In situ estimation of ephyrae liberated from polyps of Aurelia aurita using settling plates in Tokyo Bay, Japan

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Abstract

The continuous changes in the number of newly established polyps of Aurelia aurita (L.) on settling plates under natural conditions were observed from August 1998 to September 1999 in Tokyo Bay, Japan. A sharp decline in survivorship of newly settled polyps was observed within the first few days, however, survivorship of polyps settled in October increased by budding up to 399% after two months. The number of discs in each strobila varied from 1 to 6, however, most of the strobilae formed single discs. The percentage ratios of the total number of ephyrae to the initial number of polyps on settling plates were generally lower than 10%, but the highest ratio of 594.4% was estimated for the polyps settled in October. It is considered that most of the liberated ephyrae originate from the polyps settled in October in Tokyo Bay. This study suggests that the occurrence of ripe medusae with planula larvae throughout the year contributes to the success of settlement and growth of the polyp stage in Tokyo Bay.

Introduction

The scyphomedusan Aurelia aurita (L.) is a cosmopolitan jellyfish observed in many coastal waters (e.g. Yasuda, 1971; Van Der Veer & Oorthuysen, 1985; Matsakis & Conover, 1991; Lucas & Williams, 1994; Schneider & Behrends, 1994; Miyake et al., 1997; Ishii & Bämstedt, 1998; Dawson & Martin, 2001; Lucas, 2001) and some previous studies described their large predation impact on pelagic zooplankton communities (Möller, 1984; Van Der Veer & Oorthuysen, 1985; Behrends & Schneider, 1995; Schneider & Behrends, 1998). In Tokyo Bay, mass occurrences of medusae are frequently observed in summer and autumn (Ishii et al., 1995; Omori et al., 1995; Toyokawa et al., 2000) and a decisive role of medusae in the food web is suggested (Ishii & Tanaka, 2001).

The life cycle of A. aurita includes an alternation between the benthic polyp and the pelagic medusa stages. The polyp stage reproduces asexually by budding and strobilation (Lucas, 2001), and each disc of a strobila liberates an ephyra. The number of ephyrae produced is equal to the number of discs in each strobila. Therefore, it is important for the prospect of mass occurrence of the medusae to know the in situ changes in the numbers of polyps and discs in each strobila.

Most of the previous studies on polyps were performed by laboratory experiments, and in situ observation of polyps under natural conditions is rare (Thiel, 1962; Hernroth & Gröndahl, 1983, 1985a, b; Gröndahl & Hernroth, 1987; Gröndahl, 1988a, 1989). All previous studies described the reduction of polyps under natural conditions, and some studies implicated the predation impact on polyp population (Thiel, 1962; Hernroth & Gröndahl, 1985a, b). Thiel (1962) found that the nudibranch, Facelina bostonensis (Couthouy), was an important predator in Kiel Fjord, Germany. Hernroth & Gröndahl (1985a, b) carried out in situ observations and laboratory experiments and stated that predation on A. aurita polyps, especially on older polyps by the nudibranch, Coryphella verrucosa (M. Sars), was one of the significant factors regulating the size of A. aurita medusae populations. However, the degree and seasonal trends of predation effects have not been elucidated.

Strobilation in A. aurita is usually induced by decreasing water temperature (Kakinuma, 1962; Cus­tance, 1964; Kato et al., 1980). This phenomenon coincided with in situ observations. Thiel (1962) found
that most polyps (ca. 100%) strobilated between January and March and the maximum number of discs in each strobila was 3–10 in Kiel Fjord, Germany. In situ observations of *A. aurita* polyps on settling plates were also made in Gullmar Fjord, Sweden (Hernroth & Gröndahl, 1983, 1985a, b, Gröndahl & Hernroth, 1987, Gröndahl, 1988a, 1989). Hernroth & Gröndahl (1983, 1985a) reported that strobilating polyps of *A. aurita* formed plural discs during autumn and a single disc during winter. In spite of observations of various numbers of discs in each strobila, the crucial factor affecting the number of discs is unknown. These in situ investigations gave information about predation and strobilation of *A. aurita* polyps, however, seasonal changes in the number of newly settled polyps and total number of ephyrae liberated in each polyp are unknown.

In Tokyo Bay, the female medusae with planula larvae occur throughout the year (Miyake et al., 1997). The planula larvae are always present in the water and always potentially can settle on suitable substrates. In this study, we observe the changes in the number of newly settled polyps of *A. aurita* on settling plates under natural conditions and estimate the percentage ratio of the number of ephyrae liberated from polyps to the initial number of newly settled polyps. This is the first study on polyps in Tokyo Bay and the first in situ observation of polyps on settling plates continuously throughout one year.

**Materials and methods**

**Sampling and in situ experiments**

Sampling of *Aurelia aurita* medusae was conducted in daytime once a month with the T.S. “Hiyodori” of Tokyo University of Fisheries in Tokyo Bay, Japan from August 1998 to June 1999 (Fig. 1). 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 a pipette from the brood sacs of the oral arms of ripe female medusae and were 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 330 μm mesh net into a 1200 ml bowl filled with 1 μm filtered seawater. Planula larvae were immediately transferred to glass bowls containing 200 ml of 1 μm filtered seawater, and a settling plate made of acrylic plastic (5×6 cm) was floated in each glass bowl for the settlement of the planula larvae. After 1 week, the settling plates with newly settled polyps were transferred to petri dishes with 1 μm filtered seawater and the number of polyps on each settling plate counted using a dissecting microscope. The median and estimated standard error of the number of polyps on each plate was 318±99.8. These settling plates were kept in a plastic container filled with 1 μm filtered seawater and were carried to Stations A and B within 3 h (Fig. 1).

At the stations, 3–12 settling plates were attached on the upper and lower sides of the base plates (25×25 cm) in a large container (50×67×23 cm) filled with ambient seawater (Fig. 2). Each base plate with the settling plates was horizontally moored from the piers at 0.8 and 2.3 m depths at Station A, and at 0.8 m depth at Station B. We conducted 11 different series with different starting dates. We identified the series by the starting dates of each observation.

The observations of polyps on the settling plates at both stations were made on day 1, 2, 3, 5 and 7 during the first week, and once a week thereafter. For these observations, the base plates were lifted from the sea and placed into large containers (50×67×23 cm) filled with ambient seawater, and the settling plates were detached from the base plates. The settling plates were immediately moved to a transparent plastic box (13.5×13.5×7 cm) filled with ambient seawater. Polyps on the settling plates were observed with a dissecting microscope during the daytime, and the number and diameter of polyps, the number of strobilae and the number of discs in each strobila were determined. Strobilae were defined as polyps with distinctly formed discs. Other organisms that settled on the settling plates were also identified and counted. After the observations, the settling plates were reattached to the base plates and were moored again. All observations were carried out until 27 September 1999.

Surface temperature and salinity were also measured simultaneously with the polyp observations. Vertical profiles of temperature and salinity were measured once a month using a CTD (AST-1000S, Alec Co., Japan). Water sampling was carried out once a month using a Van-Dorn Bottle (3 l) at 1.5 m and 0.8 m depths at Stations A and B, respectively. The water sample was concentrated through a 20 μm mesh net and subsequently filtered through 1 μm Whatman GF/C filters. The salt contained in any water remaining...
on the filters was eliminated with isotonic ammonium formate. The filters were immediately frozen and transferred to the laboratory. For the determination of the total dry weight of micro- and small zooplankton, the filters were dried at 60 °C for 24 h and weighed.

Calculations

The mean survivorship of polyps on the settling plates on t day (MS, %) was calculated from the following equation;

\[ MS = \left[ \frac{\sum_{i=1}^{n} (P_{it_i} / P_{i0}) \cdot 100}{n} \right] \]

where \( P_{it_i} \) is the number of surviving polyps including strobilae on each settling plate on t day, \( P_{i0} \) is the initial number of polyps on each settling plate and \( n \) is the total number of settling plates.

The cumulative strobilation ratio (R, %) on the settling plates on t day was calculated from the following equation;

\[ R = \left[ \frac{\sum_{i=1}^{n} S_{it_i} / \left( \sum_{i=1}^{n} S_i + \sum_{i=1}^{n} P_{i1} \right) \right] \cdot 100, \]

where \( S_{it_i} \) is the cumulative number of strobilae on each settling plate on t day, \( S_i \) is the total number of strobilae on each settling plate during the investigated period and \( P_{i1} \) is the number of surviving polyps on each settling plate on the day the last strobila was found.

The ratio of the total number of strobilae to the initial number of polyps (N, %) was calculated from the following equation;

\[ N = \left( \frac{\sum_{i=1}^{n} S_i / \sum_{i=1}^{n} P_{i0}}{100} \right) \]

The ratios of the total number of ephyrae liberated from polyps to the initial number of polyps (E, %) were estimated from the following equation;

\[ E = \left( \frac{\sum_{i=1}^{n} D_i / \sum_{i=1}^{n} P_{i0}}{100} \right) \]

where \( D_i \) is the total number of discs on each settling plate.
Results

Temperature and salinity

Monthly changes of water temperature and salinity at Stations A and B from September 1998 to September 1999 are shown in Figure 3. The maximum surface temperatures were 29.2 °C and 29.8 °C in August and the minimum surface temperatures were 9.4 °C and 10.4 °C in February, at Stations A and B, respectively. Variation of salinity among observation dates was higher in surface waters. The maximum surface salinity was 32.9 psu in March and January, and the minimum surface salinity was <0.1 psu and 1.3 psu in August, at Stations A and B, respectively.

Zooplankton biomass

Monthly changes in biomass as mg dry weight l⁻¹ of zooplankton at Stations A and B from November 1998 to September 1999 are shown in Figure 4. The biomass increased from winter to spring and it decreased during summer and autumn at both stations. Maximum biomass was 4.7 and 3.8 mg dry weight l⁻¹ on 8 April, 1999 at Stations A and B, respectively. Minimum biomass was 0.86 and 0.69 mg dry weight l⁻¹ on 7 July, 1999 at Stations A and B, respectively.

Survivorship

Figure 5 shows the changes in mean survivorship of polyps on the upper side of the settling plates at Stations A and B. The numbers of polyps on the settling plates rapidly decreased during the first few days after the start of observations. Polyps on each plate with different starting dates disappeared within 4 months at both stations, except for polyps on the settling plates of 2 October at Station B. A different pattern was found on the settling plates of 2 October; mean survivorship reached 159.0% on 20 November 1998. Significant differences in the mean survivorship of polyps between 0.8 m and 2.3 m depths at Station A and between Stations A and B were not observed except two and four cases, respectively (Table 1).

Figure 6 shows changes in mean survivorship of polyps on the lower side of the settling plates at Stations A and B. The numbers of polyps on the settling plates decreased rapidly with variable patterns dur-
Table I. Results of the statistical analyses by Two-way ANOVA without replication for survivorship of *Aurelia aurita* polyps on the settling plates on each starting date. The results of the analyses among sampling dates were omitted from the table. *F* and *p* indicate *F*-ratios and probability values, respectively (*: *p* < 0.05, **: *p* < 0.01). Degrees of freedom of each result was 1 on each analysis.

<table>
<thead>
<tr>
<th>Starting date</th>
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<th>Lower side 0.8 m–2.3 m</th>
<th>Sta. A – Sta. B</th>
<th>Upper Side – Lower Side 0.8 m</th>
<th>Sta. A 0.8 m</th>
<th>Sta. A 2.3 m</th>
<th>Sta. B 0.8 m</th>
</tr>
</thead>
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<tr>
<td></td>
<td><em>F</em></td>
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<td><em>F</em></td>
<td><em>p</em></td>
</tr>
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<td>0.140</td>
<td>16.595</td>
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<td>0.067</td>
<td>0.800</td>
<td>9.046</td>
<td>0.017 *</td>
</tr>
<tr>
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<td>0.044 *</td>
<td>35.877</td>
<td>&lt;0.001 **</td>
<td>9.526</td>
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<td>&lt;0.001 **</td>
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<td>0.253</td>
<td>0.492</td>
<td>0.498</td>
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<td>0.008 **</td>
</tr>
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<td>8.193</td>
<td>0.019 *</td>
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</tr>
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</table>
Figure 5. Changes in mean survivorship of *Aurelia aurita* polyps on the upper side of the settling plates at Stations A and B in Tokyo Bay. Starting date is also expressed.

ing the first few days after the start of observations. Polyps on settling plates of 31 August, 26 January, 23 February, 6 April, 5 May, 25 May and 6 June disappeared within 4 months at both stations. But polyps on settling plates of 2 October, 26 October, 24 November and 15 December survived more than 4 months. The mean survivorships of polyps of 2 and 26 October reached 320.9% and 393.3% on 10 December and 16 December 1998 at Station B, respectively. Significant differences of the mean survivorship of polyps between 0.8 m and 2.3 m depths at Station A and between Stations A and B were observed for six and eight cases, respectively (Table 1).

Polyp survivorship was usually higher on the lower side. Statistical analyses of the mean survivorship of polyps between upper and lower sides at each station also showed that there were significant differences on each settling plate, especially for the settling plates of October (Table 1). No significant differences of the survivorship between upper and lower sides of the set-
tling plates were found for the plates of 31 August at either station (Table 1).

The settling plates were usually invaded by the barnacles, *Balanus eburneus* Gould, *B. improvinus* Darwin and *B. amphitrite* Darwin, the clam worm, *Polydora ligni* Webster, the mussel, *Mytilus galloprovincialis* Lamarck, and the amphipod, *Corophium* sp, which grew rapidly on the both sides of the settling plates at both stations. All plates were frequently covered on both sides with dense aggregations of these organisms, such as *M. galloprovincialis*, which completely covered the settling plates after May 1999.

**Strobilation**

Figure 7 shows the changes in cumulative strobilation ratios on the upper and lower sides of the settling plates at Stations A and B. Strobilae were first observed on the lower side of settling plates of 2 October at Station B on 10 December 1998. At Station A,
Figure 7. Changes in cumulative strobilation ratio of *Aurelia aurita* polyps on the upper and lower sides of the settling plates at stations A and B in Tokyo Bay. A and B = Station; 0.8 and 2.3 = depth of the settling plates; U and L mean the upper and lower side, respectively. Starting dates of the observations are also shown.

<table>
<thead>
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<th></th>
<th>Upper side</th>
<th>Lower side</th>
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<tbody>
<tr>
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<td>2.3 m</td>
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</tr>
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<td>[Diagram]</td>
</tr>
<tr>
<td>6 Apr 1999</td>
<td>[Diagram]</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 8. The frequency of *Aurelia aurita* strobilae having various number discs in each strobilae. 0 denotes no strobilae observed.
the cumulative strobilation ratios on the upper sides were less than 50%, however, on the lower side, 96.9–98.4% of polyps strobilated on the settling plates of 2 October. By contrast, the cumulative strobilation ratios at Station B were nearly 100% on both sides and for all settling plates. Strobilation continued for more than one month. On 1 May 1999, the last strobila was observed on the lower side at Station B, and all polyps disappeared by 31 May 1999.

Number of discs in each strobila

Figure 8 shows the frequency of strobilae having various numbers of discs on each strobila on the settling plates. The number of discs varied from 1 to 6 in each strobila, however, 54.9–100% of the strobilae had single disc. Strobilae having plural discs were only observed on the settling plates of 2 and 26 October. Six discs in a strobila was observed on the lower side of the settling plate of 2 October at Station B.

Number of ephyrae

We estimated the percentage ratios of the total number of strobilae and anticipated ephyrae to the initial number of polyps (Table 2). The percentage ratios were generally lower than 10%, however, greater than 200% was observed on the lower side of the settling plates of 2 and 26 October at Station B. The highest percentage ratio of 594.4% was observed on the settling plates of 26 October at Station B. Comparisons between the upper and lower sides showed that the estimated ratios of ephyrae liberated from polyps were significantly higher on the lower side of the settling plates at 2.3 m depth at Station A (Wilcoxon’s signed-ranks test, $P < 0.01$) and at Station B ($P < 0.025$).

Discussion

Survivorship

The higher survivorship of polyps on the lower side of the settling plates suggests that naturally settled polyps will also be observed on the lower side of substrata in situ. This phenomenon is frequently observed in other coastal waters (e.g. Hernroth & Gröndahl, 1983; Gröndahl & Hernroth, 1987; Gröndahl, 1988a; Miyake et al., 1997). In Japanese waters, SCUBA divers observed that polyps settled only on the lower side of floating piers (Miyake et al., 1997). In laboratory experiments, more than 90% of the planula larvae recruited on the lower side of plastic coverslips (Brewer, 1978). These studies suggest that cnidarian planulae preferentially settle on the lower side of substrata, perhaps enabling polyps to avoid sedimentation. In coral reefs, sedimentation is a serious problem for the survivorship of polyps in many habitats (e.g. Babcock & Davies, 1991; Babcock & Mundy, 1996; Gilmour, 1999). In the present study, sedimentation was observed only on the upper side, where polyp survivorship was lower.

A rapid decrease in the survivorship of newly recruited larvae is also observed in other benthic organisms (Gosselin & Qian, 1997; Hunt & Scheibling, 1997), indicating that one of the significant causes of their mortality is predation by other benthic organisms. Gröndahl (1988b) reported that the mortality rate of newly settled polyps in Gullmar Fjord was 4.5–28% within 10 days after placement in situ.

In our present study, invasion and growth of other organisms were observed on all settling plates. From February to September, other organisms such as M. galloprovincialis Lamarck completely covered the surface of the settling plates on both sides as a mussel bed. The invasion and growth of other organisms on the plates decreased from October to December, and the abundance of A. aurita polyps increased by budding during this period. Of course in nature, some polyps can establish colonies which is different from our investigations; the importance of the colony effect, which could eliminate open space for other organisms, remains to be elucidated. In the present study, some polyps (i.e. plates of October on lower side in Station B) established dense colonies on the settling plates and the lower mortality was recorded on this plate. If polyps grow continuously without initial reduction by competition, they would survive for a long period. These findings suggest that competition for space with other organisms influence to the survivorship of A. aurita polyps.

Strobilation

A high cumulative strobilation ratio in this study means that most of the polyps surviving throughout the strobilation period will strobilate and liberate ephyrae. Thiel (1962) also reported that ca. 100% of the A. aurita polyps in Kiel Fjord, Germany strobilated. Previous laboratory experiments indicated that strobilation by A. aurita is initiated by reduction in water temperature (Kakinuma, 1962; Custance, 1964; Kato et al., 1980). Because of water temperature de-
increases from autumn to winter, the autumn recruitment and growth of polyps observed in this study should reduce the dangerous period when polyps are exposed to competition for space with other benthic organisms. On the other hand, the reduction and loss of the number of polyps after strobilation suggests that polyp lifetime is less than 1 year or until late spring. As mentioned above, the new invasion of other benthic organisms, such as *M. galloprovincialis*, may cause the reduction of the post-strobilated polyps of *A. aurita*. The *in situ* observation of natural polyps of Grøndahl (1988b) and Hernroth & Grøndahl (1985a, b) revealed that the predation impact by other organisms is greater on older polyps of *A. aurita*. We could not observe actual predation by other organisms on the settling plates, however, from the observation that all polyps disappeared by August, we assume that the *in situ* lifetime of polyps is less than 1 year in Tokyo Bay.

Cessation of strobilation and loss of polyps may also be explained by lowering salinity (Purcell et al., 1999). In the present study, water salinity decreased from winter to spring with a minimum of <0.1 psu on 17 August. Purcell et al. (1999) also stated that the low salinity (<11 psu) inhibits strobilation and the production of *Chrysaora quinquecirrha* (DeSor) polyps in Chesapeake Bay, U.S.A.

**Table 2.** Percentage ratios of the total number of strobilae and ephyrae liberated from polyps to the initial number of polyps. 0 denotes no strobilae observed.

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<th>Started date</th>
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<th>Station B</th>
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<tbody>
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<td>0.8 m</td>
<td>2.3 m</td>
</tr>
<tr>
<td>Upper side</td>
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<td></td>
</tr>
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<td>0</td>
</tr>
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<td>0</td>
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<td>24 Nov. 1998</td>
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</tr>
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<td>0.3</td>
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<td>0</td>
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<td>Lower side</td>
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</table>

**Number of discs in each strobila**

Most of the strobilae in the present study formed single discs. In Gullmar Fjord, Sweden, Hernroth & Grøndahl (1983) found plural discs in each strobila during autumn and spring with *in situ* observations and a single disc in each strobila only in midwinter. Hernroth & Grøndahl (1983) and Grøndahl & Hernroth (1987) suggested that the zooplankton biomass in ambient seawater correlated with the occurrence of plural discs. An increase in the numbers of discs in each strobila was reported with an increase in food availability in laboratory experiments by Spangenberg (1967, 1968). Polyps of *A. aurita* usually formed a single disc after starvation (Spangenberg, 1967). Spangenberg (1968) also reported that the sizes of *A. aurita* polyps apparently influenced the number of discs of strobilae and that very small polyps formed a single disc. By contrast, Watanabe (unpublished) found that each strobila produced 22–30 discs when supplied with excess *Artemia* nauplii as food in laboratory experiments. All results suggest that the food availability was not enough to produce plural discs in each strobila during the strobilation period in Tokyo Bay. However, further experiments are needed to know the relationship with food availability and the number of discs produced in each strobila.
The number of ephyrae liberated from polyps reflects the survivorship at the polyp stage. The present study revealed that most of the liberated ephyrae would originate from polyps recruited in October. On the lower side in Station B, it was surprising that 2–5 times the initial numbers of settled polyps were produced after several months as polyps. If the ephyrae were produced continuously from December to April, as observed in this study, the cumulative numbers of ephyrae collected by net would be highest from March to April. This suggestion agrees with previous results of the occurrence of ephyrae by net sampling in Tokyo Bay (Sugiura, 1980; Toyokawa & Terazaki, 1994; Omori et al. 1995). Sugiura (1980) reported that ephyrae occurred from December to April. Toyokawa & Terazaki (1994) reported that ephyrae were abundant from January to March, and peaked in March. Omori et al. (1995) also reported that ephyrae appeared in March. This suggests that the number of polyps newly settled in autumn should contribute to the mass occurrence of medusae in next year in Tokyo Bay.

Most of the settled substrate in Tokyo Bay is occupied by the other benthic organisms such as M. galloprovincialis (see Furuse & Furota, 1985). This observation means that A. aurita polyps are exposed to keen competition for space with other organisms, especially during spring and summer as observed in this study. If the recruitment of planula larvae is restricted to summer as observed in many waters (Van Der Veer & Oorthuysen, 1985; Matsakis & Conover, 1991; Lucas & Williams, 1994; Schneider & Behrends, 1994; Miyake et al. 1997; Ishii & Bämstedt, 1998), the consequent production of ephyrae could be low in the following spring. In Tokyo Bay, ripe medusae with planula larvae are frequently observed throughout the year (Miyake et al., 1997). It is believed that it depends on the abundance of zooplankton, such as Oithona davisae Ferrari & Orsi, as food (Ishii & Tanaka, 2001) or on rather warm water temperatures during the winter (Hamner et al., 1982). The presence of ripe medusae with planula larvae, even in autumn and winter, would contribute to increasing settlement and survival of polyps during the period of low recruitment and growth of other benthic organisms, resulting an abundant settlement and high survival during the polyp stage. This flexibility will explain their success in many coastal waters.

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