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CHINA JELLYFISH PROJECT

Population dynamics of *Aurelia* sp.1 ephyrae and medusae in Jiaozhou Bay, China

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Abstract The scyphozoan *Aurelia aurita* (Linnaeus) s. l., is a cosmopolitan species-complex which blooms seasonally in a variety of coastal and shelf sea environments around the world. We hypothesized that ephyrae of *Aurelia* sp.1 are released from the inner part of the Jiaozhou Bay, China when water temperature is below 15°C in late autumn and winter. The seasonal occurrence, growth, and variation of the scyphomedusa *Aurelia* sp.1 were investigated in Jiaozhou Bay from January 2011 to December 2011. Ephyrae occurred from May through June with a peak abundance of 2.38 ± 0.56 ind/m^3 in May, while the temperature during this period ranged from 12 to 18°C. The distribution of ephyrae was mainly restricted to the coastal area of the bay, and the abundance was higher in the dock of the bay than at the other inner bay stations. Young medusae derived from ephyrae with a median diameter of 9.74 ± 1.7 mm were present from May 22. Growth was rapid from May 22 to July 2 with a maximum daily growth rate of 39%. Median diameter of the medusae was 161.80 ± 18.39 mm at the beginning of July. In August, a high proportion of deteriorated specimens was observed and the median diameter decreased. The highest average abundance is 0.62 ± 1.06 ind/km^2 in Jiaozhou Bay in August. The abundance of *Aurelia* sp.1 medusae was low from September and then decreased to zero. It is concluded that water temperature is the main driver regulating the life cycle of *Aurelia* sp.1 in Jiaozhou Bay.

Keywords *Aurelia* sp.1 · Ephyrae and medusae · Population dynamics · Jiaozhou Bay

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Introduction

Climate change and human activities are destabilizing coastal marine ecosystems (Sun et al., 2011); during the past several decades, high numbers of gelatinous zooplankton species have been reported from many estuarine and coastal ecosystems around the world

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(Mills, 2001; Condon et al., 2012). The common moon jellyfish, *Aurelia aurita* (Linnaeus) s. l., is a cosmopolitan species-complex with a worldwide distribution in neritic waters between 70°N and 40°S (Kramp, 1961; Lucas, 2001). Mitochondrial and nuclear DNA sequence data indicate that there are many sibling species of *A. aurita* s. l. worldwide, and the species found in the seas of Japan, Korea, and China is *Aurelia* sp.1 (Dawson & Martin, 2001; Ki et al., 2008).

Blooms of *Aurelia* spp. have increased since the 1980's, especially in semi-enclosed seas (Ishii & Tanaka, 2001). As *Aurelia* spp. usually bloom in the coastal area of the sea where it is easier to cause more damage (Sun et al., 2011), jellyfish blooms negatively affect industry as they clog water intake at coastal power plants (Dong et al., 2012), and affect the health of marine ecosystems as they compete with fish for food and feed on fish larvae and small fish (Sabates et al., 2010). In some areas, the annual average biomass of *Aurelia* spp. is higher than that of other large zooplankton, and they control the zooplankton population through a top-down effect (Makabe et al., 2012). Many ecologists have suggested that increasing numbers of jellyfish could ultimately result in an ecological disaster in which they replace fish and dominate marine ecosystems (McNamara et al., 2013).

The life cycle of *Aurelia* spp. varies in different areas since environmental factors such as water temperature, food availability, iodide concentration, and substrate affect the abundance of scyphistoma, the strobilation period of the polyps, the growth of the medusa stage, and longevity of the population (Di Camillo et al., 2010; Bonnet et al., 2012; Miller & Graham, 2012). Generally, strobilation of *Aurelia* spp. polyps occurs during the cold season, and ephyrae are released in late winter and early spring (Lucas, 2001). In Tokyo Bay ephyrae of *Aurelia* sp.l occur from October to May with the highest abundance during February, and a high polyp density has been observed on the underside of pontoons (Toyokawa et al., 2011). Medusae of *Aurelia* sp.5 in the Veliko Jezero, Croatia are present all year round, as the lake bathymetry enables medusae to vertically migrate to deeper and cooler water layers, avoiding the high temperatures which develop in the upper layer during the summer (Kogovsek et al., 2012). The longevity of *Aurelia* spp. in Kagoshima Bay, Japan and Jellyfish Lake of Palau exceed 1 year (Yasuda, 1971; Hamner & Jenssen, 1974). Miyake et al. (2002) observed that *Aurelia* spp. in Kagoshima Bay can survive through the winter and even spawn twice (Miyake et al., 2002).

Although a number of studies on the life cycle of *Aurelia* spp. have been conducted, multi-site comparisons of the seasonal patterns of *Aurelia* spp. are scarce, particularly in the northern Yellow Sea where there has been little research on its population dynamics (Dong et al., 2012). Jiaozhou Bay is a semi-enclosed bay affected by human activities such as industry and agriculture, both around the bay and on the Yellow Sea coast on the southern side of the Shandong Peninsula. In this study, we hypothesized that ephyrae of *Aurelia* sp.1 are released from the inner part of the Jiaozhou Bay when water temperature is below 15°C in late autumn and winter. Combined with laboratory experiments and field surveys, we focused on the population dynamics of *Aurelia* sp.1 in Jiaozhou Bay, in order to reveal the population dynamics of *Aurelia* sp.1 in Jiaozhou Bay.

Materials and methods

Sampling of ephyrae and medusae in Jiaozhou Bay

Surveys were conducted at six stations in Jiaozhou Bay from January to December 2011 (Fig. 1). Station Z is at a dock in the mouth of Jiaozhou Bay, while the other five stations are all located in the inner part of the bay. Samples of ephyrae and young medusae were collected monthly by vertical tows from near the bottom to the surface, using a conical plankton net of about 145 cm long, 50 cm inner diameter at the net mouth and 500 μm mesh. These samples were collected monthly. At dock station Z, however, samples were taken weekly from April 1 to July 1 and monthly during the rest of the period. Ephyrae and young medusae were selected and identified under a dissecting microscope immediately after towing, and measured with a vernier caliper. To determine the variation of biomass, visual counts were carried out seven times during August and September in station C4, C3, C1, A3, and D1 (Doyle et al., 2007). To determine the abundance, visual counts were carried out for 20 min at each station, the speed of survey vessel was limited to 2 kn. during visual count, and the maximum width of visual range was about 20 m. To determine bell diameter, medusae collected from the surface of the sea using a hand net (10 mm mesh size)

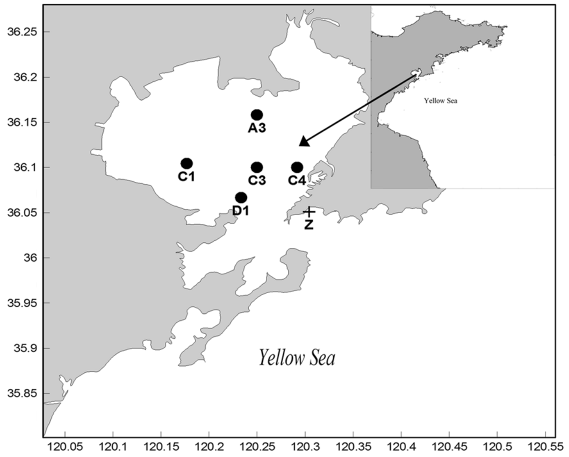

Fig. 1 Ephyrae and medusae sampling stations in Jiaozhou Bay, China (*filled circle* monthly, *plus* weekly from April 1 to July 1 and monthly in the rest of the period)

were measured with a ruler. Planula larvae in the brood sacs on the oral arms were examined using a dissecting microscope. Growth rate (GR) was calculated according to the formulae: $GR = (BD_t - BD_0)/t$, where BD_t and BD_0 are the mean bell diameters at time t and time 0, respectively.

Vertical profiles of salinity and temperature were obtained using a CTD (AAQ1183-1F, Alec CO., Japan) before each collection.

Laboratory culture of ephyrae

In order to confirm whether the ephyrae released in late autumn can survive and grow over winter, a total of 60 ephyrae were used. The ephyrae used in this experiment were released from *Aurelia* sp.1 polyps obtained from the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. Strobilation was induced by changing the temperature from 20 to 15°C, and ephyrae were collected immediately after release. Ephyrae were kept in an aquarium and cultured in 0.45-µm-filtered seawater without food for 24 h before the experiment. The photoperiod was maintained at 12 h light:12 h dark, simulating the light conditions in late spring and early summer. Four temperatures (5, 10, 15, and 20°C), spanning the temperature range in late spring and early summer in Jiaozhou Bay, were used for ephyrae culture. Incubators were used to maintain these temperatures. Five ephyrae of the same size were arbitrarily kept at each of the four temperatures, with three replicates at each level. Ephyrae were placed in 1-l bottles (Nalgene 11 cm inner diameter and 12 cm high wide-mouth) and cultured in 0.45-µm-filtered seawater. The water used in this experiment was obtained from Jiaozhou Bay, and the salinity was approximately 31 psu. Ephyrae were fed daily with sufficient food (300 ind/L *Artemia* sp. nauplii). Each day, 1 h after feeding, the ephyrae were transferred to a new bottle containing clean 0.45-µm-filtered seawater of the same temperature and salinity. During data collection, they were exposed to indirect room light and microscope illumination for approximately two min, once per week. The diameter of ephyrae and medusae were measured weekly. The experiment lasted for 61 days. Growth rate and survival rate were calculated. Microsoft Excel and Surfer 8.0 were used for descriptive statistics and figure drawing.

Results

Temperature and salinity

Water quality parameters in Jiaozhou Bay during the study period are shown in Fig. 2. The mean surface water temperature varied during the survey period between 4 and 27.4°C. Water temperature was lowest in February and was highest in September. Annual salinity varied little between 30 and 33 psu.

Occurrence, distribution, and abundance of ephyrae and medusae

There were totally 56 ephyrae collected and measured, only one ephyra collected in station C3, other 55 ephyrae were all collected in station Z. The distribution of ephyrae was mainly restricted to the coastal area of the bay, and the abundance was highest in the dock of the bay than at the inner bay stations. Ephyrae abundance varied between 0.14 ± 0.14 and 2.38 ± 0.56 ind/m^3, the bell diameter of ephyrae collected varied little, and the average bell diameter was 3.34 ± 0.41 mm at station Z (Fig. 3). In the inner bay, ephyrae of *Aurelia* sp.1 were observed mainly at station C3, with very low abundance at the other stations. At station Z, ephyrae of *Aurelia* sp.1 occurred from May through June with a peak abundance of

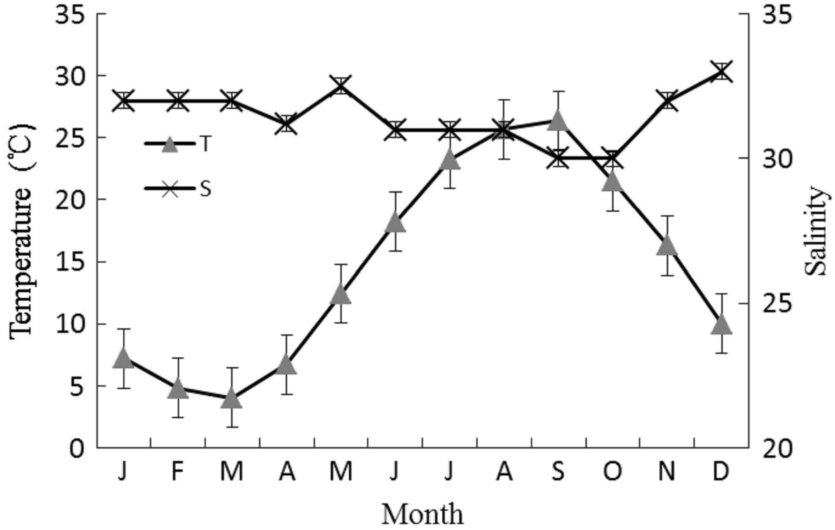

Fig. 2 Annual variation in temperature and salinity. *Error bars* represent standard deviation

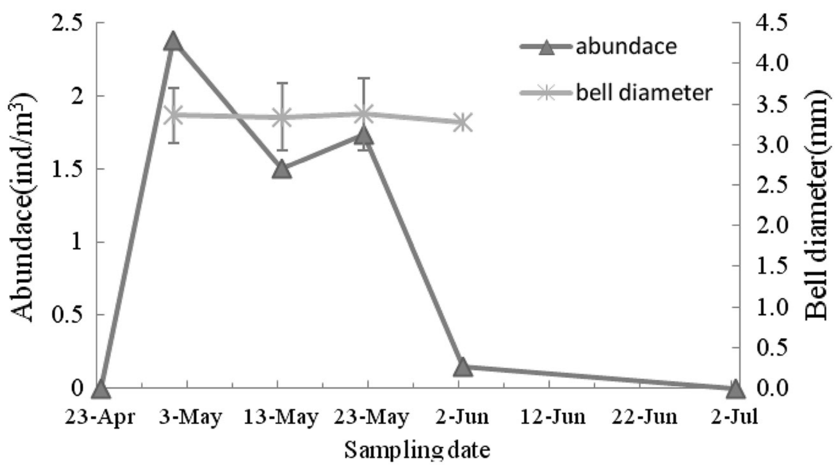

Fig. 3 Abundance and bell diameter of ephyrae at station Z in Jiaozhou Bay 2011. *Error bars* represent standard deviation

2.38 ± 0.56 ind/m^3 in May. The temperature ranged from 12 to 18°C during the period ephyrae occurred, and was 13 to 16°C when abundance was relatively high (Fig. 2). Only one meta-ephyrae with diameter of 9.74 mm was collected in May 22 at station Z.

A total of 104 individual *Aurelia* sp.1 medusae were recorded in the visual count during the survey. The average number of medusae decreased with time during August and September. As shown in Fig. 4, the highest average abundance was 0.62 ± 1.06 ind/km^2, and the highest abundance was 2.51 ind/km^2 at station A3 on August 1. The abundance of *Aurelia* medusae was low from September onward and decreased to zero.

The variation of bell diameter in young and adult medusae is shown in Fig. 5. Young medusae derived from ephyrae were observed only on May 22 at station Z. Young medusa were then collected, whose median diameter was 9.74 ± 1.7 mm. The maximal diameter was observed in July, 161.80 ± 18.39 mm. The growth rate of ephyrae to young medusae was 8.6%, and growth was rapid from May 22 to July 2 with a maximum daily growth rate of 39%. The median diameter was 161.80 mm at the beginning of July. Planula larvae were observed in brood sacs on the oral arms of the specimens in July. In August the proportion of deteriorated specimens was about 75% and the median diameter decreased to 100.00 ± 26.11 mm in September.

As shown in Fig. 6, during the experimental period ephyrae in groups 15 and 20°C developed into young medusae, and the growth rate of ephyrae was higher at

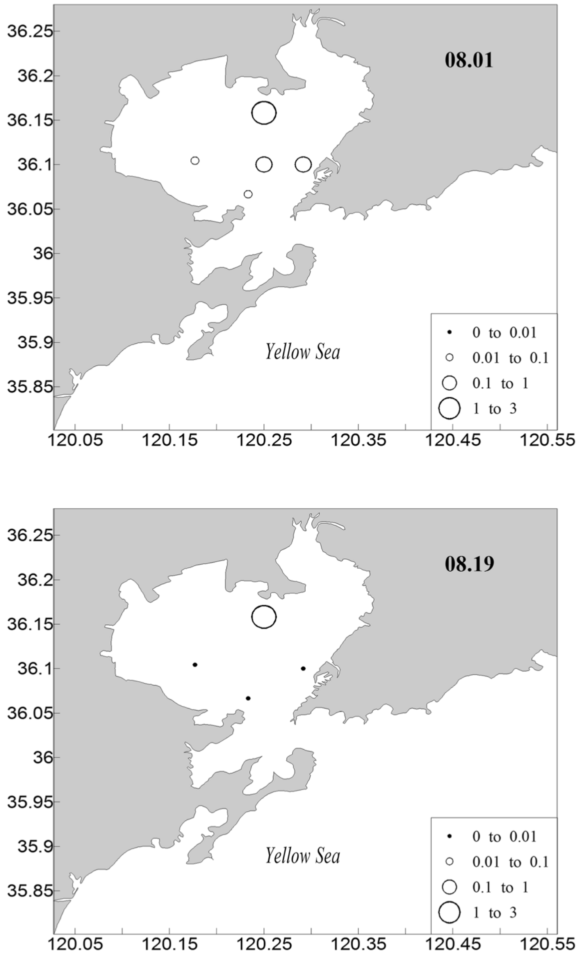

Fig. 4 Abundance (ind/km^2) of *Aurelia* sp.1 medusae in Jiaozhou Bay 2011

15°C than at 20°C. The bell diameter of ephyrae at 10°C was constant, and decreased at 5°C.

The survival rate of ephyrae was significantly different ($P < 0.01$) at different temperatures. As shown in Fig. 7, during the first 25 days of this experiment, the survival rate of ephyrae was approximately 46% at 20°C, being the lowest of the four temperature groups. The survival rate was 73% at 15°C. The survival rate of ephyrae at 5 and 10°C was higher than that at 15 and 20°C, 93 and 80% at 10 and 5°C, respectively, during the 61-day experimental period.

Discussion

The plankton stage of jellyfish occurs seasonally, usually with a life span of four to eight months (Bonnet et al., 2012; Kogovsek et al., 2012). With increased temperature when spring food conditions are suitable for exponential growth (Uye & Shimauchi, 2005), while the bell diameter decreases after sexual reproduction in late summer and early autumn (Thein et al., 2012). However, population dynamics show different characteristics in different habitats (Kogovsek et al., 2012; McNamara et al., 2013). Ephyrae were collected from April to June in 2009 in the inner part of Jiaozhou Bay (Wan & Zhang, 2012). In our survey, ephyrae of *Aurelia* sp.1 appeared seasonally in Jiaozhou Bay when the temperature increased in spring, the ephyrae release process lasted for approximately 1 month, and ephyrae were not only collected from the station in the inner part of the bay, but also collected from the station Z in the mouth of the bay. Construction, in the last 20 years, of raft culture, pontoons, and a cross-sea bridge in the bay provides

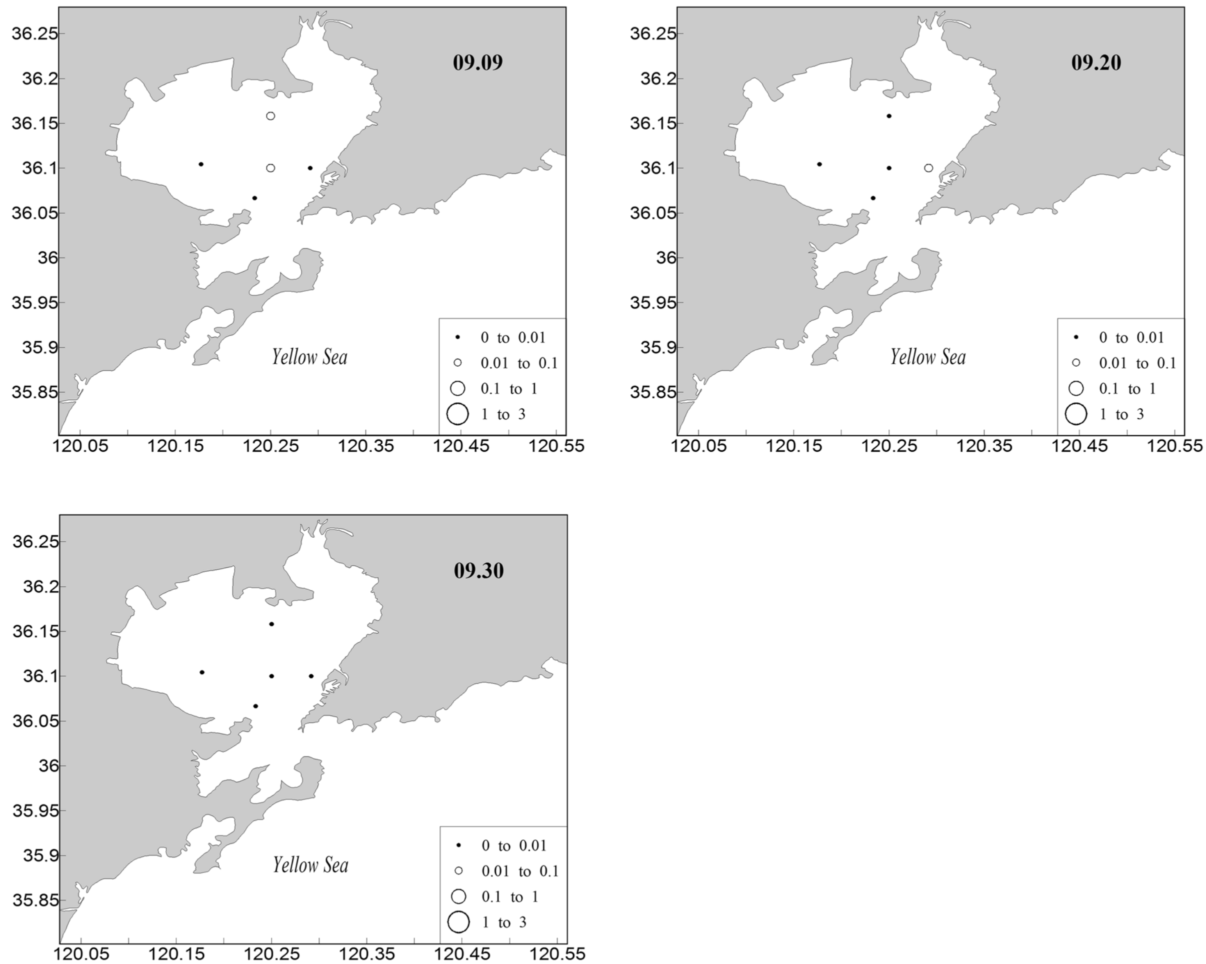

Fig. 4 continued

suitable substrates for the polyps, and facilitates the survival and reproduction of the *Aurelia* sp.1 population (Toyokawa et al., 2011). We found the abundance of ephyrae to have been in the range of 0.14–2.38 ind/m^3 in 2011, which was lower than that in 2009 (Wan & Zhang, 2012). Ephyrae of *Aurelia aurita* appeared from October to May with a higher abundance of 0.39–0.64 ind/m^3 in February in Tokyo Bay (Toyokawa et al., 2011). Ephyrae occurred from November to the middle of April with a maximum abundance of 3.3 ind/m^3 in May 2011 in Thau lagoon, in the Northwestern Mediterranean Sea (Bonnet et al., 2012). In Jiaozhou Bay, the abundance of *Aurelia* sp.1 ephyrae was similar to that reported in other coastal areas, but the period of occurrence was shorter.

Temperature is the most important environmental factor for the occurrence of strobilation and the growth of medusae. A drop in temperature may be the primary cue for strobilation in the Suez Canal, as the release of ephyrae seems to be induced by a lowering of ambient temperature to below 16°C, with peak release occurring in December−February (El-Serehy & Al-Rasheid, 2011). Laboratory experiments showed that strobilation of *Aurelia* sp.1 polyps occurs at 10 and 15°C in Jiaozhou Bay (Wang et al., 2012). In the present survey, the temperature ranged from 12 to 18°C, and the temperature had begun to increase in spring when the ephyrae were captured. But in the North Adriatic sea the temperature range is similar to that of Jiaozhou Bay, and the strobilation occurs when temperature goes below 15°C in the cold season (Di Camillo et al., 2010). The existence of a thermocline layer ensures that polyps attach to the rocky substrate

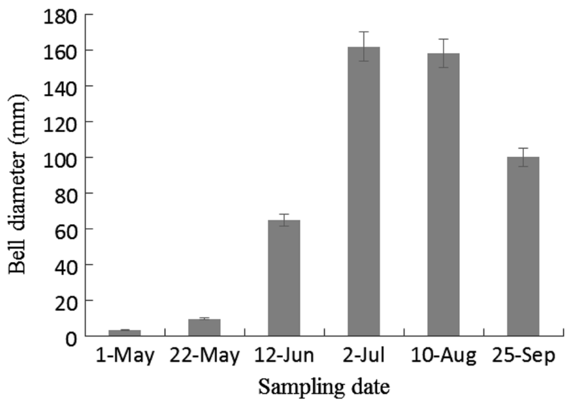

Fig. 5 Annual variation in bell diameter of *Aurelia* sp.1 medusae in Jiaozhou Bay 2011. *Error bars* represent standard deviation

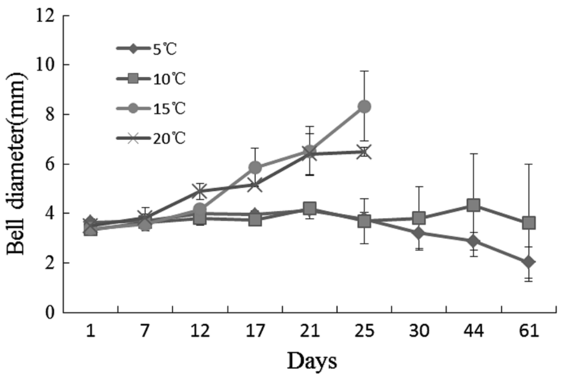

Fig. 6 Bell diameter of ephyrae at different temperatures during the experiment. *Error bars* represent standard deviation

below 20 m depth allowing continuous strobilation and stability of the *Aurelia* medusae population all year round in the Veliko Jezero (Kogovsek et al., 2012). The character of life cycle of *Aurelia* spp. differ, and sometimes appear confusing, mainly because polyps in different areas have different temperature preferences, and appear to have evolved different life cycle strategies according to their ambient conditions.

Temperature controls the growth and development also of ephyrae. In our experiments the survival rate of ephyrae was high, but they did not develop into medusae at 5 and 10°C. Ephyrae grow fast and can develop into medusae at 15 and 20°C in 3 weeks. A survey in Gullmar Fjord, western Sweden found a high abundance of *Aurelia* spp. ephyrae in November, and

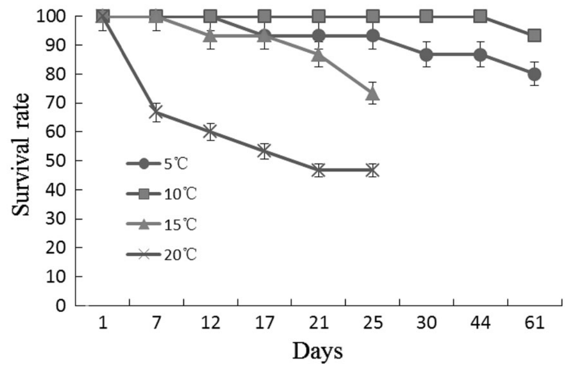

Fig. 7 Survival rate of ephyrae at different temperatures during the experiment. *Error bars* represent standard deviation

these ephyrae survived in deep water over the winter without growth until April when the temperature was suitable for ephyrae growth (Hernroth & Grondahl, 1983, 1985). In our survey, the temperature was approximately 14°C when the first ephyrae was caught. This is in agreement with our experimental results which showed that temperature was the limiting factor controlling the development of ephyrae to larval jellyfish, and these findings were concordant with previous survey results (Albert, 2009).

In our survey, medusae appeared from May to September, with the largest bell diameter of 16.18 cm in July, 2011 in Jiaozhou Bay. The maximum bell diameter of *Aurelia* spp. in Thau lagoon in the Northwestern Mediterranean Sea reached 11.3 cm on the 7th May (Bonnet et al., 2012). The life span of *Aurelia* spp. is longer than 1 year in Kagoshima Bay and Jellyfish Lake, Palau (Yasuda, 1971; Hamner & Jenssen, 1974). Miyake demonstrated that the life span of *Aurelia* spp. in Kagoshima can extend to 2 years, and they can spawn twice (Miyake et al., 2002). Adult medusae are larger in non-bloom years than in bloom years mainly because food is limited when jellyfish abundance is high (Kogovsek et al., 2012). The abundance of *Aurelia* spp. in south-west Wales sea is 0.33 ind/km^2, is lower than the abundance of *Aurelia* sp.1 in August 1 (Doyle et al., 2007). The life span of *Aurelia* sp.1 in Jiaozhou Bay, approximately 5 months from May to September, is shorter than that of *Aurelia* spp. in Horsea lake England (Lucas, 1996). Zooplankton biomass is highest in May in Jiaozhou Bay, providing good food conditions for the growth of medusae (Wan & Zhang, 2012). Body shrinkage and death of medusae occurred in August and September,

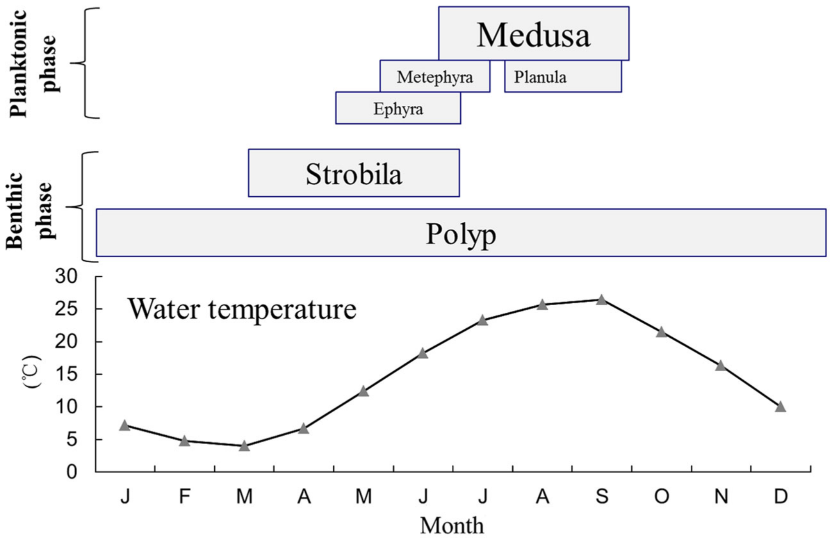

Fig. 8 Schematic representation of typical seasonal life cycle of *Aurelia* sp.1 in Jiaozhou Bay, China

mainly because zooplankton production cannot support the energy needed due to increased respiration-based consumption in adult medusae when the temperature is high and the zooplankton biomass is decreasing (Frandsen & Riisgard, 1997). Kogovsek et al. (2012) suggested that *Aurelia* medusae respond to the changing environment, in particular to enhanced temperature, by reducing their body size. Medusae in the Veliko Jezero are present all year round as the lake bathymetry enables them to vertically migrate to deeper and cooler water layers, avoiding the limiting temperatures which develop in the upper layer during the summer, and these conditions may prolong the life span of *Aurelia* medusae (Kogovsek et al., 2012).

In Jiaozhou Bay where the water temperature ranges from approximately 5 to 26°C during the year, the occurrence of *Aurelia* sp.1 medusae shows a particular seasonal pattern, schematically depicted in Fig. 8. The experimentally determined effects of temperature on development of the different stages in the life cycle of *Aurelia* sp.1, match the timing of the different stages appearing at Jiaozhou Bay (Fig. 8). This would be consistent with driving of yearly cycle of *Aurelia* sp.1 exclusively by in situ temperature, although auxiliary controlling factors cannot be excluded. Typically, strobilation indicated by the presence of ephyrae, occurs during early spring when the water temperature begins to increase, giving rise to ephyrae in the plankton from May to June. Medusae grow to a bell diameter of approximately 16 cm, and attain sexual maturity in mid-summer, when the population biomass reaches its annual peak. After mid-summer, the population steadily declines and disappears from the water column. The life span of individuals is equal to or less than the period of occurrence of the medusa population, the life span of an individual being no more than 5 months. That *Aurelia* sp.1 medusae appear each year in Jiaozhou Bay, and a large number of ephyrae appear at near shore stations, which indicates a high abundance of non-specific polyps growing in this area. Further investigations of *Aurelia* sp.1 polyps in situ should be conducted to address the life cycle of this species.

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