Experimental study of growth and asexual reproduction in *Aurelia aurita* polyps

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**Abstract**

A series of experiments to investigate the effects of different combinations of water temperature and food availability on the growth, budding, and strobilation of *Aurelia aurita* polyps was conducted in the laboratory. The growth rate of *A. aurita* polyps increased with higher ambient water temperature and greater food availability. Asexual reproduction including daughter polyp production and strobilation also increased with increasing food availability. The highest mean number of discs per strobila was 20.8, when an excess of food was supplied continuously. Strobilation is induced not only by a lowering of water temperature but also by food depletion. The relationship of this finding to mass occurrences of medusae is discussed.

**Key words:** jellyfish, *Aurelia aurita*, polyp, strobilation, growth

**Introduction**

The scyphozoan jellyfish *Aurelia aurita* (L.) is found in many coastal waters (e.g. Möller, 1980) and its life cycle includes an alternation between benthic polyp and planktonic medusa stages. The polyps asexually produce daughter polyps by budding and planktonic ephyrae by strobilation. It is important to know the environmental factors affecting the asexual reproduction process, since the latter is directly correlated to consequent mass occurrence events of medusae. Such mass occurrences often result from an increase in the number of polyps that are actively undergoing asexual reproduction.

Recent physiological studies on the asexual reproduction process have shown that the induction of strobilation in *A. aurita* polyps requires a change in environmental temperature (Berrill, 1949; Kakinuma, 1962; Custance, 1964, 1966; Kato et al., 1980; Kroicher et al., 2000). For example, Berrill (1949) suggested that one of the factors necessary to induce strobilation is a low critical temperature usually observed during the winter, and this suggestion has been supported in naturally occurring populations of *A. aurita* polyps (Watanabe and Ishii, 2001). Although correlations between sudden increases or decreases in temperature and the subsequent appearance of strobilae have been shown in some of the above-mentioned studies, quantitative studies of the asexual reproduction of polyps, including growth, budding, and the strobilation process have not yet been carried out. We conducted a series of incubation experiments to investigate the simultaneous effects of water temperature and food supply on the growth, budding, and strobilation of *A. aurita* polyps in the laboratory. Regarding water temperature, we paid special attention to the length of time before a temperature drop.

**Materials and Methods**

Sampling of *Aurelia aurita* medusae was conducted in daytime aboard the T.S. “Hiyodori” of the Tokyo University of Fisheries in Tokyo Bay, Japan, on 21 June, 1994. Female medusae with planula larvae were scooped from surface aggregations with a hand net (10 mm mesh size) and kept in buckets with ambient seawater. Planula
larvae were collected with a pipette from the brood sacs of the oral arms of ripe female medusae and immediately transferred to glass bottles filled with ambient seawater. Ambient water temperature was measured at a station in the innermost part of Tokyo Bay once a month.

In the laboratory, the samples of planula larvae were cleaned by carefully pouring the larvae through a 0.33 mm mesh net into a 1200 ml bowl filled with GF/C-filtered seawater. Planula larvae were immediately transferred to petri dishes filled with GF/C-filtered seawater and incubated under the light conditions of 8L16D. Water temperature was maintained at 22°C. After 10 days the petri dishes with newly settled polyps were transferred into plastic containers (4-l) filled with GF/C-filtered seawater. The number of polyps in each petri dish was reduced to 30 individuals by removing the excess with a plastic cutter, and then the experiments were started.

A series of experiments using different combinations of water temperature and food supply was carried out for 147 days. Water temperature was 22°C before the experiments were started, but in different treatments it was lowered to 15°C after 0, 20, or 40 days from the start of the experiment. Artemia nauplii were supplied as food for A. aurita polyps once a day. In one treatment Artemia nauplii were supplied until the end of the experiment. The various combinations of experimental treatment and the abbreviations for each treatment are summarized in Table 1. When food was supplied to the polyps, each petri dish was removed from its plastic container and Artemia nauplii were added in excess. After 1-3 hours, the incubation water in the dish was replaced with fresh GF/C-filtered seawater and the dish with its polyps was placed back into plastic container.

Observations of the settled polyps in the petri dishes were made every day. For these observations, each petri dish was removed from its container, and the diameter of polyps and strobilae, the number of daughter polyps produced by budding, the number of discs in each strobila, and the number and outer diameter of liberated ephryae were immediately determined under a dissecting microscope. Daughter polyps and other organisms attached to the dish were carefully removed using a plastic cutter. After the observations, each petri dish was replaced into its plastic container.

Table 1. Combinations of temperature regime and food availability to which polyps of Aurelia aurita were expressed in the present study, showing abbreviations for each experimental treatment.

<table>
<thead>
<tr>
<th>Food supply after lowering of temperature</th>
<th>Elapsed days from start of experiment until lowering of temperature to 15°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>No food supply</td>
<td>A0  A20  A40</td>
</tr>
<tr>
<td>10 days supply</td>
<td>B0  B20  B40</td>
</tr>
<tr>
<td>Continuous food supply</td>
<td>C0  C20  C40</td>
</tr>
</tbody>
</table>

Fig. 1. Water temperature in the innermost part of Tokyo Bay measured monthly from April to December, 1994.
Experimental study of growth and asexual reproduction in *Aurelia aurita* polyps

No apparent increase in polyp diameter was detected until the end of the experiment.

The cumulative number of daughter polyps increased with a higher food supply and a longer period between the start of the experiment and the lowering of the temperature (Table 2). No daughter polyps were produced in the A0 and B0 treatments. With a continuous food supply, the mean number of daughter polyps produced from an original polyp reached as high as 122.7 individuals (C40 treatment).

Strobilation was not observed in polyps subjected to experimental treatments in which the water temperature was lowered just after the start of the experiments (A0, B0, and C0). In some other treatments, strobilations were observed (Fig. 3). Strobilae were first observed 20 days after the start of the experiments in treatment A20. Higher strobilation ratios and earlier strobilation initiation were observed in the polyps deprived of food (A20 and B20). Significant differences in cumulative strobilation ratios were not recognized among the other experimental groups.

The number of discs, period of strobilation, daily ephyra production rate and total number of liberated ephyrae per strobila, and outer diameter of ephyrae are summarized in Table 3. Treatments, A0, B0, and C0, are not included because no strobilae were observed throughout the study. Many discs per strobila were observed in treatments where food was supplied in excess continuously, up to 20.8 discs on average in treatment C40. Production rate, total number of liberated ephyrae, and ephyra size also increased with a greater food supply. The maximum average size of ephyrae was 4.0 mm.

### Table 2. Cumulative number of daughter polyps produced per polyp of *Aurelia aurita* in each treatment. Initial number of polyps in each treatment is 30. Data denote means ± S.D.

<table>
<thead>
<tr>
<th>Food supply after lowering of temperature</th>
<th>Elapsed days from start of experiment</th>
<th>0</th>
<th>20</th>
<th>40</th>
</tr>
</thead>
<tbody>
<tr>
<td>No food supply</td>
<td>0</td>
<td>5.1 ± 3.3</td>
<td>30.3 ± 11.1</td>
<td></td>
</tr>
<tr>
<td>10 days supply</td>
<td>0</td>
<td>9.8 ± 9.1</td>
<td>44.5 ± 6.5</td>
<td></td>
</tr>
<tr>
<td>Continuous food supply</td>
<td>104.1 ± 30.0</td>
<td>114.0 ± 27.0</td>
<td>122.7 ± 13.7</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 2. Changes in polyp size of *A. aurita* during the experiment. Open and solid triangles show the date of water temperature reduction to 15°C and the date when food supply was stopped, respectively. Initial number of polyps in each treatment is 30. The abbreviations for each experimental treatment are explained in Table 1.
Discussion

We observed apparent relationships between the growth rate of *Aurelia aurita* polyps and both water temperature and food supply. The water temperature in Tokyo Bay ranged from 13.7 to 28.3°C, which is essentially the range of temperature measured every year. However, the monthly pattern of change of water temperature are variable year-to-year. It is well known that induction of strobilation of *A. aurita* polyps requires changes in environmental temperature (Berrill, 1949; Kakinuma, 1962; Custance, 1964, 1966; Kato et al., 1980; Kroither et al., 2000), and our results confirm this; water temperature reduction induced polyp strobilation. It is also well known that growth rate increases with a rise in environmental water temperature. Considering the changing pattern of water temperature, the date of water temperature reduction may be important in determining polyp growth. If the water temperature abruptly decreases in late autumn, polyps cannot grow sufficiently. But if the water temperature is maintained at a higher level until early winter and then abruptly decreases, polyps will be able to grow enough to produce many discs in their strobila.

The size of polyps increased with greater food availability. Shrinkage of polyp size just after food depletion was considerable (treatments A and B). This finding suggests that eutrophicated waters having much zooplankton as prey for polyps would be most suitable for polyp growth.

Production of daughter polyps was also correlated with the food supply, and this correlation is more obvious than that of polyp growth. Although there was a maximum polyp size of around 4.0 – 4.5 mm, daughter polyp production was never saturated within the range of our experiments. In the process of polyp production, energy obtained as food will be used for polyp growth up to a certain size, but it will also be transferred to daughter polyps simultaneously. Daughter polyp production will not be saturated by food availability as long as space for daughter polyps exists.

Previous laboratory experiments revealed that strobilation by polyps of *A. aurita* is initiated by a reduction in water temperature (Kakinuma, 1962; Custance, 1964; Kato et al., 1980), as was also observed in this study. However, strobilation was not observed in polyps that experienced a lowering of temperature just after the start of the experiment despite a continuous supply of food. We suggest that the water temperature stimulus to induce the strobilation is not effective for small polyps just after settlement. Early strobilation, only 20 days after the temperature was lowered, was observed in treatment A20, which was relatively food-limited and could not grow sufficiently due to the early onset of lower-temperature conditions. The cumulative strobilation ratio

### Table 3. Number of discs, period of strobilation, daily ephyra production rate and total number of liberated ephyrae per strobila

<table>
<thead>
<tr>
<th>Food supply after lowering of temperature</th>
<th>Number of discs</th>
<th>Period of strobilation (days)</th>
<th>Production rate (ind/lmday)</th>
<th>Total liberated number (ind)</th>
<th>Diameter (mm)</th>
<th>Number of discs</th>
<th>Period of strobilation (days)</th>
<th>Production rate (ind/lmday)</th>
<th>Total liberated number (ind)</th>
<th>Diameter (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No food supply</td>
<td>1.7 ± 0.5</td>
<td>9.2 ± 4.2</td>
<td>0.2</td>
<td>1.6</td>
<td>2.4 ± 0.7</td>
<td>3.7 ± 1.1</td>
<td>7.1 ± 2.0</td>
<td>0.4</td>
<td>2.9</td>
<td>2.9 ± 0.5</td>
</tr>
<tr>
<td>10 days supply</td>
<td>3.3 ± 2.1</td>
<td>6.8 ± 1.5</td>
<td>0.4</td>
<td>3.3</td>
<td>2.8 ± 0.4</td>
<td>4.5 ± 1.6</td>
<td>9.3 ± 1.6</td>
<td>0.3</td>
<td>4.0</td>
<td>2.8 ± 0.5</td>
</tr>
<tr>
<td>Continuous food supply</td>
<td>17.3 ± 2.7</td>
<td>29.4 ± 10.8</td>
<td>0.8</td>
<td>29.4</td>
<td>3.8 ± 1.6</td>
<td>20.8 ± 2.2</td>
<td>20.3 ± 5.1</td>
<td>1.0</td>
<td>22.0</td>
<td>4.0 ± 0.8</td>
</tr>
</tbody>
</table>

Fig. 3. Changes in cumulative strobilation ratios of *A. aurita* polyps during the experiment. The abbreviations for each experimental treatment are explained in Table 1.
also increased abruptly in the A20 treatment. Similar pattern was also observed in the A40 treatment, which was also food-limited. These findings suggest that strobilation is induced by a combination of water temperature reduction and food depletion. Lowering the water temperature and food depletion have negative effects on polyp growth. We think that polyps change their life stage from benthic to planktonic by strobilation to avoid such an unsuitable environment.

The number of discs per strobila and number of ephyrae produced were significantly correlated with food supply. In laboratory experiments, an increase in the number of discs per strobila with an increase in food availability was also reported by Spangenberg (1967, 1968). Spangenberg (1967) showed that polyps of *A. aurita* usually formed a single disc after starvation, and Spangenberg (1968) also reported that polyp size apparently influenced the number of discs and that very small polyps formed a single disc. These findings, including our results, suggest that food availability is the most important factor for regulating the number of discs, and consequently the ephyra production rate. Regarding the diameter of ephyrae, larger ones were found in the treatment supplied foods in excess. However, this relationship is not as clear as those for disc number and ephyra production rate. In the process of ephyra production, energy obtained as food is applied to strobila growth, i.e. ephyra size, up to a maximum size, however, it is also reflected in the number of discs in a strobila, i.e. the number of ephyrae being produced simultaneously. Any increase in the number of produced ephyrae will not be saturated by a larger amount of food. In this respect ephyra production seems much the same as daughter polyp production, mentioned above.

Our study revealed that the polyp growth increased with higher ambient water temperature and greater food availability, and that asexual reproduction including daughter polyp production and strobilation also increased with increasing food availability. To liberate many ephyrae, polyp size just before strobilation seems to be one of the most important factors. Watanabe and Ishii (2001) reported that most strobilae of *A. aurita* observed on settling plates in natural seawater in Tokyo Bay have a single disc. It is considered that polyps of *A. aurita* are usually food-limited even in Tokyo Bay. The number of individuals of prey available as food for polyps, such as micro- and small zooplankton, decreases from autumn to winter simultaneously with the decreasing water temperature (Anakubo and Murano, 1991; Nomura et al., 1992). But if more ripe female medusae are present and more planula larvae settle even in the early autumn, or if a high water temperature and abundant zooplankton biomass are maintained until the late autumn, it will contribute to increasing the polyp growth and asexual reproduction of *A. aurita*. We want to emphasize that food availability for polyps must be regarded as one of the most important factors for inducing a mass occurrence of medusae in the next summer.

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**References**


