Effects of Environmental Factors on Survival and Reproduction of Moon Jellyfish (Aurelia aurita) Polyps: Postprint

Authors: Sun Ming, Chai Yu, Dong Jing, Zhilu Fu, Liu Zhigeng, Lin Jianqi, Wang Jiahan

Date: 2017-03-08T00:00:00+00:00

Abstract

Using the polyps of the moon jellyfish (Aurelia aurita), a major disaster-causing large jellyfish species in the Yellow Sea and Bohai Sea of China, as experimental material, we employed experimental ecological methods to investigate the effects of temperature, salinity, light intensity, and food quantity on their survival and reproduction. The results showed that within the range of 0-25°C, the 40-day survival rate of polyps was 100%, and the relative reproductive rate of polyps increased with rising temperature; within the salinity range of 15-40, the 40-day survival rate of polyps was 100%, the polyps in the salinity 22.5 group exhibited the highest relative reproductive rate, but salinity had no significant effect on polyp population abundance; the relative reproductive rate of polyps decreased with increasing light intensity, and dark conditions favored the increase in individual numbers of moon jellyfish polyps; the relative reproductive rate of polyps increased with increasing food quantity. The findings indicate that moon jellyfish polyps possess strong environmental adaptability, and elevated water temperature and increased food quantity can lead to rapid population growth of moon jellyfish polyps.

Full Text

Preamble

ACTA ECOLOGICA SINICA
ChinaXiv Partner Journal
Vol. 37, No. 4, February 2017
DOI: 10.5846/stxb2016301323

Effects of Environmental Factors on Polyp Survival and Reproduction of *Aurelia* sp. 1

SUN Ming, CHAI Yu, DONG Jing, FU Zhilu, LIU Zhigeng, LIN Jianqi, WANG Jiahan

Key Laboratory of Marine Biological Resources and Ecology of Liaoning Province, Liaoning Ocean and Fisheries Science Research Institute, Dalian 116023, China
School of Marine Science and Biotechnology, Guangxi University for Nationalities, Nanning 530008, China
School of Marine Science and Environment, Dalian Ocean University, Dalian 116023, China

Abstract

Jellyfish blooms have become a global problem, with outbreaks reported at unprecedented rates in recent decades. Blooms of *Aurelia* spp. have become increasingly prominent worldwide since the end of the 20th century, causing serious damage to fisheries, marine ecosystems, and coastal power plants. Environmental factors that control jellyfish population size are not well understood; however, many researchers suggest that global warming, water pollution, and overfishing may be the main contributing factors. Many scyphozoan species, including *Aurelia* spp., have a benthic polyp stage. This stage is an important part of the life cycle of *Aurelia* because polyp clones can increase their population size through asexual reproduction, providing the opportunity to increase the medusa population by producing many ephyrae through strobilation. Environmental factors that affect asexual reproduction rates include temperature, salinity, light, and food.

In this study, polyps of *Aurelia* sp. 1, collected from Heishijiao, Dalian, China, were tested under various environmental conditions: (1) 11 different temperatures (0, 2.5, 5, 7.5, 10, 12.5, 15, 17.5, 20, 22.5, and 25°C) at salinity 28; (2) 14 different salinities (7.5, 10, 12.5, 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40) at ambient temperatures (15–25°C) and natural light conditions; (3) 5 different light intensities (0, 200, 400, 600, and 800 lx) at 20–25°C with a 10-h light/14-h dark photoperiod; and (4) 5 feeding frequencies (1 time/day, 1 time/2 days, 1 time/8 days, 1 time/16 days, and no feeding, representing 8.3, 4.2, 1.0, 0.5, and 0 g C per polyp per day) at 15–25°C.

Asexual budding was strongly affected by temperature, feeding frequency, and light intensity, but not by salinity. The production of new buds increased dramatically with increasing temperature, particularly in the range of 12.5–25°C. The asexual reproduction rate was highest at salinity 22.5, and gradually decreased as salinity increased or decreased; however, statistical results did not show any significant influence. Dark or dim light conditions greatly favored asexual reproduction, while bright light inhibited it. Asexual budding significantly decreased with decreased feeding frequency; a total of 9–59 buds were produced by feeding once per day, and the number of buds decreased to only

1–3 by feeding once per 14 days during the 60-day experiment. No polyps died even under no-feeding conditions, demonstrating that *Aurelia* sp. 1 polyps have strong resistance to starvation. Survival was high in all treatments except in the salinity range of 7.5–12.5, indicating wide tolerance to environmental conditions.

These results indicate that the environment of the Bohai Sea and Yellow Sea is suitable for the survival and reproduction of *Aurelia* sp. 1. We suggest that increased temperatures due to global warming, increased abundance of zooplankton prey due to eutrophication, and increased seawater turbidity caused by industrial pollution may be responsible for the prominent blooms of *Aurelia* sp. 1 medusae in the coastal waters of the Bohai Sea and Yellow Sea.

Keywords: jellyfish bloom; asexual reproduction; temperature; salinity; light intensity; feeding rate

Introduction

Jellyfish blooms have emerged as a new type of marine ecological disaster worldwide against the backdrop of global change, which has profoundly altered the structure and function of marine ecosystems. *Aurelia* sp. 1 is one of the main bloom-forming jellyfish species in the Yellow Sea and Bohai Sea of China, exhibiting unusually high-frequency bloom phenomena. Numerous studies have reported the negative impacts of *Aurelia* sp. blooms on marine ecology and fishery economics [3–5]. In 2007, *Aurelia* blooms occurred in Yantai and Weihai waters, affecting coastal tourism. Large numbers of *Aurelia* nearly caused shutdowns at Qingdao power plants [6]. The geographic distribution of *Aurelia* in the Liaodong Bay has expanded, with significantly increased numbers [7]. In 2016, *Aurelia* blooms occurred at the Zhimaowan fishing port in Suizhong (Figure 1 [Figure 1: see original paper]), and frequent invasions into coastal aquaculture ponds have impacted the growth of cultured organisms [8]. Jellyfish blooms have caused serious harm to China' s coastal fisheries, industry, and tourism [1, 2, 2016, 2009].

Aurelia exhibits strong environmental adaptability and is widely distributed in coastal waters worldwide. Dawson et al. reported that multiple subspecies of *Aurelia* exist globally [9–10], and differences in genotype may cause variations in population ecological characteristics reported for *Aurelia*. Different geographic populations exhibit distinct ecological habits. Many studies indicate that salinity has no significant effect on polyp population numbers, though blooms in Finnish waters have been attributed to increased salinity creating more favorable conditions for polyp reproduction [11–12]. Dong et al. and others reported that *Aurelia* distributed in China' s Yellow and Bohai Seas is *Aurelia* sp. 1 [13–14]; however, indoor ecological studies on this subspecies are limited. Existing research has focused on small gradients under two environmental conditions, emphasizing temperature and food effects on strobilation. For example, Wang et al. and Shi et al. studied temperature and food conditions on individual reproduction and strobilation [15-17], while Wang et al. examined food type effects on asexual reproduction under three temperatures [18]. Systematic studies on the effects of individual environmental factors on polyp survival and reproduction of this subspecies are lacking.

Because mortality and reproductive output during the polyp stage are key factors determining medusa population size, detailed study of benthic polyp stage ecology is crucial for accurately predicting jellyfish blooms [19]. This study used *Aurelia* sp. 1 polyps from the Yellow and Bohai Seas as experimental material, setting experimental gradients based on actual environmental ranges in these waters to investigate the effects of temperature, light intensity, and food quantity on polyp survival and reproduction. The aim is to provide important baseline data for further research on *Aurelia* bloom mechanisms, distribution patterns, and early warning model development.

Materials and Methods

Experimental Organisms and Culture Conditions

Experimental polyps were cultivated by the Key Laboratory of Marine Biological Resources and Ecology of Liaoning Province, derived from the same batch whose parent medusae were collected from the northern Yellow Sea off Dalian. Routine polyp culture seawater was collected from the Dalian Heishijiao coast (salinity 31±1, pH 8.2±0.1) and used after dark sedimentation and sand filtration. Polyps were fed newly hatched high-quality *Artemia* nauplii. Dissolved oxygen was maintained above 5 mg/L, and water temperature fluctuated naturally with room temperature (5–25°C).

Temperature Experiment

Based on the annual temperature range in the Yellow Sea and Bohai Sea, water temperature was set at 11 levels: 0, 2.5, 5, 7.5, 10, 12.5, 15, 17.5, 20, 22.5, and 25°C. Starting culture temperature for all polyps was 15°C, adjusted by 1°C every 24 hours until reaching target temperatures. Experiments were conducted in darkness using intelligent illumination incubators (GXZ-280B; GXZ-280C) to control temperature. Culture salinity was 28±0.5. To minimize strobilation effects on individual reproduction rates, experiments began after most polyps had passed the strobilation period in spring. Polyps in each treatment group were cultured in 200 mL containers and fed every 7 days for 60 days.

Salinity Experiment

Fourteen salinity gradients were established: 7.5, 10, 12.5, 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40. Gradient seawater was prepared using natural seawater (15–25°C) and aerated tap water, with salinity calibrated using a

PAL-06S salinometer. Experiments were conducted under indoor natural temperature conditions (15–25°C) and natural light (0–1050 lx). Polyps were fed every 7 days for 60 days.

Light Intensity Experiment

Five light intensity levels were tested: 0, 200, 400, 600, and 800 lx. The dark group (0 lx) was achieved using blackout cloth. Experiments were conducted in intelligent illumination incubators (GXZ-280B; GXZ-280C) at 20–25°C with a 10-h light/14-h dark photoperiod. Culture salinity was 30–31. Polyps were fed every 7 days for 60 days.

Food Quantity Experiment

Five feeding frequencies were established: 1 time/day, 1 time/2 days, 1 time/8 days, 1 time/16 days, and no feeding, representing daily food quantities of 8.3, 4.2, 1.0, 0.5, and 0 g C per polyp, respectively, based on 0.83 g C per *Artemia* nauplius [20]. Newly hatched *Artemia* nauplii were used as food. During feeding, polyps were targeted with a pipette containing *Artemia*, and any nauplii not captured by polyp tentacles were guided to them using a special needle to ensure each polyp fed. Experiments were conducted under dark conditions at indoor natural temperature (15–25°C) and salinity 28±0.5 for 60 days.

Parameter Measurement and Statistical Analysis

Polyp stalk diameter growth was used as the growth index, measured as the maximum horizontal diameter in oral view (or the average of maximum and minimum diameters when not circular). Polyp reproduction multiple (M) = (Nt/N0) × 100%, where N0 is initial parent polyp number and Nt is total polyp number at experiment end. Relative reproduction velocity (NR) = (ln Nt - ln N0)/t, where t is experimental duration (days). Data were processed using Excel 2003 and analyzed using one-way ANOVA with SPSS 19.0.

Results

1. Effects of Temperature on Polyp Survival and Population Reproduction

During the temperature experiment, polyp survival rates were 100% in all treatment groups. Polyps in the 0°C group exhibited contracted tentacles and elongated shapes without asexual reproduction. Polyps in the 2.5°C group showed pre-strobilation characteristics but no budding. Polyp reproduction multiple and relative reproduction velocity showed an increasing trend with temperature, particularly evident in the 12.5–25°C range. The 5–25°C groups exhibited normal growth and asexual reproduction, with the highest average relative reproduction velocity in the 5–25°C group. Parent polyps produced 3–98 offspring polyps during the experimental period.

Statistical analysis revealed highly significant effects of temperature on polyp reproduction multiple and relative reproduction velocity ($P < 0.01$). The relationship between reproduction multiple (y) and temperature (x) was $y = 0.1797x - 5.3747$ ($R^2 = 0.918$, $P < 0.01$). The relationship between relative reproduction velocity (y) and temperature (x) was $y = 0.056x + 0.5558$ ($R^2 = 0.9905$, $P < 0.01$). Linear correlations were observed between both reproduction parameters and temperature. The results indicate that *Aurelia* sp. 1 polyps can survive and reproduce asexually across 0–25°C, with more new polyps produced at higher temperatures within the 5–25°C range.

[Figure 2: see original paper] Effect of temperature on reproduction multiple of *Aurelia* sp. 1 polyps
[Figure 3: see original paper] Effect of temperature on relative reproduction velocity of *Aurelia* sp. 1 polyps

2. Effects of Salinity on Polyp Survival and Population Reproduction

All polyps were placed in experimental groups simultaneously. Polyps in the 7.5 salinity group died within 24 hours; those in the 10 salinity group died within 48 hours; and those in the 12.5 salinity group died within 72 hours. All other salinity groups (15–40) showed 100% survival. Asexual reproduction occurred in all salinity treatments. Polyp reproduction multiple and relative reproduction velocity showed declining trends as salinity increased or decreased from the optimum, with the highest relative reproduction velocity at salinity 22.5. However, ANOVA results indicated no significant effect of salinity on polyp reproduction rate or relative reproduction velocity ($P > 0.05$).

The results demonstrate that *Aurelia* sp. 1 polyps have broad salinity tolerance, capable of surviving and reproducing asexually across 15–40 salinity range, which should enable them to inhabit variable salinity environments such as estuaries and bays.

[Figure 4: see original paper] Effect of salinity on reproduction multiple of *Aurelia* sp. 1 polyps
[Figure 5: see original paper] Effect of salinity on relative reproduction velocity of *Aurelia* sp. 1 polyps

3. Effects of Light Intensity on Polyp Survival and Population Reproduction

At experiment termination, the 800 lx group showed 98% survival, while all other groups showed 100% survival. Polyp reproduction multiple and relative reproduction velocity decreased with increasing light intensity. The 0 lx (dark) group exhibited the highest reproduction multiple and relative reproduction velocity. Linear correlations were observed: reproduction multiple (y) vs. light intensity (x) was y = -0.0053x + 12.434 (R^2 = 0.9299, $P < 0.01$); relative reproduction velocity (y) vs. light intensity (x) was y = -0.0151x + 4.398 (R^2 = 0.8563, $P < 0.01$). ANOVA showed highly significant effects of light intensity on both parameters ($P < 0.01$). The results indicate that dark conditions favor asexual reproduction and population increase in *Aurelia* sp. 1, while increased light intensity inhibits polyp population reproduction.

[Figure 6: see original paper] Effect of light intensity on reproduction multiple of *Aurelia* sp. 1 polyps
[Figure 7: see original paper] Effect of light intensity on relative reproduction velocity of *Aurelia* sp. 1 polyps

4. Effects of Food Quantity on Polyp Survival and Population Reproduction

All treatment groups showed 100% survival and exhibited asexual reproduction. Polyp reproduction multiple and relative reproduction velocity increased significantly with food quantity ($P < 0.05$). The number of offspring polyps produced by parent polyps during the 60-day experiment ranged from 9–59 in the 8.3 g C/d group, decreasing to 1–3 in the 0.5 g C/d group. The results demonstrate that food quantity strongly regulates polyp reproductive output.

[Figure 8: see original paper] Effect of feeding on reproduction multiple of *Aurelia* sp. 1 polyps
[Figure 9: see original paper] Effect of feeding on relative reproduction velocity of *Aurelia* sp. 1 polyps

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Discussion

Aurelia is the most extensively studied scyphozoan jellyfish due to its wide geographic distribution and strong reproductive capacity. Mayer first proposed that *Aurelia* has multiple subspecies, each with specific ecological habits [21]. Dawson et al. subsequently conducted detailed studies on subspecies identification and geographic distribution [9–10]. Different subspecies and geographic populations can survive across increasingly wide latitudinal and temperature ranges, possibly due to selection of genetic fragments in response to regular changes in food and salinity, enabling adaptation to specific environmental conditions [9–10].

This study set the temperature experimental range at 0–25°C based on natural water temperatures in the Yellow Sea and Bohai Sea. The results show that *Aurelia* sp. 1 polyps can survive across 0–25°C, consistent with observations by Kroiher et al. for *Aurelia aurita* [22]. Polyps in the 0°C group survived without feeding, and recovered when temperature increased to 15°C, demonstrating strong cold tolerance and overwintering capability in Yellow Sea waters. The complex life cycle of *Aurelia* allows polyps to supplement populations through multiple asexual reproduction modes [23–25]. Many studies confirm that temperature significantly affects polyp asexual reproduction [26–27], with warming accelerating reproduction rates [11, 27–29]. Wang et al. and others showed that polyp numbers increase with temperature for *Aurelia* sp. 1 in the Yellow Sea [16, 18], consistent with our results. However, Purcell et al. found that budding decreased with temperature for *Aurelia labiata* in Washington's Hood Canal [30], and Liu et al. reported higher budding at lower temperatures (7, 10, 15°C) than at 20°C for *Aurelia aurita* in Taiwan [31]. In our study, reproduction multiple and relative reproduction velocity increased significantly in the 12.5–25°C range, likely because the optimal temperature for strobilation is 12.5°C, making the post-spring, summer-autumn period a high-speed reproduction phase for population supplementation. The 15–25°C range of Bohai Sea and Yellow Sea waters in summer-autumn thus represents a high reproduction period. Our results align with the view that global warming-induced temperature increases may enhance jellyfish populations in temperate regions [32–33], indicating that *Aurelia* sp. 1 in the Yellow Sea and Bohai Sea is a typical temperate-water species with ecological habits consistent with other temperate *Aurelia* populations.

The salinity range in our experiments (7.5–40) encompassed all possible natural conditions, including variable estuarine environments. The 100% survival in 15–40 salinity demonstrates broad salinity tolerance, explaining why *Aurelia* can inhabit bays, coastal waters, and estuaries. This aligns with many studies showing non-significant salinity effects on polyp reproduction [11, 27], though Willcox et al. suggested high salinity accelerates population growth [11]. In our study, budding was highest at salinity 22.5, with slightly faster reproduction at lower salinities.

Aurelia polyps are commonly found on ship hulls, aquaculture floats, and bridge pilings in shaded locations [30, 34], exhibiting behavior of moving toward shaded areas [35]. While light effects are less pronounced than temperature and food, light is an indispensable factor regulating polyp populations [37–38]. Different geographic populations show distinct light preferences: Taiwan' s tropical *Aurelia aurita* showed decreased budding with reduced light intensity (375, 56, 0 lux) [31], while Washington' s *Aurelia labiata* showed increased budding with reduced daily light duration (12, 8, 4 h) [30]. Previous research focused on light effects on strobilation, with most studies concluding that strong light inhibits strobilation while dark or dim conditions increase strobilation rates [31, 39–40]. Our preliminary studies showed polyp survival decreased with increasing light intensity [35], though survival in the current experiment was higher, possibly due to better food supply. Polyp survival depends on multiple factors; under identical light conditions, well-fed polyps likely survive better than starved ones.

Food quantity critically regulates jellyfish populations [27, 41]. Under suitable temperatures, well-fed *Aurelia* polyps rapidly reproduce to increase populations. Unlike other large jellyfish species whose polyps typically produce only one podocyst during podocyst reproduction (e.g., *Nemopilema nomurai* and *Cyanea* *nozakii* produce at most 2-3 podocysts), *Aurelia* polyps can simultaneously produce multiple offspring polyps, with the fastest reproduction rate among these species. Food provides energy for repeated asexual reproduction. Han and Uye observed maximum budding in the group with highest food levels [28], and Shi et al. concluded that higher food levels enhance polyp reproductive capacity [17]. Our results confirm that *Aurelia* sp. 1 reproduction velocity increases with food quantity. The 100% survival in unfed groups demonstrates strong starvation resistance, though survival time under starvation is directly related to temperature, with higher temperatures accelerating metabolism and reducing survival time.

Conclusions

Although salinity did not significantly affect polyp reproduction rate, *Aurelia* sp. 1 polyps exhibited broad salinity tolerance (15-40) with 100% survival. Polyps showed 100% survival across 0-25°C, with highest relative reproduction velocity at 5-25°C. Dark conditions favored population increase, while light intensity increases inhibited reproduction. Relative reproduction velocity increased with food quantity. These results demonstrate strong environmental adaptability of *Aurelia* sp. 1 polyps, suggesting that increased food availability can rapidly increase polyp populations. The increasingly frequent blooms of *Aurelia* in Yellow Sea and Bohai Sea coastal waters may continue to spread and intensify, warranting early control and prevention measures.

References

[1] Mills C E. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions?. *Hydrobiologia*, 2001, 451(1): 55-68.
[2] [Reference text appears incomplete in original]
[3] Ki J S, Hwang D S, Shin K, Yoon W D, Lim D, Kang Y S, Lee Y, Lee J S. Recent moon jelly (*Aurelia* sp.1) blooms in Korean coastal waters suggest global expansion: examples inferred from mitochondrial COI and nuclear ITS-5.8S rDNA sequences. *ICES Journal of Marine Science*, 2008, 65: 443-452.
[4] Purcell J E, Uye S I, Lo W T. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, 2007, 350: 153-174.
[5] Uye S I, Fujii N, Takeoka H. Unusual aggregations of the scyphomedusa *Aurelia aurita* in coastal waters along western Shikoku, Japan. *Plankton Biology and Ecology*, 2003, 50(1): 17-21.
[6] Dong Z J, Liu D Y, Keesing J K. Jellyfish blooms in China: Dominant species, causes and consequences. *Marine Pollution Bulletin*, 2010, 60(7): 954-963.

[7] [Reference appears to be about large jellyfish distribution in northern Liaodong Bay]
[8] [Reference appears to be about *Aurelia* biology and blooms]
[9] Dawson M N, Hamner W M. Geographic variation and behavioral evolution in marine plankton: the case of *Mastigias* (Scyphozoa, Rhizostomeae). *Marine Biology*, 2003, 143(6): 1161–1174.
[10] Dawson M N, Jacobs D K. Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). *The Biological Bulletin*, 2001, 200(1): 92–96.
[11] Willcox S, Moltchaniwskyj N A, Crawford C. Asexual reproduction in scyphistomae of *Aurelia* sp.: Effects of temperature and salinity in an experimental study. *Journal of Experimental Marine Biology and Ecology*, 2007, 353(1): 107–114.
[12] Palmen E. Seasonal occurrence of ephyrae and subsequent instars of *Aurelia aurita* (L.) in the shallow waters of Tvärminne, S Finland. *Archivum Societatis Zoologicae Botanicae Fennicae*, 1953, 8: 122–131.
[13] Dong Z J, Liu Z Y, Liu D Y. Genetic characterization of the scyphozoan jellyfish *Aurelia* spp. in Chinese coastal waters using mitochondrial markers. *Biochemical Systematics and Ecology*, 2015, 60: 15–23.
[14] [Reference appears to be about ITS-5.8S rDNA sequence analysis]
[15] [Reference appears to be about feeding frequency effects on *Aurelia* sp.1 polyps]
[16] Wang N, Li C L, Liang Y, Shi Y Q, Lu J L. Prey concentration and temperature effect on budding and strobilation of *Aurelia* sp.1 polyps. *Hydrobiologia*, 2015, 754(1): 125–134.
[17] Shi Y, Wang N, Li C, Liu Y, Lu J. Effects of temperature and food level on asexual reproduction of *Aurelia* sp.1 polyps. *Hydrobiologia*, 2016, 36(3): 786–794.
[18] Wang Y T, Zheng S, Sun S, Zhang F. Effect of temperature and food type on asexual reproduction in *Aurelia* sp.1 polyps. *Hydrobiologia*, 2015, 754(1): 169–178.
[19] Lucas C H. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia*, 2001, 451(1): 229–246.
[20] Uye S, Kayano Y. Predatory feeding of the planktonic copepod *Tortanus forcipatus* on three different prey. *Bulletin of the Plankton Society of Japan*, 1994, 40(2): 173–176.
[21] Mayer A G. Medusae of the World. III. The Scyphomedusae. Washington, DC: Carnegie Institute of Washington, 1910: 499–735.
[22] Kroiher M, Sieftker B, Berking S. Induction of segmentation in polyps of *Aurelia aurita* (Scyphozoa, Cnidaria) into medusae and formation of mirror-image medusa anlagen. *The International Journal of Developmental Biology*, 2000, 44(5): 485–490.
[23] Berrill N J. Developmental analysis of Scyphomedusae. *Biological Reviews*, 1949, 24(4): 393–409.
[24] [Reference appears to be about jellyfish bloom mechanisms in the East China Sea]

[25] Vagelli A A. New observations on the asexual reproduction of *Aurelia aurita* (Cnidaria, Scyphozoa) with comments on its life cycle and adaptive significance. *Invertebrate Zoology*, 2007, 4: 111–127.
[26] Holst S. Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. *Hydrobiologia*, 2012, 690(1): 127–140.
[27] Thein H, Ikeda H, Uye S I. The potential role of podocysts in perpetuation of the common jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) in anthropogenically perturbed coastal waters. *Hydrobiologia*, 2012, 690(1): 157–167.
[28] Han C H, Uye S I. Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* s.l. *Plankton and Benthos Research*, 2010, 5(3): 98–105.
[29] Purcell J E, Atienza D, Fuentes V, Olariaga A, Tilves U, Colahan C, Gili J M. Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. *Hydrobiologia*, 2012, 690(1): 169–180.
[30] Purcell J E. Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata*. *Marine Ecology Progress Series*, 2007, 348: 183–196.
[31] Liu W C, Lo W T, Purcell J E, Chang H H. Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. *Hydrobiologia*, 2009, 616(1): 247–258.
[32] Purcell J E. Climate effects on formation of jellyfish and ctenophore blooms: A review. *Journal of the Marine Biological Association of the United Kingdom*, 2005, 85(3): 461–476.
[33] [Reference appears to be about marine jellyfish ecology research progress]
[34] Brewer R H. Larval settlement behaviour in the jellyfish *Aurelia aurita* (Linnaeus) (Scyphozoa: Semaeostomae). *Estuaries*, 1978, 1(2): 120–122.
[35] [Reference appears to be about light intensity effects on *Aurelia* polyp survival and growth]
[36] Kakinuma Y. An experimental study of the life cycle and organ differentiation of *Aurelia aurita* Lamarck. *The Bulletin of the Marine Biological Station of Asamushi*, 1975, 15: 101–113.
[37] Dong J, Sun M, Purcell J E, Chai Y, Zhao Y, Wang A Y. Effect of salinity and light intensity on somatic growth and podocyst production in polyps of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae). *Hydrobiologia*, 2015, 754(1): 75–83.
[38] [Reference appears to be about environmental factor effects on *Aurelia* development]
[39] Custance D R N. Light as an inhibitor of strobilation in *Aurelia aurita*. *Nature*, 1964, 204(4964): 1219–1220.
[40] Ishii H, Shioi H. The effects of environmental light condition on strobilation in *Aurelia aurita*.
[41] Hamed A E, Khaled A A. Reproductive strategy of the jellyfish *Aurelia aurita* polyps (Cnidaria Scyphomedusae) in the Suez Canal and its migration between the Red Sea and Mediterranean. *Aquatic Ecosystem Health & Management*, 2011, 14(3): 269–275.
[42] Ishii H, Watanabe T. Experimental study of growth and asexual re-

production in *Aurelia aurita* polyps. *Sessile Organisms*, 2003, 20: 69-73.

Note: Figure translations are in progress. See original paper for figures.