Marine Biology (2006) 149: 1047–1058
DOI 10.1007/s00227-006-0285-5

RESEARCH ARTICLE

Yoko Nozawa · Mutsunori Tokeshi · Satoshi Nojima

Reproduction and recruitment of scleractinian corals in a high-latitude coral community, Amakusa, southwestern Japan

Received: 20 December 2004 / Accepted: 12 February 2006 / Published online: 11 March 2006

Abstract Reproduction and recruitment in high-latitude coral populations in Japan have been little studied. A comprehensive study of the reproduction and early life history was conducted on nine common scleractinian coral species in Amakusa, southwestern Japan (32°N) from 2001 to 2003 including; (1) fecundity (the proportion of colonies with mature eggs), (2) timing and synchrony of spawning, (3) initial larval settlement pattern, (4) recruitment, (5) post-settlement mortality. The fecundity was high (76.7–100%) in six of seven species examined in 2002 and 2003. Annual spawning of the seven species occurred from mid July to August in 2001–2003, when seawater temperature was at the annual maximum. Spawning was highly synchronised among conspecific colonies and species in 2002 and 2003, with five species spawning five to nine nights after the full moon and another two spawning around the new moon. Temporal patterns of larval settlement of three spawning species during the first 10 days after spawning were similar to those of other spawning species from low latitudes. The number of scleractinian recruits on settlement plates, deployed from July to October (the major recruitment period at the study site), was low (2 recruits/m^2) for the three consecutive years. Post-settlement mortality of 1–1.5 month old spat of five species ranged between 88 and 100% over 3–10 months in the field, similar to the values reported for both high and low latitude species (>94–99%). Among the key stages examined, the low recruitment rate may be the most important step in limiting successful reproduction and recruitment of these high-latitude scleractinian populations. The low recruitment rate may be attributable to (1) the reduced influx of larval supply from other coral populations, which are smaller and more isolated at high-latitudes and (2) the longer precompetent larval phase of broadcast-spawning corals which results in an increased chance of larvae being dispersed away from parent populations.

Communicated by T. Ikeda, Hakodate

Y. Nozawa (✉) · M. Tokeshi · S. Nojima
Amakusa Marine Biological Laboratory, Kyushu University,
Tomioka, Reihoku-Amakusa, 863-2507, Kumamoto, Japan
E-mail: yokon@ambl-ku.jp
Tel.: + 81-90-19476637
Fax: +81-90-69352413

Introduction

Scleractinian coral species have a wide latitudinal range of distribution. While they exhibit a distinct biogeographical pattern of reduced biodiversity with increasing latitude, most coral reefs are also restricted to the tropics despite the occurrence of many coral communities with extensive coral cover at higher latitudes (Stehli and Wells 1971; Veron 1995, 2000). A number of biophysical factors have been proposed as influencing the latitudinal limits of coral and coral reef distribution, including water temperature, light availability, competition with other biota including macroalgae and failure in reproduction and/or recruitment (reviewed in Veron 1995; Kleypas et al. 1999; Harriott and Banks 2002).

Reproduction and recruitment are two crucial processes for the development and maintenance of coral populations. Although early theories suggested that lower water temperatures restricted reproduction in high-latitude coral populations (Yonge 1940; Wells 1957; Veron 1974), recent studies have documented successful gametogenesis and subsequent broadcast-spawning in many scleractinian species at high latitude locations (e.g. Shlesinger and Loya 1985; Yeemin 1991; Babcock et al. 1994; van Woesik 1995; Shlesinger et al. 1998; Harii et al. 2001; Thamrin et al. 2001; Tioho et al. 2001; Goffredo et al. 2002; Wilson and Harrison 2003). However, the pattern and timing of reproduction in high-latitude coral populations varies greatly and there have been only a few studies of coral reproduction on limited number of species at high latitudes in Japan (Yeemin 1991; Harii et al. 2001; Thamrin et al. 2001; Tioho et al. 2001).

With respect to the coral recruitment, there appears to be a decline in recruitment with increasing latitude, especially in broadcast-spawning corals (see review in Hughes et al. 2002). Although proximate factors causing this pattern have not fully been elucidated, recent studies suggest the direct influences of lower water temperatures on various stages of recruitment process, e.g. reduced larval development rates (Wilson and Harrison 1997), extended larval pre-settlement-competency periods (Wilson and Harrison 1998; Nozawa and Harrison 2002) and reduced larval settlement rates (Wilson and Harrison 1997; Y. Nozawa and P.L. Harrison, unpublished data).

In order to test the hypotheses that the failure of coral reproduction and/or recruitment processes in high-latitude scleractinian populations limits population growth, the present study examined the following key stages on nine common scleractinian coral species in a high-latitude coral community in Amakusa, southwestern Japan (32°N) from 2001 to 2003; (1) fecundity (i.e. the proportion of colonies with mature eggs), (2) timing and synchrony of broadcast spawning, (3) initial larval settlement pattern, (4) recruitment, (5) post-settlement mortality. In addition to these, the minimum reproductive size was also examined, since it was likely to be negatively affected by harsh environmental conditions at high-latitudes (see review in Harvell and Grosberg 1988).

Materials and methods

Study site and environmental variables

The present study was conducted in a high-latitude coral community (ca. 5 m in depth) at Satsukigaura, Amakusa, southwestern Japan (32°10′N, 130°02′E) (Fig. 1). A total of 98 scleractinian coral species have been recorded from Amakusa (Veron 1992; Nishihira and Veron 1995). At the study site, scleractinian corals form a patchy community, growing on the upper part of rocky substrata, where sand and pebbles fill the benthos between rocky outcrops. A total of eight common broadcast-spawning scleractinian species (*Acropora* cf. *hyacinthus*, *Acropora solitaryensis*, *Cyphastrea serailia*, *Echinophyllia aspera*, *Favia favus*, *Hydnophora exesa*, *Montastrea valenciennesi*, *Platygyra contorta*) and one brooding scleractinian species (*Alveopora japonica*) were used in the present study. Coral species were identified from sections of colonies using Veron (2000). Percentage cover for these species at the study site ranges between 0.3 and 3.9% (Y. N., unpublished data). Seawater temperature at the study site was monitored at 2-h intervals for the 3-year study period using Optic Stow-Away Temp data loggers (accuracy: ±0.2°C) (Onset Computer Corporation, Pocasset, MA, USA).

Reproduction

Fecundity and minimum reproductive size

This survey was conducted in 2002 on five broadcast-spawning scleractinian species (*A*. cf. *hyacinthus*, *C. serailia*, *E. aspera*, *F. favus*, *M. valenciennesi*) and repeated in 2003 with an addition of two species, *H. exesa* and *P. contorta*. Minimum reproductive size and fecundity [the proportion of colonies that contain mature (pigmented) eggs] (after Hughes et al. 2000) were determined simultaneously. Eighteen to 50 colonies of various sizes were sampled for each species by measuring diameter just before the predicted annual spawning periods in 2002 and 2003 (Yeemin 1991) (for sampling dates, refer to Table 1, Fig. 4). More samples

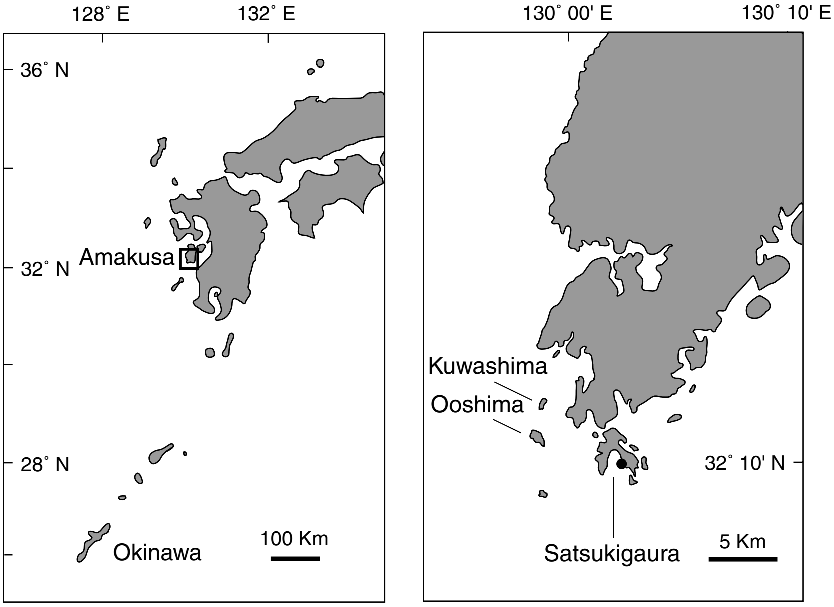


Fig. 1 Map of Amakusa, southwestern Japan showing the study site Satsukigaura indicated by a *closed circle*

Table 1 Sampling dates (lunar month) for annual fecundity estimates in 2002 and 2003

Species	Lunar month	2002	2003
Acropora cf. *hyacinthus*	July	NM	–
Cyphastrea serailia	July	NM	FM
Echinophyllia aspera	July	5 dAFM	2 dAFM
Favia favus	August	1 dANM	–
Montastrea valenciennesi	July	FM	1 dAFM
Platygyra contorta	July	–	FM

were taken from smaller size classes to determine the minimal reproductive size (for the number of colonies in different size classes, refer to Fig. 2). Each colony was photographed with a scale and three section samples (including >3 polyps) were taken with a hammer and a chisel from the inner part of each colony to avoid sterile zones. For small colonies, a whole colony was sampled. The presence of mature eggs was examined in >3 polyps in each of the section samples, or in all polyps for small colonies, under a dissecting microscope. Colonies were scored as fecund when mature eggs were observed in at least one of three section samples from each colony, or in a single polyp for small colonies. Relative colony-size (i.e. projected area) was determined from the photographs using Scion Image software (Scion Corp.). For the five species examined in 2002 and 2003, minimum reproductive size was determined from a pool of the two years' data of each species. Annual fecundity was calculated only from colonies larger than minimum reproductive size.

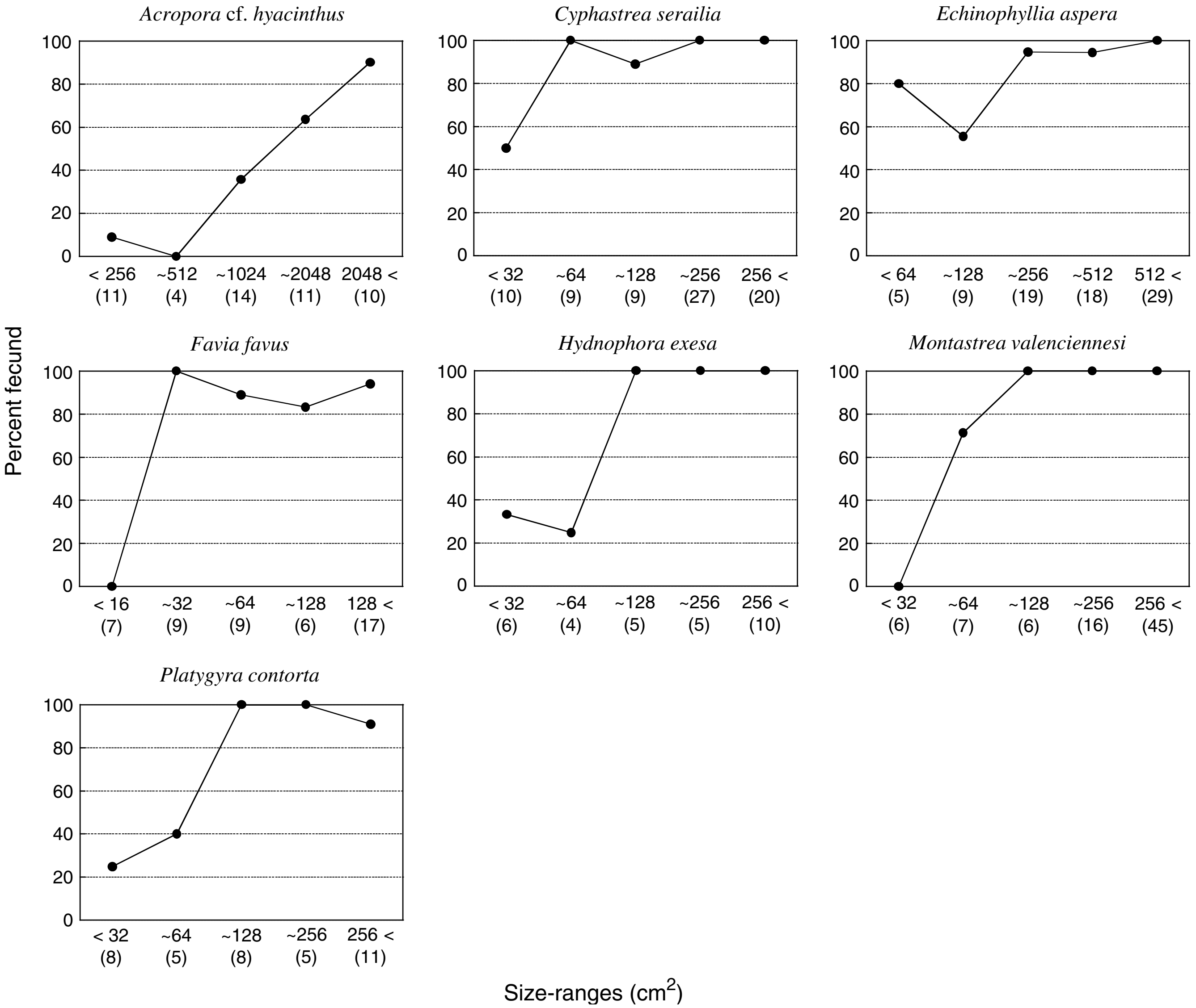


Fig. 2 Fecundity (the proportion of colonies with mature eggs) of seven broadcast-spawning scleractinian corals in different size ranges (cm^2, log scale). Note that the scale is different for each graph. Data were pooled from 2002 and 2003, except for *Acropora* cf. *hyacinthus* where only data from 2002 were used

Timing and synchrony of spawnings

This survey was conducted on the seven species examined for fecundity. Annual spawning of the species has been confirmed by Yeemin (1991) with monthly or bimonthly examinations at Kuwashima, near the study site (Fig. 1). A preliminary survey on the timing of spawning was done in 2001 with six species, *A.* cf. *hyacinthus*, *C. serailia*, *E. aspera*, *F. favus*, *M. valenciennesi* and *H. exesa* based on the previous records of spawning under laboratory conditions (Yeemin 1991). For each species, the approximate timing of spawning in the field was determined by approximately weekly examinations of ten middle-sized colonies chosen haphazardly at each examination. Three section samples (including >3 polyps) were taken from the inner part of each colony and examined under a dissecting microscope for the presence of mature eggs.

In 2002, a more detailed survey on the timing and synchrony of spawning among conspecific colonies was performed on six broadcast-spawning species. These included five of the six species studied in 2001, *A.* cf. *hyacinthus*, *C. serailia*, *E. aspera*, *F. favus*, *M. valenciennesi* and *P. contorta*. For each species, ten colonies with mature eggs, separated by a distance of 5–10 m from one another, were haphazardly chosen approximately 1 week before the predicted spawning period. An 'egg-capture' device, consisting of the top-half of a transparent plastic bottle and a transparent vinyl tube with one opening, was deployed by anchoring it with lines and nails to the base of a colony, which was floated a few centimetre above the colony with a small amount of air in the vinyl tube. Spawning of each colony was monitored by checking the presence of spawned eggs in the egg-capture device every morning. When spawned eggs were present, an approximate quantity of eggs was examined visually and recorded. The monitoring was continued until a few days after the last spawning night and then the monitored colony was examined for the presence of mature eggs by taking three section samples (including >3 polyps) from the inner region of the colony.

In 2003, this survey was repeated with four species, *C. serailia*, *E. aspera*, *M. valenciennesi* and *P. contorta*. Additional 30 middle-sized colonies were haphazardly chosen after the spawning period and examined for the presence of mature eggs. In *E. aspera* and *P. contorta*, this examination was done twice in July and August spawning periods due to split-spawning observed in the species in 2003 (for sampling dates, refer to Table 2, Fig. 4).

Table 2 Sampling dates for the proportion of spawned colonies during spawning periods in 2003

Species	Lunar month	
Cyphastrea serailia	July	4 dANM
Echinophyllia aspera	August	4, 11 dAFM
Montastrea valenciennesi	July	2 dANM
Platygyra contorta	August	4, 11 dAFM

Recruitment process

Initial larval settlement pattern

An experiment to determine the larval precompetent period and initial larval settlement rates was done on three broadcast-spawning scleractinian species, *A. solitaryensis* (relatively branched basal plate type) (cf. completely fused basal plate type), *C. serailia* and *F. favus* in 2002. Spawned gametes of *A. solitaryensis* were collected directly from the water surface just after spawning one night after the new moon (nANM) in August at Ooshima (Fig. 1), where *A. solitaryensis* was a dominant species. Subsequent observation on some features (size, colour and behaviour) of larvae developed from the gametes confirmed few larvae of other species being mixed in the sample. For *C. serailia* and *F. favus*, spawned gametes were obtained using 'larvae-capture' devices in the field. Five colonies of each species with mature gametes were collected just before the predicted spawning period and placed under a 'larvae-capture' device, which is a large, pyramidal, transparent plastic bag with some air at the top, being anchored to the sea bottom at four points of its opening with strings and stones. Spawned gametes of *C. serailia* and *F. favus* were collected on the fifth night after the full moon (nAFM) in July and the fourth nANM in August, respectively.

For each species, six to eight groups of 200 larvae were counted and placed into separate plastic aquaria ($10{\times}9{\times}15$ cm^3) (settlement aquaria) 2 days after spawning. The size of 10–15 larvae of each species was also measured under a dissecting microscope (×20 magnifications) with a calibrated eyepiece micrometer (the minimum scale of 50 μm). Each aquarium contained an artificial slate plate (hereafter settlement plate) ($5{\times}5{\times}0.4$ cm^3) that had been conditioned at the study site for a month. The plates were checked prior to experiments to ensure that no coral spat were present. The plate was placed horizontally 1 cm above the bottom of the aquarium by putting a conical plastic support glued onto the bottom of the aquarium through a centre hole of the plate. Each settlement aquarium was aerated by an air-stone to supply oxygen and create gentle currents. Settlement aquaria were placed in a large tray with running seawater to maintain temperature close to ambient seawater temperature. Temperatures during the experimental periods were recorded with a maximum–minimum thermometer and ranged 26.5–28°C for *C. serailia* and 23.5–27.5°C for *A. solitaryensis* and *F. favus*. Seawater in the settlement aquaria was carefully changed every 3 days by gently siphoning out the old seawater while retaining larvae with a 115 μm plankton-mesh filter submerged in the aquaria.

The plates were examined every day until 10 days after spawning (i.e. 8 days after the start of experiments). Each plate was transferred into a shallow tray of seawater and the numbers of attached and settled larvae on two plate surfaces (top and bottom) were counted under a dissecting microscope (×10–15 magnifications). Larvae were counted as (a) 'attached', when they were firmly attached to the settlement plate by the aboral end before undergoing metamorphosis and (b) 'settled', when they had begun to metamorphose (pumpkin-shaped appearance as against pear-shaped), with little or no possibility of active detachment and further migration. Settled larvae were marked with a fine line nearby on the plate surface using a sharp pencil to distinguish them in subsequent examinations. Larvae that had detached during the examination were collected by filtering through a 100 μm mesh plankton net and returned to the settlement aquarium.

Recruitment

A total of 50, 100 and 50 settlement plates ($10 \times 10 \times 0.4$ cm^3) were deployed at the study site in 2001, 2002 and 2003, respectively. Each plate was fixed horizontally by bolts and nuts 2–3 cm above the substratum and >10 cm away from the nearest corals. The plates were submerged for 3 months, from July to October, covering the major recruitment period of scleractinian corals at the study site (Yeemin 1991; Tioho et al. 2001; Thamrin 2001). The top and bottom plate surfaces were examined under a dissecting microscope (×10–15 magnifications), and coral recruits were counted and identified to family or genus level where possible (after Baird and Babcock 2000; Babcock et al. 2003; Y. N. unpublished data).

Post-settlement mortality

A preliminary experiment was conducted with *F. favus* and *H. exesa* in 2001–2002. For each species, larvae were obtained on the fifth nANM in August 2001 from spawnings of colonies that had been collected before the predicted spawning period. Larvae were maintained with running seawater in a laboratory until being used. Ten groups of 300 larvae were counted and placed into separate settlement aquaria ($20 \times 12 \times 12$ cm^3), each containing a settlement plate ($10 \times 10 \times 0.4$ cm^3). The settlement aquaria were maintained in the same manner as in the settlement experiment. After one and a half months, each plate was examined for the number of spat on the top and bottom surfaces and tagged with a small plastic plate and a plastic line. The plates with spat were carefully transferred to the study site and fixed in the same manner as in the recruitment experiment. The plates were retrieved after 10 months, and the number of surviving spat was counted under a dissecting microscope.

A more detailed experiment was conducted with three broadcast-spawning species, *A. solitaryensis*, *C. serailia* and *F. favus* and a brooding species, *A. japonica* in 2002–2003. For the three spawning species, larvae that had settled during the settlement experiment were used. The plates with spat were placed vertically and maintained in large trays with running seawater under indirect natural light until being used in the experiment. For *A. japonica*, planula larvae that were released on the ninth day after the new moon (dANM) in September (Thamrin et al. 2001) were collected from ten colonies in the laboratory. Larvae were placed in a tray with gently overflowing running seawater containing five settlement plates ($5 \times 5 \times 0.4$ cm^3) that had been conditioned for a month in the study site. Each plate was placed horizontally on a small piece of plastic to make a gap for larval settlement on the bottom plate surface.

For each species, the number of spat on the top and bottom surfaces of each plate was counted under a dissecting microscope (×10–15 magnifications) at 3–4 week post-settlement. The plates with spat were tagged with small plastic plates and plastic lines, carefully transferred to the study site and fixed 2–3 cm above the substrata and >10 cm away from the nearest corals. The plates were deployed vertically to prevent the influence of sedimentation that may have caused high mortality of spat in the preliminary experiment. The plates were retrieved approximately every month to count the number of surviving spat and returned to the site until three months after the start of the experiments when most spat on the plates had died. At each examination, the size (maximum diameter) of spat was also measured under a dissecting microscope (×20 magnifications) with a calibrated eyepiece micrometer (the minimum scale of 50 μm). Three to 20 spat, depending on the available number of surviving spat that looked healthy and were isolated from other spat, were chosen haphazardly for the measurement.

Statistics

Statistical analyses were done with Statistica software. A logistic regression analysis was used to test whether colony-size (independent variable) influenced the presence of mature eggs (dependent variable). Data were pooled from 2002 and 2003 prior to the analysis, except for *A.* cf. *hyacinthus* where only data from 2002 were used. A one-way ANOVA was used for the comparison of spat sizes among species. A Tukey HSD test was used for the multiple comparisons. Homogeneity of variance was tested using Bartlett's test. Where variances were not homogeneous ($P < 0.05$), a Kruskal–Wallis test was used to compare survivorship among species with multiple comparisons tested using a Dunn's test. Proportional survivorship data were arcsine transformed before applying statistical tests.

Results

Reproduction

Fecundity and minimum reproductive size

Fecundity of the six scleractinian species examined was quite high (76.7–100%), except for *A.* cf. *hyacinthus* (47.8 and 0% in 2002 and 2003, respectively) (Table 3). Few immature eggs, i.e. eggs of white or pale colour, were observed during the examination. Minimum reproductive size varied among the seven species, ranging from 6 cm^2 for *C. serailia* to 193 cm^2 for *A.* cf. *hyacinthus* (Table 3). The fecundity increased with colony size (logistic regression with Bonferroni's correction; $P < 0.001$ for *A.* cf. *hyacinthus*, *C. serailia*, *H. exesa*, *M. valenciennesi*; $P < 0.01$ for *F. favus*, *P. contorta*; $P < 0.05$ for *E. aspera*) but the pattern was different among the species (Fig. 2). While the fecundity in the six species increased to ca. 100% in colonies > 64 cm^2, the fecundity in *A.* cf. *hyacinthus* increased gradually with increasing colony size to the largest size-class (> 2,048 cm^2).

Timing and synchrony of spawnings

Annual spawning of the seven scleractinian species occurred from mid July to August in 2001–2003 (except *A.* cf. *hyacinthus* in 2003 due to zero fecundity), when seawater temperature was at the annual maximum at the study site (Figs. 3, 4). In six of the seven species, synchronous spawning among conspecific colonies was confirmed on a daily basis for two to four consecutive days in 2002 and 2003 (Fig. 4). Spawning of the four species, *A.* cf. *hyacinthus*, *E. aspera*, *M. valenciennesi* and *P. contorta* occurred synchronously from the seventh to ninth nAFM in July 2002. This synchronous spawning was repeated in July 2003 (the seventh to eighth nAFM) among three of the four species, i.e. *M. valenciennesi* and some colonies of *E. aspera* and *P. contorta*, plus *C. serailia*.

There were two separate spawning periods for *E. aspera* and *P. contorta* in 2003, occurring synchronously between the two species at the seventh to eighth nAFM in July and the seventh to ninth nAFM in August (Fig. 4). Section samples indicated that the majority of colonies spawned during the second spawning period in both species. All 30 colonies of *E. aspera* and 22 of 30 colonies of *P. contorta* had mature eggs after the first spawning period but no colony contained mature eggs after the second spawning period. For *C. serailia* and *M. valenciennesi*, the occurrence of a second spawning period by a small proportion of colonies was also suggested in August 2003, as eight of 30 *C. serailia* colonies and seven of 30 *M. valenciennesi* colonies had mature eggs after their spawning period in July.

Table 3 Fecundity (percent colonies with mature eggs) and minimum reproductive size in seven scleractinian corals

Species	Minimum reproductive size (cm^2)	Fecundity	
		2002	2003
Acropora cf. *hyacinthus*	193	47.8 (46)	0 (30)
Cyphastrea serailia	6	90.9 (43)	96.7 (30)
Echinophyllia aspera	11.3	95.9 (49)	86.7 (30)
Favia favus	16	88.5 (26)	100 (15)
Hydnophora exesa	24.5	–	76.7 (28)
Montastrea valenciennesi	36.1	97.7 (44)	96.7 (30)
Platygyra contorta	20.4	–	81.8 (33)

The number of colonies above the minimum reproductive size that were used for the calculation of fecundity was shown in parenthesis

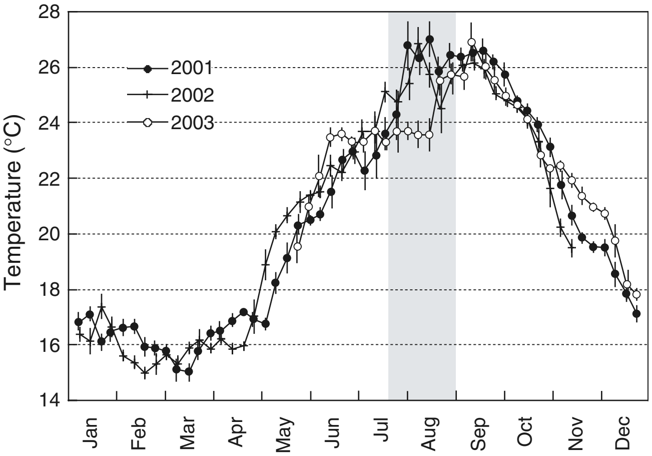


Fig. 3 Seawater temperature at 5 m depth at Satsukigaura, Amakusa in 2001–2003. *Grey zone* indicates spawning season at Amakusa. Values represent weekly average ± SD

Recruitment process

Initial larval settlement pattern

Fertilized eggs of the broadcast-spawning corals, *A. solitaryensis*, *C. serailia*, *F. favus* became pear-shaped mobile larvae within 48–72 h after spawning. Larvae measured 863.3 ± 154.1 μm long and 390 ± 68.7 μm wide (mean ± SD, $n = 15$) for *A. solitaryensis*, 380 ± 35 μm long and 230 ± 25.8 μm wide for *C. serailia* ($n = 10$) and 559.1 ± 58.4 μm long and 250 ± 0 μm wide for *F. favus* ($n = 11$). For the three species, larval attachment rate was initially high and decreased gradually with time (Fig. 5a). For *C. serailia* and *F. favus*, some settled larvae were observed on day three (Fig. 5b). Mean daily larval settlement rates of these species peaked at 3–4 days after spawning, and decreased gradually to the end of the experiments. In contrast, some larvae of *A. solitaryensis* began to settle 3–4 days after spawning with a peak occurring at 6–7 days (Fig. 5b). Cumulative settlement rate over the 8-day experimental period was 15.9 ± 8.0% (mean ± SD) in *C. serailia*, 18.3 ± 11.1% in *F. favus* and 13.6 ± 10.4% in *A. solitaryensis*.

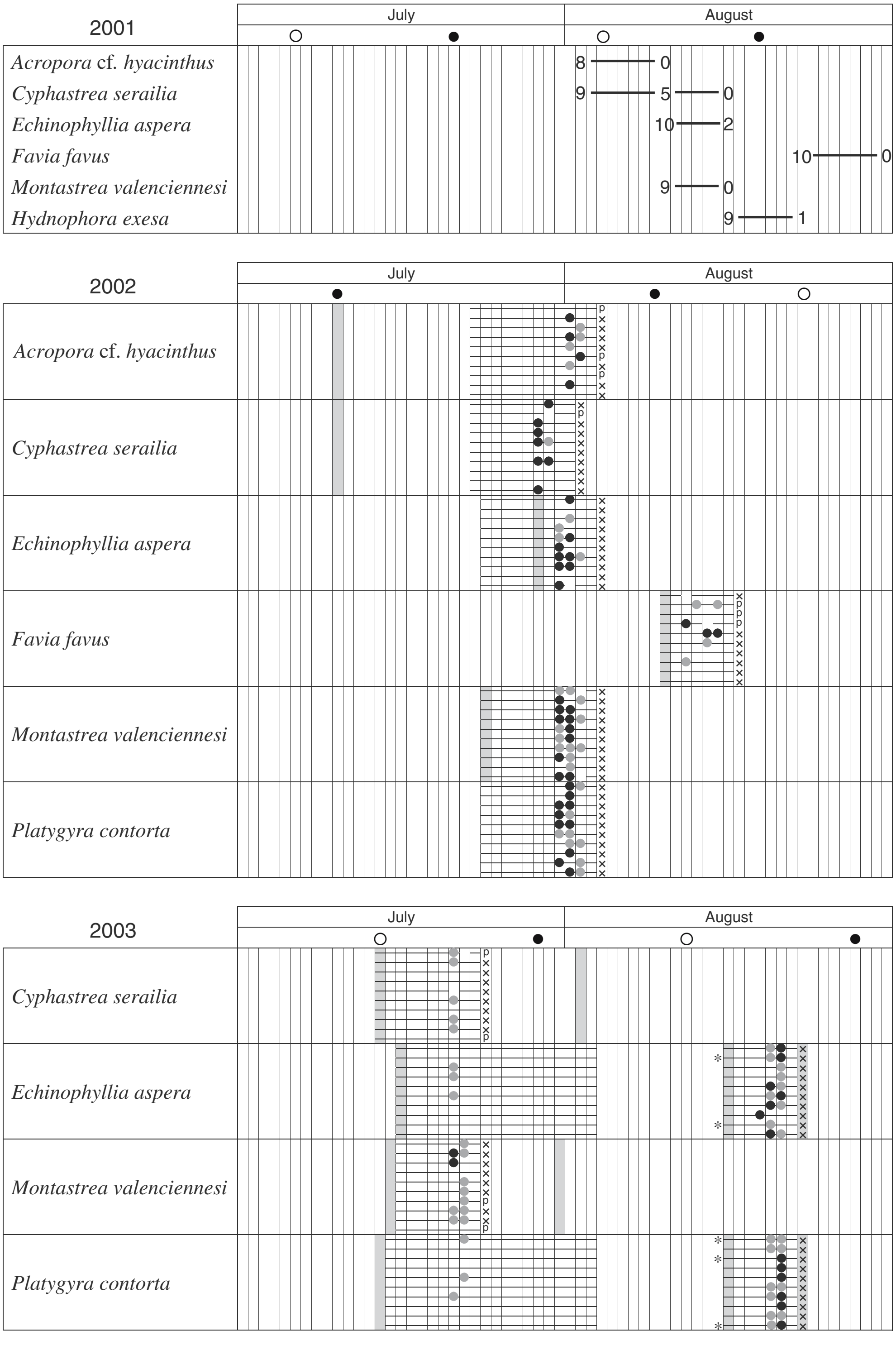
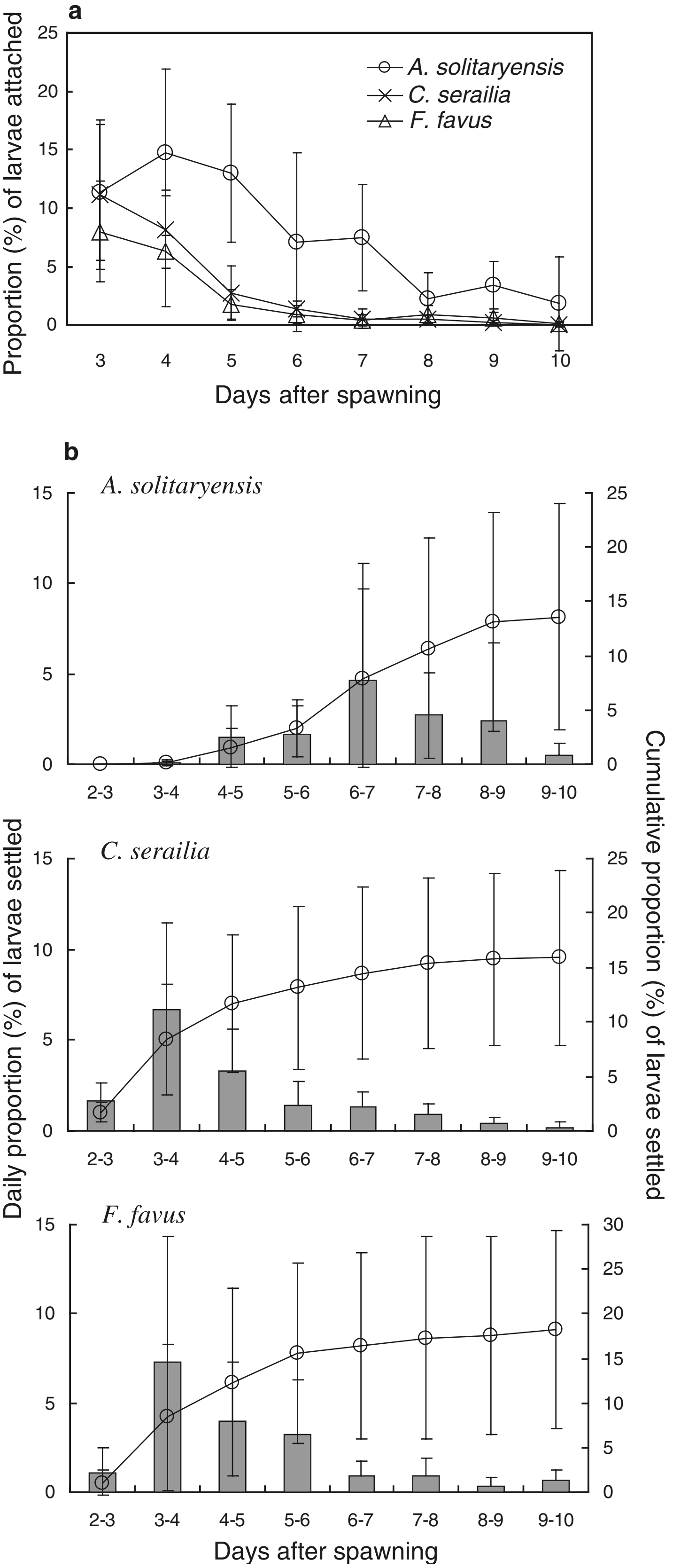


Fig. 4 Timing and daily synchrony of broadcast-spawning in seven scleractinian corals at Satsukigaura, Amakusa in 2001–2003. Species names, lunar cycle (*open circle* full moon, *closed circle* new moon) and dates (*a thin column* a single day) are shown in each year's diagram. For 2001, each horizontal bar denotes a period over which spawning may have occurred with the number of colonies (out of ten) with mature eggs observed on a particular sampling date. In 2002 and 2003, a horizontal bar denotes a monitoring period for a single colony. Disconnected part of the line means disruption due to device malfunctioning. *Filled circles* on the lines denote the presence of spawned eggs in capture devices (*closed circle* many, *grey shaded circle* few). Marks at the end of the lines show the presence (*p*) and absence (*crosses*) of mature eggs in monitored colonies at termination. *Grey cells* show dates of sampling of additional colonies for annual fecundity estimates (before spawning) or to determine the proportion of population that had spawned (after spawning in 2003). For *Echinophyllia aspera* and *Platygyra contorta* in 2003, *asterisks* indicates colonies without mature eggs after the July monitoring were replaced with new colonies for the August monitoring. Note that the smaller number of eggs observed in July 2003 may be due to malfunctioning of the device under rough sea conditions

Fig. 5 Proportion (%) of larvae attached (**a**) and settled (**b**) on the plates ($n=8$ replicate aquaria for *Cyphastrea serailia* and *Favia favus* and 6 for *Acropora solitaryensis*). Average ± SD are shown



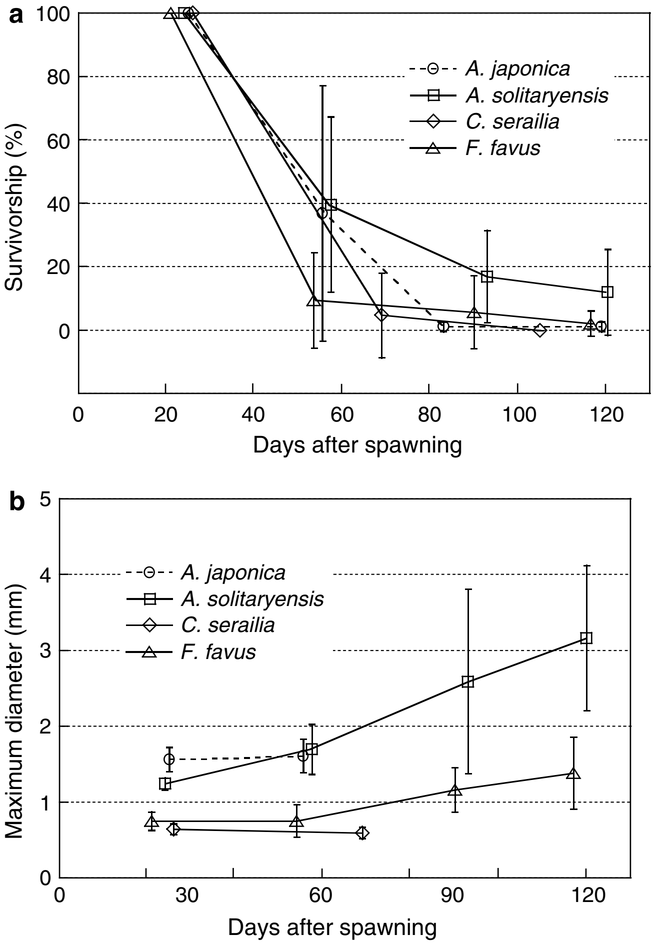


Fig. 6 **a** Survivorship of 1–1.5 month old recruits over the 3-month experimental period. **b** Change in maximum diameter of recruits [$n = 6$–20 (*Acropora solitaryensis*), 20 (*Alveopora japonica*), 20 (*Cyphastrea serailia*), 3–20 (*Favia favus*)]. Average ± SD are shown

Recruitment

There were only one or two scleractinian recruits observed on a total of 50–100 plates deployed every year from 2001 to 2003. In 2001, one recruit (species unidentified, 750 μm diam.) was found on the bottom plate surface among 50 plates. In 2002, two recruits were found on two separate plates among 100 plates. One of them was a spawning *Acropora* sp. (1.5 mm diam.) settled on the top plate surface and the other was a brooding *Alveopora* sp. (2 mm diam.) settled on the bottom surface. In 2003, one recruit of a spawning *Acropora* sp. (1.3 mm diam.) was found on the top surface among 50 plates.

Post-settlement mortality

In the preliminary experiment conducted in 2001–2002, none of 498 *F. favus* spat and 86 *H. exesa* spat survived until the first examination 10 months after being placed in the study site. A more detailed experiment conducted in 2002–2003 showed high mortality at the initial post-settlement stages in the three broadcast-spawning species, *A. solitaryensis*, *C. serailia* and *F. favus*, and the brooding species, *A. japonica* (Fig. 6a). At the end of the 3-month experimental period, the survivorship of *A. solitaryensis* was significantly higher than that of *C. serailia* and *F. favus* ($P < 0.05$). The numbers of spat surviving at the end of the experiments were three out of 117 *A. japonica* spat, 35 of 238 *A. solitaryensis* spat, zero of 200 *C. serailia* spat and six of 269 *F. favus* spat.

Spat size

The size of *A. japonica* larvae was 1,660 ± 229.6 μm in length and 562 ± 48.5 μm in width (mean ± SD, $n = 25$) (see the previous section for the other spp.). Spat of the four species were significantly different in size (max. diam.) at the start of experiment (ca. 3–4 week post settlement); *A. japonica* (1.59 ± 0.13 mm: mean ± SD, $n = 25$) > *A. solitaryensis* (1.24 ± 0.09 mm, $n = 24$) > *F. favus* (0.75 ± 0.12 mm, $n = 25$) > *C. serailia* (0.65 ± 0.08 mm, $n = 26$) ($P < 0.05$) (Fig. 6b). Spat sizes of *A. solitaryensis* and *F. favus* increased 255 and 186% on average for the next 3 months, attaining 3.17 ± 0.96 mm (mean ± SD) ($n = 6$) and 1.38 ± 0.47 mm ($n = 3$), respectively.

Discussion and conclusion

Reproduction

Fecundity and minimum reproductive size

The six scleractinian corals examined, except *A.* cf. *hyacinthus*, showed high fecundity (76.7–100%) at the high-latitude study site (32°N) where the annual mean water temperature ranged from 15 to 27°C (Fig. 3). Wilson and Harrison (1997) also reported high fecundity in 21 scleractinian corals from the Solitary Islands (30°S) where the annual water temperature was 16.6–26.6°C. Hence, these studies confirmed that many scleractinian corals are capable of producing gametes in the low temperature ranges at high-latitudes.

Low fecundity of *A.* cf. *hyacinthus* (0–47.8%) observed in 2002–2003 may not be a general feature of the species at the study site, since high fecundity (80%) was observed in the preliminary survey in 2001 (Fig. 4). Low fecundity may be attributable to split-spawning (reviewed in Baird et al. 2000), i.e. colonies had spawned their gametes before the observed spawning period in July, and/or to environmental disturbances (reviewed in Ward and Harrison 2000).

It is unlikely that spawning was triggered in June prior to examination as water temperatures were around 2–3°C lower than July. However, environmental disturbances were experienced in 2002–2003. Typhoons occurred a few times per year in 2002–2003, and in 2003 an outbreak of a seaweed *Colpomenia sinuosa* occurred from the end of March to the beginning of April which covered most colonies for a couple of weeks. Although these events did not cause high whole colony mortality, significant physical and tissue damage (e.g. partial tissue death or bleaching) was observed in colonies of some vulnerable species such as *Pocillopora damicornis* and acroporid corals (Y. N., personal observation).

Although there are few published data on the minimum reproductive size of scleractinian coral species, the values for the four faviid species in this study (6–36.1 cm^2) are similar to values reported for other faviids at low latitude sites (ca. 7–50 cm^2) (Babcock 1984, 1991; Sakai 1997; Hall and Hughes 1996). In contrast, *A*. cf. *hyacinthus* had a much larger minimum reproductive size (193 cm^2) than other coral species examined in this study, and published values for other acroporid species from low latitude sites (38–59 cm^2) (12°S) (Hall and Hughes 1996). This may be due to reduced fecundity during the study as a result of environmental stressors.

The positive relationship between colony-size and fecundity found in the seven species in the present study is consistent with other published studies (Babcock 1984; Hall and Hughes 1996; Kapela and Lasker 1999). This may be due to differential resource allocation between growth and reproduction among colonies of different sizes. Smaller colonies may allocate more resources to growth in order to escape the higher risk of mortality (Harvell and Grosberg 1988; Babcock 1991) and they may use up resources for survival under stressful conditions or disturbances, thus becoming non-reproductive. This hypothesis also suggests that the minimal reproductive size for each species may vary at different times and locations, depending on the extent of stresses and disturbances experienced (see also review in Harvell and Grosberg 1988).

Timing and synchrony of spawnings

Water temperature is a significant factor determining the general timing of annual spawning at high-latitudes (e.g. Shlesinger and Loya 1985; van Woesik 1995; Wilson and Harrison 2003; but see Babcock et al. 1994). In this study, reduced water temperature in July 2003 was associated with split spawning in all four species examined. Wilson and Harrison (2003) also observed less synchronous sporadic spawning among conspecific colonies in many scleractinian corals at the Solitary Islands, where colonies experience highly variable water temperatures during the spawning season.

Recruitment process

Initial larval settlement pattern

The pre-settlement competency periods of larvae of *A. solitaryensis*, *C. serailia* and *F. favus* from the present study site (2–4 days) were much shorter than those reported for broadcast-spawning species from high-latitudes (6–12 days) (Shlesinger and Loya 1985, 1991; Wilson and Harrison 1998). However, these values were comparable to those reported from lower latitudes (1–7 days) (Babcock and Heyward 1986; Heyward et al. 1987; Baird 2001; Schwarz et al. 1999; Nozawa and Harrison 2002, 2005; Miller and Mundy 2003). The patterns of larval attachment and settlement in the three species were similar to those for other species from low latitudes (Nozawa and Harrison 2002, 2005; Miller and Mundy 2003), except the larval settlement pattern of *A. solitaryensis* (Fig. 5). *A. solitaryensis* showed a delayed peak in settlement which may result in more larvae being swept away from natal populations and contribute to lower local recruitment.

Recruitment

The recruitment rate of 2 m^{-2} in this study was considerably lower than values reported from low-latitude areas in the Pacific (57–4,590 recruits/m^2) (reviewed in Glassom et al. 2004). Yeemin (1991) reported a similar number of scleractinian recruits at Kuwashima, near the present study site (Fig. 1). On a total of 490 settlement tiles (10×10×2 cm^3), consisting of five types of tiles; ceramic tiles, beach rock, rhyolite rock, Takiron and shell, deployed from 1988 to 1990, only two recruits of the brooding species, *P. damicornis* were observed in 1988. These recruitment rates were consistent with values from high latitude sites in eastern Australia, except that there, brooding species were the dominant recruits (Harriott 1992, 1999; Harriott and Banks 1995; Harriott and Simpson 1997; Hughes et al. 2002). Tioho et al. (2001) observed ca. 70 recruits of the brooding coral *P. damicornis* on 90 ceramic tiles (10×10×2 cm^3) every year for 2 years, which were deployed within a distance of 10 m from *P. damicornis* colonies at Ooshima, near the present study site (Fig. 1). Hence, low recruitment rates of brooding species at the present study site may be due to low density of brooding species (Y. N., unpublished data). The plate material is unlikely to be the cause, since many larvae settled on the plates in laboratory experiments in the present study.

Probable factors creating the general pattern of recruitment at high-latitude may be (1) reduced larval supply from other coral populations, which are smaller and more isolated at high-latitudes, and (2) different larval dispersal patterns of broadcast-spawning and brooding coral species. Short precompetent period of brooding larvae results in high contribution to local recruitment (Harriott 1992; Smith 1992; Tioho et al. 2001). In contrast, longer precompetent period in broadcast-spawned larvae means they are vulnerable to passive drift and may recruit some distance from parent colonies (reviewed in Harrison and Wallace 1990). Similar results (i.e. low recruitment in highly fecund broadcast-spawning coral populations) reported from another high-latitude site, the Solitary Islands suggest that the pattern may not be a local phenomenon (Harriott 1999; Wilson and Harrison 1997).

Yeemin (1991) examined juvenile scleractinian corals (≤ 50 mm in diameter) on natural rocky substrata at Kuwashima (Fig. 1) and found 188 juveniles in an area of 52.5 m^2 (3.58 juveniles/m^2). Given that juvenile corals may include a number of cohorts, the density of coral recruits recorded in the present study for 1 year (2 recruits/m^2) may reflect natural levels of recruitment onto the natural substrata in the study site. Harriott (1999) reported similar densities of coral recruits on settlement panels and of juvenile corals on natural substrata (2.3 recruits/m^2/year) in the Solitary Islands and slightly lower mortality rates of the juveniles tracked over 5 years (2.0 corals/m^2/year). She concluded that the low recruitment rates must be sufficient to maintain the high-latitude coral communities.

Post-settlement mortality

Post-settlement mortality of five scleractinian corals ranged 88–100% over the 3-month period in the present study. Similar values were reported from other high-latitude sites (> 94–99%) (Shlesinger and Loya 1991; Wilson 1998; Fairfull and Harriott 1999) and also from a low latitude site (> 94–98%) (Babcock 1985; Babcock and Mundy 1996). Hence, high mortality appears to be a general feature of scleractinian recruits in the first year of settlement with little difference between low and high latitude sites.

A positive correlation between colony-size and survivorship has been reported for the two scleractinian corals, *Platygyra sinensis* and *Oxypora lacera* during the period of four to nine month post settlement (Babcock and Mundy 1996). Results of the present study largely supported the correlation where the survivorship of larger spat (i.e. *A. solitaryensis*) was higher than those of smaller spat (i.e. *C. serailia* and *F. favus*). In contrast, Babcock (1985) reported a slightly higher mortality in *A. millepora* (86%) than in *Goniastrea aspera* (66%) and *P. sinensis* (74%), even though the spat of *A. millepora* were three to four times larger than those of *G. aspera* and *P. sinensis*. The reason why the correlation was not always observed among species may be species-specific tolerance to various environmental stresses and disturbances affecting their survivorship. The study site of Babcock (1985) had relatively high sedimentation (cf. Babcock and Mundy 1996), which may reduce the survivorship of recruits of species vulnerable to sedimentation such as acroporids.

Conclusion

The present study examined the several key stages in the reproduction and recruitment processes of scleractinian corals in high-latitude coral populations. Among the key stages examined, synchrony of spawning and recruitment were identified as key stages which may limit successful reproduction and recruitment. Synchrony of spawning among conspecific colonies may be disturbed by unusually low or variable water temperature, resulting in a reduction of locally produced larval supply. The low recruitment recorded at high-latitude sites may limit the formation and development of coral populations. Hence these results support the argument that the processes of population replenishment may be a significant factor influencing the latitudinal limit of coral distribution.

Acknowledgements We thank Mr K. Tanaka for the collection of *A. s.* larvae and Mr H. Tomikawa for the provision of water temperature data. We also thank Dr A. Baird, Dr J. Wilson and two anonymous reviewers for reviewing a manuscript and productive comments. Y. N. was supported by a Research Fellowship for Young Scientists and M. T. and S. N. by Grants-in-Aid for scientific research (Nos. 14255013 and 11480150, respectively), administered by the Japan Society for the Promotion of Science. The experiments performed here complied with the current laws of Japan.

References

Babcock RC (1984) Reproduction and distribution of two species of *Goniastrea* (Scleractinia) from the Great Barrier Reef Province. Coral Reefs 2:187–195

Babcock RC (1985) Growth and mortality in juvenile corals (*Goniastrea*, *Platygyra* and *Acropora*): the first year. In: Proceedings of the 5th international coral reef congress, Tahiti, vol 4, pp 355–360

Babcock RC (1991) Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. Ecol Monogr 61:225–244

Babcock RC, Heyward AJ (1986) Larval development of certain gamete-spawning scleractinian corals. Coral Reefs 5:111–116

Babcock R, Mundy C (1996) Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. J Exp Mar Biol Ecol 206:179–201

Babcock RC, Willis BL, Simpson CJ (1994) Mass spawning of corals on a high latitude coral reef. Coral Reefs 13:161–169

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool Stud 42:211–226

Baird AH (2001) The ecology of coral larvae: settlement patterns, habitat selection and the length of the larval phase. Phd Thesis, James Cook University

Baird AH, Babcock RC (2000) Morphological differences among three species of newly settled pocilloporid coral recruits. Coral Reefs 19:179–183

Baird AH, Marshall PA, Wolstenholme J (2000) Latitudinal variation in the reproduction of Acropora in the Coral Sea. In: Proceedings of the 9th international coral reef sympsium, Bali, vol 1, pp 385–389

Fairfull SJL, Harriott VJ (1999) Succession, space and coral recruitment in a subtropical fouling community. Mar Freshw Res 50:235–242

Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Mar Biol 144:641–651

Goffredo S, Arnone S, Zaccanti F (2002) Sexual reproduction in the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). Mar Ecol Prog Ser 229:83–94

Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950–963

Harii S, Omori M, Yamakawa H, Koike Y (2001) Sexual reproduction and larval settlement of the zooxanthellate coral *Alveopora japonica* Eguchi at high latitudes. Coral Reefs 20:19–23

Harriott VJ (1992) Recruitment patterns of scleractinian corals in an isolated sub-tropical reef system. Coral Reefs 11:215–219

Harriott VJ (1999) Coral growth in subtropical eastern Australia. Coral Reefs 18:281–291

Harriott VJ, Banks SA (1995) Recruitment of scleractinian corals in the Solitary Islands Marine Reserve, a high-latitude coral-dominated community in Eastern Australia. Mar Ecol Prog Ser 123:155–161

Harriott VJ, Banks SA (2002) Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. Coral Reefs 21:83–94

Harriott VJ, Simpson CJ (1997) Coral recruitment in Western Australia. In: Proceedings of the 8th international coral reef symposium, Panama, vol 2, pp 1191–1196

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the world, vol 25, coral reef ecosystems. Elsevier, Amsterdam, pp 133–207

Harvell CD, Grosberg RK (1988) The timing of sexual maturity in clonal animals. Ecology 69:1855–1864

Heyward A, Yamazato K, Yeemin T, Minei M (1987) Sexual reproduction of corals in Okinawa. Galaxea 6:331–343

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81:2241–2249

Hughes TP, Baird AH, Dinsdale EA, Harriott VJ, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2002) Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. Ecology 83:436–451

Kapela W, Lasker HR (1999) Size-dependent reproduction in the Caribbean gorgonian *Pseudoplexaura porosa*. Mar Biol 135:107–114

Kleypas JA, McManus JW, Menez LAB (1999) Environmental limits to coral reef development: where do we draw the line? Am Zool 39:146–159

Miller K, Mundy C (2003) Rapid settlement in broadcast spawning corals: implications for larval dispersal. Coral Reefs 22:99–106

Nishihira M, Veron JEN (1995) Hermatypic corals of Japan (in Japanese). Kaiyusha Publishers, Tokyo

Nozawa Y, Harrison PL (2002) Larval settlement patterns, dispersal potential, and the effect of temperature on settlement of larvae of the reef coral, *Platygyra daedalea*, from the Great Barrier Reef. In: Proceedings of the 9th international coral reef symposium, Bali, vol 1, pp 409–415

Nozawa Y, Harrison PL (2005) Temporal settlement patterns of larvae of the broadcast spawning reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea aspera* from Okinawa, Japan. Coral Reefs 24:274–282

Sakai K (1997) Gametogenesis, spawning, and planula brooding by the reef coral *Goniastrea aspera* (Scleractinia) in Okinawa, Japan. Mar Ecol Prog Ser 151:67–72

Schwarz JA, Krupp DA, Weis VM (1999) Late larval development and onset of symbiosis in the scleractinian coral *Fungia scutaria*. Biol Bull 196:70–79

Shlesinger Y, Loya Y (1985) Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. Science 228:1333–1335

Shlesinger Y, Loya Y (1991) Larval development and survivorship in the corals *Favia favus* and *Platygyra lamellina*. Hydrobiologia 216/217:101–108

Shlesinger Y, Goulet TL, Loya Y (1998) Reproductive patterns of scleractinian corals in the northern Red Sea. Mar Biol 132:691–701

Smith SR (1992) Patterns of coral recruitment and post-settlement mortality on Bermuda's reefs: comparisons to Caribbean and Pacific reefs. Am Zool 32:663–673

Stehli FG, Wells JW (1971) Diversity and age patterns in hermatypic corals. Syst Zool 20:115–126

Thamrin (2001) Reproductive biology of a scleractinian coral *Alveopora japonica* Eguchi in Amakusa, South-western Japan. PhD dissertation, Kyushu University

Thamrin, Nojima S, Tokeshi M (2001) Experimental analysis of planula release in a scleractinian coral *Alveopora japonica*. Galaxea. JCRS 3:25–30

Tioho H, Tokeshi M, Nojima S (2001) Experimental analysis of recruitment in a scleractinian coral at high latitude. Mar Ecol Prog Ser 213:79–86

van Woesik R (1995) Coral communities at high latitude are not pseudopopulations: evidence of spawning at 32°N, Japan. Coral Reefs 14:119–120

Veron JEN (1974) Southern geographic limits to the distribution of Great Barrier Reef hermatypic corals. In: Proceedings of the 2nd international coral reef symposium, vol 2, pp 465–473

Veron JEN (1992) Hermatypic corals of Japan. Australian Inst Mar Sci Monogr Ser 9, Townsville

Veron JEN (1995) Corals in space and time: the biogeography and evolution of the Scleractinia. UNSW Press, Sydney

Veron JEN (2000) Corals of the World. Aust Inst Mar Sci & CRR Qld Pty Ltd, Townsville

Ward S, Harrison P (2000) Changes in gametogenesis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorus during the ENCORE experiment. J Exp Mar Biol Ecol 246:179–221

Wells JW (1957) Coral reefs. Mem Geol Soc Am 67:609–631

Wilson JR (1998) Reproduction and larval ecology of broadcast spawning corals at the Solitary Islands, eastern Australia. PhD dissertation, Southern Cross University

Wilson JR, Harrison PL (1997) Sexual reproduction in high latitude coral communities at the Solitary Islands, eastern Australia. In: Proceedings of the 8th international coral reef symposium, vol 1, pp 533–538

Wilson JR, Harrison PL (1998) Settlement-competency periods of larvae of three species of scleractinian corals. Mar Biol 131:339–345

Wilson JR, Harrison PL (2003) Spawning patterns of scleractinian corals at the Solitary Islands—a high latitude coral community in eastern Australia. Mar Ecol Prog Ser 260:115–123

Yeemin T (1991) Ecological studies of scleractinian coral communities above the northern limit of coral reef development in the western Pacific. PhD dissertation, Kyushu University

Yonge CM (1940) The biology of reef-building corals. Sci Rep Great Barrier Reef Exped 1:353–391