

The effects of environmental light condition on strobilation in *Aurelia aurita* polyps

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Abstract

The effects of light condition on strobilation of *Aurelia aurita* polyps were investigated in the laboratory. Significant differences in changes in the cumulative proportion of strobilae among total polyps were found between polyps incubated under light and dark conditions. Under dark conditions 94.8% of polyps strobilated during 65 days of incubation experiment, but only 30% did so under light conditions. Polyps incubated under dark conditions liberated, on average, eight times more ephyrae by strobilation than polyps incubated under light conditions. Increased strobilation in the dark may be an adaptive behavior for polyps since strobilation in nature occurs during the winter, when light intensity is low. It is likely that highly eutrophicated waters such as Tokyo Bay will contribute to the asexual reproduction of polyps due to the blocking of light and a concomitant in ephyra populations.

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

Introduction

The scyphozoan jellyfish *Aurelia aurita* (L.) is found in many coastal waters (e.g., Möller, 1980). The life cycle of *A. aurita* includes an alternation between benthic polyp and planktonic medusa stages; the polyp stage reproduces asexually by releasing planktonic ephyrae by strobilation (i.e., multiple transverse fission of the polyp), and the ephyrae soon become medusae.

The environmental conditions under which strobilation of *A. aurita* occurs are incompletely understood. In previous studies it has been shown that changes in environmental temperature are necessary to induce strobilation in this species (Berrill, 1949; Custance, 1964, 1966; Kato et al., 1980; Kroiher et al., 2000). For example, Berrill (1949) suggested that one of the factors needed to induce strobilation is a low critical temperature, usually observed during the winter; this suggestion was supported by a study of naturally occurring populations of *A. aurita* polyps (Watanabe and

Ishii, 2001). Although correlations between sudden increases or decreases in temperature and subsequent appearances of strobilae have been demonstrated in the above-mentioned studies, there have been few quantitative studies of other environmental factors that may play a role in inducing strobilation. Correlations between reduction of food supply and strobilation were studied by Spangenberg (1967), and those between environmental light condition and strobilation were studied by Custance (1964). We devised a series of experiments to investigate the effects of certain environmental conditions, especially light condition, on strobilation of *A. aurita* polyps in the laboratory. In particular, we wished to show whether the decreasing light intensity in highly eutrophicated waters such as Tokyo Bay might enhance the asexual reproduction of polyps by strobilation, and this lead to increased ephyra densities and medusa blooms (Toyokawa et al., 1997, 2000).

Materials and Methods

Sampling of medusae *Aurelia aurita* was conducted in daytime on 11 June 1993 aboard the T.S. "Hiyodori" of the Tokyo University of Fisheries in Tokyo Bay, Japan. 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 by pipette from the brood sacs of the oral arms of ripe female medusae and immediately transferred to glass bottles filled with ambient seawater.

In the laboratory, the samples of planula larvae were cleaned by carefully pouring the planulae through a 0.33 mm mesh net into a 1200 ml bowl filled with GF/C filtered seawater. Planula larvae were immediately transferred to 30 petri dishes (6cm diameter) filled with GF/C filtered seawater and incubated under light conditions of 8L16D (150 lx: L; Light, D; Dark). Water temperature was 22°C. After 1 week, the petri dishes with newly settled polyps were transferred into plastic containers (5-l) filled with GF/C filtered seawater. *Artemia* nauplii were supplied to polyps once a day.

By 141 days after planula settlement, the number of polyps had increased enough for incubation experiments. Polyp densities in each petri dish were controlled as leaving a space (ca. 1 cm) among polyps by eliminating the excess polyps with a small plastic cutter. About 20 polyps in each petri dish were used for incubation experiments. The petri dishes were divided among four treatments (6-8 petri dishes were used in each treatment), with light conditions and water temperatures as: 1) 24L-15°C, 2) 8L16D-22°C, 3) 8L16D-15°C, and 4) 24D-15°C. Water temperatures of 22 and 15 °C were referred to the data of September-October and December in Tokyo Bay, respectively. Incubation water was changed once a day, and then the *Artemia* nauplii were supplied. New buds of polyps were eliminated by a small plastic cutter.

Polyps in the petri dishes were observed with a dis-

secting microscope every day, and their number and diameter, the number of strobilae, and the number of discs in each strobila were determined. The number of liberated ephyrae was also counted following filtration of the incubation seawater with a hand net (0.33 mm mesh). Strobilae were defined as polyps with distinctly formed discs. After the observations of polyps and strobilae, the petri dishes were returned to the plastic containers filled with GF/C filtered seawater. The experiment continued for 65 days.

Results

The number and initial sizes of polyps used in this experiments are shown in Table 1. No strobilae were observed in polyps in the 22°C treatment which experienced no change from the acclimation temperature. In the other treatments, in which the water temperature was lowered from 22°C to 15°C, strobilae were observed. The cumulative proportion of strobilae among total polyps in each of these three treatments is shown in Fig. 1. First strobilation was observed 20 days after the start of the

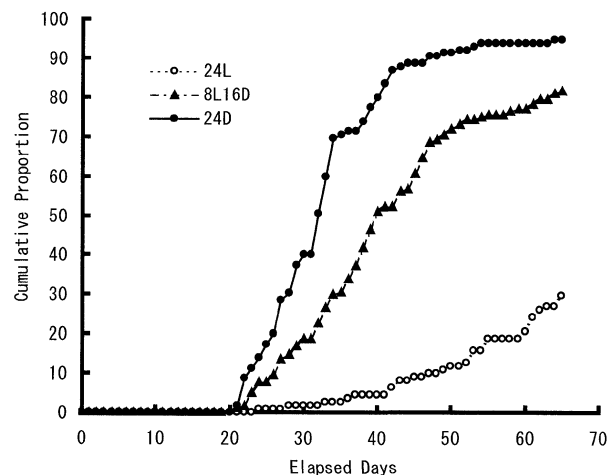


Fig. 1. Changes in the cumulative proportion of strobilae among total polyps of *A. aurita* in each 15°C treatment group during the experiment. The 22°C group is excluded.

Table 1. The size of polyps and the proportions of strobilae and of polyps that have ceased ephyra liberation to the initial number of polyps. Mean numbers of discs and total number of liberated ephyrae per polyp are also shown. 0 denotes no strobilae observed.

Experimental treatment	Number of polyps	Initial size of polyps (mm; Mean±SD)	Strobilae			Polyps that have ceased to liberate ephyrae			Total number of liberated ephyrae per all polyps
			Number of individuals	Proportion (%)	Mean number of discs	Number of individuals	Proportion (%)	Size of polyps (mm; Mean±SD)	
24L (15°C)	111	1.67±0.39	33	29.7	16	6	5.4	0.77±3.64	1.59
8L16D (22°C)	121	1.63±0.33	0	0	0	0	0	0	0
8L16D (15°C)	153	1.54±0.29	125	81.7	14	73	47.7	0.96±5.00	9.17
24D (15°C)	115	1.60±0.32	109	94.8	14	91	79.2	1.08±6.84	12.54

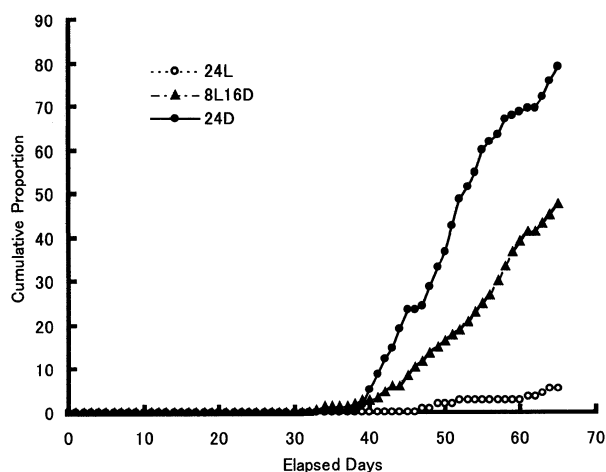


Fig. 2. Changes in the cumulative proportion of residual polyps that have ceased ephyra liberation among total polyps of *A. aurita* in each 15°C treatment group during the experiment. The 22°C group is excluded.

experiment in the 8L16D treatment, but after 24 days in the 24L treatment. In the 24D treatment, strobilae abruptly increased from the first observation and the cumulative proportion of strobilae was the highest, attaining 94.8% within 65 days. In the 24L treatments, only 30% of the polyps had strobilated by the end of the experiment.

The cumulative proportion of residual polyps that have ceased ephyra liberation in each of the three 15°C treatments is shown in Fig. 2. Polyps that had ceased ephyra liberation were first observed 33 days after the start of the experiment in the 8L16D treatment, and after 47 days in the 24L treatment. The cumulative proportion of such exhausted polyps was the highest in the 24D treatment, about 80% of polyps having ceased ephyra

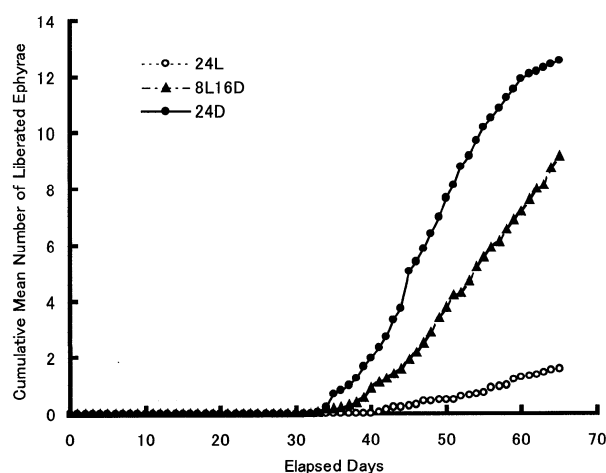


Fig. 3. Changes in cumulative mean number of liberated ephyrae per all polyps of *A. aurita* in each 15°C treatment group during the experiment. The 22°C group is excluded.

liberation within 65 days. In the 24L treatment, only 5% of the polyps had ceased ephyra liberation by the end of the experiment.

No significant difference was found in the mean number of discs per strobilae among the experimental treatments except for the non-strobilating 22°C treatment (Table 1), and it ranged from 14 to 16 discs. However, significant differences were found in the total numbers of liberated ephyrae per all polyps, the highest mean value being 12.54 in the 24D treatment. The cumulative mean numbers of liberated ephyrae per all polyps in each group during the experiment are also shown in Fig. 3 with clear difference between the 24D and 24L treatments.

Discussion

It is well known, as the result of previous studies, that changes in environmental temperature induce polyp strobilation and that constant temperature inhibits strobilation (Berrill, 1949; Custance, 1964, 1966; Kato et al., 1980; Kroiher et al., 2000). Our results agree with these observations. Our experiment furthermore suggests that light act as an inhibitor of the polyp strobilation process. Custance (1964) also found that light was an inhibitor of strobilation for the polyp of *A. aurita* and suggested that the progressive decrease in illumination that occurs in late autumn might be a positive stimulus for the onset of strobilation. We think it would be adaptive for polyps to have darkness as a positive inducer for strobilation, as Custance (1964) proposed.

The onset of strobilation is observed from late autumn to early winter in natural waters (Watanabe and Ishii, 2001), accompanying the seasonal decrease in light intensity. The change in light regime occurs simultaneously with the lowering of temperature at that time of year. In the winter, strobilae suddenly increase in natural waters (Watanabe and Ishii, 2001) which is also demonstrated by the timing of ephyra appearance. The highest numbers of ephyrae are observed in March in Tokyo Bay (Toyokawa and Terazaki, 1994; Omori et al., 1995; Toyokawa et al., 2000). In our experiment, a time lag of about 30 days between the onset of the strobilation and ephyra liberation was observed. This suggests that the strobilation of *A. aurita* polyps should be most extensive about one month before the appearance of ephyrae, that is, in the middle of winter when both illumination and temperature are low.

Planula larvae of *A. aurita* tend to settle on the underside of rocks and artificial plates (Hernroth and

Gröndahl, 1983; Gröndahl, 1988), and Brewer (1978) observed by experiment that more planulae settle on the underside of coverslips than the uppersurface. It is obvious that planulae preferentially settle, and polyps grow, on the underside of rocks, ships, artificial constructions, and so on, where there is a low level of light intensity. Recent increases in the sediment load and phytoplankton abundance due to eutrophication in coastal waters cause the blocking of light. This should contribute to the success of the strobilation of polyps for asexual reproduction and concomitantly result in an increase in ephyra populations (Ishii, 2001). Such a response of *A. aurita* polyps to eutrophication and the increase in artificial substrates may be one of the reasons for the recent medusa blooms observed in many coastal waters.

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