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AN OVERVIEW OF THE BREEDING AND LARVAL REARING TECHNIQUES OF PEARL OYSTER *Pinctada maxima*

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ABSTRACT

Pinctada maxima is a pearl oyster species in the *Pinctada* genus that produces some of the world's highest-value pearls. In past decades, the pearl culture industry relied heavily on wild stocks of this species for pearl production. To reduce the exploitation of wild populations while simultaneously supporting industry expansion and ensuring sustainable pearl culture, proper broodstock management, breeding techniques, and larval rearing practices are essential. Although information on the breeding techniques and larval rearing practices of *Pinctada maxima* is relatively abundant, it has not been systematically compiled or organised. Therefore, this review summarises and discusses information reported in previous studies on the breeding techniques and larval rearing practices of *Pinctada maxima*. The breeding section covers early broodstock selection, intensive broodstock conditioning, previously reported breeding techniques, and egg incubation. The larval rearing section includes larval feeding and nutrition, comparisons of food rations and stocking densities, water quality parameters, and larval settlement, with particular emphasis on the types of spat collectors used. In addition, this review highlights existing knowledge gaps that warrant further investigation.

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INTRODUCTION

Pearl oyster *Pinctada maxima*, also known as the white-, silver-, or golden-lipped oyster, is a marine bivalve mollusc belonging to the family Pteriidae. This species is widely distributed across the Indo-Pacific region and occurs in the waters of several countries, including China (Wang et al., 2016), Australia (Hart and Friedman, 2004; Scarratt et al., 2012), the Solomon Islands (Skewes, 1990; Hawes et al., 2011), Papua New Guinea (George, 1978), Myanmar (Rao et al., 2009), Indonesia, the Philippines (Strack, 2008), and Malaysia (Lim, L.-S., pers. comm.). *Pinctada maxima* is the largest species within the *Pinctada* genus and possesses a thick layer of nacre, also known as mother-of-pearl (Wada and Tëmkin, 2008). Nacre is an organic–inorganic composite material that forms both the inner shell layer and the outer coating of pearls (Jackson et al., 1988; Nudelman et al., 2006). The pearls produced by *P. maxima* are known as South Sea cultured pearls and represent the leading category in the global pearl market (Southgate et al., 2008). Consequently, the mariculture of *P. maxima* has been developed primarily for pearl production. In addition to *P. maxima*, other *Pinctada* species commonly cultured in the pearl industry include *P. fucata, P. martensii*, and *P. margaritifera* (Southgate et al., 2008).

To date, breeding and larval rearing techniques for *Pinctada* species have been well developed (Gervis and Sim, 1992; Southgate, 2008). However, most reported studies have focused on *P. fucata, P. martensii,* and *P. margaritifera*, with comparatively less attention given to *P. maxima*. Although general hatchery procedures for pearl oysters share many similarities, species-specific considerations are essential to ensure optimal breeding success (Liang et al., 1999; Aji, 2011). Despite the availability of numerous studies on the breeding and larval rearing of *P. maxima*, the available information remains scattered and has not been synthesised into a comprehensive species-specific protocol. Therefore, this review provides an overview of the breeding and larval rearing techniques of *P. maxima* and highlights existing knowledge gaps that warrant further investigation.

Broodstock selection and intensive conditioning to promote gonad maturation

Healthy and actively growing *Pinctada maxima* individuals should be selected as broodstock. Suitable broodstock are typically identified by well-developed shells that are large, intact, and have sharp edges. The sex of broodstock can be readily determined using the method described by Rose (1990). Prior to introduction into spawning tanks, broodstock should be thoroughly cleaned to remove biofouling organisms from the shell surface and disinfected by immersion in freshwater or potassium permanganate solution to minimise contamination (Rose, 1990; Liang et al., 1999; Liu et al., 2007; Pu et al., 2012). For induced spawning in tanks, a sex ratio of three females to one male has been recommended (Liang et al., 1998, 1999).

Following selection, broodstock are typically subjected to intensive conditioning in tanks prior to spawning induction. Table 1 summarises broodstock conditioning parameters for *P. maxima* reported in previous studies. In general, conditioning involves feeding broodstock with nutritious microalgae for a period of 5 to 20 days. Liang et al. (1998) reported that intensively conditioned broodstock exhibited higher spawning success, fertilisation rates, and larval production, with values of 25–50%, 96–98.4%, and 13–500 × 10^4 individuals, respectively, compared with unconditioned broodstock, which recorded 6.2–13.2%, 68.2–71.0%, and 8.0–9.0 × 10^4 larvae, respectively.

The type of microalgae used for conditioning also influences spawning performance. Xie et al. (2011) observed that a higher proportion of *P. maxima* broodstock reached gonadal maturity when fed a mixed diet containing cultivated algae collected originally from the sea (50%), compared with those fed *Chaetoceros muelleri* (34.8%), *Platymonas subcordiformis* (25%), or a mixed diet of *C. muelleri, P. subcordiformis*, and *Chlorella* spp. (34.8%). Moreover, broodstock fed the mixed sea-collected microalgae also exhibited the highest spawning success and fertilisation rates, with values of 45.5% and 97%, respectively. This was followed by broodstock fed *C. muelleri* (30.4% and 95%, respectively), the mixed diet of *C. muelleri, P. subcordiformis*, and *Chlorella* spp. (30.4% and 93%, respectively), and *P. subcordiformis* (20% and 92%, respectively).

Intensive conditioning is therefore a crucial step in broodstock management, with the type of microalgae used being a key factor influencing reproductive performance. This is likely related to the nutritional requirements of *P. maxima* during gonadal maturation. However, information on the specific nutritional requirements of this species remains limited. Therefore, further studies on the nutritional requirements of *P. maxima* broodstock are strongly recommended to improve feeding management and enhance spawning success.

Breeding techniques

Several methods have been developed for breeding *Pinctada maxima*. Table 2 summarises the breeding techniques reported in previous studies. The conventional approach involves artificial fertilisation, in which broodstock are sacrificed to obtain sperm and eggs, which are then mixed in ammoniacal seawater to achieve fertilisation. Liu et al. (2007) confirmed that an ammonia concentration of 30 ppm yielded the highest fertilisation rate (98%) among the ten tested concentrations, which ranged from 0 to 90 ppm.

Given the high value of *P. maxima* broodstock, non-invasive breeding methods are preferred (Liang et al., 1998).

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Table 1. Broodstock conditioning parameters for *P. maxima*, reported in previous studies

Broodstock sizes - Shell height (SH) - Shell length (SL)	Conditioning duration (days)	Water quality parameters	Feeding (types of microalgae used)	References
SH 220 - 250 mm	6 - 10	28 - 30 ˚C 26 - 31 ppt pH 8.0 - 8.4	*Platymonas subcordiformis,* *Isochrysis zhanjiangensis,* *Isochrysis galbana*	Liang et al. (1998)
SH 220 - 250 mm	5 - 7	28.1 - 30.0 ˚C 30 - 33 ppt pH 8.1 - 8.3	*Platymonas subcordiformis,* *Isochrysis zhanjiangensis,* *Isochrysis galbana* *Spirulina* powder	Liang et al. (1999)
SH 220 - 250 mm	10 - 15	25 - 28 ˚C	*Platymonas subcordiformis,* *Isochrysis zhanjiangensis,* *Skeletonema costatum,* *Spirulina* powder	Liu et al. (2007)
SH 140 - 160 mm	5 - 7	24 - 30 ˚C 30.8 - 32.5 ppt pH 8.0 - 8.3	*Platymonas subcordiformis,* *Chaetoceros muelleri,* *Chlorella* spp. Mixture of algae	Xie et al. (2011)
SL 180 - 320 mm	15 - 20	N/A	*Platymonas* sp., *Chaetoceros* sp., *Dunaliella* sp., *Spirulina* powder *Chlorella* powder	Pu et al. (2012)

Table 2. Breeding techniques for *Pinctada maxima* broodstock reported in previous studies

Breeding / Induction methods	Descriptions	References
Artificial fertilisation	Sacrifice broodstock and surgical-ly collect sperm and eggs, then perform fertilisation in ammoniacal seawater.	Wada (1953) Wada (1963) Minaur (1969) Xu and Li (1980) Tanaka and Kumeta (1981) Liu et al. (2007)
Air exposure stimulation	Expose broodstock to air for 1 - 6 h under shading and return it to the tank for spawning.	Liang et al. (1998) Liang et al. (1999) Zhao et al. (2003) Pu et al. (2012
Heat stimulation	Increase water temperature by 1 - 5°C for 2 - 3 h.	Rose (1990) Rose and Baker (1994) Liang et al. (1998) Liang et al. (1999) Pu et al. (2012)
Water flow stimulation	Create water flow in the tank to induce spawning.	Pu et al. (2012)
Algal stimulation	Immerse broodstock in the spawn-ing tank containing a high concentration of *Platymonas subcordiformis* and *Isochrysis zhanjiangensis* microalgae.	Pu et al. (2012)
Chemical stimulation	Injection of ammonium hydroxide (NH_4OH).	Winanto (2013)
Semen stimulation	Introduce conspecific sperm into the spawning tank.	Pu et al. (2012) Taylor et al. (2018)

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Inducing natural spawning in captivity has been shown to be feasible, with several stimulation techniques reported, including air exposure (drying), temperature elevation, increased water flow, chemical stimulation, and the introduction of microalgae or conspecific sperm into the water. Descriptions of these methods are presented in Table 2.

To date, few studies have systematically compared the efficiency of spawning induction methods. Nevertheless, the combined use of multiple stimulation techniques has been reported to be more effective than the application of a single method. Pu et al. (2012) observed that combined stimulation methods reduced the latency period before spawning and resulted in the release of larger quantities of eggs and sperm. However, this was also accompanied by a higher proportion of unfertilised eggs and deformed larvae (Table 3). The authors attributed this to overstimulation, which may cause broodstock to release both mature and immature gametes, thereby increasing the incidence of fertilisation failure and larval deformities.

Unfortunately, the study by Pu et al. (2012) remains the only study to date that has reported optimisation of spawning induction methods for *P. maxima*. Moreover, the physiological responses of *P. maxima* broodstock to these stimulation techniques, which are crucial for understanding the underlying induction mechanisms, remain poorly understood. Further studies are therefore needed to elucidate these physiological responses and optimise spawning induction methods to achieve shorter latency periods, higher fertilisation success, and lower incidences of larval deformities.

Egg incubation

Few studies have investigated the optimal conditions for incubating fertilised eggs of *Pinctada maxima*. The limited available information primarily focuses on the influence of egg density on larval survival. In the *P. maxima* production manual, Rose (1990) recommended an incubation density of 30 eggs mL^{-1}, a value that was later supported by Liang et al. (2017). However, Southgate et al. (1998) reported that egg density could be increased to 100 eggs mL^{-1}. Although larval survival tended to decline with increasing egg density, the survival rate at 100 eggs mL^{-1} remained high at 74.1%, which falls within the 60–80% range typically achieved in successful hatchery operations. Southgate et al. (1998) further emphasised that, in addition to egg quality, environmental parameters such as salinity and temperature play important roles in determining hatching success and larval survival. Future studies should therefore investigate the effects of these parameters in greater detail to establish optimised incubation protocols for *P. maxima*.

Larval rearing

The larval development of *Pinctada maxima* comprises several distinct stages, beginning with the D-stage, also known as the D-shaped stage, and progressing through the early umbo, umbo, and pediveliger stages, before transitioning to the plantigrade stage and finally settling as spat, which subsequently develop into juveniles. The larval morphology and biology of *P. maxima* throughout these developmental stages have been well documented in previous studies (Wada, 1942, 1953; Minaur, 1969; Tanaka and Kumeta, 1981; Rose and Baker, 1994; Winanto, 2009) and are therefore not discussed in detail in this review.

Table 3. Summary of spawning stimulation methods and reproductive outcomes for *Pinctada maxima* broodstock reported by Pu et al. (2012)

Stimulation method (s)	Spawning after stimulation (min)	Released eggs (%)	Fertilised eggs (%)	Deformed larvae (%)
D 4 h	380	30.33	99.74	1.62
D 3 h + **MA** 1 h	204	43.50	98.37	1.33
D 3 h + **MA** 1 h + **CS**	93	51.20	97.08	2.85
D 2 h + **MA** 1 h + **H** 1 h + **CS**	42	86.43	88.64	13.24
D 1.5 h + **MA** 0.5 h + **H** 0.5 h + **CS** + **WF**	26	92.24	87.36	19.56

D = Dryness; **MA** = Micro-algae; **CS** = Conspecific sperm; **H** = Heat; **WF** = Water flow

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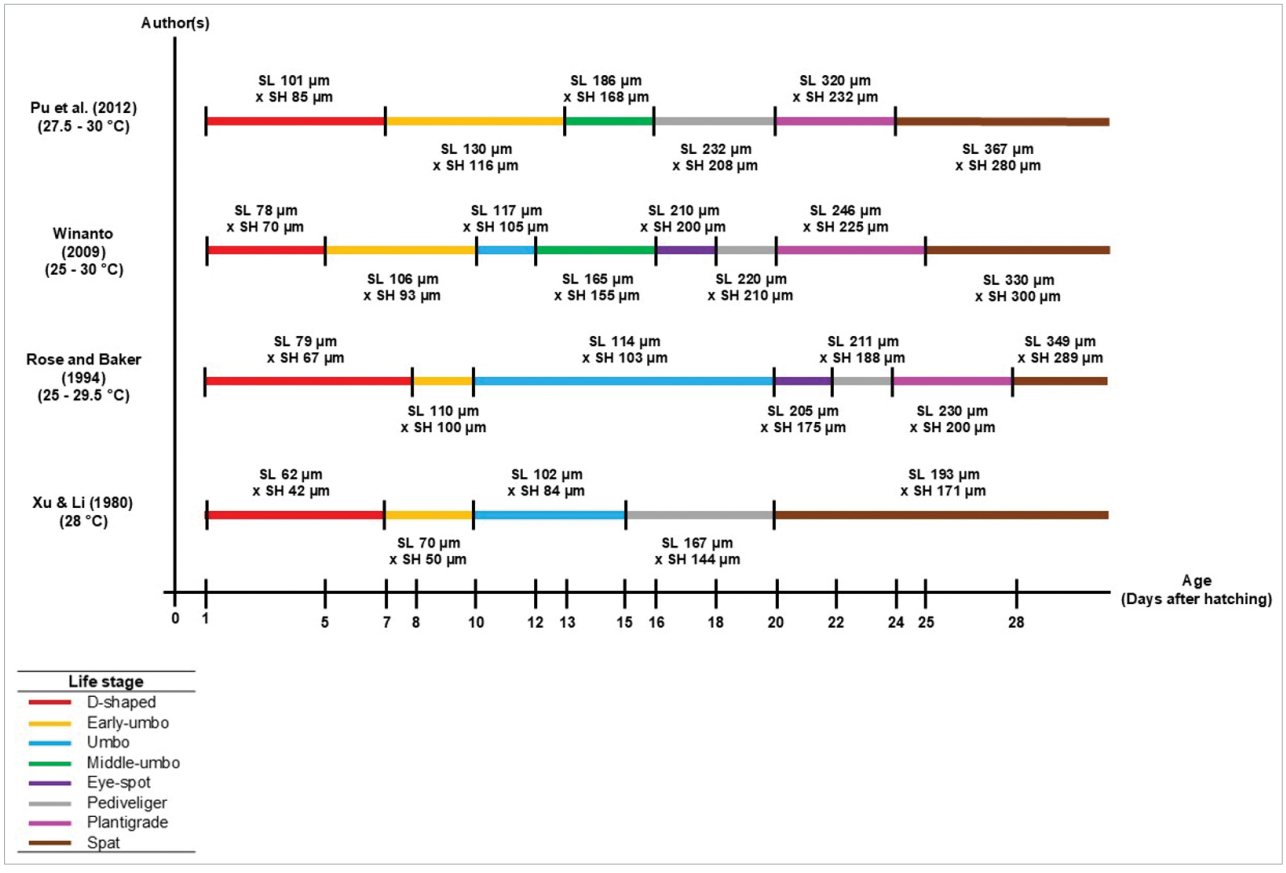


Fig 1. Larval developmental stages of *Pinctada maxima* reported in previous studies

Fig. 1 illustrates the approximate duration required for *P. maxima* larvae to develop from the D-shaped stage to the spat stage. Under optimal rearing conditions, with water temperatures maintained between 25 and 30°C, larval development typically takes approximately one month to complete. Throughout this period, feeding is one of the most critical factors influencing larval survival, growth, and successful metamorphosis. The selection of suitable microalgal species is therefore a major consideration, as it directly affects ingestion efficiency, digestion, and the availability of essential nutrients required for larval development.

Larval feeding and nutrition

The suitability of microalgae as a diet for *Pinctada maxima* larvae depends on several criteria, including appropriate particle size and morphology for ingestion, digestibility, and nutritional composition. Table 4 summarises the microalgal species used for the culture of *P. maxima* larvae at different developmental stages, as reported in previous studies.

The morphological characteristics of microalgae should correspond to the larval stage to ensure efficient ingestion. For example, the diatom *Chaetoceros gracilis* is unsuitable for early-stage larvae because its elongated spines may impede ingestion (Rose and Baker, 1994). Brown (2002) reported that microalgae suitable for ingestion by filter-feeding bivalve larvae generally range from 1 to 15 µm in diameter. Similarly, Xie and Xu (1980) observed that newly hatched *P. maxima* larvae ingested microcharcoal particles smaller than 1.3 µm but, after two days, were capable of ingesting *Platymonas subcordiformis* cells of up to 15 µm in diameter.

Digestibility is another critical factor in selecting suitable microalgae for larval feeding. Rose and Baker (1994) reported that *Nannochloropsis oculata* was poorly digested by *P. maxima* larvae owing to its thick cell wall. Among the species listed in Table 4, *Isochrysis zhanjiangensis* was more readily digested than *P. subcordiformis* and yeast throughout the D-stage to pediveliger stage, as indicated by its shorter gut clearance time (Liu et al., 2007). However, the digestibility of other microalgae commonly used in *Pinctada* spp. larval culture, including *Chaetoceros* spp., *Dunaliella* sp., *Tetraselmis* spp., and *Pavlova* spp., has yet to be evaluated for *P. maxima*, although such information is available for *P. margaritifera* (Doroudi and Southgate, 2003).

Information on the nutritional requirements of *Pinctada* spp. larvae remains limited. Martínez-Fernández et al. (2006) demonstrated that the growth of *P. margaritifera* D-stage larvae fed seven microalgal species was significantly correlated with dietary protein, lipid, and carbohydrate contents, whereas the growth of umbo-stage larvae was significantly correlated only with carbohydrate content.

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Table 4. Microalgal species fed to different developmental stages of *Pinctada maxima* larvae, as reported in previous studies

	Xu and Li (1980)	Rose and Baker (1994)	Xie et al. (2011)	Pu et al. (2012)	Liang et al. (2015)	Liang et al. (2017)
D-stage	*P. subcordiformis* Yeast	*I. galbana* *N. oculata* *C. calcitrans* *C. gracilis*	*I. zhanjiangensis* Yeast *Spirulina* powder	*I. zhanjiangensis* *D. salina*	*I. zhanjiangensis* *P. viridis* Yeast	*I. zhanjiangensis* Yeast
Early umbo to pediveliger	*P. subcordiformis* Yeast	*I. galbana* *N. oculata* *C. calcitrans* *C. gracilis*	*P. subcordiformis* Yeast *Spirulina* powder	*P. subcordiformis* *I. zhanjiangensis* *D. salina* *C. muelleri* Yeast *Spirulina* powder	*P. subcordiformis* *I. zhanjiangensis*	*P. subcordiformis* *I. zhanjiangensis* *Chlorella* spp. Yeast
Plantigrade	*P. subcordiformis*	*T. chuii* *N. oculata* *I. galbana* *C. calcitrans* *C. gracilis*	*P. subcordiformis* *C. muelleri* *Chlorella* spp. Yeast *Spirulina* powder	*P. subcordiformis* *C. muelleri* *I. zhanjiangensis* *D. salina* Yeast *Spirulina* powder	*P. subcordiformis* *C. muelleri* *Chlorella* spp. Yeast	*P. subcordiformis* *C. muelleri* *Chlorella* spp
Spat	N/A	*T. chuii* *N. oculata* *I. galbana* *C. calcitrans* *C. gracilis*	*P. subcordiformis* *C. muelleri* *Chlorella* spp. Yeast *Spirulina* powder	*P. subcordiformis* *C. muelleri* *I. zhanjiangensis* *D. salina* Yeast *Spirulina* powder	*P. subcordiformis* *C. muelleri* *Chlorella* spp. Yeast	*P. subcordiformis* *C. muelleri* *Chlorella* spp.

Full names of microalgae: 1. *Platymonas subcordiformis*, 2. *Isochrysis zhanjiangensis*, 3. *Isochrysis galbana*, 4. *Nannochloropsis oculata*, 5. *Dunaliella salina*, 6. *Pavlova viridis*, 7. *Chaetoceros calcitrans*, 8. *Chaetoceros gracilis*, 9. *Chaetoceros muelleri*, 10. *Tetraselmis chuii*

In addition, the concentrations of saturated fatty acids, polyunsaturated fatty acids (PUFAs), docosahexaenoic acid (DHA), and the combined DHA + eicosapentaenoic acid (EPA) were also significantly associated with larval growth. Among the seven species tested, *Pavlova salina* and *Pavlova* sp., which contained the highest levels of these fatty acids, supported the greatest growth of both D-stage and umbo-stage larvae (Martínez-Fernández et al., 2006). According to Strugnell and Southgate (2003), lipid accumulation during the early developmental stages of *P. margaritifera* larvae suggests that lipids serve as an important energy source during metamorphosis. Therefore, crude lipid content and fatty acid composition are likely to be key nutritional factors in microalgal diets for *Pinctada* spp. larvae. Nonetheless, further studies are required to verify whether this also applies to *P. maxima*. Taylor et al. (1997a) emphasised that the nutritional value of a given microalgal species depends on the comparative context, the *Pinctada* species under investigation, and the larval stage. They evaluated the nutritional value of *Isochrysis galbana*, *Pavlova lutheri*, *Chaetoceros muelleri*, *C. calcitrans*, and *Tetraselmis suecica* for *P. maxima* spat and found *C. muelleri* to be the most effective single-species diet. In contrast, Minaur (1969) reported *P. lutheri* and *I. galbana* as the most suitable species for feeding *P. maxima* larvae, suggesting ontogenetic variation in dietary requirements between larval and spat stages.

Although previous studies have identified suitable microalgal species for *P. maxima* larval feeding, knowledge of the species-specific nutritional requirements of this species remains scarce. Future research should therefore focus on defining these requirements to improve larval performance and survival. Furthermore, the use of locally available microalgal strains that satisfy both the nutritional and morphological requirements of *P. maxima* larvae should be prioritised to enhance the sustainability of *Pinctada* spp. larval culture.

Food ration and larval stocking density

In addition to the choice of microalgal species for feeding *Pinctada* spp. larvae, several other factors, including larval developmental stage, algal ration, and larval stocking density, also influence feeding performance. However, studies investigating optimal algal rations for *Pinctada* spp. larvae at different developmental stages and culture densities remain scarce.

Liang et al. (2017) conducted a series of experiments to determine the optimal culture density for *P. maxima* larvae at three developmental stages, namely D-stage, early umbo stage, and eye-spot stage, under fixed algal rations. They recommended that, to achieve the highest growth, survival, and metamorphosis rates, *P. maxima* larvae should be cultured under the conditions summarised in Table 5.

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Table 5. Optimal culture density and feeding conditions for *Pinctada maxima* larvae recommended by Liang et al. (2017)

Larval stage	Larval density (larvae mL^{-1})	Feeding
D-stage	1.0 - 3.0	*I. zhanjiangensis* (0.4 - 2.0 × 10^4 cells mL^{-1} d^{-1})
Early umbo	1.0 - 1.5	*P. subcordiformis* (0.6 - 2.0 × 10^3 cells mL^{-1} d^{-1}) + *I. zhanjiangensis* (2.0 - 5.0 × 10^4 cells mL^{-1} d^{-1}) + *Chlorella* spp. (2.0 - 5.0 × 10^4 cells mL^{-1} d^{-1})
Eye-spot	0.4 - 0.8	*P. subcordiformis* (0.2 - 0.4 × 10^4 cells mL^{-1} d^{-1}) + *C. muelleri* (2.0 - 5.0 × 10^4 cells mL^{-1} d^{-1}) + *Chlorella* spp. (2.0 - 5.0 × 10^4 cells mL^{-1} d^{-1})

Although Liang et al. (2017) established the optimal culture densities for *P. maxima* larvae, information regarding the interaction between larval density and algal ration at different developmental stages remains lacking.

Similarly, Doroudi and Southgate (2000) investigated the effects of algal ration and larval density on the growth and survival of *P. margaritifera* larvae. Their experiments involved two larval age groups, 1- and 13-day-old larvae, using a 3 × 4 factorial design comprising three larval densities, 1.0, 2.0, and 5.0 larvae mL^{-1}, and four algal rations. Larvae were fed a 1:1 mixture of *Isochrysis galbana* and *Pavlova salina*. For 1-day-old larvae, the algal rations were 0, 2,500, 5,000, and 12,500 cells mL^{-1} day^{-1}, whereas for 13-day-old larvae, the rations were 0, 7,500, 15,000, and 37,500 cells mL^{-1} day^{-1}. Based on their findings, Doroudi and Southgate (2000) recommended that *P. margaritifera* larvae from 1 to 8 days of age be fed approximately 8,000 cells mL^{-1} day^{-1} and cultured at a density of 3 larvae mL^{-1}. Older larvae, from 13 to 20 days of age, should be fed approximately 25,000 cells mL^{-1} day^{-1} and cultured at a density below 2 larvae mL^{-1}.

These studies demonstrate that knowledge of the feeding performance of *P. maxima* larvae remains incomplete. Further research is required to evaluate and compare the effects of different algal rations and larval stocking densities across various developmental stages. In addition, the potential effects of different microalgal combinations and dietary compositions should also be investigated.

Water quality parameters

Apart from food and nutrition, water temperature and salinity are two major environmental factors influencing the growth and survival of *Pinctada* spp. larvae. Over the past decades, *Pinctada maxima* larvae have typically been reared at water temperatures ranging from 24 to 30°C and salinities between 27 and 36 ppt. Table 6 summarises the water temperature and salinity conditions used for *P. maxima* larval culture, as reported in previous studies. Doroudi et al. (1999) investigated the combined effects of temperature and salinity on the embryos and larvae of *P. margaritifera*. Their experiment employed a 4 × 4 factorial design with four temperature levels, 20, 25, 30, and 35°C, and four salinity levels, 25, 30, 35, and 40 ppt. The results indicated that the optimal conditions for maximum survival and growth of *P. margaritifera* larvae, from 1 to 15 days of age, were 26–29°C and 28–32 ppt. For *P. maxima*, Taylor et al. (2004) reported that the most suitable salinity range for nursery rearing of spat was 30–34 ppt, while Deng et al. (2013) found that spat reared at salinities of 27–30 ppt exhibited higher growth and survival rates than those cultured at lower salinities of 21–24 ppt. However, both studies focused solely on salinity and did not examine the effects of temperature. Moreover, no study has yet determined the optimal culture conditions for early-stage *P. maxima* larvae.

Consequently, information on the combined effects of temperature and salinity on *P. maxima* larvae remains limited. Determining these optimal parameters is essential for developing more efficient large-scale hatchery techniques. Therefore, future research should focus on identifying optimal temperature–salinity combinations to enhance larval performance and survival in *P. maxima* culture.

Larval settlement

Larval settlement or spat collection in *Pinctada maxima* typically begins when pediveliger larvae develop a visible eyespot. To optimise survival and growth, Taylor et al. (1998a) recommended a setting density of not more than 1 larva mL^{-1} and a spat density of approximately 70 spat per 100 cm² of collector surface. The timely introduction of suitable settlement substrates, or collectors, during this stage is therefore critical. In the absence of collectors, larvae may settle on tank surfaces, requiring manual removal by scraping or water jets, which can damage fragile larvae and result in high mortality (Taylor et al., 1997b). The detailed settlement process in *Pinctada* species has been well described in previous studies (Rose, 1990; Rose and Baker, 1994; Southgate, 2008) and is therefore not further elaborated here. Table 7 summarises the artificial substrates used for *P. maxima* spat settlement, as reported in previous studies, with efficiency largely influenced by substrate type, material, and colour.

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Table 6. Water quality parameters for larval rearing of *Pinctada maxima* reported in previous studies

Larval life stage	Water tempera-ture (˚C)	Salinity (ppt.)	pH	References
D-shaped to spat	25.0 - 29.5	35.0 - 36.0	N/A	Rose and Baker (1994)
Spat	N/A	30.0 - 34.0	N/A	Taylor et al. (2004)
D-shaped to spat	24.0 - 26.0	30.8 - 32.5	8.0 - 8.3	Xie et al. (2011)
D-shaped to spat	25.1 - 29.6	28.8 - 30.2	N/A	Deng et al. (2013)
Spat	27.6 - 29.2	27.0 - 30.0	N/A	Deng et al. (2013)
D-shaped to spat	24.0 - 30.0	30.8 - 32.5	8.0 - 8.3	Liang et al. (2015)
D-shaped to spat	27.5 - 31.0	30.8 - 32.5	8.0 - 8.3	Liang et al. (2017)

Table 7. Examples of artificial substrates used for *Pinctada maxima* spat collection, as reported in previous studies

Introduction of collector at (life stage)	Types/ Colours/ Materials of artificial substrates	Results	Reference
Plantigrade	– Monofilament nylon fishing line – Dark plastic shade cloth – Dark glass – Grey plastic plate	Glass or plastic plates appeared to yield greater spat settlement per unit area.	Rose and Baker (1994)
Pediveliger	– Curved PVC slat – Polypropylene rope – Combination of PVC slat and polypropylene rope – Monofilament nylon	Rope and combined PVC slat with polypropylene rope produced the highest spat numbers.	Taylor et al. (1998b)
	– PVC slat with epifloral biofilm – PVC slat without epifloral biofilm	PVC slat with epifloral biofilm produced the highest spat numbers.	
Eye-spot	– Black plastic plate – Red plastic plate – Plastic mesh cloth	Black and red plastic plates showed inconsistent performance in spat collection. The combined use of plastic plates and cloth collectors yielded the best results in spat collection.	Liang et al. (1999)
Eye-spot	– Tabular adhering apparatus – PVC rope adhering apparatus	PVC rope adhering apparatus produced better results in spat collection.	Liu et al. (2007)
Pediveliger	– Asbestos – Bamboo – Fibrous filamentous polyethylene – Ceramic roof	Polyethylene achieved the highest settlement rate, followed by bamboo, asbestos, and ceramic roof.	Arini and Jaya (2011)

Settlement substrates are commonly categorised into three main types: plates, also referred to as sheets or slats, ropes, and mesh cloth. These collectors are manufactured from materials such as glass, plastic, PVC, polypropylene, and polyethylene, and may exhibit different surface characteristics, including smooth, rough, corrugated, porous, or twisted structures. Rough-surfaced substrates consistently enhance byssal attachment and spat settlement (Taylor et al., 1998b; Xie et al., 2011). For example, Liang et al. (2015) reported that rough black plastic sheets supported significantly higher spat recruitment than smooth sheets, shade cloth, or nylon nets. However, plate-type collectors may obstruct water flow within culture tanks, leading to uneven spat distribution (Liang et al., 2015), disrupted aeration, and irregular dispersion of algal feed, thereby negatively affecting larval feeding and growth (Liang et al., 1999; Liu et al., 2007). In addition, the accumulation of dead microalgae, larval debris, and waste products on plate surfaces may further reduce spat survival (Liang et al., 1999; Liu et al., 2007; Pu et al., 2012). To mitigate these limitations, porous plastic plates have been recommended

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(Xie et al., 2011), while shade cloth or shading nets have been suggested to improve water flow and reduce fouling (Pu et al., 2012). Furthermore, combining shade cloth with plate collectors has been shown to enhance spat recruitment while reducing associated drawbacks (Liang et al., 1999, 2015).

In addition to physical characteristics, colour plays an important role in larval settlement. *Pinctada maxima* larvae exhibit negative phototactic behaviour and preferentially settle on dark-coloured substrates. This has been confirmed by Liang et al. (2015) and Wang et al. (2017) who reported significantly higher settlement on black and red plastic sheets compared with lighter-coloured substrates such as yellow, green, or white. Similar trends have been observed in other *Pinctada* species, including *P. mazatlanica* (Saucedo et al., 2005) and *P. martensii* (Su et al., 2007), further supporting the preference for dark substrates. Overall, these findings indicate that dark-coloured collectors are more suitable for enhancing larval settlement.

Beyond substrate type and colour, biofilm development on collector surfaces is also a key factor influencing settlement success. Rose and Baker (1994) reported delayed settlement in *P. maxima*, which was attributed to insufficient biofilm development on collectors conditioned in seawater for only two weeks. In contrast, Taylor et al. (1998b) prepared collectors by conditioning them in aerated tanks containing *Chaetoceros muelleri* for 72 hours, allowing adequate biofilm formation. Both Taylor et al. (1998b) and Wang et al. (2017) demonstrated that biofilm significantly enhances spat recruitment, likely by providing chemical cues that induce settlement and potentially supplying nutritional support during metamorphosis. However, the precise mechanisms underlying biofilm-mediated settlement remain unclear and require further investigation.

Finally, economic and environmental considerations should also be taken into account when selecting settlement substrates. Natural, locally available, and low-cost materials are preferable for sustainable hatchery operations. Ompi et al. (2018) compared polypropylene ropes with natural fibre ropes derived from sugar palm *Arenga pinnata* and coconut *Cocos nucifera* and found no significant differences in settlement success, demonstrating that natural fibres are viable alternatives. Similarly, Arini and Jaya (2011) reported successful settlement on bamboo substrates. Wang et al. (2017) further showed higher settlement on palm fibre ropes than on polypropylene ropes, likely due to their rough texture and dark coloration. Collectively, these studies suggest that natural materials have strong potential to replace synthetic collectors; however, research on alternative natural substrates for *P. maxima* remains limited. Future studies should therefore explore environmentally friendly materials to improve the sustainability of hatchery practices.

CONCLUSION

This review summarises and evaluates current knowledge on the breeding and larval rearing techniques of pearl oyster *Pinctada maxima*. While considerable advances have been achieved in the hatchery production of other *Pinctada* species, such as *P. fucata*, *P. martensii*, and *P. margaritifera*, information specific to *P. maxima* remains comparatively limited and fragmented.

Critical knowledge gaps persist in understanding the effects of environmental factors, particularly temperature and salinity, on the embryonic and larval development of *P. maxima*. Similarly, although settlement and metamorphosis have been widely studied, the chemical and biological cues governing larval attachment remain poorly defined. Future research should therefore prioritise the determination of optimal environmental parameters for larval culture and further elucidate the role of biofilm-associated chemical signals in promoting settlement success.

In addition, the use of cost-effective and environmentally sustainable natural materials as spat collectors represents a promising approach for large-scale hatchery operations. Further research is also required to refine broodstock conditioning, spawning induction, and larval feeding strategies specifically tailored to *P. maxima*. Collectively, advances in these areas will contribute to the development of more standardized, efficient, and sustainable hatchery techniques for *P. maxima*, ultimately supporting the growth and stability of the South Sea pearl aquaculture industry.

PREGLED TEHNIKA UZGOJA I UZGOJA LIČINKI BISERNE KAMENICE (*Pinctada maxima*)

SAŽETAK

Pinctada maxima je vrsta biserne kamenice iz roda *Pinctada* koja proizvodi neke od najvrjednijih bisera na svijetu. Tijekom proteklih desetljeća industrija uzgoja bisera uvelike se oslanjala na prirodne populacije ove vrste za proizvodnju bisera. Kako bi se smanjilo iskorištavanje tih zaliha, a istovremeno podržalo širenje industrije i osigurao održiv uzgoj bisera, ključno je pravilno upravljanje matičnjacima, kao i učinkovite tehnike uzgoja i uzgoja ličinki. Iako je dostupno relativno mnogo podataka o tehnikama uzgoja i praksama uzgoja ličinki *Pinctada maxima*, nisu sustavno prikupljeni ni objedinjeni. Stoga ovaj pregledni rad sažima i razmatra informacije objavljene u prethodnim istraživanjima o tehnikama uzgoja i praksama uzgoja ličinki *Pinctada maxima*. Odjeljak o uzgoju obuhvaća rani odabir matičnjaka, intenzivno kondicioniranje matičnjaka, razne prethodno objavljene tehnike uzgoja i inkubaciju jaja. Odjeljak o uzgoju ličinki uključuje hranjenje i prehranu ličinki, usporedbe obroka hrane i gustoće naseljenosti,

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parametre kakvoće vode i naseljavanje ličinki, što se prvenstveno odnosi na vrste korištenih kolektora. Osim toga, ovaj pregledni rad ukazuje na postojeće nedostatke u znanju koji zahtijevaju daljnja istraživanja.

Ključne riječi: južnomorska biserna kamenica, upravljanje matičnjacima, proizvodnja ličinki

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DECLARATION OF COMPETING INTEREST

The authors declare no conflict of interest.

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Formal ethical approval and specific permits were waived for this study, as it was based solely on a literature review and did not involve invasive experiments on live animals.

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REFERENCES

Aji, L. P. (2011): A review of pearl oyster (*Pinctada maxima*) culturein general. Jurnal Saintek Perikanan, 6, 2, 85-91. https://doi.org/10.14710/ijfst.6.2.85-91

Arini, E., Jaya, N. T. S. P. (2011): The effect of various spat collector materials for spat attachment of pearl oyster (*Pinctada maxima*). Journal of Coastal Development, 15, 1, 34-44.

Brown, M. R. (2002): Nutritional value of microalgae for aquaculture. In: Cruz-Suarez L. E., Ricque-Marie, D. Tapia-Salazar, M., Gaxiola-Cortes, M. G., Simoes, N. (eds), Avances en Nutrición Acuícola VI. Memorias del VI Simposium Internacional de Nutrición Acuícola; 2002 Sep 3-6, Cancún, Quintana Roo, México, p. 281-292.

Deng, Y. W., Fu, S., Liang, F. L., Du, X. D., Xie, S. H. (2013): Growth and survival of pearl oyster *Pinctada maxima* spat reared under different environmental conditions. Journal of Shellfish Research, 32, 3, 675-679. https://doi.org/10.2983/035.032.0308

Doroudi, M. S., Southgate, P. C. (2000): The influence of algal ration and larval density on growth and survival of blacklip pearl oyster *Pinctada margaritifera* (L.) larvae. Aquaculture Research, 31, 8-9, 621-626. https://doi.org/10.1046/j.1365-2109.2000.318483.x

Doroudi, M. S., Southgate, P. C. (2003): Embryonic and larval development of *Pinctada margaritifera* (Linnaeus, 1758). Molluscan Research, 23, 101-107.

Doroudi, M. S., Southgate, P. C., Mayer, R. J. (1999): Growth and survival of blacklip pearl oyster larvae fed different densities of microalgae. Aquaculture International, 7, 3, 179-187.

George, C. D. (1978): The pearl, a report to the government of Papua New Guinea. Food and Agriculture Organization of the United Nations, and the Asian Development Bank. Samarai, Milne Bay Province, Papua New Guinea. p. 169.

Gervis, M. H., Sims, N. A. (1992): The Biology and Culture of Pearl Oysters (Bivalvia: Pteriidae). ICLARM, Manila Philippine. 49pp.

Hart, A. M., Friedman, K. J. (2004): Mother-of-pearl shell (*Pinctada maxima*): Stock evaluation for management and future harvesting in Western Australia. FRDC Project 1998/153, Fisheries Research Contract Report No. 10, Department of Fisheries, Perth, Western Australia. 84pp.

Hawes, I., Lasiak, T., Lincoln Smith, M., Oengpepa, C. (2011): The status of silverlip pearl oyster *Pinctada maxima* (Jameson) (Mollusca, Pteriidae) in the Solomon Islands after a 15- year export ban. Journal of Shellfish Research, 30, 255-260. https://doi.org/10.2983/035.030.0209

Jackson, A. P., Vincent, J. F. V., Turner, R. M., Alexander, R. M. (1988): The mechanical design of nacre. Proceedings of the Royal Society of London Series B, 234, 1277, 415-440. https://doi.org/10.1098/rspb.1988.0056

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Liang, F. L., Lin, W. C., Deng, Y. W., Xie, S. H. (2015): Effect of water exchange frequency and artificial substrates on hatchery production of *Pinctada maxima*. Chinese Agricultural Science Bulletin, 31, 29, 33-38. (in Mandarin with English abstract).

Liang, F. L., Liu, D. C., Deng, C. M. (1999): Study on the techniques for artificial breeding of *Pinctada maxima* (Jameson). Transaction of Oceanology & Limnology, 9, 2, 55-59. (in Mandarin with English abstract).

Liang, F. L., Xu, G. L., Deng, C. M. (1998): Study on artificial promoting maturation and inducing spawning in *Pinctada maxima* (Jameson). Transactions of Oceanology and Limnology, 8, 2, 34-37. (in Mandarin with English abstract).

Liang, F. L., Wang, Q. G., Deng, Y. W., Xie, S. H. (2017): Effects of stocking density on hatching, growth, survival and metamorphosis at larval stages of pearl oyster *Pinctada maxima*. Transaction of Oceanology and Limnology, 26, 6, 75-81. (in Mandarin with English abstract).

Liu, Y., Yu, X. Y., Deng, C. M., Liang, F. L., Zhang, C. F. (2007): Study on artificial reproduction of *Pinctada maxima* (JAMESON). Journal of Guangdong Ocean University, 27, 3, 38-44. (in Mandarin with English abstract).

Martínez-Fernández, E., Acosta-Salmón, H., Southgate, P. C. (2006): The nutritional value of seven species of tropical microalgae for black-lip pearl oyster (*Pinctada margaritifera*, L.) larvae. Aquaculture, 257, 1-4, 491-503. https://doi.org/10.1016/j.aquaculture.2006.03.022

Minaur, J. (1969): Experiments on the artificial rearing of the larvae of *Pinctada maxima* (Jameson) (Lamellibranchia). Australian Journal of Marine and Freshwater Research, 20, 2, 175-187. https://doi.org/10.1071/MF9690175

Nudelman, F., Gotliv, B. A., Addadi, L., Weiner, S. (2006): Mollusk shell formation: Mapping the distribution of organic matrix components underlying a single aragonitic tablet in nacre. Journal of Structural Biology, 153, 2, 176-187. https://doi.org/10.1016/j.jsb.2005.09.009

Ompi, M., Lomoindong, F., Mandagi, S. V. (2018): Effects of artificial and natural materials ropes as substrates for settling and metamorphosis of pediveliger pearl oyster, *Pinctada maxima* (Jameson, 1901). Aquaculture, Aquarium, Conservation & Legislation - International Journal of the Bioflux society, 11, 3, 796-803.

Pu, L. Y., Chan, G. C., Chen, F. X., Tan, W., Sui, Z. (2012): Research on the breeding and larval rearing techniques of the pearl oyster (*Pinctada maxima* Jameson). Fisheries Science and Technology Information, 39, 1, 1-5. (in Mandarin).

Rao, G. S., Pattnaik, P., Dash, B. (2009): Growth and biometric relationships of the silver or gold-lip pearl oyster, *Pinctada maxima* (Jameson, 1901) under land-based culture system. Indian Journal of Fisheries, 56, 4, 249-255.

Rose, R. A. (1990): A manual for the artificial propagation of the silverlip or goldlip pearl oyster, *Pinctada maxima* (Jameson) from Western Australia. Fisheries Department, Perth. 41pp.

Rose, R. A., Baker, S. B. (1994): Larval and spat culture of the Western Australian silver- or goldlip pearl oyster, *Pinctada maxima* Jameson (Mollusca: Pteriidae). Aquaculture, 126, 1-2, 35-50. https://doi.org/10.1016/0044-8486(94)90246-1

Saucedo, P. E., Bervera-Leon, H., Monteforte, M., Southgate, P. C., Monsalvo-Spencer, P. (2005): Factors influencing recruitment of hatchery reared pearl oyster (*Pinctada mazatlanica*; Hanley 1856) spat. Journal of Shellfish Research, 24, 1, 215-219. https://doi.org/10.2983/0730-8000(2005)24[215:FIROHR]2.0.CO;2

Scarratt, K., Bracher, P., Bracher, M., Attawi, A., Safar, A., Saeseaw, S., Homkrajae, A., Sturman, N. (2012): Natural pearls from Australian *Pinctada maxima*. Gems & Gemology, 48, 4, 236-261. https://doi.org/10.5741/GEMS.48.4.236

Skewes, T. (1990): Marine resource profiles: Solomon Islands. FFA report 90/61. Honiara, Solomon Islands, South Pacific Forum Fisheries Agency. 52pp.

Southgate, P. C. (2008): Pearl oyster culture. pp. 230-272. In: Southgate, P. C, Lucas, J. S. (eds), The Pearl Oyster 1st Edition. Elsevier BV, Oxford, UK.

Southgate, P. C, Strack, E., Hart, A., Wada, K. T., Monteforte, M., Cariño, M., Langy, S., Lo, C., Acosta-Salmón, H., Wang, A. M. (2008): Exploitation and culture of major commercial species. pp. 303-355. In: Southgate, P. C., Lucas, J. S. (eds), The Pearl Oyster 1st Edition. Elsevier BV, Oxford, UK.

Southgate, P. C., Taylor, J. J., Ito, M. (1998): The effect of egg density on hatch rate of pearl oyster (*Pinctada maxima* and *P. margaritifera*) larvae. Asian Fisheries Science, 10, 3, 265-268. https://doi.org/10.33997/j.afs.1998.10.3.010

Strack, E. (2008): Introduction. pp. 1-35. In: Southgate, P. C, Lucas, J. S. (eds), The Pearl Oyster 1st Edition. Elsevier BV, Oxford, UK.

Strugnell, J. M., Southgate, P. C. (2003): Changes in tissue composition during larval development of the blacklip pearl oyster, *Pinctada margaritifera* (L.). Molluscan Research, 23, 2, 179-183.

Su, Z. X., Huang, L. M., Yan, Y., Li, H. X. (2007): The effect of different substrates on pearl oyster *Pinctada martensii* (Dunker) larvae settlement. Aquaculture, 271, 1-4, 377-383. https://doi.org/10.1016/j.aquaculture.2007.02.039

Tanaka, Y., Kumeta, M. (1981): Successful artificial breeding of silver-lip pearl oyster, *Pinctada maxima* (Jameson). Bulletin of National Research Institute of Aquaculture, 2, 21-28. (in Japanese with English abstract).

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Taylor, A., Mills, D., Wang, T., Ntalamagka, N., Cummins, S. F., Elizur, A. (2018): A sperm spawn-inducing pheromone in the silver lip pearl oyster (*Pinctada maxima*). Marine Biotechnology, 20, 4, 531-541. https://doi.org/10.1007/s10126-018-9824-6

Taylor, J. J., Southgate, P. C., Rose, R. A., Keegan, A. J. (1998a): Effects of larval set density on subsequent growth and survival of the silver-lip pearl oyster *Pinctada maxima* (Jameson). Journal of Shellfish Research, 17, 1, 281-283.

Taylor, J. J., Southgate, P. C., Rose, R. A. (1998b): Assessment of artificial substrates for collection of hatchery-reared silver-lip pearl oyster (*Pinctada maxima*, Jameson) spat. Aquaculture, 162, 3-4, 219-230. https://doi.org/10.1016/S0044-8486(98)00213-0

Taylor, J. J., Southgate, P. C., Rose, R. A. (2004): Effects of salinity on growth and survival of silver-lip pearl oyster, *Pinctada maxima*, spat. Journal of Shellfish Research, 23, 2, 375-377.

Taylor, J. J., Southgate, P. C., Wing, M. S., Rose, R. A. (1997a): The nutritional value of five species of microalgae for spat of the silver-lip pearl oyster, *Pinctada maxima* (Jameson) (Mollusca: Pteriidae). Asian Fisheries Science, 10, 1, 1-8.

Taylor, J. J., Rose, R. A., Southgate, P. C. (1997b): Inducing detachment of silver-lip pearl oyster (*Pinctada maxima*, Jameson) spat from collectors. Aquaculture, 159, 1-2, 11-17. https://doi.org/10.1016/S0044-8486(97)00201-9

Wada, S. (1942): Artificial insemination and development in *Pinctada maxima* (Jameson). Kagaku-Nanyo (Science of South Seas), 4, 3, 26-32.

Wada, S. (1953): Biology of the silver-lip pearl oyster, *Pinctada maxima* (Jameson). I. Artificial fertilization and development. Margarita, 1, 1-15.

Wada, K. T., Tëmkin, I. (2008): Taxonomy and phylogeny. pp. 37-76. In: Southgate, P. C, Lucas, J. S. (eds), The Pearl Oyster 1st Edition. Elsevier BV, Oxford, UK.

Wang, X. X., Chen, Z. Z., Huang, Z. R., Xu, S. N., Chen, T. (2016): Preliminary analysis of *Pinctada maxima* in nature reserves along coastal area in the northern South China Sea. South China Fisheries Science, 12, 2, 110-115. (in Mandarin with English abstract).

Wang, Q. H., Li, J. H., Liang, F. L., Xie, S. H., Du, X. D., Deng, Y. W. (2017): Effects of different substrates on settlement and growth of pearl oyster (*Pinctada maxima*) larvae in hatcheries. Aquacultural Engineering, 77, 15-19. https://doi.org/10.1016/j.aquaeng.2017.02.001

Winanto, T. (2009): The study of growth and development of larvae and spat of pearl oyster *Pinctada maxima* (Jameson) in different rearing environmental conditions. PhD Thesis. (in Indonesian with English abstract).

Xie, S. H., Liang, F. L., Fu, S. (2011): Experiments on artificial breeding of *Pinctada maxima* from Indonesia. Journal of Guangdong Ocean University, 31, 4, 42-45. (in Mandarin with English abstract).

Xie, Y. K., Xu, Z. J. (1980): The early feeding habits of the larvae of *Pinctada maxima*. Acta Zoologica Sinica, 26, 1, 80-85. (in Mandarin with English abstract).

Xu, Z., Li, K. (1980): A preliminary study on the rearing of artificially fertilized larvae of *Pinctada maxima* (Jameson). Journal of Fisheries of China, 4, 3, 295-301. (in Mandarin with English abstract).

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