Ex situ reproduction and recruitment of scleractinian coral Galaxea fascicularis

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Research Article

Keywords: early life history, post-settlement survival, growth, larvae, metamorphosis, sexual reproduction

Posted Date: June 23rd, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1648572/v1

Version of Record: A version of this preprint was published at Marine Biology on January 24th, 2023. See the published version at https://doi.org/10.1007/s00227-023-04175-7.

Abstract

Sexual reproduction plays an important role in the population and community structure maintenance in scleractinian corals, particularly in growth and development after larvae settlement. Despite this, only few studies have been conducted to monitor the post-settlement growth and development of scleractinian coral larvae. This study aimed to obtain this data by collecting adult *Galaxea fascicularis* colonies from Weizhou Island coast (21°00'–21°10' N, 109°00'–109°15' E) and recording their complete life cycle, from fertilization to recruitment, for one year *ex situ*. The results demonstrated that *G. fascicularis* could reproduce sexually when reared in a tank for 2 y. Their embryo produced a “prawn chip” that lacked a blastocoel, indicating that *G. fascicularis* is a complex coral. Larvae evidently showed association with zooxanthellae four days after settlement and completed metamorphosis after 1 month. The mean diameter of *G. fascicularis* recruits was 4.74 ± 1.12 mm, and the survival rate was only 5.60% in the first year, which may be attributed to their competition with algae. To increase their survival rate without the interference of algae, we suggest that the recruits of *G. fascicularis* be reared *ex situ* to complete metamorphosis (1 month) and then transferred to the field. This study improved our understanding of the early life cycle of scleractinian corals.

1. Introduction

Scleractinian corals are the dominant reef-building organisms present in coral reefs (Jones et al. 2004). Successful reproduction and recruitment are critical for the maintenance and recovery of scleractinian coral species as well as underpin reef resilience (Harrison 2011). The natural replenishment of coral population mainly occurs by sexual and asexual reproduction. Compared to the latter, sexual reproduction has the advantage of higher fertility and greater genetic diversity (Ayre and Hughes 2000; Edwards 2010; Huang et al. 2018). However, high mortality after settlement is a key factor in shaping the adult population size and distribution of scleractinian corals (Gosselin and Qian 1997; Wilson and Harrison 2005; Penin et al. 2010). Although the importance in the life cycles has been recognised, only few studies have addressed the causes of high post-settlement mortality rates in reef-building corals, especially during the period when juveniles become visible to the naked eye of the diver, often call ‘coral recruitment’, which usually takes about 1 y (Harrison and Wallace 1990; Chiappone and Sullivan 1996). Most studies conducted on the early post-settlement mortality of corals have focused on short-term observations (< 6 m), reared in a nursery or hatchery setting. For example, it was reported that the larval survival of *Acropora muricata* and *A. valida* decreased substantially to approximately 50% by the first week of the experiment and to approximately 10% by the third week (Nozawa and Harrison 2008). Henry et al. (2019) reported that the survival rate of *A. cervicornis* recruits in 38 L glass aquaria for four months was approximately 86% in the first month, which gradually decreased during the following two months leading to 56% survival in the fourth month. However, subsequent survival and growth of the recruits were not monitored. Babcock (1985) showed the growth and mortality rates for three scleractinian corals *in situ* but only recorded the data in the third, fifth, and ninth months. Although some long-term *in situ* observation studies were conducted, most of them examined after the coral recruits were visible to the

naked eye (Guest et al. 2014; dela Cruz and Harrison 2017; Henry et al. 2021). Considering that this drastic bottleneck has profound implications on the population structure, dynamics, and capacity for recovery after disturbance, it is necessary to monitor the complete life cycle of corals after settlement.

There are two methods which can be used to harvest gametes (Edwards 2010). The first is to collect gametes directly from the field, including collection from spawn slicks and coral colonies *in situ*, which is suitable for large mass spawning events. The second is to remove mature colonies from the reef a few days or a month prior to spawning and maintain them *ex situ* in aquaria tanks or a land-based hatchery on shore. *Ex situ* spawning is not only cost-effective but also reduces the reliance on *in situ* spawning, but it is not convenient for long-term observation and research. However, little information exists on whether corals could reproduce sexually when they are raised in captivity for a long time (> 1 year). Successful sexual reproduction has only been reported for broadcast spawning (13 species) in public aquariums (Petersen et al. 2007). Therefore, it is still necessary to survey sexual reproduction of the coral when reared *ex situ* for an extended period.

The coral species *Galaxea fascicularis* (Linnaeus 1767) is widely distributed in the Indo-Pacific region and is an ecologically important species in the South China Sea(Veron 2000; Zou 2000). The adult corals are not affected by large-scale thermal stress and can withstand the synergistic effects of high temperature and low salinity (Yu et al. 2019; Dias et al. 2019). However, little information is available on the embryonic and larval development of *G. fascicularis* (Okubo et al. 2013) and no information is available on the post-settlement and survival rates of their primary polyps.

In this study, adult *G. fascicularis* colonies were reared in a pond two years in advance. After spawning *ex situ*, a complete life cycle from fertilization to recruitment was recorded for one year and data on post-settlement growth and mortality was obtained. The result provides a greater understanding required to increase the coral larvae survival rate and population density, in the context of global warming, through coral ecological protection and restoration through *ex situ* sexual reproduction.

2. Methods

2.1 Sample Collection

On July 20, 2017, samples of scleractinian coral *G. fascicularis* (> 10 cm in diameter) were collected at depths 3–5 m from the coast of Weizhou Island (21°00'–21°10' N, 109°00'–109°15' E) (Fig. 1). Ten adult colonies separated by at least 5 m were collected. The samples were carefully transported in seawater to the pond (4 ×5 ×2 m) at the aquaculture facility for breeding (Fig. 2a). The corals were maintained in the pond with flowing sand-filtered seawater and natural light, and fed artemia twice a week. The temperature was maintained at 26 ± 2 ℃ and the salinity was maintained at 30.

2.2 Experimental Methods

On April 13, 2019, six colonies of *G. fascicularis* (three female and three male) were transferred to two tanks (50 ×50 ×60 cm) from the pond (Fig. 2b). Prior to transfer, colonies were observed by carefully removing a few branches to determine the presence of mature oocytes, as indicated by their pigmentation. Seawater flow in the tank was stopped daily by turning the taps off after sunset (ca. 19:00 at Beihai). The methods outlined by Wei et al. (2020) were followed. Briefly, colonies were monitored approximately every 30 min from sunset until midnight allowing for detection of spawning activity. If no spawning was observed on any day, seawater flow was restored after midnight. If spawning was observed, the egg-sperm bundles were collected with a plastic cup and transferred to a 10 L plastic cask in filtered sea water with 100–300 μm mesh plankton nets. Because the bundles of *G. fascicularis* were naturally divided into red and white types (Harrison 1988), the two different coloured bundles were separated and gently agitated to facilitate bundle disintegration and cross-fertilised using pipettes. Developmental stages were observed, and photographs were taken using a stereomicroscope (Olympus SZX16) hourly for the first 12 h after spawning and every 4 or 6 h thereafter. Fertilization success was defined as the percentage of eggs that were fertilised (normal and abnormal embryos) divided by total number of eggs and embryos under a stereomicroscope after 2 h. The terracotta tiles had previously been used for most experiments involving coral larval rearing and transplantation to reefs (Heyward and Smith 2002; Nozawa and Harrison 2008; Edwards 2010). Thus, 6 terracotta tiles (5 × 4 × 1 cm) were used to induce the settlement of larvae at the end of the planula stage.

The substrates were biologically conditioned for 6 months in the pond with flow-through seawater. After successful metamorphosis, living recruits present on the tiles were counted, the settlement rate was analysed (Eq. (1)). For this experiment, the larvae were defined as metamorphosed when they had changed from either free swimming or casually attached pear-shaped forms to squat, firmly attached disc-shaped structures with pronounced flattening of the oral-aboral axis (Heyward and Negri 1999). The recruits were reared in the pond for 1 y from successful metamorphosis. They were photographed with Olympus SZX16 monthly for the first 4 months, and every 2 or 4 months thereafter. The number of recruits on the tiles were counted, and all macroalgae and turf algae were cleaned by hand when observed. The diameter of 10 corals was recorded; to measure skeletal dimensions (with retracted live tissue) following Van Moorsel (1988) the surrounding substratum was gently tapped.

The settlement rate = N ind / area (cm^2) (1)

Where, N is the number of metamorphosis larvae and area is the area of substrates.

3. Results

3.1 Embryonic and larval early development of *G. fascicularis*

Four colonies of *G. fascicularis* (two female and two male) spawned around 20:20 on 29 April 2019 (10 nights after the full moon) (Fig. 3a, b), and the spawning continued for about 30 min. Buoyant egg-sperm

bundles were released which break up on their way to the surface. The red eggs (about 300 μM) were partly fertilised and the fertilisation rate was 30% (Fig. 3c). On 25 May 2019 around 20:30 (5 nights after the full moon), the same four samples of *G. fascicularis* spawned again and almost all the red eggs were fertilised (Fig. 3d). All oocytes did not contain zooxanthellae.

Cleavages produced 4 cells after 2 h and embryos of 32 cells after approximately 3.5 h (Fig. 4a, 4b). However, some eggs were unfertilised (indicated by the white arrows Fig. 4b-d). After 5 h, during which cleavage proceeded, the embryos passed through the prawn chip stage consisting of an extended cellular bilayer lacking a blastocoel (Fig. 4c). Through changes in cell shape, this extended sheet of cells shrunk in diameter and thickened, while the sides bent inward, forming a bowl-shaped embryo(Fig. 4d, 4e). The embryo gradually thickened and became spherical, reaching the blastula stage after 10.5 h (Fig. 4f). However, some eggs which had not been fertilised began to dissolve (Fig. 4g) forming a hole through which cellular contents were drained out (Fig. 4h). The larvae started to rotate without a direction after 26 h (Fig. 4i). The two germ layers of the larvae were evident at approximately 37 h (Fig. 4j). After 69 h, the sphere gradually elongated to form a spindle shaped planula larva and crawled slowly to find an appropriate place for attachment (Fig. 4k, 4l).

3.2 Larval development after metamorphosis of *G. fascicularis*

We selected terracotta tiles for coral larvae settlement. After 69 h, the larvae started exploring the substratum with their aboral end and began to settle inside the holes (Fig. 5a1, 5a2). The larvae became flattened and six primary septa were observed approximately 5 d after spawning, which indicated that the larvae settled successfully (Fig. 5b). There were 183 individual larvae and the settlement rate was 1.53 ind/cm^2. After 9 d, the larvae metamorphosed into a primary lotus-like polyp, in which the tentacles and the zooxanthellae began to appear and the recruits began to secrete calcium carbonate and formed a wall (Fig. 5c1, 5c2). After approximately 1 month, 12 tentacles with more zooxanthellae (Fig. 5d1), six primary septa and the completely formed wall with the secondary septa were visible (Fig. 5d2), indicating that the larvae had completely metamorphosed, and the mean diameter was about 0.52 ± 0.05 mm (n = 10) (Table 1). After 2 months, the tentacles and the septa were longer and thicker (Fig. 5e1, 5e3). Once stimulated, they retracted into the body cavity (Fig. 5e2). There was no significant difference(P > 0.05)between the diameter (0.53 ± 0.15 mm; n = 10) of the second and first month (Table 1). We found some recruits that were dead with intact skeletons (Fig. 5e4). After three months, the recruits had grown and developed longer and thicker tentacles (Fig. 5f1, 5g, 5h1, 5i1, 5j), the diameter significantly increased from 0.64 ± 0.16 mm (n = 10) to 4.74 ± 1.12 mm (n = 10) after one year (P < 0.01) (Fig. 5f2, 5h2, 5i2) (Table 1).

Table 1
The diameter and larval survival rate over time

time	diameter(mm)	survival rate
5 d	—	100%
1 m	0.52 ± 0.05	81.87%
2 m	0.53 ± 0.15	50.82%
3 m	0.64 ± 0.16	43.72%
4 m	0.92 ± 0.16	26.55%
6 m	1.41 ± 0.28	21.86%
8 m	1.96 ± 0.29	14.76%
12 m	4.74 ± 1.12	5.46%

According to the fitting equation with diameter, it conforms to the parabolic growth trend ($y = 0.0371x^2 - 0.1076x + 0.6305$; $R^2 = 0.9954$) (Fig. 6a), the mean growth rate was 19.23% in the first four months after settlement. In the next 4 months (from the fifth to eighth months), the growth rate was 28.26%. The most rapid growth of 35.46% occurred in the last 4 months (from the ninth to twelfth months) (Fig. 6a). The number of larvae that were successfully settled at 5 d was recorded as 100% (Fig. 6b), the survival rate of the recruits decreased continuously during the experimental period, particularly in the first 4 months, the survival rate was only 26.55% in the fourth month. The most serious decline occurred in the second month from 81.87–50.82%. The later survival rate decreased slightly to 5.60% after one year (Fig. 6b, Table 1).

4. Discussion

4.1 Adult *G. fascicularis* rearing two years *ex situ* could reproduce sexually

This study found that *G. fascicularis* reared in a tank for two years spawned and fertilised successfully, indicating that corals could reproduce sexually *ex situ*. Several environmental signals (such as seasonal temperature, lunar, and diel cycles) have been shown to influence gametogenesis and spawning of corals in the wild (Babcock et al. 1986; Harrison and Wallace 1990; Babcock et al. 1994; Nozawa et al. 2006; Kongjandtre et al. 2010), however, few studies are about coral reproduction *ex situ*, as a result, the environmental factors that influence reproduction of corals remain unclear. Petersen et al. (2007) reported that broadcast spawners (13 species) and brooders (11 species) in public aquariums mainly reproduced in open systems under natural light conditions. Survey research thought that temperature fluctuation and nature moonlight might be beneficial to enhance reproduction in captivity, but it is not necessary. In

addition, they assumed more species might reproduce in public aquariums without being noticed by the staff owing to the lack of recruitment and of experimental design (larval collection). Broadcast coral of four *Acropora* species (*A. hyacinthus*, *A. tenuis*, *A. millepora*, and *A. microclados*) spawned for the first time in a fully closed artificial *ex situ* closed system mesocosm aquarium design that utilised a microprocessor technology to accurately replicate environmental conditions, including photoperiod, seasonal insolation, lunar cycles, and seasonal temperature (Craggs et al. 2017). After that, they completed the life cycle (i.e., production of an F2 generation) of the coral *A. millepora* in a fully closed artificial *ex situ* mesocosm (Craggs et al. 2020). This breakthrough has numerous implications for our understanding of reproductive biology in an *ex situ* environment, but it is still not clear what direct environmental factors are required to trigger spawning. In our study, the system used natural seawater and light; therefore, moonlight may trigger spawning of *G. fascicularis.* However, further studies should be conducted to determine the factors affecting their reproduction *ex situ*.

4.2 *G. fascicularis* larvae quickly acquire zooxanthellae after settlement which improve early survival rate

The zooxanthellae began to appear 9 d after spawning (4 d after settlement) and were not present in the eggs when observed under a stereomicroscope, which indicated that the zooxanthellae of *G. fascicularis* larvae came from ambient environment. The juveniles of three species (*Goniastrea aspera, Platygyra sinensis*, and *A. millepora*) contained zooxanthellae 10 d after settlement (Babcock 1985). Shlesinge and Loya (1991) found that zooxanthellae of *Favia favus* and *P. lamellina* appeared 26–30 d and 16–18 d, respectively, after spawning. *G. fascicularis* that acquired zooxanthellae earlier could acquire nutrition quicker which facilitated their calcification and metamorphosis, thereby improving their early survival rate. The first days or weeks following settlement are characterised by very high rates of mortality, for example, the survival rate of one-month-old primary polyps is approximately 0.21% and 0.25% in *F. favus* and *P. lamellina*, respectively (Shlesinge and Loya 1991); larval survival rate of *A. muricata* and *A. valida* decrease substantially to around 50% by the first week and to approximately 10% by the second to third week in the settlement aquaria (Nozawa and Harrison 2008). Our study showed the survival rate of *G. fascicularis* recruits was 81.87% in the first month which was higher than the above studies and may be related to the rapid acquisition of zooxanthellae. In addition, the appearance time of zooxanthellae is not only associated with species but also with the number of zooxanthellae present in the environment. Asymbiotic coral larvae of *A. monticulosa* in sediment-containing treatments acquired *Symbiodinium* earlier and had greater *Symbiodinium* densities when compared to seawater-only treatments (Adams et al. 2009). The combination of an adult coral and sediment resulted in the highest symbiont acquisition rates by *A. millepora* recruits, which were up to five-fold greater than those in seawater alone (Nitschke et al. 2016). In this study, we used filtered natural seawater, which provided a source of zooxanthellae for rapid acquisition. The appearance time of zooxanthellae in juvenile *G. fascicularis* is documented here for the first time.

4.3 Competition with algae is a major factor affecting the growth and survival rate of G. fascicularis recruits

The mean diameter of *G. fascicularis* recruits was 4.74 ± 1.12 mm in the first year. Because little is known about the growth rate of the massive corals for one year *ex situ*, we compared the diameter to the others *in situ* and found that the growth rate of *G. fascicularis* recruits was slower than those reported in the literature for other broadcast corals (Table 2). The survival rate of juveniles decreased continuously during the growth process, particularly in the first four months. The survival rate was only 26.55% in the fourth month and 5.60% after one year. The survival rate of *A. tenuis* juveniles was 59% at 10 months and 56% at 4 months for *A. cervicornis* (Nakamura et al. 2011; Henry et al. 2019). Compared to the above studies, the survival rate of *G. fascicularis* in each month was lower in this study.

Table 2
Growth rates of juvenile corals

Species	Mean diameter (mm)	Age	Literature
Favia favus	10	1 yr	Shlesinge and Loya 1991
Platygyra lamellina	10	8 m	Shlesinge and Loya 1991
Diploria labyrinthiformis	3	6 m	Chamberland 2017
Platygyru sinensis	3–4	8 m	Babcocka and Mundyb 1996
Acropora millepora	5.1	9.3 m	Babcocka 1995
Acropora solitaryensis	3.17 ± 0.96	3 m	Nozawa et al. 2006
Galaxea fascicularis	4.74 ± 1.12	1 yr	This study

We assume that the slow growth and low survival rate of juveniles might be due to their competition with algae. The main reasons for post-settlement mortality are competition, sedimentation, and predation (Penin et al. 2010, 2011). Among the dead recruits, there were two types: ones with completely removed or heavily damaged skeletons (i.e., “missing recruits”) who likely faced predation or were dislodged by grazers, and other ones with intact skeletons (i.e., “dead-intact recruits”) who were probably killed by other factors such as sedimentation, competition, or starvation (Sato 1985; Hunte and Wittenberg 1992). Due to their small size at settlement, predation faced by coral recruits in their benthic life could be overlooked (Penin et al. 2011). In this study, the intact skeletons of dead recruits were observed in the second month, the recruits were placed on a shelf where there were no benthic organisms fixed and no sediment coverage in the pond, and there was sufficient food with natural seawater. Thus, we concluded that competition with algae was the main factor that affected the growth and survival rate of *G. fascicularis* recruits. Macroalgae can be a dominant space occupier and can inhibit coral recruitment at multiple stages of the lifecycle (Box and Mumby 2007; Ritson-Williams et al. 2010; Craggs et al. 2019; Henry et al. 2019; Liao et al. 2021). Algae may also affect the development and survival of recruits by producing allelopathic substances or by interfering with the microbial community on corals (Rinkevich and Loya 1987; Thacker et al. 1998; Rasher and Hay 2010). Therefore, harmful algae should be timeously removed during juvenile growth.

In conclusion, this study reveals that adult *G. fascicularis* could sexually reproduce when kept *ex situ* for two years. The rapid acquisition of zooxanthellae by larvae helpful to improve early survival rate. The mean diameter of *G. fascicularis* recruits was 4.74 ± 1.12 mm and the survival rate was 5.60% in the first year. We concluded that the slow growth and low survival rate of recruits may be attributed to competition with algae. We recommend that recruits of *G. fascicularis* be reared 1 month *ex situ* and then transferred to the field. There are two reasons for this recommendation: firstly, the larvae will have completed metamorphosis and adapted to the ambient environment *ex situ* for a period of time, and the survival rate can be relatively improved when transplanted into the wild; secondly, the mortality of recruits increase continuously when kept *ex situ* for an extended period of time, wasting labour and money. Our results suggest that reef rehabilitation methods that aim to harness coral sexual reproduction might benefit from focusing on the rearing of juveniles through early post-settlement mortality bottlenecks.

Declarations

Author contributions

All authors contributed to the study conception and design. KY and FW conceived the research, FW, MC, WH, YW and XL contributed the materials and performed the experiments. MC and FW conducted the data analyses, XZ and HS involved in species identification, KY and FW wrote the manuscript.

Acknowledgements

This research was funded by the National Natural Science Foundation of China (Nos. 42090041, 42030502 and 41666005), Science and Technology Project of Guangxi (Nos.AA17204074, AD17129063, 2018GXNSFBA050023), the BaGui Scholars Program Foundation (2014BGXZGX03), and the Basic Ability Promotion Project for Young and Middle-aged Teachers in Universities of Guangxi (No. 2019KY0034). We thank the reviewers for providing many meaningful comments.

Data Availability

All data generated during this study are included and are openly available on this published article.

Declarations

Conflict of interest

All authors declare that they have no conficts of interest.

Ethical approval

Permits for coral sampling and breed were provided by Ministry of Agriculture and Rural Affairs of the People's Republic of China, and the local Department of Ocean and Fisheries. All applicable international, national and/or institutional guidelines for sampling, care, and experimental use of organisms for the study have been followed by the authors.

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Figures

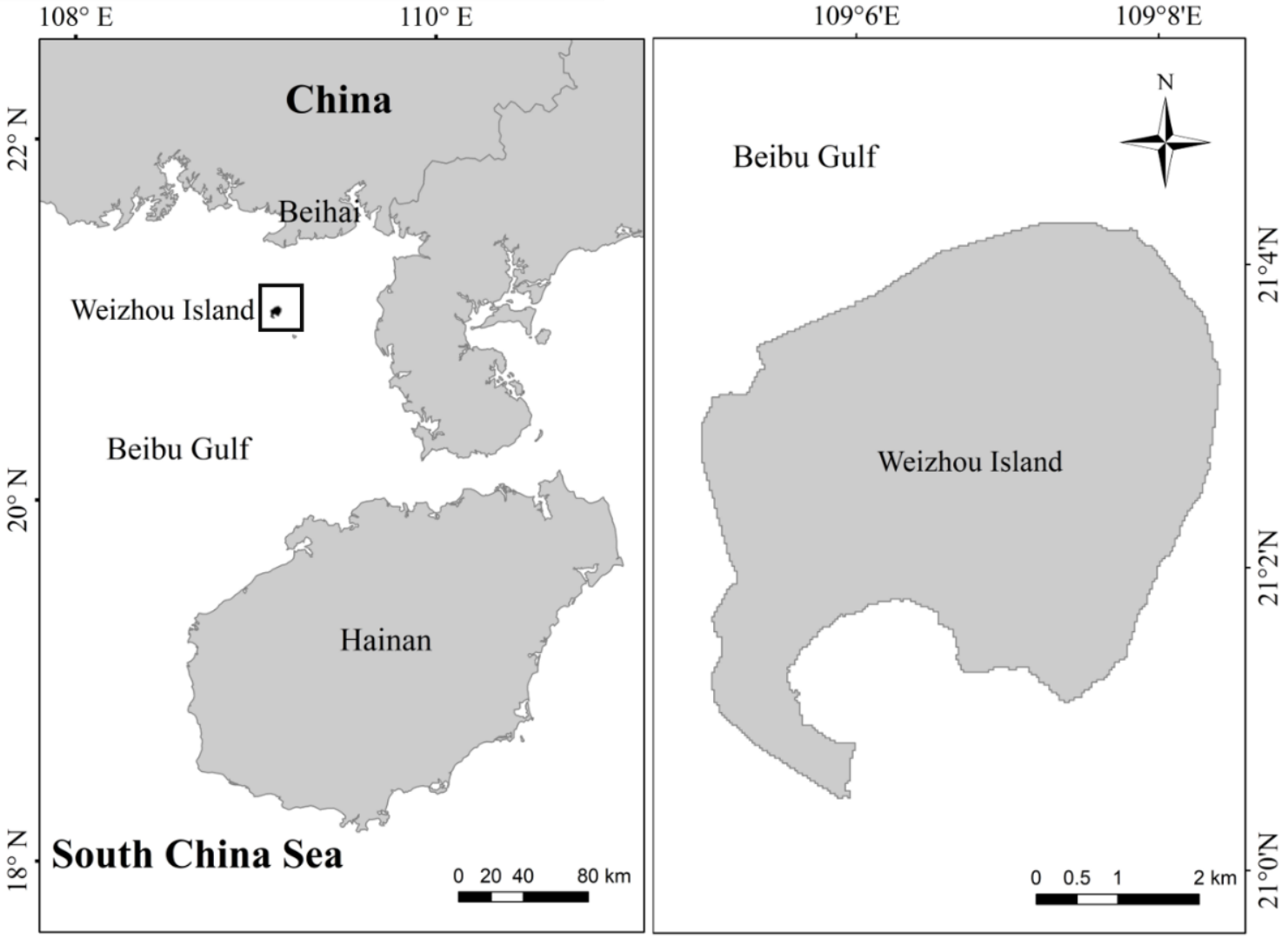

Figure 1

Map of the South China Sea showing the study site Weizhou Island indicated by a closed square

Figure 2

G. fascicularis nursery

(a) the breeding pond at the aquaculture facility (4 × 5 × 2 m); (b) spawning tank (50 × 50 × 60 cm)

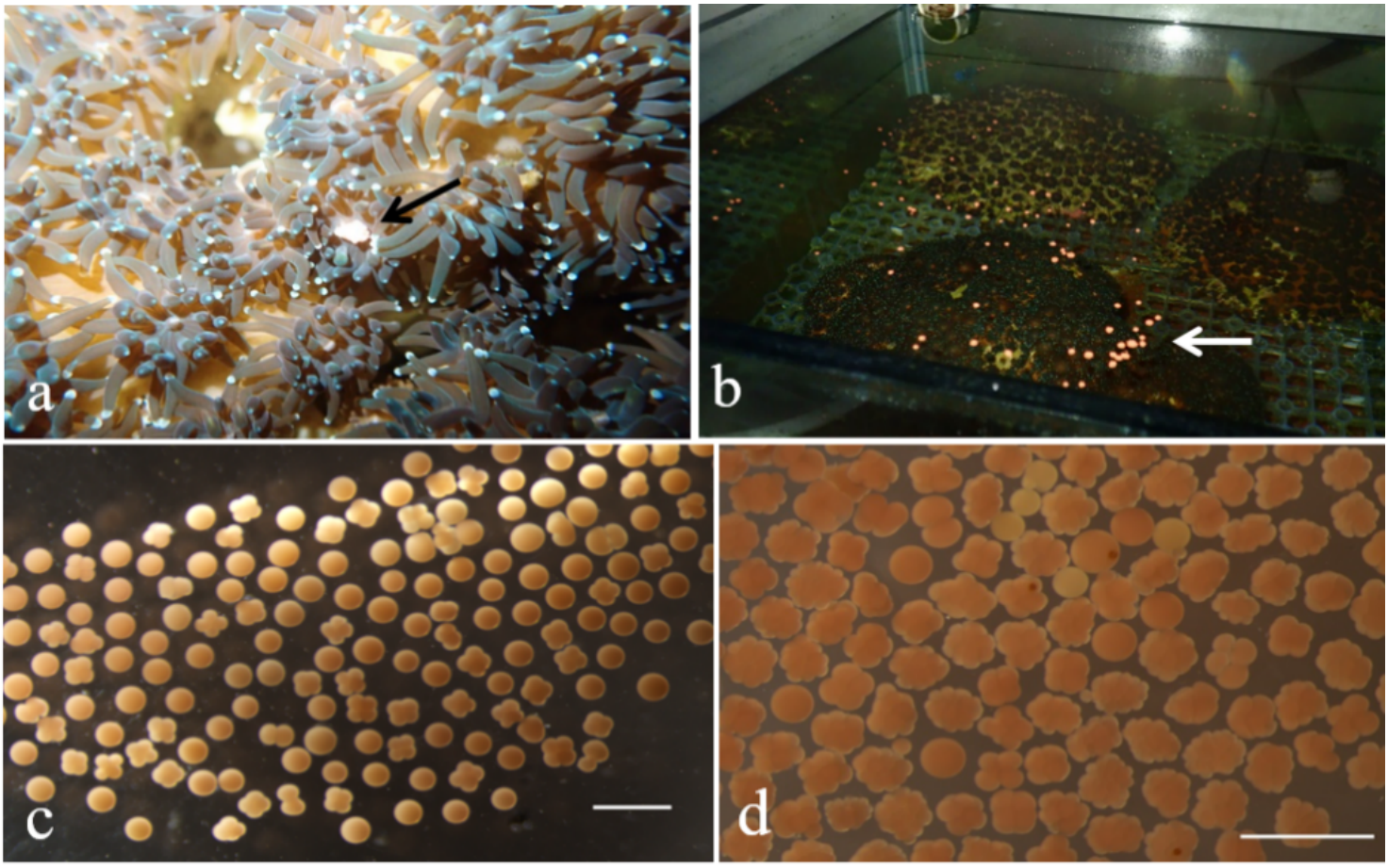

Figure 3

G. fascicularis spawning and eggs

(a) black arrow shows egg-sperm bundles; (b) white arrow shows eggs; (c) red eggs of 29 April, 2019; (d) red eggs of 25 May, 2019.

All rulers indicate 1 mm.

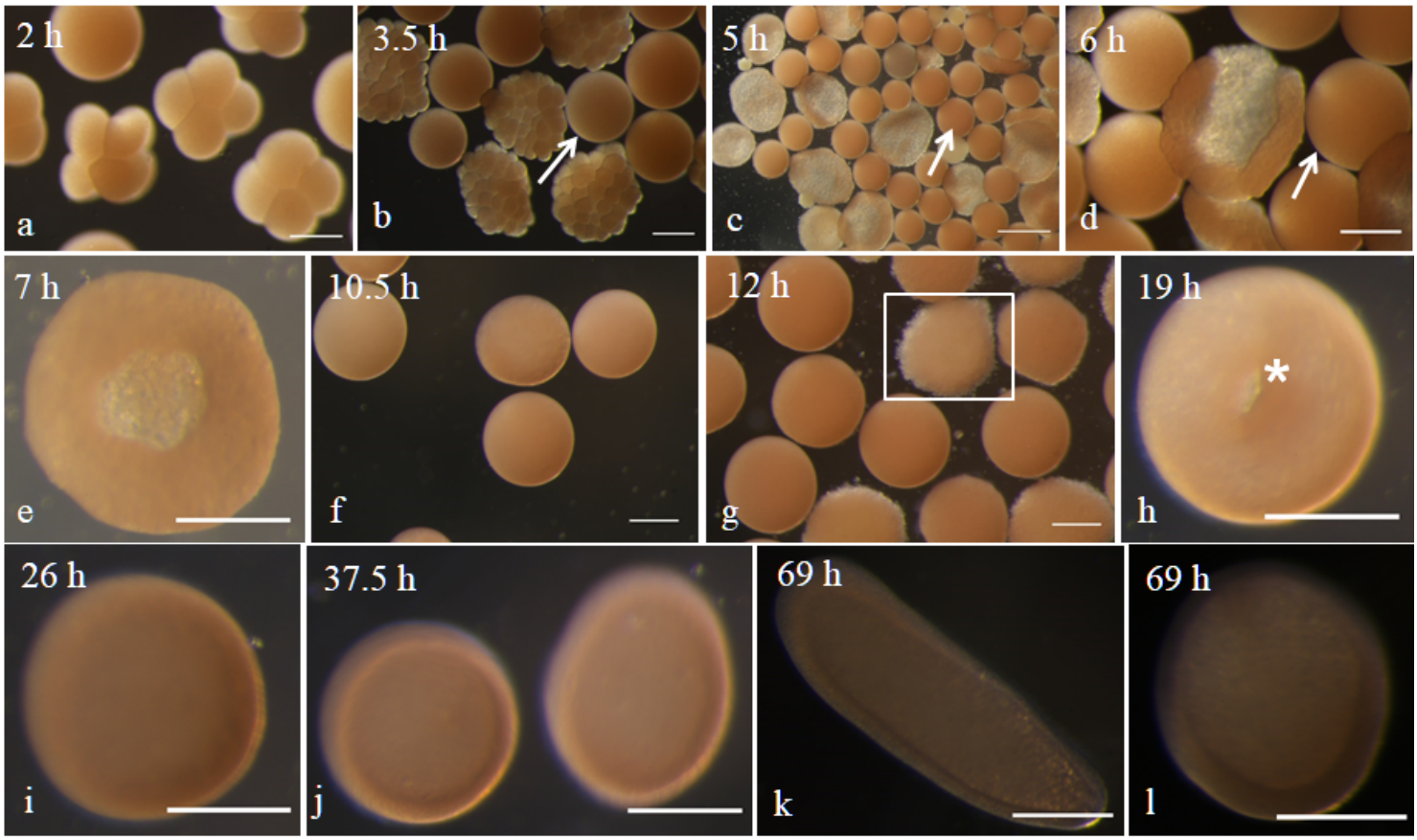

Figure 4

G. fascicularis early development

(a) 4-cell stage; (b) 32-cell stage, the white arrow shows unfertilised eggs; (c) prawn chip stage; (d, e) bowl stage; (f) blastula stage; (g) some eggs began to dissolve, the box indicates a dissolving egg; (h) the eggs dissolved from the hole; asterisk represents the hole; (i) early planula stage; (j) middle planula stage; (k, l) later planula stage.

All rulers indicate 200 μm, except Fig. 4(c) which indicates 500 μm.

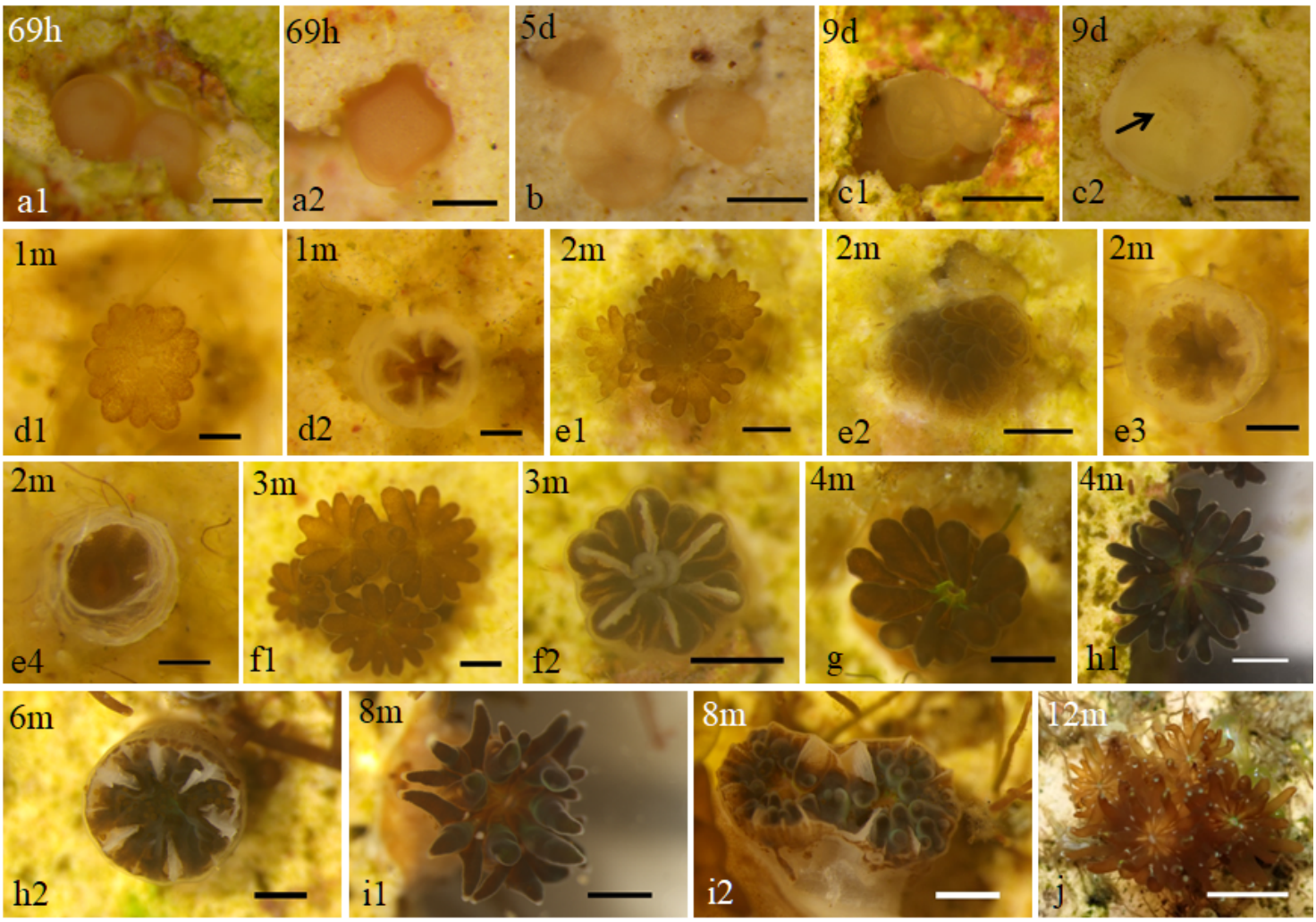

Figure 5

G. fascicularis post-settlement development

(a1, a2) larvae started settling into holes; (b) larvae settled successfully; (c1, c2) larvae metamorphosed into a primary polyp and showed zooxanthellae; (d1, d2) 12 tentacles and 6 primary septa evident with more zooxanthellae; (e1, e2) tentacles grew longer and retracted into the body cavity once stimulated; (e3) the septa and body wall were thicker; (e4) recruit was dead but skeleton was intact; (f1, g, h1, i1, j) recruits continued to develop, the tentacles grew longer and thicker; (f2, h2, i2) diameter was 0.64–4.74 mm.

(a1, a2, d1, d2, e3, e4) indicate 200 μm; (b, c1, c2, e1, e2, f1, f2, g, h1, h2) indicate 500 μm; (i1, i2) indicate 1 mm; (j) indicates 0.5 cm.

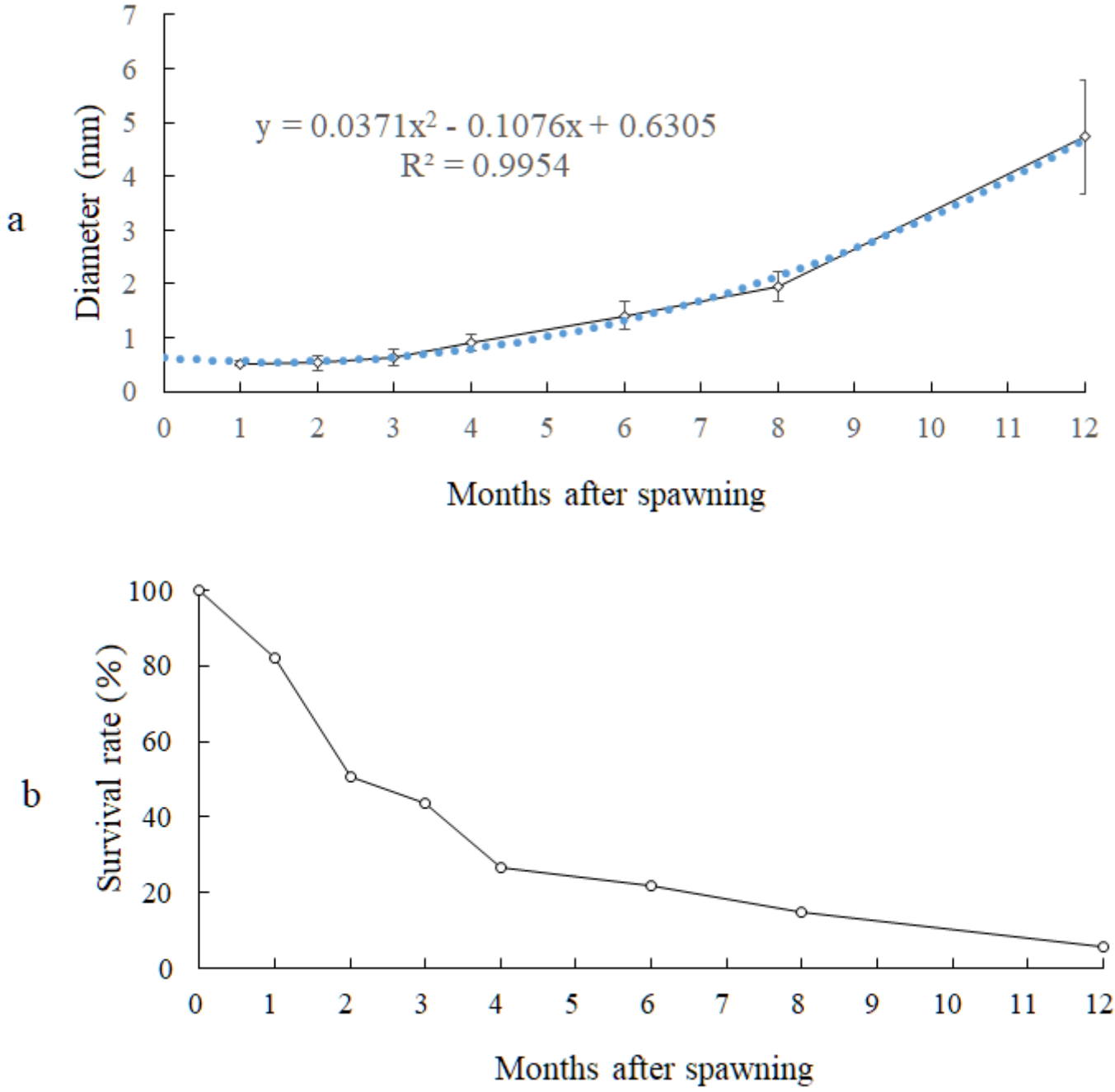

Figure 6

The diameter (a) and the survival rate (b) of *G. fascicularis* recruits