Seasonal variations in the trophic relationship between the scyphomedusa *Aurelia aurita* s.l. and mesozooplankton in a eutrophic brackish-water lake, Japan

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Abstract: The seasonal variations in trophic relationship between the moon jelly *Aurelia aurita* s.l. and mesozooplankton were investigated in a brackish-water lake, Honjo District, Japan from June 2005 to August 2006. The medusae occurred abundantly (average abundance and biomass: 0.55 medusae m⁻³ and 58.8 mg C m⁻³, respectively) during warm seasons (i.e. June–November, 2005), but were very scarce or absent during the remaining seasons. The mesozooplankton biomass fluctuated from 1.3 to 150 mg C m⁻³ (overall average: 60.5 mg C m⁻³) irrespective of the medusa biomass variation. Mesozooplankton were preyed upon by medusae almost non-selectively; the small copepod *Oithona davisae* and bivalve larvae were the predominant prey, comprising 52–99% (average: 85%) of the gastric pouch contents. The medusa population ingestion rate on mesozooplankton varied from 0.11 to 12.8 mg C m⁻³ d⁻¹, which corresponded to 0.6 to 29% of the mesozooplankton biomass per day and to 1.6 to 47% of mesozooplankton daily production rate. *A. aurita* medusae were certainly a key component of the zooplankton community, but they did not exert any significant top-down control as to suppress mesozooplankton biomass in this eutrophic lake.

Key words: *Aurelia aurita*, Japan, mesozooplankton, predation impact, seasonal occurrence

Introduction

The ecological importance of large gelatinous carnivorous zooplankton such as cnidarians and ctenophores has been increasingly recognized, since their unusual aggregations and population increases have been reported frequently in many parts of the world's ocean in recent decades (Arai 2001, Mills 2001, Brodeur et al. 2002, Purcell 2005, Kawahara et al. 2006, Purcell et al. 2007). Previous studies suggest that the abundance of such jellyfish can be a key factor in regulating the trophic structure of marine plankton communities; when they occur abundantly, their predation impact may be so intensive as to affect the population size and species composition of the plankton communities (Lindahl & Hernroth 1983, Olesen 1995, Schneider & Behrends 1998, Pagès et al. 2001). At the same time, jellyfish also reduce fish standing stocks, either by direct predation on fish eggs and larvae or by competing with planktivorous fish and fish larvae for available zooplankton prey (Möller 1980, Purcell & Arai, 2001, Hansson et al. 2005). In addition, jellyfish hamper fishing activity by clogging

and bursting fishing nets, and cause problems to coastal power plants by blocking cooling water intakes (Kuwabara et al. 1969, Rajagopal et al. 1989, Purcell et al. 2007).

In Japanese coastal waters, like many other coastal waters, the moon jelly *Aurelia aurita* s.l. Linnaeus is the most common and abundant scyphozoan species (see Dawson 2003, Dawson & Martin 2001 for sibling species), and it is particularly abundant in eutrophic waters such as Tokyo Bay and the Inland Sea of Japan. In Tokyo Bay, the mass occurrence of *A. aurita* medusae began in the 1960s, when associated problems of clogged screens of power plant seawater intakes were reported (Kuwabara et al. 1969, Yasuda, 1983). Since then, *A. aurita* has become the most dominant species in the zooplankton community (Omori et al. 1995) and exerts high predation pressure, equivalent to 5 to 162% of mesozooplankton biomass per day in spring and summer (Kinoshita et al. 2006). In the Inland Sea of Japan, the increase in *A. aurita* population became significant in the 1990s, when both increasing water temperature, particularly in winter, and decreasing of zooplanktivorous fish populations were prominent (Uye et al. 2003, Uye & Ueta 2004). In Ondo Strait, a central part of the Inland Sea of Japan,

the average biomass of *A. aurita* (66.0 mg C m^{-3}) was much higher than the micro- and mesozooplankton biomass (average: 23.7 mg C m^{-3}) and its predation impact was equivalent to 26% of zooplankton biomass per day from May to August (Uye & Shimauchi 2005).

Honjo District is an enclosed shallow brackish-water lake (area: 16.2 km^2 , average depth: 5.1 m) in the northern part of Lake Nakaumi, Shimane Prefecture (Fig. 1). The Honjo District was separated from other waters by construction of a bank in 1981, but with connections via two narrow inlets so that the water exchange between the Honjo District and the Lake Nakaumi is limited (daily exchange rate: 2.26% of water volume of the Honjo District, Koike et al. 1999). Frequent mass occurrences of *A. aurita* medusae during summer were reported by local fishermen after the embankment, but no research has been conducted on their seasonal population dynamics in the Honjo District. Meanwhile, this eutrophic lake harbors one of the world's highest mesozooplankton biomasses (annual average: 71 mg C m^{-3} , Uye et al. 2004), and hence it is our prime aim to understand the prey and predator relationship between mesozooplankton and *A. aurita* medusae. We investigated the seasonal variations in abundance, biomass, gut contents and population ingestion rate of *A. aurita* medusae, together with mesozooplankton abundance, taxonomic composition, biomass and production rate.

Materials and Methods

Aurelia aurita medusa abundance, biomass and gut contents

Prior to the initiation of our regular samplings, we conducted a sighting survey on the geographical distribution of *A. aurita* medusae by running a boat along 3 cross transects of the Honjo District. Since we encountered aggregated

medusae most often in the central part of the lake and very few near the shore, we set up a sampling area (approximate diameter: 3 km) in the central Honjo District (Fig. 1) during our investigation (at ca. 2-week intervals) from June 2005 to August 2006. On each sampling occasion, surface and bottom (depth: ca. 6 m) water temperatures, salinities and dissolved oxygen concentrations were measured by a multiple water checker (Horiba, U-20). To lessen the sampling variance due to heterogeneous distribution (see Results), medusae were caught by 5 to 7 horizontal tows of a net (0.6 m mouth diameter, 2.0 m length, $505 \mu\text{m}$ mesh size and fitted with Rigosha flowmeter) at 1–3 m depth at $1.0\text{--}1.5 \text{ m s}^{-1}$ for 3–5 minutes. Total wet weight and numbers of medusae caught by each tow were determined, and the bell diameter and wet weight were measured for specimens caught during separate tows.

Wet, dry and carbon weights were determined for medusae collected in August 2005. Medusae were transported alive to the laboratory in 20 L containers. After rinsing with distilled water and blotting, wet weight was measured. Dry weight was then measured after drying in an electric oven at $60\text{--}65^\circ\text{C}$ for 4–6 days until constant weight was reached. Carbon contents of 15–22 mg aliquots of pulverized dried medusa were determined using a CHN analyzer (Yanagimoto, MT-3) with antipyrine as the standard.

On each sampling date, 5 to 10 medusae were collected by a scoop net, and were individually preserved in 10% formalin lake-water solution. Within several days of sampling, the gastric pouch was dissected and the food contents removed from the gastric filaments by using a jet of tap water. The gut contents in the wash were retained with a $40 \mu\text{m}$ sieve and examined under a dissecting microscope. Appropriate body length of zooplankters (e.g. prosome length for copepod copepodites, body length for copepod nauplii, cladocerans and polychaete larvae, body width for bivalve

Fig. 1. Sampling site of *Aurelia aurita* medusae and mesozooplankton (shaded) in Honjo District, Shimane Prefecture, Japan.

Table 1. Summary of daily predation impact of *Aurelia* medusa populations on prey zooplankton biomass and production rates.

Location and season	Medusa abundance or biomass	Medusa bell diameter	Prey type	Ingestion rate or clearance rate	Daily predatory impact on zooplankton	Reference
Kiel Bight, Germany Summer	0.002–0.16 med. m ⁻³ 2–44 mg C m ⁻³	20 cm	Mixed zooplankton	40–80 mg C med. ⁻¹ d ⁻¹	64% of production rate	Schneider & Behrends (1994)
Bornholm Basin, Germany Spring-fall	≤0.023 med. m ⁻³	7–15 cm	Copepods & cladocerans	≤385 prey med. ⁻¹ d ⁻¹ ≤4,815 prey med. ⁻¹ d ⁻¹	~0–1.2% of copepod biomass 0.1–7.9% of cladoceran biomass	Barz & Hirche (2005)
Kertinge Nor, Denmark Spring-fall	2–248 med. m ⁻³	2–6 cm	Rotifers	0.01–2.4 l ⁻¹ med. ⁻¹ h ⁻¹	~0–351% of biomass	Olesen (1995)
Prince William Sound, USA Summer	<0.003 med. m ⁻³	7–26 cm	Copepods & cladocerans	506 prey med. ⁻¹ d ⁻¹ 634 prey med. ⁻¹ d ⁻¹	0.05% of copepod biomass 2.3% of cladoceran biomass	Purcell (2003)
Inland Sea of Japan, Japan Summer	65 mg C m ⁻³	21 cm	Mixed zooplankton	6.07 mg C med. ⁻¹ d ⁻¹	26% of biomass	Uye & Shimauchi (2005)
Tokyo Bay, Japan Spring-summer	18.3–236 mg C m ⁻³ *	13–18 cm	Mixed zooplankton	0.16 l ⁻¹ gWW ⁻¹ h ⁻¹	5–162% of biomass	Kinoshita et al. (2006)
Honjo District, Japan Summer-fall	0.6–1.3 med. m ⁻³ 20.6–120 mg C m ⁻³	11–19 cm	Mixed zooplankton	0.06–29.8 mg C med. ⁻¹ d ⁻¹	0.6–29% of biomass 1.6–47% of production rate	Present study

* Converted from average depths (24 and 44 m) of stations in Tokyo Bay.

larvae, see Uye 1982) were measured with a video micrometer (Mitani, WinRoof) and automatically converted to carbon weights using predetermined length-weight regressions (see Uye & Shimazu 1997 for details).

Mesozooplankton abundance, biomass and production rate

Mesozooplankton samples were collected by vertical hauls of a plankton net (25 cm mouth diameter, 80 µm mesh size) from the bottom to the surface and immediately fixed with 5% formalin lake-water solution. Because of the relatively homogeneous distribution of mesozooplankton in the Honjo District (overall average of variance of their abundance among 7 samples: 22%) found in a previous study (24 sampling occasions for two years, Uye et al. 2004), a single sample was examined on each occasion. The sample was split into 1/16–1/32 subsamples with a Motoda box splitter, from which at least 200 specimens were identified and counted under a dissecting microscope. Their appropriate body lengths were measured and converted to carbon weights, as described above. The production rate of each taxonomic group (P , mg C m⁻³ d⁻¹) was estimated based on its biomass (B , mg C m⁻³) and experimentally determined specific growth rates (g , d⁻¹) (see Table 1 of Uye & Shimazu 1997):

$$P = B \times g.$$

Summation of this for all taxonomic groups gives the mesozooplankton community production rate (CP , mg C m⁻³ d⁻¹):

$$CP = \Sigma P.$$

Feeding selectivity and predation impact

The feeding selectivity of *A. aurita* was determined based on the Chi-square (χ^2) method comprising of two × two configured comparisons between the average number of each prey taxon in the gastric pouch and corresponding number in the ambient water (see Pearre 1982 for details) as has been commonly used in many jellyfish prey selectivity studies (Graham & Kroutil 2001, Purcell & Sturdevant 2001, Sullivan et al. 1994). Selectivity, C , is given by:

$$C = \pm (\chi^2/n)^{1/2}$$

where n is the total number of a given prey taxon both in the medusa and in the water.

The *A. aurita* population ingestion rate on mesozooplankton was estimated by:

$$PIR = 24 \times GC \times DT^{-1} \times N$$

where PIR is the population ingestion rate (mg C m⁻³ d⁻¹), GC is the average carbon weight of gut contents (mg C medusa⁻¹), N is medusa abundance (medusae m⁻³) and DT is digestion time (h). The digestion time was not measured but assumed to be 1.0 h according to the previous studies by Ishii & Tanaka (2001) and Uye & Shimauchi (2005), because of similar prey taxa (i.e. *Oithona davisae*

Ferrari & Orsi, *Acartia omorii* Bradford, bivalve larvae and gastropod larvae), medusa bell diameter: (range: 10–25 cm) and temperature (range: 18–22°C) in these studies.

Results

Environmental parameters

Temperature fluctuated greatly from 3.2 to 30.7°C at the surface and from 3.2 to 28.3°C at the bottom (Fig. 2a). Salinity varied from 12 to 24 at the surface and from 14 to 25 at the bottom with overall averages of 19.8 and 20.8, respectively (Fig. 2b). Dissolved oxygen concentration was usually saturated (>7.5 mg O₂ L⁻¹) at the surface, but hypoxic at the bottom (minimum: 0.5 mg O₂ L⁻¹) during summer (Fig. 2c).

Mesozooplankton abundance, biomass and production rate

Mesozooplankton abundance showed considerable fluctuations with season, occurring more abundantly from June to October (average: 23.4×10^4 ind. m⁻³) than in the remain-

ing periods (average: 4.4×10^4 ind. m⁻³) (Fig. 3a). The annual peak abundance was recorded on 5 August 2005 (44.4×10^4 ind. m⁻³) and on 12 July 2006 (73.3×10^4 ind. m⁻³).

In terms of biomass, mesozooplankton also fluctuated markedly from 1.3 to 150 mg C m⁻³ over the study period (Fig 3b). Largely according to the seasonal numerical variation, the biomass was also high from June to October (average: 70 mg C m⁻³) with prominent peaks on 5 July (116 mg C m⁻³) and on 16 October (150 mg C m⁻³) in 2005 and on 20 August (128 mg C m⁻³) in 2006. These biomass peaks were composed primarily (65–99%) of the small

Fig. 2. The seasonal variations in surface and bottom (6 m) temperature (a), salinity (b) and dissolved oxygen (c) concentration in Honjo District.

Fig. 3. The seasonal variations in abundance (a), biomass (b), production rate (c) and biomass-based taxonomic composition of mesozooplankton (d) in Honjo District.

copepod *Oithona davisae* and bivalve larvae (Fig. 3d).

Mesozooplankton production rate varied from 2.2 to 260 mg C m⁻³ d⁻¹ (Fig. 3c). As a result of positive temperature effects on the specific growth rate, the production rate tended to be higher relative to biomass during warm seasons. An extremely high production rate on 16 October 2005 was attributed to the dominance of small-sized bivalve larvae.

Aurelia aurita medusa abundance, biomass and gut contents

Measurements of 600 *A. aurita* specimens from the Honjo District gave the following relationship between wet weight (*WW*, g) and bell diameter (*BD*, cm) (Fig. 4):

$$WW = 0.089 BD^{2.70}$$

Dry weight and carbon contents were measured for 18 medusae, with wet weights ranging from 13 to 78 g. Average dry weight was 2.6% (SD=1.1%) of wet weight, and average carbon weight was 4.8% (SD=2.3%) of dry weight. There was no significant size-dependent difference in these relative weights. Hence, the average wet:dry:carbon weight ratio for *A. aurita* medusae from the Honjo District was 100:2.6:0.13, which was used for converting wet weight biomass to carbon biomass.

Although we repeated 5–7 net tows at randomly selected locations in the central Honjo District to alleviate the sampling variance (overall average: 60%), the sample size of each tow differed greatly, particularly in summer of 2005 when medusae were often in patchy aggregations. In an extreme case on 5 August 2005, one towed sample contained 193 medusae but the next one contained only 2 medusae. Hence, the sampling variance among 7 tows on this date

Fig. 4. Relationship between bell diameter and wet weight of *Aurelia aurita* caught in Honjo District.

was as large as 144%.

The abundance of *A. aurita* medusae increased from 0.29 medusae m⁻³ in June, peaked on 20 August (1.33 medusae m⁻³) and then suddenly declined on 8 September 2005 (Fig. 5a). A strong typhoon, No. 14 (maximum wind speed in Shimane Prefecture: 97 km h⁻¹), passed on 6 September. Although only a few medusae were caught by our regular net samplings on 8 September, our scuba diving observations revealed that a large number of medusae were concentrated in the well-aerated bottom layer (Fig. 2c). After this sudden decline, the abundance recovered to 0.59 medusae m⁻³ in October and then disappeared until resurgence in June 2006 (Fig. 5a). The medusa population was much smaller in 2006 (maximum abundance: 0.12 medusae m⁻³) than in 2005 (Fig. 5a).

Fig. 5. The seasonal variations in abundance (a), bell diameter (b), carbon weight (c) and biomass (d) of *Aurelia aurita* in Honjo District. Vertical lines denote SD. Open circles indicate zero.

In 2005, the size of medusae was smallest in June (average bell diameter and carbon weight: 10.5 cm and 20.6 mg C, respectively), and gradually increased until November, when average bell diameter and carbon weight was 14.3 cm and 153 mg C, respectively (Fig. 5b, c). There were no significant changes in the frequency distributions of medusa bell diameter in 2005 and individual cohorts could not be identified. The growth of medusae was, however, clearly traced during June and July 2006, when the average bell diameter and carbon weight increased from 10.4 to 17.1 cm and from 60.3 to 278 mg C, respectively.

The pattern of seasonal variation in medusa biomass was similar to that of abundance; increasing from 20.6 mg C m⁻³ in June to 120 mg C m⁻³ in August then decreasing to 35.7 mg C m⁻³ in November (Fig. 5d). The average biomass between June and November was 58.8 mg C m⁻³. The average medusa biomass in June and July 2006 was 10.0 mg C m⁻³.

The daily ingestion rate varied markedly from 0.06 to 29.8 mg C medusa⁻¹ d⁻¹ in 2005 (Fig. 6a). The highest ingestion rate was recorded on 16 October 2005, when prey biomass and production rate were also highest (Fig. 3a).

The gut content examination revealed that *A. aurita* medusae ingested all the mesozooplankton taxa present in the Honjo District. The small copepod *O. davisae* and bivalve larvae were the most important prey items (Fig. 6b),

Fig. 6. The seasonal variations in ingestion rate (a) and carbon biomass composition of gut contents (b) of *Aurelia aurita* in Honjo District. Vertical lines denote SD.

Fig. 7. The seasonal variations in feeding selectivity of *Aurelia aurita* estimated from gut contents and ambient mesozooplankton in Honjo District.

Fig. 8. The seasonal variations in population ingestion rate (a), predation impact on mesozooplankton biomass (b) and predation impact on mesozooplankton production rate (c) of *Aurelia aurita* in Honjo District. Vertical lines denote SD.

accounting for 52 to 99% (average: 85%) of the gut contents, reflecting their dominance in the plankton. Other major prey taxa were copepods (*Acartia hudsonica* Pinhey and *A. sinjiensis* Mori) and gastropod larvae.

The feeding selectivity of medusae was determined for 5 prey categories, i.e. *A. hudsonica*, *A. sinjiensis*, *O. davisae*, bivalve larvae and gastropod larvae. It ranged from -0.26 for *O. davisae* to 0.25 for bivalve larvae, both recorded on 13 November, but usually stayed near zero (Fig. 7), indicating that *A. aurita* medusae fed on mesozooplankton prey largely non-selectively.

***Aurelia aurita* population impact on mesozooplankton**

The ingestion rate of the population of medusae on the mesozooplankton community varied from 0.11 to 12.8 mg C m^{-3} from June to November (Fig. 8a), which corresponded to 0.6 to 29% (average: 8.9%) of the mesozooplankton biomass per day (Fig. 8b), and to 1.6 to 47% (average: 13.0%) of the mesozooplankton daily production rate (Fig. 8c).

Discussion

The present study demonstrated the seasonality of the *A. aurita* medusa population in the Honjo District for the first time, where the population culminated during warm seasons (Fig. 5a), similar to that observed in other Japanese waters such as Lake Hamana (Kuwabara 1969), Urazoko Bay (Yasuda 1983), Tokyo Bay (Omori et al. 1995) and the Inland Sea of Japan (Uye & Shimauchi 2005). In 2005, medusae already occurred before our survey started and they seemed to grow relatively slowly to the maximum size in autumn. In 2006, the resurgence of medusae occurred in June after the disappearance of the population in the preceding winter and spring. This indicates that a new medusa generation might start in spring, as has been commonly observed in other Japanese coastal waters (Yasuda 1969, Miyake et al. 1997, Watanabe & Ishii 2001). Unfortunately, the very scarce occurrence of ephyrae in our zooplankton samples failed to identify the precise timing of ephyra liberation from benthic polyps, which also remained undiscovered despite our scuba diving searches. Hence, it is still uncertain when and where medusa recruits come from for *A. aurita* population in the Honjo District.

Compared to 2005, the medusa population size was much smaller in 2006, but vice versa for medusa body size (Fig. 5), indicating population density effect (Schneider & Behrends 1998). Such an annual variation in the occurrence of medusae has been noticed by a local fisherman (S. Nakashima, personal communication), who has been operating set-net fisheries in the Honjo District for >50 years. He also mentioned that medusae can persist during warm and mild winters and they tend to be more abundant in the following summer. The 2005–2006 winter was very severe; average local air temperature in December 2005 was 4.0°C , while the corresponding average for the previous 10 years

was 7.0°C (Meteorological Agency of Japan). An unusually rapid decline of water temperature to the annual minimum (3.2°C in January 2006) might hamper the overwintering of medusae as well as recruitment of a new population.

Uye et al. (2004) reported that due to sufficient phytoplankton food supply (average chlorophyll *a* concentration: $4.7 \mu\text{g L}^{-1}$), the Honjo District is very productive for mesozooplankton; the average biomass and production rate were 71.0 mg C m^{-3} and $17.6 \text{ mg C m}^{-3} \text{ d}^{-1}$, respectively, during a two-year survey from 1997 to 1999. The average mesozooplankton biomass (60.5 mg C m^{-3}) was similar to that of Uye et al. (2004) but the average production rate ($32.4 \text{ mg C m}^{-3} \text{ d}^{-1}$) was higher in our study. The predominance of bivalve larvae in our plankton samples boosted the mesozooplankton production rate, since small-sized bivalve larvae have higher specific growth rates ($g=0.4\text{--}1.0 \text{ d}^{-1}$) than copepods ($g=0.05\text{--}0.5 \text{ d}^{-1}$). During the warm period from June to November, 2005, the average medusa biomass (58.8 mg C m^{-3}) was equivalent to the average mesozooplankton biomass (56.2 mg C m^{-3}), demonstrating that *A. aurita* was certainly the most dominant species in the zooplankton community in the Honjo District.

Sullivan et al. (1994) reported that slow swimming prey such as hydromedusae and barnacle larvae were more vulnerable to predation by *A. aurita*. Graham & Kroutil (2001) also demonstrated that small copepods were more vulnerable than large copepods ($>1 \text{ mm}$) since the latter has a higher escape ability. Zooplankton appearing in the Honjo District almost entirely consists of meso- and microzooplankton (Godhantaraman & Uye 2003, Uye et al. 2004, present study) and hence they may be highly vulnerable. In fact, 5 major prey taxa (i.e. *Oithona davisae*, *Acartia hudsonica*, *A. sinjiensis*, bivalve larvae and gastropod larvae) were ingested in an almost non-selective manner (Fig. 7).

The mesozooplankton ingestion rates by a medusa determined in the Honjo District ranged from 0.06 to $28.9 \text{ mg C medusa}^{-1} \text{ d}^{-1}$, which were similar to those reported in previous studies (i.e. $8\text{--}15 \text{ mg C medusa}^{-1} \text{ d}^{-1}$ in Kiel Bight, Schneider & Behrends 1994, $2.2\text{--}22.8 \text{ mg C medusa}^{-1} \text{ d}^{-1}$ in Tokyo Bay, Ishii & Tanaka 2001, $6.07 \text{ mg C medusa}^{-1} \text{ d}^{-1}$ in the Inland Sea of Japan, Uye & Shimauchi 2005). Previous studies estimated the predation impacts by *Aurelia* medusa populations on zooplankton communities in the field, although different methods were employed depending on the study; the results are summarized in Table 1. An extremely high predation impact was reported by Olesen (1995) in Kertinge Nor, a brackish-water fjord in Denmark, where the *A. aurita* population ingested 351% of the rotifer biomass per day. In Kiel Bight, Germany, the medusa predation impact was equivalent to 64% of daily zooplankton secondary production (Schneider & Behrends 1994). In Tokyo Bay, the predation pressure was estimated to vary from 5 to 162% of the zooplankton biomass per day (Kinoshita et al. 2006). In the Inland Sea of Japan, it was estimated to be 26% of the zooplankton biomass per day (Uye & Shimauchi 2005). In contrast, the predation impacts re-

ported by Purcell (2003) in Prince William Sound, Alaska, and Barz & Hirche (2005) in Bornholm Basin, the Baltic Sea, were low (<ca. 8% of zooplankton biomass per day). In the Honjo District, the highest predation impact was recorded on 1 November 2005, when the *A. aurita* population (biomass: 81.4 mg C m⁻³) ingested 29% of the mesozooplankton biomass (31.7 mg C m⁻³) per day and 47% of the daily production rate (19.8 mg C m⁻³ d⁻¹). The corresponding average impacts between June and November 2005 were 8.9 and 13.0%, respectively.

In conclusion, in a brackish-water lake called the Honjo District, *A. aurita* medusae occurred only in warm seasons, and in terms of biomass this species was the most dominant component of the zooplankton community. All major taxa of mesozooplankton were equally vulnerable to this gelatinous predator, and the predation pressure by the medusa population was highest in autumn. However, no significant top-down control by *A. aurita* was observed since the zooplankton biomass did not decrease concurrently. Mesozooplankton production potential might surpass the predation loss. This further suggests that *A. aurita* medusae might not be food-limited but their seasonal population fluctuation might be affected primarily by physical parameters such as temperature and deoxygenation in this eutrophic lake.

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