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Research article

Spawning behaviour and activity in seven species of ornamental dottybacks

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Abstract

The marine aquarium fish industry has been growing rapidly, but still heavily relies on wild-caught organisms. Dottybacks (Pseudochromidae) are among the most popular cultured marine fishes, but issues related to pair formation and filial cannibalism commonly prevent mass production. This study investigated the behavioural aspects of dottyback aquaculture, mainly the events surrounding pair formation and spawning activity. Broodstock pairs of seven species were acquired and aggression level monitored daily for each pair, as well as spawning activity and frequency. All pairs successfully bonded, but the time until bonding varied; trends were observed in aggression level for some species. Time in between bonding and spawning also presented a high variability (5.7 ± 4.2 weeks). The spawning frequency was somewhat fixed for each pair, but variable among species. Egg masses were frequently cannibalised and most pairs required many spawning events (8.7 ± 8.2) for the first egg mass to hatch. Dottybacks present no sexual dimorphism, therefore the aggression levels and variability in bonding time are probably related to sex changes. The egg mass cannibalism decreased with time and was likely related to broodstock inexperience. The results presented should aid in enhancing aquaculture protocols and hopefully stimulate worldwide dottyback aquaculture.

Introduction

The marine aquarium trade is a commercial industry that has been expanding all over the world (Olivotto et al. 2011). It has been estimated that this economic sector is worth around US$ 15 billion (Olivotto et al. 2006), but heavily relies on wild-caught rather than cultured specimens. In the past decade it has been reported that 24 million marine fishes belonging to 1,470 species were harvested yearly, exclusively for the aquarium trade (Wabnitz et al. 2003). In that same period, only about 50 species of marine aquarium fishes were commercially cultured, out of more than 1,000 economically important species (Arvedlund et al. 2000). Nowadays a little over 80 different species of aquacultured marine ornamental fish are mass-produced and frequently available in the largest commercial hatcheries. While marine ornamental aquaculture is growing, it is still not as successful as that of ornamental freshwater fish, where over 90% of commercially available fish are cultured (Tlusty 2002). The main hindrances in the production of new marine species are the difficulty in getting broodstock to spawn, larval nutrition and scaling up from laboratory culture to mass production (Holt 2003; Olivotto et al. 2008).

Along with Pomacentridae and Gobiidae, the family Pseudochromidae features among the most popular of the cultured marine ornamental fish. Also known as dottybacks, this group has caused a revolution in the ornamental aquaculture industry like no other, apart from clownfishes, because of their resilience and reduced size (Wittenrich 2007). Members of the Pseudochromidae are widespread in the Pacific Ocean, but many are endemic to areas located in the Indian Ocean, such as the Red Sea (Lubbock 1976; Gill 2004). Several species have been described in the last few years (Gill and Allen 2011; Gill et al. 2012), with roughly 153 valid species in total (Froese and Pauly 2011). Most species of dottybacks exhibit protogynous hermaphroditism with bi-directional sex change also reported for some (Wittenrich and Munday 2005). This feature facilitates

their aquaculture, considering that the random placement of a randomly chosen pair of fish will result in pair formation and spawning. Once the pair is formed and spawning initiates, the female lays a demersal egg mass that is tended by the male until hatching (Olivotto et al. 2006; Wittenrich 2007).

Even though dottybacks are successfully cultured and produced, they still display a few characteristics that prevents culturing them from becoming a worldwide activity. The most notable issues are related to larval rearing. Larval mortality is relatively high (Wittenrich and Turingan 2011) and associated with physiological changes and nutrition (Olivotto et al. 2006; Wittenrich 2007; Holt 2011). In addition, there are many problems associated with events prior to larval rearing. Firstly, pairing is often a difficult task considering that some species (e.g. *Pictichromis* spp.) show extreme aggression that may eventually result in death (Wittenrich 2007). Then, once pairing is successful and spawning activity begins, it may take place over irregular time intervals and with males frequently cannibalizing the egg masses, not allowing them to hatch (M. Mies, pers. obs.).

The present study investigated and identified the main issues related to pair formation and spawning activity in several species of Pseudochromidae. During the experiments, spawning behaviour, activity and frequency were recorded, as well as successful egg hatching. The study aims to contribute to improvements in pairing dottybacks, managing spawns and establishing standard practices for aquaculture protocols, which will hopefully enhance worldwide production of pseudochromids.

Methods

Broodstock acquisition

A total of 11 pairs of seven different species of dottybacks were acquired through local fish suppliers and breeders. Each one of the 22 fishes was purchased separately and their gender unknown. Seven pairs belonged to the genus *Pseudochromis* and included three pairs of *Pseudochromis fridmani*, two pairs of *P. flavivertex*, one pair of *P. aldabraensis* and one pair of *P. springeri*. Of the remaining four, two were *Pictichromis paccagnellae*, one was *Pictichromis diadema* and one was *Manonichthys splendens*. None of these species present sexual dichromatism or dimorphism. All fishes were randomly chosen generating heterogeneity of sizes. Fishes shorter than 4.0 cm in length (TL) were defined as small, fishes longer than 6.0 cm as large and fishes 4.0–6.0 cm long as medium-sized. All fishes were cultured specimens, except for the *Pictichromis* pairs. It was also known that *P. fridmani* pair "C" were actually siblings, originally from the same parents and spawn. The same was the case for *P. flavivertex* pair "B".

Broodstock maintenance

All pairs were kept in a recirculating system and maintained in rigorously stable physical and chemical water conditions. Temperature was maintained at 27° C, specific gravity at 1,024 kgm^{-3} and photoperiod at 10L:14D. Nitrogen compounds were controlled by a protein skimmer and kept below 0.01 mg L^{-1} for NH_4^+ and NO_2^- and below 0.1 mg L^{-1} for NO_3^-. Each pair was placed in a 60 L rectangular glass tank with numerous PVC pipe segments to provide shelter and hiding places. Three hermit crabs and a single ophiuroid (*Ophioderma cinerea*) were placed in each tank to help clean detritus and food remnants. Aragonite substrate and heavy aeration were also employed to stimulate biological filtering and prevent the growth of undesired algae and cyanobacteria. Each pair was fed three times a day with 10 to 15 pellets (0.5 mm in diameter) of Sustainable Aquatics Hatchery Diet (55% crude protein and 19% crude fat; Sustainable Aquatics LLC, Jefferson City, TN, USA). The behaviour of all pairs was monitored for eight months immediately after the fish were introduced to the system.

Bonding and aggression – internal tank method

Many individuals exhibited aggressive behaviour towards their conspecifics when placed together in the broodstock tank. The level of aggressive behaviour was monitored daily and classified as: low – dominant fish may occasionally chase the submissive fish, but no physical evidence of aggression is present apart from slightly torn fins; medium – dominant fish frequently chases the submissive fish, with torn fins and bite marks evident on the body; and high – dominant fish incessantly chases and bites the submissive fish, significantly threatening the life of the latter. If a high level of aggression was observed between a pair, these were separated. In such cases, a smaller glass tank with a lid made of 7.5-mm plastic mesh was positioned inside the 60 L tank. The submissive fish was then placed inside the smaller tank so the dominant fish could observe and grow accustomed to the presence of the submissive fish. These non-bonding individuals were completely exposed to each other every two weeks for half an hour until aggression level decreased and a bond was finally established, defined as when both individuals swam together and aggression ceased.

Recording of spawning and hatching events

Throughout the eight-month period, spawning activity was monitored and recorded. For all pairs, every day at noon and after lights-out, the PVC pipe guarded by the male individual was inspected with a flashlight for the presence of egg masses. When spawning had occurred, the egg masses were left to the care of the male and eventually were either eaten or hatched. Whenever eggs survived past the fourth night post-spawn and eye spots were bright gray, the egg mass was removed and kept in an artificial incubator. Egg masses were artificially incubated by placing them inside an oval cup connected to an air compressor. This cup was placed inside a tank connected to recirculating system; a gentle airflow kept the egg mass in constant motion. Hatching events were considered successful and recorded only when more than 50% of the larvae had successfully hatched from the egg mass.

Results

Bonding

Except for *P. flavivertex* pair "A", all pairs belonging to the genus *Pseudochromis* presented moderate to low aggression (Table 1) and were kept together until effectively bonded, at which point aggression halted and pairs were occasionally observed swimming together. Many pairs bonded immediately, especially the sibling pairs of *P. fridmani* "C" and *P. flavivertex* "B". On the other hand, *P. flavivertex* pair "A" and the pairs of *M. splendens* and *Pictichromis* spp. showed a high level of aggression and had to be separated by the internal tank method to prevent deaths. The internal tank method resulted in a 100% success rate with all pairs eventually bonding. However, the pair of *M. splendens* took approximately 6 months to effectively bond (Table 1).

Spawning behaviour and activity

The time elapsed after bonding and before spawning is denoted the "bonding–spawning interval". This interval took as little as two weeks for some pairs (e.g. *P. diadema*) and over four months for others (*P. paccagnellae*). Average time for all pairs was 5.7 ± 4.2 weeks, excluding the data for *M. splendens* and *P. springeri*.

Prior to spawning events, females exhibited a swollen belly and males demonstrated courting behaviour. The male would constantly swim towards the female and quickly make a U-turn and return to his shelter, vigorously waving his tail back and forth. After this ritual was repeated three or four times, the female would follow the male into his PVC pipe shelter and lay an egg mass (Fig. 1). This egg-laying procedure inside the shelter lasted an average of about 20 minutes. After first spawning, all pairs began to spawn at a somewhat fixed interval (Table 2). The pair that

Table 1. Main characteristics of the 11 pairs of Pseudochromidae used in this study. Fishes were randomly chosen for the experiments, generating heterogeneity and disparities in size between the pairs. All pairs were originally cultured, except for the *Pictichromis* pairs; aggression was determined according to the level of stress and damage inflicted by the dominant fish. Time to bond was designated as time spent by a pair to completely bond and cease aggression.

Pair	Origin	Aggression level	Size difference	Pair size	Time to bond
Pseudochromis fridmani pair "A"	aquacultured	low	no	both small	immediately
P. fridmani pair "B"	aquacultured	low	no	both medium	immediately
P. fridmani pair "C"	aquacultured	low	yes	small and medium	immediately
Pseudochromis flavivertex pair "A"	aquacultured	high	yes	medium and large	7 weeks
P. flavivertex pair "B"	aquacultured	low	no	both medium	immediately
Pseudochromis aldabraensis	aquacultured	medium	yes	medium and large	6 weeks
Pseudochromis springeri	aquacultured	low	no	both medium	immediately
Pictichromis paccagnellae pair "A"	wild-caught	high	yes	small and large	19 weeks
P. paccagnellae pair "B"	wild-caught	high	no	both medium	8 weeks
Pictichromis diadema	wild-caught	high	yes	medium and large	8 weeks
Manonichthys splendens	aquacultured	high	yes	medium and large	25 weeks

presented the highest spawning frequency was *P. fridmani* pair "B", spawning every 5.8 ± 0.5 days, and the lowest was presented by *P. flavivertex* pair "B", spawning every 11.2 ± 1.1 days. Every pair would spawn at a specific time during daylight, either in the morning or afternoon. The only exception was *P. fridmani* pair "C", which always spawned after dark.

A few events of note occurred with some pairs. The *M. splendens* pair started spawning even before bonding and while separated. The female would lay the eggs on the bottom of the internal tank. When released from the internal tank she was vigorously chased and attacked by the male. The *P. diadema* pair stopped spawning after five spawning events and began to demonstrate aggression once again, suggesting that the pair disbanded. Lastly, the *P. springeri* pair was the only one to never spawn after being together for eight months.

Hatching

Most pairs did not allow the egg mass to hatch until after several unsuccessful spawning events. The average number of spawns until the first hatch was 8.7 ± 8.2, excluding the data for the pairs that presented no hatches in the 8-month period (*P. paccagnellae* pair "A", *P. diadema* and *M. splendens*) and the pair of *P. springeri*, for which no spawns were recorded. The males would frequently eat the egg mass on day two or three post-spawn. These males would also frequently eat the egg mass in small increments, decreasing its size every day until the third day when they cannibalised the last remnants of the egg mass. The highest contrast in time until a successful hatch was within the species *P. fridmani*: pair "A" spawned 24 times before allowing an egg mass to hatch, while pair "B" had a successful hatch for the second spawn (Table 2). Most egg masses hatched successfully in spawns subsequent to

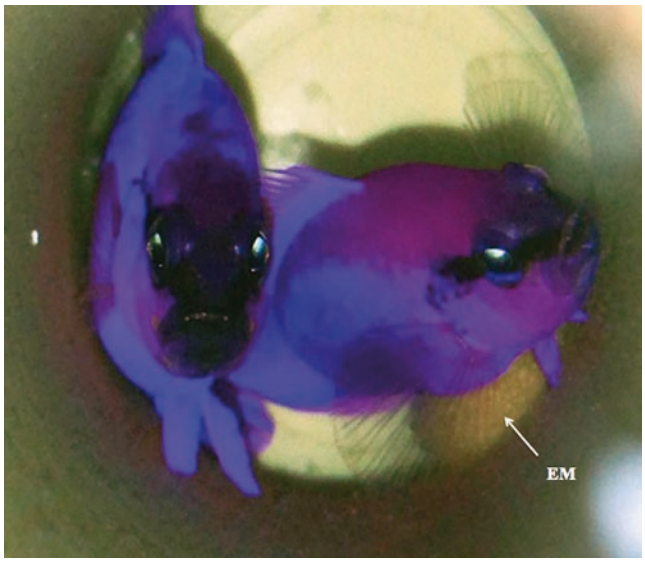

Figure 1. Spawning event of *Pseudochromis fridmani* pair "B" taking place inside the PVC pipe guarded by the male. The male is on the left; an egg mass (EM) is being laid and visible just below and to the right of the female. Shortly after this stage of the process, the male would constantly rub on the egg mass and fertilise it.

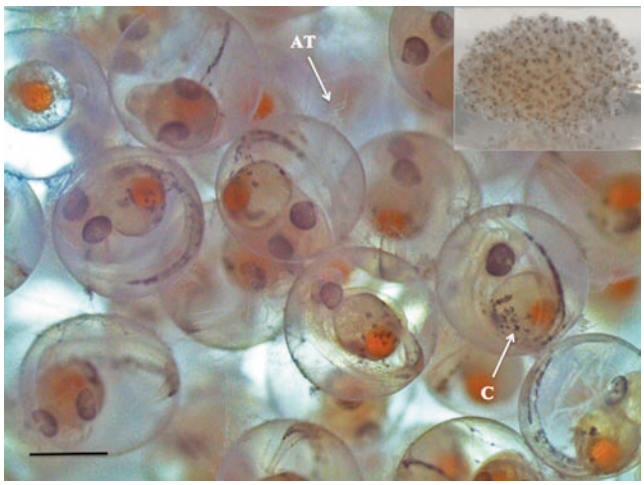

Figure 2. Details of an egg mass (96 h post-spawn) laid by the pair of *Pseudochromis aldabraensis.* Embryos are kept together by adhesive threads (AT). At this stage they display large visible eyes and chromatophores (C) in the tail. Scale bar = 500 µm. Top right: the same egg mass, 2.5 cm in diameter, when removed from the PVC pipe guarded by the male.

Table 2. Spawning and hatching results presented by the 11 pairs of Pseudochromidae. Spawning results include bonding–spawning interval (time in between bonding and first spawn), spawning frequency (in days) and spawning period of the day. Hatching results include how many spawning events took place until the first hatching and at which day post-spawn the eggs hatched. Data marked with an asterisk were phases that were still incomplete at the end of the 8-month experiment.

Pair	Bonding–spawning interval	Spawning frequency interval (n)	Spawning period	Spawns until first hatch	Hatching day (post-spawn)
Pseudochromis fridmani pair "A"	6 weeks	7.2 ± 1.0 (27)	PM	24	5th
P. fridmani pair "B"	4 weeks	5.8 ± 0.5 (27)	AM	1	4th
P. fridmani pair "C"	5 weeks	7.3 ± 0.9 (22)	PM (after dark)	6	5th
Pseudochromis flavivertex pair "A"	8 weeks	9.9 ± 0.8 (12)	PM	2	6th
P. flavivertex pair "B"	4 weeks	11.2 ± 1.1 (17)	PM	4	5th
Pseudochromis aldabraensis	3 weeks	8.4 ± 1.8 (19)	PM	9	5th
Pseudochromis springeri	32 weeks*	–	–	–	–
Pictichromis paccagnellae pair "A"	4 weeks	6.9 ± 1.4 (17)	PM	15	5th
P. paccagnellae pair "B"	16 weeks	10.0 ± 0.0 (1)	AM	2*	–
Pictichromis diadema	2 weeks	10.2 ± 3.0 (4)	PM	5*	–
Manonichthys splendens	immediately	10.0 ± 1.4 (4)	AM	5*	–

the first successful egg mass hatch, but it was still common for the pairs to occasionally eat them. Many eaten egg masses had a white coloration and no eyespots, indicating poor development.

When an egg mass reached day four or five post-spawn, pigmented eyes were visible (Fig. 2) indicating a readiness to hatch. All hatching events took place when light intensity significantly varied, either when a strong light was positioned above the incubator or 1–2 hours after the lights went out.

Physiological characteristics of eggs and larvae

Egg masses averaged 3 cm in diameter and each contained about 1,200 embryos (Fig. 2). Upon microscopic inspection, adhesive filaments were observed on the surface of all eggs keeping the embryos together. Embryos measured 1.0 mm, while hatched larvae were an average of 3.5 mm in total length. Very few or no chromatophores were visible in the larvae of most species, except for *P. aldabraensis* and *P. paccagnellae* larvae, which contained dozens of chromatophores and darker pigmentation when compared to the other species analysed in this study.

Discussion

Bonding

The pair formation issue in dottyback aquaculture is related to bonding and aggression between the pair. Dottybacks are known to display bi-directional sex change, being able to switch gender back and forth according to either physiological or ecological necessities (Wittenrich and Munday 2005). When pairing dottybacks, it is generally extremely difficult to determine the sex of the individuals; it is very common for same-sex individuals to be placed together. Considering that in many coral reef fishes, aggression is more intense between conspecifics of the same sex (Fricke 1980; Black et al. 2011) due to endocrinal regulation (Oliveira et al. 2002; Black et al. 2011), it is possible that some of our extremely aggressive pairs (e.g. *M. splendens*) were not originally heterosexual. Therefore, some pairs might have required sex reversal and the bonding time was correspondingly longer and positively related to aggression level. However, some species demonstrated a trend in aggression level. All pairs of *P. fridmani* were extremely docile, even when size differed between the individuals (Table 1). *Pictichromis paccagnellae* pairs, however, demonstrated high levels of aggression throughout. Such trends corroborate the reports of many commercially oriented and non-scientific dottyback breeders (R. Rio, pers. comm.).

Most dottybacks are protogynous hermaphrodites and sex reversal in the opposite direction (male to female) can take as much as twice as long and over three months to successfully take place (Wittenrich and Munday 2005; Wittenrich 2007). This may be an explanation for the difference in the time to bond for the two pairs of *P. paccagnellae* (Table 1). Perhaps pair "A" consisted originally of two males, while pair "B" was either heterosexual or consisted of two females. Time to bond also differed significantly among the *P. flavivertex* pairs. Considering that *P. flavivertex* pair "B", as well as *P. fridmani* pair "C", was formed by individuals that spent their entire life cycles together, including larval stages, it is likely that a heterosexual pair was naturally established as juveniles matured.

In the case of aggressive broodstock, the internal tank method proved effective in achieving successful pairing and bonding. Another possibility may be stocking several broodstock conspecifics together. Aggressive behaviour will likely occur but the most physically fit heterosexual individuals are also likely to quickly bond and start spawning (Sayadi et al. 2012).

Spawning

Dottybacks readily spawn in captivity if water conditions and feeding regimens are adequate (Wittenrich 2007). It has been reported that dottybacks may start spawning as early as three weeks after bonding (Olivotto et al. 2006). Some of our pairs corroborate such reports, considering that five of 11 pairs spawned within a month after bonding (Table 2). However, other pairs took much longer to start spawning, especially *P. paccagnellae* pair "B", spawning only after four months post-bonding. The bonding–spawning interval showed no correlation with time to bond, showing that a

readiness to spawn may be more influenced by aspects pertaining to reproductive physiology and successful gonadal maturation rather than social ecology.

Dottybacks are known to spawn early in their life cycle, as early as six months of age (Moe 1997). The spawning frequency has been described for some ornamental species such as gobies (Wittenrich et al. 2007), but never for dottybacks. When a dottyback pair begins spawning activity, it generally takes place over a relatively fixed interval (Table 2). However, this frequency was shown to vary among conspecific pairs and is in accordance with studies stating that dottybacks spawn in intervals fixed between six and ten days (Moe 1997; Wittenrich 2007). Furthermore, dottybacks tend to spawn at a fixed time of day (Table 2). Each of our 11 pairs always spawned at the same time of day, either in the morning or afternoon.

Hatching

Pseudochromidae spawn demersal egg masses and are one of the few fish to have them wrapped together by adhesive threads (Mooi 1990). The male fish tends these egg masses inside his shelter by vigorous oxygenation and constant tumbling (rotating and spinning the egg mass through 360 degrees). He seldom ventures out when caring for the eggs, even when food is available. Most of our spawns hatched during the fifth day post-spawn, similar to results reported for dottybacks kept at 27° C (Olivotto et al. 2006). However, the males ate many of the egg masses before hatching (Table 2) on day two or three post-spawn. The eaten egg masses often seemed poorly developed, with no embryos visible inside the egg case, in contrast to well-developing egg masses. *Pseudochromis fridmani* pair "A" spent six months spawning and constantly eating the egg masses until the first hatch, while pair "B" had a successful hatch for the second spawn.

The production of poor-quality egg masses may be a consequence of two events: 1) the male is not taking proper care of the eggs; or 2) the female is not laying eggs that are physically fit enough to successfully undergo embryonic development and hatch. The first hypothesis is supported by the fact that many inexperienced males may leave their shelter and therefore not provide appropriate oxygenation to the egg mass, leading embryos to develop under hypoxic conditions (Payne et al. 2002; 2004). The second hypothesis may relate to the fact that the females of coral reef fishes tend to increase fecundity and egg quality over time and with increased experience (Sargent 1992; Klug 2009).

Conclusions

Of the three main bottlenecks in dottyback aquaculture, two were addressed in this study: pair formation and the delay in successful egg mass hatching. A wide variety of events may take place when attempting to pair and spawn dottybacks: size, sex and behaviour are some of the factors that may influence both bonding and spawning, either quickening or retarding the processes. Our data indicate that aggression and time to bond are intimately related.

Regarding pair formation, the breeder can make one of two major decisions: pairing young fish that may take longer to spawn quality eggs or pairing large fish that may spawn quality eggs, but take longer to bond. Either way, patience seems to be a requirement. When commercially culturing these specimens and considering the variability in our results, it is recommended that having a large broodstock available would facilitate the mating and spawning of pairs. The delay in successful hatching may be related to size and inexperience of the pairs, as large and older broodstock appeared to spawn higher-quality eggs. However, more research focusing on this specific aspect may contribute and add to our results.

The methods and results produced in this study may enhance dottyback breeding protocols, especially for the pairing stage. For example, avoiding *Pictichromis* spp. and starting operations with more docile species such as *Pseudochromis fridmani* and *P. springeri* is highly recommended for less experienced breeders. Our data may also stimulate breeders all over the world to engage in dottyback aquaculture, especially in places where these fishes are currently absent or in low supply, fighting high prices and mortality related to importation.

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