Benefits of Male Monosex Culture of Giant Freshwater Prawn (*Macrobrachium rosenbergii*): Improving Growth Performance, Production Yield, and Profitability

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ABSTRACT

We evaluated the advantages of all-male giant freshwater prawn (*Macrobrachium rosenbergii*) culture over traditional mixed-sex and all-female systems in the aspects of growth performance, production yield, and profitability. The prawn post-larvae were reared in a nursery pond for 43 days until the male sexual characteristics (gonopore complex) could be distinguished externally, then they were sexed and transferred to monosex grow-out ponds (two ponds per sex) and cultured for another 140 days. The prawn post-larvae in the mixed-sex group were reared for 60 days in the nursery phase and 165 days in the grow-out phase. At harvest, the male prawns from the all-male group had higher body weight (93.02 g), average daily growth (0.66 $g \cdot day^{-1}$), and specific growth rate (3.41 $\% \cdot day^{-1}$), compared to the males in the mixed-sex system (69.38 g, 0.41 $g \cdot day^{-1}$, and 2.56 $\% \cdot day^{-1}$, respectively). The proportion of an unfavorable "small male" morphotype was reduced from 20.11 % in the mixed-sex culture to 4.67 % in the all-male system, whereas that of a desirable "orange claw" morphotype was increased from 38.59 to 61.33 %. Ultimately, the production yield of the all-male group was 2,076.6 $kg \cdot ha^{-1}$, whereas that of the mixed-sex system was 1,273.8 $kg \cdot ha^{-1}$. The cost-benefit analysis revealed that the former was 155.78 % more profitable than the latter. The all-female group showed the best survival rate and feed conversion ratio, yet it was the least profitable system. In conclusion, the all-male culture was the most productive and profitable system of giant freshwater prawn farming.

Keywords: Aquaculture, Cost-benefit analysis, Giant freshwater prawn, Mixed-sex culture, Monosex culture

INTRODUCTION

Giant freshwater prawn (*Macrobrachium rosenbergii* [De Man, 1879]) is a commercially important aquatic animal in Thailand and other Asian countries. Native to the Indo-West Pacific region, it lives in tropical freshwater environments, particularly in extremely turbid water. Gravid females spawn in estuaries since the planktonic larvae require brackish water for their survival. After metamorphosis into post-larvae, they adapt to a more benthic lifestyle and begin to migrate upstream within one or two weeks after metamorphosis (New, 2002, 2022). In 2019, the global production of giant freshwater prawn from aquaculture was 273,738 tonnes. China is by far the top producer of farmed giant freshwater prawn, with a production yield of 139,609 tonnes, followed by Bangladesh (52,197 tonnes), Thailand (31,345 tonnes), and Vietnam (20,129 tonnes) (FAO, 2022). The farmed production from these four Asian countries was greater than the rest of the world combined.

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Traditionally, the giant freshwater prawn farming method is to stock male and female prawns in the same pond (mixed-sex culture) and grow them out for 6-8 months. Although apparently simple, the major drawbacks of this approach are a low survival rate, sometimes less than 30 % (Prakob Subyodkeaw, pers. comm.), low production yield, and large variation in the growth rate between male and female prawns (Brody *et al*., 1980; Cohen *et al*., 1981; Levy *et al*., 2017). After culturing for about 4-6 months, the growth rate of the female prawn generally reaches a plateau with an average weight of about 25-35 g, because more energy is allocated to reproductive system development and egg production (Siddiqui *et al*., 1997; Tidwell *et al*., 2015). The growth of females nearly stops after maturation (Ra'anan *et al*., 1991). The situation for male giant freshwater prawns is different. Adult males can be differentiated into three types according to their size and morphology, namely, small male (SM), orange claw (OC), and blue claw (BC). The male prawns are capable of transforming from one morphotype into another in the following order: SM to OC to BC. The transformation occurs most frequently when larger individuals are removed or die (Ra'anan and Sagi, 1985; Karplus and Barki, 2019). At harvest, SM prawns have an average body weight of about 10 g, while OC and BC prawns have similar body weights of 40-70 g (Ra'anan *et al*., 1991; Siddiqui *et al*., 1997; Dinh and Nguyen, 2014; Tidwell *et al*., 2015). The SM has small claws and grows very slowly. The BC often shows territorial and aggressive behavior, and it develops large blue-colored spinous claws suited for fighting against other males for a higher chance of mating with female prawns. In contrast, the OC possesses medium-sized orange-colored claws and spends less energy for fighting and mating (Ra'anan and Sagi, 1985), thus more energy is available for somatic growth. Unfortunately, often only a small percentage of the male prawns in mixed-sex culture develop as OC (the most desirable morphotype) at harvest, whereas the rest become either SM or BC (Prakob Subyodkeaw, pers. comm.). Therefore, it is conceivable that if the male and female prawns could be separated for monosex culture as soon as possible, the reproductive organ development in both sexes would be retarded, and higher growth rates would likely be obtained.

The idea of improving growth performance by monosex culture has been successfully applied in livestock and aquaculture productions, especially Nile tilapia (Beardmore *et al*., 2001; Kembenya and Ondiba, 2021). Studies on monosex culture of giant freshwater prawn are available in the literature and generally reveal that all-male culture (Siddiqui *et al*., 1997; Nair *et al*., 2006; Tidwell *et al*., 2015) has significantly higher production yields and is more profitable than mixed-sex culture, although some researchers preferred all-female culture (Malecha, 2012; Levy *et al*., 2017). Monosex culture can be performed by manually separating the two sexes based on external morphology, namely, the presence (male) or absence (female) of the gonopore complex (Siddiqui *et al*., 1997; Nair *et al*., 2006). Alternatively, genetic manipulation by selective breeding with neofemales, produced from the removal of the androgenic gland (andrectomy) or by RNAi technology (Na-Nakorn and Jintasataporn, 2012; Tan *et al*., 2020), can also be successfully applied to produce all-male offspring (Rungsin *et al*., 2006; 2012; Tidwell *et al*., 2015).

Even though the advantages of all-male giant freshwater prawn culture over the traditional mixed-sex culture in terms of improving the production yield have been demonstrated by previous studies, to our knowledge most of them separated the prawns by sex at a relatively late stage, often at around two months after first stocking or when the prawns reached a size of 4-6 g (Sagi *et al*., 1986; Siddiqui *et al*., 1997; Nair *et al*., 2006). It is wise to separate the males and females as early as possible, to minimize interactions between the two sexes that potentially retard somatic growth. In addition, a cost-benefit analysis of an all-male culture system was usually not performed in prior research, except for one field trial in India in which the profit gained from the monosex system over the mixed-sex system was only moderate, i.e., 63 % (Nair *et al*., 2006). Thus, the economic feasibility of this system is still uncertain in real-farm conditions, given the comparatively high cost and complicated procedures associated with sex separation. One possible reason for the moderate economic benefits of Nair *et al*. (2006) might be that the sex separation was done at a relatively late stage (60 days after stocking) in the nurseries, when the prawns reached an average body weight of 4.5 g. If the sex separation of the prawn post-larvae was carried out as early as possible, the improved production yield and economic return from the monosex culture should have been more prominent.

To provide more comprehensive evidence supporting all-male culture of the giant freshwater prawn, the present study compared the differences among all-male, all-female, and mixed-sex culture systems in various aspects including growth performance, production yield, and profitability under field conditions. The prawn post-larvae were inspected weekly to identify the earliest stage of sexual differentiation before being transferred to the monosex culture ponds. The results of this study can provide practical guidelines that might be helpful for the development of monosex giant freshwater prawn aquaculture in the future.

MATERIALS AND METHODS

Experimental design

This study was conducted at a commercial giant freshwater prawn farm in Ratchaburi Province, central Thailand. The post-larvae were obtained from 20 female broodstock (20,000-30,000 larvae/female). In the nursery phase, prawn post-larvae (age 25 days after hatching) were stocked in two nursery ponds at the density of 32 prawns·m^{-2}. One nursery pond was used for mixed-sex culture, and the other was used for monosex culture in the grow-out phase. The prawns designated for the mixed-sex and monosex cultures were reared in the nursery ponds for 60 and 43 days, respectively (see below). The average body weights of prawns from the two nursery ponds were similar (Table 1). It should be noted that it is a common practice for Thai prawn farmers to transfer the juvenile giant freshwater prawns from nursery ponds to grow-out ponds after having been cultured for about two months so that the stocking densities can be reduced, leading to faster growth rates (Limsuwan and Chanratchakool, 2004).

After the prawns from the mixed-sex group had been reared in the nursery pond for 60 days, they were transferred to two new grow-out ponds at a density of 6 prawns·m^{-2} (Limsuwan and Chanratchakool, 2004) until harvest (165 days in the grow-out phase, or 225 days in total). For the monosex culture pond, the prawns were reared in the nursery pond until morphological differences between male and female were distinguishable (43 days after stocking in the nursery pond); then, the post-larvae were sexed and transferred to four new grow-out ponds (two all-male ponds and two all-female ponds) at a density of 6 prawns·m^{-2}. All four of the monosex groups were cultured until harvest, which was 140 days in the grow-out phase (183 days in total). A diagram of the experimental design is presented in Figure 1. All of the prawns were fed with commercial pelleted feed (36 % protein)

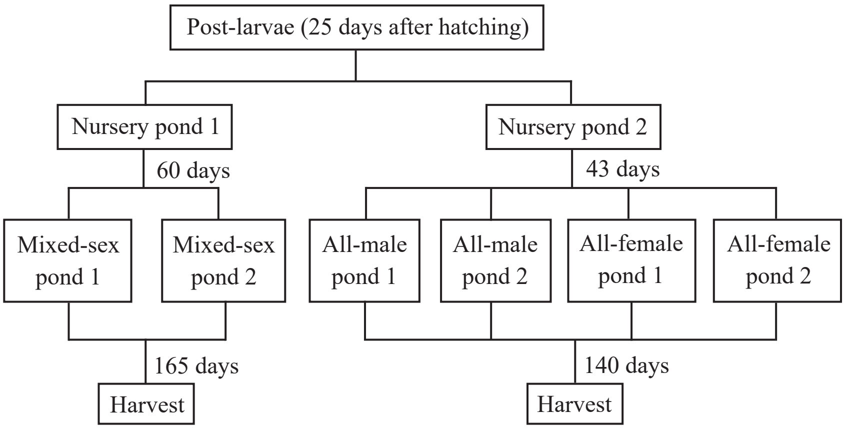

Figure 1. Experimental design for comparing monosex and mixed-sex culture of giant freshwater prawn.

four times per day. The feeding rate was generally 2-5 % of body weight, depending on the prawn size and environmental conditions (Limsuwan and Chanratchakool, 2004). Water quality parameters were measured weekly. No water change was performed throughout the culture period.

Sex determination

During the nursery period, 50 prawns were sampled weekly from each study pond. The prawns were weighed and the sex of individuals was determined by observing the presence (male) or absence (female) of the gonopore complex at the fifth pereiopod under a stereomicroscope. To examine the development of male and female reproductive organs histologically, the prawns were fixed with Davidson's fixative and processed for histological study (Bell and Lighter, 1998).

Growth performance, production yield, and cost-benefit analysis

After transferring the prawns to the grow-out ponds at 60 days (for mixed-sex culture) and 43 days after stocking (for monosex culture), 25 prawns from each pond were sampled and weighed weekly. Average daily growth (ADG), specific growth rate (SGR), survival rate, feed conversion ratio (FCR), and production yield were determined at harvest. The formulae to calculate ADG, SGR, and FCR are as follow:

$$\text{ADG } (\text{g}\cdot\text{day}^{-1}) = \frac{\text{Final weight-Initial weight}}{\text{Days}}$$

$$\text{SGR } (\%\cdot\text{day}^{-1}) = \frac{\ln(\text{Final weight})-\ln(\text{Initial weight})}{\text{Days}} \times 100$$

$$\text{FCR} = \frac{\text{Feed intake}}{\text{Body weight gain}}$$

At the end of the field trial, around 150-200 male prawns/pond were sampled and classified according to their morphotypes as SM, OC, or BC. The proportion of each morphotype was recorded. The cost of production and profitability of each group was also calculated at the end of the trial. The difference in average body weight between the two culturing systems during the grow-out phase was compared using an independent t-test by IBM SPSS Statistics version 27 software (IBM Corporation, Armonk, NY, USA). Differences were considered statistically significant if $p<0.05$.

RESULTS

The average weights of the prawns during the nursing period are shown in Table 1. The prawns designated for the mixed-sex culture system were cultured for 60 days after stocking and attained the average body weight of 1.02 g before being transferred into the grow-out ponds. The prawns designated for the monosex culture system were reared until the two sexes could be distinguished (at 43 days); their average body weight was 0.78 g.

For the sex determination, there were no recognizable external differences between the male and female prawns from 15 to 36 days after stocking. Histologically, the sexual difference of the primordial germ cells (PGC), located under the heart and above the hepatopancreas, was also not discernible (Figure 2). At 43 days, the external opening of the vas deferens organ, a part of the gonopore complex of the male prawn, was distinguishable at the fifth pereiopod (Figure 3). At 50 days, the male and female prawns started to develop their testes and ovaries, respectively, with varying stages of the germ cells. At 57 days, the seminiferous tubules appeared in the males, while the female ovarian development was more advanced than at 50 days (Figure 4).

Table 1. Average body weight (g) (mean±SD) of giant freshwater prawns during the nursery phase.

Days after stocking	Nursery pond 1 (designated for mixed-sex culture)	Nursery pond 2 (designated for monosex culture)
15	0.21±0.06	0.22±0.03
22	0.44±0.15	0.40±0.10
29	0.66±0.15	0.65±0.10
36	0.71±0.30	0.72±0.13
43	0.75±0.27	0.78±0.20
50	0.93±0.27	-
57	1.02±0.24	-

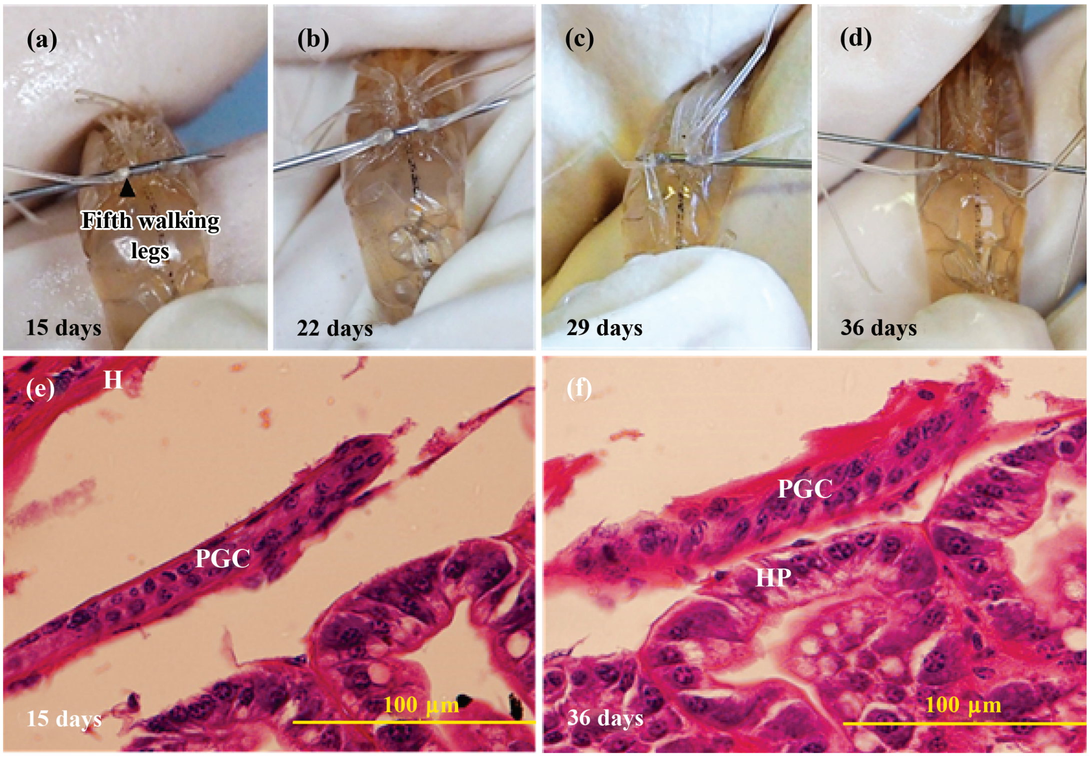

Figure 2. External appearance (a-d) and histological sections (e-f) of giant freshwater prawn at 15, 22, 29, and 36 days after stocking in a nursery pond. During this period, there was no discernible sexual difference between the two sexes. The primordial germ cells (PGC) were visible under the heart and above the hepatopancreas (e and f). H, Heart; HP, hepatopancreas; PGC, primordial germ cells.

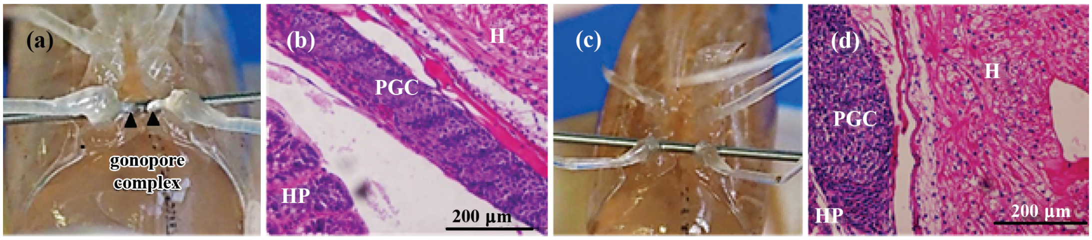

Figure 3. External appearance (a and c) and histological sections (b and d) of giant freshwater prawn at 43 days after stocking in a nursery pond. Externally, the male prawn could be differentiated from the female by the presence of the gonopore complex at the fifth pereiopod (a), which is absent in the female (c). Histologically, the gonads were more developed but any differential characteristics between the male (b) and female (d) was still unrecognizable in the histological sections. Note that the primordial germ cells were more numerous than in earlier stages. H, Heart; HP, hepatopancreas; PGC, primordial germ cells.

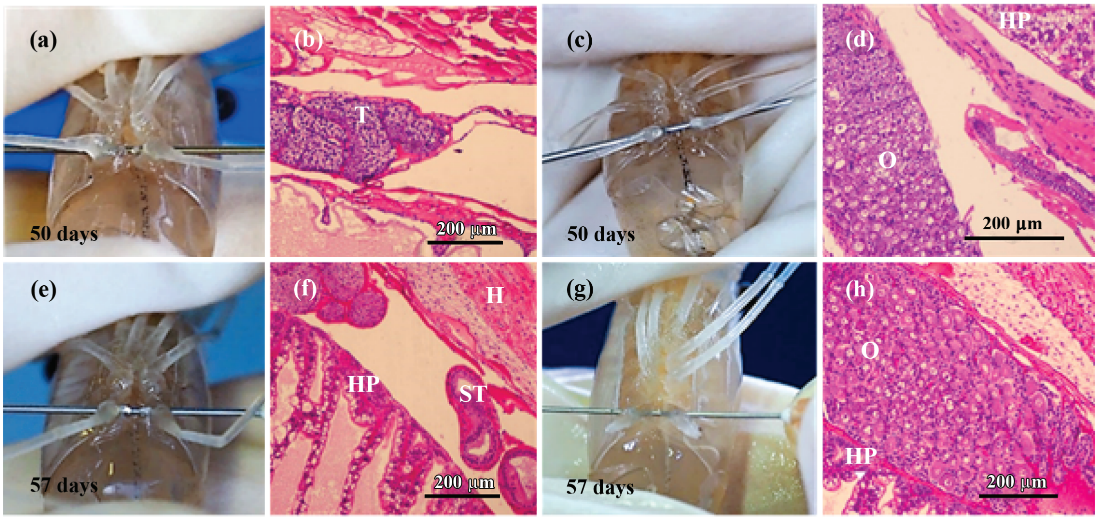

Figure 4. External appearance (a, c, e and g) and histological sections (b, d, f, and h) of giant freshwater prawn at 50 and 57 days after stocking. The testis and seminiferous tubule of the male prawn (b and f) and the ovary of the female (d and h) are distinguishable. H, heart; HP, hepatopancreas; O, ovary; ST, seminiferous tubule; T, testis.

Throughout the grow-out phase, the average body weight, ADG, SGR, and production yield of the male prawns were much higher than the females, regardless of the culturing system (Tables 2 and 3). When comparing the growth performance between the mixed-sex and monosex systems, the benefit of monosex culture was evident. The male prawns in the all-male pond attained the average final body weight of 93.02 g at harvest (183 days in total), which was significantly higher ($p<0.05$) than those reared in the mixed-sex pond (40.14 g) for the same period (Table 2). It is worth mentioning that the average body weight of the males from the mixed-sex group never reached the size of those in the monosex group, even after being cultured for a longer period (69.38 g at 225 days in total). At 183 days, the average weight of the female prawns in the all-female group was 30.28 g, which was significantly higher ($p<0.05$) than those of the mixed-sex culture group (27.64 g).

All water quality parameters throughout the study period, namely dissolved oxygen (>4 $mg \cdot L^{-1}$), temperature (30-33 °C), salinity (0 ppt), pH (7.4-8.5), alkalinity (95-105 $mg \cdot L^{-1}$ as $CaCO_3$), ammonia (<1 $mg \cdot L^{-1}$), and nitrite (<0.1 $mg \cdot L^{-1}$) were suitable for giant freshwater prawn farming in both culturing groups.

Given that the male prawns in the all-male group had the highest body weight at harvest, it is not unexpected that their growth performance (ADG 0.66 $g \cdot day^{-1}$ and SGR 3.41 $\% \cdot day^{-1}$) and production yield (2,076.6 $kg \cdot ha^{-1}$) were also superior to the other groups (Table 3), despite a lack of statistical support due to the limited number of replications. It should be noted that this study was conducted at a commercial farm, thus only two replicates which already occupied a total of eight ponds could be assigned. However, owing to small variation of means (see Table 3), the differences between treatments were apparent. The survival rate for the all-male pond (53.46 %) was higher than that

Table 2. Average body weight (g) (mean±SD) of giant freshwater prawns cultured in different systems during the grow-out phase.

Total days after stocking	Male prawns		Female prawns	
	Mixed-sex culture	Monosex culture	Mixed-sex culture	Monosex culture
64	2.66±0.54^a	13.09±1.40^b	1.32±0.21^a	1.43±0.12^a
71	5.70±2.52^a	17.98±2.39^b	1.80±0.55^a	2.06±0.30^a
78	7.61±2.69^a	23.47±2.36^b	2.31±0.34^a	2.20±0.28^a
85	10.56±3.04^a	28.26±3.11^b	2.41±0.49^a	2.56±0.17^a
92	13.01±2.13^a	33.12±2.76^b	2.60±0.34^a	3.14±0.34^b
99	15.92±3.02^a	38.30±5.67^b	3.26±0.21^a	4.27±0.56^b
106	20.07±3.76^a	43.24±4.35^b	3.71±0.49^a	5.52±0.50^b
113	25.28±5.90^a	48.00±5.19^b	4.82±0.46^a	7.14±0.78^b
120	32.54±9.90^a	51.00±8.52^b	6.29±1.05^a	8.43±0.62^b
127	33.26±5.40^a	55.66±6.38^b	11.98±2.41^a	10.17±1.25^b
134	33.72±5.04^a	60.02±5.26^b	14.96±3.33^a	14.03±2.07^a
141	34.10±3.48^a	64.42±9.15^b	17.22±3.07^a	18.11±3.82^a
148	34.68±5.40^a	67.46±9.85^b	20.42±3.33^a	19.10±2.78^a
155	35.10±4.30^a	72.10±10.81^b	22.12±3.71^a	21.56±3.17^a
162	36.06±4.55^a	75.88±8.24^b	22.62±4.01^a	25.14±3.27^b
169	37.04±3.54^a	85.41±6.42^b	23.82±3.53^a	28.74±4.20^b
176	38.50±6.27^a	89.00±5.35^b	25.74±3.30^a	28.99±4.29^b
183	40.14±6.89^a	93.02±5.72^b	27.64±5.18^a	30.28±3.27^b
190	49.60±6.94	-	28.24±4.13	-
197	51.88±7.04	-	28.70±2.52	-
204	64.56±9.69	-	30.00±3.07	-
211	66.00±7.97	-	31.94±3.23	-
218	67.52±8.80	-	34.38±3.99	-
225	69.38±9.18	-	36.94±5.53	-

Note: Mean weights are compared between mixed-sex and monosex cultures (separately for males and females); means with different superscripts within the same row are significantly different from each other ($p<0.05$).

of males in the mixed-sex system (36.19 %), but lower than for the all-female pond (89.60 %). In addition, a difference in the proportions of the three male morphotypes (SM, OC, and BC) between the two systems was evident (Table 4). The unfavorable morphotype SM was about five times more abundant in the mixed-sex pond (20.11 %) than in the monosex pond (4.67 %). In contrast, the preferred morphotype OC was dominant in the all-male pond (61.33 %) but not in the mixed-sex system (38.59 %). The percentage of BC was similar between the two culture systems (about 30-40 %).

Compared to the male prawns, the differences in the female body weight, ADG, and SGR between the mixed-sex and monosex ponds were less dramatic. However, the survival rate (89.60 %), FCR (1.44), and production yield (1,745.0 kg·ha^{-1}) of the all-female culture were better than those from the mixed-sex system (53.08 %, 1.89, and 613.8 kg·ha^{-1}, respectively).

A cost-benefit analysis of the different prawn culture systems is shown in Table 5. The total production cost of the mixed-sex culture system was 228,148 THB·ha^{-1} (6,800 USD·ha^{-1}), less than that of the all-male (347,735 THB·ha^{-1} or 10,400 USD·ha^{-1}) and all-female systems (325,813 THB·ha^{-1} or 9,700 USD·ha^{-1}). Although the total cost of the all-male production system was the most expensive, this was compensated by the highest income (523,294 THB·ha^{-1} or 15,600 USD·ha^{-1}). Thus, the all-male culture was the most profitable for giant freshwater prawn farming (175,558 THB·ha^{-1} or 5,200 USD·ha^{-1}). By comparison, the net profits from the mixed-sex and all-female cultures were 68,636 THB·ha^{-1} (2,000 USD·ha^{-1}) and 23,188 THB·ha^{-1} (700 USD·ha^{-1}), respectively.

Table 3. Growth performance and production yield of giant freshwater prawn cultured in different systems during the grow-out phase.

Parameters	**Male prawns**		**Female prawns**	
	Mixed-sex culture	**Monosex culture**	**Mixed-sex culture**	**Monosex culture**
Average body weight at harvest (g)	69.38±2.74	93.02±2.98	36.94±0.14	30.28±0.17
ADG (g•day^{-1})	0.41±0.02	0.66±0.02	0.22±0.00	0.21±0.00
SGR (%•day^{-1})	2.56±0.02	3.41±0.02	2.18±0.00	2.61± 0.00
Survival rate (%)	36.19±0.27	53.46±2.21	53.08±2.60	89.60±4.24
FCR	1.89±0.00	1.87±0.10	1.89±0.00	1.44±0.01
Production yield (kg•ha^{-1})	660.0±10.6	2,076.6±121.5	613.8±30.05	1,745.0±12.4

Note: ADG, average daily growth; SGR, specific growth rate; FCR, feed conversion ratio

Table 4. Percentages of the three morphotypes of male giant freshwater prawns cultured in different systems during the grow-out phase.

Morphotype	**Mixed-sex culture**		**Monosex culture**	
	Number	**Percentage**	**Number**	**Percentage**
Small male (SM)	37.00±2.83	20.11±2.94	7.00±4.24	4.67±2.61
Orange claw (OC)	71.00±9.90	38.59±2.72	92.00±8.94	61.33±2.77
Blue claw (BC)	76.00±5.66	41.30±0.22	51.00±5.66	34.00±5.38
Total	184.00±12.7	100	150.0±7.1	100

Table 5. Cost-benefit analysis of giant freshwater prawn production in different systems during the grow-out phase.

Costs/Revenue	Mixed-sex culture	Monosex culture	
		All-male culture	All-female culture
Costs ($THB{\cdot}ha^{-1}$)			
Giant freshwater prawn seed	10,238	13,125	13,650
Commercial pelleted feed	86,760	139,819	90,675
Electricity	30,734	16,042	18,125
Fuel	29,844	18,229	16,875
Labor	18,750	12,500	15,000
Chemicals and probiotics	15,000	11,823	11,738
Maintenance costs	4,438	3,385	1,938
Sex separation	-	104,167	125,000
Land lease	6,250	5,208	6,250
Harvest expense	15,000	12,500	15,000
Miscellaneous	11,134	10,938	11,563
Total cost	228,148	347,736	325,814
Revenue ($THB{\cdot}ha^{-1}$)	296,784	523,294	349,002
Net profit ($THB{\cdot}ha^{-1}$)	68,636	175,558	23,188

DISCUSSION

It has long been known that giant freshwater prawns cultured in an all-male monosex system generally grow faster and attain higher production yield than those reared in a mixed-sex system (Siddiqui *et al*., 1997; Nair *et al*., 2006; Tidwell *et al*., 2015). Due to the influence of female prawns in promoting the development of the male reproductive system, which in turn leads to somatic growth retardation, the key to success might be early separation of the male and female post-larvae, soon after their reproductive organs can be identified. Our study revealed that the external male characteristics (gonopore complex) could be distinguished under a stereomicroscope at 43 days after stocking in the nursery pond, when the prawns attained the average body weight of 0.78 g, although histologically their gonads had yet to be differentiated into testes and ovaries. This finding is in agreement with Rungsin *et al*. (2006), who reported the presence of the gonopore complex in giant freshwater prawns at 45 days of the post-larval stage. Consequently, our culturing of all-male and all-female prawns in the monosex grow-out ponds began after the post-larvae had been reared in the nursery pond for 43 days, which was sooner than the previous studies (Sagi *et al*., 1986; Siddiqui *et al*., 1997; Nair *et al*., 2006). The fact that the prawns' testes and ovaries develop after the appearance of the gonopore complex suggests that the histological technique is not suitable for sexual differentiation at the earliest stage. Nevertheless, histological sections can be helpful to confirm the accuracy of sex separation from 50 days onward. It is worth mentioning that around 10 % of the post-larvae died during the sex separation process at 43 days. The mortality during sexing has rarely been reported in the literature, but is usually assumed negligible from a practical perspective.

The males from the all-male monosex pond attained a higher average individual weight (93.02 g) than the males from the mixed-sex system (69.38 g), despite having been cultured for a shorter period (183 and 225 days, respectively). The female prawns, on the other hand, reached a lower average body weight compared to the males, only 30.28 g for the monosex culture at 183 days and 36.94 g for the mixed-sex culture at 225 days, respectively. Similarly, many previous researchers also noticed that the average prawn body weight was greatest in the all-male system, followed by mixed-sex and all-female systems (Siddiqui *et al*., 1997; Nair *et al*., 2006; Tidwell *et al*., 2015). Not surprisingly, the highest production yield at harvest was seen in the all-male pond (2,076.6 $kg \cdot h^{-1}$), whereas the lowest yield was recorded in the mixed-sex pond in our study (1,273.8 $kg \cdot h^{-1}$, when the yields from the males [660.0 $kg \cdot h^{-1}$] and females [613.8 $kg \cdot h^{-1}$] were combined).

The improvement of male prawn production from the monosex pond over the mixed-sex pond can be attributed to the higher proportion of the large-sized, less aggressive OC males in the population (61.33 vs 38.59 %, respectively) and lower proportion of the tiny, submissive SM males (4.67 vs 20.11 %), even if the proportion of the large-sized, more aggressive BC males was slightly reduced (34.00 vs 41.30 %). A similar shift in composition of male morphotypes as a result of monosex culture was observed in previous works, in which the SM proportion was generally reduced 2-5 times compared to the mixed-sex system (Siddiqui *et al*., 1997; Tidwell *et al*., 2015) or even eliminated in one study (Sagi *et al*., 1986). In contrast, the OC proportion usually increased 1.2-1.5 times (Sagi *et al*., 1986; Siddiqui *et al*., 1997; Tidwell *et al*., 2015). In another study, with the absence of female prawns, mating competition among male prawns was absent (Karplus and Barki, 2019), the male development from OC to BC was reduced, and the SM males were not inhibited from transforming into OC, allowing a significant proportion of the male population to become OC (Sagi *et al*., 1986; Tidwell *et al*., 2015).

The observation that the all-male culture was the most productive system, followed by the all-female and mixed-sex cultures is consistent with previous studies, as well (Sagi *et al*., 1986; Nair *et al*., 2006). Note that the all-female system was reported to be less productive than the mixed-sex group in one study (Siddiqui *et al*., 1997). The reason the production yield from all-female ponds was usually greater than that of the mixed-sex system despite the smaller size of the individual female prawns is that the survival rate of the females was greater than the males, regardless of the culture system (Sagi *et al*., 1986; Siddiqui *et al*., 1997; Nair *et al*., 2006; Levy *et al*., 2017). The less aggressive behavior of the female prawn is most likely responsible for the higher survival rate compared to the male prawn, for which agonistic behavior is common, especially the BC morphotype (Ra'anan and Sagi, 1985; Levy *et al*., 2017).

Regarding the profitability of the different culture systems, the cost-benefit analysis revealed that the all-male culture resulted in the highest revenue and became the most profitable system for giant freshwater prawn farming. Despite being the most expensive system, the all-male group was 155.78 and 657.11 % more profitable than the mixed-sex and all-female systems, respectively. Authors of another study made a similar conclusion, but their profit difference was less dramatic; Nair *et al*. (2006) reported that the net profit from all-male culture was 63 and 60 % greater than that from mixed-sex and all-female farming. Several factors can account for the difference in net profit between our trial and Nair *et al*. (2006), including the onset of post-larvae sex separation, which was 43 days in our study and 60 days in the other (with corresponding average body weights of 0.78 and 4.5 g, respectively). Whether and to what extent the sex separation time plays a critical role in the success of all-male monosex culture is worth further investigation. Nevertheless, it is wise to separate the sex of post-larvae and stock all-male prawns as early as possible.

It should be noted that although some researchers favored all-female over all-male culture (Malecha, 2012; Levy *et al*., 2017), our results showed that with our experimental setting, the all-female group was the least profitable system; the higher productive yield of the all-female monosex culture (compared to the mixed-sex group) was offset by the high production costs. Hence, the economic viability of the all-female system is disputable.

CONCLUSION

The male sexual characteristics (gonopore complex) of the giant freshwater prawn post-larvae first appeared at 43 days (0.78 g) after stocking in the nursery pond, enabling the sex separation and monosex grow-out at this stage. Culturing all-male prawns had several advantages over the traditional mixed-sex and all-female cultures. In the absence of females, the male prawns grew faster and had a higher survival rate. The proportions of SM and OC males were also favorably shifted, leading to greater production yield and net profit compared to the other two systems. In short, the all-male monosex culture was the most productive system and is economically justifiable.

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