



## Effect of Stocking Density on Growth, Size Variation, Condition Index and Survival of Discus, *Symphysodon aequifasciatus* Pellegrin, 1904

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### Abstract

Juveniles of the tropical ornamental fish, Discus (*Symphysodon aequifasciatus*) of mean standard length,  $3.58 \pm 0.03$  cm and mean weight,  $3.36 \pm 0.03$  g, were reared at four stocking densities (1 juvenile/10 L, 1 juvenile/7.5 L, 1 juvenile/5.0 L and 1 juvenile/2.5 L) with three replicates each, for a period of 12 weeks, to evaluate effect of stocking density on growth, condition index, size variation and survival. Growth and survival were recorded after every two weeks. At the end of the culture period, lower densities of 1 juvenile/10 L and 1 juvenile/7.5 L showed significantly higher growth and survival ( $p < 0.05$ ). The condition index and coefficient of variation did not vary significantly ( $p > 0.05$ ) among the stocking densities but coefficient of variation (CV) increased towards the end of the culture period. Results indicated that discus juveniles may be reared at the highest density of 1 juvenile per 2.5 l up to a period of two weeks without affecting growth parameters significantly, at a density of 1 juvenile per 5.0 l up to a period of six weeks and at a density of 1 juvenile per 7.5 l for a period of twelve weeks. It can, therefore, be concluded that a stocking density of 1 juvenile per 7.5 l is optimal for rearing juveniles of this fish without compromising on specific growth, survival and well-being.

**Keywords:** Discus, stocking density, growth, survival, condition index.

### Introduction

Discus is colourful, attractive and one of the costly freshwater ornamental fish (Chong *et al.*, 2002). The market price of discus depends upon its colour, pattern, shape, size, condition, activity and health status. Even though ornamental fish farmers rear them in glass aquaria equipped with sponge filters, very often, they are stocked in very high densities, compromising on their general wellbeing. Scientific data on optimized stocking densities to achieve consistent production of healthy discus is lacking.

The stocking density is one of the most important variables in aquaculture as it directly influences survival, growth, behaviour, health, water quality, feeding and production (de Oliveira, 2012). Several studies have been carried out to record the influence of stocking density on growth, survival, welfare and production of fishes. Both positive and negative relationships between stocking density and growth have been reported and the pattern of this interaction appears to be species specific (Rahman and Marimuthu, 2010).

An increase in density leads to enhanced

energy requirements due to stress (Leatherland and Cho, 1985) causing reduced growth and food utilization (Hengsawat *et al.*, 1997). On the other hand, culturing the fishes at densities less than optimal reduces the efficiency and profitability of culture system. It has been demonstrated that rearing fish at inappropriate stocking densities may impair growth and reduce immune competence due to factors such as social interaction and water quality deterioration which can affect both feed intake and conversion efficiency of the fish (Ellis *et al.*, 2002). The optimum stocking density needs to be determined for each species and the production phase to ensure well-being of the animal, enable efficient management and to maximize production and profitability. Hence, the present study was undertaken to determine the optimum stocking densities for the best growth and survival of juveniles of discus.

### Materials and Methods

#### Experimental Fish

Juvenile discus, *Symphysodon aequifasciatus* (mean standard length,  $3.58 \pm 0.03$  cm and mean

body weight  $3.36 \pm 0.03$  g) were stocked randomly in all-glass aquarium tanks of 120 L capacity equipped with thermostatic heater (set at  $28^{\circ}\text{C}$ ) and sponge filter (Diameter = 120 mm, Height = 90 mm) and filled with filtered freshwater, at four different stocking densities viz. 1 juvenile/10 L, 1 juvenile/7.5 L, 1 juvenile/5.0 L and 1 juvenile/2.5 L of water in triplicate, for a period of 12 weeks..

### Feed and Feeding

The juveniles were fed frozen moist feed (crude protein: 25.8%, mixture of beef heart (90%), *Spirulina* powder (9%) and vitamin-mineral mixture (1%) twice a day (10.00 h and 17.00 h) at the rate of 8% of body weight per day for first eight weeks and at the rate of 7% of body weight per day from ninth week. Dry feed (Tetra bits, having crude protein: 47.7%) was provided at the rate of 1% of body weight once a day at 14.00 h throughout the culture period.

### Water Exchange

The tank water exchanged daily at the rates of 20%, 30%, 40%, 50% and 60% were carried out from first, second to sixth, seventh to eighth, ninth to tenth and 11<sup>th</sup> to 12<sup>th</sup> week, respectively. The sponge filters were squeezed and washed after every three days.

### Growth and Survival

The standard length and weight of the juveniles were recorded after every two weeks and the growth expressed as length gain (%), weight gain (%) and Specific Growth Rate (SGR):

$$\text{Length gain (\%)} = \frac{(\text{Final length} - \text{Initial length}) \times 100}{\text{Initial length}}$$

$$\text{Weight gain (\%)} = \frac{(\text{Final weight} - \text{Initial weight}) \times 100}{\text{Initial weight}}$$

$$\text{SGR} = \frac{(\ln(\text{final weight}) - \ln(\text{initial weight})) \times 100}{\text{Time interval (days)}}$$

Coefficient of variation (CV) for weight within tanks was calculated at the start and end of the experiment to assess size variation by using the formula:

$$\text{CV (\%)} = \frac{\text{Weight standard deviation} \times 100}{\text{Mean weight}}$$

The Condition index was calculated at the start and end of the experiment by using the formula:

$$\text{Condition index (K)} = \frac{\text{Weight in g} \times 100}{(\text{length in cm})^3}$$

Survival was calculated at the end of each sampling period by the formula:

$$\text{Survival (\%)} = \frac{\text{Final number of fishes} \times 100}{\text{Initial number of fishes}}$$

### Analysis of Water Quality

The water quality of each tank was analysed on a weekly basis. Temperature and pH were measured by a mercury thermometer, and pH meter, respectively (Eutech Instruments, Cyberscan pc 510). Dissolved oxygen, total hardness, ammonia-nitrogen ( $\text{NH}_3\text{-N}$ ), nitrite-nitrogen ( $\text{NO}_2\text{-N}$ ) and nitrate-nitrogen ( $\text{NO}_3\text{-N}$ ) were estimated by following standard methods (APHA, 1998).

### Statistical Methods

The data on standard length, weight, length gain, weight gain, specific growth rate (SGR), survival, coefficient of variation (CV) and condition index (K) of juveniles reared at different stocking densities are presented as arithmetic mean  $\pm$  standard error (SE). A one-way analysis of variance (ANOVA) was used to test significant differences in these parameters of juveniles reared at different stocking densities. Wherever significant differences ( $P < 0.05$ ) were found in multiple comparisons, Tukey's HSD test was used to determine which particular pairs differed. Student's *t*-test was employed to test the significant difference in condition index (K) and coefficient of variation (CV) at the start and end of the experiment for each stocking density. These analyses were performed using the statistical software SPSS 16.0.

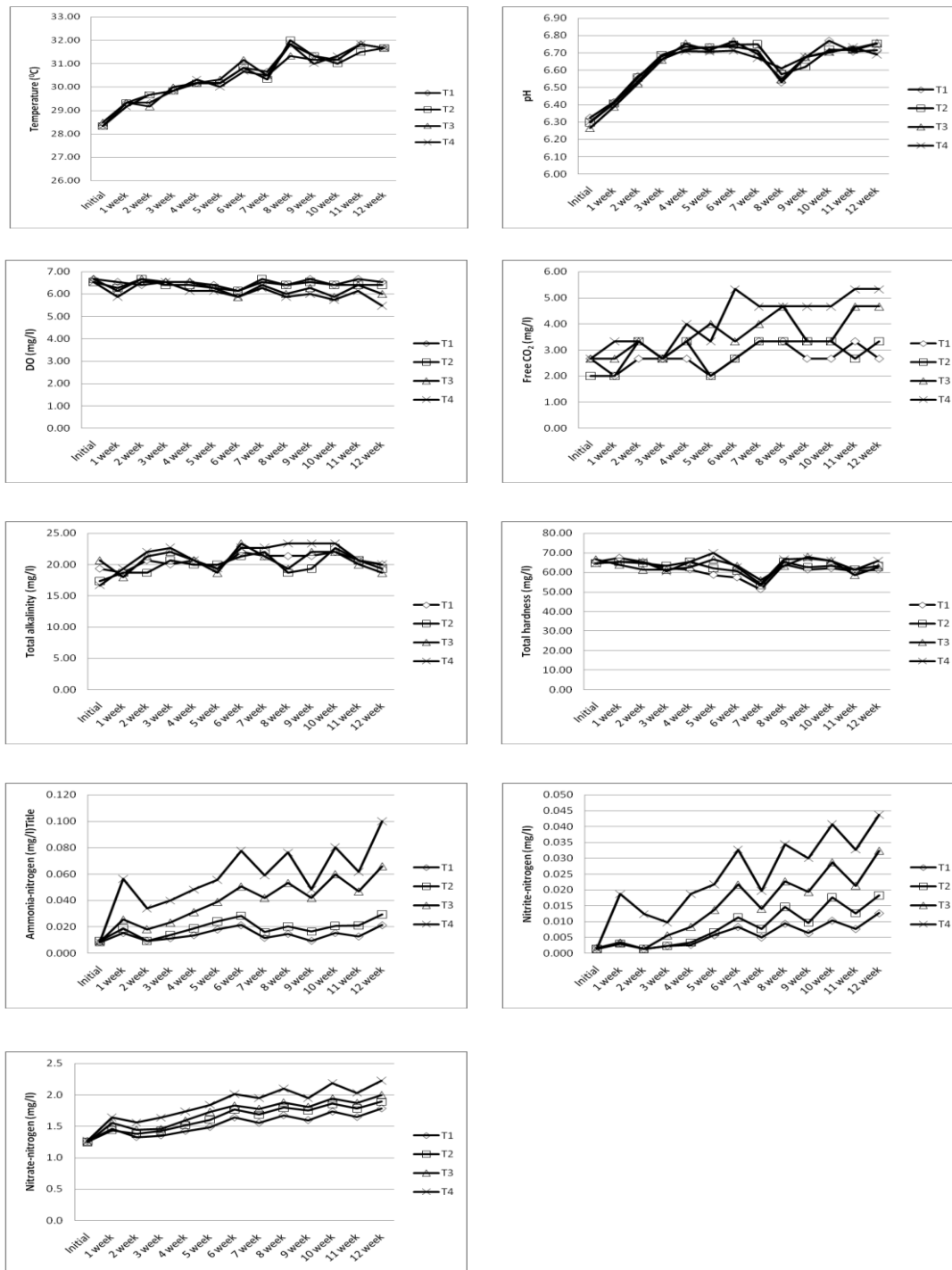
## Results

### Water Quality

All water quality parameters tested except  $\text{NH}_3\text{-N}$  and  $\text{NO}_2\text{-N}$  were within permissible range (Figure 1). The concentration of ammonia-nitrogen ( $\text{NH}_3\text{-N}$ ) and nitrite-nitrogen ( $\text{NO}_2\text{-N}$ ) increased with increase in stocking density. Levels of  $\text{NH}_3\text{-N}$  and  $\text{NO}_2\text{-N}$  exceeded 0.05 mg/l and 0.02 mg/l at the end of the first week and the fifth week of culture at the highest stocking density, increasing above 0.05 mg/l and 0.02 mg/l at the stocking density of 1 juvenile per 5 L, at the end of the sixth week of culture and remained below the threshold level of 0.5 mg/L and 0.02 mg/L at lower stocking densities (1 juvenile per 7.5 L and 1 juvenile per 10 L) till the end of the culture period.

### Survival

At the stocking densities of 1 juvenile per 10 L and 1 juvenile per 7.5 L, no mortality was observed till the end of the culture period. At a density of 1



**Figure 1.** The water quality parameters observed during culture of *S. aequifasciatus* at different stocking densities over a period of twelve weeks.

juvenile per 5 L, mortality was recorded during sixth week of culture whereas, at a density of 1 juvenile per 2.5 L, mortality was observed from the second week onwards. The majority of fishes which died became isolated from the rest of the fishes, refused feed, emaciated and got darkened before death. White faecal strands (infected with ciliates) were observed from the seventh week of culture at the stocking densities of 1 juvenile per 5 L and 1 juvenile per 2.5 L. Survival was calculated after every two weeks and

represented in Table 1.

Survival of juveniles reared at different densities differed significantly ( $P < 0.05$ ). The lowest survival was recorded at the highest density which differed significantly from the rest of the densities. No significant difference ( $p > 0.05$ ) was found in the survival of juveniles reared at the densities of 1 juvenile/10 L, 1 juvenile/7.5 L and 1 juvenile/5 L up to a period of eight weeks. At the end of tenth and twelfth week, 100% survival was recorded in

**Table 1.** The survival of juveniles of *Symphysodon aequifasciatus* reared at various densities over a culture duration of twelve weeks

Culture period	Survival (%)			
	T1 (1 juvenile/10l)	T2 (1 juvenile/7.5l)	T3 (1 juvenile/5l)	T4 (1 juvenile/2.5l)
After 2 weeks	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	97.22 ± 0.6967 <sup>b</sup>
After 4 weeks	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	95.14 ± 0.6933 <sup>b</sup>
After 6 weeks	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	92.36 ± 0.6933 <sup>b</sup>
After 8 weeks	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	95.83 ± 0.00 <sup>a</sup>	89.58 ± 0.00 <sup>b</sup>
After 10 weeks	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	88.89 ± 1.39 <sup>b</sup>	84.02 ± 0.70 <sup>c</sup>
After 12 weeks	100± 0.00 <sup>a</sup>	100± 0.00 <sup>a</sup>	84.72 ± 1.39 <sup>b</sup>	77.78 ± 0.6944 <sup>c</sup>

The values are expressed as mean ± Standard Error (SE).

<sup>a, b, c</sup> The values in a row with different superscript varies significantly ( $p < 0.05$ ).

densities of 1 juvenile/10 L and 1 juvenile/7.5 L which differed significantly ( $p > 0.05$ ) from the densities of 1 juvenile/5 L and 1 juvenile/2.5 L.

### Growth

The standard length and weight of juveniles observed at various densities over a culture duration of twelve weeks are depicted in Figure 2 and 3, respectively. Length gain, weight gain and specific growth rate (SGR) are recorded in Table 2.

The standard length, weight, length gain (%), weight gain (%) and SGR of juveniles of discus fish reared at various densities did not differ significantly ( $p > 0.05$ ) at the end of two weeks of culture. The growth decreased significantly ( $p < 0.05$ ) with an increase in stocking density after the second week of culture. However, the growth of juveniles cultured at densities of 1 juvenile/10 L, 1 juvenile/7.5 L and 1 juvenile/5 L did not differ significantly ( $p > 0.05$ ) till the sixth week of culture. At the end of 12<sup>th</sup> week, the highest growth was observed at the lowest density *i. e.* 1 juvenile/10 L but was not significantly different ( $p > 0.05$ ) from that of juveniles reared at the density of 1 juvenile/7.5 L. The lowest growth was observed at a density of 1 juvenile/2.5 L followed by 1 juvenile/5 L.

### The Condition Index (K) and Coefficient of Variation (%)

The condition index (K) and coefficient of variation (%) calculated at the beginning and end of the experiment are presented in Table 3. The condition index of juveniles reared at the various stocking densities did not differ at the beginning as well as at the end of the experiment although, it decreased significantly ( $p \leq 0.05$ ) towards the end of the culture period in treatments having densities of 1 juvenile/10 L and 1 juvenile/5 L. K of fishes reared at densities of 1 juvenile/7.5 L, and 1 juvenile/2.5 L, however, did not differ significantly at the beginning and end of the culture period ( $P > 0.05$ ).

The coefficient of variation for weight among the various stocking densities did not vary significantly ( $P < 0.05$ ), from the beginning to the end

of the experiment. However, it increased significantly ( $P < 0.05$ ) from beginning to end of the culture period in each treatment. Social hierarchy was evident at all treatments with presence of a few aggressive and dominant juveniles, who prevented other fellow inmates within their territory from taking feed. This behavior was more pronounced after the sixth week of culture.

### Discussion

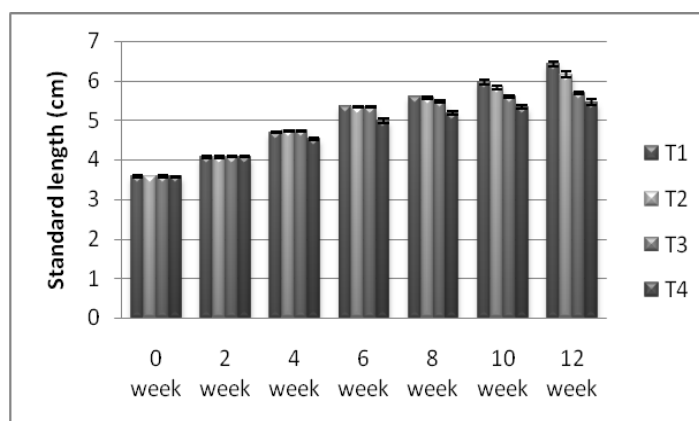
#### Survival

100% survival was recorded till the end of the experimental period at lower stocking densities, *i.e.* up to a density of 1 juvenile per 7.5 L. However, survival decreased significantly with increase in stocking density. Mortality that occurred prior to second week at the highest stocking density, can possibly be attributed to injury caused by accidental contact of fishes with water exchange apparatus and built up suction pressure therein. The mortality occurring at higher densities thereafter is attributed to the combined effects of water quality deterioration due to high level of  $\text{NH}_3\text{-N}$  and  $\text{NO}_2\text{-N}$ , due to social interactions and aggressive encounters, reduction in habitat space and sheltered areas, gut ciliate infection and voluntary suppression of food intake.

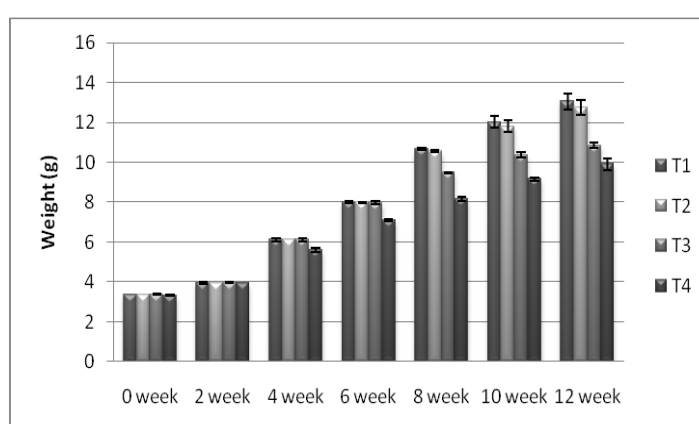
The high survival observed at lower densities in other studies were linked to availability of more space and food (Narejo et al, 2005), optimal water quality and less competition whereas incidence of mortality at higher densities were attributed to behavioural changes, rapid spread of virulent pathogens (Cruz and Ridha, 1991), stress, as a result of competition for food and space (Akinwole et al., 2014), decreased water quality due to increased biomass (Ronald et al., 2014), poor handling (Vera Cruz and Mair, 1994) and deterioration of health due to positive interaction of stressful factors (Barton and Iwama, 1991).

#### Growth

At the end of the culture period of 12 weeks, the



**Figure 2.** The standard length of juveniles of *Symphysodon aequifasciatus* reared at various densities over a culture duration of twelve weeks.



**Figure 3.** The weight of juveniles of *Symphysodon aequifasciatus* reared at various densities over a culture duration of twelve weeks.

stocking density above 1 juvenile per 7.5 L showed a negative impact on growth. Lower growth at higher stocking densities could be attributed to reduced water quality (Ruane et al., 2001; Ellis et al., 2002; Foss et al., 2006), onset of hierarchies and dominant relationships (Bolasina et al., 2006), competition for food and living space (Diana et al., 2004), greater expenditure of energy in antagonistic interactions (Bachellos and Lulhier, 1999), voluntary appetite suppression and increased stress (Ruane et al., 2001; Abdel-Tawwab, 2012).

### Condition Index (K)

The condition index of discus juveniles was not influenced by stocking density. As the condition index was calculated only for live fishes remaining at the end of the culture and that of emaciated fishes which died in high-density treatments was not taken into account, similarity was observed in condition index of fishes among all the densities tested. Similarity in the condition index of fishes reared at different densities was also recorded in *Oreochromis niloticus* (Abdel-Tawwab, 2012); *Siganus rivulatus*

(Saoud et al., 2007) and *Brycon insignis* (Tolussi et al., 2010). On the other hand, Lambert and Dutil (2001) found a negative effect of increasing stocking density on the condition index of *Gadus morhua* and postulated decreased food intake as the cause.

Condition index decreased significantly ( $P < 0.05$ ) from start to end of the culture of the present study, at two densities (1 juvenile per 10 L and 1 juvenile per 5 L), indicating a gradual deterioration of well-being. Jorgensen et al. (1993) found that the condition index of *Salvelinus alpinus* reared for nine weeks at high stocking densities improved with time, while the condition of the same fish stocked at low densities did not improve over the same time. On the contrary, Saoud et al. (2007) attributed improvement in the condition index (from 1.09 to 1.31-1.33) of *Siganus rivulatus* grown at different densities over the period of eight weeks to the fact that, the feed given to the fish was nutritionally rich as compared to what they consume in nature.

### Coefficient of Variation (CV) for Weight

The coefficient of variation for weight increased

**Table 2.** The growth and SGR of juveniles of *Symphysodon aequifasciatus* reared at various densities over a culture duration of twelve weeks

Growth Parameter	Stocking density	Culture period (Week)					
		2	4	6	8	10	12
Length gain (%)	T1	13.79 ± 0.95 <sup>a</sup>	31.01 ± 0.27 <sup>a</sup>	49.35 ± 0.26 <sup>a</sup>	56.33 ± 0.44 <sup>a</sup>	66.49 ± 2.04 <sup>a</sup>	79.32 ± 1.87 <sup>a</sup>
	T2	13.86 ± 0.75 <sup>a</sup>	32.10 ± 0.67 <sup>a</sup>	48.66 ± 0.50 <sup>a</sup>	55.44 ± 0.23 <sup>ab</sup>	62.60 ± 0.87 <sup>a</sup>	72.06 ± 2.85 <sup>a</sup>
	T3	13.76 ± 0.89 <sup>a</sup>	31.68 ± 1.14 <sup>a</sup>	48.49 ± 1.52 <sup>a</sup>	52.56 ± 0.46 <sup>b</sup>	56.09 ± 0.52 <sup>b</sup>	58.45 ± 0.52 <sup>b</sup>
	T4	14.27 ± 0.43 <sup>a</sup>	26.40 ± 1.11 <sup>b</sup>	39.66 ± 2.14 <sup>b</sup>	44.97 ± 1.36 <sup>c</sup>	49.07 ± 1.51 <sup>c</sup>	52.77 ± 2.28 <sup>c</sup>
Weight gain (%)	T1	17.27 ± 1.70 <sup>a</sup>	82.05 ± 1.73 <sup>a</sup>	138.16 ± 0.79 <sup>a</sup>	217.96 ± 2.11 <sup>a</sup>	257.51 ± 8.35 <sup>a</sup>	287.98 ± 12.87 <sup>a</sup>
	T2	17.31 ± 0.22 <sup>a</sup>	82.05 ± 0.81 <sup>a</sup>	137.18 ± 2.08 <sup>a</sup>	214.38 ± 2.19 <sup>a</sup>	251.37 ± 9.55 <sup>a</sup>	279.18 ± 9.33 <sup>a</sup>
	T3	17.01 ± 0.43 <sup>a</sup>	81.42 ± 2.22 <sup>a</sup>	136.97 ± 2.91 <sup>a</sup>	180.96 ± 1.81 <sup>b</sup>	207.32 ± 4.50 <sup>b</sup>	221.99 ± 4.87 <sup>b</sup>
	T4	18.49 ± 0.31 <sup>a</sup>	68.03 ± 2.54 <sup>b</sup>	112.37 ± 2.20 <sup>b</sup>	145.17 ± 3.71 <sup>c</sup>	174.71 ± 3.19 <sup>c</sup>	197.51 ± 9.57 <sup>b</sup>
SGR	T1	1.14 ± 0.10 <sup>a</sup>	2.14 ± 0.04 <sup>a</sup>	2.07 ± 0.01 <sup>a</sup>	2.07 ± 0.01 <sup>a</sup>	1.82 ± 0.03 <sup>a</sup>	1.61 ± 0.04 <sup>a</sup>
	T2	1.14 ± 0.01 <sup>a</sup>	2.14 ± 0.02 <sup>a</sup>	2.06 ± 0.02 <sup>a</sup>	2.05 ± 0.01 <sup>a</sup>	1.79 ± 0.04 <sup>a</sup>	1.59 ± 0.03 <sup>a</sup>
	T3	1.12 ± 0.03 <sup>a</sup>	2.13 ± 0.04 <sup>a</sup>	2.05 ± 0.03 <sup>a</sup>	1.84 ± 0.01 <sup>b</sup>	1.60 ± 0.02 <sup>b</sup>	1.39 ± 0.01 <sup>b</sup>
	T4	1.21 ± 0.02 <sup>a</sup>	1.85 ± 0.06 <sup>b</sup>	1.79 ± 0.02 <sup>b</sup>	1.60 ± 0.03 <sup>c</sup>	1.44 ± 0.17 <sup>c</sup>	1.29 ± 0.04 <sup>b</sup>

T1 = 1 juvenile/10l, T2 = 1 juvenile/7.5l, T3 = 1 juvenile/5l and T4 = 1 juvenile/2.5l.

The values are expressed as mean ± Standard Error (SE). <sup>a, b, c</sup> The values of each growth parameter in a column with different superscript varies significantly (p < 0.05).

**Table 3.** The condition index (K) and coefficient of variation (CV) of juveniles of *Symphysodon aequifasciatus* reared at various densities at the start and end of the culture period

Stocking density	Condition index (K)			Coefficient of variation (%)		
	At the start	At the end	t-test for comparison of K at the start and end of culture	At the start	At the end	t-test for comparison of CV at the start and end of culture
T1	3.65 ± 0.02 <sup>a</sup>	3.19 ± 0.12 <sup>a</sup>	t(2) = 4.302, p = 0.05	7.43 ± 0.14 <sup>a</sup>	33.15 ± 1.26 <sup>a</sup>	t(2) = 18.433, p = 0.003
T2	3.57 ± 0.05 <sup>a</sup>	3.18 ± 0.16 <sup>a</sup>	t(2) = 1.931, p = 0.193	7.46 ± 0.47 <sup>a</sup>	33.29 ± 0.8 <sup>a</sup>	t(2) = 60.108, p = 0.000
T3	3.63 ± 0.07 <sup>a</sup>	3.26 ± 0.08 <sup>a</sup>	t(2) = 25.924, p = 0.001	8.76 ± 0.81 <sup>a</sup>	28.73 ± 3.18 <sup>a</sup>	t(2) = 7.755, p = 0.016
T4	3.53 ± 0.02 <sup>a</sup>	3.34 ± 0.21 <sup>a</sup>	t(2) = 0.838, p = 0.49	10.2 ± 0.94 <sup>a</sup>	32.91 ± 1.54 <sup>a</sup>	t(2) = 9.532, p = 0.011

T1 = 1 juvenile/10l, T2 = 1 juvenile/7.5l, T3 = 1 juvenile/5l and T4 = 1 juvenile/2.5l.

The values are expressed as mean ± Standard Error (SE). <sup>a</sup> The values in a column with same superscript do not vary significantly (p > 0.05).

significantly over the culture period in each stocking density. This increment suggests that growth hierarchy may be an inherent feature of reared population as observed in *Solea senegalensis* (Salas-Leiton et al., 2011). This high size variation could be attributed to the establishment of the social hierarchy in each density group irrespective of the availability of sufficient food and suppression of growth of certain individuals. At the beginning of culture period, all fishes were active and consumed feed readily when distributed. With progress in culture, the social

hierarchy was discernible in all the groups and dominant individuals developed their territory and did not allow others to feed in those zones. This behavior may be one of the reasons for the suppression of feed intake in subordinates. Such observations of the present study are supported by the considerable difference in food consumption and growth in *Pleuronecte splatessa* under conditions where rations are not limiting (Purdom, 1974). It is also supported by Koebele (1985) who demonstrated that dominant fish ingested more food either by acquiring a limiting

ration first and preventing subordinates from obtaining food or behaviourally inhibiting the subordinates' feeding behaviour. The stocking densities tested in the study had shown no influence on size variation of discus, much in accordance with studies on *Brycon insignis* (Tolussi et al., 2010) and *Solea senegalensis* (Salas-Leiton et al., 2011) where homogenous CV was observed in different stocking densities. On the contrary, the conditions of both high and low CV were reported at higher densities. Large size variation at higher densities found in *Gadus morhua* (Lambert and Dutil, 2001) was attributed mainly to the establishment of hierarchical groups. Low size variation at very high densities was reported by Kailasam et al. (2002) in *Lates calcarifer* and Ronald et al. (2014) in *Oreochromis niloticus*. Very high densities lead to reduced territorial behaviour, disruption in the dominance hierarchy and reduction in chronic stress which ultimately improved growth in slow growers and reduced growth of shooters due to reduced dominance over food. Most researchers concluded that the size variation depended on many factors, mainly species behaviour and the range of stocking density considered in experiments.

The influence of stocking density on growth and survival varies with species, size, culture period, culture system and practice adopted. The present study revealed that discus juveniles may be reared at the highest density of 1 juvenile per 2.5 L up to a period of two weeks without affecting growth parameters significantly. It also showed the possibility of rearing juveniles at a density of 1 juvenile per 5.0 L up to a period of six weeks and at a density of 1 juvenile per 7.5 L for twelve weeks. This study indicated the use of a strategy of growing the juveniles at the highest density in the beginning with periodical reduction in density by removing individuals showing higher growth and aggressiveness and rearing them as a separate group. This practice may ensure homogenous growth in each group or tank and make the availability of marketable size fishes at different times during the culture period.

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