



Reproduction of the dog snapper *Lutjanus jocu* in captivity, linking ecological, and production observations

Evandro Malanski^{1*} ⁽ⁱ⁾, Ana Cecilia Gomes Silva Malanski¹ ⁽ⁱ⁾, Luiz Fernando Loureiro Fernandes¹ ⁽ⁱ⁾

¹ Universidade Federal do Espírito Santo 🔅 - Centro de Ciências Humanas e Naturais, Departamento de Oceanografia e Ecologia, Base Oceanográfica – Aracruz (ES), Brazil.

*Corresponding author: evanmal@gmail.com

ABSTRACT

Snappers' domestication for reproductive purposes is a first step to allow future offering of high quality, more sustainable fish products, generating ecological advantages to the marine ecosystem such as the reduction on the pressure of current stocks. The dog snapper *Lutjanus jocu* is a very important species with very little information on its capability for domestication. For that reason, dog snappers were collected in the coastal area and maintained in laboratory to verify their capacity to be domesticated and achieve reproductive success. A specific protocol was designed for their maintenance in recirculating aquaculture systems and is presented in the methods section. The domestication of wild specimens until they achieved reproductive success and produced viable eggs in captivity took approximately 2.5 years. Spawning events produced an average of about 25,000 eggs, or about 2,100 eggs·kg¹ of broodstock, with an average of three events per week. During new and full moon, the viability of eggs was higher, showing a strong influence of the lunar cycle in their reproduction. Spawning activities only happened during the night, and embryo development took about 535 degree-hours. Our results concluded that the dog snapper *L. jocu* can be conditioned in captivity for reproductive purposes, with consistent production of eggs in a weekly basis, enabling the possibility of a large-scale production to help reduce the pressure on the natural stocks.

Keywords: Reproduction; Snapper; Fish culture; Egg production; Broodstock management.

Reprodução do vermelho-dentão *Lutjanus jocu* em cativeiro, relacionando observações ecológicas e de produção

Resumo

A domesticação dos pargos para fins reprodutivos é um primeiro passo para permitir a oferta futura de produtos pesqueiros mais sustentáveis e de alta qualidade, gerando vantagens ecológicas ao ecossistema marinho, como a redução da pressão aos estoques atuais. O vermelho-dentão *Lutjanus jocu* é uma espécie muito importante e com poucas informações sobre sua capacidade de domesticação. Por esse motivo, vermelhos-dentão foram coletados na área costeira e mantidos em laboratório para verificar sua capacidade de serem domesticados e alcançarem sucesso reprodutivo. Um protocolo específico foi elaborado para sua manutenção em sistemas de recirculação em aquicultura e é apresentado na seção de metodologia. A domesticação de espécimes selvagens até alcançarem sucesso reprodutivo e produzirem ovos viáveis em cativeiro levou aproximadamente 2,5 anos. Os eventos de desova produziram cerca de 25 mil ovos, ou 2.100 ovos·kg⁻¹ de reprodutores, com média de três eventos por semana. Durante as luas nova e cheia, a viabilidade dos ovos foi maior, mostrando a forte influência do ciclo lunar na sua reprodução. As atividades de desova só aconteciam durante a noite, e o desenvolvimento do embrião demorava 535 graus-hora. Nossos resultados concluíram que o vermelho-dentão *L. jocu* pode ser acondicionado em cativeiro para fins reprodutivos, com produção consistente de ovos semanalmente, habilitando a possibilidade de produção em larga escala para ajudar a reduzir a pressão sobre os estoques naturais.

Palavras-chave: Reprodução; Pargo; Piscicultura; Produção de ovos; Manejo de reprodutores.

Received: October 28, 2023 | Approved: August 15, 2024 Section editor: Fabiana Garcia ()



INTRODUCTION

Marine fish farming has attracted the attention of scientists and producers to develop a diverse supply of animal protein to society, with the possibility of being raised offshore at sea to avoid land usage, and thus meeting the current demands for this type of food through high-quality products, contributing directly and indirectly to the economy of several coastal and inland regions in the world (FAO, 2018).

To reduce pressure on fish stocks in the natural environment, solutions must be presented, and aquaculture is the best alternative. Species of relevant commercial interest, such as snappers, have suffered from overfishing and consequent decline in their stocks (FAO, 2018), forcing technological and practical developments in aquaculture, both at local and global scales, aiming to prevent the collapse of fisheries.

In Southeast Brazil, the dog snapper *Lutjanus jocu* is a species of relevant commercial interest due to its white and tasty meat. This contributes to a high demand for this fish and, consequently, high commercial value. In estuarine systems, *L. jocu* is very abundant in the juvenile stage, suggesting that the environmental conditions are favorable for their development into the adult stage (Pimentel & Joyeux, 2010). However, finding larger mature adults of this species is not an easy task. Their behavior of creating spawning aggregations in places far off the coast (Bezerra et al., 2021), also with fishers informing that the dog snapper has been disappearing from their catches in recent years, suggests that natural and artificial pressures (fisheries, pollution, habitat degradation) on their stock have been impacting its populations.

The spawning aggregations of snapper species in the natural environment are documented for several places, and it is also common to relate their spawning events to the moon or tide phases (Boza-Abarca et al., 2008; Grimes, 1987). This knowledge is tentatively used to explain egg production in laboratory facilities (Emata, 2003), where controlled conditions are applied to simulate the natural environment to best control the spawning events, although artificial/semi-artificial spawning attempts are also applicable (Boza-Abarca et al., 2008; Emata, 2003).

Although several studies have been performed with snappers regarding its domestication (Baesjou & Wellenreuther, 2021) and reproduction (Arnold et al., 1978; Phelps et al., 2009), no information is presented for the dog snapper *L. jocu*. The main goal of this study was to provide novel information on the domestication and reproduction of the dog snapper *L. jocu*, establishing the necessary protocols for successful egg production, and information on hatching success.

MATERIALS AND METHODS

This study was conducted at the Marine Organisms Rearing Laboratory (LABCOM) at the Universidade Federal do Espírito Santo Oceanographic Station, in Aracruz, Espírito Santo, Brazil. The LABCOM is located 200 m from the beach, where seawater was collected for the experiments. This beach is influenced by an estuarine system (Piraquê-Açu and Piraquê-Mirim rivers); consequently, the water quality is always changing, and the salinity varies considerably along the year, even during a single day. Seawater was collected and treated prior to its use in the rearing tanks by physical equipment (decanters and sequence of filters with several particle sizes retention) and chemical compound (chlorination).

Adult dog snappers were sampled with a hook and line in the estuarine system near the laboratory, SISBIO collecting license numbers 64108-2 and 77273-1. There was no evidence of mature *L. jocu* individuals in this estuarine system despite its availability, being generally small in size with less than 500 g. Larger individuals (> 1 kg) were only found distant from shore. Consequently, most of the individuals used in the experiment grew and matured in the laboratory after approximately three years of confinement.

Once fish was captured, it was brought to a quarantine system prior to their introduction into the production system. The quarantine procedure comprised of freshwater and formaldehyde (10 mg \cdot L⁻¹) baths during 10–30 minutes, in separate containers, every other day, for two weeks, and daily full seawater exchange in the quarantine tank. During the first five days, fish were not fed so they could empty their guts. After one month, if the fish had no signs of disease during the entire period (skin ulcer or hemorrhage, popped eyes, fin rot, abnormal swim behavior), and was feeding normally, they were tagged with a microchip and moved to the production system. Fish returned to the quarantine system when any problem was detected, and the quarantine protocol was applied until the problem was solved.

The Lyfe Support Systems (LSS) used throughout this investigation were composed of two production units using recirculating aquaculture system (RAS) technique: RAS1 had 11 tanks with 400 L of volume each, and RAS2 was a single tank with 5,000-L volume. Both systems had their own water treatment unit composed by a pump, a sump, physical and biological filters, a skimmer, an ozone generator, and an ultraviolet-C (UV-C); this increased the water volume in about 1,000 L to each system. The RAS1 was used as a recovery system in which fish was kept isolated in each tank, while the RAS2 was used as a reproduction system in which the broodstock was kept in shoal, with an egg collector tank (0.5-mm mesh size sieve) on the side of the tank continuously receiving water from the upper 25 cm of the water column. In both production systems, the drainage of the tanks was done centrally from the bottom flowing to the sump, but in the reproduction tank it had a 0.5-mm mesh size net attached at the end of the pipe, prior to its flow to the sump, to retain eggs missed by the egg collector. Salinity, temperature, pH, and dissolved oxygen were recorded at least three times a week. The photoperiod was kept 12/12-h light/dark using a timer.

In the production system, the broodstock was fed to satiation. Chopped sardine, squid, and shrimp were used for feeding, as well as commercially available extruded or pelleted fish food. This variety of food fulfilled the energy requirements for the broodstock to reach maturity. The pelletized food is the first one given as it is the least preferred by the broodstock, although it has important nutrients and vitamins that may not be available in other food provided. The protocol applied routinely is presented in Fig. 1.

Initially, 16 dog snapper (average of 957.5 g and 32.9 cm SL) were kept in the reproduction tank (RAS2) under controlled

environmental conditions. Every morning, prior to feeding the broodstock, the egg collector and the tank were checked for any signs of reproductive activity. As far as behavior, this species is very aggressive when mating, so the signs of reproductive activity does not include only the presence of eggs (spawn), but also the presence of an injured fish. When spawning was observed, eggs were gently collected, rinsed for few seconds with tap water, and quantified volumetrically. The volumetric estimation was done with the use of a calibration obtained, when several subsamples of 0.5 mL had the eggs quantified (1,400 eggs/mL, approximately), and other subsamples of eggs had biometric data and pictures obtained. The presence of buoyant eggs represents the viable eggs (or the eggs that were fertilized), and these were separated from the non-buoyant eggs, placed in a hatching container (2-L Becker), filled with filtered and sterilized seawater, with constant slow aeration to keep the eggs in movement and with oxygen. When larvae were observed, the water container was gently poured into the larviculture tank with green water and aeration. The estimated embryo development, in degree-hours, was measured by the difference between time

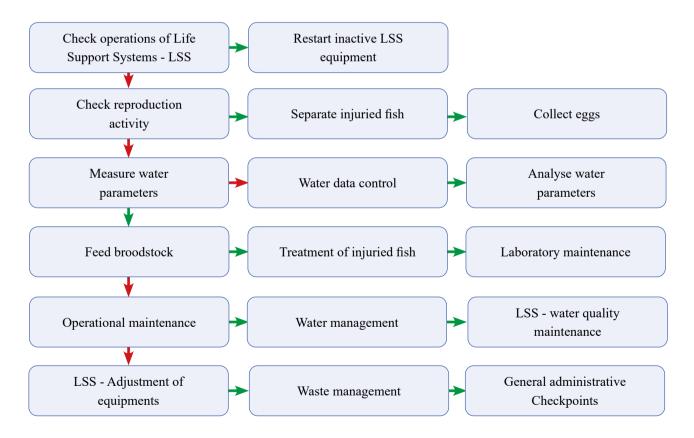


Figure 1. Daily routine protocol applied in the rearing laboratory facility during the domestication and reproduction activities. The activity flow is defined by arrows and levels; green arrow has preference over the red ones; top levels must be completed previously than the below ones.

of spawning and time of hatching, multiplied by the mean water temperature throughout the period.

If an injured fish was detected in RAS2, it was removed and transferred to a secondary recovery system (RAS1); the sooner the injured fish was isolated for recovery, the higher the chance of its survival. After transferring the injured fish from RAS2, the tank was cleaned, and scales that had fallen due to aggression were collected and weighed.

Biometric data was obtained before and after the study. No measurement was taken after the first spawning event to avoid stress to the broodstock. The estimated average weights of the fish at a specific date were based on the growth observed between the two measurements. Also, for analytical purposes, all the fish kept at RAS1 and RAS2 were considered the broodstock for food uptake evaluation, while only the fish kept at RAS2 were considered the broodstock for egg production estimates. The lunar cycle was registered to evaluate its influence over egg production and viability, and broodstock reproduction attempts.

RESULTS

During the first 18 weeks of 2022, that corresponds to the duration of this experiment, from the initial broodstock in the RAS2 reproduction unit (16), only seven individuals remained until the end (Fig. 2). The decrease of the broodstock was due mainly to the aggressive behavior of this species—one fish becomes the focus of the aggression during and after the spawning stimulus, until the fish becomes completely exhausted and critically injured. This could be also related to some dominance within the shoal, as the aggressions also happen without the presence of eggs in the tank. These were considered

the negative reproductive attempts of the species, possibly promoted by the dominant female that had no egg to be released and needed to repel the males that kept approaching its genital duct. Scales that had fallen from a single injured fish in one night weighted 23 g, leaving the fish almost without scales in both sides, and with several scratches and severe punctures in its skin. Despite injured fish being transfer to RAS1 for recovery, two individuals died after few days due to the severe injuries related to this aggressive mating behavior.

Considering weekly food consumption, an average of 2 kg of food was supplied to the broodstock (i.e., 12% of their total weight) for both the reproduction and recovery tanks. The food supplied was composed of chopped fresh sardine (83%), chopped fresh squid (9%), commercial extruded fish feed pellet (7%), and chopped fresh shrimp (1%). Food was always given to satiation.

Regarding the positive reproductive attempts, 41 spawning events in the reproduction tank were detected (Fig. 2). Categorizing spawning by moon phases, 10 happened in the new moon, seven in the first quarter, 11 in the full moon, and 13 in the last quarter. Within the 18 weeks period, only two weeks (weeks 11 and 16) did not have spawning events; that could be related to some induced stress when capturing injured fish to move to RAS1. First week was represented by one day and is not considered as a full week. In general, when spawning was observed, an average of three events occurred in a week, commonly with one day resting between spawning events, although it also happened in three consecutive days. The spawning activity only happened when the facilities were in the dark, being checked for eggs at about half an hour after the lights were off, when possible, which was at 6:30 p.m., although not always confirmed.

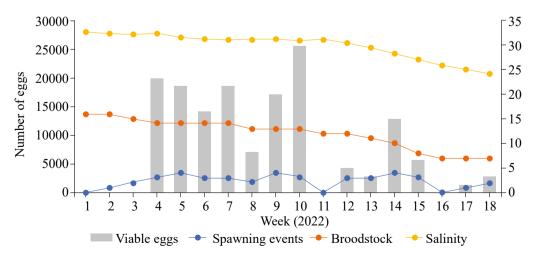


Figure 2. Variability of the sum of viable eggs produced (grey bars, left axis), and for the right axis the following: number of spawning events (blue line), number of the broodstock (orange line), and the average of salinity measurements (yellow line) along the weeks of 2022.

With the periodic observation of events during this investigation (Fig. 2), some details can be highlighted: the broodstock did not produce viable eggs in their first attempts (weeks 2 and 3); the quantity of spawning events per week was increasing until stabilized by week 7; the ratio of viable eggs started to increase until reaching its peak in week 10. After week 10, despite other possible disturbances, the seawater available in the laboratory for the experiments had its salinity lowered, a situation that might have led to a decrease in viable eggs, and even the discouragement to reproduce. The overview of all these situations suggests that the broodstock was still learning how to succeed when mating.

An estimated 1.05 million eggs were produced in the 18week period, of which only 14.3% were viable. The spawning events produced between 4,254 and 76,572 eggs (average of 25,593), and the viability of eggs in these spawning events were between 0 and 57.1%. Regarding egg production per broodstock size, it ranged between 289 and 9,638 eggs \cdot kg⁻¹ of broodstock (average of 2,167). When observing the viability of eggs by the moon phases, the most viable eggs were produced in the new and full moons (17.7 and 16.5%, respectively), while the first and last quarter moons produced less viable eggs (5.9 and 13.1%, respectively).

The water parameters at the RAS2 were kept as constant as possible after the first successful spawning event, intentionally to avoid fish stressors. However, that was not possible for salinity. The salinity at the RAS2 varied due to natural environmental changes in water salinity, water exchange, and cleaning of the system. The water exchange for the system was 8% per day, generating a weekly water consumption of about 3.5 m³. The averages and ranges for the environmental parameters were: temperature 26.8°C (26.1-27.4°C), salinity 29.7 (23.9-32.6), pH 8.2 (7.9–8.4), and dissolved oxygen 6.1 mg \cdot L⁻¹ (4.4–8.9 mg \cdot L⁻¹). The broodstock started reproducing when salinity was at 32.6. The decrease in salinity reached its lowest value at week 18, when it reached 24.1. Considering the viability of eggs with salinity, the higher the salinity, the higher the percentage of viable eggs (Fig. 3). Also, when salinity was higher, most of the eggs flowed straight to the egg collector (Fig. 3).

The egg collector was always verified early in the morning, when eggs were collected, quantified, and transferred to the hatching containers. Even though non-buoyant eggs were considered unfertilized, few larvae could have hatched from them, meaning that few fertilized eggs are also non-buoyant, and, in this case, these early hatched larvae were transferred to the larviculture tank. It could happen due to a thicker and heavier eggshell (chorion), and/or smaller oil globules, although none of these conditions were checked. Regarding viable eggs, the number of embryos that did not hatch was not quantified, just visually estimated by experienced observer, and, according to this observation, the hatching rates were higher than 97% (i.e., it is assumed less than 500 eggs not hatching from a batch of 15,000 eggs, using the visual experience acquired during egg measurements), when there was no salinity or temperature variation between the reproduction tank and the egg container. This occurred without the use of the green water technique. However, when the available seawater reached lower salinities (i.e., collected and treated available seawater below 25, while the seawater in the tank was still higher than 28), the difference between clean seawater available used in the container to hatch the larvae (25) and that of the reproduction tank in which the eggs were spawned (28) caused no hatching. Consequently, it is better to use poorer water quality from the reproduction tank to hatch the eggs than change it to the cleaner seawater with lower salinities.

Hatching was very synchronized for the whole batch of eggs, estimated to last no more than 30 minutes after the first larvae hatched, and all of them floated straight to the surface, while the eggshells (chorion) dropped to the bottom, facilitating the transfer of only hatched larvae to the larviculture tank. Eggs were in average 0.882-mm wide (n = 30, range: 0.828–0.922 mm) (Fig. 4).

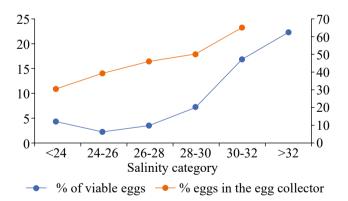


Figure 3. Percentages of viable eggs (left axis, blue line) and eggs in the egg collector (right axis, orange line), according to the salinity categories. The > 32 salinity category has no observation for % of eggs in the egg collector due to lack of data; the few data available for this category have no counting of eggs that flowed straight to the sump, but the % of viable eggs is still possible to obtain despite of the possibility of being inaccurate as it is valid only for the eggs that flowed straight to the egg collector.

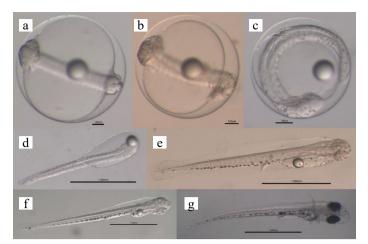


Figure 4. Embryonic and early larval development of dog snapper Lutjanus jocu. (a) C-shaped embryo, 6 hours to hatch; (b) s-shaped embryo, 3 hours to hatch; (c) s-shaped embryo, 30 minutes to hatch; (d) early hatched, yolk-sac larvae; (e) 1-day-old yolk-sac larvae; (f) 2-day-old yolk-sac larvae; (g) 3-day-old pre-flexion larvae.

The early yolk-sac larvae hatched around 3:30 p.m. local time the next day after the spawning, with a size of about 2.1-mm SL, without pigmented eyes and developed mouth (Fig. 4). It means that the estimated embryo development is reached in about 535 degree-hours. The mouth opened two days post hatch (DPH), while the yolk-sac was fully consumed in three DPH, when the pre-flexion larvae presented pigmented eyes and started consuming exogenous food (Fig. 4). At the three DPH pre-flexion stage, the pectoral fins were already present, helping the larvae to stabilize its position in the water column, consequently helping capture food.

DISCUSSION

The reproductive mating behavior of the dog snapper *L. jocu* in captivity has shown a strategy based on aggressiveness in a controlled environment. These aggressive mating attempts that looks like a rape must prompt the female to release their eggs in the water column for the males to fertilize them. Despite linking their aggressiveness to their reproductive strategy, this behavior is also related to some dominance within the shoal, where individuals were injured even without eggs in the tank. Such interactions occur whenever the interest of individuals conflict by the limitation of resources (Xu et al., 2021), considering that territory and mates in the controlled, confinement reproduction tank are considered limiting factors to the dog snapper, while neither food nor nesting sites can be considered limiting factor to individuals.

However, dominance was observed from late larval stages (data not shown) when some specimens started to attack others to scare them off from their surroundings. Based on that observation, we infer that this is probably the primary evolutionary characteristic leading to its aggressiveness as a dominance behavior. This observation also comes from its natural habitat, where early juveniles found in intertidal rocky shores usually settled between rocks, protect their cleft by repelling any other individual that might cross it (personal observation).

Territorialism and aggression are natural components of a species behavior, intrinsic from natural selection that produces individuals that behave selfishly (Briffa, 2010). Consequently, it is understandable when early life stages of fish that pursuit a large mouth gape start to play the aggressive behavior during the progress of a domestication program, sometimes even practicing cannibalism (Duk et al., 2017). In the wild, the balance between benefits and costs modulates the behavior of species, in which hormones play an important role within the aggressive behavior (Duque-Wilckens et al., 2019). The behavior of the dog snapper broodstock follows exactly the social experience of wild animals, even after three years in captivity, hypothesizing the accumulation of hormones in the culture water as verified in other investigations (Good et al., 2017; Hamlin et al., 2008), although not checked in the current investigation. Other Lutjanidae species are also reported to behave in the same way (Turano et al., 2000).

This dominance behavior caused several losses of individuals before successfully achieving reproduction in our investigation. However, at higher density, less losses of individuals occurred. This might be explained by the following: the aggressive interactions has an outcome from a subsequent conflict, meaning that the winner of a conflict interaction is more likely to win again, and the loser is more likely to lose again, even against another opponent (Xu et al., 2021). Consequently, the loser keeps being bitten wherever it moves in the confinement reproduction tank.

The smaller densities result in lower number of potential mates (Holubová et al., 2019) and, as a consequence, less possibilities of new, better interactions. It means that the fish memory and the interaction possibilities are playing an important role in the reproductive strategy of *L. jocu*. Consequently, we assume that, when a shoal is large enough, the dominant individual has a lot more targets to be aware of, while, when the shoal is minimal, the dominant individual just keeps interacting as winner until the loser is gone. In the literature, we could find snappers that reached reproductive success with six specimens in their tank at 0.3 individual $\cdot m^{-3}$ (Boza-Abarca

et al., 2008), and with densities of 1.5-3 individuals·m⁻³ (25 and 50 specimens) (Turano et al., 2000). Here, we succeed with an intermediate density of 3.2 individuals·m⁻³, while neither at the lower (1.2 individual·m⁻³) nor the higher (6.4 individuals·m⁻³) densities succeeded to reproduce.

The conflict between individuals is not desirable in aquaculture, and selections should be made to promote domestication. Considering that natural selection may not be an important scenario for developing aquaculture as individuals should not behave selfishly (Briffa, 2010), there is the need of intentional selection of specimens that grow more and faster, resistant to diseases, and less aggressive. These phenotypes and genotypes can be selected in a hatchery facility through breeding programs (Lhorente et al., 2019), with the most profitable fish being kept at the aquaculture facility. Using individuals from such selections, the management techniques for rearing dog snapper in captivity successfully reached spawning naturally, without the use of hormones. Also, when natural spawning is achieved by the broodstock, it is possible to control it by pairing them in a shoal at the reproduction tank when egg production is required and impairing them individually in tanks to calm them down.

Several species of the Lutjanidae family are known for aggregating in selected areas for reproduction, when they are shoaling in early evening and start spawning activity during night (Grimes, 1987). Some authors even correlate their spawning activity to the moon phase and the tide (Boza-Abarca et al., 2008; Grimes, 1987), where the new and full moons are highlighted for reproduction activity. Indeed, the results obtained also indicate that new and full moon phases produce the most viable eggs, and these results suggest that this signature, within their life cycle, can be selected for controlling spawning activity and synchronization.

It is also important to highlight that reproduction in our broodstock just happened after 2.5 years of confinement of the individuals inside the laboratory, without their perception of the external natural environment, but still the moon phase seems to have effects on reproductive success (Table 1). Despite this success, the ratio of viable eggs is still low when compared to other cultured snappers (Turano et al., 2000), and variation between spawning events was also observed. However, our broodstock were most likely in their first reproductive attempts, still learning how to succeed in mating. It is also possible to suggest that the reproductive season was heading towards its end, but we are unsure if this is the case for the dog snapper, since other authors found other snappers reproducing in laboratory yearround (Turano et al., 2000).

According to our findings, the dog snapper is reaching its sexual maturity at about 1 kg in captivity, what is already a considerable market size. Other Lutjanidae species may mature with lower weights, although it seems they are always older than 2 years old, as discussed by Turano et al. (2000). When metabolic rate is compartmented, it can be partitioned into active, growth, and maintenance components (Barneche & Allen, 2018), meaning that fish do not spend energy for gonadal maturation before reaching maturity. Consequently, any energy acquired is mostly directed to somatic growth. However, when food is given at the production tank, dog snappers are mostly eating when they are shoaling (personal observation), otherwise they eat very little when individually or with few fish kept in the tank (personal observation). This is a key point when farming this fish, and a benefit for keeping a shoal to get a better growth performance. In fact, some Lutjanidae species only need little food requirements to keep them alive (Wakeman et al., 1979), so if they are eating well, and they do so when in a shoal, any extra energy consumed is just assimilated to its body.

CONCLUSION AND CONSIDERATIONS

The dog snapper *L. jocu* can be conditioned in captivity for reproductive purposes, with consistent natural production of eggs in a weekly basis. The correlation between egg production, broodstock, and natural events has shown that, despite the weekly egg production, there is a tendency of producing more eggs during new and full moons, and more viable eggs in higher salinities and broodstock weight.

The reproductive behavior of dog snapper is linked to aggressive interactions, situation that led to the loss of broodstock specimens. This situation requires some effort when dealing with this species, and incidents should be avoided by applying good management practices.

With the reproduction success for this species in captivity and the development of a technological package, the reduction of the pressure of anthropogenic activities (i.e., fisheries, pollution) to their natural stocks is expected if the aquaculture stakeholders start its production. Such investment might not only be good for the enterprise, but also for the environment, as this species has important ecological issues within its occupancy area.

CONFLICT OF INTEREST

Nothing to declare.

DATA AVAILABILITY STATEMENT

The data will be available upon request.



AUTHORS' CONTRIBUTION

Conceptualization: Malanski E; Methodology: Malanski E; Investigation: Malanski E, Malanski ACGS; Data acquisition: Malanski E, Malanski ACGS; Data curation: Malanski E; Formal Analysis: Malanski E, Malanski ACGS; Funding acquisition: Malanski E; Project administration: Malanski E; Supervision: Fernandes LFL; Writing – original draft: Malanski E, Malanski ACGS; Writing – review & editing: Fernandes LFL; Final approval: Malanski E.

FUNDING

Fundação de Amparo à Pesquisa do Espírito Santo Grant No.: 522/2020 Conselho Nacional de Desenvolvimento Científico e

Tecnológico ROR

Grant No.: 316224/2020-0

ACKNOWLEDGEMENTS

We thank the Laboratório de Cultivo de Organismos Marinhos, at Base Oceanográfica/Universidade Federal do Espírito Santo, for providing the infrastructure to the development of this project; and the reviewers for improving this paper with the valuable discussion.

REFERENCES

- Arnold, C. R., Wakeman, J. M., Williams, T. D., & Treece, G. D. (1978). Spawning of red snapper (Lutjanus campechanus) in captivity. *Aquaculture*, 15(3), 301-302. https://doi. org/10.1016/0044-8486(78)90040-6
- Baesjou, J.P., & Wellenreuther, M. (2021). Genomic signatures of domestication selection in the Australasian snapper (Chrysophrys auratus). *Genes*, 12(11), 1737. https://doi. org/10.3390/genes12111737
- Barneche, D. R., & Allen, A. P. (2018). The energetics of fish growth and how it constrains food-web trophic structure. *Ecology Letters*, 21(6), 836-844. https://doi.org/10.1111/ele.12947
- Bezerra, I. M., Hostim-Silva, M., Teixeira, J. L. S., Hackradt, C. W., Félix-Hackradt, F. C. & Schiavetti, A. (2021). Spatial and temporal patterns of spawning aggregations of fish from the Epinephelidae and Lutjanidae families: An analysis by the local ecological knowledge of fishermen in the Tropical Southwestern Atlantic. *Fisheries Research*, 239, 105937. https://doi.org/10.1016/j.fishres.2021.105937
- Boza-Abarca, J., Calvo-Vargas, E., Solis-Ortiz, N., & Komen, H. (2008). Induced spawning and larval rearing of spotted rose snapper, Lutjanus guttatus, at the Marine Biology Station, Puntarenas, Costa Rica. *Ciencias Marinas*, 34(2), 239-252. https://doi.org/10.7773/cm.v34i2.1246

- Briffa, M. (2010). Territoriality and Aggression. *Nature Education Knowledge*, *3*, 81.
- Duk, K., Pajdak, J., Terech-Majewska, E., & Szarek, J. (2017). Intracohort cannibalism and methods for its mitigation in cultured freshwater fish. *Reviews in Fish Biology* and Fisheries 27, 193-208. https://doi.org/10.1007/ s11160-017-9465-2
- Duque-Wilckens, N., Trainor, B. C., & Marler, C. A. (2019). Aggression and Territoriality. In: Choe, J. C. (Ed.). *Encyclopedia of Animal Behavior* (pp. 539-546). Elsevier. https://doi.org/10.1016/B978-0-12-809633-8.90064-5
- Emata, A. C. (2003). Reproductive performance in induced and spontaneous spawning of the mangrove red snapper, Lutjanus argentimaculatus : a potential candidate species for sustainable aquaculture. *Aquaculture Research*, *34*, 849-857. https://doi.org/10.1046/j.1365-2109.2003.00892.x
- Food and Agriculture Organization (FAO). (2018). *The State* of World Fisheries and Aquaculture 2018: Meeting the sustainable development goals. FAO.
- Good, C., Davidson, J., Earley, R. L., Styga, J., & Summerfelt, S. (2017). The effects of ozonation on select waterborne steroid hormones in recirculation aquaculture systems containing sexually mature Atlantic salmon Salmo salar. *Aquacultural Engineering*, 79, 9-16. https://doi. org/10.1016/j.aquaeng.2017.08.004
- Grimes, C. B. (1987). Reproductive biology of the Lutjanidae: a review. In: Polovina, J., Ralston, S., Munro, J. L., Powers, J. E., & Fox Jr., W. W. (Eds.). *Tropical snappers and groupers: biology and fisheries management* (pp. 239-294). Westview Press.
- Hamlin, H. J., Moore, B. C., Edwards, T. M., Larkin, I. L. V., Boggs, A., High, W. J., Main, K. L., & Guillette, L. J. (2008). Nitrate-induced elevations in circulating sex steroid concentrations in female Siberian sturgeon (Acipenser baeri) in commercial aquaculture. Aquaculture, 281(1-4), 118-125. https://doi.org/10.1016/j. aquaculture.2008.05.030
- Holubová, M., Čech, M., Vašek, M., & Peterka, J. (2019). Density dependent attributes of fish aggregative behaviour. *PeerJ*, 7, e6378. https://doi.org/10.7717/peerj.6378
- Lhorente, J. P., Araneda, M., Neira, R., & Yáñez, J. M. (2019). Advances in genetic improvement for salmon and trout aquaculture: the Chilean situation and prospects. *Reviews* in Aquaculture 11(2), 340-353. https://doi.org/10.1111/ raq.12335
- Phelps, R. P., Papanikos, N., Bourque, B. D., Bueno, F. T., Hastey, R. P., Maus, D. L., Ferry, A., Davis, D. A. (2009). Spawning of red snapper (Lutjanus campechanus) in response to hormonal induction or environmental control in a hatchery setting. *Reviews in Fisheries Science*, 17(2), 149-155. https://doi.org/10.1080/10641260802505689

- Pimentel, C. R., & Joyeux, J.C. (2010). Diet and food partitioning between juveniles of mutton Lutjanus analis, dog Lutjanus jocu and lane Lutjanus synagris snappers (Perciformes: Lutjanidae) in a mangrove-fringed estuarine environment. *Journal of Fish Biology*, 76(10), 2299-2317. https://doi. org/10.1111/j.1095-8649.2010.02586.x
- Turano, M. J., Davis, D. A., & Arnold, C. R. (2000). Observations and Techniques for Maturation, Spawning, and Larval Rearing of the Yellowtail Snapper Ocyurus chrysurus. *Journal of the World Aquaculture Society*, 31(1), 59-68. https://doi.org/10.1111/j.1749-7345.2000.tb00698.x
- Wakeman, J. M., Arnold, C. R., Wohlschlag, D. E., & Rabalais, S. C. (1979). Oxygen Consumption, Energy Expenditure, and Growth of the Red Snapper (Lutjanus campechanus). *Transactions of the American Fisheries Society*, 108(3),288-292. https://doi.org/10.1577/1548-8659(1979)108%3C28 8:OCEEAG%3E2.0.CO;2
- Xu, X., Guo, H., Zhang, Z., Wang, Y., Qin, J., & Zhang, X. (2021). Impact of pre-aggressive experience on behavior and physiology of black rockfish (Sebastes schlegelii). *Aquaculture*, 536, 736416. https://doi.org/10.1016/j. aquaculture.2021.736416