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Advancements in hatchery production of red snapper *Lutjanus campechanus*: Exclusive use of small strain rotifers as initial prey for larval rearing

Yole Buchalla[1] | Charles James McGuigan[1] | John D. Stieglitz[1] | Ronald H. Hoenig[1] | Carlos E. Tudela[1] | Kimberly G. Darville[1] | Leonardo Ibarra-Castro[2] | Daniel Benetti[1]

[1]Department of Marine Biology and Ecology, University of Miami—Rosenstiel School of Marine, Atmospheric, and Earth Science, Miami, Florida, USA

[2]School of Forest, Fisheries & Geomatics Sciences, University of Florida—Whitney Laboratory for Marine Bioscience, St Augustine, Florida, USA

Correspondence
Yole Buchalla, Department of Marine Biology and Ecology, University of Miami- Rosenstiel School of Marine, Atmospheric, and Earth Science, 4600 Rickenbacker Causeway, Miami, FL 33149, USA.
Email: ybuchalla@iattc.org

Present address
Yole Buchalla, Inter-American Tropical Tuna Commission, 8901 La Jolla Shores Drive, La Jolla, California 92037, USA.

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Abstract

The red snapper (*Lutjanus campechanus*) has one of the most valued fisheries in the southeastern United States and has been largely studied for its aquaculture potential with varied results that revealed production challenges. This study focused on addressing challenges in larval rearing and juvenile production of this species. Broodstock fish were acclimated in a 60 m^3 tank equipped with recirculating aquaculture system (RAS) and temperature control. After 1 year in captivity, fish volitionally spawned and larval rearing trials were conducted in replicated flow-through seawater tanks ranging from 0.4 to 2.4 m^3, at a temperature range of 24–26°C. Enriched s-strain rotifers, *Brachionus rotundiformis* (lorica length of 100–210 μm), were used for first feeding. Enriched *Artemia* sp. were gradually introduced after 18 days post hatch (DPH). The survival rate before metamorphosis (12 DPH) averaged 66.09 ± 0.08%. Survival rate from yolk-sac larvae to post-metamorphic early juvenile averaged 4.43 ± 0.01%. At 40 DPH, early red snapper juveniles averaged 0.35 ± 0.02 g in weight and 28.83 ± 0.60 mm in standard length. A total of 31,849 fully

weaned juveniles were harvested. This study demonstrates that small strain rotifers can be used exclusively as first feeding prey organism for red snapper larvae, representing a significant advancement for red snapper juvenile production.

KEYWORDS
aquaculture, broodstock, first feeding, larval husbandry, marine, rotifers

1 | INTRODUCTION

The red snapper *Lutjanus campechanus* is one of the most economically important marine fish species in the Gulf of Mexico and South Atlantic coast of United States (Bardon-Albaret & Saillant, 2017). Overfishing led to intensive management of the red snapper stock since 1990 (Bardon-Albaret et al., 2013); and since 2018 the species is no longer considered overfished (NOAA, 2020). Nonetheless, fishery closures remain in place throughout most of their range. The popularity of red snapper as a gamefish, its high market value, and its importance to commercial fisheries suggests that the development of husbandry techniques for this species could potentially lead to the development of its aquaculture industry, as well as provide a source of fry for stock enhancement programs (Bardon-Albaret, 2014; Bardon-Albaret & Saillant, 2017; Chávez et al., 2014; Ogle & Lotz, 2006; Watanabe et al., 2005).

Previous research conducted on red snapper focused on describing the early larval stages as well as spawning induction techniques for wild-caught broodstock (Arnold et al., 1978; Bardon-Albaret et al., 2013; Hastey et al., 2013; Papanikos et al., 2008; Rabalais et al., 1980; Saillant et al., 2013; Williams et al., 2004). While providing the baseline for hatchery technology development for this species, much of this work was constrained by difficulties in obtaining volitional spawning in captivity and high mortalities during the early developmental stages associated with first feeding of the larvae. Similar to other *Lutjanids*, red snapper larvae experience rapid yolk-sac absorption coupled with small mouth gape, creating a delicate phase during the switch from endogenous reserves to exogenous feeding (Estrada-Godínez et al., 2015; Gutiérrez-Sigeros et al., 2018).

Several authors have reported that the success of red snapper larval rearing was dependent upon the use of copepods as a first-feeding prey item due to their small sizes (50–180-μ length) and high natural nutritional value (Ogle et al., 2005; Ogle & Lotz, 2006; Phelps et al., 2005; Rhodes & Phelps, 2008; Watanabe et al., 2005). Calanoid copepods (*Acartia*, *Calanus*, and others), harpacticoid (*Euterpina*, *Tisbe*) and cyclopoid (*Corycaeus*, *Oithona*, and others) were successfully used during the first feeding of several snapper species including: golden snapper (*Lutjanus johnii*), mangrove red snapper (*Lutjanus argentimaculatus*), spotted rose snapper (*Lutjanus guttatus*) (Alvarez-Lajonchère et al., 2012; Doi et al., 1997; Schipp, 2006), as well as in ornamental marine fish species with small mouth gapes (DiMaggio, 2020; Lee et al., 2018). However, the scale of copepod culture necessary to support mass aquaculture production would likely be cost-prohibitive and require extensive space in a commercial setting (Stottrup, 2000), suggesting that live prey alternatives are necessary to support the development of commercial aquaculture of marine fish species such as the red snapper.

Snapper species have mouth width of approximately 190–220 μm at first feeding, and *L. campechanus* has a mandibular length of 221 μm at 60 h post fertilization (Castaños, 1997; Williams et al., 2004; Zavala-Leal et al., 2015). Small strain rotifers (s-strain rotifer), *Brachionus rotundiformis*, have a lorica length of 100–210 μm, which is slightly over 60% of the relative predator's mouth width. Studies on prey selectivity of marine fish larvae have repeatedly reported that larvae consume prey sizes that are 20–80% of their mouth width during first feeding (Castaños, 1997; Saillant et al., 2013), which indicate that the size of s-strain rotifers could be adequate for first feeding of snappers. It has also been suggested that the lack of successful attempts to feed red snapper larvae with rotifers could be related to inadequate enrichment rather than to prey size (Saillant et al., 2013).

Moreover, the size threshold of prey ingested by the larvae may not only be a function of larvae length or mouth width but can also be affected by the density of available food (Duray & Kohno, 1990). Castaños (1997) have found s-strain rotifers ranging 62–166 μm in the gut of *L. argentimaculatus* during the first days of feeding in an experimental larval rearing, potentially indicating that the excess rotifers in the tank likely grew, reproduced, and the neonates were ingested by the larvae. Physical processes operating on a microscale level can also affect the first feeding of marine fish larvae (Margulies et al., 2001). Hence, there are more factors other than prey size that can determine the first-feeding success of marine fish larvae.

Along with copepods, enriched rotifers have been used effectively as first feeding organisms for snapper species (Duray et al., 1996; Ibarra-Castro et al., 2020), small mouth-gape marine fish larvae (Alvarez-Lajonchère et al., 1996; Geng et al., 2019; Wullur et al., 2011), and even challenging species that also exhibit rapid yolk-sac absorption and high nutritional demand, such as scombrid larvae (Blanco et al., 2020; Kaji et al., 1999; Sawada et al., 2005; Stein et al., 2018). S-strain rotifers are relatively easy to culture in large scale, compared to copepod species (Saillant et al., 2013). Therefore, demonstrating the viability of using enriched rotifers during the initial feeding can provide a viable alternative source of live prey and facilitate the development of mass production of *L. campechanus*, and other marine species known to be difficult to raise.

In 2018 the University of Miami Experimental Hatchery (UMEH) began conducting research with red snapper aimed at developing hatchery technology of economically important reef fish species of the Gulf of Mexico and Caribbean. The objective of the present study was to test if the use of enriched s-strain rotifers (*B. rotundiformis*) could be adequate as first feeding prey and enable success in the scaling-up of hatchery production for this species. Data and results obtained on broodstock volitional spawning, larval rearing, and juvenile production of red snapper at 40 days post hatch (DPH) are reported.

2 | MATERIALS AND METHODS

2.1 | Egg production

A group of thirteen (13) wild fish (seven females averaging 6.14 ± 0.33 kg and six males averaging 5.30 ± 0.25 kg in body weight after acclimation) was captured using hook-and-line techniques off the Atlantic coast of Florida. The broodstock fish were conditioned over a period of 1 year in a maturation system previously described by Benetti et al. (2008) and Stieglitz et al. (2012, 2017).

Salinity was consistent at 36-ppt, and pH was 8.1. A shade-cloth cover was placed approximately two meters above the tank to attenuate light intensity, whereas photoperiod was natural (25°44′2″N, 80°9′43″W).

Broodstock red snapper were fed with a diet of previously-frozen cut fish—sardines (*Sardina* sp) and mackerel (*Scomber* sp)– and market squid (*Loligo* sp), given six times a week to 2–3% of the total biomass. As a complementary diet, a semi-moist feed (MADMAC-MS; Aquafauna Bio-Marine Inc. Hawthorne, CA) with the addition of a vitamin and mineral mix was given to the fish once a week. The broodstock diet was supplemented with shrimp and polychaetes (ProChaete; Sea Farms Nutrition, Miami, FL) in the 2 months preceding the spawning season.

The broodstock were conditioned to spawn volitionally through temperature control. Temperature regimes were set to follow natural temperature fluctuations in the ocean in the fall and summer in the southeastern United States. The first natural spawns were obtained when temperatures reached 25.8°C, and subsequent spawns were observed regularly while temperature was maintained 25.9 ± 0.04°C. Fish spawned during the night and eggs were collected in the morning from a 0.2 m^3 collector tank with a 0.2-mm nylon mesh screen when embryos were at the early development stages. To determine the number of eggs/ml, three samples of 1-ml were counted from the spawns. The mean ± standard error of the mean (SEM) of 1932 ± 63 eggs/ml was obtained. The total number of eggs were estimated volumetrically using a 2-L graduated beaker and the fertilization rate was estimated by the relation between the total number of floating eggs with the total number of eggs collected (floating and sinking).

Egg measurements were obtained from sub-samples of 10 eggs in 10 different spawns with the use of an optical microscope (Leica Microscopes CME; Buffalo, NY).

Hatch rates were determined by volumetric sampling and visual counts of yolk-sac larvae 30 h post hatch (HPH) taken directly from the incubation tanks. The averages were estimated from three samples, and the values are expressed as mean ± SEM.

2.2 | Larval rearing

Two larval rearing trials were conducted using s-strain rotifers as first-feeding prey item in an experimental system consisting of eight replicated 0.4 m^3 tanks, and in a pilot-scale system of four replicated 2.4 m^3 tanks with flow-through seawater. The cylindrical fiberglass tanks had dark green/blue walls and light green/blue bottoms. Seawater was filtered by two sand filters filled with broken glass filter medium (Vitroclean; Trivitro Corporation, Kent, WA), followed by a series of cartridge filters (10, 5, 1, and 0.05 μm) and a 200 W UV sterilization filter (Aqualogic; Inc, San Diego, CA).

Egg collection and treatment were described in detail by Benetti et al. (2008) and Stieglitz et al. (2012, 2017). Approximately 30 min after collection, the eggs were stocked in one 0.4 m^3 and one 2.4 m^3 tank and treated with 100-ppm Formalin (Parasite-S; Syndel Laboratories, Ferndale, WA) for 1 h. After that, water exchange was set to 1000% of the volume of the tank per day to flush the Formalin. Medium to strong aeration was supplied by an air pump through an air ring placed around the bottom of the center standpipe of the incubation tanks and pure oxygen was also provided to maintain saturation levels between 7 and 9 mg/L. Eggs were incubated at a mean density of 351 ± 13.96 eggs/L at a temperature of 25.5 ± 1°C.

After the eggs hatched and the number of yolk-sac larvae was estimated, larvae (1 DPH) were evenly transferred via beaker between the eight 0.4 m^3 tanks at a density of 35 larvae/L and to the four 2.4 m^3 tanks at a density of 73.08 ± 9.73 larvae/L. Each larval culture tank was fitted with a 200-μ mesh screen in the center standpipe to allow water exchange. During larval rearing, the mesh size was increased to 300 μ after 15 DPH, and 500 μ after 25 DPH.

Water exchange and aeration was gradually increased as larvae developed. During the incubation period, the water flow was set to 1000% of the volume of the tank per day, and aeration was maintained strong enough to avoid agglomeration of the eggs on the surface. Once the eggs hatched, water flow was set to 250–300% of the volume of the tank per day and a gentle aeration was provided to avoid any mechanical shock and stress to the yolk-sac larvae. Water exchange was maintained at the same rate for the first 6 days and it was gradually increased throughout the run, as the biological load increased in the culture tanks and the larvae became more resilient. After 6 DPH, water exchange was set to 400–500% of the volume to the tank per day until 14 DPH; then increasing to 500–600% from 14 DPH to 24 DPH and finally, 900–1000% after 25 DPH.

Water quality parameters during the larval rearing trials were maintained as follow: 25.5 ± 1°C temperature; 6.0–10.5 mg/L dissolved oxygen; 36-ppt salinity. The photoperiod was maintained 16-h light: 8-h dark, with exception of four 0.4 m^3 tanks that had extended light period (McGuigan et al., 2021). Surface skimming was performed manually with paper towels regularly throughout the day, as well as with the use of surface skimmers, which were cleaned every 30 min after feeding to remove oil and particulate buildup. After 6 DPH all tanks were siphoned once a day to remove detritus from the bottom.

As an effort to reduce bacterial load of the tanks, a passive transfer was done in each tank during the first days of introduction of *Artemia* sp. The passive transfer consisted of connecting two tanks by a 5 cm diameter flexible hose and siphoning water from one tank (with larvae) to the other tank. The larvae were passively transferred over a period of 12 h to a clean and disinfected tank. According to Stuart et al. (2016) passive transfer can considerably reduce the bacterial load in *Seriola lalandi* larval rearing tanks, contributing directly to improved survival. A positive effect was also observed when using this technique in high-performance species as cobia and mahi-mahi (Benetti et al., 2008; Stieglitz et al., 2017).

The larval rearing protocol established for both production trials is presented in Figure 1.

2.3 | Live feed production and feeding regime

The s-strain rotifer (*B. rotundiformis*) used in this study were cultured in a semi-continuous indoor system consisting of two 1 m^3 cylindrical tanks and three 0.4 m^3 conical tanks. The initial density of the culture was 1000 rotifer/ml and after a 3-day cycle when the rotifers were harvested, the density was 1800–2000 rotifer/ml. Rotifers were fed with OriOne (Skretting, Tooele, UT), and 24 h prior to larval feeding, rotifers were harvested, rinsed with filtered seawater, placed in the 0.4 m^3 conical tanks, and fed with another enrichment diet developed at UMEH (Table 1) containing Rotigreen, N-Rich (Reed Mariculture Inc., Campbell, CA), Protein Plus, AlgaMac 3050, Astaxanthin (Aquafauna Bio-Marine Inc., Hawthorne, CA), and yeast (Lesaffre Corporation, Milwaukee, WI). This enrichment mix (OriOne and UMEH enrichment diet) allows the rotifers to assimilate significant amounts of fatty acids in the tissue and guts, which is essential for marine fish larvae (Tocher, 2010; Watanabe, 1993). Taurine, a component that has been proven to impart positive effects on the growth and survival rate of marine fish larvae (Chen et al., 2004, 2005; Matsunari et al., 2013; Salze et al., 2012), was also utilized in the rotifer enrichment for the last 24 h prior to larval

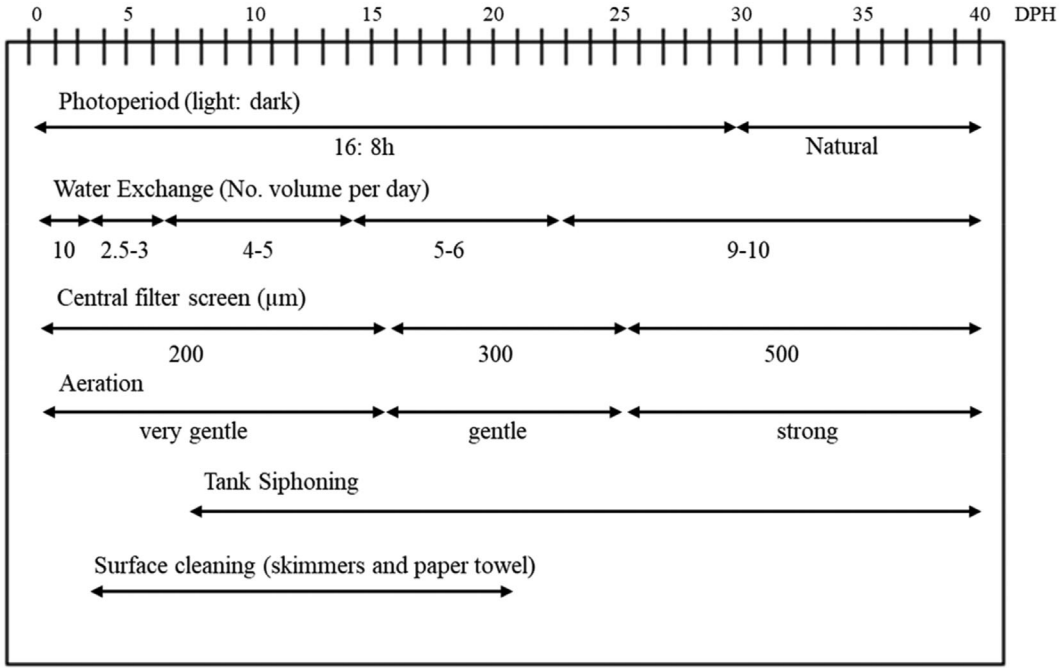

FIGURE 1 Rearing protocol of red snapper *Lutjanus campechanus* larvae.

TABLE 1 UMEH culture and enrichment protocol for s-strain rotifers (*Brachionus rotundiformis*).

Culture day	Culture density (rotifers/ml)	Media diet	Feeding rate (g mill rot^{-1})
Day 1	1000	OriOne	0.45–0.55
Day 2	1200–1500	OriOne	0.35–0.45
Day 3	1500–2000	OriOne	0.3–0.25
24 h UMEH enrichment	1000	Rotigreen (20%) N-Rich (5%) Protein Plus (2.5%) AlgaMac (30%) Astaxantin (2.5%) Yeast (40%)	0.3

feeding at a rate of 4 g/L. The addition of dissolved taurine in the rotifers culture can result in internal taurine concentrations identical to that of wild copepods (Hawkyard et al., 2016).

Rotifers were harvested before each feeding period, at 06:00 a.m., 10:30 a.m., 01:30 p.m., 04:30 p.m., and 07:30 p.m., after counting the residual quantities of rotifers in each larval tank. The number of rotifers fed to each tank was calculated to maintain a concentration of 15 rotifers/ml in the first day of feeding, 20 rotifers/ml between the 4–5 DPH, and 25 rotifers/ml from 6 to 20 DPH. After 20 DPH, the number of rotifers was gradually decreased until 25 DPH, when the fish were fed exclusively *Artemia* sp. metanauplii. Rotigreen algae in paste was used as green water in the larval tanks, added prior to each rotifer feeding in concentrations of 6–20 ml of algae/m^3, depending on the intensity of water exchange, to maintain a concentration of 500,000–700,000 cells/ml in the rearing tanks. Green water has been widely used in larval fish aquaculture as a form of mitigating light-intensity and enabling efficient establishment of exogenous feeding, as well as a nutritional supplement for live feed (Schwarz et al., 2008; Van der Meeren et al., 2007; Wang et al., 2019).

Artemia sp. nauplii and metanauplii were supplied to the larvae from 18 DPH until 35 DPH. Recently hatched nauplii were provided for the first 3 days, and enriched metanauplii for the rest of the period. *Artemia* sp. metanauplii were enriched with a diet developed at UMEH containing 85% Algamac 3050 (Aquafauna Bio-Marine Inc., Hawthorne, CA), 10% N-rich, 5% Astaxanthin, 1 g/L of taurine, and 0.5 g/L of sodium bicarbonate. A commercial water-conditioner Sanocare Ace (INVE Aquaculture Inc., Salt Lake City, UT) was used in both the hatching and enrichment process. *Artemia* sp. used for the daily feedings were maintained in a cold storage container with temperatures ranging from 8–12°C. The *Artemia* sp. were fed to the larvae at 07:00 a.m., 09:00 a.m., 12:00 p.m., 02:00 p.m., 04:00 p.m., 07:00 p.m., starting with a concentration of 0.05 *Artemia* sp/ml per feeding at 18 DPH, reaching 7 *Artemia* sp/ml per feeding at 30 DPH. At this point, co-feeding with dry feed began and the amount of *Artemia* sp. that were supplied for each feeding gradually decreased until juveniles were completely weaned onto dry feeds.

An artificial diet of 350-μ sized crumble with 56.3% of crude protein (Otohime; Reed Mariculture Inc., Campbell, CA) was first introduced ad libitum at 30 DPH, and the particle size of inert diet was gradually increased until the fish were completely weaned at 35 DPH. During the weaning, the inert diet was supplied 30 min before each feeding of *Artemia* sp., and after the co-feeding concluded, it was supplied each hour.

The feeding protocol for red snapper larval rearing developed in this study is presented in Figure 2.

2.4 | Sample and data analysis

Larvae were sampled daily during the first 6 days of feeding. In the first larval rearing trial, an estimation of survival rate was determined at 12 DPH by collecting three subsamples of tank water to estimate the total number of larvae in the tank. A 5 cm diameter straight pipe with a valve was submerged in each tank to collect the samples from the entire water column (vertical sample). The contents of the samples were poured over a 200-μ filter, and the total number of larvae were counted. The result was expressed as a mean of three samples. The survival rate at this period (pre-flexion stage) was used to determine the adequacy of rotifers as first prey for red snapper larvae. In the second larval rearing trial, the survival rate was determined at 20 DPH by similar methodology. The estimation of the survival rate at this point could be useful for understanding the most important periods of mortality during larval rearing that are not related to first feeding.

At 40 DPH, juveniles were collected from all tanks and transferred to different nursery systems. In the first larval rearing trial, all larvae were manually counted during transfer, and in the second larval rearing trial, as the tanks had higher density, fish were sedated using clove oil at a concentration of 2 ppm to reduce handling stress during transfer; and batched weighed with the use of fish nets and 15 L buckets to obtain the total biomass in each tank. Three samples of 50 juveniles per sample were collected and weighed to obtain the average weight per fish. The total number of harvested fish from each tank was obtained by dividing the total biomass harvested by the average juvenile weight. Measurements of standard length (mm) were made at 3 DPH and at time of transfer with an optical microscope (Leica Microscopes CME; Buffalo, NY).

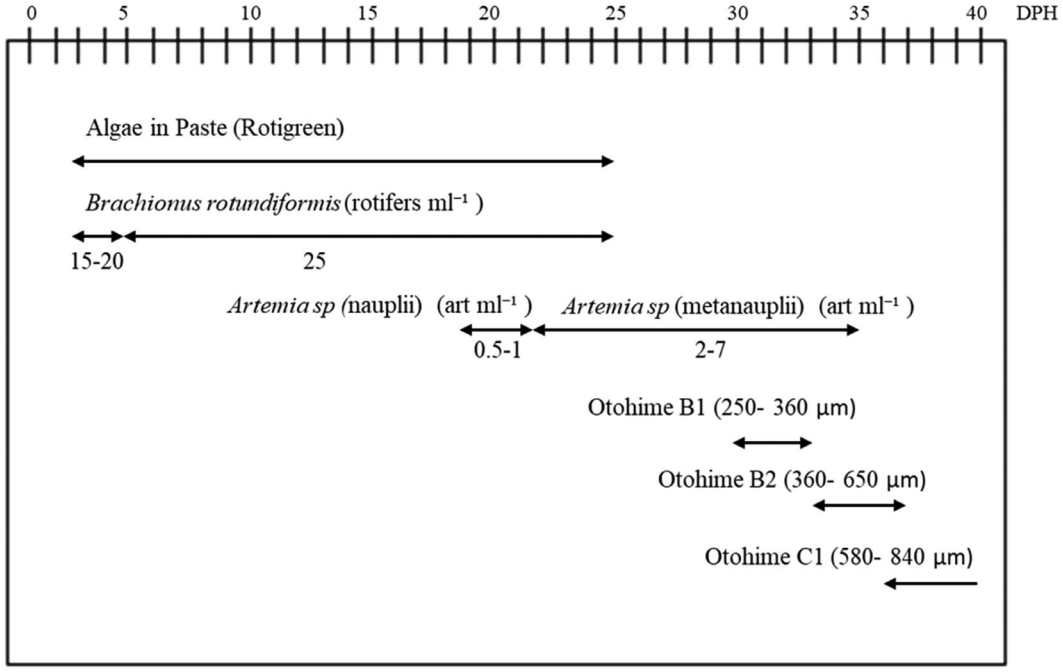

FIGURE 2 Feeding protocol of red snapper *Lutjanus campechanus* larvae in culture conditions.

Productivity (juveniles/L) and final survival were calculated for each tank and trial. Final survival rates from each trial were arcsine-transformed and a student's *t*-test (Microsoft Excel, 2016) was used to compare mean survival rates among the two trials (Zar, 1996). The coefficient of variation (CV) was calculated for the mean percentage final survival of each trial.

3 | RESULTS

3.1 | Egg production

Over the course of the spawning season reported in this study, a total of 6.44 million eggs was collected from 23 viable natural spawns from the broodstock cohort, with fertility rate averaging 68.0 ± 6.35%. For the larval rearing trials reported in present study, 1.01 million fertilized eggs were used: a total of 135,000 eggs for the first larval rearing trial and 877,000 eggs for the second larval rearing trial.

The average diameter of the eggs was 847.75 ± 5.78 µm, and the mean oil droplet diameter was 151.11 ± 1.36 µm. For the two spawns used in the larval rearing trials, the mean fertilization rate was 95.50%, and the mean hatch rate was 82.22%. At 25.5°C, the incubation period was 24 h. The standard length of newly hatched larvae averaged 2.11 ± 0.03 mm.

3.2 | Larval and juvenile production

The larvae exhibited fully pigmented eyes and open mouths by the end of 2 DPH. At the start of the first feeding (at 3 DPH), the yolk-sac reserves and oil globules were almost fully consumed. At the end of the first day of feeding, 60% of larvae exhibited enriched rotifer content in their guts. At 4 DPH, all larvae had rotifers in their guts.

The formation of the swim bladder started at 6 DPH, and its inflation occurred until 12 DPH, when swim bladder inflation was >95% in all larval rearing tanks. The survival rate of the tanks calculated at 12 DPH averaged 66.09 ± 0.08% (Table 2), and at 20 DPH averaged 23.32 ± 0.02% (Table 3).

A delicate period was observed with the introduction of the *Artemia* sp. at 18 DPH, and persisted until 30 DPH, when the larvae are going through metamorphosis. Settlement behavior at the bottom of the tank became apparent, and it was possible to alleviate this behavior throughout metamorphosis by manipulating light intensity and aeration. Overall, the larvae exhibited considerable high mortality during this critical phase.

After 30 DPH, cannibalistic behavior was very evident. Size heterogeneity in the larvae and juveniles was observed as early as 12 DPH, but it was also noted that the cannibalism was not solely a size related issue, as a general aggressive behavior was characteristically of larvae of red snapper at this stage. This behavior was more evident in tanks with higher densities. In the present study, higher mortalities were related to cannibalism after the period of metamorphosis, persisting until 40 DPH.

A total of 5253 juveniles were harvested at 40 DPH from the eight 0.4 m^3 tanks, with survival rates ranging from 1.54% to 11.27%. The average survival rate was 4.61 ± 0.01% at the same age (Figure 3), and calculated CV was 0.64. The mean final density of this larval rearing trial was 1.64 ± 0.40 juveniles/L. A total of 26,596 juveniles were produced in the four 2.4 m^3 tanks with survival rates at 40 ± 2.8 DPH ranging from 3.10% to 5.56%. The average survival rate was 3.95 ± 0.01%, and calculated CV was 0.28. Fish averaged 0.35 ± 0.02 g in body weight and 28.83 ± 0.06 mm in standard length, and the mean final density was 3.69 ± 0.44 juveniles/L. Mean final survival rates were not statistically different among the two larval rearing trials (student's *t*-test, $p > 0.05$). In total, 31,849 early-juveniles were harvested at 40 ± 2.8 DPH across all tanks, with a mean final survival of 4.43% ± 0.01, and mean final density of 2.20 ± 0.42 juveniles/L.

4 | DISCUSSION

Enriched s-strain rotifers were successfully used as the sole first-feeding prey item for *L. campechanus* larvae, leading to pilot-scale production quantities of fully weaned juveniles that meet or exceed those reported in other studies using copepod nauplii for first feeding (Bootes, 1998; Ogle & Lotz, 2006). In addition, when tracking larval growth and development from first-feeding larvae to early-juveniles, the results achieved here mirrored the study conducted

TABLE 2 Summary of stocking density, survival rates, number of larvae and juveniles produced of red snapper *Lutjanus campechanus* during Trial 1.

Tank	Volume (m^3)	Larvae stocked 1 DPH	Number of larvae at 12 DPH	Survival at 12 DPH	Number of juveniles at 40 DPH	Survival at 40 DPH	Juveniles/L
S1[a]	0.4	14,250	2420	16.98%	689	4.84%	1.72
S2[a]	0.4	14,250	9696	68.04%	950	6.67%	2.37
S3[a]	0.4	14,250	10,181	71.45%	418	2.93%	1.04
S5[a]	0.4	14,250	10,666	74.85%	337	2.36%	0.84
S6	0.4	14,250	12,120	85.05%	629	4.41%	1.57
S7	0.4	14,250	13,090	91.86%	1606	11.27%	4.01
S8	0.4	14,250	9212	64.65%	220	1.54%	0.55
S10	0.4	14,250	7957	55.84%	404	2.84%	1.01
Mean ± SEM				66.09 ± 0.08		4.61% ± 0.01	1.64 ± 0.40

[a]Tanks had photoperiod of 24 h light until 12 DPH.

TABLE 3 Summary of stocking density, survival rates, number of larvae and juveniles produced, and size parameters of red snapper *Lutjanus campechanus* during Trial 2.

Tank	Volume (m^3)	Larvae stocked 1 DPH	Number of larvae at 20 DPH	Survival at 20 DPH	Number of juveniles at 40 DPH	Survival at 40 DPH	Mean weight at 40 DPH (g)	Standard length at 40 DPH (mm)	Juveniles
A1	2.4	108,000	30,000	27.78%	9211[a]	3.10%	0.32	28	3.83
A2	2.4	188,800	40,000	21.19%					
A3	2.4	188,800	40,000	21.19%	10,503	5.56%	0.4	30	4.37
A4	2.4	216,000	50,000	23.15%	6882	3.19%	0.34	28.5	2.86
Mean ± SEM				23.32 ± 0.02		3.95 ± 0.01	0.35 ± 0.02	28.83 ± 0.60	3.69 ± 0.44

[a]Tank A2 was combined with A1 before the final count at 40 DPH.

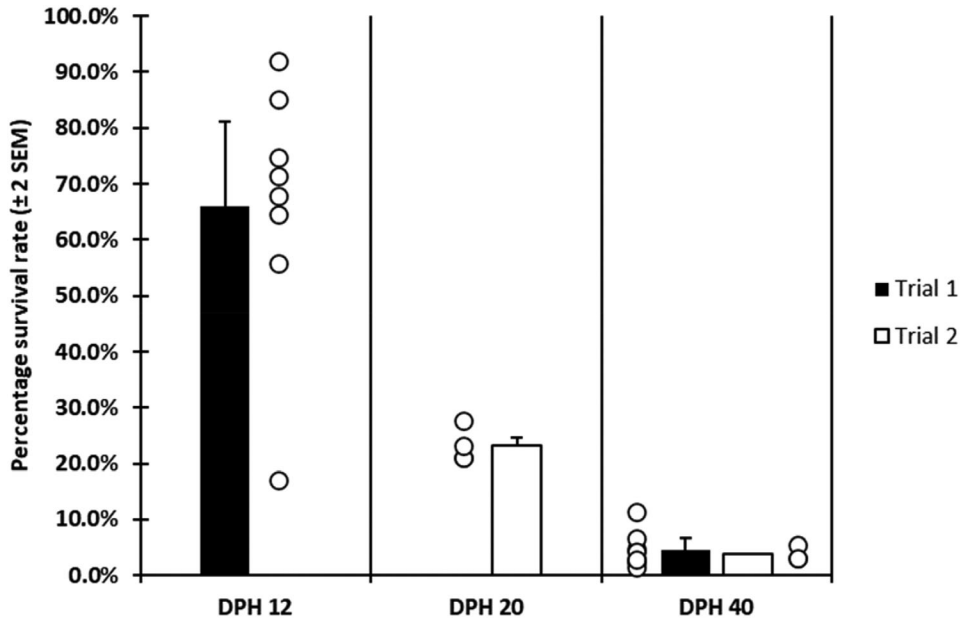

FIGURE 3 Survival rates of *Lutjanus campechanus* for Trial 1 (initial stock density of 35 larvae L^{-1}), and for Trial 2 (initial stock density of 75 larvae L^{-1}). Bars indicate mean percentage survival rate from each trial at different stages of development, and circles indicate survival of individual tanks. Error bars are 2 SEM.

by Drass et al. (2000) which fed copepods as first prey item, suggesting that the larvae in the current study did not suffer from any nutritional deficiencies as a result of diet. Such results suggest that providing high-quality enriched s-strain rotifers can result in successful first feeding of this species (60% feeding success during the first day of feeding, and 100% during the second day of feeding) and establish a sufficient diet for downstream success throughout the entire larval period.

In many studies involving *L. campechanus*, major bottlenecks were reported during the first days of larval rearing related with the first feeding, and high mortalities were observed as a consequence after 8 DPH (Bardon-Albaret, 2014; Bardon-Albaret et al., 2013; Bardon-Albaret & Saillant, 2017; Ogle & Lotz, 2006; Saillant et al., 2013; Williams et al., 2004). Such issues were not observed in the present study. The estimated survival rate (Figure 3) at 12 DPH (66.09 ± 0.08%) was high when compared to survival rates at this stage of development in other challenging marine fish species (Alvarez-Lajonchère et al., 2012; Gutiérrez-Sigeros et al., 2018; Ogle & Lotz, 2006) demonstrating the success in the first feeding using exclusively rotifers. When compared with the mean final survival rate (4.43 ± 0.01%) at 40 DPH, results indicate that the high mortalities during larval rearing were observed in three further phases: (a) metamorphosis, after 20 DPH, (b) introduction of *Artemia* sp. and (c) weaning and cannibalism after 30 DPH. These critical periods were also reported in other snapper species (Gutiérrez-Sigeros et al., 2018; Leu et al., 2003; Watanabe et al., 1998).

These limitations can be avoided and further work with red snapper larval rearing should consider: (a) alleviating the stress of the larvae through manipulation of light, water current, aeration, and improved larval nutrition (Ibarra-Castro et al., 2020); (b) providing a high-quality, clean and disinfected *Artemia* sp., since it can be the source of introduction of bacteria in the culture environment (Høj et al., 2009); and (c) improving feeding and size-grading protocol after weaning to avoid the cannibalism associated with size heterogeneity of the cohort (Folkvord, 1991).

Mean final survival rates were not statistically different among the two larval rearing trials, suggesting that final survival was not density-dependent, and initial stock densities ranging 35–75 larvae/L can be suitable for red snapper larval rearing (Figure 3).

Although copepods have been successfully used for a variety of snapper species that also exhibit small mouth gapes, their culture is reportedly more complex, expensive, and require more production area than rotifer culture (Saillant et al., 2013; Stottrup, 2000), especially when considering the production of commercial amounts of live prey. Consequentially, the exclusive use of rotifers as first-feeding prey items for this species is a very encouraging result for the development of commercial-scale red snapper aquaculture industry.

While no direct comparison was made between the use of rotifers and copepods during the first feeding of red snapper in this study, future research should consider investigating differences that may occur with the use of each prey type during the larval rearing of this species. Furthermore, integrating the use of rotifers and copepods during the first feeding could be an alternative for small-mouth marine fish species, and likely optimize results. However, as private production companies raising red snapper seek immediate methods to improve larval production, the protocol presented in this study represents an important alternative that does not necessitate copepod culture.

The development of a reliable and intensive protocol for larval rearing production of a species is one of the first steps in realizing commercial-scale culture feasibility. This study builds upon results of previous trials conducted on this species. As reported, the exclusive use of rotifers as first-feeding prey for red snappers overcomes a significant bottleneck for the reliable mass production of this species and makes an important contribution towards a collective effort to support the development of commercial-scale aquaculture of this iconic species.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Yole Buchalla https://orcid.org/0000-0003-0600-6131
John D. Stieglitz https://orcid.org/0000-0003-3926-4364

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