Ingestion and growth rates of *Aurelia coerulea* polyps fed naturally occurring copepods as food

Haruto Ishii* and Yoko Takahashi

Tokyo University of Marine Science and Technology, 4–5–7 Konan, Minato-ku, Tokyo 108–4177, Japan

* Corresponding author: Haruto Ishii  E-mail: ishii@kaiyodai.ac.jp

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Abstract

The ingestion rates and somatic growth of *Aurelia coerulea* polyps fed *Artemia* nauplii or *Oithona davisae* were estimated. The ingestion rates of polyps fed *O. davisae* increased with increasing prey densities, and they were not saturated in all polyp size groups. Furthermore, the ingestion rates of polyps fed *O. davisae* were not attained to the level of the ones fed *Artemia* even if the highest density of *O. davisae* was supplied. The specific growth rates of polyps fed *Artemia* were also significantly higher than the ones fed *O. davisae* under all prey densities. The ingestion and growth rates of polyps fed *Artemia* will not be realistic to apply to the polyps settled in natural seawaters given the prey densities in ambient seawaters. In this study, it is appeared that *A. coerulea* polyps can utilize the most dominant copepods *O. davisae* as a food source, and the estimated ingestion and specific growth rates will be applied to the naturally settled *A. coerulea* polyps in ambient seawaters.

Keywords: jellyfish, polyp, *Aurelia*, *Oithona*, Tokyo Bay

Introduction

The mass occurrence and dense aggregations of jellyfish have been reported from several waters in the world (Möller, 1980; Behrends and Schneider, 1995; Brodeur et al., 1999; Graham, 2001; Mills, 2001; Purcell et al., 2007), and the outbreaks of *Aurelia coerulea* are frequently observed in coastal waters around Japan (Kuwahara et al., 1969; Uye et al., 2003; Uye and Ueta, 2004). The life cycle of *A. coerulea* involves pelagic medusa and benthic polyp stages. Polyps can expand their population size by asexual budding reproduction and produce asexually ephyrae through strobilation during the benthic stage. Ephyra production in each strobila can directly contribute to medusa recruitment. Knowing the ecology of *A. coerulea* polyps during the benthic stage is highly important since the population dynamics of polyps consequently influence the mass occurrence of medusae in ambient seawater (Ishii, 2001; Purcell et al., 2007; Lo et al., 2008; Toyokawa et al., 2011; Yoon et al., 2018).

Among the environmental factors, temperature and food concentrations have been revealed to be significant factors for the asexual reproduction of *A. coerulea* polyps (Ishii and Watanabe, 2003; Han and Uye, 2010; Wang et al., 2015). Moreover, it has been affirmed that plenty of food supply enhances the somatic growth and asexual reproduction of polyps by budding (Ishii and Watanabe, 2003; Han and Uye, 2010). Food supply can be a major factor for polyp production, however, most of the previous studies have preferentially used *Artemia* nauplii as a major food source (Ishii and Watanabe, 2003; Han and Uye, 2010; Wang et al., 2015), which does not reflect natural prey composition. In Tokyo Bay, where the outbreak of *A. coerulea* is frequently observed, large amounts of small cyclopoid copepod *Oithona davisae* are distributed. *Oithona davisae* is known as the most dominated zooplankton in Tokyo Bay (Anakubo and Murano, 1991; Nomura, 1994; Ito and Aoki, 2010) and is employed as one of the major food sources of *A. coerulea* medusae throughout the year (Ishii and Tanaka, 2001). Nonetheless, no studies have explored the feeding behavior of *A. coerulea* polyps toward the naturally occurring copepods despite their dominance in the coastal marine ecosystems. It will be very favorable for *A. coerulea* polyps if they can utilize these small dominant copepods as a food source.

The present study aimed to know whether *A. coerulea* polyps can utilize naturally occurring copepods, such as *O. davisae*, as food. The ingestion and growth rates of the polyps fed naturally occurring small copepod *O. davisae* was estimated. In the experiment, *Artemia* nauplii, which are generally used for aquaculture, were also supplied as the control prey to compare with *O. davisae*. This was the first estimation of the ingestion and growth rates of *A. coerulea* polyps using naturally occurring copepods as food.

Materials and methods

*Aurelia coerulea* medusae were sampled scooping with a hand net by “Hiyodori” that belongs to the Tokyo University of Marine Science and Technology (TUMSAT) on the 31st of August, 2001, in the innermost part of Tokyo Bay. The planula larvae were collected from the female medusa with a
pipette and poured into the glass bottles (900ml) filled by an ambient seawater, and they were transferred to the land laboratory. In the land laboratory, the planula larvae were settled to the floating acrylic plates (5 cm × 5 cm) in the 60-cm square aquarium with 1-µm filtered seawater in 17°C and dark conditions. All the polyps on the acrylic plates were incubated in a glass bowl with 200-mL filtered seawater at 17°C and dark conditions suppling Artemia nauplii as food until the experiments were started. The polyp diameter (mouth disk diameter) was measured once every few days under a dissecting microscope (Nikon SMZ10) with an ocular micrometer.

Newly hatched Artemia nauplii were used for the experiments (Utah, USA, body length; ca. 0.3 mm). Oithona davisae (copepod IV–VI) were carefully collected at the harbor in the TUMSAT using a plankton net (0.1 mm mesh size) by oblique tows. In the land laboratory, O. davisae were sorted under the dissecting microscope (Nikon SMZ10). The prosome length of sorted O. davisae was adjusted around 0.3 mm. Oithona davisae were also collected every day and were stocked in the 1-µm filtered seawater under 17°C and dark conditions until they were supplied for polyps.

Several polyps were controlled as one polyp on each plate before the experiments were started, and the residuals were removed from a plate with small tweezers and scalpels. The polyps were put into two prey groups fed Artemia or O. davisae for the ingestion experiment. In each prey group, three size groups of polyps were prepared (Table 1). Four to seven polyps were put into two prey groups fed O. davisae or Artemia instead of Artemia for the growth experiment, and O. davisae instead of Artemia were supplied 3 days before the start of the experiments for acclimation for the polyps fed O. davisae in the experiment. At the beginning of the experiments, we prepared the similar diameters (mm; means ± S.D.) of polyps, which were 0.468 ± 0.030 (n = 20) and 0.480 ± 0.029 (n = 20) for polyps fed Artemia and for ones fed O. davisae, respectively. All the experimental plates were immersed in the glass bowls filled with 200-mL filtered seawater, supplying following densities of Artemia or O. davisae (20, 100, 250, and 500 individuals 200 ml−1). During the experiment, the diameter of polyps on each plate was measured under the dissecting microscope every day. After the measurement of polyp diameters, the seawater was changed and new preys were supplied. In addition, the growth experiment continued 14 days under 17°C and dark conditions. Five polyps were utilized in each prey density. The daughter polyps reproduced during the growth experiments were removed at once with small tweezers and scalpels. The dry weight of each polyp was determined from polyp diameters using the following equation of Watanabe (2001):

\[
W = 0.074 \cdot D^{2.35} \quad r^2 = 0.87,
\]

where \(W\) is the dry weight of polyps (mg) and \(D\) is the central disk diameter of polyps (mm). The specific growth rate (\(\mu\; day^{-1}\)) of polyps was determined as follows:

\[
\mu = \ln \left( \frac{W_t}{W_0} \right) \cdot t^{-1},
\]

where \(W_t\) is the dry weight of polyps (mg) after \(t\) days from the start of the experiment and \(W_0\) is the one at the start of the experiment.

### Results

The ingestion rates of polyps fed Artemia abruptly increased with increasing prey densities under low prey densities, but they showed trends of saturation under high prey densities regardless of the polyp diameter (Fig. 1). The ingestion rates increased with increasing polyp diameters, and significant differences were observed among the polyp diameters, except for the lowest prey density (one-way ANOVA; Tukey method, \(p<0.01\)). The highest ingestion rate was 184 individuals polyp⁻¹ day⁻¹ for a large size group under the

### Table 1. Diameter of Aurelia coerulea polyps in each size group fed Artemia nauplii or Oithona davisae used in the ingestion experiments. Data are shown in means ± S.D.

| Size group | Artemia nauplii n | Oithona davisae n |
|------------|-------------------|-------------------|
| Small      | 0.507 ± 0.009     | 22                | 0.535 ± 0.013 | 20 |
| Medium     | 0.998 ± 0.025     | 21                | 0.999 ± 0.017 | 19 |
| Large      | 1.456 ± 0.040     | 22                | 1.556 ± 0.029 | 19 |
Ingestion growth of polyp fed copepods

The ingestion rates of polyps supplied *O. davisae* increased with increasing prey densities, and they were not saturated in all the polyp size groups (Fig. 2). The relationships between prey densities and ingestion rates were correlated by linear regression equations with a zero x intercept in each size group. The ingestion rates increased with increasing polyp diameters, and the significant differences were observed among the polyp size groups, except for the lowest prey density (one-way ANOVA; Tukey method, \( p < 0.05 \)). The highest ingestion rate was 86 individuals polyp\(^{-1}\) day\(^{-1}\) for a large size group under the highest prey densities.

Figure 3 exhibits the growth of *A. coerulea* polyps fed *Artemia* nauplii, and during the incubation experiments, the dry weights of polyps gradually increased. Further, Fig. 4 displays the growth of *A. coerulea* polyps fed *O. davisae*, and during the incubation experiments, the dry weights of polyps gradually increased.

Table 2 presents the specific growth rates of *A. coerulea* polyps throughout the experimental periods (14 days). The specific growth rates were relatively low under the lowest prey densities. Nonetheless, the significant differences of specific growth rates in polyps fed *Artemia* were not observed among the prey densities. On the polyps fed *O. davisae*, the specific growth rates were significantly low under the lowest prey densities (one-way ANOVA; Tukey method, \( p < 0.05 \)), but significant differences were not observed among the polyps under the other prey densities. The mean specific growth rate (day\(^{-1}\); means±S.D.) of polyps fed *Artemia* was 0.17±0.03, and that of the ones fed *O. davisae*, except for the lowest prey densities, was 0.089±0.018. A significant difference between these specific growth rates of polyps fed *Artemia* and ones fed *O. davisae* was observed (ANOVA, \( p < 0.01 \)).

**Discussion**

Previous studies have noticed the importance of food supply on jellyfish polyps such as *A. coerulea* for the estimation of their ingestion and growth rates (Ishii and Watanabe, 2003; Han and Uye, 2010; Wang et al., 2015). Nevertheless, the feeding behavior and growth of polyps have been observed using artificially hatched *Artemia* as food in the most of previous studies, and it has been discussed regarding the utilization of naturally occurring copepods by a few studies (Chi et al., 2019). Chi et al. (2019) used cultured calanoid copepod,
Acartia tonsa fed Rhodomonas baltica, as a food source of Aurelia aurita polyp, and active ingestion to A. tonsa by polyps was observed. Our results also validated that A. coerula polyps can ingest small copepods such as O. davisae.

The growth experiments in the present study verified that the effects of prey densities were not so reflected to the somatic growth of polyps. It is well known that produced organic matters by ingestion are employed for the somatic growth and asexual reproduction of polyps (Ishii and Watanabe, 2003; Han and Uye, 2010). In this study, asexually produced daughter polyps were removed to measure the somatic growth of each polyp itself. That is, prey densities more efficiently affect the asexual reproduction by budding than the somatic growth of polyps. It is well known that produced organic matters will depend on the quality of prey items. For somatic growth or asexual reproduction by budding, it is considered that how productive matters are utilized will determine the rates of polyps fed O. davisae in all size groups (ANOVA, p<0.01). It is considered that these differences of the ingestion rate among preys depend on the swimming speed and weight–length ratio in prey items. Slow and fat swimmers, such as Artemia, are easy to capture and obtain organic matters for polyps. Conversely, Chi et al. (2019) observed no differences relating to the growth and the asexual reproduction between the A. aurita polyps fed Artemia and ones fed A. tonsa. This will depend on the volume of the incubation container that is only 4 ml in Chi et al. (2019), and it is considered that A. tonsa will easily be ingested by polyps compared with our present study. Careful attention must be paid because the ingestion rate estimated by polyps fed Artemia may be evaluated as an over-estimation to apply the naturally settled polyps.

In Tokyo Bay, Nomura (1994) revealed that O. davisae is the most dominant zooplankton and is observed throughout the year by the long-term fluctuations of the zooplankton community based on the result of a 10-year investigation. Moreover, most of stomach contents in the A. coerula medusae are also occupied by O. davisae (Ishii and Tanaka, 2001). The highest abundance of O. davisae was observed in summer and winter (2520inds l\(^{-1}\)), and their mean abundance was 657 inds l\(^{-1}\) (Nomura, 1994). The highest and mean abundance of O. davisae approximately corresponds to the densities of 500 and 100 inds 200 ml\(^{-1}\) of prey densities in our experiments, respectively. Prey densities used in this study are in the range of actual densities in ambient seawaters. It is indicated that the estimations of ingestion and specific growth rates in this study will be applied to the naturally settled A. coerula polyps in Tokyo Bay.

In addition to O. davisae, tintinnids are also one of the dominant plankton species in Tokyo Bay (Nomura, 1994). The micro- and meso-zooplankton (20–2000 µm) collected by water bottle were dominated more than 99% tintinnids and O. davisae throughout the year (Nomura, 1994). Kamiyama (2011) estimated the ingestion rates of A. coerula polyps as a function of the ciliate density with tintinnids Favella ehrenbergii that commonly appeared in Tokyo Bay (Nomura et al., 1992). Under the highest density of tintinnids observed in Tokyo Bay, the ingestion rate of polyps fed F. ehrenbergii was 0.28µgC polyp\(^{-1}\)hr\(^{-1}\) (Kamiyama, 2011). Assuming that the individual carbon contents of O. davisae are 0.08 µg (Uye, 1982), the highest ingestion rate of polyp fed O. davisae in this study is 0.28µgC polyp\(^{-1}\)hr\(^{-1}\), and it is almost same as the ingestion rate with tintinnids. Kamiyama (2011) also estimated the ingestion rate of polyps as a function of the other small non-loricate ciliates, but their ingestion rates were very low and negligible. These estimations using naturally occurring zooplankton will also be very essential to infer the ingestion rates of polyps naturally settled in ambient seawaters.

### Table 2. Specific growth rate of Aurelia coerula polyps fed Artemia nauplii or Oithona davisae in each prey density. Data are shown in means±S.D.

| Prey density (inds 200 ml\(^{-1}\)) | Specific growth rate (day\(^{-1}\)) | Artemia nauplii | n | Oithona davisae | n |
|-----------------------------------|-----------------------------------|-----------------|---|-----------------|---|
| 20                                | 0.145±0.012                       | 5               | 0.042±0.019          | 5  |
| 100                               | 0.166±0.014                       | 5               | 0.065±0.014          | 5  |
| 250                               | 0.185±0.023                       | 5               | 0.078±0.024          | 5  |
| 500                               | 0.176±0.037                       | 5               | 0.165±0.009          | 5  |
In coastal waters, many polyp colonies of *A. coerulea* have been observed on the surface of rocks, shells, and artificial structures, such as pier, pontoon, pylon, or ship bottom (Mi- yake et al., 2002; Ishii and Katsukoshi, 2010; Toyokawa et al., 2011). It is suggested that polyp is a passive and opportunistic predator; thus, utilizing the dominant prey items in the ambient waters for their ingestion and growth is highly effective. The current study confirmed that *A. coerulea* polyps can utilize the most dominant copepods *O. davisae* as a food source. Further studies on polyps using dominant prey species will be required to estimate the applicable ingestion and growth rates in each coastal water.

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