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Horizontal distribution and growth of jellyfish, *Aurelia aurita* (Linnaeus 1758) *sensu lato*, in Mikawa Bay, Japan

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Abstract—We investigated the occurrence, growth, and horizontal distribution of the moon jelly, *Aurelia aurita sensu lato*, in Mikawa Bay from April 2007 to November 2008. In May and August 2007, dense populations of adults occurred in the bay mouth. After August, larger individuals with no planula larvae had involuted bells. In March 2008, adults were highly abundant in the western part of the bay. Small-sized moon jellies were observed from March to June, and dense swarms of adults and semi-adults shifted from the western part to the eastern part of the bay from spring to summer. In August 2008, very few adults were observed, and all were damaged or involuted without planula larvae. After August, no adults were observed. The estimated biomass of the *Aurelia* medusa in Mikawa Bay was much higher than that of the preceding reports. Therefore, the growth of the *Aurelia* medusae population in Mikawa Bay was comparable to previous observations. A life cycle model of *Aurelia* medusae that explains the spatio-temporal distribution of young and adult medusae and the appearance of sessile polyps in Mikawa Bay is discussed.

Key words: *Aurelia aurita s.l.*, spatio-temporal distribution, Life cycle, Mikawa Bay

Introduction

Recent studies on the life history of jellyfish have reported the increase in the number of mass break-outs in the world's oceans (Parsons 1977, Möller 1979, 1980, Purcell 1985, Hay et al. 1990, Matsakis and Conover 1991, Lucas and Williams 1994, Schneider and Behrends 1994). Harmful jellyfish blooms have increased around the world in recent decades as a result of human-induced degradation of ecosystems (Purcell et al. 2007). The moon jelly, *Aurelia aurita sensu lato* (Linnaeus 1758) (hereafter simply referred to as *Aurelia aurita*), is widely distributed in the neritic zone and in inland seas in a higher position in neritic food web, and mass break-outs are reported frequently (Yasuda 1969, 1971). The moon jellies create problems by clogging trawler nets (e.g. Hela 1952, Russell 1970) and clogging cooling water intakes in power plants (Mawatari et al. 1962, Matsueda 1969).

The moon jelly also causes problems for neritic fisheries by eating eggs and larvae of commercial fish species (Möller 1980, 1984, Kideys and Niermann 1994). Dense swarms feed intensely on zooplankton communities and thus suppress the neritic food webs (Lindahl and Hernroth 1983, Van der Veer and Oorthuysen 1985, Omori et al. 1995, Schneider and Behrends 1998). Top-down control of the plankton community by the jellyfish changes the zooplankton community structure and alters the conformation of marine ecosystems (Schneider and Behrends 1998). In the coastal waters of western Sweden, feeding pressure by moon jellies on copepods diminished feeding pressure by the copepods on algae and induced a dinoflagellate bloom (Lindahl and Hernroth 1983). Parsons (1979, 1993) proposed that over-fishing of commercial fish species released the jellyfish from competition, allowing them to eat various food sources, from microzooplankton to fish larvae.

In the Northern Hemisphere, *Aurelia* medusae with a life span of several months to over a year predominate from winter through spring as ephyrae (reviewed in Lucas and Williams 1994). Adults predominate in spring through summer (Nomura and Ishimaru 1998, Möller 1984, van der Veer and Oorthuysen 1985, Toyokawa 1995). A high abundance of *Aurelia* medusae has frequently been observed in the mouth of Mikawa Bay, Japan. Mikawa Bay is separated from Ise Bay to the west by the Chita Peninsula. The surrounding land, especially in the innermost part of the bay, is highly populated and industrialized. The coastal area of the bay and peninsula accounts for much of Aichi Prefecture, where 7.25 million people reside, the fourth largest population in Japan (Statistics Bureau 2010). Mikawa Bay is one of the most eutrophicated bays in Japan on account of its semi-enclosed state and loadings from two major rivers, the Yahagi River from the northwest and the Toyo River from the east (Yamamoto and Okai 2000). In this region ika-nago, or Japanese sand lance (*Ammodytes personatus*), and katakuchi-iwashi, or Japanese anchovy (*Engraulis japonica*), are commercially important species, and compete with moon jellies for zooplankton (Uye and Ueda 2004). The jellies frequently block water intakes of thermal power plants that use sea water to cool the condenser system, and cause operational difficulties or further shut-down of the power plants (Hamada 2003).

Little is known about the general distribution pattern of adult *A. aurita* in this bay. A few studies have focused on the distribution of polyps (Hamada 2003), but no comprehensive work on the life cycle has been done to date. Studies of the population dynamics of *A. aurita* should encompass the whole of Mikawa Bay and cover the whole life cycle from polyp to medusa. As an initial stage to fill this gap, this study examines the distribution of adult moon jellies in Mikawa Bay with particular reference to their seasonal and horizontal patterns.

Materials and Methods

Adult moon jellies were collected at 39 stations in Mikawa Bay (Fig. 1, Table 1) in fish larva nets (conical; 130 cm mouth diameter, 3.5 m long, 0.5 mm mesh) and modified NORPAC nets (conical; 45 cm mouth diameter, 2.1 m long, 27.5 mm mesh in upper 1/3, 18.0 mm mesh in middle 1/3, and 3.5 mm mesh in bottom 1/3). A flow meter was attached to each net. The fish larva nets were towed obliquely and the NORPAC nets were towed vertically to collect adult moon jellies. The average towing speed was ca. $0.3\,\mathrm{m\,s^{-1}}$. A memory depth recorder was attached to the bridle cable of each net. The volume of water filtered was calculated from the flow meter revolution. The modified NORPAC net was specifically used in the eastern part of the bay, where the water depth is too shallow to deploy fish larva nets from large research vessels. Vertical profiles of water temperature (°C) and salinity (PSU) were drawn from CTD data. All adult moon jellies were sorted immediately after sampling. Bell diameters (BD) were measured to the nearest 0.5 cm by putting the medusae upside down on a plastic plate with a grid, followed by wet weight (WW) measurement to the mearest 0.5 g on an electronic balance. The BD of damaged specimens was estimated from the radius. The carbon biomass (C) was esti-

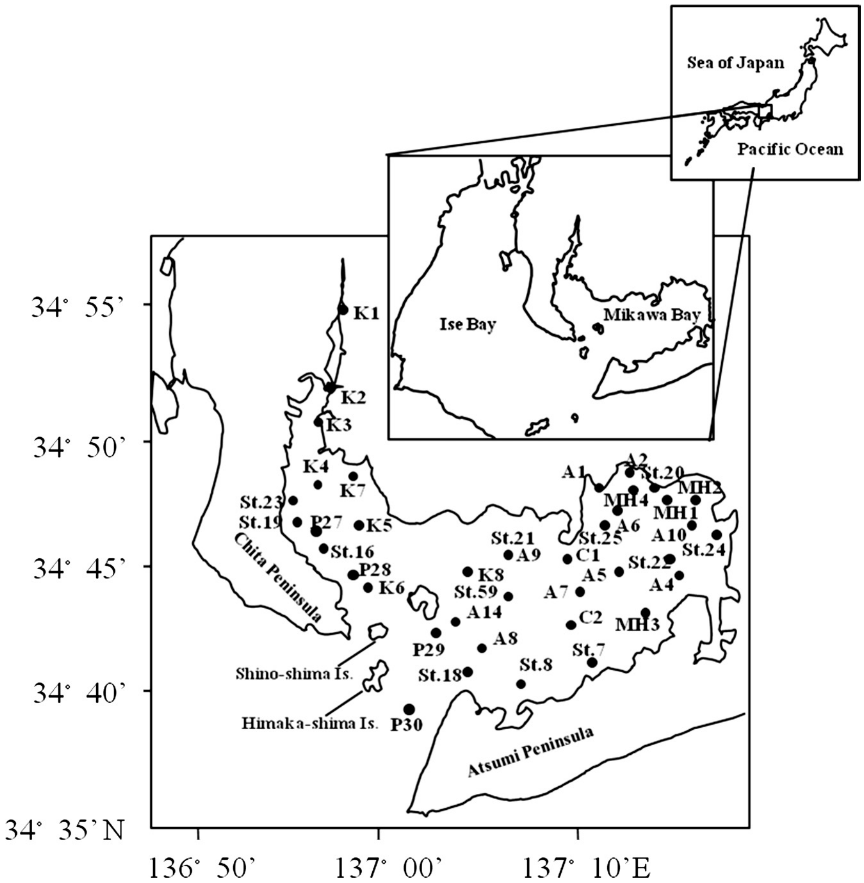

Fig. 1. Locations of sampling stations in Mikawa Bay, Japan

Table 1. Sampling details.

Year	Date	Station	Net	Cruise
2007	14-May	P27, P28, P29, P30	Fish larva net	R/V Kaiko-Maru
	30-May	K4, P27	Fish larva net	R/V Kaiko-Maru
	12-Jun	K4, P27	Fish larva net	R/V Kaiko-Maru
	26-Jun	K4, P27, P29, P30	Fish larva net	R/V Kaiko-Maru
	6-Jul	P30, P29, K4, P27, P28	Fish larva net	R/V Kaiko-Maru
	26-Jul	P30, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	28-Aug	P30, P29, K4, P27, P28, C1, C2, C3, A4, K8	Fish larva net	Fishing boat
	14-Sep	P27, K4, P29, P30	Fish larva net	R/V Kaiko-Maru
	9-Oct	K8,C1, A13, A4, C2	Fish larva net	Fishing boat
	12-Oct	P28, P27, K4, P29, P30	Fish larva net	R/V Kaiko-Maru
2008	11-Mar	P30	Fish larva net	Fishing boat
	13-Mar	P29, C2, A4, K8, K4, P27	Fish larva net	Fishing boat
	17-Apr	P30, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	8-May	A14, K6, St.16, K5, St.19, K4, K3, K2, K1, K7, K8,	Modifided NORPAC net	R/V Shiranami
	9-May	MH1, MH2, St.24, A10, A4, MH3, A5, A7, St.7, St.8, St.18, A8, A9, St.25, MH4, A1, A2, A6	Modifided NORPAC net	R/V Shiranami
	12-May	P30, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	3-Jun	St. 20, MH1, MH2, St. 24, A10, St.22, A4, MH3, A5, A7, St.7 St. 8, St. 18, A8, A9, St. 21, St. 25, MH4, A1, A2, A6, A8, St.18, St.8	Modifided NORPAC net	R/V Shiranami
	5-Jun	P30, S7, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	9-Jun	A5	Modifided NORPAC net	R/V Shiranami
	10-Jun	A5, A8	Modifided NORPAC net	R/V Shiranami
	2-Jul	St.59, A14, K6, St.16, K5, St.19, K4, K3, K2, K1, K7, K8	Modifided NORPAC net	R/V Shiranami
	3-Jul	St. 20, MH1, MH2, St. 24, A10, St. 22, A4, MH3, A5, A7, St. 7 St. 8, St. 18, A8, A9, St.21, St. 25, MH4, A1, A2, A6	Modifided NORPAC net	R/V Shiranami
	8-Jul	P30, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	7-Aug	P30, S7, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	10-Sep	P30, S7, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	7-Oct	P30, S7, P29, K4, P27	Fish larva net	R/V Kaiko-Maru
	11-Nov	P30, S7, P29, K4, P27	Fish larva net	R/V Kaiko-Maru

mated with the equation of Larson (1986):

$$C = 1.63 * 10^{-3}\,WW\,.$$

Growth rate (G) was estimated from the equation of Toyokawa (2000):

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

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 diameter at day i and day $i+t$ respectively.

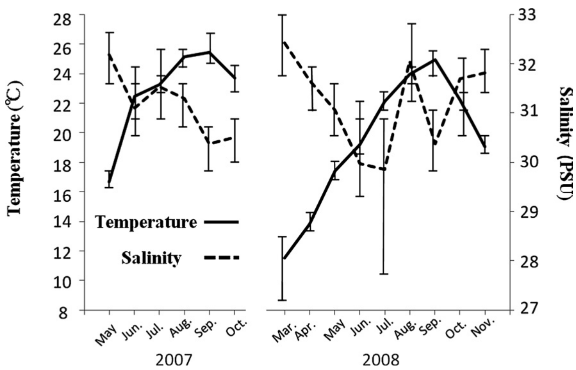

Fig. 2. Seasonal changes of average water temperature and salinity in Mikawa Bay. Bars indicate ranges.

Results

The maximum mean water temperature was 25.5°C in September 2007 and the minimum was 11.6°C in March 2008 (Fig. 2). Mean salinity fluctuated between 29.8 in July 2008 and 32.4 in March 2008.

Sampling data of *Aurelia aurita* in this study is summarized in Table 2. Relationship between BD (cm) and WW (g) of the adult moon jellies in this study was represented as follows (see Fig. 3.):

$$WW = 0.1034 * BD^{2.6591}\,.$$

Moon jellies appeared in the water column at temperatures of 8.3–26.5°C and salinities of 27.5–32.8 (Fig. 4).

In May and August 2007, adults appeared at high densities at several stations in the bay mouth area; the highest den-

Table 2. Sampling data of *Aurelia aurita* in Mikawa Bay.

Year	Month	No.	Bell Diameter (cm)		Wet Weight (g)	
			Range	Average	Range	Average
2007	May	147	2.2–30.3	14.8±5.9	0.8–899.1	180.3±166.7
	June	79	8.2–32.1	19.9±5.2	27.8–1048.3	339.6±213.9
	July	20	3.2–17.5	11.3±4.0	2.3–208.9	81.6±59.3
	August	141	3.0–23.1	15.7±3.3	1.9–437.0	170.3±81.2
2008	March	67	1.2–15.0	5.7±2.9	138.6–0.2	17.0±22.0
	April	42	4.0–25.0	15.8±5.2	4.1–539.2	192.5±134.8
	May	74	1.8–32.6	12.8±7.4	0.5–1092.2	159.6±207.4
	June	320	2.0–29.8	16.4±6.3	0.7–860.2	229.2±177.8
	July	49	6.2–25.0	16.3±4.7	13.2–539.2	203.7±127.4
	August	3	—	—	—	—

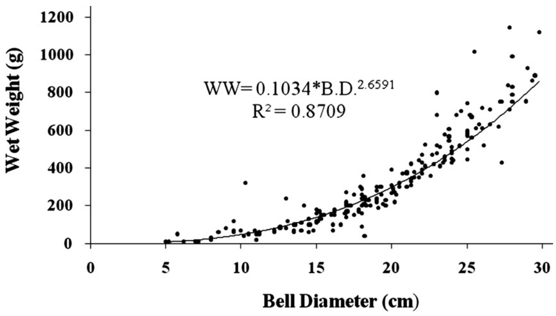

Fig. 3. Relationship between wet weight (WW) and bell diameter of *Aurelia aurita* in Mikawa Bay.

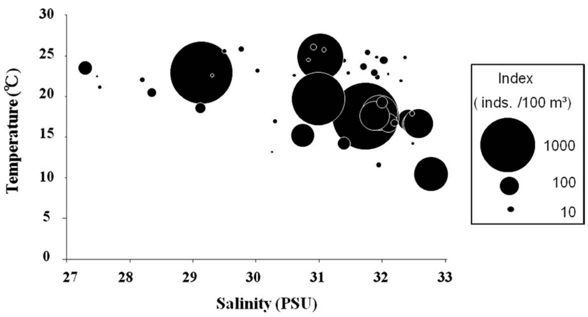

Fig. 4. Occurrence of *Aurelia aurita* in relation to water temperature and salinity in Mikawa Bay.

sities were recorded at St. P29 in May (91.4 ind./100 m^3) and August (44.7 ind./100 m^3) (Fig. 5). No jellies were observed after August in 2007. In March 2008, a moderately high density (24.8 ind./100 m^3) was recorded at St. P27, in the western part of Mikawa Bay. In April, adult *Aurelia* medusae were observed in the inner part of the western end of the bay (St. K4, 11.3 ind./100 m^3). From May till July, the distributional area shifted from the western part to the eastern part of Mikawa Bay. From May to August 2007 and from May to July 2008 mature adult medusae with planula larvae appeared in the bay mouth area. Most individuals caught in July were damaged. In August 2008, only three individuals, all damaged, appeared at St. 7, off Atsumi Peninsula. After August 2008, no moon jellies were observed in any area of Mikawa Bay. The highest abundance (1559.7 ind./100 m^3) was recorded at St. A5 in June 2008.

In May 2007, BD showed a wide range, from <5.0 to >25.0 cm, with a mean of 14.8 cm (Fig. 6). In June, large specimens (>20 cm) were abundant (mean=19.9 cm). In July, smaller specimens (10.0–15.0 cm) were more abundant. In August, most specimens were in the 15.0–20.0 cm range. In March 2008, individuals with BD <10.0 cm accounted for more than 90% of all specimens (mean=5.7 cm). In April, individuals with BD >10.0 cm accounted for more than 80% of all specimens (mean=15.8 cm). In May, BD showed a wide range, from <3.3 to >33.2 cm; most specimens larger than 10.0 cm carried planula larvae. In June, BD showed a wide range (3.5–30.7 cm, mean=16.4 cm). In July, the BD of jellies collected from southeastern Mikawa Bay, off Atsumi Peninsula, was in the range of 5.0–25.0 cm, and no large jellies >25.0cm in BD appeared in eastern part of Mikawa Bay. Most of the larger specimens carried planula larvae with involution of bells. Maximum growth rate in 2007 and 2008 was estimated at 0.06 day^{-1} between May 30 and July 12 and 0.08 day^{-1} between March and April, respectively.

Discussion

Relative abundance and growth of Aurelia aurita *in Mikawa Bay*

In the Northern Hemisphere, *Aurelia* medusae appears from May to August (Nomura and Ishimaru 1998), with a life span of several months to more than a year (reviewed in Lucas and Williams 1994). In Tokyo Bay, medusae occurred from April to May, with a maximum biomass of 45 mgC m^{-3} (Toyokawa et al. 2000). In the Kiel Bight, Germany, medusae occurred from May to June, with a maximum biomass of 55

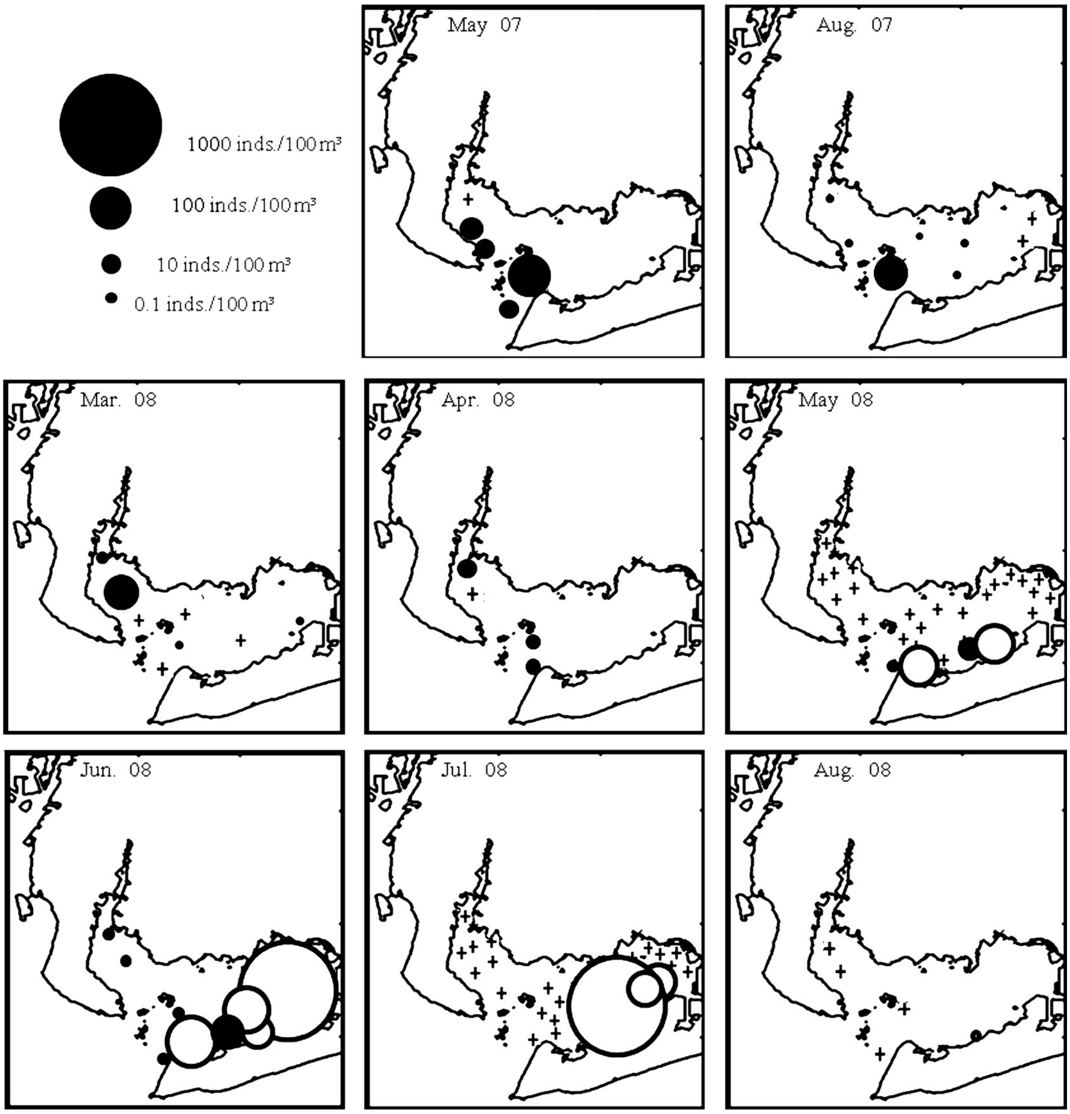

Fig. 5. Horizontal distribution of *Aurelia aurita* in Mikawa Bay. Black circles, fish larva net; White circles, modified NORPAC net. +indicates absence of *A. aurita* in the collection.

mgC m^{-3} (Möller 1984). In the western part of the Wadden sea, the Netherlands, medusae had a maximum biomass of 17.5 mgC m^{-3} in June (van der Veer and Oorthuysen 1985). The highest medusa biomass in Mikawa Bay, 262.5 mgC m^{-3}, was 4.8–15.0 times higher than that of preceding reports from the world ocean. Adult moon jellies release planula larvae in summer and then lower their bioactivity with drastic involution to death (Ishii et al. 1995). After August in both years, no medusae were recorded in Mikawa Bay. This drastic decline may be related to the release of planula larvae.

Growth rate of *Aurelia aurita* from preceding studies in 2007 and 2008 are summarized in Table 3. Moon jelly populations in Mikawa Bay showed similar growth rates to 0.09 day^{-1} in Denmark (Olesen et al. 1994) and in Tokyo Bay (Toyokawa 2000).

Table 3. Maximum growth rates of *Aurelia aurita* in different areas.

Area	Growth rate (day^{-1})	Reference
Kiel Bight, Germany	0.18	Möller (1980)
Kertinge Nor, Denmark	0.07–0.09	Olesen, et al. (1994)
Tokyo Bay	0.06	Toyokawa (2000)
Kagoshima Bay	0.25	Miyake (1997)
Mikawa Bay	0.06–0.08	This study

Effects of temperature and salinity on Aurelia aurita *in Mikawa Bay*

Occurrence ranges of temperature and salinity of natural populations of *A. aurita* are summarized in Table 4. In Mikawa Bay, moon jellies were found in water temperatures of 8.3–26.5°C. Our results are comparable to the results of Urazoko Bay (Yasuda 1968) and Tokyo Bay (Omori et al.

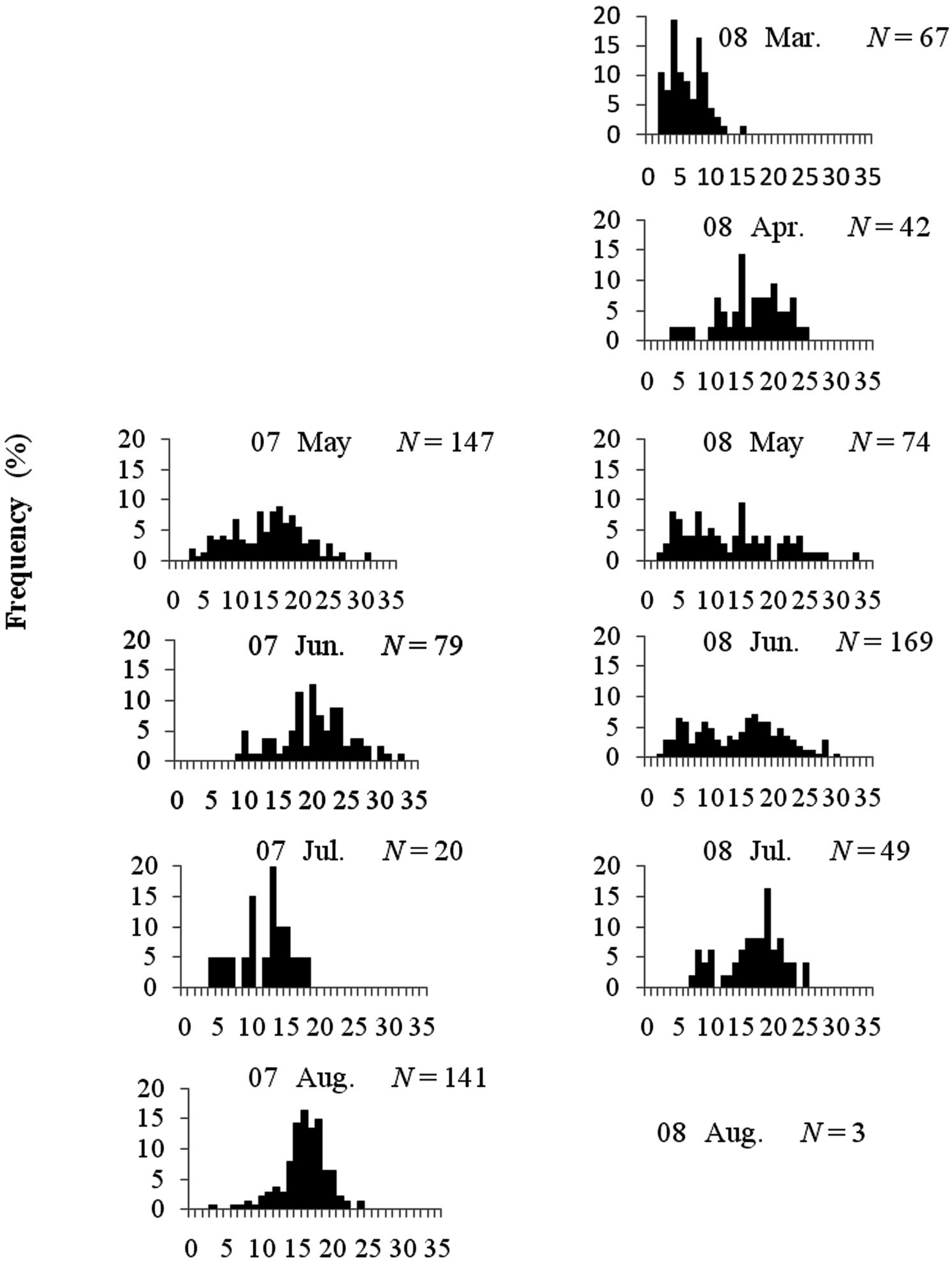

Fig. 6. Seasonal changes in bell diameter of *Aurelia aurita* in Mikawa Bay.

Table 4. The range of appearance, water temperature and salinity for natural populations of *Aurelia aurita* in different areas.

Area	Temperature (°C)	Salinity (PSU)	Reference
Urazoko Bay	7.0–28.0	28.8–34.3	Yasuda (1968)
Kagoshima Bay	15.0–23.0	2.4–35.6	Miyake (1998)
Tokyo Bay	10.0–25.0	—	Omori et al. (1995)
Kiel Bight	2.0–22.0	14.0–22.0	Möller (1980)
Mikawa Bay	8.3–26.5	27.5–33.4	This study

1995). In Kagoshima Bay (Miyake et. al. 1997), southern Kyushu, the lowest value of the range of appearance (15.0°C) is much higher than that of our study. On the other hand, in the Kiel Bight, the lowest value (2.5°C) is much lower than that of our study. These results show that natural moon jelly populations have wide range adaptation to temperature.

Moon jellies in Mikawa Bay showed high growth rates between May and June 2007 and between March and April 2008, when the water temperature ranged between 11.6 and 22.9°C (Fig. 2). This agrees with reports of the relationship between the growth of *A. aurita* and water temperature from the world's oceans (Yasuda 1971a, Hamner and Jenssen 1974, Möller 1980), which showed high growth between 13.0 and 26.0°C.

During the appearance of swarms in Mikawa Bay, the salinity ranged between 27.5 and 32.8 and the most of sawrms appeared between 29.0 and 32.5 (Fig. 4). These ranges are similar to that in Urazoko Bay (Yasuda 1968). No jellies were observed at salinities under 27.0.

Hirst and Lucas (1998) reviewed the influence of salinity on body weight in the *Aurelia aurita* on the basis of preceding research data from the world ocean and reported significant differences in the relationships between BD and dry, ash-free dry and ash weights at different salinities, where weight increased with increase of the ambient salinity and no relationship was found between BD and WW. In Mikawa Bay, the range of salinity during the research period was narrower (27.5–32.5) than those in Hirst and Lucas (1998), and there were no clear salinity effects observed on the carbon biomass and growth of natural *Aurelian* medusa population. These results show the capacity of *A. aurita* to adapt to a wide range of temperatures and salinities, and their ability to grow rapidly in spring at water temperatures ranging from 11 to 23°C.

Larval recruitment

In Mikawa Bay ephyra larvae appeared in winter (late January to mid February), with a dense population in the bay mouth (Toyokawa et al. 2011). In Urazoko Bay, most ephyra larvae developed directly from planula larvae (Yasuda 1969). However, most ephyra larvae around the world are reported to appear through the polyp and strobila stages (Kakinuma 1962, 1975, Yasuda 1969, Hernroth and Gröndahl 1983, 1985a, 1985b, Gröndahl 1988, 1989). In Mikawa Bay, no direct development from planula to ephyra larvae has been observed.

Yasuda (1988) reported that *Aurelia* medusae reached their sexual maturity at ca. 7.0 cm BD in Urazoko Bay. Mature medusae can release planula larvae into the water column. The larvae, whose swimming ability is weak, search for substrate and settle within 24 h (Miyake 1997). Thus, the distribution area of adult medusae with planula larvae and the settling point of polyps may be close to each other. In fact, great numbers of mature medusae were observed in the area near the dense polyp colonies in the bay mouth area in May 2007 (Toyokawa et al. 2011). Therefore, the size and horizontal distribution of sexually mature adults can give important information on the population dynamics. In contrast, in the eastern part of Mikawa Bay off Atsumi Peninsula, where dense populations of mature medusae were distributed in July, no ephyra larvae have been discovered (Toyokawa et al. 2011). This fact suggests that no sessile polyps live in this area, perhaps because environmental conditions are not suitable for their settlement (Ishii et al. 2008).

The population of *A. aurita* in the mouth of the western Seto Inland Sea, Japan, apparently increased in the 1990s (Uye and Ueda 2004). This increase is partly attributable to the increase of substrates for the settlement of polyps, such as floating piers and aquaculture rafts (Holst and Jarms 2007, Hoover and Purcell 2009). In the mouth area of Mikawa Bay, there are several islands with fishing ports. Toyokawa et al. (2011) reported massive colonies of moon jelly polyps on the undersurface of floating piers and mooring ships in each of these ports. This is the same area as where we observed dense populations of ephyra larvae in winter (Toyokawa et al. 2011). We suspect the occurrence of dense populations of ephyra larvae in the water column through the benthic polyp and strobila stages here.

Numerical simulation combined with Hydrodynamic modeling and Lagrangian particle tracking model analysis with the addition of suspended particles as ephyra larvae was conducted (Kazuhiro Aoki et al. personal communication). Behavior of particles as young jellies one month later in the ephyla stage were analyzed on the basis of four anticipated cases as follows: young jellies of a) active diel vertical migrant; b) non-migrant and passive drifter; c) non-diel vertical migrants with surface layer dweller; d) non-diel vertical migrant with bottom layer dweller. As a result, active diel vertical migration of *Aurelian* medusa was very important to develop horizontal distribution structures in the bay and this behavior contributes to sustaining the medusa population in the bay.

For the life cycle and horizontal distribution of *Aurelia aurita* in Mikawa Bay, the bay mouth area with small islands is an important geographic feature for the early sessile stage and larval recruitment of medusae into the water column.

On the basis of the present observations and information from previous research, the life cycle of *A. aurita* in Mikawa Bay may be summarized as follows. *Aurelia aurita* starts its life cycle as the ephyra stage during the winter in the bay mouth area. From March to April, it spends its young medusa period growing rapidly in the western end of the bay as the water temperature increases. After May, mature adult medusae carrying planula larvae appear in the bay mouth and start to release larvae into water column. After July, the spent adults shrink, become damaged, and are driven to the easternmost part of Mikawa Bay by tidal currents, where they die.

Our findings suggest that the Mikawa Bay mouth is a key site for the early life stages and population dynamics of *A. aurita* in Mikawa Bay, and that most jellies spend their entire lives in the bay, with negligible population exchange with those outside of the bay.

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