Morphological characteristics of ephyrae of *Aurelia coerulea* derived from planula strobilation

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Abstract

Ephyrae are produced through the strobilation of polyps in the general life cycle of *Aurelia coerulea*. However, it has been reported that planulae can also metamorphose directly into ephyrae, without passing through the polyp stage. There is a mixture of ephyrae developed from planulae (planula-strobilated ephyrae) and ephyrae developed from polyps (polyp-strobilated ephyrae) in the ephyra population. However, the effect of the planula-strobilated ephyrae on the ephyra population is yet to be determined, since their morphological characteristics have not yet been elucidated. This study aimed to determine the morphological characteristics to distinguish between planula-strobilated and polyp-strobilated ephyrae. The differences in body dimensions, such as total body diameter (TBD), central disc diameter (CDD), lappet stem length (LStL), rhopalial lappet length (RLL), and total marginal lappet length (TMLL) were compared between the two types of ephyra. Thus, we show that body proportions can be used to identify planula- and polyp-strobilated ephyrae. The ranges for identifying planula-strobilated ephyra were 35.0–38.3% for CDD/TBD, 56.7–64.9% for LStL/CDD, 84.7–99.5% for TMLL/CDD, and 31.0–37.5% for RLL/TMLL. This method could be an important basis for devising countermeasures for jellyfish blooms in areas where ephyrae deriving from planula strobilation occur.

Keywords Life cycle · Polyp · Body proportion ratio · Marginal lappet · Planula strobilation

Introduction

The mass occurrence of the scyphozoan moon jellyfish, *Aurelia* spp., disrupts coastal economic activities, especially electric power plants and fisheries (Purcell and Arai 2001; Purcell et al. 2007). The scyphozoan moon jellyfish *Aurelia* spp., alternate between asexual benthic polyp and

sexual planktonic medusa stages in their life cycle. Fertilized eggs develop into planulae, which attach to a suitable substrate, and metamorphose into polyps. Polyps produce clones asexually and create colonies. The polyps subsequently then transform into strobilae, releasing planktonic ephyrae in winter and regenerate into polyps again. The released ephyrae grow into sexually mature medusae during

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summer. However, it was reported that *A. aurita* in Germany, and *A. aurita* [later changed to *A. coerulea* (Scorrano et al. 2016)] in Japan (Fig. 1) have shown another variation in their life cycle, where the planula ostensibly metamorphoses directly into an ephyra, omitting the polyp stage after settling on substrate (Haeckel 1881; Hirai 1958; Kakinuma 1975; Miyake et al. 2019; Suzuki et al. 2019; Yasuda 1975, 1979; Lucas 2001). This was called ‘*Ephyra pedunculata*’ by Haeckel (1881) and Hirai (1958) and is currently referred to these days as ‘direct development’ (Berrill 1949; Hirai 1958;

Kakinuma 1975; Yasuda 1975, 1979; Arai 1997; Lucas 2001). However, Arai (1997: p 159) noted direct development of ephyrae from planulae only in *Pelagia*, a phenomenon also observed in *Periphylla* by Jarms et al. (1999), where the planula develops into an ephyra without settling on substrate. Miyake et al. (2019) suggested that the direct development of *A. coerulea* may be due to the strobilation of planulae because large planulae developed into ephyrae in low water temperature conditions, and into polyps in high water temperature conditions, similar to normal strobilation

Fig. 1. Map of distribution of the planula-strobilation type *Aurelia* in Japan (○) and sampling points (☆)

from polyps. Therefore, the direct development of *A. coerulea* planulae should be called ‘planula strobilation’ as it includes a benthic stage. The following details have been reported regarding this kind of development in *Aurelia*.

1. The planula size of the planula-strobilation type is 500–800 μm ; while that of the polyp-strobilation type is 200–300 μm (Kakinuma 1975; Yasuda 1988).
2. The mature oocytes of medusae in the areas where the planula-strobilation type is distributed are large (Kon and Honma 1972; Yasuda 1988; Suzuki et al. 2019).
3. Medusae inhabiting the area where the planula-strobilation type is distributed produce large planulae from winter to spring and small planulae from summer to autumn (Yasuda 1988; Suzuki et al. 2019).
4. The planula-strobilation type *Aurelia* was identified as *A. coerulea* using DNA barcodes of the cytochrome oxidase subunit I (COI) and the internal transcribed spacer 1 (ITS-1) region (Miyake et al. 2019; Suzuki et al. 2019).

Yasuda (1988) and Suzuki et al. (2019) reported that medusae with large planulae appear only during the low water temperature period ($< 20\text{ }^{\circ}\text{C}$) from winter to spring. These reports suggested that most of the ephyrae appearing during this period are produced by direct development from planulae (planula strobilation), and that this is one of their reproductive strategies during the low water temperature period. In contrast, polyp strobilation occurred during the low water temperature period ($< 20\text{ }^{\circ}\text{C}$) from March to May in Urazoko Bay (Yasuda 1988). It is also suggested that polyp strobilation may occur during the same period as planula strobilation in Maizuru Bay (Suzuki et al. 2019), implying that ephyrae from both planula- and polyp-strobilation coexist in the same ephyra population. It is important to study the life cycle strategies of the planula-strobilated ephyrae to determine their effect on the *Aurelia* medusa population. However, there are currently no methods for estimating these effects, since there is no genetic difference in DNA barcodes between planula-strobilated ephyrae and polyp-strobilated ephyrae. Moreover, the morphological differences between the two types are unclear. This study aimed to determine the morphological characteristics for distinguishing between planula- and polyp-strobilated ephyrae.

Materials and methods

The planula-strobilation type of *A. coerulea* is found in Nanao Bay (Miyake et al. 2019). Two hundred and forty-one medusae of *A. coerulea* were collected near the Notojima Aquarium (Nanao, Ishikawa Prefecture, Japan), which is located in Nanao Bay, in April 2020 (Fig. 1). The medusae

were kept in an exhibition tank at the Notojima Aquarium. Water temperature was maintained at approximately $15\text{ }^{\circ}\text{C}$. On 23 June 2020 planulae were collected from three medusae (approximately 300 individuals per medusa) in the exhibition tank, and each set of planulae from the three medusae was transferred into separate Petri-dishes (63 mm in diameter, 34.6 mm in height). The planulae were transferred to the laboratory in a cooler box to maintain a low temperature and were kept in an incubator at $15\text{ }^{\circ}\text{C}$ to collect ephyrae strobilated from large planulae. The ephyrae strobilated from large planulae were defined as E1 (Fig. 2).

On 19 March 2020, large planulae ($n = 66$) were collected from a medusa in Miyazu Bay (Kyoto Prefecture) next to Maizuru Bay (Fig. 1), where the planula-strobilation type is distributed (Suzuki et al. 2019). Individual planulae were placed in each well of 12-well plates and incubated at $15\text{ }^{\circ}\text{C}$ in the laboratory to distinguish polyps developed from residua after planula strobilation (PRP: planula-residuum polyp in Fig. 2) and polyps developed directly from planulae (IPP: large-planula polyp in Fig. 2). Polyps (nPP: normal-size planula polyp in Fig. 2) collected from Aburatsubo (Kanagawa Prefecture) were used as a control strain of *A. coerulea*, common along the Pacific coast of Japan (Fig. 1). The polyps from Aburatsubo were identified as *A. coerulea* by rearing the medusa generation as well as DNA barcoding using cytochrome oxidase subunit I (COI). The polyps were fed *Artemia* nauplii every 2 days and kept at a temperature of $23\text{ }^{\circ}\text{C}$. Three to four hours after feeding, the rearing water was replaced with filtered seawater (pore size: $1\text{ }\mu\text{m}$). Polyp strobilation was induced in an incubator by decreasing the temperature to $15\text{ }^{\circ}\text{C}$ to obtain ephyrae. The ephyrae were divided into two categories and four types of ephyra in this study, as follows in Fig. 2.

- E1: Ephyra strobilated from a large planula.
- E2: Ephyra derived from polyp strobilation.
- E2.1: Ephyra liberated through strobilation of the residual polyp after the strobilation of a large planula.
- E2.2: Ephyra liberated through strobilation of the polyp developed directly from a large planula.
- E2.3: Ephyra liberated from a normal-sized planula.

Ephyrae were photographed using a digital camera (EOS Kiss X6i; Canon, Tokyo, Japan) mounted on a stereomicroscope (SZX12; Olympus, Tokyo, Japan) within 24 h after liberation. Body dimensions like the total body diameter (TBD), central disc diameter (CDD), lappet stem length (LStL), rhopalial lappet length (RLL), and total marginal lappet length (TMLL) of ephyrae were measured according to Straehler-Pohl and Jarms (2010), using the image analysis software, ImageJ (Schneider et al. 2012) (Fig. 3). Statistical analysis was performed in R version 4.0.3 (Team 2020). An ANCOVA was used to compare the differences in the

Fig. 2. Different types of ephyra formation. E1: Ephyra strobilated from a large planula. E2: Ephyra derived from polyp strobilation. E2.1: Ephyra liberated through strobilation of the residual polyp (PRP: planula-residual polyp) after strobilation of large planula. E2.2: Ephyra liberated through strobilation of polyp developed directly from large planula (IPP: large-planula polyp). E2.3: Ephyra liberated through strobilation of polyp developed directly from normal-sized planula (nPP: normal-size planula polyp)

Fig. 3. Measuring parts of ephyra. TBD total body diameter, CDD: central disc diameter, LSIL lappet stem length, RLL rhopalial lappet length, TMLL total marginal lappet length. Scale bar = 1 mm

regression coefficients between each measurement part and Tukey's multiple comparison test was used to compare the difference in the ratios of each body proportion between the four types of ephyrae.

Results

Planulae in one of three sets of Petri-dishes, which were collected at the Notojima Aquarium, strobilated and released single ephyrae 4 days after collection. Ephyrae with a perfect marginal lappet were selected for measurement of the body dimensions ($n = 105$, E1 in Figs. 2, 4). The size range of these large planulae was 389–558 μm , and the average size was $444.0 \pm 35.8 \mu\text{m}$ ($n = 50$).

Forty-four planulae collected in Miyazu Bay released ephyrae by planula-strobilation and produced residua, 16 planulae developed into polyps, and six planulae died.

Fig. 4. Morphology differences between the four types of ephyrae. (a) Strobilation from planula attached to substrate, releasing only a single ephyra, white arrow indicates a residuum with already developed calyx and hypostome still lacking tentacles; (b) polyps developed

from residua; (c) ephyra from planula strobilation (E1 in Fig. 2); (d) ephyra from polyp strobilation type 2.1 (E2.1 in Fig. 2), (e) ephyra from polyp strobilation type 2.2 (E2.2 in Fig. 2); (f) ephyra from polyp strobilation type 2.3 (E2.3 in Fig. 2). Scale bar = 1 mm

Seventeen out of 44 residua disappeared. The remaining 27 residua developed into polyps within 2 days. These polyps were kept at 23 °C for 2 months and they strobilated after 30 days when the temperature was decreased to 15 °C. The number of ephyrae produced by residual polyps (E2.1 in Figs. 2, 4), those from polyps developed directly from large planulae (E2.2, Figs. 2, 4), and those produced by normal-sized planulae (E2.3, Figs. 2, 4) were 84, 72, and 19 ephyrae, respectively.

Table 1 shows body dimensions of all types of ephyrae.

The ratios between TBD and CDD, CDD and LStL, CDD and TMLL, and RLL and TMLL differed significantly among the four ephyrae types (ANCOVA: $p < 0.001$, Fig. 5). Tukey's multiple comparison test ($p < 0.001$) demonstrated that the ratios (%) of CDD/TBD, LStL/CDD, TMLL/CDD, and RLL/TMLL were significantly different between the ephyrae derived from planula strobilation (E1) and ephyrae derived from polyp strobilation (E2: E2.1, E2.2, and E2.3). There were no significant differences among the polyp-strobilated ephyrae (E2: E2.1, E2.2, and E2.3). The results

Table 1. The sizes of the parts of the all types of ephyrae

	E1 (<i>n</i> = 105)	E2.1 (<i>n</i> = 84)	E2.2 (<i>n</i> = 72)	E2.3 (<i>n</i> = 19)	E2 (<i>n</i> = 175)
TBD	1.63 ± 0.24	2.98 ± 0.28	3.06 ± 0.34	3.09 ± 0.33	3.02 ± 0.31
CDD	0.60 ± 0.09	1.20 ± 0.16	1.24 ± 0.16	1.19 ± 0.14	1.21 ± 0.16
LStL	0.36 ± 0.05	0.58 ± 0.05	0.58 ± 0.07	0.57 ± 0.07	0.58 ± 0.06
RLL	0.19 ± 0.05	0.37 ± 0.07	0.39 ± 0.06	0.44 ± 0.05	0.38 ± 0.06
TMLL	0.55 ± 0.09	0.95 ± 0.10	0.96 ± 0.10	1.00 ± 0.19	0.96 ± 0.10

E1, E2.1, E2.2, E2.3, and E2 shown in Fig. 2

Fig. 5. Relationships between TBD, CDD, LStL, RLL, and TMLL. ***Shows significant difference $p < 0.001$

showed that the three types of ephyra strobilated by polyps (E2: E2.1, E2.2, and E2.3) can be clearly distinguished

from planula-strobilated ephyrae. Body proportion ratios are depicted in Fig. 6 and given in Table 2.

Fig. 6. The difference of the ratios of each body proportion between the four types of ephyrae. Asterisk shows significant differences: *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

Discussion

The total body diameter (TBD) of the planula-strobilated ephyrae (1.63 ± 0.24 mm) was approximately half the size of the TBD of the polyp-strobilated ephyrae (3.02 ± 0.31 mm) (Table 1 and Fig. 7). Almost all planula tissue was used to produce a small ephyra by planula strobilation. As a result, only a small number of tiny residua was produced (27 out of 44). Only 27 residua developed into tiny polyps while 17 disappeared, suggesting that strobilating planulae use their energy to release an ephyra that can swim away rather than producing polyps or regenerative tissue residua for further polyp development.

Fu et al. (2014) studied the point of no return from starvation in the ephyrae of *A. aurita* sensu lato (later *A. coerulea*). They determined that the PNR_{50} (the starvation period at which 50% of ephyrae recovered from starvation and grew to the advanced ephyrae stage) was the point at which the disc diameter decreased by 30% compared with ephyra size just after liberation from strobila, and was longer under lower water temperature conditions. The average TBD at PNR_{50} was 1.36 mm at 15 °C, 1.69 mm at 12 °C, and 1.65 mm at 9 °C, similar to those of the planula-strobilated ephyrae. The starvation tolerance of ephyrae is an adaptive strategy to survive in the primary season of ephyrae liberation when zooplankton biomass is low (Fu et al. 2014). This suggests

Table 2 Differences in the body proportion ratios between the ephyrae of the E1 and E2 types

		E1	E2
CDD/TBD (%)	Mean $\pm$ SD	36.7 $\pm$ 2.6	40.1 $\pm$ 2.3
	First quartile	35.0	38.4
	Third quartile	38.3	41.7
LStL/CDD (%)	Mean $\pm$ SD	60.9 $\pm$ 6.5	47.8 $\pm$ 4.5
	First quartile	56.7	44.9
	Third quartile	64.9	50.7
TMLL/CDD (%)	Mean $\pm$ SD	92.9 $\pm$ 11.1	79.3 $\pm$ 7.4
	First quartile	84.7	74.4
	Third quartile	99.5	84.1
RLL/TMLL (%)	Mean $\pm$ SD	34.1 $\pm$ 3.9	40.0 $\pm$ 4.2
	First quartile	31.0	37.1
	Third quartile	37.5	42.6

Fig. 7. Total body diameter values for the four types of ephyrae. *** Shows significant difference ($p < 0.001$)

that the size of the planula-strobilation ephyrae is the biological minimum size of ephyrae for survival in nature. Thus, planula strobilation is an adaptive strategy to increase fitness by releasing a minimum-sized ephyra, which can survive on minimal energy, during the low water temperature season.

The ephyra types can be distinguished by body dimensions (Table 1). However, Suzuki et al. (2019) reported no differences in size between ephyrae strobilated by planulae and polyps. Any difference may depend on the difference in planula sizes ($679 \pm 142 \mu\text{m}$ in Suzuki et al. (2019) and $444.0 \pm 35.8 \mu\text{m}$ in the current study). The ratios of these planula sizes are also similar to the ratios of ephyra sizes (2.5 mm in Suzuki et al. (2019) and 1.6 mm in the current study). However, the mean TBD and CDD were 2.5 mm and

0.9 mm, respectively, and the CDD/TBD ratio was 36% for Suzuki et al. (2019); and the CDD/TBD value was within 35.0–38.3% of the interquartile range of the CDD/TBD ratio in our study. In addition, among the planula-strobilated ephyrae observed in this study, an ephyra with a TBD of 2.5 mm had a CDD/TBD value of 31.5%, which does not fall within the range but indicates that the ratio of CDD/TBD is remarkably small. Moreover, this specimen had an LStL/CDD value of 60.1%, a TMLL/CDD value of 99.2%, and an RLL/TMLL value of 39.5%. All these values fall within the range to identify planula-strobilated ephyrae, except for RLL/TMLL. Even if TBD is similar to that of polyp-strobilated ephyrae, it is possible to identify the strobilation type of ephyrae based on body dimensions.

Therefore, CDD/TBD, LStL/CDD, TMLL/CDD, and RLL/TMLL ratios can be used to distinguish between planula-strobilated and polyp-strobilated ephyrae. In addition, the interquartile ranges of the ratios can be used for identifying the strobilation type. The ranges for identifying planula-strobilated ephyrae were 35.0–38.3% for CDD/TBD, 56.7–64.9% for LStL/CDD, 84.7–99.5% for TMLL/CDD, and 37.5–31.0% for RLL/TMLL. These results indicate that the planula-strobilated ephyrae have long marginal lappets compared with central disk diameter. The lack of difference in the RLL/CDD ratio indicates no difference in the lappet's crack depth between the ephyra types, suggesting that planula-strobilated ephyrae have long marginal lappet stems. The body size of planula-strobilated ephyrae was smaller than that of polyp-strobilated ephyrae, and the swimming ability of planula-strobilated ephyrae was low, regardless of the long marginal lappet of planula-strobilated ephyrae acting as a paddle (Higgins et al. 2008; Feitl et al. 2009), and generating propulsion to allow the ephyrae to swim.

The appearance of planula-strobilating moon jellyfish has been observed only in a few places in Japan (Mutsu Bay, Aomori Prefecture; Urazoko Bay, Fukui Prefecture; Maizuru Bay, Kyoto Prefecture; and Nanao Bay, Ishikawa Prefecture) (Hirai 1958; Kakinuma 1975; Miyake et al. 2019; Suzuki et al. 2019; Yasuda 1975, 1979) and Germany (Haeckel 1881). However, planula-strobilated ephyrae have been observed in areas with thermal and nuclear plants in the Wakasa and Maizuru Bays (Yasuda 1988; Suzuki et al. 2019). To prevent power plant accidents due to invasion of the water intake by a large number of *A. coerulea*, a series of ecological studies of *A. aurita* were conducted by Dr. Toru Yasuda (1988). The bell-size of mature medusae, oocyte, and planula sizes were the only parameters used to distinguish between planula strobilation and polyp strobilation in previous studies (Kon and Honma 1972; Kakinuma 1975; Yasuda 1975; Suzuki et al. 2019). This study provides a method to discriminate between the strobilation types based on the morphology of ephyrae. Yasuda (1975) and Suzuki et al. (2019) speculated that the *Aurelia* population was

mixed, with both planula-strobilated and polyp-strobilated ephyrae occurring in their sampling field. The methodology of this study could clarify the proportion and population dynamics of planula-strobilated ephyrae in the field. Elucidation of the population dynamics of planula strobilation ephyrae using this method could be an important basis for preparing countermeasures for jellyfish blooms in areas where planula strobilation occurs.

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References

- Arai M (1997) A functional biology of Scyphozoa. Chapman & Hall, p 316
- Berrill NJ (1949) Developmental analysis of scyphomedusae. *Biol Rev Camb Philos Soc* 24:393–410
- Feitl KE, Millett AF, Colin SP, Dabiri JO, Costello JH (2009) Functional morphology and fluid interactions during early development of the scyphomedusa *Aurelia aurita*. *Biol Bull* 217:283–291
- Fu ZL, Shibata M, Makabe R, Ikeda H, Uye SI (2014) Body size reduction under starvation, and the point of no return, in ephyrae of the moon jellyfish *Aurelia aurita*. *Mar Ecol Prog Ser* 510:255–263
- Haeckel E (1881) Metagenesis und hypogenesis von *Aurelia aurita*. Ein Beitrag zur Entwicklungsgeschichte und zur Teratologie der Medusen. Gustav Fischer, Jena
- Higgins JE, Ford MD, Costello JH (2008) Transitions in morphology, nematocyst distribution, fluid motions, and prey capture during development of the scyphomedusa *Cyanea capillata*. *Biol Bull* 214:29–41
- Hirai E (1958) On the developmental cycles of *Aurelia aurita* and *Dactylometra pacifica*. *Bull Mar Biol Stat Asamshi* 9:81
- Jarms G, Båmstedt U, Tiemann H, Martinussen MB, Fosså JH (1999) The holopelagic life cycle of the deep-sea medusa *Periphylla periphylla* (Scyphozoa, Coronatae). *Sarsia* 84:55–65
- Kakinuma Y (1975) An experimental study of the life cycle and organ differentiation of *Aurelia aurita* Lamarck. *Bull Mar Biol Stat Asamshi* 15:101–112
- Kon T, Honma Y (1972) Studies on gonad maturity in some marine invertebrates-V. Seasonal changes in the gonads of the moon jelly. *Bull Jpn Soc Sci Fish* 38:545–553
- Lucas CH (2001) Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* 451:229–246
- Miyake H, Ikeguchi S, Takayama K, Yoshikawa M, Arima S, Suzuki N (2019) On the moon jelly which develops to ephyra directly from planula. *Aquabiology* 41:54–59 (in Japanese with English abstract)
- Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451(18):27–44
- Purcell JE, Uye S, Lo W (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar Ecol Prog Ser* 350:153–174
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671
- Scorrano S, Aglieri G, Boero F, Dawson MN, Piraino S (2016) Unmasking *Aurelia* species in the Mediterranean Sea: an integrative morphometric and molecular approach. *Zool J Linn Soc*. <https://doi.org/10.1111/zoj.12494>
- Straehler-Pohl I, Jarms G (2010) Identification key for young ephyrae: a first step for early detection of jellyfish blooms. *Hydrobiologia* 645(1):3–21
- Suzuki KS, Suzuki KW, Kumakura E, Sato K, Oe Y, Sato T, Sawada H, Masuda R, Nogata Y (2019) Seasonal alternation of the ontogenetic development of the moon jellyfish *Aurelia coerulea* in Maizuru Bay Japan. *PLoS ONE* 14:e0225513
- Yasuda T (1975) Ecological studies on the jelly-fish, *Aurelia aurita* (L.), in Urazoko Bay, Fukui Prefecture-XI. An observation on ephyra formation. *Publ Seto Mar Lab* 22:75–80
- Yasuda T (1988) Studies on the common jelly-fish, *Aurelia aurita* (Linné). Japan Fisheries Resource Conservation Association

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