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RESEARCH

# Broodstock spawning activity and filial cannibalism in orchid dottyback *Pseudochromis fridmani* (Klausewitz, 1968) under different rearing temperatures

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## Abstract

The orchid dottyback *Pseudochromis fridmani* is considered one of the most attractive species in the marine ornamental fish trade because of its bright colour, resilience, and relatively small size. Orchid dottyback aquaculture faces bottlenecks related to broodstock management and spawning conditioning, which make large-scale production challenging but can be addressed through targeted improvements. The present study addresses the knowledge gaps with regard to the management of *P. fridmani* under artificial conditions, describing the pair formation process with the associated behaviours, and the histological maturation process of gonads. The effects of low (25 °C) and high (28 °C) temperature on spawning activity and filial cannibalism were studied by monitoring six pairs for a period of 6 months. Water temperature strongly influenced broodstock spawning activity and filial cannibalism. The spawning rate increased significantly at 28 °C, but concurrent filial cannibalism also increased, leading to spawn losses. Notably, the total monthly number of viable spawns that successfully developed until hatching did not differ significantly between the 28 and 25 °C treatments. Examination of the size and shape of specimens sexed by histology ($n = 6$) suggested that these criteria may allow rapid visual sex identification in this species. Males tended to be longer and exhibited a more slender body shape, while females were comparatively shorter and showed a rounder body shape with a more pronounced belly. However, the accuracy of this method needs to be evaluated using larger sample sizes. In summary, maintaining the broodstock temperature around 25 °C facilitates the management of spawns and improves the performance of this highly demanded species.

**Keywords** Pseudochromidae · Rearing temperatures · Filial cannibalism · Reproductive behaviour · Gonad histology

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## Introduction

Aquaculture of marine ornamental species plays a key role in the aquarium fish trade and is considered a sustainable alternative to wild-capture fisheries (Holt 2003; Olivotto et al. 2003, 2011). Over the past decades, this trade has expanded worldwide, becoming a multi-million-dollar industry exceeding 340 million US$ per year in value in 2014 (Calado et al. 2017; Biondo et al. 2020). Approximately 90% of the marine fish sold are still captured in the wild, and in some countries, destructive capture methods are still employed, resulting in negative repercussions on coral reefs and the surrounding marine ecosystems (Olivotto et al. 2003; Calado et al. 2017). Consequently, concerns have been raised regarding the overexploitation of natural stocks, leading to an increasing interest in the development of aquaculture techniques (Pouil et al. 2019). Moreover, hatchery-produced juvenile fish exhibit greater hardiness and reduced susceptibility to disease, displaying a higher survival rate under artificial conditions compared to wild-caught specimens (Tlusty 2002; Olivotto et al. 2017; Chen et al. 2020; Watson et al. 2023). The study of the reproductive biology of marine ornamental fish is essential for achieving successful production (Chen et al. 2020; Watson et al. 2023). However, the reproductive behaviour and spawning of reef fish are frequently difficult to observe in field studies, which typically focus only on describing species distribution, habitat, and morphology (Lubbock 1975; Zander 2017). Consequently, relevant information is scarce in the literature, and the production of new marine species under artificial conditions is often constrained by knowledge gaps in captive spawning and larval nutritional requirements, which are generally the main bottlenecks in scaling up to mass production (Holt 2003; Olivotto et al. 2017; Chen et al. 2020, 2023; Martino et al. 2023).

Dottybacks (Pseudochromidae) are a family of small, vibrantly coloured marine reef fish found in the Indo-Pacific region (Thresher 1984; Wittenrich 2007). They are among the most traded marine ornamental fish and are popular choices for home aquariums, along with damselfish (*Pomacentridae*), because of their aesthetics, bright colour, resilience, and relatively small size (Thresher 1984; Wittenrich 2007; Calado et al. 2017). Dottybacks comprise more than 150 species in 24 genera, and new species are still being discovered (Gill 2004; Gill and Allen 2011; Gill et al. 2012). The orchid dottyback *Pseudochromis fridmani* (Klausewitz, 1968) is a small, captivating dottyback endemic to the Red Sea (Lubbock 1975; Moe 1997; Gill 2004) and is considered one of the most commercially attractive dottybacks in the marine aquarium trade (Wittenrich 2007). Orchid dottybacks are characterised by a bright purple, elongated body with a black stripe across the eyes. They are also known for their hardiness and resilience in aquarium culture (Moe 1997). While *Pseudochromis fridmani* was once considered challenging to rear in artificial condition, it is now routinely produced by multiple aquaculture companies, with nearly all specimens in the ornamental fish trade being captive-bred rather than wild-caught. Optimising the breeding management for this species is of significant interest to the aquarium industry. In this context, it is important to understand the reproduction and behaviour of this fish under artificial conditions. Although orchid dottybacks have been successfully bred under artificial conditions (Brons 1996; Moe 1997; Chen et al. 2023; Martino et al. 2024), they display several characteristics which make large-scale production challenging. Similar to most dottybacks, *P. fridmani* was described as a protogynous hermaphrodite, developing first as a female and becoming a male later; the timing of sex change is influenced by social dynamics (Wittenrich 2007). There is limited evidence for bidirectional sex change in this species, although it is hypothesized to occur in wild populations (Wittenrich and Munday 2005; Wittenrich 2007; Kuwamura et al. 2014). To date, some of the most critical challenges for the culture of orchid dottybacks are related to broodstock and spawning management (Chen et al. 2023), as comprehensive studies on pair formation, sexual behaviour, spawning dynamics, gonadal development, and filial cannibalism (FC) are limited or completely lacking (Wittenrich 2007; Mies et al. 2014; Chen et al. 2023). Recently, Chen et al. (2023) described the early embryonic and larval ontogeny of *P. fridmani* under artificial conditions. This work documented year-round spawning and high FC, encouraging future studies to understand and manage cannibalism by broodstock and optimise larval dietary nutrition during the first 14 days post-hatching (DPH). Indeed, previous studies on *P. fridmani* breeding and larval culture lack detailed descriptions and analyses (Brons 1996; Moe 1997). However, recent studies focused on the production of high-quality live feeds (Martino et al. 2023), a key factor for larval survival. The best culture performance was observed when *P. fridmani* larvae were fed enriched calanoid copepods during the first 15 DPH (Martino et al. 2024). Pairing dottybacks can also pose challenges, considering that within the confines of a small tank, co-housing of two or more similarly sized individuals typically results in fighting (Lubbock 1975). Recommended strategies to mitigate intraspecific aggression involve keeping *P. fridmani* in groups of individuals with different sizes providing hiding structures and refuges (Lubbock 1975; Wittenrich 2007; Mies et al. 2014). In addition, introducing individuals before puberty may enhance pair formation, as juveniles tend to be less predisposed to exhibit aggressive intragroup behaviour and more likely to form mating pairs as they mature (Mies et al. 2014). When spawning begins, the female lays a demersal egg mass that may be protected or consumed by the male before hatching (Wittenrich 2007; Mies et al. 2014; Chen et al. 2023). Although different studies have documented FC in *P. fridmani,* the specific mechanisms eliciting this behaviour are unknown, rendering it an aquaculture bottleneck for this and many other dottyback species (Sargent 1992; Mies et al. 2014; Shei et al. 2017; Chen et al. 2023). Temperature strongly influences metabolism and behaviour in aquatic ectotherms, with direct consequences for key aquaculture traits such as growth, reproductive performance, and survival under controlled conditions (Pankhurst and Munday 2011; Visser 2008; Sunday et al. 2010). FC may also be influenced by temperature, while temperature-dependent effects on FC and reproductive performance have indeed been reported in other marine fishes (Donelson et al. 2010; Madhu et al. 2016). Reduced dissolved oxygen availability at higher temperatures can compromise embryonic development and increase the incidence of non-viable eggs, which males may then consume to recover energy from otherwise lost reproductive investment (Payne et al. 2002, 2004; Vallon et al. 2016). In addition, elevated temperatures may accelerate metabolic rates and the energetic costs of parental care, making egg consumption an adaptive strategy to balance the trade-off between self-maintenance and offspring survival (Manica 2004; Klug 2009). Courtship and continuous reproductive activity at higher temperatures may further exacerbate male energetic demands, increasing the likelihood of FC as a means to regain resources and potentially restart reproductive cycles (Matsumoto et al. 2018).

In the present study, we tested the effects of two temperatures on reproductive performance, and FC in the orchid dottyback *P. fridmani*. The behaviours involved in the pairing process of orchid dottybacks under artificial conditions were monitored for 6 months, and the histology of mature gonads was characterized.

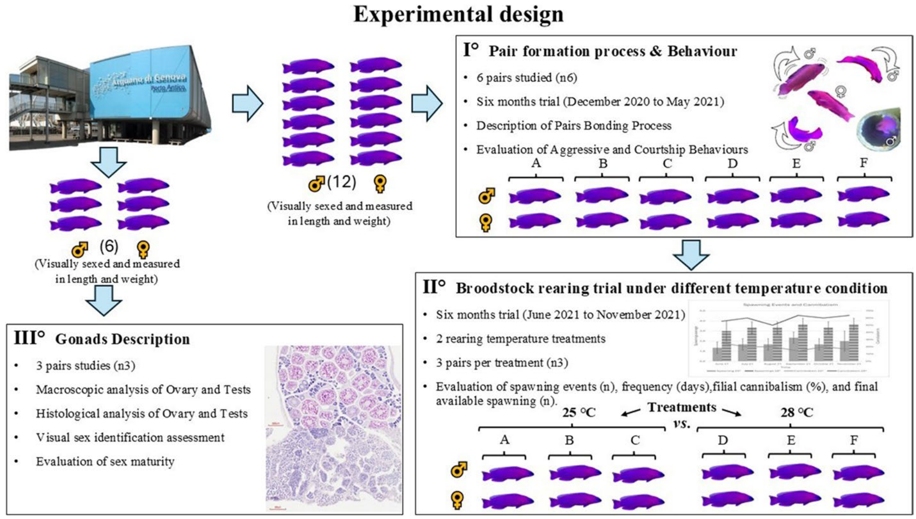

**Fig. 1** Experimental design: 6 pairs of *P. fridmani* were obtained and divided into two experimental rearing treatments ($n=3$), 25 °C and 28 °C, for 6 months studying the effects on spawning production, spawning frequency and filial cannibalism. In addition, a detailed description of pair formation behaviour and gonad histology was performed

## Materials and methods

All experiments described below (Fig. 1) were conducted in quarantine areas belonging to the Tropical Department of the Aquarium of Genoa (Genoa, Liguria, Italy). Histological analysis was performed in the laboratories of the Highly Specialized Aquaculture and Biotechnology Service (SABE), located at the Marine Scientific and Technological Park of the ECOAQUA Institute of the University of Las Palmas de Gran Canaria (Las Palmas, Canary Islands, Spain).

### Broodstock conditioning

A total of 18 adult *P. fridmani* were procured from the Aquarium of Genoa (Genoa, Liguria, Italy) and briefly acclimated in the same tank of a dedicated recirculating system for approximately 15–20 min. (Fig. 1). Since individuals were previously maintained at 25 ± 1 °C, a salinity of 35 ± 1 g $L^{-1}$, and a 12:12 h photoperiod, the same physicochemical conditions were adopted to ensure environmental consistency. At the end of the acclimation period, the total length and weight of each fish were measured (Table 1). All fish were older than 1 year (Table 1) at the beginning of the experiment, with a total length and weight of 10.2 ± 1.2 cm and 8.4 ± 1.7 g, (mean ± standard deviation, SD; Table 1) respectively. Because *P. fridmani* does not present any obvious sexual dimorphism, specimens were visually sexed assuming females to be smaller with a swollen belly and males to be larger and more slender. The sorted specimens were split into nine pairs (Table 1), three of which were euthanized (Chen et al. 2014), placed in 50 mL Falcon polyethylene tubes and preserved in buffered formalin (4%) for subsequent histological analyses (Fig. 1). The remaining six pairs (Table 1) were simultaneously placed in assigned partitions of two

**Table 1** Total length and weight of 18 *P. fridmani* individuals selected for the experimental broodstock trial (1 year) and histological analysis of gonads

| *P. fridmani* Biometry | Specimens | Pair | Sex | TL (cm) | Weight (g) |
|---|---|---|---|---|---|
| Broodstock Study | 1 | A | Male | 12.1 | 10.9 |
| | 2 | | Female | 9.8 | 6.6 |
| | 3 | B | Male | 10.3 | 7.3 |
| | 4 | | Female | 8.4 | 8.6 |
| | 5 | C | Male | 11.3 | 10.4 |
| | 6 | | Female | 9.5 | 8.1 |
| | 7 | D | Male | 11.2 | 9.6 |
| | 8 | | Female | 10.1 | 10.3 |
| | 9 | E | Male | 11.9 | 9.8 |
| | 10 | | Female | 8.6 | 5.4 |
| | 11 | F | Male | 10.4 | 6.6 |
| | 12 | | Female | 8.2 | 5.23 |
| Total mean | | | Male | 11.2 ± 0.7 | 9.1 ± 1.7 |
| | | | Female | 9.1 ± 0.8 | 7.8 ± 1.9 |
| Gonads Histology | 13 | G | Male | 11.5 | 9.6 |
| | 14 | | Female | 8.9 | 6.6 |
| | 15 | H | Male | 11.3 | 9.8 |
| | 16 | | Female | 9.6 | 8.6 |
| | 17 | I | Male | 10.8 | 7.9 |
| | 18 | | Female | 8.8 | 6.2 |
| Total mean | | | Male | 11.2 ± 0.4 | 9.1 ± 1.0 |
| | | | Female | 9.1 ± 0.4 | 7.1 ± 1.3 |
| Total | | | | 10.2 ± 1.2 | 8.4 ±1.7 |

glass aquaria connected to the same recirculating system (Fig. 1). Each aquarium was divided into three partitions of approximately 133 L (Fig. S1), without any decoration or gravel, and provided with individual aeration. Each partition housed one *P. fridmani* pair and two uncapped polyvinyl chloride (PVC) pipes (30 cm long and 3.2 cm in diameter) as shelter and spawning substrate. The use of a glass tank and an open-ended pipe in the present study provided a great opportunity to describe this behaviour. Access to the experimental area was restricted to a few people to avoid interference with behaviour and spawning activity. Water quality was maintained using biological filtration, a sand filter, a UV steriliser (Panaque, Italy), and a heat exchanger, all powered by a main pump (Astralpool, Italy). Each broodstock tank was illuminated by two 30 W fluorescent tubes (Philips, Netherlands) positioned 20 cm above the water surface. The fish were fed twice a day (9:00 a.m. and 2 p.m.) ad libitum using mixed diets based on marine chopped fish (cod and sardines), mussels, and shrimp. The diet was supplemented with a vitamin premix (1 g/kg) that contained spirulina powder (60%), ascorbic acid (10%), Astaxanthin (10%), garlic powder (10%), B-complex (5%), and trace minerals (5%). In addition, the broodstock was fed enriched live-cultured *Mysis* and frozen adult *Artemia* once a day, at a ratio of approximately 10 individuals of each prey species per fish. Daily maintenance included cleaning the drain mesh and siphoning the feed waste and debris. Water samples were collected from the recirculating system three times per week to check dissolved oxygen levels

(> 80%) salinity, pH (> 8.0), ammonia ($NH_4^+$), and nitrite ($NO_2$). The latter two parameters were maintained below 0.01 mg $L^{-1}$ throughout the trial.

## Behaviour and pair formation management

After isolation (see Sect. "Broodstock conditioning"), the behaviour of the six pairs was monitored daily for 6 months (from December 2020 to May 2021). Behavioural monitoring was performed using instantaneous interval sampling (Altmann 1974) conducted daily every 2 h over a fixed 10-min period during daytime (08:00–18:00 h; $n = 6$ per day) by two trained operators who were alternating to make observations. Aggressive and courtship behaviours were recorded through direct observations using a semi-quantitative four-point ordinal scale (0 = absent, 1 = low, 2 = moderate, and 3 = high), capturing the intensity of interactions between individuals. This approach followed the *focal animal sampling* method described by Altmann (1974), where each pair was observed for fixed time intervals each day to record the occurrence and intensity of predefined behaviours. Ordinal scoring and interval sampling allowed standardized and repeatable measurements of behavioural intensity (Lehner 1998; Bateson & Martin 2021). Aggressive behaviour was assessed daily based on the presence and intensity of three diagnostic indicators: (i) confinement of the subordinate fish in a corner, (ii) frayed fins, and (iii) visible bite marks. A score of 1 (low) was assigned when occasional chasing or brief confinement occurred without visible damage, 2 (moderate) when confinement was persistent or mild fin fraying was observed, and 3 (high) when bite marks or severe fin fraying appeared, indicating escalated aggression. Physical signs such as frayed fins or bite marks were scored only on the day of their first appearance, and not in subsequent days unless new lesions developed. Courtship behaviour was evaluated daily based on three characteristic displays: (i) the male swimming in and out of the same PVC shelter, (ii) quivering with open fins in front of the female, and (iii) the pair sharing the same PVC shelter (Fig. 3). A score of 1 (low) was assigned when courtship displays were occasional and short in duration, such as sporadic male entries into the PVC shelter or brief approach movements without response from the female. A score of 2 (moderate) indicated regular and persistent displays of quivering or fin spreading, sometimes accompanied by short episodes of cohabitation within the PVC shelter, suggesting an intermediate level of reproductive interaction. A score of 3 (high) was assigned when courtship was intense and continuous, characterized by prolonged quivering and frequent cohabitation of the pair inside the PVC shelter, often culminating in pre-spawning behaviour. The overall daily score reflected the intensity and persistence of these displays during observation periods. A single daily score was assigned to each pair by integrating the observed intensity of the diagnostic criteria (i–iii), providing a standardized quantitative index for both aggression and courtship. A detailed summary of the scoring criteria used for aggression and courtship is presented in Table S1. Direct observation was chosen instead of video recording to ensure immediate welfare monitoring and allow prompt intervention whenever aggressive interactions escalated to potentially harmful levels during pair formation, thereby providing both reliable behavioural assessment and continuous welfare supervision (Lehner 1998). The monthly aggression and courtship scores for each pair were obtained by averaging the daily observation scores. When a high level of aggressive behaviour was observed in a pair, the larger individual was temporarily placed in a separated, transparent floating cage, maintaining visual contact between the specimens. The physical isolation of the aggressive individual lasted for a maximum of 1 week. The isolated fish was released when the aggressive interactions observed during the isolation time ceased. A pair was considered bonded when they simultaneously accepted food, displayed no signs of aggression, and initiated courtship, ultimately resulting in the first spawning event. At this step, three different spawns from the same breeding pair were selected for the embryonic development study ($n = 3$). From each spawn, twenty eggs were sampled at 0, 1, 2, 3, 6, 9, 12, 15, 18, 24, 36, 48, 72, and 96 h post-fertilization (HPF), resulting in a total of 840 eggs examined. Samples were collected directly from the aquarium tanks using a sterile blade and pipette, while the remaining egg mass was left under the male parent's care. Morphological data were recorded by photographing embryos at 5 × and 10 × magnification with a stereomicroscope (Leica, Germany) connected to a digital camera (Motic, Xiamen, China). Eggs were fixed in 4% buffered formalin, and egg diameter was measured with a micrometre scale ocular.

## Spawning activity and filial cannibalism

The effects of rearing temperature on the spawning dynamics and FC of orchid dottybacks were investigated for 6 months (from June 2021 to November 2021). The six pairs obtained as described in Sect. "Behaviour and pair formation management" were divided into two groups ($n = 3$), kept at 25 ± 1 °C and 28 ± 1 °C, respectively. The temperature of 25 °C corresponds to that of the holding tank during the first period of the experiment and served as control, whereas 28 °C was selected as it has been previously associated with elevated levels of filial cannibalism in several dottyback species (Olivotto et al. 2006; Madhu et al. 2016; Chen et al. 2023). The aquarium tank selected for the 28 °C treatment was equipped with a heater, which progressively increased the temperature from 25 to 28 °C over 3 days (1 °C per day) and then maintained it stable at 28 °C during the 6-month trial. Using a flashlight, all pairs were checked at least five times per day to verify the presence of egg masses in the PVC pipe. The total number of spawning events per month, and the spawning frequency (days) were calculated. When spawning occurred, the eggs were left under the exclusive care of the male until hatching, in order to assess the occurrence of filial cannibalism (FC). In this species, only males perform brood care and filial cannibalism, while females typically remain distant from the spawning site, as the males keep them away. The rate of FC was expressed as the monthly frequency of egg masses that were completely cannibalised by the male during incubation. Partial FC was not considered, as quantifying the proportion of eggs consumed was particularly challenging due to the continuous parental care provided by the male and the variable extent of egg removal, which can make reliable estimation difficult. FC was calculated as follows (Chen et al. 2023):

$$FC = \frac{Number\ of\ egg\ masses\ cannibalised\ in\ a\ month}{Total\ number\ of\ monthly\ spawnings} \times 100\%$$

The total number of egg masses available for hatching per month was calculated by subtracting the number of egg masses cannibalised during the month from the total monthly spawning number.

## Gonadal histology

Histological analysis was conducted on the gonads of three *P. fridmani* pairs, which were not used for the observation experiment described in Sect. "Behaviour and pair formation management" (see Sect. "Broodstock conditioning"). Gonad samples were collected at the beginning of the experimental period from individuals considered sexually mature according to established size criteria for dottybacks (Mies et al. 2014; Wittenrich 2007; Table 1), further confirmed by the observation of courtship behaviour in the broodstock tanks. At this stage, the gonads were expected to be in an advanced phase of maturation. Gonads from each sampled fish were removed, macroscopically examined, and fixed in 4% paraformaldehyde at 4 °C for 48 h. Thereafter, the samples were dehydrated, embedded in paraffin (Thermo Fisher Scientific STP 120–2; Thermo Shandon Limited, United Kingdom), sectioned at 3 µm thickness using a Leica Jung Autocut 2055 microtome (Leica, Nussloch, Germany), and stained with haematoxylin and eosin (Martoja and Martoja-Pierson 1970). Six histological sections per sample were analysed, ensuring that representative regions of the entire gonadal tissue were captured. Observations were used to confirm whether orchid dottyback gonads contained exclusively testicular or ovarian tissue or had both types of tissue. The mounted sections were scanned using a Motic Easy Scan Pro digital scanner (Motic, Xiamen, China) operated using Motic DS Assistant software (Motic VM V1 Viewer 2.0) and examined using Image Pro Software (Media Cybernetics, USA). Three trained independent blind observers evaluated the slides to estimate visual differences among the samples. The classification of oocyte developmental stages followed the standardized terminology for marine teleosts proposed by Lowerre-Barbieri et al. (2023).

### Statistical analysis

Daily spawning activity (0/1) and filial cannibalism (0/1, conditional on spawning) were analysed using Generalized Estimating Equations (GEE) with a binomial distribution and logit link. *Temperature* (25 °C vs 28 °C), *Month*, and their interaction were included as fixed factors, with *Pair ID* treated as the clustering unit to account for repeated measures and the nested design. To address sparse data in some months, a simplified model including only *Temperature* was also fitted for filial cannibalism. Marginal predicted probabilities were extracted to estimate daily spawning probability and the likelihood of filial cannibalism under each treatment. Inter-spawn intervals (days between successive spawnings) were analysed using a linear mixed-effects model with *Temperature* as a fixed factor and *Pair ID* as a random factor. Aggressive and courtship behaviours (daily mean scores, 0–3) were evaluated using GEE with a Gaussian distribution, including *Day* (as a continuous covariate) and *Month* as fixed factors, and *Pair ID* as the clustering unit. This approach allowed testing both inter-pair differences and temporal trends in the decline of aggression and the concomitant increase in courtship during pair formation. All analyses were performed with IBM SPSS Statistics v27.0 (IBM Corp., Chicago, IL, USA), and statistical significance was set at $p < 0.05$.

## Results

### Pair formation and reproductive behaviour

The average time required for pair formation was 7.5 ± 2.8 weeks (Table 2). Aggression scores declined significantly over time (GEE, day effect: $\beta < 0$, $p < 0.001$), indicating a progressive reduction in agonistic interactions during pair formation (Fig. 2, Table 2). In contrast, courtship activity increased steadily over time (day effect: $\beta > 0$, $p < 0.001$), reaching consistently high levels as pairs stabilized. These results reveal a continuous behavioural

**Table 2** Monthly mean (±SD) aggression and courtship scores of six *P. fridmani* pairs during a six-month pair-formation trial (December 2020–May 2021). Behavioural levels were scored semi-quantitatively from 0 to 3 (0 = absent, 1 = low, 2 = medium, and 3 = high). Values represent descriptive monthly averages, while temporal trends and period effects in aggression and courtship were statistically tested using Generalized Estimating Equations (GEE) with *Day* (continuous covariate) and *Month* (fixed factor) and *Pair ID* as the clustering unit

| *P. fridmani* pairs | Dicember20 | | January21 | | February21 | | March21 | | April21 | | May21 | | Time to bond (weeks) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Aggression | Courtship | Aggression | Courtship | Aggression | Courtship | Aggression | Courtship | Aggression | Courtship | Aggression | Courtship | |
| A | 2.5 ± 0.6 | - | 1.3 ± 0.4 | 0.9 ± 0.2 | 0.6 ± 0.4 | 1.9 ± 0.3 | - | 2.3 ± 0.3 | - | 2.8 ± 0.5 | - | 3.0 ± 0.0 | 9 |
| B | 0.8 ± 0.2 | 1.2 ± 0.5 | - | 2.2 ± 0.7 | - | 2.8 ± 0.2 | - | 3.0 ± 0.0 | - | 3.0 ± 0.0 | - | 3.0 ± 0.0 | 4 |
| C | 0.9 ± 0.3 | 1.0 ± 0.3 | 0.7 ± 0.4 | 1.6 ± 0.2 | 0.2 ± 0.1 | 2.0 ± 0.3 | - | 2.5 ± 0.4 | - | 2.9 ± 0.5 | - | 3.0 ± 0.0 | 8 |
| D | 1.6 ± 0.3 | 0.6 ± 0.3 | 0.9 ± 0.3 | 2.0 ± 0.3 | - | 2.4 ± 0.4 | - | 2.9 ± 0.5 | - | 3.0 ± 0.0 | - | 3.0 ± 0.0 | 6 |
| E | 2.1 ± 0.5 | 0.4 ± 0.2 | 1.0 ± 0.2 | 1.9 ± 0.4 | - | 2.8 ± 0.5 | - | 3.0 ± 0.0 | - | 3.0 ± 0.0 | - | 3.0 ± 0.0 | 6 |
| F | 2.8 ± 0.7 | - | 1.7 ± 0.6 | 0.3 ± 0.2 | 0.8 ± 0.5 | 1.8 ± 0.3 | 0.3 ± 0.3 | 1.9 ± 0.6 | 0.2 ± 0.2 | 2.1 ± 0.5 | - | 2.9 ± 0.6 | 12 |
| Tot. mean + SD | 1.8 ± 0.8 | 0.5 ± 0.5 | 0.9 ± 0.6 | 1.5 ± 0.7 | 0.3 ± 0.4 | 2.3 ± 0.4 | 0.1 ± 0.1 | 2.6 ± 0.4 | 0.0 ± 0.1 | 2.8 ± 0.4 | - | 3.0 ± 0.0 | 7.5 ± 2.8 |

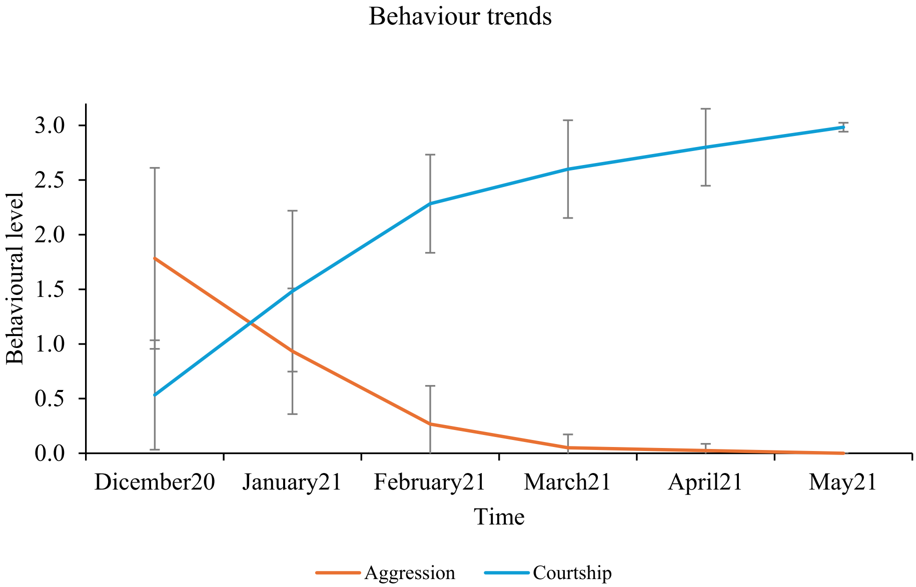

**Fig. 2** Behavioural trends (aggression and courtship) of *P. fridmani* pairs ($n = 6$) during a 6-month pair-formation trial (December 2020–May 2021). Behavioural levels are presented as monthly means ± SD, based on semi-quantitative scores ranging from 0 (absent) to 3 (high). Aggression was scored according to the level of stress and damage inflicted by the dominant fish, whereas courtship was scored based on the intensity of reproductive displays exhibited by the male. Lines represent descriptive monthly averages, while temporal trends and period effects were statistically tested using Generalized Estimating Equations (GEE) with *Day* (as a continuous covariate) and *Month* (as a fixed factor), and *Pair ID* as the clustering unit

transition from aggression to courtship, reflecting the gradual establishment and stabilization of pairs under controlled conditions. Only two pairs, A and F, exhibited high levels of aggression which negatively affected the food intake of all individuals in the tanks, as fighting continued during feeding. Different types of bite-related injuries were documented in these pairs, including haemorrhagic lesions, desquamation, and frayed fins. Therefore, physical isolation, as described in Sect. "Behaviour and pair formation management", was necessary for pairs A and F. After 2 months of experimentation, all pairs exhibited courtship behaviour (Fig. 2), and four pairs (B, C, D, and E) spawned for the first time, thereby completing the bonding process (Table 2). Males predominantly occupied the PVC pipe, while females primarily swam in open areas, occasionally using pipes as shelter. Detailed biometric measurements of both sexes are provided in Table 1. A few days before spawning (3 days), while females typically presented with a swollen abdomen, the males showed increased courtship behaviour, swimming in and out of their preferred pipe (Fig. 3). At this stage, the male was constantly courting the female, chasing and turning in front of her, quivering with open fins, and then swimming back into the chosen PVC pipe (Fig. 3). This courtship process of swimming in and out lasted until the female followed the male and shared the same PVC pipe (Fig. 3). The male then slowly encircled the female within the pipe, performing quivering movements; these behaviours were subsequently followed by the female's spawning of the egg mass. At this time, the female started to lay egg masses slowly, while the male fertilised them with sperm. This process generally took 2 h, after which the female left the PVC pipe and returned to swim in the open areas, while the male

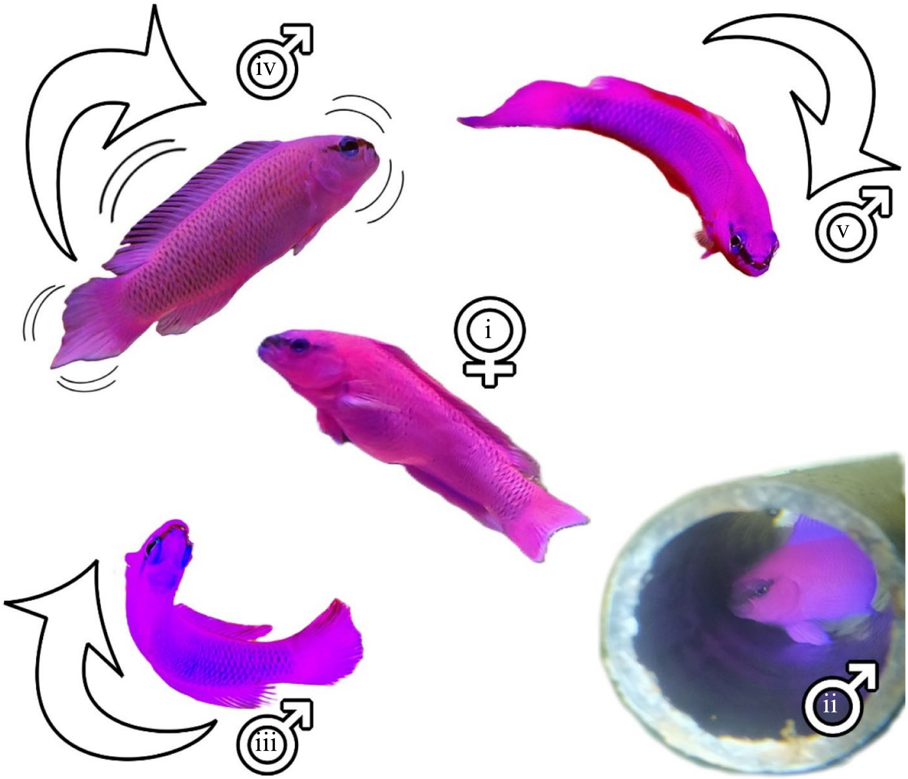

**Fig. 3** Schematization of the orchid dottyback *P. fridmani* courting behaviour: **i** female swims in open area; **ii** male prepares and defends the nest inside the PVC pipe; **iii** Male swims out of the pipe looking for the female; **iv** male swims in front of the female shaking vigorously the body; **v** male swims back into the PVC pipe, guiding the female by indicating the way

started taking care of the egg mass inside the PVC pipe, swimming out for a few seconds only for feeding. During parental care, the male actively wraps his body around the egg mass and fans with his fins, maintaining constant motion to ensure adequate oxygenation while simultaneously guarding the eggs against potential predators.

## Spawning activity and filial cannibalism

The six pairs of *P. fridmani* spawned constantly throughout the experiment, regardless of the temperature (Table 3; Fig. 4). The embryonic development of orchid dottybacks completed within approximately 96 HPF at 25 °C (Fig. S2, Table S2). After spawning, individual eggs measured 1.0 ± 0.1 mm in diameter (mean ± SD), with no significant differences detected between pairs or among spawns. Eggs were spherical and transparent, each containing a spherical yolk of 0.5 ± 0.1 mm in diameter. They were aggregated into cohesive clutches by fine adhesive threads, which provided structural stability to the egg mass without attaching it to the substrate. Spawning was observed only in the afternoon, between 2 and 7 pm. Spawning activity was significantly higher at 28 °C than at 25 °C, with daily spawning probabilities (mean ± SE) of 0.11 ± 0.01 and 0.06 ± 0.01, respectively

**Table 3** Monthly spawning events, spawning frequency, filial cannibalism rates, and number of egg batches available for hatching in six *P. fridmani* pairs reared at two water temperatures (25 °C and 28 °C) over a six-month period. Values are observed means ± SD. Statistical comparisons were performed using a Linear Mixed Model (LMM) with temperature as a fixed factor and pair ID as a random factor. Different superscript letters within rows indicate significant differences between temperatures ($p < 0.05$)

| Monthly spawning events (*n*) | | | | Spawning frequency (days) | | | | Monthly Filial cannibalism (%) | | | | Available egg batches for hatching (*n*) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pair | 25 °C | Pair | 28 °C | Pair | 25 °C | Pair | 28 °C | Pair | 25 °C | Pair | 28 °C | Pair | 25 °C | Pair | 28 °C |
| A | 1.8 ± 0.4 | D | 3.5 ± 0.5 | A | 17.8 ± 6.0 | D | 8.9 ± 1.5 | A | 27.3 ± 27.4 | D | 52.4 ± 12.5 | A | 1.7 ± 0.5 | D | 1.7 ± 0.5 |
| B | 1.7 ± 0.8 | E | 3.3 ± 0.5 | B | 22.1 ± 9.6 | E | 9.3 ± 1.3 | B | 10.0 ± 20.4 | E | 60.0 ± 15.3 | B | 1.5 ± 0.8 | E | 1.7 ± 0.5 |
| C | 1.8 ± 0.8 | F | 3.3 ± 0.8 | C | 19.6 ± 9.1 | F | 9.8 ± 3.1 | C | 18.2 ± 22.1 | F | 65.0 ± 11.4 | C | 1.7 ± 0.8 | F | 1.2 ± 0.4 |
| Tot. mean + SD | $1.8 \pm 0.1^{a}$ | | $3.4 \pm 0.1^{b}$ | | $19.8 \pm 2.2^{b}$ | | $9.3 \pm 0.4^{a}$ | | $18.5 \pm 8.6^{a}$ | | $59.1 \pm 6.4^{b}$ | | 1.6 ± 0.1 | | 1.5 ± 0.3 |

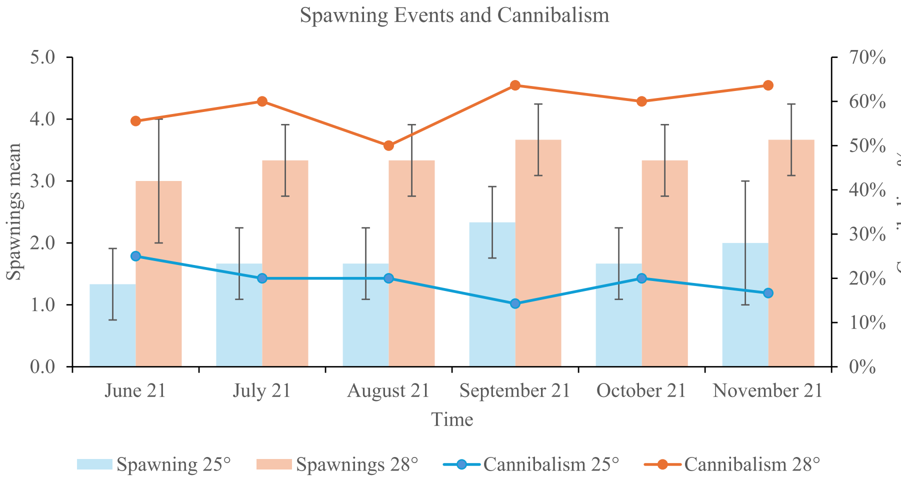

**Fig. 4** Mean monthly spawning and filial cannibalism rate (%) of six *P. fridmani* pairs exposed to different water temperature conditions ($n = 3$) over a 6-month period

(GEE, $p < 0.01$). Model-predicted inter-spawn intervals (mean ± SE) were 9.3 ± 0.4 days at 28 °C and 19.8 ± 2.2 days at 25 °C (LMM, $p < 0.001$). On a monthly scale, pairs maintained at 28 °C produced on average (mean ± SE) 3.4 ± 0.1 spawning events versus 1.8 ± 0.1 at 25 °C. These model-based estimates were consistent with the observed means reported in Table 3, confirming that higher temperature substantially reduced the time between consecutive spawnings. Filial cannibalism increased with temperature, with probabilities (mean ± SE) of 0.63 ± 0.03 at 28 °C and 0.18 ± 0.01 at 25 °C (GEE, $p < 0.05$). Monthly data indicated that males consumed about 59.1% ± 6.4% of clutches at 28 °C versus 18.5% ± 8.6% at 25 °C. The resulting total number of egg masses available after FC did not differ significantly between treatments (Table 3).

## Gonadal histology

Macroscopic analysis confirmed the phenotypic sexes inferred from size and morphology for the six specimens (three males and three females, Figs. 5 and 6; Table 1). The ovaries were lobular paired structures that occupied a substantial portion of the abdominal cavity. Their colour ranged from yellowish to orange, depending on the maturation stage of the oocytes, reflecting their advanced development. Histological sections of the ovaries (Fig. 5a, b) revealed a spectrum of oocyte developmental stages, consistent with an asynchronously spawning reproductive strategy. Primary growth oocytes were the smallest, measuring approximately 20–80 µm in diameter, and were characterized by large, centrally located nuclei with a prominent nucleolus. Their cytoplasm was thin, basophilic, and contained few organelles, reflecting the initial stages of cellular differentiation. Secondary growth oocytes ranged from about 80–450 µm in diameter and exhibited progressive accumulation of yolk granules and cortical alveoli within the cytoplasm. Early in this stage (80–200 µm), yolk granules were sparse and irregularly distributed, whereas in more advanced oocytes (200–450 µm) the cytoplasm became increasingly filled with yolk inclusions and lipid droplets, indicating active vitellogenesis. Tertiary (fully grown) oocytes were considerably larger, ranging between 450 and 500 µm in diameter, with cytoplasm

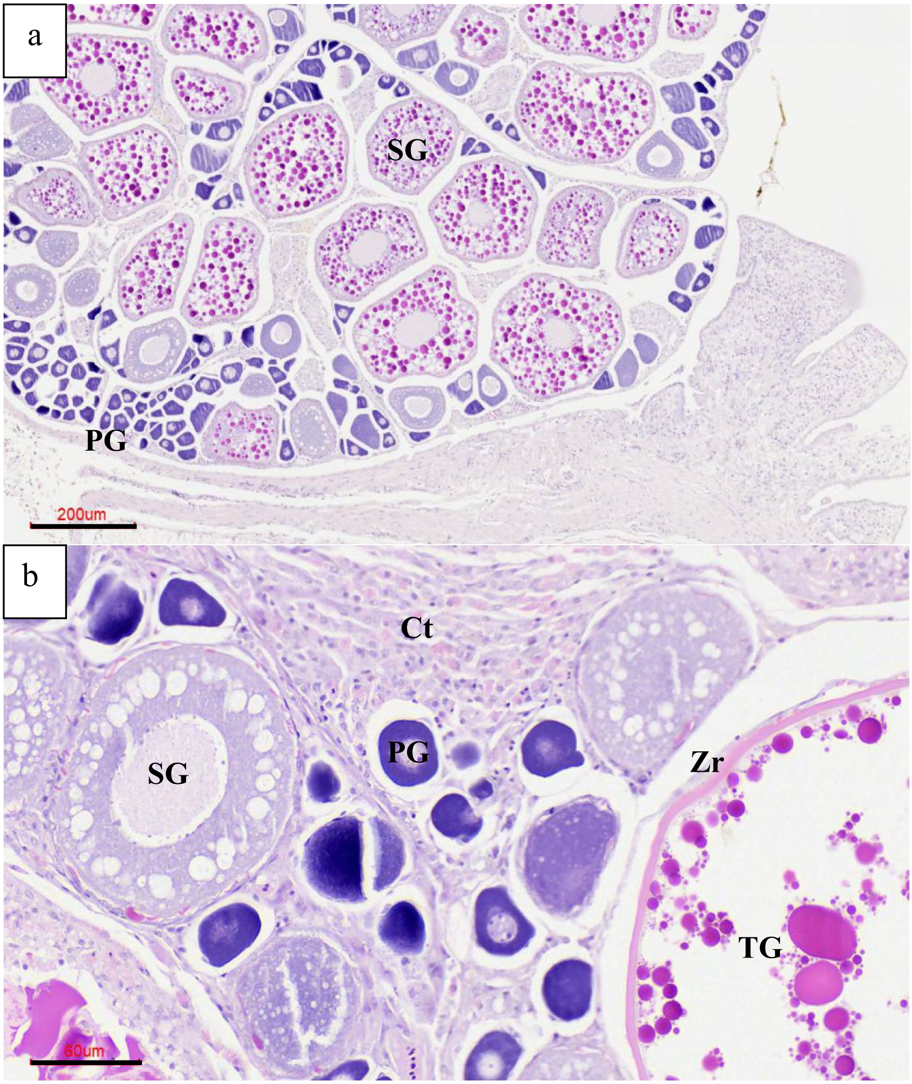

**Fig. 5** Histological examination of *P. fridmani* ovary: **a** mature ovary with different follicular development stages, scale bar 200 µm; **b** various stages of oocyte maturation; scale bar 60 µm; PG = primary growth oocyte; SG = secondary growth oocyte; TG = tertiary growth oocyte; Ct = connective tissue; Zr = zona radiate

densely packed with yolk granules and numerous lipid droplets, suggesting advanced maturation and readiness for fertilization. The zona radiata, a specialized extracellular glycoprotein layer surrounding the oocytes, was well-defined around the larger, more mature oocyte. The testes were elongated, symmetrical, and paired organs located along the ventral side of the body cavity. They appeared whitish to pale cream in colour, indicative of sexual maturity. Histological sections of the tests revealed well-organized seminiferous tubules, which were predominantly round to slightly oval in cross-section, with clearly

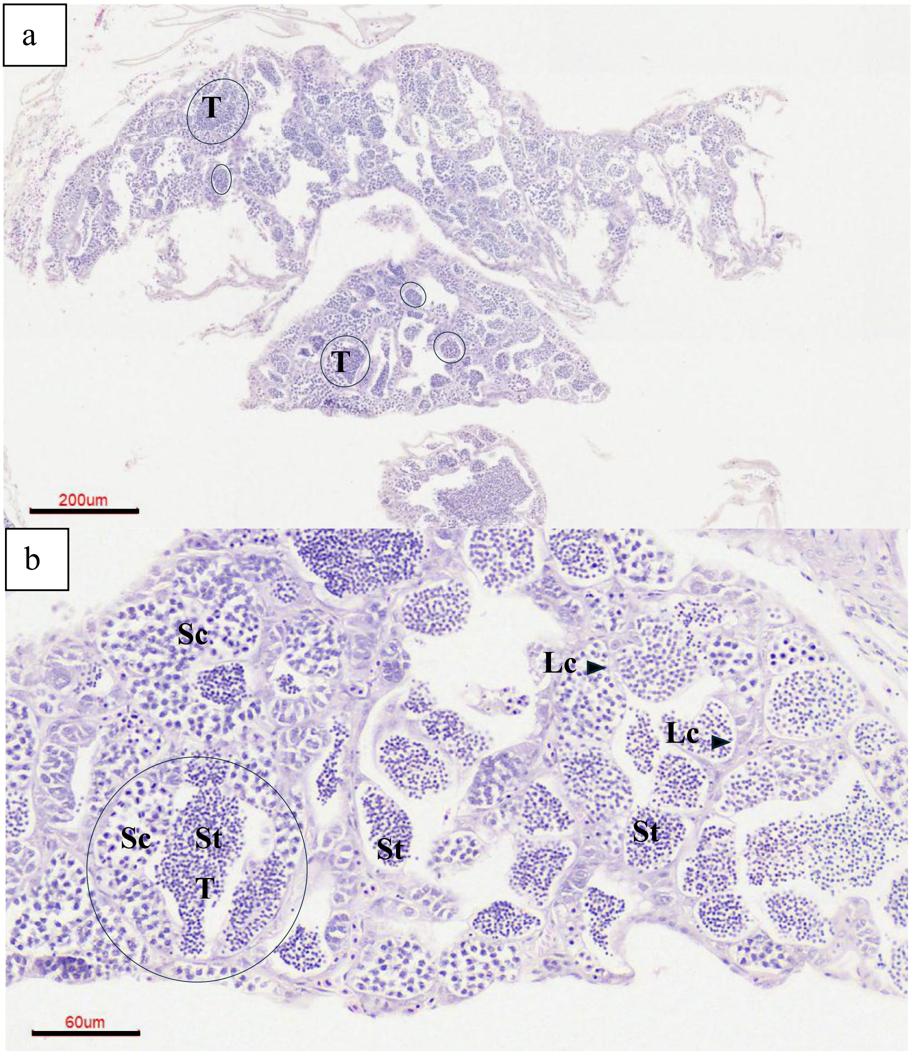

**Fig. 6** Histological examination of *P. fridmani* testicular tissue: **a** mature testis at various stages of spermatogenesis scattered in the gonad, scale bar 200 μm; **b** various maturation stages, scale bar 60 μm; Sc = spermatocyte; St = spermatid; T = seminiferous tubules (highlighted by a black circle); Lc = Leydig cells (highlighted by a black arrow)

delineated boundaries between the tubular epithelium and the surrounding interstitial tissue (Fig. 6a, b). The diameter of individual seminiferous tubules ranged from approximately 60 to 180 μm, reflecting natural variability among tubules. The tubular lumen appeared centrally located and varied in diameter depending on the stage of spermatogenic activity. Each seminiferous tubule exhibited spermatocytes, and spermatids near the luminal surface (Fig. 6b). Interstitial tissue between the tubules was moderately vascularized and contained clusters of Leydig cells, which appeared polygonal with centrally located nuclei and eosinophilic cytoplasm, consistent with their role in androgen synthesis (Fig. 6b). In addition, small capillaries were observed within the interstitial space, indicating a well-maintained microenvironment for tubular function.

## Discussion

The present study analysed critical behavioural and reproductive traits in orchid dottyback, *P. fridmani* bred in captivity. The analysis of daily aggression and courtship scores at 25 °C revealed significant temporal trends, with aggression gradually declining and courtship increasing over time. This continuous behavioural shift, captured by the inclusion of *Day* as a covariate in the GEE model, reflects a progressive transition from dominance interactions to reproductive cooperation as pairs stabilized. Such a trajectory aligns with the establishment of social hierarchies and stable pair bonds reported in other *Pseudochromis* and reef-associated species (Mies et al. 2014; Kuwamura et al. 2020). The progressive reduction in aggression also underscores the importance of monitoring pair dynamics to safeguard animal welfare, as excessive agonistic interactions can compromise both health and reproductive output. The timing of pair formation varied among pairs and was closely related to aggression and courtship levels. Therefore, considering that aggression is more intense among individuals of the same sex (Brons 1996; Moe 1997; Wittenrich 2007), pairs A and F may have contained two females one of which underwent sex reversal to establish a reproductive pair, as suggested by the higher aggression observed in these fish during the bonding period (Wittenrich and Munday 2005). If individuals were not of the same sex in these two pairs, the high aggression and resulting delay in pair formation may be attributed to issues related to gonadal maturation or behavioural incompatibility between individuals, thus requiring more time to establish a bond (Munday 2002; Wittenrich and Munday 2005). In contrast, pairs B, C, D, and E probably already had an established hierarchy, which fostered low aggressiveness and earlier bonding (Wittenrich and Munday 2005). Previous studies have reported that bonding between *P. fridmani* pairs occurs on average every 5 weeks (Mies et al. 2014; Chen et al. 2023) while in this study it took on average 7.5 weeks. This discrepancy with regard to the time required for pair formation may be influenced by factors such as the origin of the individuals used in the study, their age, size, sexual maturity, and pre-existing social relationships (Mies et al. 2014; Chen et al. 2023). Moreover, temporary isolation of males proved to be effective in achieving successful pairing among aggressive individuals. Indeed, continuous visual contact between specimens probably facilitated the establishment of a hierarchy and mutual acceptance, while preserving physical integrity by minimising the risk of injuries and extreme stress (Chen and Fernald 2011; Frommen 2020). The observations on the reproductive behaviour of orchid dottybacks helped better understand the pair bonding process, allowing us to identify the timing of pair formation (7.5 ± 2.8 weeks, $n = 6$) when no aggressive interactions were observed and the pair began spawning.

Orchid dottybacks are demersal spawners, with spherical eggs surrounded by a sticky, fibrillar, and elastic extracellular matrix which gave stability to the egg mass until hatch. In the present study the eggs' morphology and embryos' development sequence were in accordance with previous studies conducted at higher temperatures on *P. fridmani* (27 ± 1 °C) (Chen et al. 2023) and similar dottyback species such as *P. flavivertex* (27 ± 0.5 °C) (Olivotto et al. 2006) and *P. dilectus* (29 ± 1 °C) (Madhu et al. 2016). The present study also examined reproductive and behavioural traits at two temperatures (28 °C and 25 °C). The inter-spawn intervals at 28 °C were less than half those observed at 25 °C, and corresponded to a doubling of spawning probability at the higher temperature, confirming that elevated temperature can accelerate reproductive dynamics, as reported in other coral reef fishes where temperature acts as a primary cue for gonadal activity and spawning rhythms (Donelson et al. 2010; Madhu et al. 2016). Nevertheless, this increase in reproductive output was accompanied by a higher incidence of filial cannibalism (FC), which reduced the number of egg masses available for hatching. This aligns with theoretical and empirical studies showing that filial cannibalism can be modulated by environmental stressors (Manica 2004; Klug 2009; Matsumoto et al. 2018). These findings emphasise a key trade-off: higher reproductive activity under elevated temperature does not necessarily result in greater offspring survival, since male parental care is compromised and egg loss increases. Similar patterns have been reported in the beaugregory damselfish (*Stegastes leucostictus*), which exhibited higher FC at warmer temperatures (Payne et al. 2002; 2004). Our results are also consistent with Chen et al. (2023), who observed high levels of FC in *P. fridmani* at elevated temperatures, particularly during the later stages of incubation. In our study, the higher number of total spawning events and FC observed in pairs maintained at 28 °C may be explained by multiple, not mutually exclusive mechanisms. Elevated temperature is known to stimulate reproductive physiology, potentially through enhanced hormone synthesis and activation within the hypothalamus–pituitary gonadal axis (Donelson et al. 2010; Pankhurst and Munday 2011). At the same time, higher metabolic demands at elevated temperature could have increased energetic requirements, potentially driving males to compensate by consuming their own clutches, even under apparently adequate feeding regimes (Manica 2004; Klug 2009). While our data do not allow disentangling the relative contribution of endocrine regulation versus nutritional stress, both hypotheses remain plausible and warrant further investigation. More broadly, FC has been attributed to multiple factors, including water parameters (Payne et al. 2002; 2004), egg developmental quality (Mies et al. 2014; Chen et al. 2023), or the adaptive advantage of restarting courtship (Matsumoto et al. 2018). Thus, the causes of FC remain complex and likely multifactorial, depending on both species-specific traits and rearing conditions. It should be acknowledged that the number of replicates per treatment was limited, reflecting constraints in space and broodstock availability; nevertheless, the consistency of patterns observed across pairs supports the robustness of the conclusions. Continuous spawning observed at both temperatures indicates that reproductive activity in *P. fridmani* is also closely linked to pair bonding and may be influenced by other factors such as isolation, food availability, and overall husbandry conditions (Chen et al. 2023). Importantly, pairs maintained at 25 °C presented continuous spawning with significantly lower FC compared to those at 28 °C, thus mitigating the risk of egg loss during aquaculture operations. It is also plausible that the increased spawning frequency observed at 28 °C may have led to female exhaustion, resulting in reduced egg quality over time. Under this scenario, FC would have increased at elevated temperature if males preferentially consume eggs of lower viability. This hypothesis warrants further investigation, for instance through trend analyses of egg quality across successive spawning events. This suggests that maintaining broodstock at lower temperature represents a viable strategy for sustaining production while limiting losses due to FC. Alternatively, rearing at higher temperatures combined with the prompt collection of eggs after spawning and their subsequent removal from parental care for artificial incubation may represent a viable approach to prevent FC and to intensify larval production, although it inevitably entails increased efforts in spawn management. Overall, these findings provide a comprehensive framework for optimising broodstock management of *P. fridmani*, highlighting the dual role of temperature in enhancing reproductive activity while simultaneously increasing the risk of filial cannibalism.

The lack of clear sexual dimorphism in *P. fridmani* may lead to pairing challenges, potentially resulting in unintentional pairing of individuals of the same sex, which frequently results in aggressive behaviour (Mies et al. 2014). In our study, the analysis of the gonads suggested that the evaluation of total length and body shape of individuals may be a relatively reliable and fast proxy for visually identifying the sex of orchid dottybacks but only 6 individuals are clearly insufficient to draw a conclusion on this topic and, as discussed earlier, sexing errors may have occurred in pairs A and F in this study, indicating a non-negligible error rate. Histological analysis highlighted the presence of both primary and tertiary growth oocytes in the ovary tissue of the presumptive females, while testes were in active spermatogenesis in the 3 individuals sexed as males based on morphology. This confirmed that all sampled individuals were sexually mature. Finally, the gonads of males contained only spermatocytes and spermatozoa, and no ovarian tissues were observed, indicating that sex reversal was completed before sampling.

## Conclusions

The present study provided critical information for the management of captive reproduction in *P. fridmani*. Pair formation proved to be a critical phase of captive spawning and occurred during the first two months following the assignment of fish to pairs, with episodes of aggression observed before the establishment of stable reproductive behaviour. Courtship and spawning were clearly pair-specific and influenced by social compatibility, which could in some cases be facilitated through the temporary isolation of aggressive individuals. Rearing temperature was shown to be a key factor influencing broodstock performance. At 28 °C, spawning frequency was higher, but this was accompanied by a marked increase in FC, ultimately resulting in a comparable number of viable egg masses at the two tested temperatures. Maintaining broodstock at 25 °C, however, may represent a practical strategy to minimise management effort and risk of egg loss by fully exploiting natural parental care. Conversely, rearing at 28 °C may be advantageous if combined with the prompt collection and artificial incubation of egg masses, as this approach can prevent FC and thereby sustain higher production levels. Histological analysis of *P. fridmani* gonads confirmed sexing based on total length and body shape, indicating that these two characters may be useful indicators for sex identification in this species. Future research should further investigate the mechanisms underlying FC, including its environmental and physiological drivers, and examine the potential occurrence of bidirectional sex change to fully understand the reproductive biology of this species.

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**Data availability** No datasets were generated or analysed during the current study.

## Declarations

**Ethics approval** This study was designed and conducted in accordance with the guidelines of the current European Directive (2010/63/EU) and the Italian Legislative Decree 26/2014 on the protection of animals used for scientific purposes.

**Competing interests** The authors declare no competing interests.

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