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Life history and seasonal abundance of *Aurelia aurita* medusae in Tokyo Bay, Japan

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Abstract: Occurrence, growth and seasonal variation of the scyphomedusa *Aurelia aurita* was investigated in Tokyo Bay from January 1988 to May 1992. Ephyrae occurred from late October through May with peak abundance in February and March. The distribution of ephyrae was mainly restricted to the inner part of the bay, and the abundance was highest in the innermost part of the bay. Young medusae derived from ephyrae occurred from February. The median diameter of the young medusae was 4.8 cm in April. Growth was rapid from April to May with a maximum daily growth rate of 12.6%. The median diameter was 17.7 cm at the beginning of August. Spawning was observed in July 1991 in specimens of 14.4–20.8 cm, and in May 1992 in one specimen of 17.0 cm. In October, the proportion of deteriorated specimens was high and the median diameter decreased. The abundance of *Aurelia* medusae was low from autumn to winter. Some medusae apparently survived through winter and large specimens (>20 cm) were collected with the small young specimens in April. Some of them were still spawning. *Aurelia* medusae were scarce in the outer part of the bay. Carbon-based biomass in the inner part of the bay was 1.3–246 mgC m^{-3} in July 1990, 0.4–16 mgC m^{-3} in May 1991, and 0.4–52 mgC m^{-3} in September 1991, while it was generally below 2 mgC m^{-3} from autumn through winter. It is hypothesized that the autumn decrease in medusae biomass was due to (1) the increase in deteriorated medusae in autumn, and (2) the outflow of the upper layer of water in the inner bay grew stronger in autumn due to a prevailing north wind and increased precipitation, and a considerable part of the population was swept out from the inner part of the bay.

Key words: scyphomedusae, ephyrae, population dynamics, distribution, coastal ecosystem

Introduction

Aurelia aurita (Linnaeus) is an inshore scyphozoan species and is cosmopolitan from northern boreal to tropical waters (Russell 1970). In Tokyo Bay and the Seto Inland Sea, mass occurrences of *Aurelia* medusae have been a socio-economic problem since at least the 1960s. They frequently block water intakes of thermal power plants that use seawater to cool the condenser system, and cause operational difficulties or further shutdown of the power plant (Sato 1967; Kuwabara et al. 1969; Matsueda 1969). Knowledge of the life history, seasonal variation of standing stock and the mechanisms which regulate their abundance has been needed since then. From the aspect of ecosystem study of the highly eutrophicated Tokyo Bay, it is necessary to quantitatively assess the ecological role of *Aurelia* medusae, especially their population dynamics, horizontal and vertical distributions, and migration patterns (Nomura & Ishimaru 1998).

It is known that there are roughly two patterns in the occurrence and growth of the medusoid stage of *Aurelia aurita* in the field. One is that ephyrae occur from late winter to early spring, grow rapidly to adult size, mature in summer and then disappear from the water column or survive through the winter (Hamner & Jenssen 1974; Möller 1980; Hernroth & Gröndahl 1985; Lucas & Williams 1994). The other is that often the planulae develop directly into a single ephyra immediately after settling (Haeckel 1881; Hirai 1958; Kakinuma 1975). The former pattern is known from Kagoshima Bay, the southern coast of Japan (Miyake et al. 1997). As to the latter case, slow medusa growth with win-

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ter spawning is reported from Urazoko Bay, on the coast of the Japan Sea (Yasuda 1968, 1971, 1975), and fast medusa growth with summer spawning is reported from Mutsu Bay, the northern coast of Japan (Hirai 1958; Kakinuma 1975). In Tokyo Bay, the central part of Japan, it is known that *Aurelia* ephyrae occur from December through May (Sugiura 1980; Toyokawa & Terazaki 1994), grow rapidly, and spawn from summer through to the following year (Tsuchiya et al. 1984; Omori et al. 1995). It has been suggested that there was recruitment in autumn as well as in spring in Tokyo Bay (Omori & Fujinaga 1992). It is necessary to assess growth from ephyrae to medusae in the field to clarify the season of recruitment in Tokyo Bay.

We chose Odaiba as the main station for monthly sampling. The station is shallow and rich with underwater substrates to which scyphopolyps are expected to attach (Thiel 1962), and it was reported that at Harumi, near the station, ephyrae occur more abundantly in winter than off Funabashi (Sugiura 1980; Toyokawa & Terazaki 1994). Therefore the station was considered appropriate to assess the life cycle from the early stages. The station is semi-enclosed and the effect of advection was expected to be relatively small. Also important was that the station was easy to access from land. For the estimation of standing stock in the main body of the bay, we used a research vessel to encompass the bay from the innermost to the outermost part.

Materials and Methods

Recruitment and growth pattern

Medusae of *Aurelia aurita* were collected at Funabashi (Fig. 1A, B) in April and near the mouth of the Arakawa River (Fig. 1C, D, E) from May to October in 1990, and at Odaiba (Fig. 1F) from April 1991 through May 1992. Horizontal hauls were carried out for 3–5 minutes at 1–2-m depth with a 2-mm-mesh net (80-cm mouth diameter). The volume of water sampled was measured after May 1991 using a flowmeter attached to the mouth of the net. Surface water temperature was measured with a thermometer before each net collection. Medusae were counted and their diameters were measured along adradial axis to within 1 cm (until March 1991) and later to 1 mm (from April 1991 to the end of the sampling). For damaged medusae whose diameter could not be accurately measured, the radius was doubled instead. Medusae bearing planulae larvae or those with damaged bodies were counted and measured separately at Odaiba. Diameter of medusae was converted to wet weight by the following equation:

$$W=1.9\times10^{-4}L^{2.7},$$

where W is the wet weight (g) and L is the bell diameter (mm) (Toyokawa 1995). Daily growth rate (G, % d^{-1}) was estimated from the equation :

$$G=(\ln W_{i-t}-\ln W_i)/t\times100,$$

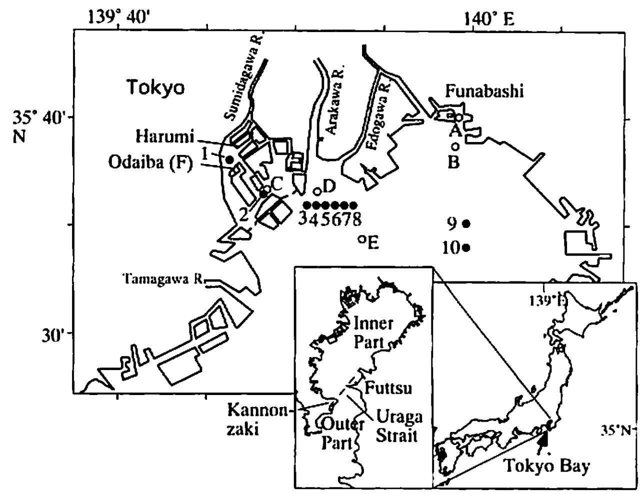

Fig. 1. Location of sampling stations in the northern part of Tokyo Bay. Medusae were collected at: Stns A, B, Funabashi, April 1990; Stns C, D, E, around the mouth of the Arakawa River, May–October 1990; Stn F, Odaiba, April 1991–May 1992. Ephyrae and young medusae were collected at: Stn B, Funabashi, January 1988–February 1989; Stn F, Odaiba, November 1991–May 1992. Also shown are Stns 1–10 where sampling for the biomass studies was carried out on 22–23 May 1991.

where t is the time between two sampling dates, and W_i and W_{i+t} are the wet weights of medusae estimated from median diameters at day i and day $i+t$.

To assess the size frequency distribution of younger stages of *A. aurita*, sampling was carried out at Odaiba (Fig. 1F) during November 1991 and May 1992. Horizontal hauls of 3 min each were made at 2-m depth using a 0.33-mm-mesh MTD net (56-cm mouth diameter) (Motoda 1971), equipped with a flowmeter, between 0900–1200 h. Samples were fixed in 2% formaldehyde and were examined later in the laboratory. Surface water temperature was measured using a thermometer. Vertical profiles of temperature and salinity were measured from 19 February through 26 May 1992 using an Alec Electronics portable TS meter. Samples collected at Funabashi (Fig. 1B) bi-weekly from January 1988 through February 1989 were also examined and added to the analysis. Details of the sampling at Funabashi have been described elsewhere (Toyokawa & Terazaki 1994). Samples were preserved in 70% alcohol. Water temperature was measured at 2-m intervals from the surface to 8 m using an STD meter.

In the laboratory, ephyrae and young medusae of scyphozoans were counted and measured under a dissecting microscope. All the diameters were measured along the adradial axis (Möller 1980) and the growth stage, from ephyra through to young medusa, was determined following Yasuda (1988). Preserved specimens were measured more than 40 d after the preservation. The bell diameter of live animals was estimated assuming a 35% shrinkage for the specimens preserved in 70% alcohol and a 10% shrinkage for those preserved in 2% formaldehyde (Toyokawa 1995).

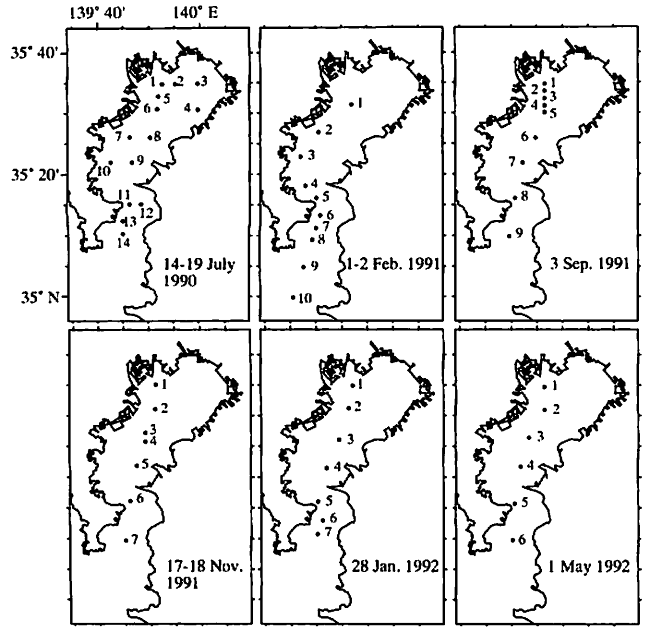

Fig. 2. Location of sampling stations for the biomass study during 1990–1992 in Tokyo Bay. Stations during the cruise on 22–23 May 1991 are shown in Fig. 1, as the stations were limited to the northern part of the bay.

Horizontal distribution and biomass

Cruises of the R/V *Tansei-Maru* and R/V *Taka-Maru* in Tokyo Bay were carried out to collect medusae of *Aurelia aurita* on seven occasions between July 1990 and May 1992 (Figs 1, 2). Sampling stations were located along a transect line from the mouth of the Arakawa River to the mouth of the bay. Apart from July 1990, stations were located to encompass the entire bay (Fig. 2), while in May 1991, stations were limited to the northernmost part of the bay (Fig. 1). For logistic reasons sampling stations were not fixed. Sampling gear and methods used during each cruise are summarized in Table 1. More than 500 m^3 of water was filtered at each station. In most cases the net was towed horizontally within the upper 5–10-m layer, for it was difficult to tow our large (mouth diameter: 1.6 m) net obliquely in the shallow (<30 m) bay. It is possible that this sampling strategy may have lead to somewhat biased results because of uneven vertical distribution of *Aurelia* medusae (Kuwabara et al. 1969; Yasuda 1972; Toyokawa et al. 1997). Considerable variation was observed in the abundance of medusae between samplings at the same station, so all samplings at a single locality were combined, in order to reflect the average abundance. The surface tows of the MTD net on 28 January 1992 were to catch ephyrae and young medusae. All the samplings were carried out during the day. Vertical profiles of water conductivity and temperature were measured with a CTD at every station. Salinity was calculated from conductivity.

Aurelia medusae were counted and bell diameters were measured as above at all stations except at Stn 9 in July 1990 and at Stn 5 in September 1991. When too many medusae were caught, they were divided arbitrarily into buckets and a portion (1/8 to 1/3) were measured. Samples collected with an MTD net on 28 January 1992 were preserved in 2% formaldehyde and were analyzed later in the laboratory. The bell diameter of live animals was estimated as described above.

Biomass at each station was estimated as follows. Diameter of medusae were converted to wet weight as described above. The sum of medusa weights at each station was divided by the total estimated volume of water filtered at the station. For stations where only a portion of the collected medusae were measured, the average wet weight for measured medusae was applied to the whole collection. The av-

Table 1. Summary of samplings in the main body of Tokyo Bay from July 1990 through May 1992. Although on many occasions stations were sampled more than once, the filtered volume of water was summed for each station.

Date	No. of stations	Gear	Mesh size (mm)	Towing method	Sampling depth layer (m)	No. of replicated tows at each station	Filtered volume (m^3)
14–19 July 1990	13	ORI[a]	1	horizontal	5–10	1[b]	548–1650
1–2 Feb. 1991	10	ORI	0.33	horizontal	0–2	1	503–1824
				oblique	from surface to above the bottom	1	
22–23 May 1991	10	ORI	2	horizontal	5–10	2[c]	475–1624
3 Sept. 1991	9	ORI	2	horizontal	5–10	2[d]	940–4829
17–18 Nov. 1991	7	ORI	2	horizontal	5–10	2	655–1449
28 Jan. 1992	7	ORI	2	horizontal	5–10	2	966–1744
		MTD	0.33	horizontal	0–3	1	38.7–51.0
1 May 1992	6	ORI	1	horizontal	5–10	1	464–1055

[a] Ocean Research Institute net (Omori 1965).
[b] Three tows at Stn 5.
[c] Four tows at Stns 4 and 6.
[d] Eight tows at Stn 3.

erage wet weight at nearby stations was extrapolated to reflect that at Stns 9 (July 1990) and 5 (September 1991) where no medusae was measured. The wet weight was converted to dry weight by assuming that the dry weight was 2.02% of the wet (Toyokawa 1995). Carbon and nitrogen content was estimated by assuming they comprised 5.3% and 1.6% respectively of the dry weight (Toyokawa 1995). All of these equations and ratios are comparable to those listed in previous publications (Larson 1986; Schneider 1988; Hirst & Lucas 1998).

Results

Hydrography

In the innermost part of Tokyo Bay, there are three major inflows of rivers (the Arakawa, Edogawa and Tamagawa Rivers) (Fig. 1). The coastline is mostly covered by concrete embankment. Station B (Fig. 1) at Funabashi is just outside of Funabashi Port and near a shipping lane. The depth was about 8 m. The water was generally well mixed from late September through May and there was a weak stratification from June to September (Toyokawa & Terazaki 1994). Surface water temperature was >25°C from late August to early September. It was <8°C from January through February. The difference between surface and bottom temperature was 2.1–6.0°C in the stratified season (June–September). From October to February, water temperature was warmer at the bottom than at the surface, with the difference 0.2–2.2°C. Salinity was 29–30 throughout the year with lower salinities (<26) at the surface during the stratified season.

The sampling station at Odaiba is in a semi-enclosed area with two openings to canals at the mouth area of the Sumidagawa River. The depth is generally shallower than 5 m except in a single narrow shipping lane and around the openings to the canals where the depth is about 9 m. Surface water temperature reached 28.5°C in early August, then decreased to 10.3°C in February. From several vertical T–S measurements from winter to spring, the difference between surface and bottom temperatures was up to 1.0°C maximum. Salinity was 23.1–24.8 at the surface and 29.6–29.8 at the bottom from February to March in 1992. In April, it was homogeneous at 20.3–20.4 between the surface and bottom, suggesting an inflow of low salinity water from the Sumidagawa River.

Tokyo Bay can be divided into an inner part and an outer part at the line which connects Cape Futtsu and Kannonzaki (Fig. 1), where the bay forms the narrow Uraga Strait. The inner part of the bay is mostly shallower than 30 m. The water mass of the bay is characterized by low salinity water, strongly influenced by inflow from rivers at the surface at the innermost station, moderately low salinity water in the middle of the bay, and high salinity water in the outer part of the bay with intrusions into the middle of the bay along the bottom layer. An estuarine front was prominent

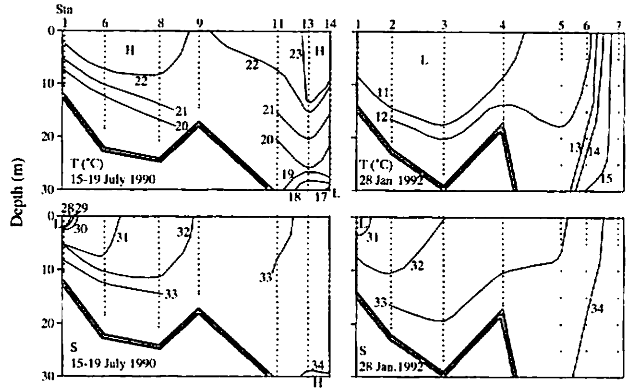

Fig. 3. The temperature (T, °C, top) and salinity (S, bottom) profile in Tokyo Bay during summer (left) and winter (right); H, higher; L, lower.

during summer off the Arakawa River. The surface salinity remained <31 even in winter (Fig. 3). The surface water temperature was >22°C during summer and was higher than that of bottom water. It was <11°C during winter and lower than that of bottom water.

Occurrence, growth and distribution of ephyrae and young medusae

Ephyrae and young medusae of *Aurelia aurita* occurred at Funabashi from January (the start of the sampling period) through May in 1988 and, besides the occurrence of a single ephyra on 29 October, from December 1988 through February 1989 (the end of the sampling period) (Fig. 4). They occurred from December 1991 through April 1992 at Odaiba. Maximum abundances at the two stations were in March, reaching 0.5 indiv. m^{-3} at Funabashi and 2.4 indiv. m^{-3} at Odaiba. Surface water temperature was less than 15°C when ephyrae were present, except for three cases at Funabashi: 28 April, 10 May, and 29 October in 1988. Larvae of other scyphozoan species did not occur except a single specimen of *Chrysaora* (7.8 mm in diameter, metephyra stage) on 19 February 1992 at Odaiba.

At both stations, ephyrae of less than 2-mm diameter were present as long as ephyrae occurred. At Funabashi, ephyrae or young medusae, greater than 2-mm diameter, occurred on 26 January, 28 March and 28 April 1988 (Fig. 5). In the following winter, the diameter of all ephyrae was less than 2 mm until 27 January 1989 apart from a single ephyra in the 2–4-mm size range on 15 December. On 20 February 1989, a young medusa up to 52 mm was present. At Odaiba, ephyrae and young medusae greater than 2 mm occurred on 19 February, 7 March and 16 April in 1992.

Occurrence of ephyrae was restricted to Stns 1–5 on 28 January 1992 (Fig. 6). The abundance of ephyrae was high at Stns 1 (0.39 indiv. m^{-3}) and 2 (0.64 indiv. m^{-3}), while it was less than 0.05 indiv. m^{-3} at Stns 3–5. The most advanced stage was metephyra II at Stn 4. The size of ephyrae at these stations was generally larger than those collected at

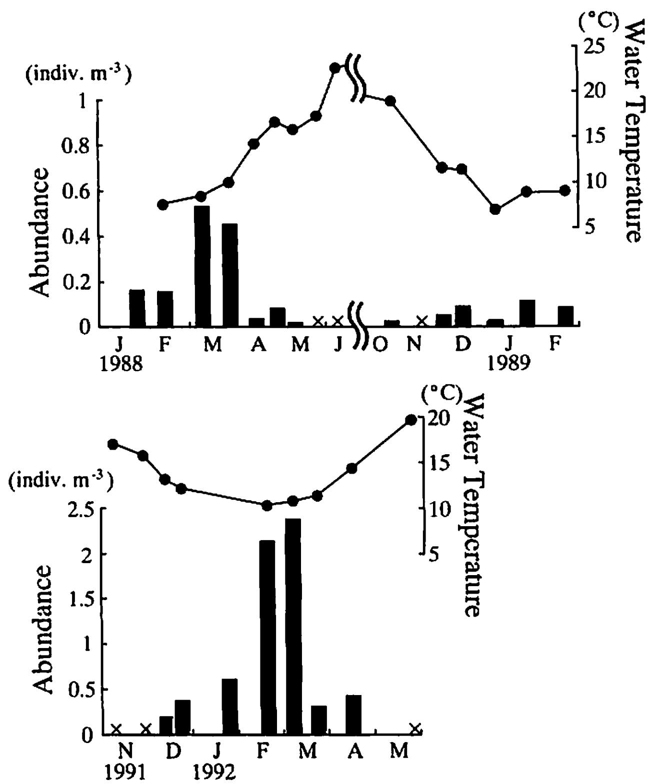

Fig. 4. *Aurelia aurita.* Water temperature and abundance of ephyrae and young medusae at the station off Funabashi, 1988–1989 (upper), and at Odaiba, 1991–1992 (lower); ×, no ephyrae occurred.

Odaiba during the same period. Median diameter was 1.8 mm at Stn 1 (n=14, 0.6–2.1 mm) and 2.3 mm at Stn 2 (n=26, 1.1–3.6 mm), while at Odaiba all the specimens were less than 2 mm. The single specimen at Stn 5 was ephyra I and the diameter was 0.5 mm. This is smaller than the average size (0.8–1.0 mm) found just after release from well-fed strobillae (Toyokawa, unpublished data). There was no significant differences among diameter distributions of Stns 1, 2 and 3/4 (combined) (p>0.05, Kruskal–Wallis one-way analysis of variance [ANOVA] by ranks) (Siegel & Castellan 1988).

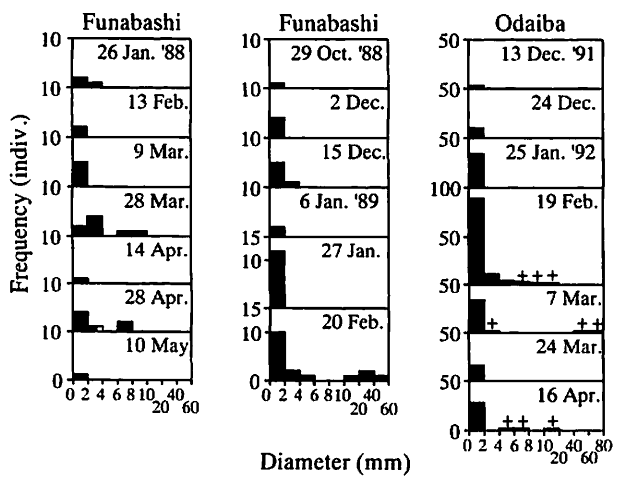

Fig. 5. *Aurelia aurita.* Size distribution of ephyrae and young medusae at the station off Funabashi, 1988–1989 (left and middle), and at Odaiba, 1991–1992 (right). Pluses denote that value is larger than 0.

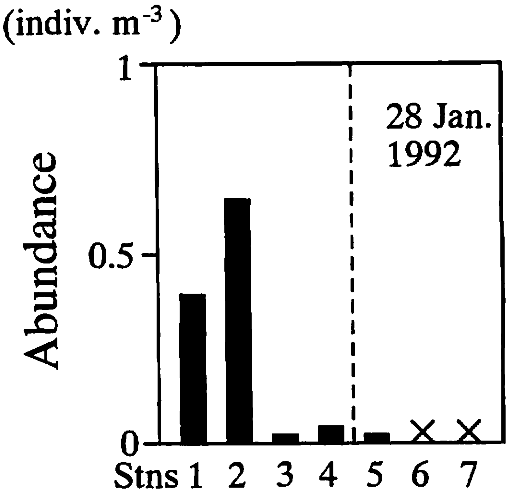

Fig. 6. *Aurelia aurita.* Distribution of ephyrae on a transect line in Tokyo Bay on 28 January 1992. Broken line denotes the boundary of the inner part (left) and the outer part (right) of the bay; ×, no ephyrae occurred.

Occurrence and growth of larger medusae

On 20 April 1990 at Funabashi, there were two size classes; 18 smaller medusae, 6–13 cm in diameter, and two larger medusae, 17 cm and 21 cm in diameter (Fig. 7). The median diameter of the smaller group was 10 cm. After 28 May, such discontinuity in size was not noticeable, and

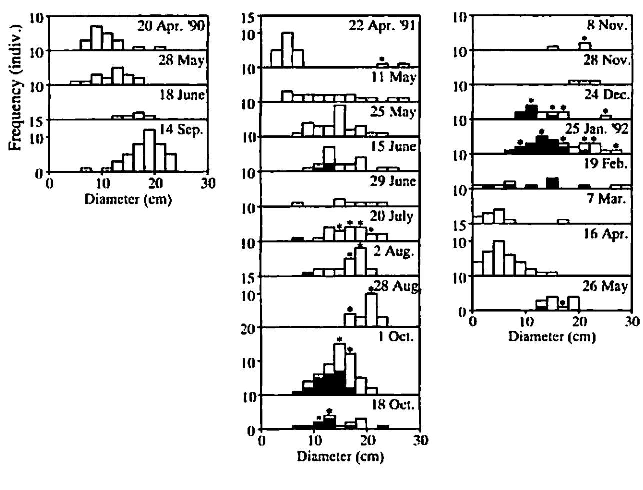

Fig. 7. *Aurelia aurita.* Size distribution of medusae at Funabashi and off the Arakawa River in 1990 (left), and at Odaiba, 1991–1992 (middle and right). Open bars denote intact specimens, black bars denote deteriorated specimens, and hatched bars denote condition not determined. Asterisk denotes that at least one mature female, bearing planulae on the oral arms, was present.

Table 2. *Aurelia aurita*. Growth and abundance of medusae in the innermost part of Tokyo Bay, indicating probably overwintered groups (*) and newly recruited groups (**). Data for November 1991 were omitted because the sample size (3) was small. Growth rate was calculated based on median diameter. Abundance was not determined in 1990 and in April 1991.

Date	n (indiv.)	Median diameter (cm)	Daily growth rate (% d^{-1})	Abundance (indiv. m^{-3})
20 Apr. 1990*	2	19		
20 Apr. 1990**	18	10		
			1.9	
28 May	17	13		
			2.7	
18 June	5	16		
			0.4	
14 Sep.	43	18		
22 Apr. 1991*	2	24.9		
			1.4	
11 May*	2	27.4		0.04
22 Apr. 1991**	20	4.8		
			12.6	
11 May**	17	11.6		0.4
			4.3	
25 May	27	14.4		1.6
			0.2	
15 June	20	14.6		0.2
			2.1	
29 June	7	16.3		0.06
			0.4	
20 July	21	16.9		0.09
			1.0	
2 Aug.	22	17.7		0.4
			1.5	
28 Aug.	20	20.5		0.1
			−2.6	
1 Oct.	54	14.8		0.09
			−1.5	
18 Oct.	15	13.5		0.03
			−0.4	
24 Dec.	13	12.3		0.03
			2.0	
25 Jan. 1992	28	15.6		0.07
			−0.1	
19 Feb.*	9	15.4		0.01
			1.3	
7 Mar.*	1	16.7		0.002
19 Feb. 1992*	3	4.3		0.004
			−2.0	
7 Mar.**	10	3.8		0.02
			2.4	
16 Apr.	35	5.4		0.09
			7.0	
26 May	12	15.2		0.01

from 28 May to 14 September, median diameter increased from 13 to 18 cm (Table 2).

On 22 April and on 11 May 1991 at Odaiba, medusae again consisted of two size groups. On 22 April, there were 20 smaller medusae, 2.1–7.4 cm, and two larger medusae, 22.2 cm and 27.6 cm. On 11 May, there were 17 smaller medusae, 4.9–21.3 cm, and two larger medusae, 26.4 cm and 28.4 cm. Differences in size class were not distinguishable after 25 May. The median diameter of the smaller size class increased from 4.8 cm on 22 April to 14.4 cm on 25 May (Table 2). The median diameter continued to increase until 28 August when it reached 20.5 cm.

On 1 October, morphological deterioration was recognizable in 43% of the population and the median diameter decreased to 14.8 cm. The condition of deterioration is summarized as follows; (1) yellowish stains were seen on parts of the umbrella or oral arms, (2) umbrella margin was damaged, and marginal lappets and tentacles were lost, (3) there were holes in the umbrella, (4) gastric pouches shrank, (5) oral arms were lost, (6) in extreme cases, all the oral arms were lost from the base of the manubrium and the gastric cavity was exposed. Shrinkage did not occur to the same extent in all four stomachs, but one or two stomachs shrank considerably. In these cases, the radius of the umbrella decreased or an oral arm was lost in the vicinity of the shrunken stomachs.

The bell diameter of deteriorated medusae was significantly smaller than intact medusae on 1 October ($P<0.001$), on 18 October ($P<0.05$), on 24 December ($P<0.01$), on 25 January ($P<0.001$), and on 19 February ($P<0.05$, except for young medusae) (Wilcoxon–Mann–Whitney test) (Siegel & Castellan 1988). Deteriorated medusae occurred through February 1992, and the medians of their diameters on each sampling date during this period were in the range of 10.8–13.2 cm. On the other hand, the median diameters of intact medusae during the same period were in the range of 16.0–27.3 cm.

On 19 February 1992, the first young medusae of the year were collected. The diameter ranged from 2.0 to 6.8 cm, and the median diameter was 4.3 cm. On 7 March, all medusae, with one exception, were young medusae. The diameter of young medusae ranged from 1.5 to 6.3 cm and the median diameter was 3.8 cm. The exception was an intact large medusa (diameter: 16.7 cm), which had survived through the winter. On 16 April, overwintered medusae were undistinguishable from others. Diameters were from 1.0 to 16.0 cm (median: 5.4 cm). Diameters increased to 12.3–19.0 cm (median: 15.2 cm) by 26 May.

Apparent daily growth rate, expressed as a percentage of the median diameter, was high from April to May. In 1990, the daily growth rate was 1.9% d^{-1} from 20 April through 28 May and 2.7% d^{-1} from 28 May through 18 June (Table 2). In 1991, the rate was 12.6% d^{-1} from 22 April through 11 May and 4.3% d^{-1} from 11 May through 25 May. In 1992, it was 7.0% d^{-1} from 16 April through 26 May.

Mature female medusae (diameter: 22.2 cm) carrying eggs and planulae on the oral arms were collected on 22 April in 1991. Mature females were next observed on 20 July as medusae of 14.4–20.8 cm diameter. Planulae continued to be observed on the oral arms until January 1992. The maximum percentage of sampled medusae carrying planulae was on 20 July (38%). The percentage was still high on 24 December (31%) and on 25 January (32%). Planulae were observed attached to deteriorated medusae, too. The minimum diameter of intact medusae carrying planulae was 14.3 cm. In spring 1992, a single mature female (diameter: 17.0 cm) was first observed on 26 May.

In Odaiba *Aurelia* medusae was generally abundant, reaching 0.06–1.6 indiv. m^{-3} from April through August in 1991 (Table 2). From October through March they were less abundant. In the spring of 1992, medusae were less abundant than for the same period in 1991.

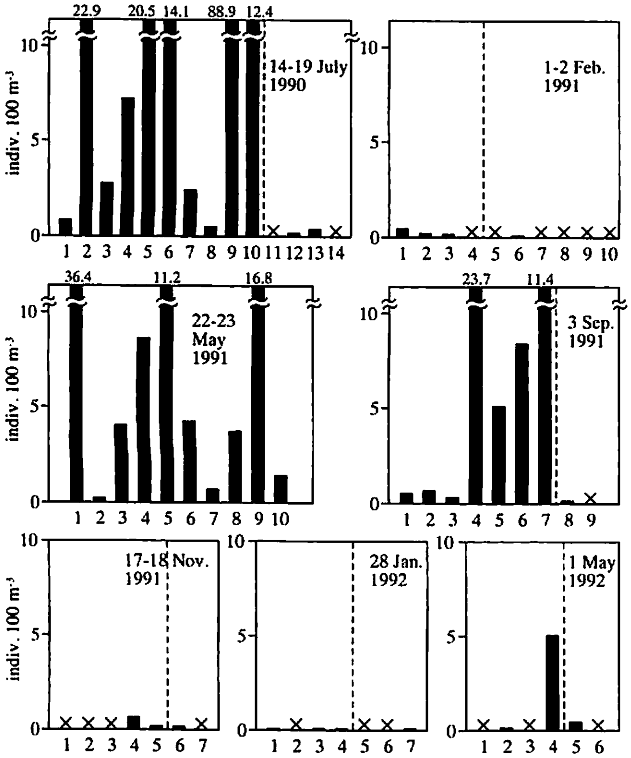

Fig. 8. *Aurelia aurita*. Distribution of medusae in Tokyo Bay from July 1990 to May 1992. Broken line denotes the boundary of the inner part (left) and the outer part (right) of the bay; ×, no medusa occurred. Numbers on the abscissa denote sampling stations.

Distribution and seasonal change of biomass

During our sampling, medusae of *A. aurita* were always scarce (<0.5 indiv. $100\,m^{-3}$) at stations in the outer part of the bay (Fig. 8). Therefore, we used only data from the inner part of the bay in the later statistical tests.

Medusae were scarce in autumn through winter. The null hypothesis that the abundance was equal for the seven sampling periods was rejected ($p<0.001$, Kruskal–Wallis one-way ANOVA by ranks) (Siegel & Castellan 1988). The a posteriori multiple comparisons showed that there were significant differences in abundances between July 1990 and November 1991, and between July 1990 and January 1992.

The total range, median and quartile of bell diameters at the stations in the inner part of the bay are shown in Table 3. Medusae diameter at the inner bay stations were tested for equality during 14–19 July 1990, 22–23 May 1991, and on 3 September 1991. Other samplings were not tested, because the sample size was small. The null hypothesis that the frequency distribution of bell diameter was equal among stations was accepted for 22–23 May 1991, but was rejected in two cases, 14–19 July 1990 and 3 September 1991 ($P<0.001$ both, Kruskal–Wallis one-way ANOVA by ranks) (Siegel & Castellan 1988). The a posteriori multiple comparisons showed significant differences in the distributions of bell diameter in July 1990 between Stns 1 (median: 14.5 cm) and 2 (19.5 cm), between Stns 2 and 5 (18 cm), and in September 1991 between Stns 4 (17.1 cm) and 7 (13.2 cm), between Stns 6 (15.8 cm) and 7.

Carbon- and nitrogen-based biomass of medusae in the inner part of the bay is summarized in Table 4. Carbon-based biomass in the outer part of the bay was always <1 mgC m^{-3}.

Discussion

Occurrence of *Aurelia* ephyrae was restricted to the inner part of Tokyo Bay. They were an order of magnitude more abundant in the northern part of the inner bay, where the three major rivers flow in, than in the southern part. The ephyrae were still more abundant in the canals (Odaiba) than outside of the canals (Funabashi). Peak abundance of ephyrae reported at Harumi (1.7 indiv. m^{-3}) (from Table 1 in Sugiura, 1980, assuming a filtering efficiency of 0.9) is

Table 3. *Aurelia aurita*. Bell diameter and percentage of deteriorated specimens during various seasons in the inner part of Tokyo Bay. Numbers of stations examined are different from those sampled, because there were stations where medusae were not collected or diameters were not determined; N: total number of samples; Q_1, Q_3: first and third quartiles. Median, Q_1 and Q_3 are the data for observation numbers $(n+1)/2$, $(n+1)/4$ and $3(n+1)/4$ when sorted in order of increasing size, respectively. n is the number of total observations. When $(n+1)$ was not divisible by 2 or by 4, a weighted mean was used (Snedecor 1956). Results of Kruskal–Wallis one-way ANOVA by ranks show that unequlityof frequency distributions of bell diameters among stations was significant (*** $P<0.001$), not significant (ns), and not tested (–). nd denotes not determined.

	No. of stations examined	N	Range (cm)	Median (cm)	Q_1 (cm)	Q_3 (cm)	K–W test between stations	% of population deterioration
14–19 July 1990	9	650	7–26	19	16	21	***	nd
1–2 Feb. 1991	3	5	10–26	19	10	25	—	60
22–23 May 1991	10	405	5.4–31.0	15.2	11.6	18.0	ns	nd
3 Sep. 1991	6	193	5.4–23.9	15.4	12.8	18.0	***	nd
17–18 Nov. 1991	2	11	12.2–22.8	17.8	14.3	21.4	—	82
28 Jan. 1992	3	9	6.8–23.4	11.5	7.0	21.0	—	78
1 May 1992	2	36	1.2–19.2	7.6	3.6	12.9	—	11

Table 4. *Aurelia aurita*. Carbon and nitrogen-based biomass during various seasons in the inner part of Tokyo Bay.

	No. of stations	Carbon-based biomass ($mgC\ m^{-3}$)		Nitrogen-based biomass ($mgN\ m^{-3}$)	
		Range	Median	Range	Median
14–19 July 1990	10	1.3–246	28	0.4–74	8.5
1–2 Feb. 1991	4	0–1.3	0.6	0–0.4	0.2
22–23 May 1991	10	0.4–16	7.6	0.1–4.8	2.3
3 Sep. 1991	7	0.4–52	11	0.1–16	3.3
17–18 Nov. 1991	5	0–1.7	0	0–0.5	0
28 Jan. 1992	4	0–0.4	0.2	0–0.1	0.08
1 May 1992	4	0–2.8	0.03	0–0.9	0.009

of the same order as that at Odaiba. Yasuda (1988) reported that occurrence of ephyrae was concentrated in the innermost part of Urazoko Bay and in Tsuruga Bay. In Kagoshima Bay, polyps of *Aurelia* were distributed exclusively on the underside of floating piers and polystyrene buoys, especially on the shells or calcareous tubes of fouling animals, and in the empty space where the occupier had recently fallen off (Miyake et al. 1997). The main origin of *Aurelia* ephyrae in Tokyo Bay is supposed to be from within the canals at the head of the bay. These canals are full of artificial underwater constructions and accompanying fouling organisms (Furota 1985) providing substrates for scyphystomae.

Aurelia ephyrae mostly appeared from December to April with peak abundances from February to March in the innermost part of the bay. The surface water temperature was below 15°C during this period. These data are in accordance with a previous publication by Sugiura (1980), except that ephyrae occurred until early June in Sugiura (1980). A decrease in water temperature has been reported as one of the most important factors that initiate strobilation (Kakinuma 1962). In her experiments, the lowering of temperature from 25°C to 15°C was the most effective way to initiate strobilation. Strobilation occurs in low rate during the spring increase in water temperature, and even during summer in very low rate (Thiel 1962). Thus, the occurrence of ephyrae from late October to early June in the innermost part of Tokyo Bay is able to be explained by the strobilation of polyps primarily caused by a decrease in water temperature. However, we do not have enough evidence that rules out direct formation of ephyrae from planulae.

Recruitment of young medusae was observed from February through April. Recruitment was not observed in autumn. Their high apparent growth rate from April to May is probably supported by an increased environmental temperature and an abundance of prey organisms. To attain a daily growth rate of 12.6% at a population density of 0.4 indiv. m^{-3} for medusae of 4.8-cm diameter (Table 2, 22 April to 11 May 1991), assuming a 6% respirative loss (Larson 1987) and an assimilation efficiency of 86% (Anninsky 1988), 0.61 $mgC\ m^{-3}\ d^{-1}$ of prey organisms is needed. The average abundance of copepodids of *Acartia omorii* was 2000–3000 indiv. m^{-3} from April to May during 1981–1988 (Nomura & Murano 1992). Although February to June is a season of low abundance for *Oithona davisae*, copepodids were present in abundances of 3000–28,800 indiv. m^{-3} in 1981 and in 1982 (Anakubo & Murano 1991). Assuming a dry weight of 6.8 μg for *A. omorii* (Hirota 1981) and 0.5-mm body length for *O. davisae* (Uchima 1984), the abundance of these two copepod species converts to 6.5–9.8 $mgC\ m^{-3}$ and 0.8–8.0 $mgC\ m^{-3}$, respectively (Hirota 1981; Uchima 1984). Considering a daily P/B ratio of 0.05–0.33 for *Acartia* spp. and 0.04–0.07 for *Oithona* spp. (reviewed by Uye 1984), these biomasses are considered to be enough to support the growth of *Aurelia* medusae at Odaiba.

Mature medusae carrying planulae occurred in April 1991, July 1991–January 1992, and again in May 1992. The percentage was still higher than 30% in winter. This suggests that *Aurelia aurita* in Tokyo Bay reproduce throughout the year as Omori et al. (1995) have mentioned. From the frequency distribution of bell diameter, and from the fact that one medusa was already carrying planulae, the large medusae that occurred in spring at Odaiba were overwintered medusae. The recruitment of newly released ephyrae was observed only during winter–spring. These facts suggest that the life span of *Aurelia* medusae in Tokyo Bay is longer than one year. Such a long life span has not been reported in Europe (Möller 1980; Hernroth & Gröndahl 1985; Lucas & Williams 1994), but has been reported in Tomales Bay, USA (Hamner & Jenssen 1974), and from previous publications from Japan (Yasuda 1971; Omori et al. 1995; Miyake et al. 1997). However, the abundance of *Aurelia* medusae (except ephyrae) was always low during winter in the inner part of the bay (<0.01 indiv. m^{-3}) (Fig. 9A). A box plot, redrawn from the Fig. 3 of Omori et al. (1995), also showed that the standing stock of *Aurelia* medusae was significantly lower in autumn–winter than in spring–summer from 1990 to 1992 (Fig. 9B) ($p<0.05$, two-way ANOVA by ranks) (Meddis 1984). Thus the contribution by the overwintered population is probably not important for the overall population dynamics.

This decrease in abundance is in accordance with the in-

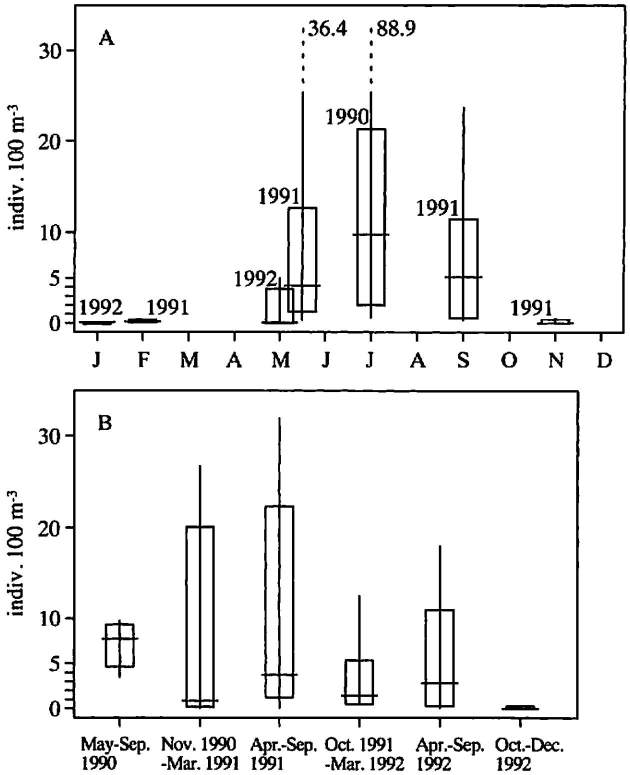

Fig. 9. *Aurelia aurita*. Box plot of the abundance of medusae in Tokyo Bay to show seasonal variations. Horizontal bar denotes median, vertical bar denotes range, and upper / lower boundary of box denotes quartile. **A.** This study. **B.** Redrawn from Fig. 3 of Omori et al. (1995).

crease in deteriorated medusae in autumn. Such a deterioration of medusae that causes a reduction in bell diameter has been reported from laboratory experiments and field observations (Spangenberg 1965; Hamner & Jenssen 1974; Möller 1980; Omori et al. 1995). Möller (1980) considered three reasons: genetic determination, starvation, and parasitization. We rarely observed parasitization in Tokyo Bay. Omori et al. (1995) excluded the possibility of starvation due to an insufficient amount of prey organisms, and concluded that the release of gametes is likely to be the trigger for reduction. Our observations at Odaiba that the radius of the umbrella often shortened in the vicinity of shrunken stomachs seem to support Spangenberg's (1965) hypothesis that starvation caused by a loss of gastric filaments at the time of spawning contributes to the death of organisms. Her hypothesis well explains the various extents of deterioration that were observed, and that deteriorated medusae continued to occur for several months at Odaiba. It also suggests that the rapid decrease in abundance of *Aurelia* medusae in autumn cannot be explained only by the death of medusae.

Physical processes in the bay, along with biological factors, are considered to affect the maintenance of the population during spring through summer and their decrease in autumn. Our results show that the distribution of *Aurelia* medusae was mostly restricted to the inner part of the bay. *Aurelia* aggregations were most frequent within a salinity range of 28–33 in Tokyo Bay (Toyokawa et al. 1997). Although patches of *Aurelia* medusae are observed occasionally at the surface near the Uraga Strait or in the outer part of the bay (Tsuchiya et al. 1984; Toyokawa, personal observation), their distribution is probably restricted to the surface layer where low salinity water has originated from the inner part of the bay (Fig. 3; Toyokawa et al. 1997). In fact, such patches were not detected using an echosounder, which cannot detect objects shallower than the bottom of the vessel (ca. 6 m) where the transducer of the echosounder was set (Toyokawa et al. 1997).

Distribution of ephyrae suggests that *Aurelia* medusae (ephyrae) mainly originate from the northern head of the bay, especially in the canals where salinity is generally lower than 30. To spread over the bay, medusae must leave the canals which are partitioned from the main body of the bay by breakwaters, and travel across the estuarine frontal region where salinity increases to greater than 30. This is thought to be one of the reasons that medusae were scarce in the bay on 1 May 1992. Canals must act as a refuge from the increased outflow of water in autumn discussed below, and this is considered to be the reason that the abundance of medusae at Odaiba remained high while they were scarce throughout the main body of the bay during autumn through winter.

Aurelia medusae resided in the main body of the bay at least from May to September in 1991. If the distribution of *Aurelia* medusae is determined only by the movement of water, they cannot reside in the bay for such a long period of time, for the residence time for water in the inner part of the bay is 0.98 to 2.08 months during May through September (Unoki & Kishino 1977). It is assumed that some biological factors such as vertical migration (Yasuda 1974; Mackie et al. 1981; Toyokawa et al. 1997) or horizontal migration (Hamner et al. 1994) allowed the population to be retained longer than the surrounding waters.

However, this form of population maintenance may be weakened in deteriorated medusae such as found in autumn. Damaged medusae are often found at the surface at the mouth of the bay (Fisheries Stations of Kanagawa Prefecture 1981–1984). Moreover, prevailing northern winds and an increase in the inflow of river water in autumn causes an increase in outflow of the upper layer of stratified water from the inner to the outer bay owing to gravitational circulation (Unoki & Kishino 1977, Unoki 1998), and this accelerates advection of the population towards the mouth of the bay in autumn. The residence time of water in the inner part of the bay is at a minimum (0.76–0.98 month) from August through October (Unoki & Kishino 1977). In September 1991, the distribution of *Aurelia* medusae was skewed from the central to the southern part of the bay, probably because of an increased discharge of water into the northern part of the bay (Toyokawa et al. 1997: Fig. 5). The smaller diameter of medusae at the southernmost station (Stn 7) than at the northern stations (Stns 4 and 6) and their distribution being restricted to the surface layer (shallower than 6 m) at Stn 7 (Toyokawa et al. 1997) suggests that smaller, presumably damaged, medusae were more susceptible to being advected by the outflow of water in the upper layer.

It is hypothesized that the abundance of *Aurelia* medusae in the inner part (main body) of the bay becomes smaller in autumn, because (1) the ratio of deteriorated medusae increases in autumn and they gradually are lost from the water column, and (2) the outflow of the upper layer of water from the inner part of the bay grows strong in autumn because of gravitational circulation (Unoki 1998) and a considerable portion of the population is swept out from the inner part of the bay. The fact that blockages due to jellyfish in the intakes of thermal power plants throughout the bay were less frequent in a year of frequent typhoons (Sato 1967) seems to agree with this hypothesis, because heavy rains accompanied by typhoons will cause an increase in the amount and outflow rates of river water and accelerate water exchange from summer to autumn, causing frequent losses of the *Aurelia* population from the bay.

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