



Annual Gametogenesis Patterns in Two High-Latitude Corals, *Alveopora japonica* and *Oulastrea crispata*, from Jeju Island, South Korea

Jin-Soo Park¹ · Shashank Keshavmurthy^{1,2} · Thatchaneshkanth Subramaniam¹ · Sang-Ryul Park¹ · Chang-Keun Kang³ · Kwang-Sik Choi¹

Received: 3 August 2018 / Revised: 25 February 2019 / Accepted: 26 February 2019
© Coastal and Estuarine Research Federation 2019

Abstract

Sexual reproduction in corals is pivotal for the survival of populations in the face of climate change. Off Jeju Island, which lies off the south coast of Korea, a high-latitude scleractinian coral, *Alveopora japonica*, has experienced a population explosion over the past couple of decades (at 5–15 m depths). A second species, *Oulastrea crispata*, which is generally present at high latitudes and extreme environments, has a stable population and dominates in the shallow subtidal waters of southern Jeju. This study examined the annual gametogenesis patterns of *A. japonica* off the north (33°24'N, 126°13'E) and south (33°14'N, 126°36'E) coasts of Jeju Island, and of *O. crispata* in the south. Histological analysis revealed that the oogonia and spermatogonia in *A. japonica* developed in separate mesenterial filaments, while the gonads in *O. crispata* developed in the same filament. *Alveopora japonica* had the same brooding period during late summer and early fall (Aug–Sep 2015) at both sites. The spawning period of *O. crispata* was also during late summer and early fall. Brooding in *A. japonica* was concordant with previous observations of its planula during the brooding period. This study provides the first data on the timing of reproduction of these two high-latitude corals from Jeju Island, which may help our understanding of the population dynamics of corals in other high-latitude environments.

Keywords *Alveopora japonica* · *Oulastrea crispata* · Planula · High-latitude · Reproductive physiology · Korea

Introduction

Understanding the reproductive traits of corals is important for managing and maintaining coral populations (Harrison 2011),

Communicated by Judy Grassle

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12237-019-00539-9>) contains supplementary material, which is available to authorized users.

✉ Kwang-Sik Choi
skchoi@jejunu.ac.kr

¹ School of Marine Biomedical Science (BK 21 PLUS), Jeju National University, 102 Jejudaehakno Jeju 63243, Republic of Korea

² Biodiversity Research Center, Academia Sinica (BRCS), 128 Academia Road Sec. 2, Nankang, Taipei 11529, Taiwan

³ School of Environmental Science and Engineering, Gwangju Institute of Science and Technology, Gwangju 61005, Republic of Korea

and this is especially true for corals at high latitudes (see Fellegara et al. 2013). As a result of climate change, corals in tropical and sub-tropical areas are predicted to undergo a poleward migration or range shifts to high-latitude areas (Riegl and Piller 2003; Yamano et al. 2011). Understanding how corals at high latitudes maintain their populations may serve as a predictor for the future status of corals and coral reefs (Guinotte et al. 2003). While several studies have examined the reproductive behavior of corals at high latitudes (Yamazato et al. 2008; Masse et al. 2012; Fellegara et al. 2013; Baird and Thomson 2018), no studies have been undertaken of the corals in Jeju Island, South Korea. Jeju Island has seven species of scleractinian corals (Sugihara et al. 2014), with *Alveopora japonica* and *Oulastrea crispata* being the dominant species.

Located off the south coast of Korea, Jeju Island is influenced by the Tushima Current, a branch of the warm Kuroshio Current, where the sea surface temperature (SST) ranges from 13 to 18 °C during the winter (Sugihara et al. 2014; Vieira et al. 2016). The annual SST differs by ~0.5–1.0 °C between the

north and south coasts of Jeju Island during the summer season. Coinciding with the increased SST, the environmental conditions of high-latitude locations will also experience changes (Yamano et al. 2011; Denis et al. 2013, 2015; Chang et al. 2014; Hong et al. 2015; De Palmas et al. 2015; Vieira et al. 2016). Moreover, the SST around Korea has risen by 1.2–1.3 °C over the last 100 years (Sugihara et al. 2014). For the past 20 years, *A. japonica* has been commonly found off Jeju and has formed large populations off the north and south coasts of the island (Song 1991; Denis et al. 2013, 2015; B. I. Kim, local SCUBA diving shop, pers. comm.; Vieira et al. 2016); however, *O. crispata* has been reported only in the south.

Alveopora japonica is distributed across the north-west Pacific Ocean, including Korea (Jeju Island), Taiwan, and Japan (Veron 2000). Populations of *A. japonica* usually inhabit shallow areas and growth may be inhibited by environmental stressors such as wave and wind action (Harii et al. 2001; Sugihara et al. 2014; Vieira et al. 2016). Colonies of *A. japonica* are hemispherical in shape, discrete, and usually measure 2–3 cm in diameter, but can be > 10 cm (Harii et al. 2001; Sugihara et al. 2014; Vieira et al. 2016). In addition, *A. japonica* is a hermaphroditic brooder; each polyp possesses both male and female gonadal functions (oocyte and spermary) and produces planulae following internal fertilization during September and October (Igarashi et al. 1992; Harii et al. 2001; Thamrin et al. 2001; Sugihara et al. 2014; Eyal-Shaham et al. 2016; Vieira et al. 2016).

Oulastrea crispata is widely distributed from the Great Barrier Reef to Japan (Veron 1993). Colonies form encrusting, sub-massive forms, and range from a few centimeters to ~ 10 cm across in size (Kawaguti and Sakumoto 1952; Yajima et al. 1986; Lam 2000; Chen et al. 2011). According to Lam (2000), *O. crispata* is a simultaneous hermaphrodite, with a spermary just above the ovary in the mesoglea of the same mesentery (Clark 1997; Collinson 1997; Lam 2000). Nakano and Yamazato (1992) reported that *O. crispata* in Okinawa spawns gametes, broods, and releases asexual planula containing algal symbionts. In a recent study, Zayasu et al. (2015) reported the release of eggs and sperm from *O. crispata* colonies reared in a laboratory.

The aims of the present study were to investigate the breeding patterns of the high-latitude scleractinian corals *A. japonica* and *O. crispata*, and to ascertain differences between the reproductive seasons along the north and south coasts of Jeju Island.

Materials and Methods

Coral Sampling

Coral colonies were collected from the north (33°24'N, 126°13'E) and south (33°14'N, 126°36'E) coasts of Jeju

Island (Fig. 1). *Alveopora japonica* was collected from both locations; however, *O. crispata* only occurred on the southern coast. From January to December 2015, three to five colonies were collected monthly at each site from a depth of 10 m by SCUBA diving. Whole colonies of *A. japonica* were easily collected since *A. japonica* occurs as individual colonies. Unlike *A. japonica*, partial *O. crispata* specimens were collected from entire colonies, since these encrust on hard substrates. Between August and September 2015, during the predicted reproductive periods, sampling was carried out bi-weekly. The *A. japonica* colonies and *O. crispata* fragments collected were fixed immediately in a 10% seawater-formalin solution for 48 h before being stored in 70% ethanol. SST was monitored at depth of 5 m (attached to the side of a rock near the coral, not on the bottom) at sampling sites by HOBOT (Onset Corporation, USA) temperature loggers, which were installed at the beginning of March 2015 and recovered in December 2015.

Histology

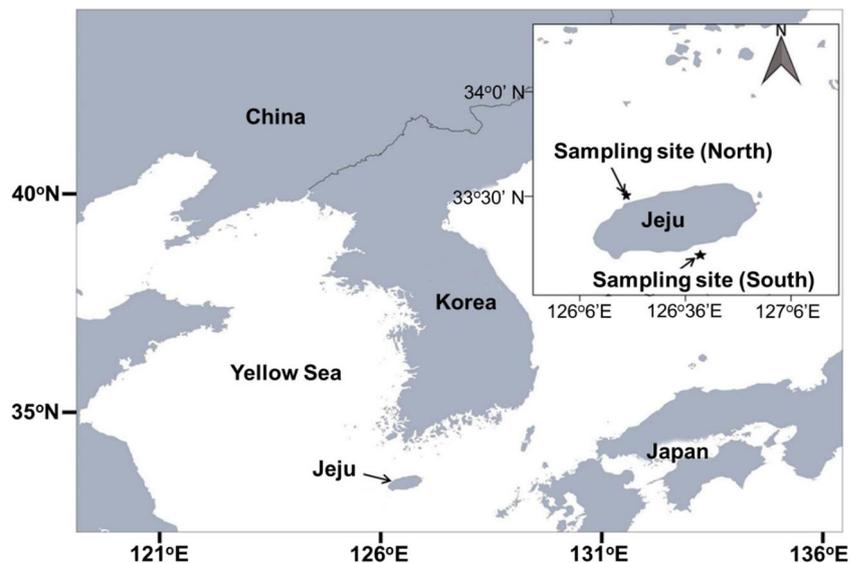
To extract coral tissues from the preserved colonies or fragments, formalin-fixed coral specimens were placed in a decalcification solution consisting of 20% citric acid and 50% formic acid (Harithsa et al. 2005) to remove the skeletal parts of the corals. After decalcification, the isolated soft coral tissues were cut into sections of ~ 1 × 1 cm and fixed in Davidson's fixative for 24 h. For histological analyses, the coral tissues were dehydrated using a series of ethanol solutions and an automatic tissue processor. After dehydration, the coral tissues were embedded in paraffin and sectioned transversely at a thickness of 6 μm. The tissue sections were stained with Harris's hematoxylin then counterstained using eosin Y.

Statistical Analysis of the Reproductive Stage

Transverse sections of the coral tissues prepared as histology slides were examined using a polarized light microscope. To trace an annual reproductive cycle, gametogenic conditions of the ovaries and testes were categorized into five developmental stages according to Szmant-Froelich (1985), as resting, primordial, early development, late development, and mature. From the digitized images of the coral tissues, oocyte size was determined by measuring the longest axis of the eggs (D1). In addition, the distance perpendicular to the longest axis was also measured (D2) using the image analysis program, ImageJ (Schindelin et al. 2015). Based on D1 and D2, the geometric mean diameter (GMD) of each oocyte was calculated (Guest et al. 2012):

$$\text{GMD} = \sqrt{(D1 \times D2)}$$

Fig. 1 Map showing the sampling sites on the north and south coasts of Jeju Island



All statistical tests were performed using the Aabel software platform (Gigawiz). Differences in GMD were tested by the Wilcoxon rank sum test and described with one-way box and whisker plots (10th and 90th percentiles) between species and sampling locations.

Planula Release

In late August and early September 2015, while most *A. japonica* colonies were actively engaged in planulation, 12 colonies of *A. japonica* were collected from the south sampling site and placed in flow-through aquaria (30 × 20 × 13 cm) to collect the planulae. Outlets of the aquaria were covered with 100- μ m mesh and filled with seawater (salinity 33), which was filtered through 1.2- μ m filters. The aquaria provided a photoperiod of 12 h light: 12 h dark and the water temperature was maintained at 22–24 °C. The seawater was renewed every 2 days. The planulae released from *A. japonica* colonies were harvested and fixed in 2.5% glutaraldehyde at 4 °C overnight for scanning electron microscopy (SEM; SUPRA-55VP, Carl Zeiss, Germany). The glutaraldehyde-fixed planulae were dehydrated in an ethanol series, before further processing in an iso-amyl acetate series. The planulae were finally coated with platinum and observed using SEM at an accelerating voltage of 15 kV.

Results

Seawater Temperature at Sampling Sites

In the north, the lowest SST recorded was 13.7 ± 0.4 °C in March, whereas the highest SST recorded was 24.0 ± 1.4 °C in August. In the south, the lowest SST recorded was $14.7 \pm$

0.2 °C in March, while the highest SST recorded was 25.0 ± 1.5 °C in August (Fig. 2).

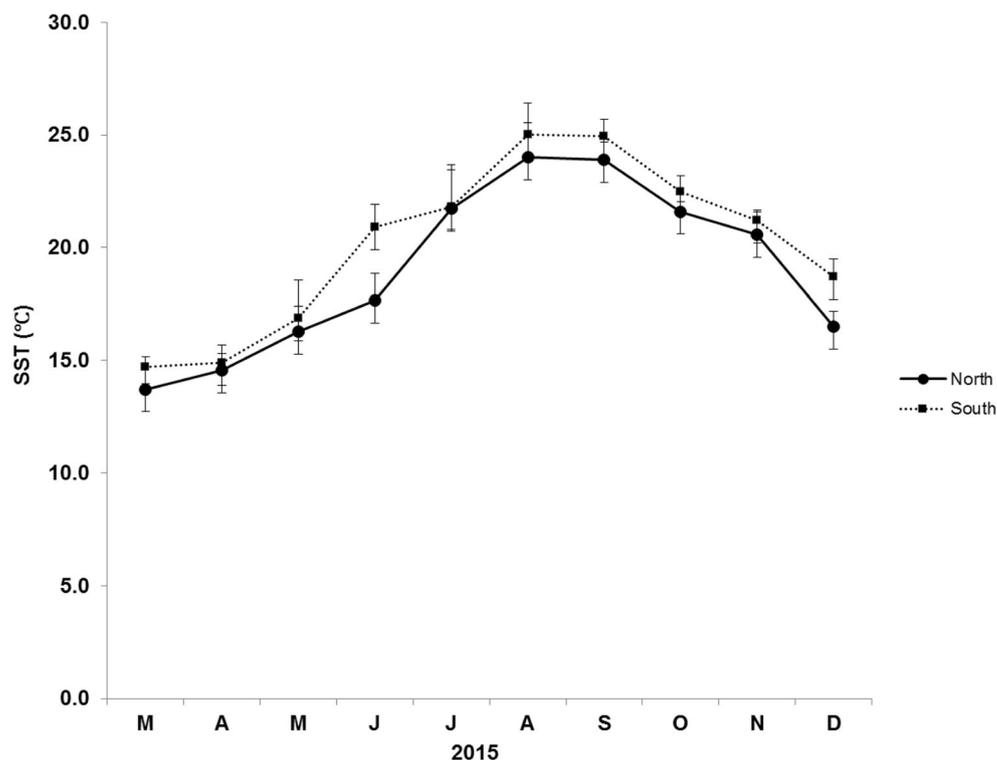
Gonad Development in *A. japonica* and *O. crispata*

The microscopic features of gonad development in *A. japonica* and *O. crispata* are shown in Figs. 3 and 4. Histological analyses revealed that oocytes and spermaries of *A. japonica* developed in separate mesenterial filaments in each polyp, while the gametes of *O. crispata* were present in the same mesenteries. During the early stage, the follicles were expanded and cytoplasm accumulated around the nuclei of the oocytes (Figs. 3 and 4c). During the mature stage, the oocytes attained their maximum size; oocytes could be seen clearly in the mesenteries and had indented nuclei and distinct vitelline membranes (Figs. 3 and 4e). During the primordial stage of spermaries of *A. japonica* and *O. crispata*, small clusters of interstitial cells (spermatocytes) began to enter and multiply in the mesoglea (Figs. 3 and 4f). Mature spermatocytes of both species were characterized by a small quantity of cytoplasm in the lumen (Figs. 3 and 4i).

Oogenesis and Spermatogenesis in *A. japonica*

Histological analysis indicated that oogenesis in *A. japonica* in the north commenced in September when the SST reached 23.9 °C, and the primordial oocytes were observed as early as late September, with a mean GMD of 40.7 μ m (Fig. 5a). The proportion of those at the primordial stage increased and reached its annual maximum in November (23.1%, Fig. 6a). The oocytes in the early and late development stages were first noticed in January, with a mean GMD of 64.8 ± 17.7 μ m (Fig. 5a). The proportion of those at the mature stage increased from March onwards and reached its annual peak in August

Fig. 2 Monthly mean sea surface temperature (SST) recorded from the north and south coasts of Jeju Island in 2015



(94.1%), with a mean GMD of 172.8 μm . The proportion of mature oocytes decreased markedly from August to September, suggesting that brooding occurred during this period (Fig. 6a). Follicles with empty lumens were clearly observed in September as most of the corals completed release of their planulae.

Alveopora japonica in the north initiated spermatogenesis in January, when the coral had primordial spermaries (Fig. 6b). In January, some polyps also exhibited spermaries in the late and mature stages. During June and July, the proportion of mature spermaries increased dramatically from 14.8 to 86.8%, and this dropped markedly during August and September, indicating that most of the sperm were released during this period.

In the south, *A. japonica* commenced oogenesis in October (Fig. 7a), as small primordial oocytes (GMD of $55.5 \pm 2.8 \mu\text{m}$, Fig. 5b) were identified in the mesenteries. In January, small oocytes ($72.6 \pm 16.2 \mu\text{m}$) appeared in the mesenteries, indicating that they were in the early developmental stage. In February, the proportion of those at the late development stage began to increase, while the proportion of mature oocytes increased from April (18.8%) to August (80%, Fig. 7a). The proportion of those in the mature stage declined dramatically in September (0%), indicating that most *A. japonica* in the south brooded in late August and September. During September and February, most of the mesenteries had no gametes, indicating that the corals were in the resting stage (Fig. 7a).

The onset of spermatogenesis in *A. japonica* in the south was first recognized in January, 3 months after oogenesis

began, when 50% of the examined colonies exhibited primordial spermaries (Fig. 7b). Spermaries in the early (12.5%) and late development stages (12.5%) were also observed in January. The proportion of those at the early development stage increased continuously to March (25.9%), while the late stage dominated in April (41.1%, Fig. 7b). The first mature spermaries appeared in May (3.4%), although the mature stage dominated in August. During August and September, the proportion of mature spermaries decreased from 55.3–8.6% (Fig. 7b).

Oogenesis and Spermatogenesis of *O. crispata*

Oulastrea crispata on the southern coast of Jeju Island commenced oogenesis in January, exhibiting small primordial oocytes (GMD $19.8 \pm 9.0 \mu\text{m}$, Fig. 5c) in the mesenteries. Oocytes at the early development stage were also identified in January (7.1%), and these reached their annual maximum in May (37.5%). In May, a small number (4.2%) of mature *O. crispata* oocytes (GMD of $47.2 \pm 14.4 \mu\text{m}$) first appeared, and these peaked in September (81.5%, Fig. 8a). In October, the proportion of mature oocytes dropped dramatically (to 0%), indicating that most *O. crispata* in the south spawned during this period when the SST dropped from 24.9 to 22.5 $^{\circ}\text{C}$ (Fig. 2).

Oulastrea crispata in southern Jeju Island commenced spermatogenesis in March, as the colonies had primordial and early spermaries (Fig. 8b). Spermaries in the late development stage first appeared in April, and this increased to

Fig. 3 Photomicrographs of the different reproductive stages observed for *Alveopora japonica*. **a** Resting stage, follicle with empty lumen. **b** Developmental stage of primordial oocyte. **c** Early stage of oocytes. **d** Late stage of the ovary. **e** Mature stage of the ovary. **f** Developmental stage of the primordial spermaries. **g** Early stage of testis, spermary with thick connective tissue. **h** Late stage of testis showing the mature spermary. **i** Fully mature stage of the testis. **j** Planula (P) of *A. japonica*. PO primordial oocyte, N nucleus, O oocytes, Nu nucleolus, S spermaries, SP primordial spermaries, L lumen

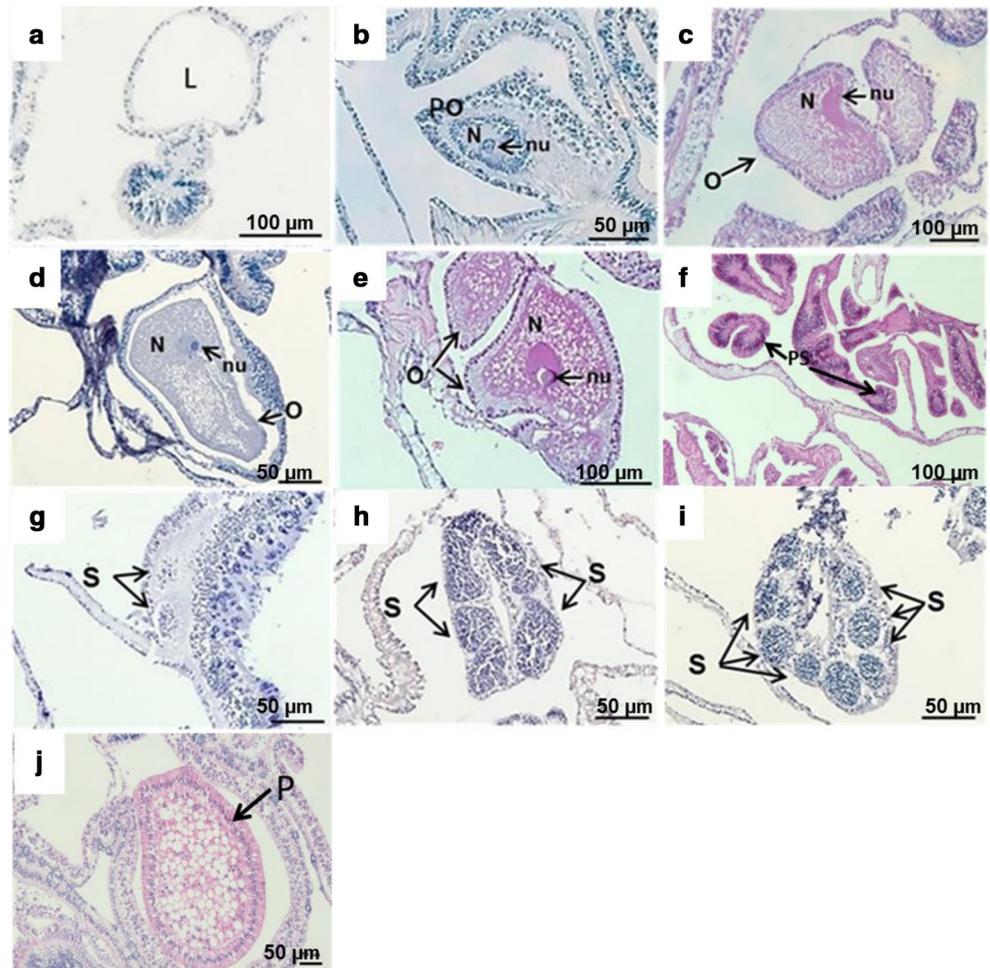
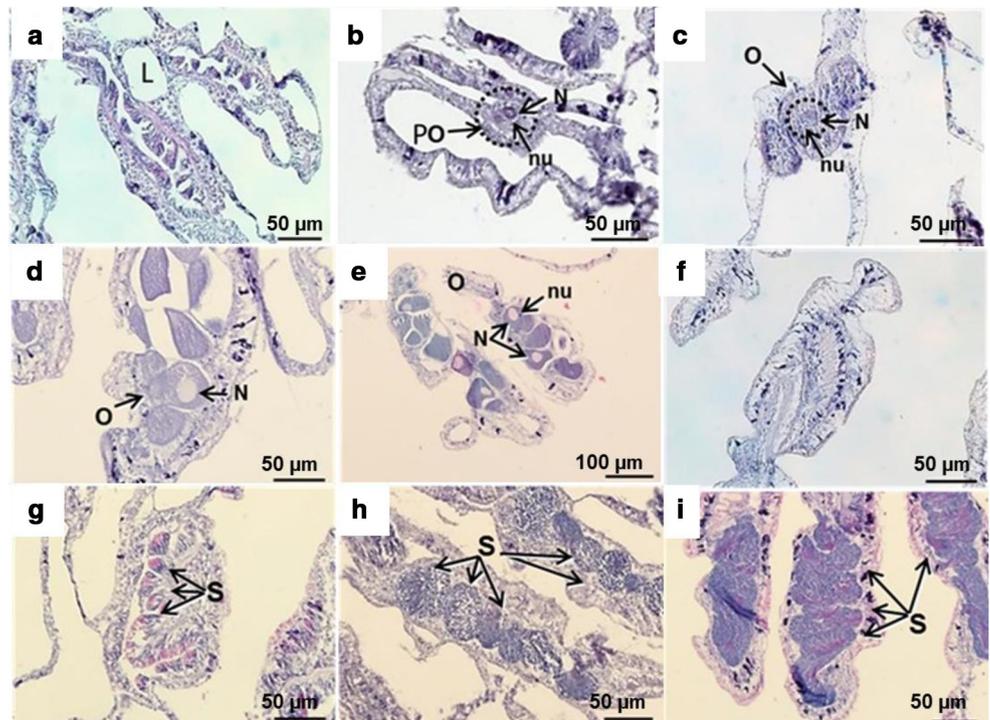


Fig. 4 Photomicrographs showing the different reproductive stages of *Oulastrea crispata*. **a** Resting stage with empty lumen in the follicle. **b** development of the primordial oocyte. **c** Early stage of the ovary. **d** Late stage of the ovary. **e** Mature stage of the ovary. **f** Development of the primordial spermaries. **g** Early stage of the testis. **h** Late stage of the testis. **i** Mature stage of the testis showing dense sperms in the spermaries. PO primordial oocyte, N nucleus, O oocytes, Nu nucleolus, S spermaries, SP primordial spermaries, L Lumen



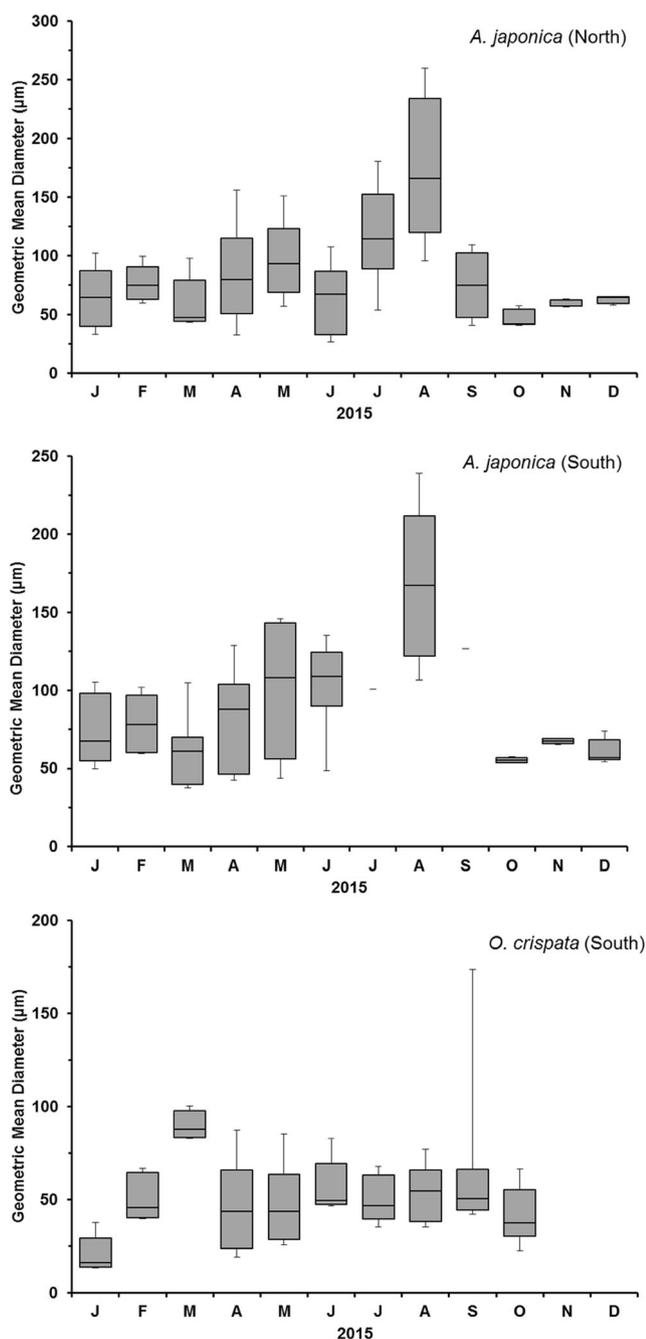


Fig. 5 Monthly geometric mean diameter (GMD) of oocytes of *A. japonica* from the north and south of Jeju Island. GMD of oocytes of *O. crispata* from the south of Jeju Island

73.9% in July. In October, 80% of the corals examined exhibited mature spermaries, whereas this dropped to 0% in November (Fig. 8b). Histological analysis suggested that *O. crispata* in the south released sperm between October and November when the mean SST decreased from 22.5 to 21.2 °C (Fig. 2). Most *O. crispata* in the south had no gametes in the mesenteries in November and February, indicating that the corals were sexually inactive and resting (Fig. 8b).

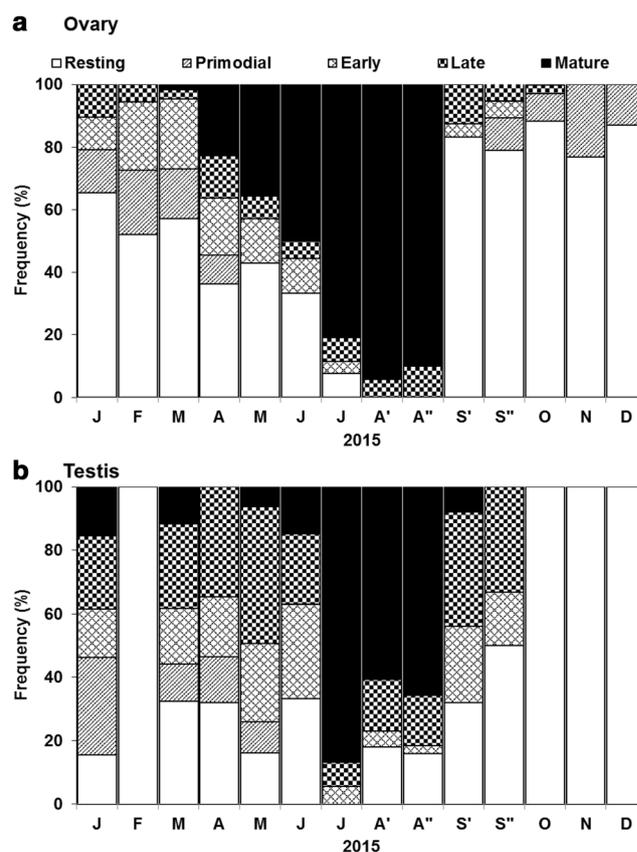


Fig. 6 Monthly frequency distribution of the different reproductive stages of *A. japonica* collected from the north of Jeju Island. During August and September, the coral was sampled bi-weekly, and the first samplings in the month were denoted as A' and S', while the second samplings were denoted as A'' and S''

Transmission of Algal Symbionts from the Mesentery to the Oocyte

Results showed vertical transmission of algal symbionts in *A. japonica*. During the late development stage, the algal symbionts were clearly visible in the mesenteries surrounding the oocytes (Fig. S1B). The presence of the algal symbionts in the ooplasm of fully mature oocytes were evident during July and August, and the algal symbionts were transmitted from the mesentery (i.e., the mother coral) to the oocytes in the late development and/or fully mature stages (Fig. S1C). SEM also demonstrated that the planula contained algal symbionts in the epithelium (Fig. S1D). In contrast, no algal symbionts were observed in any stage of gametogenesis in *O. crispata*.

Observation of Planula Release

The planulae released from *A. japonica* were ellipsoid or spherical with active locomotion and were estimated to be $539 \pm 57.2 \mu\text{m}$ in size (Fig. S1E). Cross-sections of the larvae also revealed numerous algal symbionts. However, we did not observe any planulae in the *O. crispata* tanks.

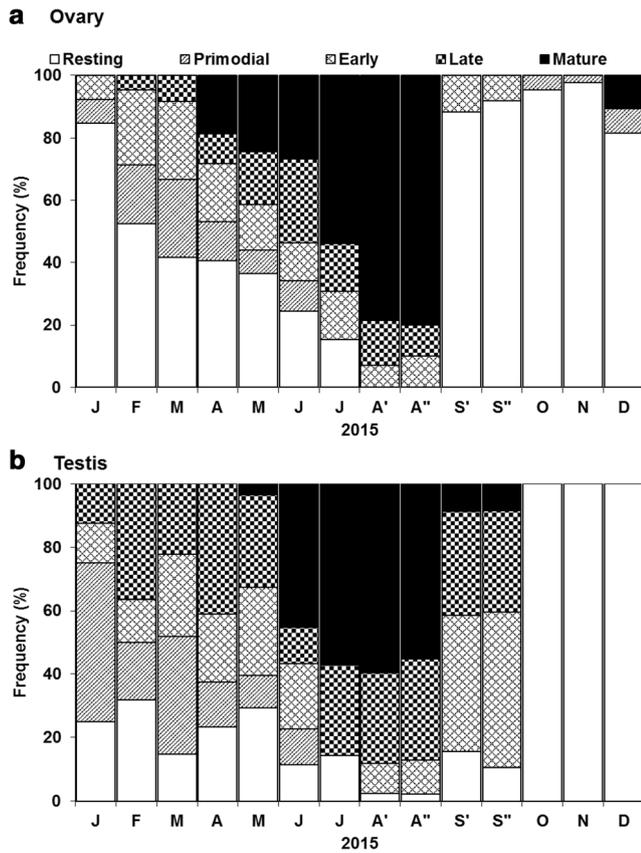


Fig. 7 Monthly frequency distribution of the different reproductive stages of *A. japonica* collected from the south coast of Jeju Island. During August and September, the coral was sampled bi-weekly, and the first samplings in the months were denoted as A' and S', while the second samplings were denoted as A'' and S''

Discussion

This is the first study to examine sexual reproduction in corals from Jeju Island, and histological analyses indicated that populations of *A. japonica* in the north and south brooded between late August and September, when the SST was stable at 24–25 °C. This represents the first step towards understanding various aspects of reproductive biology of *A. japonica* and *O. crispata* corals from Jeju Island.

This observation is similar to that from Tateyama Bay Japan, where *A. japonica* released planulae in late August and September (Harii et al. 2001) when seawater temperature was 24 °C. Oogenesis began in September (in the north) and October (in the south), suggesting that the reproductive cycle is annual, and that oogenesis takes ~10 months. Harii et al. (2001) also reported that oocytes of *A. japonica* in Tateyama Bay appeared in October, and oogenesis was estimated to be 11 months. Eyal-Shaham et al. (2016) investigated an annual reproductive cycle of *A. allingi* and *A. ocellata* from the mesophotic reefs of Eilat, in the Red Sea. Histological analysis also indicated that the primordial oocytes of *A. allingi* and *A. ocellata* in Eilat (29°32'N, 34°57'E) became fully mature

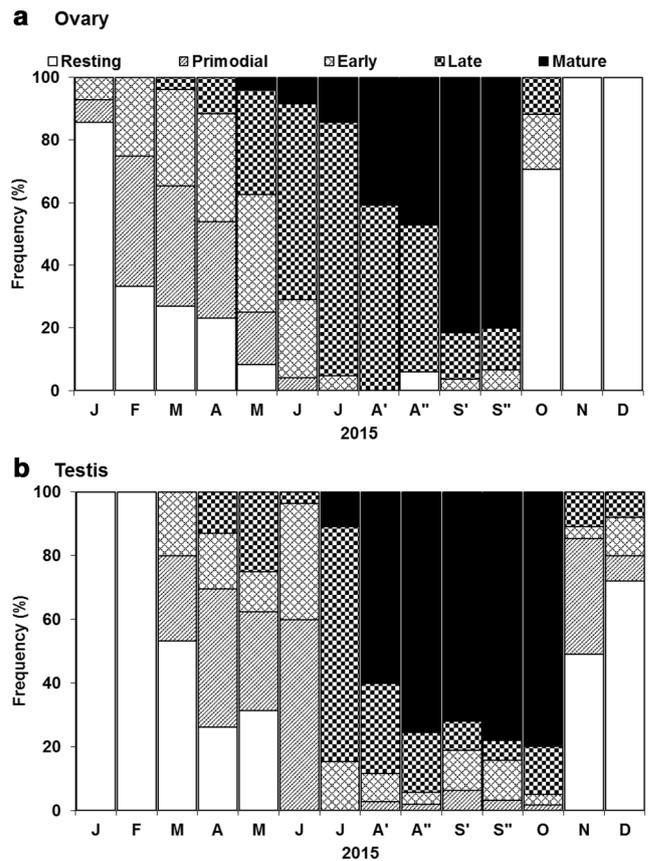


Fig. 8 Monthly frequency distribution of the different reproductive stages of *O. crispata* collected from the south coast of Jeju Island. During August and September, the coral was sampled bi-weekly, and the first samplings in the month were denoted as A' and S', while the second samplings were denoted as A'' and S''

10 months after the onset of oogenesis, and the reproductive cycle was annual.

Alveopora japonica in the north and south of Jeju Island initiated spermatogenesis in January, 3 to 4 months after oogenesis began. Contrary to the present study, Harii et al. (2001) observed the onset of spermatogenesis of *A. japonica* in Tateyama Bay in May, 7 months after oogenesis. In May, some of the *A. japonica* colonies in the north and south of Jeju Island were in late development or mature stages, although most of the corals exhibited mixed reproductive modes. In general, the onset of oogenesis in corals precedes that of spermatogenesis by 2 to 4 months, although maturation of the oocytes and spermaries progresses simultaneously, and spawning is synchronized in most cases (see Harrison and Wallace 1990).

In south Jeju Island, *O. crispata* commenced oogenesis in January, although primordial oocytes were observed until June. While mature oocytes were predominant in the mesenteries during late August to September, such mature oocytes were not observed in October, indicating that spawning occurred during late September and October, as the SST decreased from 25.0 to 22.5 °C in southern Jeju. *Oulastrea*

crispata has an annual reproductive cycle, and oogenesis lasts approximately 9 months, which is comparable to that of *A. japonica* (10 months). Histological analysis showed that the onset of spermatogenesis occurred in March, which was 2 months later than oogenesis. According to Lam (2000), *O. crispata* in Hoi Ha Wan in Hong Kong (22°28'N, 114°20'E) spawn from July to October, as the SST stays above 27 °C. In Hong Kong, oogenesis of *O. crispata* takes 6–7 months, while spermatogenesis lasts for 3 months. This comparatively fast oogenesis and spermatogenesis of *O. crispata* in Hong Kong is, in part, attributed to the relatively high SST, with an annual SST 2–3 °C higher than that off Jeju Island.

Table 1 compares the annual reproductive patterns of the two coral species observed in Jeju Island, with the same species that had been previously reported from the west Pacific Ocean. The patterns of annual gametogenesis of *A. japonica* and *O. crispata* observed in this study were similar to those reported in previous studies (see Table 1). However, the oocyte diameters reported in these studies were very different from those in our study. The differences are large enough that it seems unlikely that they can be explained by differences in fixation and measurement of the oocytes, or by phenotypic differences among corals from different geographic areas. It seems more probable that the “species” *A. japonica* and *O. crispata* each represent more than one distinct taxonomic unit in the north-western Pacific, and this is a topic for future investigation.

According to Baird et al. (2009), ~90% of the brooding corals have algal symbionts in their planulae, which are directly inherited from the parent (i.e., vertical transmission). Vertical transmission of algal symbionts was reported in the reef-building scleractinian corals in Okinawa, and the algal symbionts were transferred from the mother corals to the mature oocytes a few days before they were released (Hirose et al. 2001). Harii et al. (2001) also reported vertical transmission of algal symbionts in *A. japonica* in Japan. In this study, we observed that the color of *A. japonica* oocytes changed from white to brown in September, due to the accumulation of algal symbionts in the outer layer of the mature oocytes between June and August (see also Fig. S1D). Unlike *A. japonica*, *O. crispata* has no algal symbionts in the oocytes in any developmental stage.

The egg size (i.e., GMD) of *A. japonica* measured in this study ranged from 55.0 μm (primordial stage) to 166.2 μm (mature stage) in the north and 64.8 μm (primordial stage) to 172.8 μm (mature stage) in the south. The GMD of *O. crispata* ranged from 19.8 μm (primordial stage) to 56.3 μm (mature stage). Oogenesis of *A. japonica* in the south takes approximately 10 months from the onset in October to brooding in August. Similarly, oogenesis in *O. crispata* in the south takes approximately 9 months from January to

Table 1 Summary of the reproductive patterns of *A. japonica* and *O. crispata* reported from the north-west Pacific Ocean

Species Name	Methodology	Onset of oogenesis	Spawning	SST (°C) at spawning	Egg diameter (μm)	Location	Reference
<i>A. japonica</i>	histology	Oct	LATE Aug–early Sep	24	800	Tokyo, Japan (34°58'03"N, 139°46'05"E)	Harii et al. 2001
<i>A. japonica</i>	Direct observation	na	Sep	na	na	Amakusa, Japan (32°31'50"N, 130°02'29"E)	Thamrin et al. 2001
<i>A. japonica</i>	Histology	Sep	Late Aug–early Sep	23.9–24	173	Northern Jeju Island, Korea (33° 24'03"N, 126°13'58"E)	Present study
<i>A. japonica</i>	Histology	Oct	Late Aug–early Sep	24.9–25	166	Southern Jeju Island, Korea (33° 14'54"N, 126°36'18"E)	Present study
<i>O. crispata</i>	Histology	Feb	Jul–Oct	28	130	Hong Kong, China (22°28'N, 114°20'E)	Lam (2000)
<i>O. crispata</i>	Histology	na	Jul	na	130	Okinawa, Japan (26°48'14"N, 128°10'45"E)	Nakano and Yamazato (1992)
<i>O. crispata</i>	Direct observation	na	Jul	28.5	150	Wakayama, Japan (33°41' 24"N, 135°20'9"E)	Zayasu et al. (2015)
<i>O. crispata</i>	Histology	Jan	Late Sep–Oct	22.5–24.9	56	Southern Jeju Island, Korea (33°14'54"N, 126°36'18"E)	Present study

Not all egg diameter values are in GMD
na not available

September. The relatively long period of oogenesis of *A. japonica* observed in this study is believed to be linked to the size of the mature eggs, which may take longer to produce. These larger eggs may contain higher levels of nutrients, which could enhance the survival of the planulae and promote their dispersal (Fan and Dai 1995; Acosta and Zea 1997).

In summary, we performed histological investigations into the annual gametogenesis of the high-latitude *A. japonica* and *O. crispata* corals from Jeju Island, off the south coast of Korea. Both species showed a clear seasonal gametogenesis pattern, with major brooding and spawning periods in August and September, when the SST ranged from 24 to 25 °C. Histological analyses revealed that *A. japonica* populations in the south and north of Jeju Island exhibited the same annual gametogenic patterns, suggesting that the small SST difference between the north and south exerts no significant influence on coral reproductive physiology. The recent expansion and explosion of the *A. japonica* population from the south into the north might be linked to the increase in SST in the East China Sea; however, this needs to be substantiated through long-term monitoring of patterns of coral reproduction and population dynamics.

Acknowledgments We thank the staff of the Shellfish Research and Aquaculture Laboratory at Jeju National University for their help with data analysis.

Funding Information This work was supported by funding from the Ministry of Oceans and Fisheries of Korea, through the “Long-term changes of structure and function in marine ecosystems of Korea (2018)” project.

References

- Acosta, A., and S. Zea. 1997. Sexual reproduction of the reef coral *Montastrea cavernosa* (Scleractinia: Faviidae) in the Santa Marta area, Caribbean coast of Colombia. *Marine Biology* 128 (1): 141–148.
- Baird, A.H., and D.P. Thomson. 2018. Coral reproduction at Hall Bank, a high latitude coral assemblage in Western Australia. *Aquatic Biology* 27: 55–63.
- Baird, A.H., J.R. Guest, and B.L. Willis. 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics* 40 (1): 551–571.
- Chang, S.J., M. Rodriguez-Lanetty, K. Yanagi, S. Nojima, and J.I. Song. 2014. Two anthozoans, *Entacmaea quadricolor* (Order: Actiniaria) and *Alveopora japonica* (Order: Scleractinia), host consistent genotypes of *Symbiodinium* spp. across geographic ranges in the north western Pacific Ocean. *Animal Cells and Systems* 15: 316–325.
- Chen, K.S., H.J. Hsieh, S. Keshavmurthy, J.K.L. Leung, I.T. Lien, Y. Nakano, S. Plathong, H. Huang, and C.A. Chen. 2011. Latitudinal gradient of morphological variations in Zebra coral *Oulastrea crispata* (Scleractinia: Faviidae) in the West Pacific. *Zoological Studies* 50: 43–52.
- Clark, T.H. 1997. The ecology of indigenous and transplanted corals in the Cape D’Aguilar Marine Reserve, Hong Kong. Hong Kong: Dissertation, University of Hong Kong.
- Collinson P.R.J. 1997. The ecology of a peripheral, subtropical coral community in Hong Kong. Hong Kong: Dissertation, University of Hong Kong.
- De Palmas, S., V. Denis, L. Ribas-Deulofeu, M. Loubeyres, S. Woo, S.J. Hwang, J.I. Song, and C.A. Chen. 2015. *Symbiodinium* spp. associated with high-latitude scleractinian corals from Jeju Island, South Korea. *Coral Reefs* 34 (3): 919–925.
- Denis, V., C.A. Chen, J.I. Song, and S. Woo. 2013. *Alveopora japonica* beds thriving under kelp. *Coral Reefs* 32 (2): 503–503.
- Denis, V., L. Ribas-Deulofeu, M. Loubeyres, S. De Palmas, S.J. Hwang, S. Woo, J.I. Song, and C.A. Chen. 2015. Recruitment of the subtropical coral *Alveopora japonica* in the temperate waters of Jeju Island, South Korea. *Bulletin of Marine Science* 91: 85–96.
- Eyal-Shaham, L., G. Eyal, R. Tamir, and Y. Loya. 2016. Reproduction, abundance and survivorship of two *Alveopora* spp. in the mesophotic reefs of Eilat, Red Sea. *Scientific Reports* 6 (1): –11.
- Fan, T.Y., and C.F. Dai. 1995. Reproductive ecology of the scleractinian coral *Echinopora lamellosa* in northern and southern Taiwan. *Marine Biology* 123 (3): 565–572.
- Fellegara, I., A.H. Baird, and S. Ward. 2013. Coral reproduction in a high-latitude, marginal reef environment (Moreton Bay, south-east Queensland, Australia). *Invertebrate Reproduction and Development* 57 (3): 219–223.
- Guest, J.R., L.M. Chou, and B. Goh. 2012. Reproductive seasonality of the reef building coral *Platygyra pini* on Singapore’s reef. *The Raffles Bulletin of Zoology* 25: 123–131.
- Guinotte, J.M., R.W. Buddemeier, and J.A. Kleypas. 2003. Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* 22 (4): 551–558.
- Harii, S., M. Omori, H. Yamakawa, and Y. Koike. 2001. Sexual reproduction and larval settlement of the zooxanthellate coral *Alveopora japonica* Eguchi at high latitudes. *Coral Reefs* 20: 19–23.
- Harithsa, S., C. Raghukumar, and S.G. Dalal. 2005. Stress response of two coral species in the Kavaratti atoll of the Lakshadweep archipelago, India. *Coral Reefs* 24 (3): 463–474.
- Harrison, P.L. 2011. Sexual reproduction of scleractinian corals. In *Coral reefs: an ecosystem in transition*, ed. Z. Dubinsky and N. Stambler, 59–85. Dordrecht: Springer.
- Harrison, P.L., and C. Wallace. 1990. Reproduction, dispersal and recruitment of scleractinian corals. In *Ecosystems of the world 25: coral reefs*, ed. Z. Dubinsky, 133–207. Amsterdam: Elsevier.
- Hirose, M., R.A. Kinzie, and M. Hidaka. 2001. Timing and process of entry of zooxanthellae into oocytes of hermatypic corals. *Coral Reefs* 20: 273–280.
- Hong, H.K., S. Keshavmurthy, C.K. Kang, K. Hwang, S.R. Park, S.H. Cho, and K.S. Choi. 2015. *Alveopora japonica* repopulation of a bare substrate off Jeju Island, Korea. *Bulletin of Marine Science* 91 (4): 477–478.
- Igarashi, T., T. Higashi, and T. Hamada. 1992. Planulation of a coral *Alveopora japonica* in Izu, Central Japan. *Proceedings of the 7th International Coral Reef Symposium* 1: 501.
- Kawaguti, S., and D. Sakumoto. 1952. Pigment of skeleton of a reef coral, *Oulastrea crispata*. *Biological Journal of Okayama University* 1: 265–270.
- Lam, K.K.Y. 2000. Sexual reproduction of a low-temperature tolerant coral *Oulastrea crispata* (Scleractinia: Faviidae) in Hong Kong, China. *Marine Ecology Progress Series* 205: 101–111.
- Masse, L.M., M.G. Sere, A.J. Smit, and M.H. Schleyer. 2012. Sexual reproduction in *Pocillopora damicornis* at high latitude off South Africa. *Western Indian Ocean Journal of Marine Science* 11: 55–65.
- Nakano, Y., and K. Yamazato. 1992. Ecological study of reproduction of *Oulastrea crispata* in Okinawa. *Zoological Science* 9: 1292.
- Riegl, B., and W.E. Piller. 2003. Possible refugia for reefs in times of environmental stress. *International Journal of Earth Sciences* 92 (4): 520–531.

- Schindelin, J., C.T. Rueden, M.C. Hiner, and K.W. Eliceiri. 2015. The ImageJ ecosystem: an open platform for biomedical image analysis. *Molecular Reproduction and Development* 82 (7-8): 518–529.
- Song, J.I. 1991. The systematic study on the Korean Anthozoa 12. Order Scleractinia. *Animal Systematics, Evolution and Diversity* 7: 127–150.
- Sugihara, K., H. Yamano, K.S. Choi, and K. Hyeong. 2014. Zooxanthellate scleractinian corals of Jeju Island, Republic of Korea. *Ecological Research Monographs* 2: 111–130.
- Szmant-Froelich, A.M. 1985. The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). In *Proceedings of the 5th International Coral Reef Congress*, eds. C. Gabrie and B. Salvat 4: 295–300. Tahiti: Antenne Museum.
- Thamrin, S. Nojima, and M. Tokeshi. 2001. Experimental analysis of planula release in a scleractinian coral *Alveopora japonica*. *Journal of Coral Reef Society* 2001 (3): 25–30.
- Veron, J.E.N. 1993. *Corals of Australia and the Indo-Pacific*. Hawaii: University of Hawaii Press.
- Veron, J.E.N. 2000. *Corals of the world*. Townsville: Australian Institute of Marine Science.
- Vieira, C., S. Keshavmurthy, S.J. Ju, K. Hyeong, I. Seo, C.K. Kang, H.K. Hong, C.A. Chen, and K.S. Choi. 2016. Population dynamics of a high-latitude coral *Alveopora japonica* Eguchi from Jeju Island, off the southern coast of Korea. *Marine & Freshwater Research* 67 (5): 594–604.
- Yajima, T., O. Sano, T. Okamoto, Y. Shirai, T. Shinya, and M. Matada. 1986. Ecological distribution of the reef coral, *Oulastrea crispata* (Lamarck) at the shore region in the vicinity of Tukumo Bay. *Bulletin of the Japan Sea Research Institute* 18: 21–36.
- Yamano, H., K. Sugihara, and K. Nomura. 2011. Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical Research Letters* 38: L04601.
- Yamazato, K., E. Suwardi, and S. Sultana. 2008. Reproductive cycle of brooding corals at high latitude. *Journal of the Japanese Coral Reef Society*, 10: 1–11.
- Zayasu, Y., K. Miyazaki, Y.T. Lien, and N. Okubo. 2015. Direct evidence of sexual reproduction in the zebra coral, *Oulastrea crispata* (Anthozoa, Scleractinia), in Japan. *Invertebrate Reproduction & Development* 59 (2): 61–65.