Aquacult Int
https://doi.org/10.1007/s10499-018-0261-3

Effects of salinity, stocking density, and algal density on growth and survival of Iwagaki oyster *Crassostrea nippona* larvae

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Received: 21 July 2017 / Accepted: 14 March 2018

Abstract To determine the optimal salinity, stocking density, and algal density for hatchery culture of the Iwagaki oyster *Crassostrea nippona* larvae, three experiments with salinities of 14, 18, 22, 26, 30, and 34 practical salinity unit (PSU); stocking densities of 0.5, 1, 2, 4, 8, and 12 larvae ml^{-1}; and algal densities of 10, 20, 40, and 100×10^3 cells ml^{-1} were designed, which included the developmental stages from newly hatched D-larvae to pediveligers. Results showed that larval growth of *C. nippona* was the fastest at a salinity of 26 PSU, and when salinity was adjusted to a level that was lower or higher than this salinity, survival and growth rate of larvae declined ($P < 0.05$), resulting both in a decreased mean shell length and a high mortality. Larval growth decreased significantly with increasing stocking density. Larvae reared at 4 larvae ml^{-1} had the smallest shell length (198.9 μm) and lowest survival rate (7.9%), whereas larvae reared at 0.5 larvae ml^{-1} had the largest shell length (245 μm) and highest survival rate (66.3%) on day 13. And the shell length of larvae reared at 0.5 and 1 larvae ml^{-1} was significantly ($P < 0.05$) larger than the values in other treatments, except those reared at 2 larvae ml^{-1} ($P > 0.05$). When feeding the single-algal diet of *Isochrysis galbana* (clone T-ISO), the shell length of larvae increased markedly as the algal density was increased. Larvae reared at the highest algal density (100×10^3 cells ml^{-1}) had the largest mean shell length; however, under the conditions of our experiment, there was no significant difference ($P > 0.05$) in growth and survival rates between the treatments at algal densities of 40×10^3 and 100×10^3 cells ml^{-1}. For a large-scale culture, based on the results of this study, a salinity of 26 PSU, stocking density of 0.5–1 larvae ml^{-1}, and algal density of 40×10^3 cells ml^{-1} are recommended for an early development of *C. nippona*.

Keywords *Crassostrea nippona* · Larvae · Salinity · Stocking density · Algal density · Growth · Survival

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Published online: 23 March 2018

Introduction

The Iwagaki oyster *Crassostrea nippona*, which is large and oval shelled compared to the Pacific oyster *Crassostrea gigas* (Li 2007), occurs naturally along the coast of East Asia, Japan, and Korea (Itoh et al. 2004; Yoon et al. 2008). It inhabits stones and reefs in the low tidal positions and the intertidal zones and is a commercially important fisheries resource (Tanaka et al. 2010). *C. nippona* is highly valued and the commercial price is estimated at fivefold that of the Pacific oyster in Japan, as it is edible during the summer when the other oyster species are unavailable (Itoh et al. 2004). Traditionally, the culture of *C. nippona* depends mainly on natural seed collected from wild stocks (Fujiwara 1998). Since this method of seed collection is labor intensive, often unreliable, and limited to a short season, there has been an increasing interest in hatchery production of *C. nippona* seed (Fujiwara 1995); hence, detailed information on larval culture of *C. nippona* is crucial for initiating its aquaculture.

Salinity is considered to be one of the most important environmental factors that affects biological activities, including respiration (Stickle and Sabourin 1979), energy acquisition (Gardner and Thompson 2001), development of embryos (O'Connor and Lawler 2004), and growth and survival of larvae (Xu et al. 2011), which has been described as a master factor for many marine organisms (Kinne 1964). In oceans or industrial aquaculture operations, when salinity remains constant, the stocking density can be the key factor that influences growth of shellfish. Higher densities in culture conditions may result in reduced growth and high mortality because of competition for space and food and accumulation of metabolic wastes; while unnecessarily low densities may be costly and fail to meet the demand for mass farming (Marshall et al. 2014; Lü et al. 2017). In addition to the stocking density, algal density can also affect feeding efficiency and growth of larval bivalves (Gallager 1988). In a low algal concentrations, the low encounter rates between larvae and algal cells causes reduced feeding rate resulting in retarded growth (Tang et al. 2006). High concentrations, in contrast, can inhibit ingestion by clogging the feeding apparatus and increasing the rejection of algal particles (Gallager 1988; Sprung 1984b). To date, the effects of salinity, stocking density, and algal density on larval growth and survival have been evaluated for numerous bivalve species, including pearl oysters (Doroudi and Southgate 2000; Deng et al. 2013; Taylor et al. 2004), clams (Yan et al. 2006), mussels (Lagos et al. 2015), and scallops (Rupp and Parsons 2004; Rupp et al. 2004). An adequate knowledge of these factors on growth and survival of *C. nippona* larvae will assist in improving methods to promote its seed production in hatcheries. However, biological studies on *C. nippona* adults have been limited to culture methods, chromosomes, seasonal variations in reproductive activity, and biochemical composition (Itoh et al. 2004; Okumura et al. 2005; Adachi et al. 2014). Information pertaining to effects of environmental factors on *C. nippona* is still limited.

The present study evaluated the effects of salinity, stocking density, and algal density on growth and survival of *C. nippona* larvae aiming to attribute for the development of hatchery techniques for seed supplies of this species.

Materials and methods

Adult conditioning and larval rearing

Three experiments were designed to investigate the effects of salinity, stocking density, and algal density on larval growth and survival of *C. nippona* from 31 July to 12 August, 2016. The experiments were carried out at the Haiyi Aquaculture Cooperation, Yantai, China. Brood

stock (shell height, 12.8 ± 2.4 cm; shell length, 7.6 ± 1.3 cm) were collected from Niigata Prefecture, Japan, in 2014. The animals were transported and then cultured in Rushan Bay (36° 43′–37° 36′ N and 121° 28′–121° 39′ E), Shandong province. The parental oysters were reared in the Haiyi hatchery and fed an algal diet of *Isochrysis galbana* and *Platymonas subcordigoramis* at daily rations of 3–4% (dry algal weight/dry oyster meat weight). Mature individuals ($n = 20$) were induced to spawn by air drying in the dark for 4 to 6 h and were then thermally stimulated (water temperature raised by 2–3 °C) with flowing seawater for 1 h. D-shaped larvae at 48-h post-fertilization were collected and stocked into the experimental tank containing 10 m^3 sand-filtered seawater. Water temperature and salinity were 26.7 °C and 32.5 practical salinity unit (PSU), respectively.

Effect of salinity on growth and survival of larvae

The experiment was conducted from 31 July to 12 August, 2016. Six salinities were designed: 14, 18, 22, 26, 30, and 34 PSU. D-shaped larvae were collected and then transferred into 20-l cylindrical fiberglass rearing tanks, containing 15 l of 0.45-um filtered and UV-treated seawater, at the requisite salinity. Each treatment group included three replicates. Desired salinities greater than 30 PSU were prepared by adding sea salt to ambient seawater (32 PSU); salinities less than 30 PSU were prepared by adding filtered fresh water (filtered through a 50-μm mesh sieve) to ambient seawater. The initial salinity was raised or lowered at a rate of 2 PSU/h until the desired salinity was obtained. The average initial shell length of D-larvae was 80.28 ± 4.30 μm ($n = 50$). During the rearing period, larvae cultures were slightly aerated using sterile glass tubes to provide oxygen and to minimize organic matter deposits, which might encourage bacterial concentrations. Temperature was maintained at 26 ± 1 °C, and the initial larval density was kept at 2 larvae ml^{-1}. Larvae were fed *I. galbana* (clone T-ISO) four times a day, and the concentration of 15×10^3 cells ml^{-1} was maintained until the end of test. Before the algae were added to each containers, an amount of water equal to the volume of algal culture added was removed to maintain the correct water volume. Every second day morning, 100% of the seawater was renewed; each rearing tank was fully drained, cleaned with brush, and rinsed before restocking the larvae. During the water change, the larvae were collected onto a 55-μm mesh screen and transferred into a 1-l measuring cylinder. After gently mixing, six 0.5-ml subsamples were then removed, combined to form a 3.0-ml sample (for each replicate rearing tank), and the number of larvae enumerated to determine survival rate. For each sample, lengths of 30 randomly chosen larvae were measured using a microscope with a precalibrated micrometer.

Effect of stocking density on growth and survival of larvae

The experiment was carried out from 31 July to 12 August, 2016. Six stocking densities were used: 0.5, 1, 2, 4, 8, and 12 larvae ml^{-1}. Larvae were kept in the 20-l cylindrical fiberglass rearing tanks, containing 15 l of 0.45-um filtered and UV-treated seawater, at the requisite density. Each treatment was conducted with three replicates. The rearing temperature was maintained at 26 ± 1 °C and salinity at 32 PSU with continuous aeration to supply oxygen. The average initial shell length of D-larvae was 90.63 ± 4.84 μm ($n = 50$). The larvae were fed *I. galbana* four times a day, and the concentrations of *I. galbana* (clone T-ISO) proportionately increased with stocking density to supply larvae in each treatment with the same amounts of alga (Table 1). Seawater of each rearing container was fully changed every other day, and, as previously described, the larvae were collected onto 55-μm mesh screens, transferred into a 1-l

Table 1 Daily algal ration for *C. nippona* larvae reared under different stocking densities during the experimental period

Daily algal ratio ($\times 10^3$ cells ml^{-1})	Stocking density (larvae ml^{-1})					
	0.5	1	2	4	8	12
Days 3–4	1.5	3.0	6.0	12.0	24.0	36.0
Days 5–7	2.5	5.0	10.0	20.0	40.0	60.0
Days 8–13	4.0	8.0	16.0	32.0	64.0	96.0

measuring cylinder, and six 0.5-ml subsamples taken for later determination of shell length (from random 30 larvae) and survival rate. By adjusting the rearing water volume after the water changes (based on larval survival rate), the larvae were maintained at the desired density (0.5, 1, 2, 4, 8, and 12 larvae ml^{-1}) throughout the experiment.

Effect of algal density on growth and survival of larvae

The experiment was carried out from 31 July to 11 August, 2016. Four experimental algal densities of 10, 20, 40, and 100×10^3 cells ml^{-1} were set up to examine the effect of daily ration on growth and survival of *C. nippona* larvae. The rearing temperature was maintained at 26 ± 1 °C, salinity at 32 PSU, and the initial larval density at 2 larvae ml^{-1}. The average initial shell length of D-larvae was 80.42 ± 4.47 μm ($n = 50$). A single algae species *I. galbana* (clone T-ISO) was tested in the experiment, and the algae were harvested at the exponential phase for feeding. In order to control the final concentration of microalgae in the experimental tanks, the feeding quantity was determined through measuring the original concentration of different microalgae diets exactly (by using a hemocytometer before feeding the larvae). Other experimental procedures were as described previously.

Statistical analysis

One-way ANOVA was used to test the effects of salinity, stocking density, and algal density on growth and survival of *C. nippona* larvae. Differences between treatment means were compared using the least significant difference (LSD) test and Duncan's multiple range test in the SPSS 18.0 software. Significance levels for all analyses were set at $P < 0.05$. Data are presented as means ± standard deviation.

Results

Larval growth and survival at different salinities

There was no significant ($P > 0.05$) difference of mean shell length at different salinities on day 1 and 3, but a statistical difference began to appear from day 5 ($P < 0.05$) (Fig. 1a). On day 13, larvae reared at 26 PSU achieved the highest mean shell length

of 255 μm, which was significantly ($P < 0.05$) greater than in all the other salinity treatments. There were no significant ($P > 0.05$) differences in the shell length of 14, 18, and 34 PSU, but were significantly ($P < 0.05$) lower than those at salinity of 22, 26, and 30 PSU.

At a salinity of 34 PSU, the highest salinity tested, larval survival was substantially lower than at all other salinity treatments, and all had died by day 11 of the experiment; therefore, survival data in this treatment was not included in the statistical analyses (Fig. 1b). Larvae at 26 PSU always showed maximum survival throughout the experiment. On day 13, the lowest survival was recorded at 14 (4%) and 18 PSU (6%), which were not

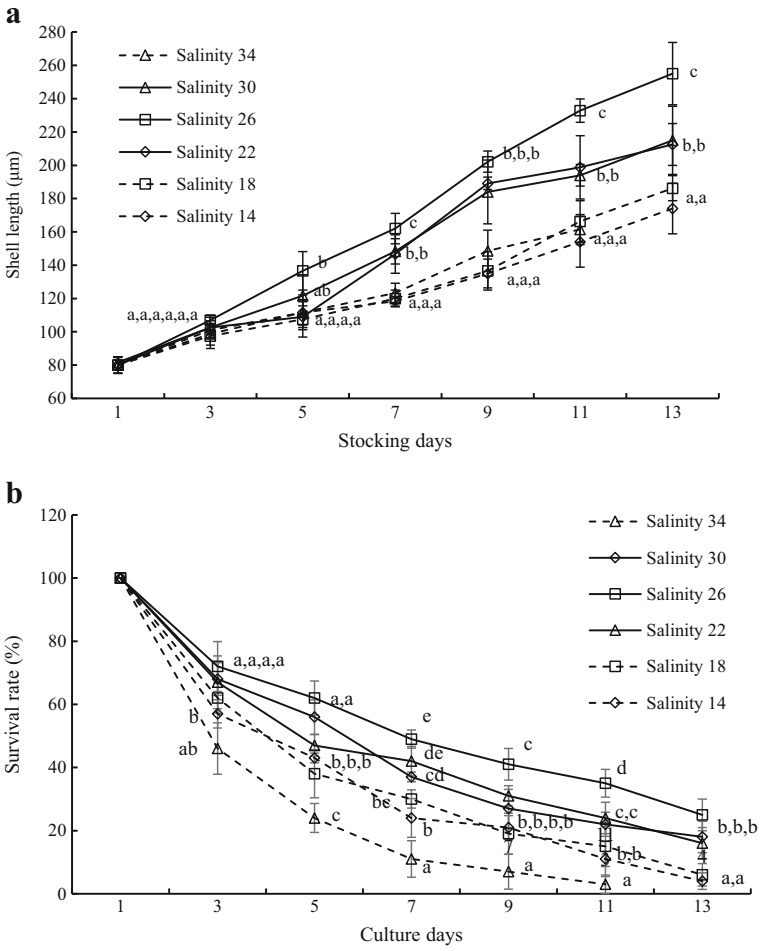

Fig. 1 **a** Mean shell length of *Crassostrea nippona* larvae reared under different salinities using a fixed stocking density of 2 larvae ml^{-1} over a 13-day period. Means within age followed by different letters were different ($P < 0.05$). **b** Mean survival rates of *C. nippona* larvae reared under different salinities using a fixed stocking density of 2 larvae ml^{-1} over a 13-day period. Means within age followed by different letters were different ($P < 0.05$)

significantly ($P > 0.05$) different, but were significantly ($P < 0.05$) lower than those at salinities of 22, 26, and 30 PSU.

Larval growth and survival at different densities

Over the sampling period from day 1 to 13, larvae reared at the highest density (12 larvae ml^{-1}) had the smallest shell length, while those at the lowest density (0.5 larvae ml^{-1}) had the highest (Fig. 2a). On days 1 and 3, the difference of mean growth rates at different densities was not significant ($P > 0.05$), while on day 5, a significant difference began to appear at different densities ($P < 0.05$), and mean shell length at the highest density showed a significant difference to other treatments on day 7 ($P < 0.05$). Shell length of larvae reared at 0.5 and 1

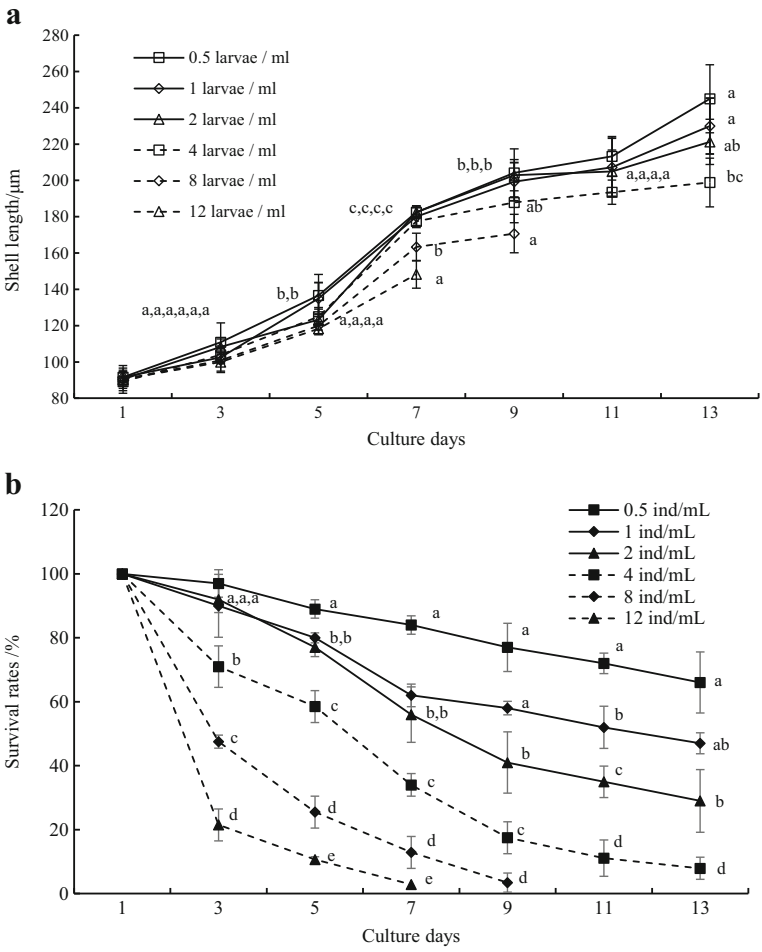

Fig. 2 **a** Mean shell length of *Crassostrea nippona* larvae reared under different stocking densities over a 13-day period. Means within age followed by different letters were different ($P < 0.05$). **b** Mean survival rates of *C. nippona* larvae reared under different stocking densities over a 13-day period. Means within age followed by different letters were different ($P < 0.05$)

larvae $ml^{-1}$was significantly ($P < 0.05$) larger than the values in other treatments, except those reared at 2 larvae ml^{-1}($P > 0.05$) on day 13.

From day 3, the survival rates of larvae recorded at low density treatments (0.5, 1, and 2 larvae ml^{-1}) were significantly ($P < 0.05$) greater than the treatments at high density treatment (4, 8, and 12 larvae ml^{-1}) (Fig. 2b). Larvae reared at 12 larvae ml^{-1} had died by day 9 of the experiment, and those reared at 8 larvae ml^{-1} had died by day 11; therefore, survival data in these treatments were not included in the statistical analyses. On day 13, the highest survival of 66.3% was observed at 0.5 larvae ml^{-1}, which is significantly ($P < 0.05$) different from the values in other stocking densities, except at 1 larvae ml^{-1} ($P > 0.05$). The lowest survival of 7.9% was observed at 4 larvae ml^{-1}, which has a significant ($P < 0.05$) difference with other larvae densities.

Larval growth and survival at different algal densities

Shell length of larvae ranged from 192.7 μm (10×10^3 cells ml^{-1}) to 253.6 μm (100×10^3 cells ml^{-1}) at the end of day 12 (Fig. 3a). On day 4, mean shell length of larvae fed at 100×10^3 cells ml^{-1} was significantly ($P < 0.05$) higher than that of larvae fed at 10×10^3 cells ml^{-1}. The same trend was observed on day 8 and day 12. However, larvae fed at 40×10^3 cells ml^{-1} were slightly smaller in shell length than the ones at 100×10^3 cells ml^{-1}, there was no significant ($P > 0.05$) difference throughout the experimental period.

Significant differences in larval survival were detected among the four different algal density treatments. Survival rate of larvae at 10×10^3 (17.4%) and 20×10^3 (27.3%) cells ml^{-1} was significantly ($P < 0.05$) lower than those of fed at 40×10^3 (54.6%) and 100×10^3 (43.1%) cells ml^{-1} (Fig. 3b). There was no significant ($P < 0.05$) difference in the survival between algal densities of 40×10^3 and 100×10^3 cells ml^{-1}, but were significantly ($P > 0.05$) higher than fed at 10×10^3 and 20×10^3 cells ml^{-1}on day 12.

Discussion

Results of the present study showed that the growth and survival of larval *C. nippona* were significantly affected by salinity. Our findings agree with Huo et al. (2014), who studied the effect of salinity on larval growth, survival, and development in the oyster *Crassostrea hongkongensis*. Previous studies have demonstrated that the influence of salinity on early life stages of marine bivalves is species specific (Yao et al. 2015; Nell and Holliday 1988; Dos Santos and Nascimento 1985). For *C. nippona*, the highest shell length and survival rate occurred at 26 PSU, indicating that this is the optimum salinity to rear *C. nippona* larvae. When salinity was adjusted to a level that was lower or higher than this salinity, growth and survival of larvae were significantly affected, resulting both in a decreased mean shell length and in higher mortalities. Similarly, the development and growth of Kumamoto oyster *Crassostrea sikamea* larvae were significantly lower at 25 ppt than at lower salinities (Xu et al. 2011). For the Pacific oyster *Crassostrea gigas* larvae, salinities higher than 27 PSU and lower than 19 PSU had significant negative effects on growth rate (Nell and Holliday 1988). The number of normal D-shaped larvae and shell length of mangrove oyster, *Crassostrea gasar* larvae reared at 28 PSU were significantly higher than those of larvae reared at higher or lower salinities (Legat et al. 2017).

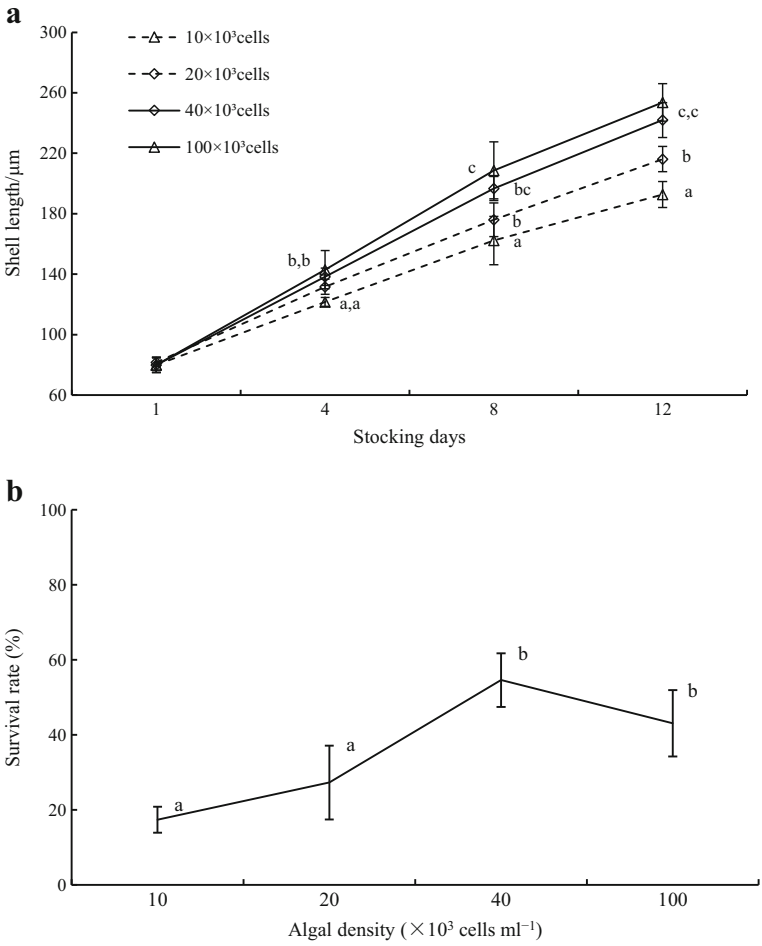

Fig. 3 **a** Mean shell length of *Crassostrea nippona* larvae reared under different algal densities using a fixed stocking density of 2 larvae ml^{-1} over a 12-day period. Means within age followed by different letters were different ($P < 0.05$). **b** Mean survival rates of *C. nippona* larvae reared under different algal densities using a fixed stocking density of 2 larvae ml^{-1} on day 12. Means with same letter are not significantly different ($P > 0.05$)

At the lowest salinity (14 PSU) and highest salinity (34 PSU), the lowest survival rate and the minimum shell length were observed on day 13. The mechanism for the effect of salinity is not entirely clear. However, previous studies showed that reversible changes of protein and RNA synthesis, alteration of the pattern of multiple molecular forms of different enzymes, and the regulation of ionic content and cell volume were shown to be of importance for the abovementioned mechanisms (Berger and Kharazova 1997). Like other marine molluscs, *C. nippona* is an osmotic conformer. Larvae close their shells at extreme salinities (14 and 34 PSU in the present study), and additional energy is required for maintenance of water and mineral balance in body fluids and cells (Berger and Kharazova 1997). Therefore, low energy utilization efficiency of the body and changes in rates of feeding, assimilation, and respiration could be the main reason for retarded growth and increased mortality in extreme salinity conditions (Berger and Sergievskii 1986). Moreover, the causes of larval death in high or low

salinities might be related to the concomitant changes in absorption and saturation coefficients of dissolved gases, particularly ambient dissolved oxygen, which is severely reduced at very high salinities (Kinne 1964; Li et al. 2011).

Stocking density of marine bivalve larvae is also an important variable to be considered in hatchery conditions. In the present study, there were significant differences in larval growth among the density treatments. The final shell length of larvae decreased with increasing stocking density. The retarded growth of shell length was noted in the larvae stocked at densities greater than 4 larvae ml^{-1}. This result indicated that a density of 0.5–4 larvae ml^{-1} was optimal for growth of the *C. nippona* larvae raised in the hatchery. However, with larval survival rate taken into consideration, the optimal initial stocking density for larval rearing was 0.5–1 larvae ml^{-1}, this being at the lower end of the suitable stocking densities of 1–20 larvae ml^{-1} generalized for larval rearing of bivalves in aquaculture (Helm and Bourne 2004).

In the present study, the mean shell length of larvae stocked at low densities (0.5, 1 larvae ml^{-1}) was significantly greater than those of larvae stocked at a density of 4, 8, and 12 larvae ml^{-1}. Previous studies have examined the negative effects of high densities on growth of many marine bivalve species. For example, a low growth rate was observed when basket cockle, *Clinocardium nuttallii* larvae were reared at high densities (Liu et al. 2010). The mean shell length of pearl oyster *Pinctada maxima* larvae stocked at densities of 1.0, 2.0, and 4.0 larvae ml^{-1} was significantly greater than those of larvae stocked at a density of 8.0 larvae ml^{-1} (Deng et al. 2013). For the clam *Meretrix meretrix*, larvae reared at 5 larvae ml^{-1} had the largest shell length, while those at 60 larvae ml^{-1} had the smallest shell length (Liu et al. 2006). The relatively small shell length at high densities can be explained in part by competition for food and physical contact between individuals (Raghavan and Gopinathan 2008; Liu et al. 2010). However, in the present study, algal concentrations were adjusted according to larval densities to ensure larvae in each treatment received an equal diet. Therefore, food should not be a limiting factor in this study. The other explanation for reduced growth at high density is due to an intraspecific competition for space. Pelagic larvae need space to swim and feed, and increased rearing density increases the possibility of collision among individuals (Avila et al. 1997). Collision causes rapid retraction of the velum, then closure of the valves, resulting in inhibition of feeding activity and increased energy expenditure (Cragg 1980).

In addition, under the conditions of our experiment, there was no significant difference in survival rates between the treatments at lower densities of 0.5 and 1 larvae ml^{-1}, but were significantly greater than those at higher densities of 4, 8, and 12 larvae ml^{-1}. Results demonstrated that when larvae were reared at optimal densities, the survival rate of larvae was independent of stocking density. Similar results also occurred in black-lip pearl oyster *Pinctada margaritifera* and the catarina scallop *Argopecten ventricosus* (Doroudi and Southgate 2000; Ibarra et al. 1997). As it has been demonstrated in other studies, the density influence on larval survival is more complex than on growth. Decreased survival rates at high densities are possibly due to bacterial contamination and oxygen depletion (Marshall et al. 2014). With increasing stocking density, more metabolic wastes accumulated in the water, resulting in high ammonia content and low oxygen level, which may be detrimental to larval growth and survival (Deng et al. 2013).

Algal density is another significant variable which should be considered in a hatchery. Optimal larval growth of *C. nippona* in the present study was observed in the treatments with the highest algal densities tested (40×10^3 or 100×10^3 cells ml^{-1}, depending on the experiment), indicating that an increase in algal density up to these levels with the respective algal

diets will not negatively affect larval growth. However, with the algal density increasing from 40 to 100 × 10^3 cells ml^{-1}, the survival rate was decreased unexpectedly. Similarly, an increase in the algal densities up to 25 and 50 × 10^3 TISO cells ml^{-1} did not significantly improve larval growth of basket cockle, *C. nuttallii* larvae, while the mean survival rate of larvae reared at 25 × 10^3 cells ml^{-1} was significantly higher than reared at 50 × 10^3 cells ml^{-1} (Liu et al. 2010). The optimal algal density of marine mollusc species should not only provide high growth rates of larvae but also avoid the side effects on water quality. When food concentration exceeds a certain threshold, the pseudo-feces production and other inhibitory effects of digestion physiology can lead to larval growth decrease as algal density increases (Sprung 1984a, b). In addition, the survival rate and shell length of larvae reared at 10 × 10^3 cells ml^{-1} were significantly lower than any other treatment. The factor likely explaining why larval growth depends largely on algal density is the rate of encounter between larvae and algae. Low food availability causes the larvae to expend more energy searching for food rather than ingesting. This can lead to a depletion of endogenous biochemical reserves (Holland and Spencer 1973) and ultimately reduced growth (Tang et al. 2006).

In summary, the effects of salinity, stocking density, and algal density on the growth and survival of *C. nippona* larvae have been described for the first time in this study. Based on our study, a salinity of 26 PSU, a density of 0.5–1 larvae ml^{-1}, and the algal density of 40 × 10^3 cells ml^{-1} provide optimal conditions for the growth and survival of *C. nippona* larvae in the hatchery. Salinity, stocking density, and algal density are controllable in hatcheries, and these results can be applied to improve artificial seed production of *C. nippona*.

Funding information This study was supported by the grants from the Shandong Province (2016ZDJS06A06), Shandong Seed Project, and Qingdao National Laboratory for Marine Science and Technology (2015ASKJ02).

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