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REPORT

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Sexual reproduction and larval settlement of the zooxanthellate coral *Alveopora japonica* Eguchi at high latitudes

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Abstract Sexual reproduction and larval settlement of *Alveopora japonica* Eguchi were studied at its northernmost distribution in Tokyo Bay (34°58′03″N, 139°46′05″E), where the annual sea temperature ranges from 13 to 27 °C. *Alveopora japonica* is a hermaphroditic brooding coral with oocytes and spermaries developing on separate mesenteries of the polyp. The oocytes first appeared in October, maturing in late August to early September of the following year, whereas the spermaries were first observed in May, and matured in approximately 4 months. The oocytes reached ca. 800 μm in diameter. Planulae containing zooxanthellae in their endoderm were released during the daytime in September and October. Well-developed planulae were able to settle and metamorphose within 7 h. The polyps started budding about 3 weeks after settlement, and took 3 years to grow to maturity. The population examined was sexually reproductive, indicating that *A. japonica* maintains local populations in Tokyo Bay by sexual reproduction.

Keywords Coral · *Alveopora japonica* · Sexual reproduction · Planulae · High latitudes

Introduction

Although sexual reproduction of scleractinian corals in subtropical and tropical waters has been well studied (Harrison and Wallace 1990), less attention has been paid to corals at higher latitudes. Recent studies have shown that coral communities at high latitudes are sexually reproductive (Yeemin et al. 1990; Babcock et al. 1994; van Woesik 1995; Wilson and Harrison 1997), but they have not detailed such processes from the onset of gamete production. In addition, these reports disagree as to whether or not high-latitude corals are locally recruited. Wilson and Harrison (1997) suggested that coral larvae at their higher latitudinal limits may not be able to recruit to their parental population, contrary to the opinion of van Woesik (1995) who considered that scleractinian corals at high latitudes in Japan contributed actively to the maintenance and proliferation of local populations.

In Japan, hermatypic corals are distributed from the Ryukyu Islands to Tateyama Bay, at the mouth of Tokyo Bay (Fig. 1; Veron and Minchin 1992). Among the 24 species of corals recorded at Tateyama Bay (Veron 1992a), the small poritid coral *Alveopora japonica* Eguchi is the most common, occurring from Tanegashima to Tateyama Bay, on the Pacific coast of Japan (Veron 1992a, 1992b). The species is a hermaphroditic brooder, which has been observed to release planulae from September to December in the Izu Peninsula (approx. 34°40′N) (Igarashi et al. 1992).

The purpose of this study was to test the hypotheses that *A. japonica* at high latitudes is sexually reproductive and able to maintain local populations. The cycle of gametogenesis, reproductive timing and larval settlement of the coral were examined, and the effects of sea temperature on reproductive season are discussed.

Methods

A study site was established 150 to 200 m offshore at Tateyama Bay, in front of the Banda Marine Laboratory, Tokyo University of Fisheries. In this area, *Alveopora japonica* form colonies up to 5 cm in diameter.

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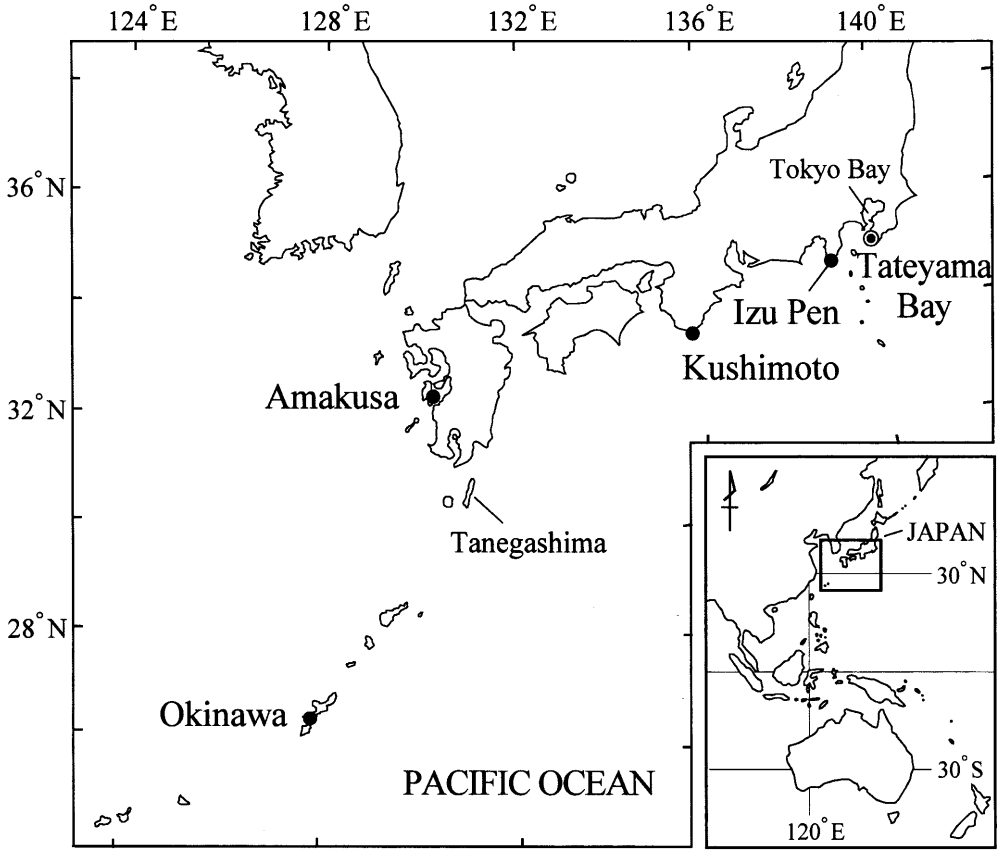

Fig. 1 Location where coral spawning has been reported in Japan. Tateyama Bay, the study site, is indicated by a *double circle*

From August 1994 to November 1995, monthly collections of up to 10 colonies of *A. japonica* were made from depths of 5 to 7 m. During the reproductive season, collections were made twice or more per month. Eighty two colonies were examined in total. In the laboratory, the length (determined as the maximum diameter) and width (taken at a right angle to the maximum diameter) of each colony was measured with calipers to the nearest 0.1 mm. The colony size (surface area) was calculated assuming the shape to be an ellipse (e.g. Hall and Hughes 1996). The samples were then dissected, decalcified with 10% HCl solution and processed for histological examination using standard techniques. Histological sections 5 to 7 μm thick were stained with hematoxylin and eosin, and developmental stages of oocytes and spermaries were determined and measured (12 to 53 oocytes per colony). After May, when oocytes became larger than 120 μm, 20 to 33 oocytes per fixed colony were measured using a dissecting microscope. In addition, the numbers of polyps and the developmental stages of their oocytes were determined in 27 colonies of different sizes (as small as 0.14 cm^2).

Planulae release from the polyps was successfully observed in eight colonies maintained in aquaria with gently running seawater (1 L min^{-1}; water and ambient temperatures similar). Two sets of observations were conducted, from early August to early September in 1994, and from late August to late September in 1995. Each colony was placed within a planula collector covered with 382-μm mesh. After release, planulae were captured and transferred by pipette to small plastic vessels filled with filtered seawater and maintained at 20 to 24 °C under 12/12 h light/dark conditions (5,000 lx). Approximately 60% of the seawater of the vessels was renewed two or three times a day. In 1995, a small rock (diameter <2 cm) collected at the study site was introduced into each plastic vessel in order to facilitate larval settlement.

Throughout the study period, sea temperatures at 5 m depth were recorded at the laboratory (Ocean-Weather Measurement System by Sanyo Technomarine Co., Tokyo), being highest in August (27 °C) and lowest in March (13 °C).

Results

Polyps of *Alveopora japonica* have 12 mesenteries per polyp. Oocytes and spermaries developed on separate mesenteries within each polyp, the numerical ratio of oocytes to spermaries in four mature polyps varying from 1 to 1.5. Recognizable oocytes became apparent by October, in the 1994 samples (Fig. 2), the number per mesentery initially being between 8 and 13 but decreasing to 1 to 4 by January of the following year. Oocytes which developed to maturity increased from an average

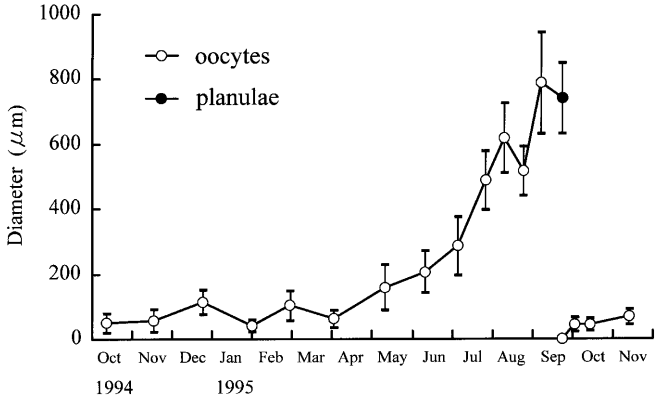

Fig. 2 Temporal pattern (mean ± 1 SD) of oocyte and planula size of *Alveopora japonica*

size of 57 μm (SD = 34.4 μm, $n = 20$) in October to a mean of 787 μm (SD = 157.4 μm, $n = 50$) by September of the following year. Their color changed from white to brown with increasing maturity due to the accumulation of numerous zooxanthellae (Fig. 3). Spermaries were first observed in the May 1995 samples with development of primordial germ cells in the mesenterial endoderm. Development continued until September. Zooxanthellae also became concentrated around the spermaries by mid-August to September. All of the oocytes and spermaries had disappeared by 24 September 1995, and planulae 740 μm long (SD = 108 μm, $n = 60$) were then observed in the coelenteron. The volume of each planulae was estimated to be 0.158 mm^3 (SD = 0.067 mm^3, $n = 60$). The smallest reproductive colony, which bore 86 polyps, measured 2.01 cm^2 (16.8 mm in diameter).

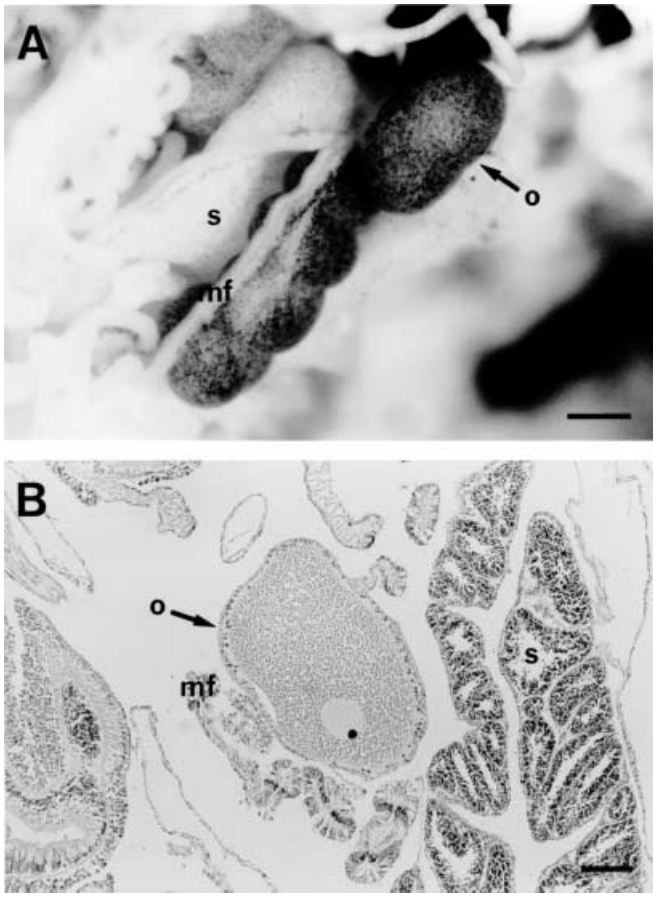

Fig. 3 Mature oocytes and spermaries of *Alveopora japonica* examined by dissection (**A**) and histological section (**B**). **A** Small dark particles around gametes are zooxanthellae; they are more abundant around oocytes than spermaries. **B** Gametes in separate mesenteries of the polyp. Nucleus and nucleolus are seen in an oocyte. *o* Oocytes; *s* spermaries; *mf* mesenterial filaments. *Scale bar*: **A** 500 μm; **B** 100 μm

In aquaria, planulae were released during the daytime (7:00 to 19:00 h) from 29 August to 24 September 1994 and from 14 to 20 October 1995. In the first set of 1994, one half of a colony (colony #1) was transferred from the sea to an aquarium on 5 August, leaving the remainder undisturbed in the field. Colony #1 released a total of 961 planulae (15 planulae $polyp^{-1}$) over ten intermittent periods from 29 August to 24 September. A second set of colonies observed in 1994, which was collected on 5 September, released 7 to 65 planulae per colony (0.2 to 0.7 planulae $polyp^{-1}$) from 17 to 23 September. In 1995, none of the 9 colonies collected on 25 August and 9 September survived collection. Two colonies collected on 24 September released planulae from 14 to 19 October. The numbers of planulae released were 127 to 341 per colony (1.1 and 2.7 planulae $polyp^{-1}$, respectively).

All of the planulae contained numerous zooxanthellae when released. The developmental stages of the planulae from colony #1 were classified on the basis of shape and movement: stage I, 621 μm long (SD = 20 μm, $n = 20$), spherical, floating motionlessly just below the surface; stage II, spherical, exhibiting rotational motion; stage III, 874 μm long (SD = 83 μm, $n = 40$), pear-shaped, mouth open and swimming incessantly near the surface; stage IV, 1,201 μm long (SD = 122 μm, $n = 48$), pear- and/or club-shaped, mesenteries well developed and swimming actively near the bottom. The stages at which the planulae were released, however, varied among different colonies. Colony #1, collected on 5 August, first released stage I planulae on 29 August, then stages II and III on 2 and 4 September, and stage IV on seven occasions on and after 14 September. Two other colonies in 1994 only released stage III and IV planulae, and the remaining 1994 colonies and all those in 1995 released stage IV planulae only. It is likely that those colonies that released few planulae may have released planulae prior to collection.

All planulae commenced crawling on the substrate at stage IV and settled within 7 h of release. In the mass culture at 20 to 24 °C, the polyps started to bud asexually about 3 weeks after settlement. In the absence of a settlement substrate, all stage I to III planulae developed to stage IV and swam for longer periods, up to 120 days before settlement.

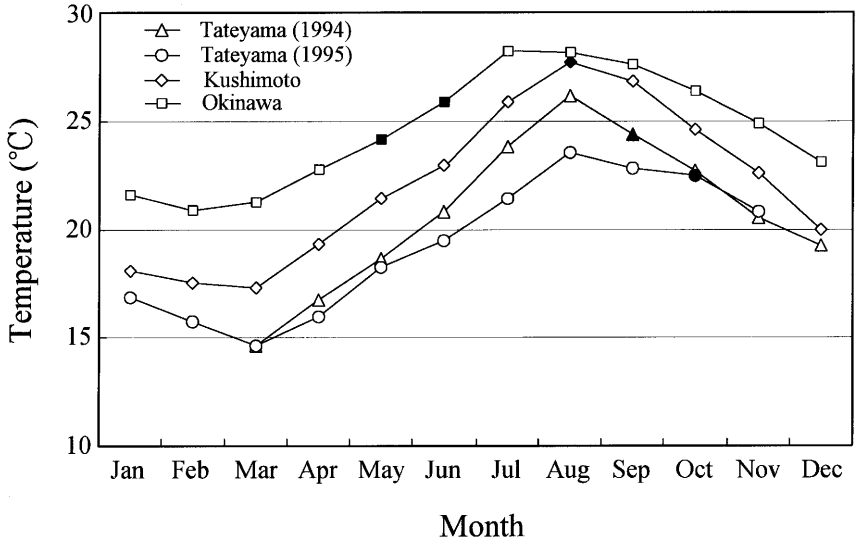

Fig. 4 Seasonal fluctuations in monthly mean sea temperatures at Okinawa, Kushimoto and study site at Tateyama (5 m depth). *Black data points* indicate major spawning months of scleractinian corals at Okinawa (Heyward et al. 1987; Shimoike et al. 1992; Hayashibara et al. 1993) and Kushimoto (van Woesik 1995), and months of planula release at Tateyama Bay (1994, 1995). Sea temperature data for Okinawa (at Aka Island; averaged from 1993 to 1997) and Kushimoto (averaged from 1906 to 1994) were obtained from the Akajima Marine Science Laboratory and from the Japan Oceanographic Data Center, respectively

Discussion

This study showed that *Alveopora japonica* is able to produce larvae and maintain local population at its northernmost distributional limit. Both the mode of sexual reproduction and seasonality agree with the findings of Igarashi et al. (1992). *Alveopora japonica* is a hermaphroditic brooding species, as is *A. daedalea* in the Red Sea (Shlesinger and Loya 1985; Shlesinger et al. 1998). Both species develop oocytes containing zooxanthellae within the mesenteries. These sexual reproductive characteristics seem to separate the genus *Alveopora* from other poritid corals.

The reproductive cycle of *A. japonica* at Tateyama Bay appeared to be annual with oogenesis requiring about 11 months, a pattern consistent with the reproductive cycle of corals worldwide (Harrison and Wallace 1990). Gametogenesis of *A. japonica* takes longer than that of *A. daedalea*, which takes less than 3 months in the Red Sea (Shlesinger et al. 1998), suggesting that lower temperatures delay the rate of gamete maturation in the former. Taking the growth rate of *A. japonica* at Amakusa as 5 mm $year^{-1}$ (see Yeemin 1991), it would take 3 years for a colony to reach sexual maturity.

In Japan, the spawning period appears to be later in the year with increasingly higher latitude (and decreasing sea temperature; Fig.4). Spawning of many scleractinian corals occurs during a period of temperature rise at Okinawa (Heyward et al. 1987; Shimoike et al. 1992; Hayashibara et al. 1993). In contrast, the reproductive season of *A. japonica* in Tateyama Bay is from late August to October, after sea temperatures have reached a maximum. According to Hagiwara (personal communication), *Acropora tumida* at Tateyama Bay also spawned gametes at the end of August and in early September. At other locations along the Pacific coast of Japan between Okinawa and Tokyo Bay, such as Amakusa and Kushimoto, spawning also occurs during the highest sea temperature (Yeemin et al. 1990; van Woesik 1995).

Alveopora japonica broods its larvae. In this regard, Harriott (1992) suggested that brooding species have an advantage in isolated reef systems because their larvae can settle soon after their release and are therefore more likely to be retained within the parental population once established.

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