Factors regulating population dynamics of the amphipod *Amphithoe valida* in a eutrophic subtropical coastal lagoon

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Abstract

Year-round investigations were carried out to address the population dynamics of amphipod *Amphithoe valida* and its potential regulating factors in the Yundang Lagoon (a eutrophic subtropical coastal lagoon in Xiamen City, China) from October 2007 to October 2008. The results show that *A. valida* population was largely composed of juveniles and reached a peak abundance (12.02×10^5 ind./m^2) in March, but sharply shrunk in July. The monthly variation pattern of *A. valida* seemed to follow that of *Ulva lactuca* which is the main food resource for *A. valida*, indicating a strong influence of food availability on *A. valida* population dynamics. Life cycle studies in laboratory indicate that *A. valida* adopted an r-selected life strategy, e.g., rapid growth rate (0.216–0.302 mm/d), consecutive breeding (4–10 times), short reproductive rhythm (9–17 d) and huge fecundity (24–192 eggs or 6–94 juveniles per brood), which contributed to the fast population growth of *A. valida* from January to March. Although temperature may also be a significant cause, *A. valida* could grow quickly and show normal reproductive traits (i.e., the timing of sexual differentiation or maturity, the reproductive rhythm, the number of broods all through its lifespan and offspring production) in temperature between 15–30℃. Therefore, the temperature variation in the lagoon water should not account for the sharp variation of *A. valida* population by affecting the survival, growth and reproduction of the amphipod. However, negative correlation between water temperature and *U. lactuca* biomass in the lagoon suggested that temperature could have indirectly affected the population dynamics of *A. valida* by affecting its food availability. The authors conclude that, in the Yundang Lagoon, the population dynamics of *A. valida* was mainly controlled by the food availability rather than water temperature.

Keywords: *Amphithoe valida*, population dynamics, food availability, *Ulva lactuca*, the Yundang Lagoon


1 Introduction

Macraoalgal blooms are increasingly common in coastal waters subjected to excessive anthropogenic inputs of nutrients (Worm and Lotze, 2006; Kraufvelin et al., 2006; Valieia et al., 1997; Balducci et al., 2001). Dense canopies of macroalgae often deteriorate the environmental quality within the canopies (Nedergaard et al., 2002; Krause-Jensen et al., 1996) and reduce biodiversity (Worm and Lotze, 2006) after degradation of blooming macroalgae. It was reported that macroalgal biomass was mainly controlled by bottom-up processes such as nutrient loading (Worm and Lotze, 2006; Valieia et al., 1997; Hauxwell et al., 1998). However, grazing pressure by small invertebrates such as amphipods should not be overlooked. Numerous literatures have shown that some species of amphipods in macroalgal-based community chose macroalgae as their diets. Amphipods are characterized by their high turnover rate, growth rate (Fredette and Diaz, 1986; Drake and Arias, 1995), and “r-selection” reproductive strategies (Neuparth et al., 2001; Aranid et al., 2007; Subida et al., 2005). They usually occur in high density (Duffy, 1990; Duffy and Hay, 2000; Balducci et al., 2001) and have quite a high secondary production (Duffy, 1990; Duffy and Hay, 2000; Balducci et al., 2001). As a result, the top-down control by grazing amphipods may significantly reduce the apparent macroalgal production (Geerz Hansen et al., 1993; Balducci et al., 2001).

The grazing pressure of an amphipod on macroalgae usually depends on its population size, hence the population dynamics of the amphipod may partially account for the seasonal variation of macroalgal biomass and production in the habitat. Temperature is widely believed to be one of the primary factors influencing the population dynamics of amphipods, as it affects amphipod’s survival, growth and turnover rate (Neuparth et al., 2001), as well as its reproductive characteristics, e.g., the number of egg or juvenile produced and the duration of embryonic development, and hence its population recruitment (Maranhão and Marques, 2003). Several field investigations also show that amphipod biomass is closely related to water temperature (Dias and Sprung, 2003; Donn and Croker, 1996; Drake and Arias, 1995). Biotic factors, such as food availability and richness (Costa and Costa, 1999; Fredette and Diaz, 1986), predation pressure (Tegner and Dayton, 1987), and other physical-chemical factors, for example salinity and dissolved oxygen (Subida et al.,...
The amphipods in the genus Amphithoe are common benthiic species in macroalgal-based communities, which are frequently found in muddy or rocky substrate of estuaries, tidal zones and coastal lagoons (Duffy and Hay, 2000; Pardal et al., 2000). They have been considered as grazers on seaweeds (Cruz-Rivera and Hay, 2000; Cruz-Rivera and Hay, 2001) or as epibenthic animals on seagrass (Valentine and Duffy, 2006; Duffy and Hay, 2001). In the Yundang Lagoon, a eutrophic coastal saline lagoon in Xiamen City, China, macroalgal blooms predominated by Ulua lactea usually develop in winter and spring, and Amphithoe valida has been identified as the primary amphipod grazer on macroalgae (Zheng et al., 2008, 2011a, b). Although this species of amphipod usually dominates in the seaweed-bed macrobenthos community, its population size has been found fluctuating dramatically throughout the year. Why such fluctuation? Is it controlled by the temperature of the lagoon water or by other factors? In addition to the existing hypothesis mentioned above, the life cycle of A. valida seems to be another key clue for us to answer the question. Pardal et al. (2000) studied the population dynamics and life history of A. valida in the Mondego Estuary, Portugal, and found that this species of amphipod had long embryonic development time from 30 d in spring to 60 d in autumn and produced a small number of eggs (6–24 eggs per breed). Another study by Borowsky (1983) reveals that the reproductive cycles of this species were 10–18 d. Although the results of the above studies may partially explain the population dynamic of A. valida in the wild, they still cannot fully explain the drastic variation of A. valida population we observed in the Yundang Lagoon.

Aiming to address the population dynamics of amphipod A. valida and its potential regulating factors (both external and internal causes) in the Yundang Lagoon, we carried out year-round investigations as well as laboratory experiments from October 2007 to October 2008. Firstly, we examined the relationships of the reported potential factors (i.e., water temperature, salinity, dissolved oxygen and food availability) with A. valida population dynamics based on field investigations. Then, we conducted the laboratory experiments on the life cycle of A. valida to test whether temperature may or may not control its population dynamics by directly affecting its growth, survival and reproduction.

2 Materials and methods

2.1 Field investigation

2.1.1 Sampling

The sampling site (ca. 0.5 m depth) was located in the inner part of the Yundang Lagoon, where Ulua lactea predominated the macroalgal community (Fig. 1). Amphithoe valida and seaweeds were sampled monthly from October 2007 to October 2008. Both amphipods and macroalgae were collected by a box sampler with 0.04 m² effective sampling area and then kept in plastic bags. Environmental variables, including temperature, salinity and dissolved oxygen, were measured in situ using a portable water quality monitor YSI 6600.

2.1.2 Sample treatment and analysis

In the laboratory, all individuals of A. valida were isolated from seaweeds by rinsing with seawater. The amphipods were weighed with an electronic balance (Sartorius BSA124S) and immediately preserved in 5% formalin solution. The wet weights of separated seaweeds were measured. A. valida abundance and sexual structure were determined under a stereoscopic microscope. The sexuality of amphipods was identified following Pardal et al. (2000). Ovigerous amphipods with different size were picked out to examine the number of eggs in their marsupium. Since intramarsupial loss of eggs may occur in different developmental stages (Cunha et al., 2005; Subida et al., 2005), females with eggs in Stage I and II were chosen. Egg developmental stage was determined according to Pardal et al. (2000). Body length of the ovigerous female was measured by a 3-Q Win image analysis system.

2.2 Life cycle experiments

2.2.1 Collection and acclimatization of Amphithoe valida

Live individuals of A. valida were picked out from filed samples, as described in Section 2.1, and reared in 15 L aquarium in the illumination incubators and acclimated in the experimental conditions for 10 d. Four experimental temperatures (15°C, 20°C, 25°C and 30°C) and one salinity (25±1), which were relevant to the field, were installed. Light regime was maintained under a 12 h light: 12 h darkness cycle with mean light intensity of (3 000±500) lx. Incubation seawater was aerated continuously and renewed every three days. Fresh U. lactea was served as diet for the amphipods.

2.2.2 Determination of growth and mortality

After 10 d acclimatization, 20 pairs of adult amphipods
were picked out and cultivated in 0.3 L of glass containers with 0.2 L of 0.45 μm filtered seawater to obtain enough newborn juveniles. After hatching, juveniles from the different ovigerous females were pooled together and were then assigned randomly to experimental devices (Fig. 2). The device comprises a 2.5 L glass square container (BSC) and nine transparent cylindrical plastic containers (TCPCs) in BSC. The TCPC’s bottom was covered by 0.1 mm sieve and four trestles were fixed on TCPC’s lateral. Thus, it assured that water in this device can flow into and out of TCPC freely through sieve. Furthermore, it also reduced the disturbance to A. valida when water was renewed. There were ten juveniles in each TCPC, thus a total of 90 individuals were used in each treatment. Experimental conditions were the same as those for A. valida acclimatization.

Fig.2. Experimental device for the incubation of Amphithoe valida. Dashed line indicates seawater level in the incubator. A and B are the top view and the lateral view of the device, respectively. 1 BSC, 2 TCPC, 3 0.1 mm sieve and 4 trestle.

Specimens of two TCPCs were sampled periodically (6 d) and transferred to six pore plates containing seawater. The amphipods were photographed under the stereoscope to determine body length, after which the amphipods were put back to the TCPCs. The number of dead individuals was recorded every day to determine the mortality. Measurements of A. valida body length were terminated when the total number of amphipod in the devices was less than nine individuals. The experiment was ended when the last amphipod died. The time from hatch to the day when the last amphipod died was defined as Life expectancy.

2.2.3 Determination of reproduction parameters

To obtain the time of sexual differentiation and first brooding of A. valida, the above-mentioned photos for body size were further analyzed for the determination of sex and identifying whether females were ovigerous or not. In ovigerous female individuals, a marked shadow could be observed on the abdomen.

To determine the reproductive rhythm and fecundity, after sexual differentiation, six pairs of mature A. valida in each temperature treatment were picked out and transferred to 0.3 L glass containers with 0.2 L of filtered seawater. The incubation seawater was renewed every day. The molting date of each female amphipod was recorded to obtain the reproductive rhythm, and the juveniles released from each female were counted to evaluate the fecundity. The experiment ended when all females died.

2.3 Data analysis

Pearson correlation analysis was employed to analyze the relationships of A. valida abundance with U. lactea biomass and the measured environmental factors. Linear regression analysis was conducted between U. lactea biomass in month 1 and A. valida abundance in month 1+1. Linear regression analysis was done between U. lactea biomass and water temperature.

The growth of amphipods followed a sigmoid pattern, though it was approximately linear during the early stages (see result section). Therefore, linear growth model was suitable for A. valida using those data in the linear section of the growth curves. Growth rates were derived from the slopes of the regression functions and compared using the analysis of covariance (ANCOVA). Mortality rates among different temperatures were compared using ANCOVA. The sex ratio of A. valida in the earlier growth stages was compared by the independent-sample t-tests.

One-way ANOVA was used to the data of reproductive traits among temperature groups, including the age and body length at first reproduction, the reproductive rhythm and the number of brood all through life span.

Juvenile number per brood among temperature treatments was also analyzed by ANCOVA, using female body length as covariate. If equal variances were assumed, Bonferroni test was selected for multiple comparisons of ANOVA; if not, Games-Howell test was employed. When P <0.05, the difference was defined as significant.

The relationships of fecundity and body length in females were analyzed by log-transformed data, determined by the regression equation (Yu et al., 2002; Jeong et al., 2007):

\[ \ln y = a + b \ln x, \]

where \( y \) is number of eggs or of juveniles released per brood, \( x \) stands for body length of ovigerous females, and \( a \) and \( b \) represent the intercept and the slope of the equation, respectively.

3 Results

3.1 Field investigation

3.1.1 Abiotic factors

The seasonal variations of temperature, salinity and disso-
lved oxygen of lagoon water are given in Fig. 3. The macroalgae appeared in the lagoon when temperature was between 12.9°C (February) and 25°C (June), and disappeared when the temperature exceeded 25°C (Fig. 3a). Salinity varied between 24.8 (July) and 30.0 (January) (Fig. 2b), and dissolved oxygen varied between 4.1 mg/L (May) and 7.8 mg/L (July) (Fig. 3c).

3.1.2 U. lactuca biomass and A. valida population dynamics

U. lactuca biomass increased progressively from December 2007, peaked in February 2008, then dramatically shrunk and disappeared in June when temperature was above 25°C. Regression analysis shows a negative relationship between U. lactuca biomass and water temperature.

A. valida could be scarcely found until January 2008. The population started to increase in February and sharply peaked in March with the abundance up to $12.02 \times 10^5$ ind./m$^2$ (Fig. 4). A. valida decreased rapidly from April to June and disappeared from July to October.

A. valida population was mainly composed of juveniles, with a percentage of immature individuals ranging from 41.9% (February) to 78.4% (March). Females were found in a higher proportion compared with males from February to April when A. valida was the most abundant in a year (Table 1).

Pearson correlation analysis shows that the fluctuation of A. valida population was neither significantly correlated to that of U. lactuca biomass, nor to that of temperature, salinity and dissolved oxygen. However, the seasonal pattern of A. valida was much similar to that of U. lactuca, but a month lag behind the later (Fig. 4a). This has been further confirmed by the correlation analysis ($r=0.89, p<0.001$).

In spite of the weak negative correlation between A. valida abundance and water temperature (Fig. 4c) in the lagoon, the effect of water temperature on the amphipod population dyna-

### Table 1. Sex ratio of Ampithoe valida population in the Yundang Lagoon

<table>
<thead>
<tr>
<th>Month</th>
<th>Sex ratios (F/M)</th>
<th>Proportion/ %</th>
<th>Abundance/ ind. m$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ju</td>
<td>M</td>
<td>NOF</td>
</tr>
<tr>
<td>January</td>
<td>1.0</td>
<td>50.0</td>
<td>25.0</td>
</tr>
<tr>
<td>February</td>
<td>3.5</td>
<td>41.9</td>
<td>12.9</td>
</tr>
<tr>
<td>March</td>
<td>2.5</td>
<td>78.4</td>
<td>6.2</td>
</tr>
<tr>
<td>April</td>
<td>2.0</td>
<td>55.0</td>
<td>14.2</td>
</tr>
<tr>
<td>May</td>
<td>1.5</td>
<td>51.6</td>
<td>19.4</td>
</tr>
</tbody>
</table>

Notes: Ju represents Juvenile, M Male, NOF Non-ovigerous female, and OF Ovigerous female.

**Fig. 4.** Monthly variation of Ampithoe valida abundance against Ulva lactuca biomass (a) and water temperature (b), and the correlation of U. lactuca biomass with water temperature (c) in the Yundang Lagoon.
mics has still been obvious. It revealed that the population size of *A. valida* sharply enlarged at low temperature (<15°C), but dramatically shrunk from March to June, when the water temperature increased from 15°C to 25°C, and disappeared during July to October, when water temperature exceeded 25°C (Fig. 4b).

3.1.3 Egg production in *A. valida*

*A. valida* displayed very high egg production ability in the Yundang Lagoon. The highest record was observed in March, up to 192 eggs per female with a body length of 13.54 mm. Significant correlation was observed between the body length of ovigerous female and the number of eggs per brood in different months (Fig. 5).

3.2 Life cycle of *A. valida*

3.2.1 Survival and growth of *A. valida* at different incubation temperatures

In the laboratory incubations, the mortality rate of *A. valida* was closely related to water temperature. The mortality rate was the highest, up to 1.25% per day, at 30°C, and gradually reduced with decreasing temperature from 0.98% per day at 25°C to 0.61% per day at 15°C. However, in the first 40 d after incubation, lower mortality rate was detected at 30°C than at other temperatures (Fig. 6). It is obvious that *A. valida* grown at lower temperature (15°C) had a longer lifespan. Their life expectancy reduced linearly from 150 d at 15°C to 77 d at 30°C with increasing temperature (Table 2, *p*<0.01).

![Fig. 5](image)

*Fig. 5.* The numbers of eggs per brood (*y*) in Stages I and II against the body length (*x*, mm) of ovigerous *Ampithoe valida* in four different months.

The growth curves of *A. valida* are shown in Fig. 7. It featured high growth rates in the early stage of life cycle and an obvious reduction in the rest lifespan. The analysis of covariance reveals significant differences in the growth rates among temperatures (*p*<0.01), and the post-hoc comparisons revealed the progressively increased growth rate from 15°C (0.216 mm/d) to 25°C (0.302 mm/d) during the linear growth period and subsequently the reduction at 30°C (0.256 mm/d).

The largest individual of *A. valida* was observed at 15°C, reaching a maximum body length of 20.40 mm, which was far

| Table 2. Life history traits in *Ampithoe valida* at different temperatures |
|------|----------------------|--------------------------|------------------------|-------------------|----------------|----------------|------|
| 15   | 150                  | 19–24                    | 20.4                   | 1.25 (21)         | 1 (21)         | 2.44 (21)      | 1    |
| 20   | 131                  | 18                       | 17.0                   | 0.94±0.31 (21)    | 4 (21)         | 2.70 (21)      | 1    |
| 25   | 92                   | 12                       | 17.2                   | 1.32±0.30 (18)    | 3 (18)         | 2.13 (18)      | 1    |
| 30   | 77                   | 12–18                    | 14.2                   | 1.05±0.01 (16)    | 4 (16)         | 3.00 (16)      | 1    |

Notes: 1) Life expectancy here was defined as the time from hatch to the day when the last amphipod died. 2) Via independent-sample *t*-tests, in the early stages of development, sex ratio was found to be close to 1 (*p* >0.05). 3) The number of replicates. 4) Total number of amphipods in each treatment was employed for the analysis of sex ratio.
Fig. 6. Growth curves of Amphipoe valida at different temperatures. Equation plots were obtained by linear regression analysis, and the growth rates were derived from the slopes of linear regression function.

longer than those at other temperatures (Table 2).

Through independent-sample t-test, the sex ratio of females vs males in A. valida was found close to 1 in the earlier growth stages, while above 2 in the later growth stages at all incubation temperatures (Table 2).

3.2.2 Reproduction of A. valida at different incubation temperatures

The increase in incubation temperature had accelerated A. valida sexual differentiation, which needed 18–24 d at 15°C and 18 d at 20°C, but 12 d at 25°C and 12–18 d at 30°C, respectively (Table 2). Similarly, the females reached ovigerous status much earlier at 25°C and 30°C than at 15°C and 20°C (Fig. 8a). A. valida grown at 25°C and 30°C began breeding around the 19th day. The body length of the first breeding female was significantly longer at 15°C than that at 25°C and 30°C (p=0.043 and p=0.001), but no significant difference was found between 15°C and 20°C (p=0.134) (Fig. 8b).

A. valida can breed continuously and actively during the life cycle. The reproductive rhythm of A. valida at 15°C was (14.7±2.1) d, almost 1.5 times longer than that at other incubation temperatures (p<0.001, Fig. 8c). The number of broods per female in its whole lifespan increased from 7.4±1.0 at 15°C to 8.8±1.3 at 20°C, then decreased to 7.2±0.7 at 25°C and 4.4±0.7 at 30°C (p<0.01, Fig. 8d).

Offspring production of A. valida was high. One female with a body length of 15.96 mm kept at 15°C released 94 juveniles, which was the highest record observed in our experiments. However, the minimum number of total released juveniles was only 6 for a female with a body length of 8.69 mm at 30°C. The analysis of covariance shows that the number of juveniles per brood was not significantly correlated to temperature (Fig. 9, p>0.1), but increased with body length of A. valida (Fig. 9, ln(y)=3.340 4ln(x)−4.9377, n=49, R²=0.685, p<0.001).

4 Discussion

4.1 Effect of food availability on A. valida population dynamics

After the year-round investigations in the Yundang Lagoon, our results show a close relationship between A. valida
and its food resource, i.e., *U. lactuca* (Fig.4a), which had agreed well with other studies (e.g., Fredette and Diaz, 1996; Drak and Arias, 1995). It is reported that *A. valida* mainly feeds on macroalgae (Browosky, 1983; Duffy and Hay, 1994; Nicotri, 1977; Zheng et al., 2008), so the abundance of this amphipod may be largely controlled by the availability of macroalgae in its habitats. Pardal et al. (2000) reported that in the eutrophic Montego estuary, where blooms of *Enteromorpha* spp. usually occurred, the abundance of *A. valida* was positively related to the biomass of *Enteromorpha* spp. Similarly, in the Yundang Lagoon, the changes in food availability in a year may be considered as one of the main causes for the fluctuation of *A. valida* population, although there was a time lag of one month for *A. valida* (Fig. 4a). The sharp decrease in *A. valida* abundance from March to July and the disappearance of the amphipod from July may thus be explained by the decrease and the absence of *U. lactuca* in the late spring and summer, when the lagoon water temperature accessed to or exceeded 25°C. The above explanation may be supported by Rivers and Peckol (1995), who found that photosynthetic efficiency and capacity of *U. lactuca* dramatically declined at 25°C, compared with the lower temperatures in their study.

### 4.2 Effect of temperature on *A. valida* population dynamics

Temperature is no doubt an important environmental factor, affecting all enzyme-catalyzed metabolisms and thus the growth of any living organisms. In our life cycle experiments, the growth of *A. valida* was also found to be obviously affected by incubation temperature, displaying a dome-shaped growth curve from 15 to 30°C (Fig. 7b), which was in accordant with that in another amphipod *Hyalella azteca* reported by Panov and McQueen (1998). Such dome-shaped growth may be explained by the differential effect of temperature leading to non-parallel changes in ingestion and metabolism with temperature (Panov and McQueen, 1998).

Despite observed stimulation for the *A. valida* growth at high experimental temperatures (20–30°C), larger final body length achieved was not detected with relation to increasing temperature (Fig. 7). In contrast, a significantly negative influence of temperature on the final body size has been widely reported in other amphipods and other aquatic animals. Panov and McQueen (1998) pointed out that net growth rate of amphipods was negligible at smaller size when temperature is higher. As a result, if larger-sized individuals are possible at higher temperature, their net growth rate should be negative. This indicates that larger individuals at higher temperature are unable to ingest enough food to meet the respiration and metabolism costs and will die rapidly, presumably because their guts impose a physical constraint on how much food can be processed per time (Cruz-Rivera and Hay, 2001).
Generally, females have often been found more abundant than males in amphipods (da Silva-Castilghoni and Buckup, 2008; Kevrekidis, 2005; Kevrekidis, 2004; Powell and Moore, 1991; Ricardo and Velos, 1998). Such was similarly the case with A. valida in the Yundang Lagoon (Table 1). Considering that the sexual ratio of A. valida in the earlier developmental stages is close to 1:1 (Table 2), a possible explanation for such female-biased sex structure in natural populations of A. valida in the Yundang Lagoon is that males die earlier than females due to their higher growth rate and their energy expenditure in the fertilization process. This process can be further hastened when one male has to fertilize two and more females. Additionally, in natural populations, higher susceptibility for males than females to predators, owing to the cruising behavior of male amphipods (Borowsky, 1983), can also be partly responsible for such sex ratio deviation.

There is no doubt that the increase of ambient temperature accelerates amphipod's growth and reduces the time accessing to its sexual maturity (Maranhão and Marques, 2003; Neuparth et al., 2001; Cunha et al., 2000; Muskó, 1992; Yu et al., 2002; Welton and Clarke, 1980). Similarly, in our laboratory study, for A. valida reared at the higher temperature, females in breeding stage were relatively smaller (Fig. 8b). This is in agreement with other studies that the size of ovigerous females observed in the field is smaller in summer and fall than in spring and winter (Muskó, 1992; Leong et al., 2007; Yu et al., 2002). Muskó (1992) believed that the breeding periodicity of amphipods was largely controlled by temperature. Our results of studying A. valida growth further confirm his conclusion (Table 2).

In temperate areas, most amphipods are iteroparous in reproductive patterns (Sainte-Marie, 1991) and feature continuous breeding (Maranhão and Marques, 2003; Prato et al., 2006). The previous studies also found that high breeding activity in A. valida during its lifespan (Borowsky, 1983; Pardal et al., 2000). In our study, it was found that the females of A. valida could be fertilized and got pregnant soon after molting during reproductive period as long as males existed. So, in our case, the time interval of 9–17 d for intermolt from 15°C to 30°C may be considered as the reproductive rhythm for A. valida. This agrees well with the finding that some Corophiidae species living in temperate areas display fortnightly reproductive rhythm (Borowsky, 1983; Fish and Mills, 1979; Moore, 1981; Sheader, 1976). However, significantly longer breeding rhythm at 15°C compared with that at higher temperatures in our experiments also suggested the inverse relationship between breeding rhythm and temperature, namely, lower temperature-prolonged embryonic development. Maranhão and Marques (2003) found that the duration of embryonic development for the amphipod Echinogammarus marinus at 10–15°C (33±0.7 d) was remarkably longer than that at 20°C (17±0.3 d). Highsmith and Coyle (1991) thought that this variation may be attributed to the slow growth rates and cleavage rates at lower temperatures.

In our case, the number of juveniles released per brood was not influenced by temperature (Fig. 9). This is different from the findings in amphipod E. marinus where the highest production of juveniles was observed at 10°C and the lowest at 20°C (Maranhão and Marques, 2003). This may be explained by differences in the intrinsic reproductive strategies between these two species. E. marinus cultivated at 20°C displayed smaller broods and shorter periods of embryonic development as compared with females at 10°C. The authors argued that high temperature resulted in increased metabolic maintenance costs and allowed a decreased amount of energy allocated in reproduction (Maranhão and Marques, 2003). Owing to decreasing energy expenditure in embryonic maintenance, intramarial loss rises under high temperature condition; whereas for A. valida at temperature ranging from 20°C to 30°C, temperature did not shorten the duration of embryonic development and produced no effect on juvenile production (Fig. 9a, Fig. 9). This means that energy allotted in reproduction could be equivalent or did not differ significantly for females among different temperature treatments.

In conclusion, although A. valida showed dome-shaped growth, small final size, increased mortality and relatively short longevity with increasing temperature, this species of amphipod survived pretty well and grew quickly at temperatures between 15–30°C. Additionally, for A. valida reared at 30°C, the mortality rate over life span was higher compared with that at lower temperatures, but it was significantly lower during the early growth stage (before Day 44). The above-mentioned results suggest that temperature fluctuation (12.4–28.9°C) in the Yundang Lagoon did not significantly restrict the development of A. valida population by affecting its survival and growth.

Higher temperature indeed caused some changes in some reproductive traits, e.g., the reduced number of broods in the life cycle due to the shortened longevity. However, our data also show the accelerated sexual maturity, the earlier first reproduction and the speed-up reproductive rhythm with increased temperature. Moreover, our findings in laboratory have confirmed that temperature did not affect A. valida offspring production. Thus, as a neutralized result, temperature actually exerted a very modest effect on A. valida reproduction. Such modest effect was neither sufficient to cause the sharp reduction of A. valida population in April, nor enough for us to explain the disappearance of A. valida in late summer and autumn when temperature was less than 30°C in the Yundang Lagoon.

A. valida appeared as an r-strategist, showing a series of characteristics for r-selection animals, e.g., quick individual growth, consecutive breeding and high fecundity. Such an effective reproductive pattern may easily lead to population balloon in a short time when environmental conditions are favor-
able. In the Yundang Lagoon, the sharply increased abundance of *A. valida* in March was mainly contributed by the increase of juveniles, which was ultimately attributed to the strong fecundity in *A. valida*, i.e., excellent egg (Fig. 5) and offspring (Fig. 9) production.

It is worth to note that, although temperature does not strongly affect *A. valida* reproductive process, we should not hence conclude that temperature produced no effect on *A. valida* population dynamics. It is well known that the large green algae *Ulva lactuca* is very sensitive to water temperature (Rivers and Peckol, 1995). Our results show a negative correlation between *U. lactuca* biomass and water temperature in the lagoon (Fig. 4c). And based on our observation and unpublished experimental data, *U. lactuca* in the Yundang Lagoon could hardly survive a water temperature above 25°C. Considering the extremely strong diet dependence of *A. valida* on *U. lactuca*, we thus conclude that temperature may indirectly account for the fluctuation and the seasonal disappearance of *A. valida* in the Yundang Lagoon.

4.3 Other potential factors affecting the population dynamics of *A. valida*

Given that the seasonal pattern of *A. valida* completely rests with the availability of *U. lactuca*, then a contradiction may exist in our data, i.e., it is very difficult to explain why the gradual increase of *U. lactuca* from November 2007 to January 2008 did not lead to a population increment in *A. valida*, when both environmental temperature (15–25°C) and food conditions in the Yundang Lagoon were advantageous to the growth and reproduction of *A. valida*. Thus, there must be additional factors, probably, the predation pressure from fishes and other predateors, which depress the population growth of the amphipod. Although we do not have any data for this, some field studies by Tegner and Dayton (1987) and Duffy and Hay (1994) may be helpful to our hypothesis. Tegner and Dayton (1987) reported that, in California, after cool waters returned in the wake of El Niño, kelp population recovered and grew profusely at the beginning. However, due to a substantial time lag of the recovery of kelp-associated fishes, the newly recovered kelp beds suffered a catastrophic decline from the explosion of amphipod *Pezamantissa hexamenala*, who have escaped the control by its predators. Duffy and Hay (1994) found that, on the sheltered sandflat at Lennoxville Point, North Carolina, *A. valida* could survive only on *Dictyota* during the season when fish was abundant because *Dictyota* released some secondary metabolites to deter fish predation. On the contrary, *A. valida*, dwelling on *Ulva* which were palatable to omnivorous fish predators, was rarely found. In Yundang Lagoon, however, *Tilapia nilotica* is a year-round predominant fish species that feed partly on amphipods (Zheng, 2011). The predation of *T. nilotica* on *A. valida* in the early developing stages of the latter may have been a decent reason for the late balloon of *A. valida* in the Yundang Lagoon, although it needs further validation.

5 Conclusions

(1) In the Yundang Lagoon, the population dynamics of *A. valida* was directly affected by its food availability. Temperature was not an obvious limiting factor that affects the survival, growth and reproduction of *A. valida* in the lagoon, and thus it was not directly responsible for the dramatic fluctuation of *A. valida* population. However, the seasonal growth of *U. lactuca* was significantly subject to temperature. Therefore, temperature may act indirectly on *A. valida* fluctuation due to strong diet dependence of *A. valida* on *U. lactuca*.

(2) *A. valida* owns a number of growth and reproductive traits as an r-strategist, such as a rapid growth rate (0.216–0.302 mm/d), cohortive breeding (4–10 times), short reproductive rhythm (9–17 d), and high fecundity (24–102 eggs and 95–94 juveniles per brood). When environmental conditions are favorable, e.g., low predation pressure, adequate food resource and appropriate abiotic conditions, the r-selected life strategy of *A. valida* will promise the amphipod quickly proliferated in a short time. This is the intrinsic reason for the *A. valida* population balloon from January to March in the Yundang Lagoon.

References


