documented to receive no growth enhancement from continuous light is the haddock (*Melanogrammus aeglefinus)* (Downing and Litvak, 1999).

Although red snapper become physoclistous as adults, with their swim bladders functioning independently of other organ systems, as larvae they are physostomous and must gulp air through their mouth and digestive system to complete initial swim bladder inflation (Render, 1995). The increased rate of swim bladder inflation in larvae in the dim light treatment indicates that a period of darkness is not necessary for

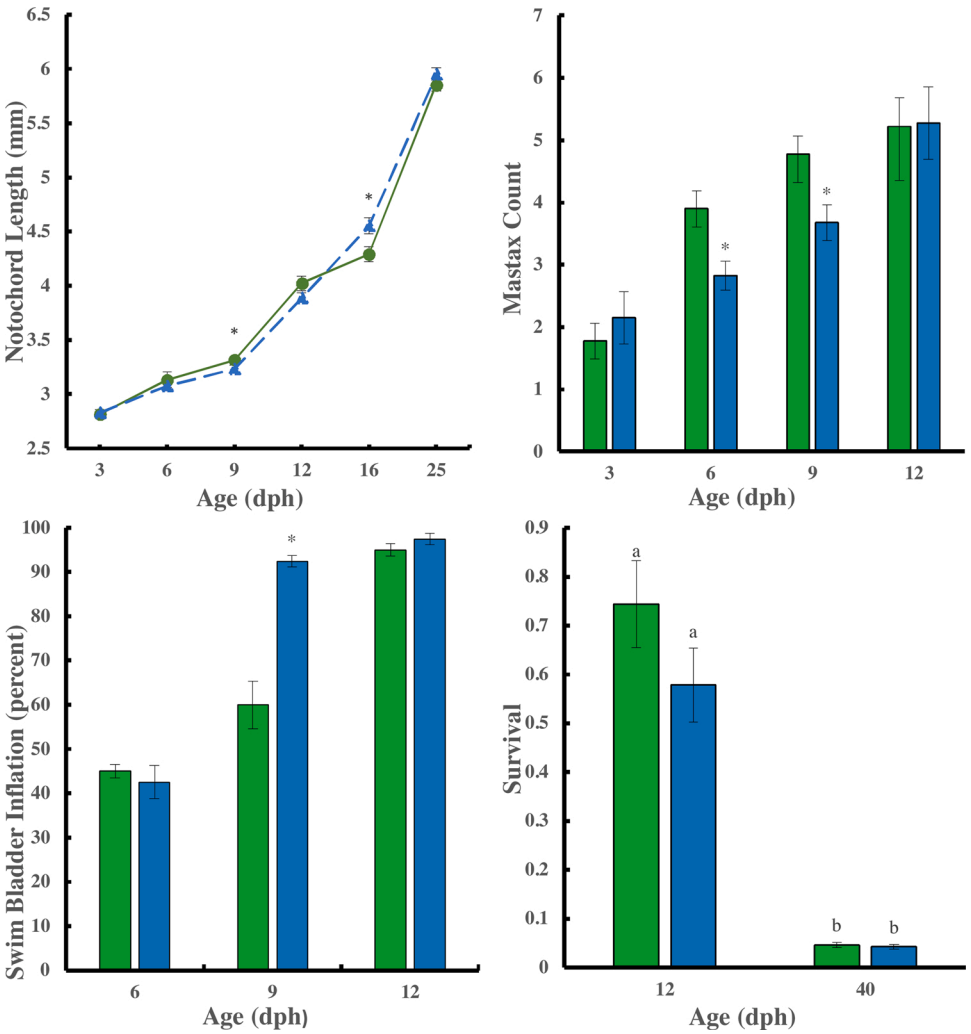

Fig. 1. Comparison of performance parameters of red snapper larvae reared under different lighting conditions. Green represents larvae raised under a 16 h light: 8 h dark regime, while blue represents a 16 h light: 8 h dim light regime. Different lighting strategies resulted in significant changes during some mid-experiment sampling, but no changes persisted by the final sampling date for any measured parameter. "*" denotes a statistically significant difference from the 16 h light: 8 h dark regime ($p < 0.05$).

this stage of larval development as has been shown in other species. Further, because larvae were observed to be positively phototactic in this trial, there is a possibility that an increased duration of time near the surface in the 16 + 8 photoperiod may have enabled successful swim bladder inflation to occur earlier in development. While incomplete or improper swim bladder inflation has been shown to have negative developmental impacts in both larvae and later life stages of marine fish including yellowfin tuna (Kurata et al., 2015), sea bass and sea bream (Chatain, 1994), and grouper (Tsuji et al., 2016), these problems did not manifest in the 16:8 photoperiod. This suggests that the delay in complete swim bladder inflation seen in the 16:8 treatment may not guarantee negative impacts to larval development. Similarly, the increased rate of successful swim bladder inflation achieved by the 16 + 8 treatment did not result in improved performance in any other metric for larval performance.

Drass et al. (2000) provided a detailed description of larval development through ontogeny which may inform some of the findings of this experiment (Drass et al., 2000). In their study, flexion began 12 dph and was completed by 16 dph. Similarly, a large proportion of spination and fin development took place from 13 to 17 dph. These processes are highly energy intensive and are likely impacted by foraging efficiency as well as other developmental precursors. By 12 dph, our study showed no significant difference in feed consumption between the two treatments. It is therefore possible that the significantly larger larvae observed in the 16 + 8 treatment at 16 dph may be a result of accelerated swim bladder inflation. Because the 16:8 treatment did not accomplish full swim bladder inflation until 12 dph, which coincides with the onset of flexion, spination, and pigmentation, there is the possibility that the energy budget available for growth was limited in comparison to the 16 + 8 treatment which had already accomplished complete swim bladder inflation by 9 dph. While growth between treatments was the same by 25 dph, these differences in the intermediate stages of larval development may prove to be relevant for the survival of larvae if exogenous stressors impact culture tanks.

The ultimate lack of difference in survival and growth between treatments demonstrates that continuous lighting provides no discernible, long-term benefit in the larval rearing of red snapper. It also suggests that the positive phototaxis of the larvae does not play a significant role in preventing contact with tank walls or exposure to potential pathogens such as bacteria and protozoans that may be present at the tank bottom. These findings are consistent with numerous other studies showing that survival was not impacted by continuous light in species such as barramundi (Barlow et al., 1995), silver seabream (Fielder et al., 2002), sole (Fuchs, 1978), flounder (Hart et al., 1996; Moustakas et al., 2004), and California yellowtail (Stuart and Drawbridge, 2012). Notably, 24 h light regimes demonstrated a negative impact on multiple species including meagre (Vallés and Estévez, 2013) and European sea bass (Barahona-Fernandes, 1979; Cerqueira et al., 1991) which was prevented here by reducing the light intensity for 8 h per day. Understanding the impacts that light may have on larval development and performance is critical to developing reliable hatchery protocols to support the growing number of private companies focusing on the

grow-out of red snapper fingerlings.

With red snapper identified as an important emergent species for aquaculture (Blaylock et al., 2000; Herrera-Ulloa et al., 2010), it is notable that this larval rearing experiment produced a significant quantity of high-quality fingerlings. The ultimate survival rate observed in this trial was comparable to a number of other high value aquaculture species such as cobia (Benetti et al., 2008), spotted rose snapper (Alvarez-Lajonchère et al., 2012), yellowtail snapper (Gutiérrez-Sigeros et al., 2018), and yellowtail kingfish (Woolley et al., 2014), and will likely improve as further trials are conducted and techniques are refined.

Author's contribution

All authors have participated in (a) conception and design, or analysis and interpretation of the data; (b) drafting the article or revising it critically for important intellectual content; and (c) approval of the final version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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