Plankton Biol. Ecol. 51 (1): 26–35, 2004

plankton
biology & ecology

Survivorship and production of *Aurelia aurita* ephyrae in the innermost part of Tokyo Bay, Japan

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Received 10 September 2003; Accepted 9 January 2004

Abstract: The survivorship and daily production rate of the *Aurelia aurita* ephyrae population in Tokyo Bay was estimated. A disc growth index, expressed as the ratio of the diameter of the central disc to the diameter over lappet tips, was used to describe the developmental process and morphological changes in the ephyrae. The number of days spent of the arbitrary developmental stages as defined by disc growth index group was also calculated, and it appears that newly liberated ephyrae become young medusae after 20–28 days. Survivorship in each stage was estimated from the changes in the total number of ephyrae belonging to each stage that were produced in the survey area over the whole observation period. Survivorship of ephyrae metamorphosing into young medusae compared to the number of newly liberated ephyrae was only 0.95%. Field observations revealed that the number of individuals, biomass and daily production rate of ephyrae was highest on March 13, being 2.8 inds m^{-3}, 0.084 mgC m^{-3} and 0.021 mgC m^{-3} day^{-1}, respectively. Total production of ephyrae over the observation period was 0.47 mgC m^{-3}. Daily P/B ratio of ephyrae was higher than other zooplankters and decreased significantly with increasing size of the ephyrae. How the population of *A. aurita* is maintained through the ephyra developmental process is discussed.

Key words: *Aurelia aurita*, ephyra, survivorship, production rate, Tokyo Bay

Introduction

The schyphomedusan jellyfish *Aurelia aurita* is found in a variety of coastal and shelf marine environments, and is recognized as an important predator in marine plankton communities (e.g. Möller 1980; Ishii & Tanaka 2001). In Tokyo Bay, mass occurrences of *A. aurita* are frequently observed in summer (Omori et al. 1995).

The life cycle of *A. aurita* includes an alternation between the benthic polyp and the pelagic medusa stages. In Tokyo Bay, ephyrae are liberated from polyps by strobilation in winter and spring and grow into adult medusa by summer (Sugiura 1980; Toyokawa & Terazaki 1994; Omori et al. 1995; Toyokawa et al. 2000). It is important for understanding the mechanisms leading to mass occurrences of this medusae to know the in situ changes in the numbers of polyps, ephyrae and medusae. Many population studies on *A. aurita* medusae have been reported, including for Tokyo Bay (e.g. Möller 1980; Schneider & Behrends 1994; Lucas & Williams 1994; Omori et al. 1995). With regard to the polyp stage, in situ population studies under natural conditions have been carried out by Watanabe & Ishii (2001) in Tokyo Bay. However, data on the quantitative changes in the number of ephyrae of different stages is lacking.

Most of the previous population studies on *A. aurita* ephyrae have been restricted to estimations of seasonal abundance (Yasuda 1968, 1969, 1976; Möller 1980; Sugiura 1980; Hernroth & Gröndahl 1983, 1985; Toyokawa & Terazaki 1994; Omori et al. 1995; Toyokawa et al. 2000), and the degree of survivorship and estimations of population production rates have not been studied, with the exception of Yasuda (1983). This is in spite of the fact that the survivorship of ephyrae is expected to be a major factor regulating the size of *A. aurita* medusa populations.

The present study documents the survivorship and daily production rate of the *A. aurita* ephyrae population based on field observations of abundance in each size class and laboratory incubation experiments on the duration of each arbitrary ephyra stage. We noticed morphological changes relating to developmental processes of the ephyrae, therefore a morphological index was used as a proxy for developmental stage in the present study. This is the first in situ estimation on the survivorship of *A. aurita* ephyrae that considers the development time of ephyra stage.

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Materials and Methods

Incubation experiments

Sampling of *Aurelia aurita* medusae was conducted in daytime aboard the T.S. "Hiyodori" of the Tokyo University of Fisheries in April and June 1997, in the innermost part of Tokyo Bay. Female medusae carrying 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 (900 ml) filled with ambient seawater. In the laboratory, the samples of planula larvae were cleaned in a large bucket filled with seawater 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 at 15°C. After 10 days the petri dishes with newly settled polyps were transferred into plastic containers (2–l) filled with GF/C-filtered seawater. Enough individuals of Artemia nauplii were supplied as prey for *A. aurita* polyps once a day. After 90 days water temperature was lowered to 8°C to induce strobilation. Liberated ephyrae were carefully collected by a pipette and incubated in a 300 ml glass bowl filled with GF/C-filtered seawater, and were used for incubation experiments within a day.

A series of incubation experiments using different prey densities was carried out for 35 days in seawater without agitation. Each ephyra was incubated separately in a 300 ml glass bowl filled with 200 ml of 1 μm mesh-filtered seawater. Water temperature was maintained at 15°C, which is approximately the same temperature as that of the ambient seawater in March. Zooplankton preys for the ephyrae were collected from surface waters in Tokyo Bay by towing a net (100 μm mesh). In the laboratory, the samples of zooplankton were cleaned by carefully pouring the specimens through a 0.33 mm mesh net into a 1200 ml bowl filled with GF/C-filtered seawater. Live specimens having ca. 300 μm body length were carefully collected using a dissection microscope and were used as prey for the ephyrae. Zooplankton prey consisted of *Oithona davisae* (Mean=83.3%), nauplius larvae (Mean=6.6%), and the other small zooplankton. Each ephyra was incubated with 10, 40, 140, or 500 individuals of zooplankton prey (N=3 in each group). During the experiments, prey density was checked and, if necessary, prey items were added to maintain the initial prey densities.

Observations of the ephyrae in the glass bowls were made every day. For these observations, the ephyra was carefully transferred into a petri dish using a pipette, and the diameter of the central disc and the diameter over lappet tips were immediately determined under a dissection microscope (Fig. 1). After the observations, each ephyra was moved to a glass bowl filled with 200 ml of 1 μm mesh-filtered seawater with zooplankton prey at the same densities.

Field observations

Sampling of *A. aurita* ephyrae was conducted in daytime one to three times a month between December 5, 2001, and April 23, 2002, aboard the T.S. "Hiyodori" of the Tokyo University of Fisheries and using a small boat at a sampling area between Tokyo and Chiba in the innermost part of Tokyo Bay. The depth at each sampling area was approximately 10 m. Ephyrae and young medusae were collected using a net (58 cm diameter; 330 μm mesh) in an oblique tow from the bottom to the surface. Specimens were immediately transferred into 20–l buckets with ambient seawater, and the number of individuals and the diameter of the central disc and the diameter over lappet tips (Fig. 1) were determined under a dissection microscope back at the land laboratory, discriminating between ephyrae and young medusae. On March 5 and 19, quantitative sampling of ephyrae was not conducted but the sizes of ephyrae were determined in the same way. Water temperature was simultaneously measured during sampling with a CTD (Alec Electronics Co.; AST-1000S).

Simultaneously with ephyra sampling, zooplankton was collected using a NORPAC net (330 μm mesh) in a vertical tow from the bottom to the surface and using a Niskin water bottle sampler (2.56 l) at 3 m depth. Water bottle samples were concentrated with a hand net (20 μm mesh). Specimens were immediately preserved in 5% buffered formalin seawater. The preserved samples were examined using a dissection microscope and specimens were identified and counted. Abundances of small zooplankters including *Acartia omorii*, *O. davisae* and nauplius larvae, were estimated from the water bottle samples, and abundances of

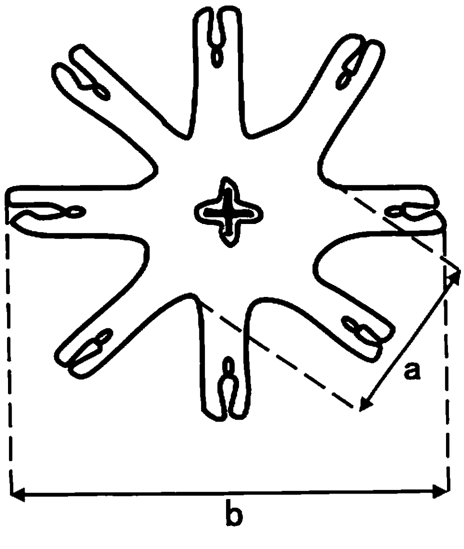

Fig. 1. Morphological illustration of *Aurelia aurita* ephyra. Diameter of central disc (a) and diameter over lappet tips (b) were determined. The disc growth index was defined as the ratio of the diameter of the central disc (a) to the diameter over lappet tips (b).

the other zooplankters was estimated from the net samples, respectively.

Some of the ephyrae collected during the observation period were brought back to the land laboratory for dry weight analysis. Specimens were rinsed with isotonic ammonium formate to remove external salts, and the diameter of the central disc was measured using a dissection microscope. Whole specimens of ephyrae were dried at 60°C for 24–48 hours and weighed.

Calculations

To analyze the developmental processes of ephyrae, a disc growth index was defined as the ratio of the diameter of the central disc to the diameter over lappet tips (a/b; Fig. 1). This index was used because during the ephyra stage the growth of the central disc is faster than the growth measured to the margin of the lappet tips. The ephyra stage was defined as the period between liberation from a polyp by strobilation and metamorphosis into early young medusa. We treated medusae having the same developmental characters as adults, involving tentacle growth, elaboration of the oral arms and gastrovascular cavity, increase of gastric cirri, and the development of radial canals, as early young medusae. The minimum disc growth index in the present study was 0.45. On the other hand, the disc growth index for early young medusae ranged between 0.90 and 0.95. We divided the ephyrae into ten developmental stages that were referable to disc growth index (from 0.45 to 0.95; every 0.05). From the relationship between elapsed days from the beginning of the incubation experiments and the index, the stage durations in days for each developmental stage were estimated.

Since the occurrence of ephyrae is restricted to our observation period, the total number of ephyrae of developmental stage i (N_i: inds m^{-3}) produced in the survey area during the whole observation period (m: day) is determined from:

$$N_i = D_i^{-1} \cdot \sum_{t=1}^{m} N_{i,t} \qquad (1)$$

where $N_{i,t}$ is the abundance of developmental stage i (inds m^{-3}) on the observation date t and D_i (day) is the stage duration in days of stage i. Survivorship of ephyrae in developmental stage i (lx_i) is determined from:

$$lx_i = N_i \cdot N_1^{-1} \cdot 1000 \qquad (2)$$

where N_1 (inds m^{-3}) is the total number of ephyrae in developmental stage 1 (the disc growth index is between 0.45 and 0.5) produced in the survey area during the whole observation period.

Biomass of ephyrae was estimated from the abundance in each size class of ephyrae and the relationship between individual diameter of the central disc and body dry weight of the ephyrae. Dry weight of ephyrae was converted to carbon weight based on the data of Ishii & Tanaka (unpublished), assuming carbon weight was 3.9% of dry weight. Mean daily production rate (mgC m^{-3} day^{-1}) of ephyra developmental stage i ($P_{i,t}$) on observation date t is determined from:

$$P_{i,t} = N_{i,t} \cdot W_i \cdot D_i^{-1} \qquad (3)$$

where W_i is the individual weight increase on a carbon basis (mgC ind^{-1}) during the developmental stage i.

Results

Temperature and zooplankton biomass

The innermost part of Tokyo Bay was well mixed during our observation period, and the water temperature difference between surface and bottom layers was small. Water temperature in the water column ranged from 9.6°C to 16.2°C during the observation period.

The following zooplankton species or groups were found in the survey area; *A. omorii*, *O. davisae*, *Centropages abdominalis*, *Paracalanus parvus*, *Rathkea octopunctata*, and so on. *Acartia omorii* numerically dominated, and the abundance ranged from 2,290 (February 5) to 121,000 inds m^{-3} (March 19). Abundance of zooplankton was converted to carbon weight based on Hirota (1981), Uye (1982) and Matsakis & Conover (1991). Mean biomass and the highest biomass of all zooplankton in the survey area were 382 and 765 (March 19) mgC m^{-3}, respectively.

Incubation Experiments

The prey densities in incubation experiments were converted to carbon weight assuming that all prey items had the same carbon content as *O. davisae*. The carbon content of *O. davisae*, 49.51% of dry weight, was after Hirota (1981), where it was referred to as O. brevicornis. Preliminary analyses of the dry weight of *O. davisae* by the senior author (H. I.) showed that its mean dry weight was 0.8 μg ind^{-1}. Therefore the carbon weight of prey items in the incubation experiments was assumed to be 0.4 μgC ind^{-1}. The prey densities supplied to ephyrae were then expressed as 20, 80, 280 and 1000 mgC m^{-3}. The relationships between days elapsed from the beginning of the incubation experiment and the diameter of the central disc and the disc growth index of ephyrae are shown in Figs. 2 and 3, respectively. Higher growth rates were observed in the higher prey density groups. However, regarding the changes in the disc growth index, significant differences among prey density groups were not observed except for in the lowest prey concentration group. The diameter of ephyrae incubated at the lowest concentration of prey gradually decreased day by day, and metamorphosis into young medusae was not observed. The other ephyra groups had entirely metamorphosed into young medusae by the end of the experiment. The first occurrence of early young medusae was 26, 20 and 14 days from the beginning of the experiment at prey

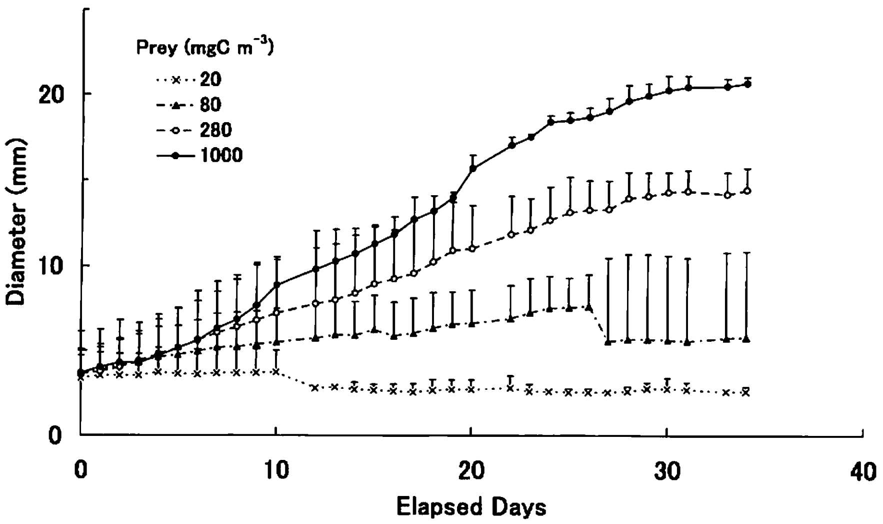

Fig. 2. Relationships between days elapsed from the beginning of the incubation experiment and the diameter of the central disc in *Aurelia aurita* ephyrae at various prey concentrations. Data are plotted as means+S.D.

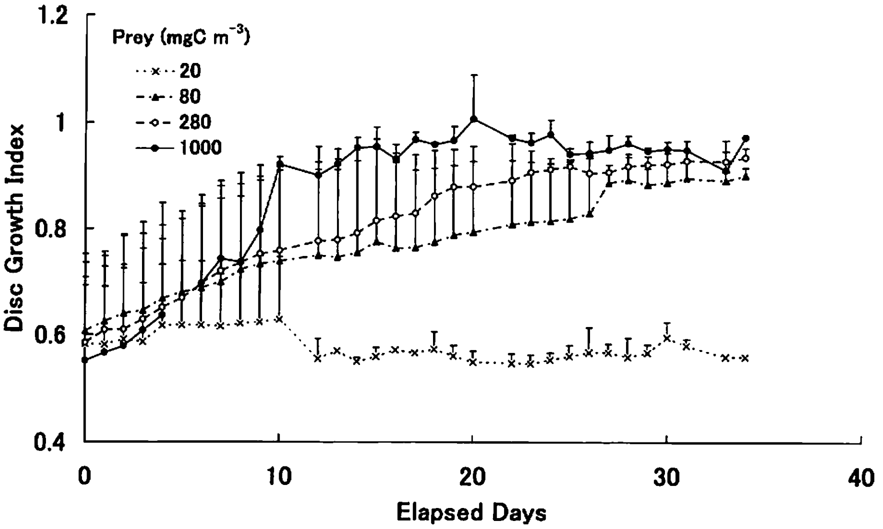

Fig. 3. Relationships between days elapsed from the beginning of the incubation experiment and the disc growth index of *Aurelia aurita* ephyrae at various prey concentrations. Data are plotted as means+S.D.

concentrations of 80, 280 and 1000 mgC m^{-3}, respectively. From microscopic examination, these early young medusae were all assignable to the 0.9–0.95 index group.

Field observations

The dry weight of ephyrae was most closely related to the disc diameter (Fig. 4; $r^2=0.86$). Changes in the standing stock of ephyrae over the 5-month period indicated that both the number of individuals and the biomass were highest on March 13, being 2.8 inds m^{-3} and 0.084 mgC m^{-3}, respectively (Fig. 5).

Size frequency distributions of the central disc diameter of ephyrae and young medusae are shown in Fig. 6. More than 50% of ephyrae had diameters of under 5 mm, except for those collected on April 2. Frequency distributions of

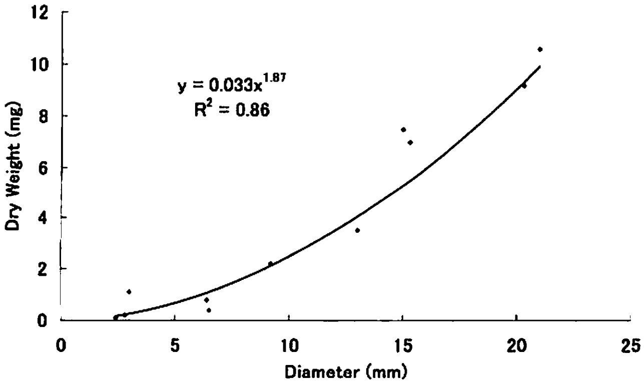

Fig. 4. Relationship between individual diameter of the central disc and body dry weight in *Aurelia aurita* ephyrae.

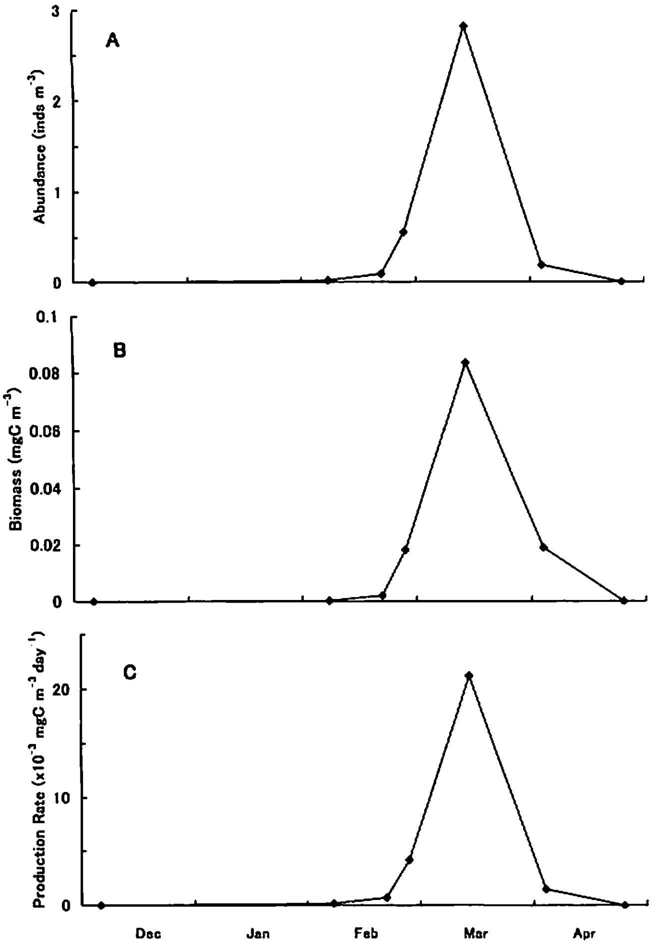

Fig. 5. Abundance (A), biomass (B) and daily production rate (C) of *Aurelia aurita* ephyrae in Tokyo Bay between December 5, 2001, and April 23, 2002.

the disc growth index of ephyrae and young medusae are shown in Fig. 7. The mode was 0.55–0.60 from February 19 to March 19 when plenty of ephyrae were present. A decrease in the number of newly liberated ephyrae was observed in late March, and many young medusae were observed on April 2.

Survivorship and production

We used data from the incubation experiments conducted at prey densities of 280 and 1000 mgC m^{-3} for calculation of survivorship and production of ephyrae. This was because the data for mean biomass of zooplankton in the survey area ranged between 280 and 1000 mgC m^{-3}, and significant differences in the curves of disc growth index for the two density groups (280 and 1000 mgC m^{-3}) were not observed. The relationship between days elapsed from the beginning of the incubation experiment and the disc growth index of ephyrae, and the relationship between central disc diameter and disc growth index of the ephyrae were used for the estimation. The regression equations of the relationships mentioned above are as follows:

$$I=0.54T^{0.17} \quad (r^2=0.86, p<0.01) \tag{4}$$

$$I=0.41S^{0.31} \quad (r^2=0.90, p<0.01) \tag{5}$$

where I is the disc growth index, T (day) is the days elapsed from the beginning of the incubation experiment and S (mm) is the central disc diameter of the ephyra. Using these equations, we converted the disc growth index into the days elapsed from the first observation of newly liberated ephyrae or the disc diameter of ephyrae. Stage duration in days for each developmental stage was calculated using the above equation for the relationship between days elapsed from the beginning of the incubation experiment and the disc growth index (Table 1).

Survivorship (lx) in each stage was calculated by equations (1) and (2) using the data for stage duration. Fig. 8 shows the survivorship of ephyrae estimated from the changes in the total number of ephyrae in each stage produced in the survey area during the whole observation period. The data were not fitted to one regression equation but were statistically fitted to two different regression equations. The cut off point of the survival curve was found at 4.6 days from the first occurrence of newly liberated ephyrae, at a disc growth index of 0.7 and at 6.9% survivorship. Survivorship of ephyrae that lived to metamorphose into young medusae compared to newly liberated ephyrae was only 0.95%.

Changes in the daily production rate of ephyrae over the 5-month observation period are shown in Fig. 5. The daily production rate was highest on March 13, being 0.021 mgC m^{-3} day^{-1}. Average daily production and total production rates of ephyrae over the observation period were 0.0034 and 0.47 mgC m^{-3}, respectively.

Table 1 summarizes the stage duration, mean daily production rate and daily P/B ratio for each developmental stage. Stage duration was estimated from the incubation experiments, and it increased with developmental stage. If a developmental stage of 0.9–0.95 coincides with the young medusa stage, newly liberated ephyrae become young medusa after 20–28 days. The daily P/B ratio abruptly decreased during the early developmental stages and thereafter gradually decreased with further development. Figure 9 shows the relationship between daily P/B ratio and ephyra diameter converted from the disc growth index using the regression equation. The regression line fitted well ($r^2=0.99$, $p<0.01$), and the daily P/B ratio significantly decreased with increasing diameter of the ephyrae. The daily P/B ratio of newly liberated ephyrae was 1.9.

Discussion

The seasonal occurrences of *A. aurita* ephyrae have been described in many previous studies, and it is known that the major abundance peak takes place between late winter and spring in Tokyo Bay (Sugiura 1980; Toyokawa & Terazaki 1994; Omori et al. 1995; Toyokawa et al. 2000) and in most other waters (Yasuda 1968, 1969, 1976; Möller 1980). The

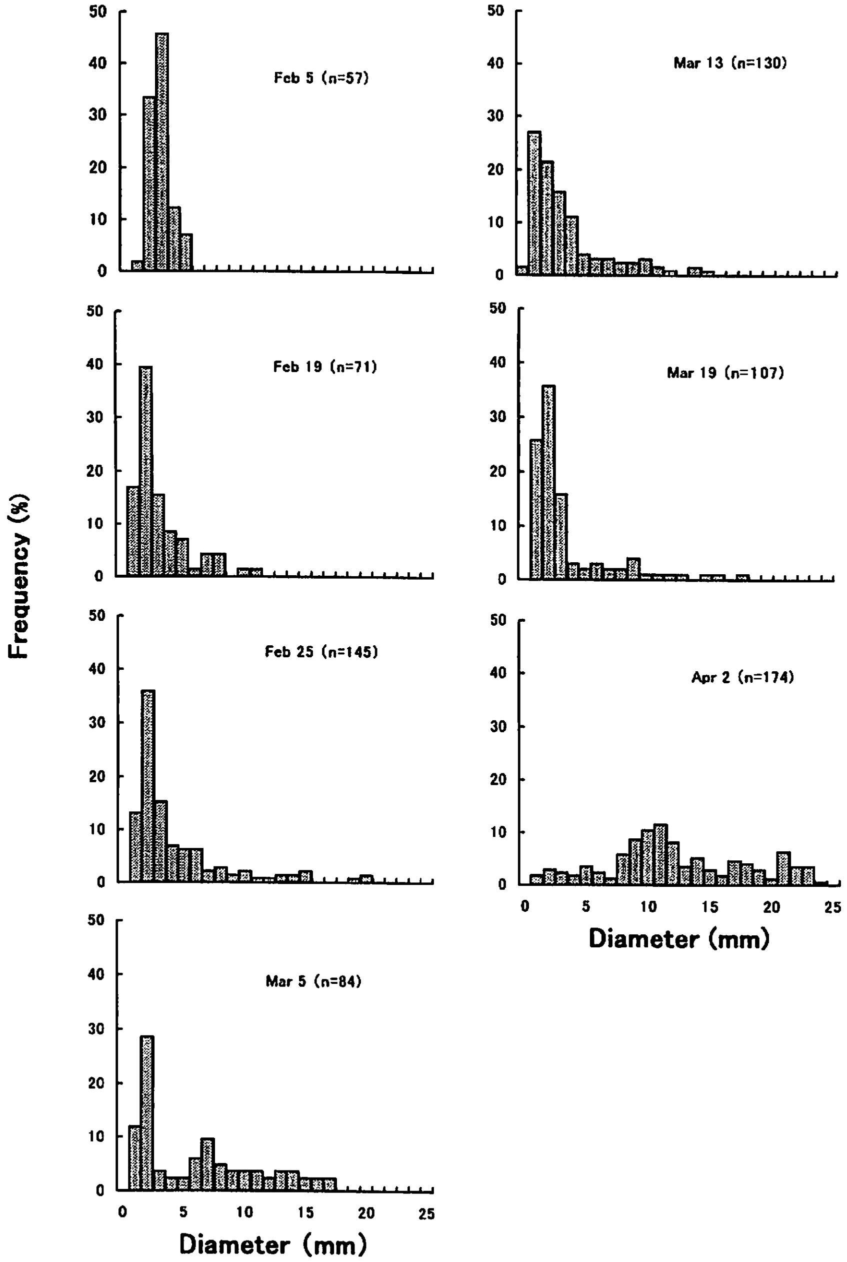

Fig. 6. Relative frequency distributions of the central disc diameter of *Aurelia aurita* ephyrae and young medusae in 2002.

exception is the observation in Gullmar Fjord, Sweden (Hernroth & Gröndahl 1983, 1985). They observed two abundance peaks of ephyrae in Gullmar Fjord in October–December and March–April. In this area, newly liberated ephyrae grew from October to December, but the growth stopped and the ephyrae entered a resting stage during the winter before growing again in April. However, in most other waters, the occurrence of ephyrae is restricted to the period between late winter and early spring as mentioned above. In the present study, ephyrae mostly appeared from February to April with an abundance peak in March. These data are in accordance with a previous study in Tokyo Bay by Toyokawa et al. (2000). During the winter, a decrease in water temperature, lower than 10°C in February in the innermost part of Tokyo Bay, induces strobilation of polyps and liberation of ephyrae (Watanabe & Ishii 2001; Ishii & Watanabe 2003). The occurrence of ephyrae in early March is explained by the strobilation caused by a decrease of water temperature during winter.

In this study recruitment of young medusae was observed from February to April with an abundance peak in April as found in previous studies in Tokyo Bay (Omori et al. 1995; Toyokawa et al. 2000). Considering the differences in timing of the abundance peaks between ephyrae and young medusae, it is assumed that the developmental period from ephyra to medusa is almost one month. This assumption is in good agreement with our incubation data, in which the developmental period was found to be 20–28

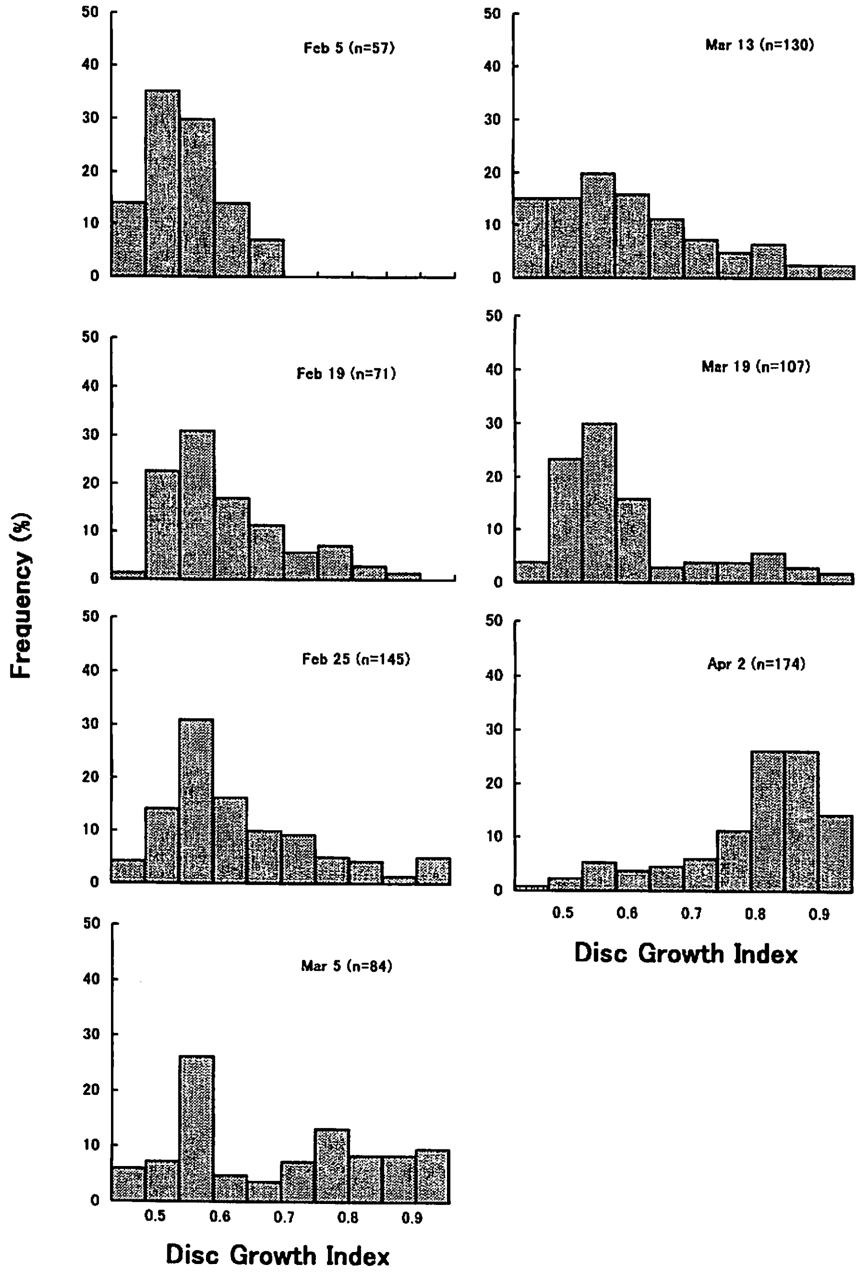

Fig. 7. Relative frequency distributions of the disc growth index of *Aurelia aurita* ephyrae and young medusae in 2002.

days.

The developmental period from ephyra to medusa deduced from incubation experiments by Yasuda (1983) was different from that found in this study. Yasuda (1983) showed that newly liberated ephyrae became young medusae after 56 days at 16–26°C supplying rotifers as prey. However, over 90% of the ephyrae died during the course of the incubation experiments. Significance of food type for growth of ephyrae is discussed by Båmstedt et al. (2001). Båmstedt et al. (2001) incubated ephyrae with various food types at 15°C and showed that the bell diameter (central disc) attained about 5 mm after 10 days from the beginning of the experiments if fresh *Mytilus* or POM were supplied as prey. We consider that the longer ephyra developmental period determined by Yasuda (1983) is caused by the difference in food type used. It is considered that naturally occurring zooplankton, consisting mainly of *O. davisae*, is preferable for ephyrae growth as it is with adult medusae (Ishii & Tanaka 2001), and it is suggested that food availability in the spring in Tokyo Bay is appropriate for *A. aurita* ephyrae.

Frequency distribution patterns of ephyra diameters showed that the abundance of small sized ephyrae is higher than larger ephyrae or young medusae as also found in previous studies (Yasuda 1983; Toyokawa et al. 2000). These results suggest lower survivorship in the early ephyra stage. Yasuda (1983) estimated survivorship as 1–11% during the ephyra stage from in situ data on ephyra abundance in each

Table 1. Stage duration, mean daily production rate and P/B ratio for each disc growth index group of the *Aurelia aurita* ephyra population in Tokyo Bay from December 5, 2001, to April 23, 2002.

Disc growth index[a]	Mean biomass ($mgC\,m^{-3}$)	Stage duration (days)	Weight increase ($mgC\,ind^{-1}$)	Mean daily production rate ($mgC\,m^{-3}\,day^{-1}$)	Daily P/B ratio
0.45–0.5	0.00022	0.29	0.0021	0.00042	1.9
0.5–0.55	0.00046	0.48	0.0035	0.00048	1.0
0.55–0.6	0.0012	0.75	0.0055	0.00068	0.59
0.6–0.65	0.0014	1.1	0.0085	0.00051	0.37
0.65–0.7	0.0015	1.7	0.013	0.00036	0.24
0.7–0.75	0.0016	2.3	0.018	0.00025	0.15
0.75–0.8	0.0016	3.3	0.025	0.00018	0.12
0.8–0.85	0.0028	4.5	0.035	0.00026	0.09
0.85–0.9	0.0015	6.0	0.047	0.00013	0.09
0.9–0.95	0.0026	7.8	0.063	0.00012	0.05

[a] Disc growth index is defined as the ratio of the central disc diameter to the diameter over lappet tips in ephyra.

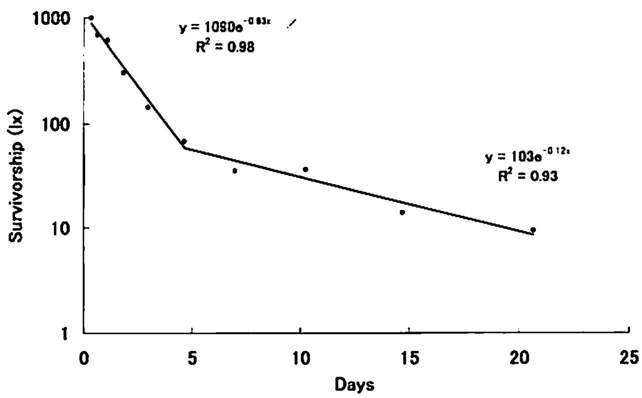

Fig. 8. Survivorship (lx) of *Aurelia aurita* ephyrae estimated from the changes in the total number of ephyrae in each stage produced in the survey area during the entire observation period.

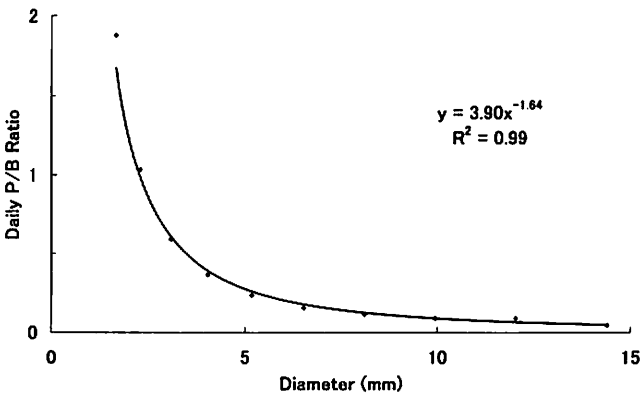

Fig. 9. Relationship between the central disc diameter and daily P/B ratio for *Aurelia aurita* ephyrae.

developmental stage in Tsuruga Bay. The estimation of Yasuda (1983) is based only on the changes in abundance of each stage and the factor of stage duration is eliminated. Our data is not able to be compared with Yasuda (1983) since the definition of ephyra stages is different and the data on stage duration is lacking. However, survivorship of ephyrae as determined by Yasuda (1983) will be lower, since the stage duration is shorter for the early ephyra stage and is longer for late ephyra stages (metephyra in his study).

The developmental stages of *A. aurita* ephyrae have been examined in several previous studies (Southward 1955; Spangenberg 1965; Yasuda 1983). Development of an ephyra into a medusa involves growth of the bell margin between the rhopalia, tentacle growth, elaboration of the oral arms and gastrovascular cavity, and sexual maturation. Of these biological changes, morphological changes involving growth of the bell margin of the central disc between rhopalia is most easily quantified. However the growth of the central disc does not always coincide with directly development of the ephyrae. For example, smaller young medusae were observed at lower prey concentrations (i.e. 80 $mgC\,m^{-3}$) as shown in Fig. 2. Our microscopic observations revealed that changes of disc growth index almost always coincided with characteristic changes in morphology such as tentacle growth, elaboration of the oral arms and gastrovascular cavity, increase in numbers of gastric cirri, and the development of radial canals. Moreover, the disc growth index of young medusae having the same morphological characters as adult ones was restricted to 0.9–0.95 in all prey concentration groups, except for the lowest one. The ratio of the diameter of the central disc to the diameter over lappet tips, i.e. disc growth index, is recommended to indicate the developmental stage easily by a numerical value.

Our data for survivorship during the ephyra stage revealed that only 1% of newly liberated ephyrae survive to become young medusae. Exponential decrease of the survivorship indicates higher mortality of newly liberated ephyrae than young medusae. The observed cut off point in the survivorship curve indicates that the mortality rate significantly decreased after 4.6 days at a disc growth index of 0.7. It is not obvious which morphological changes might contribute to decreased mortality at this point, but the development of tentacles on the bell margin at the cut off point may be a factor.

The ephyra population in Tokyo Bay is not thought to be food limited on the basis of the present incubation experiments and in situ zooplankton biomass data. Feeding pressure on the ephyra population is the most likely factor regulating the abundance of ephyrae. We couldn't infer the main consumer of ephyrae, since data indicating actual predation on *A. aurita* ephyrae through means of gut content analyses or feeding rate measurements is not available for other carnivorous predators in Tokyo Bay. Recently *A. aurita* medusae have been reported to be ingested by other medusae such as *Cyanea capillata* and *Phacellophora camtschatica* (Strand & Hamner 1988; Båmstedt et al. 1994; Hansson 1997). Preliminary observations by the senior author (H. I.) point to the existence of some dense aggregations of the sea-nettle *Chrysaora melanaster* between March and May in the innermost part of Tokyo Bay. Nomura & Ishimaru (1998) also described the occurrence of *C. melanaster* in April and May in Tokyo Bay. We consider that predation by *C. melanaster* on *A. aurita* ephyrae may in part contribute to decreases in the abundance of ephyrae in Tokyo Bay.

The highest abundance of ephyrae (2.8 inds m^{-3}) is comparable with other studies in Tokyo Bay; 0.7 inds m^{-3} in Toyokawa & Terazaki (1994) and 2.4 inds m^{-3} at Odaiba in Toyokawa et al. (2000). Even at the highest densities, the biomass of ephyrae was only 0.084 mgC m^{-3} in this study, which is about 0.05% of the total zooplankton biomass. In the ephyra stage, there are no predation effects by *A. aurita* controlling zooplankton abundance as observed for dense aggregations of adult medusae (Uye et al. 2003).

The daily P/B ratios for early ephyra stages estimated in this study were much higher than for the other zooplankton (Table 1). For example, the daily P/B ratio of the copepod, *Pseudodiaptomus marinus*, at 15°C was about 0.1 (Uye et al. 1983). Higher production compared with biomass indicates that newly liberated ephyrae abruptly grow into young medusae within one month. Kinoshita et al. (1997) inferred an adaptive mechanism in ephyrae by respiratory analyses of *A. aurita* ephyrae and medusae, and suggested that weight specific energy demand decreased during the ephyra stage to promote rapid and efficient growth. The survivorship from newly liberated ephyrae to young medusae was only 1%, that is to say 99% of newly liberated ephyrae will die during the ephyra stage. For polyp stage of *A. aurita*, survivorship of newly settled polyps settling on the lower side of the plate reached ca. 600% by active asexual reproduction in Tokyo Bay (Watanabe & Ishii 2001). Considering the stage duration that is 4–7 months in the polyp stage and 1 month in the ephyra stage, it appears that the ephyra stage has a much higher risk of predation in order to maintain their populations. To avoid the high mortality during the ephyra stage, it is very important to grow as rapidly into a young medusa as possible.

Growth rate of zooplankton, including jellyfishes, generally increases with increasing water temperature and food availability. From monthly measurements of water temperature in the innermost part of Tokyo Bay conducted by our laboratory during the past 8 years, it has been revealed that water temperature during March and early April falls within a narrow range (12–16°C), and there is no significant interannual variation. Interannual variation in the growth rate of ephyra cannot be explained by the interannual differences in water temperatures. To assess the effect of food availability, it is important to know the biomass of possible prey species for ephyrae. As mentioned above, food type is an important factor in regulating growth of ephyrae (Båmstedt et al. 2001). We used naturally occurring zooplankton, including copepods such as *Oithona davisae*, for the incubation experiments and these types of foods are the preferred prey for ephyrae as mentioned above. Recently, however, the importance of gelatinous food for growth in jellyfish has been stressed by several workers (Strand & Hamner 1988; Matsakis & Conover 1991; Båmstedt et al. 1994, 1997; Hansson 1997). Matsakis & Conover (1991) suggested that hydromedusa, *Rathkea octopunctata*, which is dominant jellyfish in spring, contributed as a preferred prey for *A. aurita*. *Rathkea octopunctata* occurs abundantly from February to April in the innermost part of Tokyo Bay (Sugiura 1980; Toyokawa & Terazaki 1994). We assumed that the abundance of preferred prey was an important factor regulating the growth of ephyrae. It is suggested that a combination of high availability of preferred food in the water and a high initial density of newly liberated ephyrae will lead to a mass occurrence of medusae in the following summer.

Acknowledgements

We are grateful to the crews of the T/S "Hiyodori" and the members of the Ecology Laboratory, Tokyo University of Fisheries, for their assistance and co-operation. Critical suggestions for the incubation experiments by Dr. M. Omori are gratefully acknowledged. We would like to thank two anonymous referees for their constructive comments.

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