

Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* s.l.

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Abstract: The polyp stage is an important part of the *Aurelia aurita* s.l. life cycle, because polyp clones are able to increase their population size by budding, providing the opportunity to increase the medusa population by the production of many ephyrae through strobilation. We investigated asexual reproduction of *A. aurita* polyps on an individual basis at 4 different temperatures (i.e. 18, 22, 26 and 28°C) and at 5 different food levels (i.e. 1.7, 3.3, 6.6, 10 and 13.3 $\mu\text{g C polyp}^{-1} \text{d}^{-1}$) in the laboratory. Three types of asexual reproduction were observed: polyps directly budded from the parent stalk (DBP), polyps budded from the parent pedal stolon (SBP), and podocysts (PC). DBP was the major reproductive method (94% of the total) and SBP and PC accounted for only 5 and 1%, respectively. PC were produced by the polyps kept under low food supply ($\leq 3.3 \mu\text{g C polyp}^{-1} \text{d}^{-1}$) and high temperature ($\geq 26^\circ\text{C}$). Production of new polyps by DBP and SBP significantly increased with increasing food and temperature. The somatic growth of parent polyps significantly increased with more food and cooler temperatures. We conclude that both increases in water temperature through global warming and increases in abundances of zooplankton prey because of eutrophication may be responsible for the prominent blooms of *A. aurita* medusae in East Asian coastal waters in recent times.

Key words: *Aurelia aurita*, bloom, eutrophication, global warming, polyp

Introduction

There is concern that large gelatinous zooplankton such as cnidarians and ctenophores have become more prevalent in many regions around the world and are causing serious socio-economic problems (Arai 2001, Graham 2001, Brodeur et al. 2002, Kawahara et al. 2006, Purcell et al. 2007). Since these gelatinous carnivores are both competitors and predators of fish (reviewed by Arai 1988, Purcell & Arai 2001), the increase of jellyfish populations may be a potential threat for sustainable fisheries (Lynam et al. 2005, Uye 2008, Pauly et al. 2009). Hence, it is important not only to elucidate the mechanisms causing the jellyfish blooms that have become increasingly frequent and prominent recently, but also to predict future blooms and to identify appropriate countermeasures.

In many coastal waters, the moon jellyfish *Aurelia aurita* (Linnaeus) s.l. (see Dawson & Martin 2001, Dawson 2003, Ki et al. 2008, for sibling species of this genus) is the most common scyphozoan species and often blooms to cause

detrimental effects on human enterprises (Yasuda 2003, Purcell et al. 2007). Particularly, in East Asian coastal waters the blooms of *A. aurita* have been associated with problems of operating power plants and commercial fisheries. For instance in Japan, the first noticeable increase of the *A. aurita* population took place in Tokyo Bay during the 1960s, when the bay was heavily eutrophicated by increased industrial and civil sewage discharge (Unoki & Kishino 1977) and aggregated medusae often clogged the screens of cooling water intakes of coastal power plants (Kuwabara et al. 1969). The *A. aurita* medusa population has since become one of the predominant zooplankton components in Tokyo Bay (Omori et al. 1995, Toyokawa et al. 2000, Ishii 2001). Since the 1980s, the *A. aurita* population has significantly increased in the Inland Sea of Japan (Seto Inland Sea), as revealed by an extensive poll of fishermen in regard to recent increases of jellyfish and associated nuisances to fisheries (Uye & Ueta 2004). In Korea, the first shut down of a nuclear power plant due to the outbreak of *A. aurita* medusae took place in 1996 (Korean Nuclear Power Plant Operational Performance Information System, <http://opis.kins.re.kr/>). Since then, the power plant shut

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downs caused by aggregated *A. aurita* medusae have become more frequent and serious, and at the same time the nuisance to fisheries has also become increasingly significant (Lee et al. 2006, Korean National Fisheries Research and Development Institution, <http://nfrdi.re.kr/>). In addition, chronic blooming of this species has now become common in eutrophicated bays and inlets, such as Masan Bay and Shiwha Lake (personal communication with researchers in Korean National Fisheries Research and Development Institute).

The increase in the *A. aurita* population in East Asia may not be attributed to a climate cycle or regime shift, which may have been responsible for jellyfish biomass fluctuation in the Bering Sea (Brodeur et al. 2002) and the North Sea (Lynam et al. 2004), but rather to regional environmental changes (Purcell et al. 2007). Although many authors have speculated about causes of the recent outbreaks of jellyfish, including increased ocean temperature by global warming, increased zooplankton prey by eutrophication, increased polyp attachment sites by marine construction, and decreased zooplanktivorous fish stocks by over-fishing (e.g. Arai 2001, Graham 2001, Lynam et al. 2006, Purcell 2005, Purcell et al. 2007, Richardson et al. 2009), little direct evidence exists.

One of the characteristic life stages of cnidarian jellyfish is the benthic polyp stage, during which clonal polyps can increase their abundance by asexual reproduction so that more ephyrae are released through strobilation. Hence, it is essential to investigate the dynamics during the polyp stage in order to understand the causes of medusa outbreaks. Previous studies have shown that temperature, salinity, light, oxygen concentration, food supply, etc. influence the polyp asexual reproduction of the genus *Aurelia* (Coyne 1973, Keen & Gong 1989, Ishii & Watanabe 2003, Ishii et al. 2008, Purcell 2007, Willcox et al. 2007, Liu et al. 2009). Most of these works examined the responses of polyps at the whole colony level, in particular how the colony size changes with environmental conditions. However, investigation at the individual polyp level (Purcell 2007, Liu et al. 2009) is needed to understand the asexual reproduction in detail. Because of recent environmental changes in East Asian coastal waters where global warming and eutrophication are remarkable (Yan et al. 2003, Gilbert et al. 2005, Wang 2006), we studied the effects of combinations of temperature and food supply on asexual reproduction and somatic growth of *A. aurita* polyps at the individual level.

Materials and methods

Polyps of *Aurelia aurita* s.l. used in this experiment were derived from our stock culture population maintained in seawater of 25 salinity at 20°C in the dark. The stock culture originated from medusae that had been collected in October 2005 from brackish-water Honjo District (part of Lake Nakaumi), Shimane Prefecture, Japan (Han et al. 2009). A hundred polyps of 2–3 weeks since budding were

carefully removed from the wall of culture containers with forceps, and 5 of them were transferred to each of 20 square polystyrene dishes (92×92×20 mm, containing filtered seawater of salinity 25). After 3 days at 20°C in the dark without food when most polyps had attached to the dish bottom, 3 healthy individuals with unshrinking body or tentacles, and being separated from each other by at least 2 cm, were selected per dish and the others were removed.

These dishes were placed at 4 different temperatures (i.e. 18, 22, 26 and 28°C±0.3°C) maintained by an incubator (Nihon-ika Co.). At each temperature, polyps were individually fed with 3, 6, 12, 18 and 24 newly hatched *Artemia* sp. (Utah, USA) nauplii (body length: ca. 200 µm, carbon weight: 0.83 µg, Uye & Kayano 1994) at every 1.5-d interval (or 1.7, 3.3, 6.6, 10 and 13.3 µg C d⁻¹). Prior to feeding, a short silicon tube (inner diameter: 25 mm, height: 20 mm) was positioned to enclose a polyp and given numbers of *Artemia* nauplii were added using a pipette inside the tubing. After consuming all foods (<15 min), the tubes were removed.

At each 1.5-d interval, all polyps were inspected under a dissecting microscope to examine the formation of new polyps, budded either from the parent stalk or pedal stolon, and podocysts. When the budded polyps separated from the parent polyps, they were excised with forceps. Podocysts were not removed. The calyx diameter, as the average of the maximum and minimum dimensions if the calyx was not round, of each parent polyp was measured with a micrometer on the first and last days of the experiment to examine somatic growth. The water in the dishes was replaced with freshly prepared and aerated (ca. 8 O₂ mg L⁻¹) water every third day. The experiment ran for 35 days in the dark, except for the time of periodic feeding and microscopic observation, which took less than 20 min.

To examine the combined effects of food supply and temperature on asexual reproduction (i.e. production of new polyps) and somatic growth of the parent polyps, two-way ANOVA was used after testing for normality and equality in variance of the data (SPSS 10.0). If the overall ANOVA results were significant, Bonferroni pair-wise comparisons were performed to test among experimental combinations. To examine the relationship between food supply and temperature on asexual reproduction and somatic growth of the parent polyps, multiple linear regression was used.

Results

Type of asexual reproduction

Aurelia aurita s.l. polyps asexually produced new polyps by budding in addition to podocysts. Two types of budding were distinguished depending on where the new polyps formed. The most common type (94% of the total, Table 1) was the directly budded polyp (DBP) off the parental stalk (Fig. 1A). Newly formed DBP attached to the substrate, and when the calyx diameter grew to 400–600 µm, it separated from the parent to develop independently. Another type was

Table 1. Mean incidents of three asexual reproduction types of *Aurelia aurita* s.l. (i.e. DBP, SBP and PC) under various combinations of food regimes and temperatures during a 35-d experiment. SD is given in parenthesis. DBP: directly budded polyp, SBP: stolonically budded polyp, PC: podocyst.

Temperature (°C)	Reproduction type	Food regime ($\mu\text{g C polyp}^{-1} \text{d}^{-1}$)					Test statistics	<i>p</i>
		1.7	3.3	6.6	10.0	13.3		
18	DBP	2.7 (0.6)	5.0 (1.0)	8.7 (1.2)	10.3 (0.6)	16.0 (<0.1)	Food, $F=79.3$, $df=4$, 19	<0.01
	SBP	0.3 (0.6)	0.7 (0.6)	0.3 (0.6)	0.3 (0.6)	0.7 (0.6)		
	PC	0	0	0	0	0		
22	DBP	5.3 (1.5)	12.3 (3.1)	14.7 (2.1)	22.3 (0.6)	27.0 (7.2)	Temp, $F=50.1$, $df=3$, 19	<0.01
	SBP	0	0	0	1.7 (0.6)	1.7 (0.6)		
	PC	0	0	0	0	0		
26	DBP	5.3 (1.2)	9.0 (1.7)	19.0 (5.3)	27.0 (3.6)	37.0 (6.6)	Food×Temp, $F=4.59$, $df=12$, 19	<0.01
	SBP	0	0	0	3.0 (<0.1)	3.3 (3.5)		
	PC	2.3 (2.1)	1.3 (2.3)	0	0	0		
28	DBP	4.3 (3.8)	14.0 (4.2)	30.0 (2.6)	31.3 (7.0)	38.3 (4.9)		
	SBP	0	0	2.0 (1.7)	2.3 (0.6)	1.3 (1.2)		
	PC	0.3 (0.6)	0.3 (0.6)	0	0	0		

the stolonically budded polyp (SBP) formed at the end of pedal stolon (Fig. 1B); the calyx diameter of recently independent SBP was 100–500 μm . The SBP were observed in high food regimes (10.0 and 13.3 $\mu\text{g C polyp}^{-1} \text{d}^{-1}$) at warm temperatures ($\geq 22^\circ\text{C}$) and in all food regimes at 18°C, but they accounted for only 5% of the total polyps produced (Table 1).

A podocyst (PC) is a cyst covered with a hard cuticle, which is formed at the pedal disc (Fig. 1C). Podocysts were produced least frequently (1% of the total) only in combinations of low food (1.7 and 3.3 $\mu\text{g C polyp}^{-1} \text{d}^{-1}$) and high temperatures ($\geq 26^\circ\text{C}$) (Table 1). The diameter of PC ranged from 200 to 300 μm . All PC remained encysted during the experiment.

Effects of food and temperature on asexual reproduction

Our preliminary experiment at lower temperatures (i.e. 10 and 14°C) revealed that although *A. aurita* polyps kept at 14°C produced new polyps by budding at extremely low rates (data not shown), most of them stopped feeding and then strobilated; at 10°C the polyps did not bud but strobilated more quickly than those at 14°C (data not shown). Hence, we performed the experiments at temperatures between 18 and 28°C, at which no strobilation took place.

In a given experimental condition, the production rate of new polyps was constant over 35 days, showing a linear relationship between cumulative numbers of new polyps and duration (Fig. 2). The total numbers of new polyps produced by budding (i.e. DBP+SBP) in each combination of

food and temperature are compared in Fig. 3. The maximum production (mean: 40.3 buds) was recorded at the combination of 13.3 $\mu\text{g C polyp}^{-1} \text{d}^{-1}$ and 26°C; the minimum production (3.0 buds) was found at the combination of 1.7 $\mu\text{g C polyp}^{-1} \text{d}^{-1}$ and 18°C (Table 1, Fig. 3). The number of buds differed significantly with food supply ($F=79.3$, $df=4$, 19, $p<0.01$), temperature ($F=50.1$, $df=3$, 19, $p<0.01$), and their interaction: $F=4.59$, $df=12$, 19, $p<0.01$) (Table 1). The multiple regression analysis revealed that the number of buds (N) increased significantly with temperature (T , °C) as well as food supply (F , $\mu\text{g C d}^{-1}$), being expressed by $N = -35.3 + 1.7T + 2.1F$ ($r^2 = 0.83$, Table 2).

Effect of food supply and temperature on somatic growth of polyps

The initial calyx diameters of parent polyps ranged from 1.1 to 1.4 mm. After 35 d, the parent polyps increased in calyx diameter to the largest at 18°C and smallest at 28°C in all food regimes (Fig. 4). The two-way ANOVA showed significant effects of food supply ($F=10.7$, $df=4$, 19, $p<0.01$), temperature ($F=76.8$, $df=3$, 19, $p<0.01$), and their interaction: $F=5.07$, $df=12$, 19, $p<0.01$) on somatic growth of the parent polyps; however, the somatic growth did not differ significantly at food levels higher than 6.6 $\mu\text{g C polyp}^{-1} \text{d}^{-1}$ (Bonferroni pair-wise comparisons). The multiple regression analysis showed that the calyx diameter increase (G , mm) was positively correlated to food supply but negatively to temperature, as expressed by $G = 1.33 -$

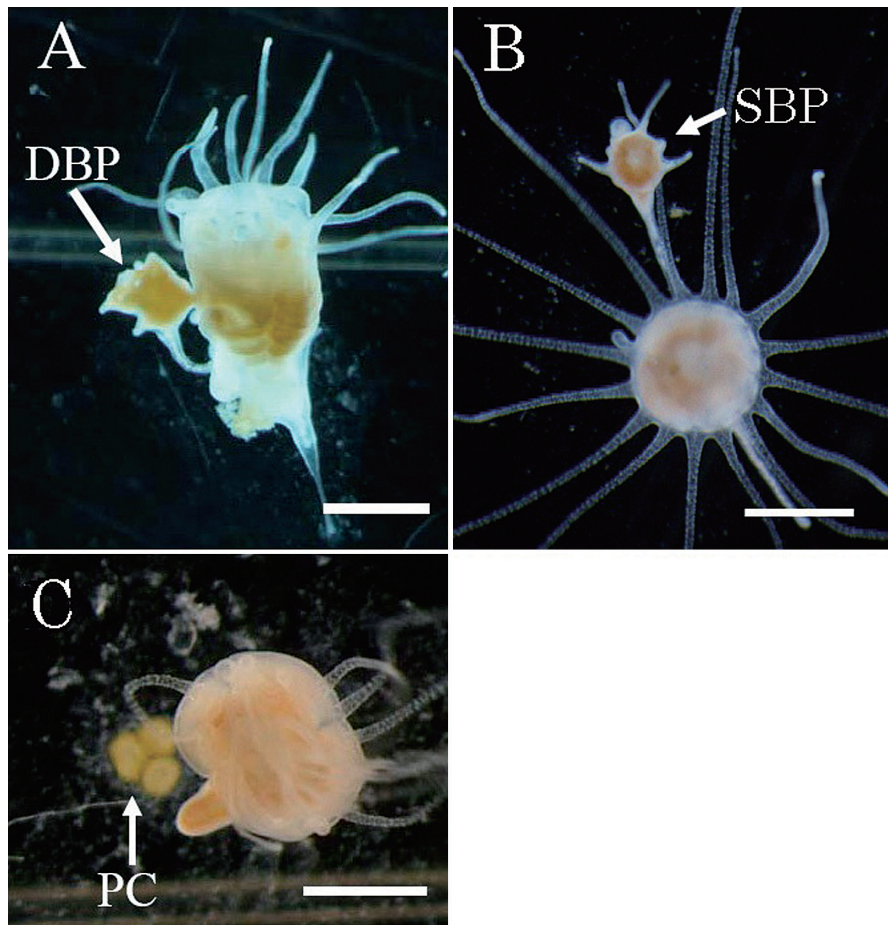


Fig. 1. Three types of asexual reproduction of *Aurelia aurita* s.l. polyps. (A) A directly budded polyp (DBP) from parent polyp's stalk, (B) a stolonical budded polyp (SBP) at the end of the pedal stolon, (C) three podocysts (PC) formed at the pedal disc. Scale bars: 1 mm.

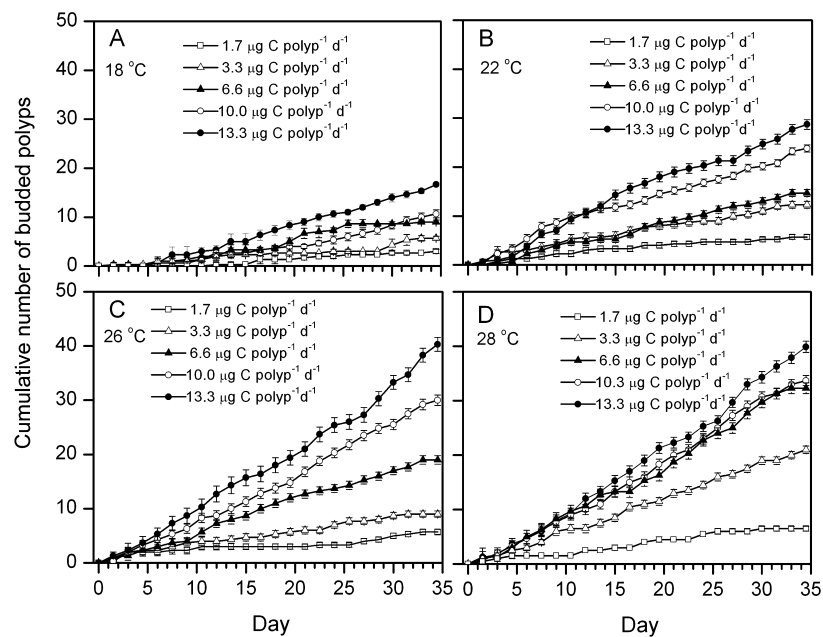


Fig. 2. Cumulative number of new polyps of *Aurelia aurita* s.l. produced under 5 food regimes at 18 (A), 22 (B), 26 (C) and 28°C (D) during a 35-d experiment. The polyp number increased linearly ($r^2 > 0.9$, $p < 0.01$ in all experiments). Vertical lines: SD.

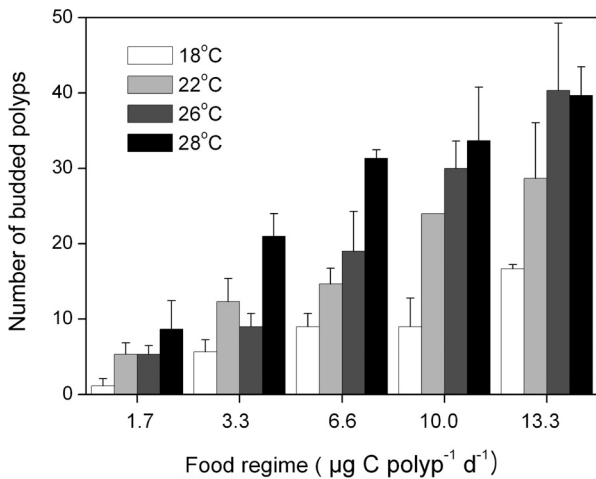


Fig. 3. Means of total new polyps (DBP+SBP) of *Aurelia aurita* s.l. produced under each combination of 5 food regimes and 4 temperatures during a 35-d experiment. Vertical lines: SD.

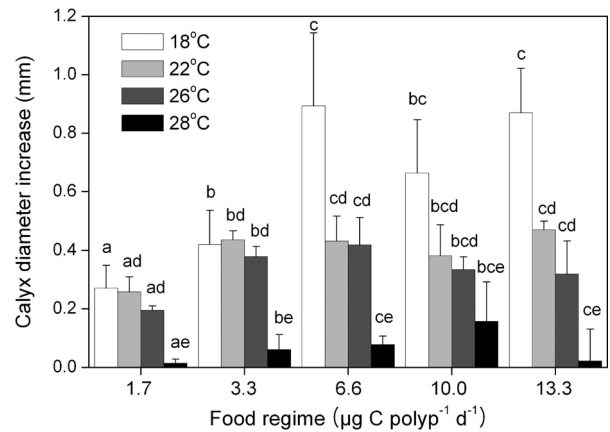


Fig. 4. Means of calyx diameter increase of *Aurelia aurita* s.l. parent polyps under each combination of 5 food regimes and 4 temperatures during a 35-d experiment. Vertical lines: SD.

Table 2. Multiple regression analysis between the number of budded polyps or calyx diameter increase of *Aurelia aurita* s.l. polyps during a 35-d experiment, food supply and temperature. Regression equations are given in text.

Variables	Coefficients	Number of new polyps			r^2	Calyx diameter increase			r^2
		t	p			Coefficients	t	p	
Intercept	-35.3	-8.3	<0.01	0.83	1.33	8.7	<0.01	0.53	
Temperature	1.7	9.6	<0.01		-0.044	-7.4	<0.01		
Food	2.1	13.6	<0.01		0.017	3.1	<0.01		

$0.044T + 0.017F$ ($r^2 = 0.53$, Table 2).

Relationship between asexual reproduction and somatic growth of polyps

The numbers of budded polyps produced at 5 different food regimes were averaged at respective temperatures; similarly, the increases in calyx diameter of the parent polyps at different food regimes were averaged at respective temperatures (Fig. 5). The averages of these parameters were significantly negatively correlated ($r^2 = 0.97$).

Discussion

Unlike most previous studies conducted at the whole colony level, our experiment of the asexual reproduction of *Aurelia aurita* s.l. polyps was carried out at the individual level using triplicate parent polyps in each of 20 combinations of food supply and temperature. In our experiment, newly formed polyps were excised immediately after they separated from the parents. The merits of our method were to provide a precise amount of food to each polyp and to avoid the inhibitive effects on budding, stolon extension, and somatic growth by over-crowding within polyp colonies. Hence, the budding rate was constant over the experimental period, indicating that the asexual reproduction and somatic growth observed here might be maximal for a given combi-

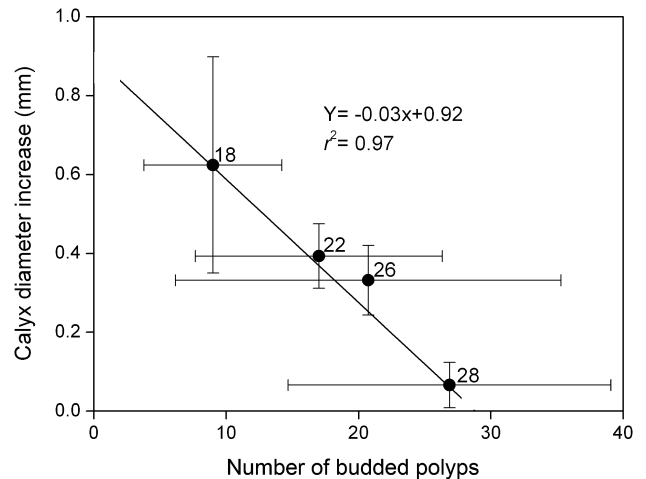


Fig. 5. Relationship between asexual reproduction (i.e. means of total new polyps) and somatic growth of parent polyps (i.e. means of calyx diameter increase) of *Aurelia aurita* s.l. at 18, 22, 26 and 28°C during a 35-d experiment. Vertical and horizontal lines: SD.

nation of food and temperature.

Among the various methods of polyp asexual reproduction, e.g. direct budding, longitudinal fission, stolon budding, planuloid budding, podocyst formation (c.f. Arai 1997, 2009, Vagelli 2007), only direct budding, stolon

budding, and podocyst formation occurred in our study. The most common reproductive method shown by our *A. aurita* polyps was direct budding as already reported by Coyne (1973) and Keen & Gong (1989). Stolonial budding was rare and restricted to certain food and temperature combinations. Podocysts were never produced by well-fed polyps, only by poorly-fed ones, suggesting that scarce food supply is an environmental cue for induction of this resting stage, as had already been speculated by Chapman (1970). The podocysts can endure through prolonged adverse environmental conditions and develop into polyps through excystment to build new polyp colonies (Arai 1997, 2009).

In Honjo District, a shallow (average depth: 5.1 m) brackish-water lake, where the medusae of our polyp specimens were derived, the wild polyp population is exposed to a wide temperature range from ca. 5 to ca. 30°C annually (Han et al. 2009). Whereas, our experiment was confined only to warm temperatures (i.e. 18–28°C), because at cold temperatures (i.e. below 14°C) the polyps ceased feeding and subsequently strobilated, as observed in our preliminary experiment. This fact indicates that some physiological changes, perhaps in preparation for metamorphosis into strobila occur in polyps at intermediate temperatures between 14 and 18°C (Kakinuma 1962). Since our SCUBA diving searches failed to find polyp colonies in the Honjo District, the actual timing of strobilation of the wild polyps remain unknown. However, a recent survey revealed that many ephyrae were collected in zooplankton samples taken between December and April (Makabe & Uye unpubl), demonstrating that strobilation and subsequent ephyra liberation take place primarily in winter and spring in the Honjo District, basically the same seasonality as observed in many Japanese waters such as Tokyo Bay (Toyokawa et al. 2000, Watanabe & Ishii 2001), Inland Sea of Japan (Uye & Shimauchi 2005) and Kagoshima Bay (Miyake et al. 2002). Since Yasuda (1975) found the direct development of planulae to ephyrae without regular strobilation for *A. aurita* in Urazoko Bay, Fukui Prefecture, the occurrence of this unusual reproductive process remains to be studied in the Honjo District.

Aurelia aurita s.l. polyps are essentially carnivorous, feeding primarily on meso- and microzooplankton (Arai 1997). Although the Honjo District harbors an extremely high biomass of both meso- and microzooplankton (annual mean: 78.4 mg C m⁻³) compared to, for example, the Inland Sea of Japan (24.0 mg C m⁻³, Uye et al. 1996, Uye & Shimazu 1997), its seasonal fluctuation is extremely wide, from ca. 10 to ca. 390 mg C m⁻³ (Raman & Uye 2003, Uye et al. 2004). Under such conditions, it is difficult to estimate the actual amount of food ingested by a wild polyp. In May 2007 when the water temperature was 18.7°C, we suspended laboratory-cultured 40 polyps on polystyrene plates at 0.8 m depth in the Honjo District for 24 h, and then retrieved them to investigate their gastric contents. A cyclopoid copepod *Oithona davisae* Ferrari & Orsi was the

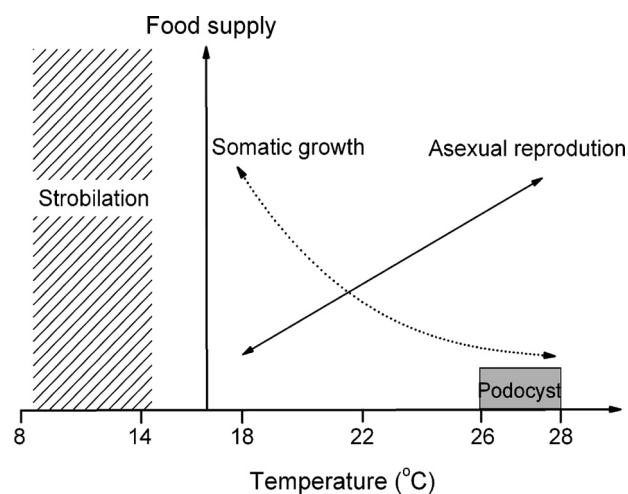


Fig. 6. Schematic representation of asexual reproduction by budding and somatic growth of parent polyps of *Aurelia aurita* s.l. in relation to temperature and food supply. Strobilation was induced at temperatures below 14°C. Podocyst formation occurred only under low food supply and high temperature combinations. Food supply scale is arbitrary.

most dominant prey (79% of total prey numbers), and the maximum ingestion rate of a polyp was 16 *O. davisae* polyp⁻¹ d⁻¹ or 4.0 µg C polyp⁻¹ d⁻¹, based on separately determined digestion time (i.e. 3 h at 18°C, Han 2009). Therefore, we assume that the wild polyps probably hardly even attain the highest ingestion rate observed in our experiment (i.e. 13.3 µg C polyp⁻¹ d⁻¹), although the laboratory cultured polyps are capable of ingesting as much as ca. 80 µg C polyp⁻¹ d⁻¹ or ca. 100 *Artemia* nauplii polyp⁻¹ d⁻¹ (Uye unpubl).

As schematically represented in Fig. 6, the rate of asexual reproduction (i.e. production of new polyps) increased with increased food supply as well as increased temperature. On the other hand, the somatic growth of parent polyps increased with increased food and decreased temperature, showing a reciprocal relationship between the somatic growth and production of offspring (Fig. 5). This fact also meant that the allocation of ingested energy by polyps to somata or reproduction varied depending on temperature. If a substantial amount of food were available, lower asexual reproduction at cooler temperatures would never be disadvantageous, since polyps of a larger size would metamorphose to strobilae with more discs and release more ephyrae (Spangenberg 1964, Ishii & Watanabe 2003).

Due to accelerated anthropogenic activities, both water temperature elevation and eutrophication are pronounced in many East Asian coastal waters. The increase of water temperature over the recent decades (i.e. 0.02 to 0.06°C per year, Takahashi & Seki 2004, Uye & Ueta 2004, Lin et al. 2005) is one of the highest in the world. This warming effect also increases the duration of warm seasons (e.g. ≥18°C). Eutrophication is also very serious particularly in

Chinese and Korean waters (Yan et al. 2003, Wang 2006) in addition to some Japanese bays near populated cities like Tokyo Bay, Ise Bay and Osaka Bay and brackish-water lakes like Honjo District and Lake Nakaumi. Eutrophication enhances phytoplankton production, which would intuitively increase the production of metazoan zooplankton such as copepods (e.g. the genus *Oithona*, in Zaitsev 1992, Uye 1994, Ishii 2001) and protozoan microzooplankton (Sanders et al. 1992, Kamiyama 1994, Uye et al. 1999). In eutrophicated waters, protozoan foods are augmented in addition to metazoan foods.

Although the growth of the benthic polyp population in situ may be influenced by many other factors, such as salinity, light, availability of attachment site, space competition with benthic organisms, predators, etc. (Watanabe & Ishii 2001, Miyake et al. 2002, Purcell 2007, Purcell et al. 2009, Willcox et al. 2008), we suggest that at least two other factors, viz. global warming and cultural eutrophication, can be responsible for the recently more prominent blooms of *A. aurita* medusae in East Asian coastal waters.

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