Introduction

Population explosions of the coral predator *Acanthaster planci* (Linnaeus) have been the most important management issue for coral communities in the Indo-Pacific region over the past four decades (Birkeland & Lucas 1990). Many coral communities occurring throughout the southern Japanese waters were impacted by chronic *A. planci* predation in recent years. Although the causes of population outbreaks are still unclear, early studies highlighted the importance of the early life stages, such high fecundity and long larval duration (Yamaguchi 1973). The larval ecology of this species indicates that only a small increase in survival rate will lead to a sudden increase in the adult population density. Moreover, larvae released by an outbreak population of *A. planci* may be transported in quantity to other reefs via ocean currents and cause another adult population outbreak (termed secondary outbreaks, Kenchington 1977). Indeed, historical records of outbreaks in the coast of mainland Japan were consistent with direction changes in the...

Latitudinal differentiation in the reproduction patterns of the crown-of-thorns starfish *Acanthaster planci* through the Ryukyu Island Archipelago

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Abstract: Chronic outbreaks of the coral eating crown-of-thorns starfish (*Acanthaster planci*) have devastated coral communities throughout the Ryukyu Islands in the past four decades. Since *A. planci* has high fecundity and long larval duration, knowledge of reproductive timing and larval dispersal are keys to understanding mechanisms of successive recruitment and consequent outbreaks of adults. As the first step to acquiring this knowledge, we monitored water temperature and peak spawning periods using gonad observation. A total of 379 *A. planci* specimens were collected from May to September in 2004 at five latitudinally different locales in the Ryukyu Islands. Peak spawning, at which starfish gonads rapidly shrunk in size, was first observed in late May in Ishigaki Island, the southernmost sampling site. Then spawning time was progressively delayed with increasing latitude, i.e. from mid to late June in Miyako Is., late June to mid July in Kerama Is., late July in Okinawa Is. and Amami Oshima Is. When we started the survey in May, some *A. planci* had already started spawning, though not at Amami Oshima. The peak spawning time in every locality coincided with the time when the water temperature exceeded 28°C. Accordingly, we can predict the approximate peak for spawning by monitoring water temperatures throughout the Ryukyu Islands. The information will be useful for: (1) numerical simulations predicting larval dispersal pathways by particle tracking through provision of the input parameter for the timing of larval release, (2) selecting times for larval sampling in the field in empirical early life history studies.

Key words: *Acanthaster planci*, coral reefs, Ryukyu Islands, spawning
Kuroshio Current, which is thought to transport *A. planci* larvae from the Ryukyu Islands to the north (Yamaguchi 1986, 1987). Population genetic data derived from highly polymorphic markers also support the secondary outbreak hypothesis through the Ryukyu Islands (Yasuda et al. 2009). The archipelago lies within the track of the Kuroshio and its associated current, and throughout these islands and other parts of Japan there is genetic homogeneity among crown-of-thorns starfish populations, suggesting possible secondary outbreaks.

For prediction and understanding of secondary outbreak phenomena, it is essential to know when and where large numbers of larvae are released as plankton and how they are subsequently dispersed by ocean currents. A number of studies have investigated larval dispersal in *A. planci* using tools ranging from numerical simulation (Dight et al. 1990a, b, Black & Moran 1991) to sampling of larvae in the field (reviewed by Birkeland & Lucas 1990). For all of these methods, information on spawning period is an absolute requirement. Predictions of larval dispersal by oceanographic modelling vary greatly with parameter inputs for reproductive timing and location (Cowen 2002). For *A. planci* in particular, empirical study of larval dispersal, ecology and dynamics also requires accurate knowledge of the timing of spawning, because the occurrence of the planktonic larvae is localized in time and space; short sampling program that is not focused on the peak breeding season may miss the larvae when they are in the water column (Birkeland & Lucas 1990, Yasuda et al. unpubl).

Because of its importance, knowledge of the spawning period of *A. planci* has been accumulated (Moran 1986, Birkeland & Lucas 1990, Idip 2003). However in Japan, spawning periods have been studied only off Okinawa main island and Iriomote Island in spite of the wide distribution of this species. *A. planci* in the Ryukyu Islands spawns in summer, but islands at different latitudes have different peak spawning periods, possibly due to the difference in water temperature; spawning occurs between late June and early August off Okinawa main island, and in June off Iriomote Island (Yokochi & Ogura 1987, Yamazato & Kiyan 1973). To better understand larval dispersal pattern and subsequent adult outbreaks, information on peak spawning periods of *A. planci* along the track of the Kuroshio Current is of great importance.

In this context, we examined the peak spawning time of *A. planci* using gonad observation together with water temperature that is possibly the most important cue for spawning of *A. planci* (Lucas 1984, Birkeland & Lucas 1990) at five latitudinally different locations (between latitudes 24°N and 28°N). The data enable us to discuss the following: (1) methods for assessing the spawning peak in this species; (2) The relationship between water temperature and peak spawning period of *A. planci*; and (3) spawning data as a basis for assessing larval dispersal of *A. planci*.

### Materials and Methods

#### Collection of *A. planci* specimens

We sampled *Acanthaster planci* from five locations in the Ryukyu Islands: Amami Ohshima Islands (28°06'59"N, 129°15'50"E), Kerama Islands (26°10'58"N, 127°18'21"E), Okinawa main island (26°30'60"N, 127°21'27"E), Miyako Islands (24°59'42"N, 125°16'02"E) and Sekisei Lagoon (24°16'85"N, 124°04'99"E) (Fig. 1). The sampling was conducted by scuba diving at depths of 1 to 20 m.

*Acanthaster planci* is gonochoristic (Lucas 1984). The sex ratio is approximately 1:1 in large wild populations (Person & Endean 1969). From 2 to 12 adult individuals with an average of 5.5 (±1.48 S.D.) of each sex were collected at approximately two-week intervals from 10 May, 29 Oct in 2004 (Table 1). Only off Okinawa, we repeated
this examination from 10 June, 26 Aug in 2005. We collected specimens larger than 200-mm diameter as far as possible, as this is the typical size of sexual maturity in the wild (Birkeland & Lucas 1990).

Gonad observations

Acanthaster planci populations often have protracted spawning periods (Babcock & Mundy 1992, Okaji 1991) and the species is also known to spawn repeatedly during reproductive peaks (Birkeland & Lucas 1990). In the laboratory, the starfish sometimes releases gametes from gonopores on only a few arms, and specimens with partially released gonads have been found in the wild (Babcock et al. 1994, Birkeland & Lucas 1990). The gonads occupy the proximal regions of the arms and extend further down toward the tips. We used the following standardized method to examine the peak spawning periods at 5 different locations. First, we dissected the roots of three arms separated by intervening arms. Then, we took close-up photographs of the dissected animals. We measured total diameter, and recorded sexual and developmental stages. Gonads were classified into three developmental stages: (1) “pre-spawning”, (2) “partially spawned” and (3) “post-spawning” (Fig. 2). In (1) “pre-spawning” stage, all disected arms were fully occupied by gonads and all gonad lobes were of similar large sizes. (2) “Partially spawned” was characterized by a decrease in gonad volume following release of sperms and eggs; ovarian bursae were of irregular sizes. In (3) “post spawning” stage, all of the dissected arms had lost most of their gonads and only a few shrunken lobes remained. According to Babcock & Mundy (1992), once this species moves into the peak spawning period, the gonad index declines dramatically. Therefore, we designated the peak spawning period as the point in time when more than half of the males and females had started spawning.

Changes in water temperature

To investigate the relationship between gonad development and water temperatures, we deployed temperature loggers (HOBO Water Temp Pro Onset, Japan) at 10 m depth near each sampling site (Fig.1) from May to October throughout the survey period in 2004 and May to end of July in 2005. We chose 10 m depth because A. planci was collected at depths of 1 to 20 m in this study and 10 m was the centre of the distribution range. In addition, water temperature at 10 m depth is relatively stable compared to surface temperature and thus indicates a more representative temperature at each site.

Results

Collected specimens

A total of 379 samples were collected (Table 1). The average diameters and numbers of specimens at each location were 25.0±5.1 cm (mean±S.D.) off Amami Oshima (n=70), 23.8±3.3 cm off the Kerama Islands (n=50), 24.3±3.3 cm off Okinawa main island (n=62) in 2004 and 25.6±5.8 cm (n=49) in 2005, 26.7±3.74 cm off the Miyako Islands (n=88) and 26.6±4.36 cm in Sekisei Lagoon (n=60). Kruskal-Wallis test indicated Okinawa specimens were significantly smaller than the other specimens.

Gonad observations

The time series of sequential observations of gonad de-
Development and changes in water temperatures smoothed to one-week moving averages are shown in Fig. 3. Off Amami Ohshima, all specimens collected in May (13 and 26 May 2004) were assigned to the (1) “pre-spawning” stage. (2) “Partially spawned” individuals were observed in 40% of the specimens from both sexes on June. The period 12–28 July was designated as the peak spawning period, as by 28 July all specimens were either (2) “partially spawned” or (3) “post-spawning”. The water temperature rose steadily from 24°C to 29°C from mid June to early August, and dropped after the end of August. The peak spawning period was estimated to have begun when water temperature had risen to 27°C to 28°C (Fig. 3).

Off Okinawa main island, there were no observable (2) “partially spawned” females at the end of May in 2004, whereas 60% of males had (2) “partially spawned” stage at this time (25 May). On June 7, 20% of females were at the (2) “partially spawned” stage, but all the males were at the (1) “pre-spawning” stage. Hence, spawning had already started in some individuals before the peak spawning period. Subsequently frequency of (2) “partially spawned” stage increased for both male and female on 28 June. Then, peak spawning period started between 21 and 27 July as all specimens on 27 July were either (2) “partially spawned” or (3) “post-spawning”. Seventy percent of specimens from both sexes were at the (3) “post-spawning” stage by September 20. The water temperature off Okinawa main island rose from 25°C in mid June to 29°C at the end of July, and then gradually decreased. Peak spawning began when the water temperature rose to around 28°C. In 2005, all the female specimens were at the (1) “pre-spawning” stage on both 10 and 24 June, whereas half of the male specimens were (2) “partially spawned” on 10 June but all the male specimens were (1) “pre-spawning” on 24 June. On 11 July, a majority of both male (3 out of 5) and female (4 out of 6) specimens were at the “partially spawned” stage, indicating that peak spawning started between 24 June and 11 July. Seventy percent of specimens from both sexes were (2) “partially spawned” on 22 July and 30% of specimens from both sexes became (3) “post-spawning” on Aug. 26. In 2005, the water temperature gradually rose from May to middle August. When we detected the initiation of peak spawning in early July, the water temperature just exceeded 28°C.

Off Kerama Islands, on 25 May, 80% of males had (2) “partially spawned” gonads suggesting that the majority has started spawning, but all of the females were at the (1) “pre-spawning” stage. Here, we could not find synchronization of sexual maturation. However, all males were (1) “pre-spawning” while only one of 6 females were at the (2) “partially spawned” stage on 17 June, suggesting almost synchronized sexual maturation this time. On 15 July, all the male and female specimens were at the “partially spawned” stage. Therefore, the spawning peak began between June 17 and July 15 when the water temperature rose to around 27°C to 28°C. On 21 Sep, all the female and 80% of males were at the (3) “post-spawning” stage. The water temperature transition off Kerama Island was comparable to that off Okinawa main island with slight fluctuation.

Off Miyako Islands, (2) “partially spawned” stages were observed in four of nine females on 10 May, but none of the males had started spawning. Nine out of 17 and 12 out of 20 specimens from both sexes were (2) “partially spawned” on 25 May and 7 June, respectively. On 25 June, 30–40% of both sexes had already been (3) “post-spawning” and the rest of the specimens were all at the (2) “partially spawning” stage. Therefore, the peak spawning period might have started around early to late June (between 7 and 25 June). On 29 Oct, possible redevelopment of gonads was observed for both sexes. The water temperature once reached up to 28°C in early June, and then suddenly dropped to 27°C due to a typhoon. The water temperature

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**Fig. 2.** Gonad development stages in *Acanthaster planci*. 

- **Male**
  - Pre-spawning
  - Partially spawned
  - Post-spawning

- **Female**
  - Pre-spawning
  - Partially spawned
  - Post-spawning

5 cm
Fig. 3. Trend of gonad development (left female, middle male) with changing one-week moving average water temperature (right) in 2004 and 2005. Shadowed areas indicate 26–30°C. Possible redevelopment was detected only on 29 Oct in Miyako.
reached 28°C again around the end of June and recorded the highest temperature (29°C) around early August. Then, the water temperature fluctuated around 27°C until the end of September. The spawning peak began when the water temperature reached around 28°C.

In Sekisei Lagoon, 40% of both female and male specimens were already at the (2) “partially spawned” stage on 13 May, indicating spawning had started before our investigation. Since nine out of ten specimens from both sexes were (2) “partially spawned” by 26 May, the peak spawning period started between 13 and 26 May. Until early July, all specimens were at the (2) “partially spawned” stage, and on July 10, 30% were in the (3) “post-spawning” stage. Water temperature exceeded 28°C in mid May, but suddenly dropped in mid June due to a typhoon, after which it gradually rose and remained above 28°C until mid August. The spawning peak started around the time when water temperature rose to ca. 28°C.

Thus, in Sekisei Lagoon, our southernmost site, spawning was already underway in some specimens collected in mid May. At our northernmost site, Amami Ohshima, all of the specimens at that time were filled with matured gonads (no gonad reduction was observed), indicating all the specimens that were (1) “pre-spawning”. The further to the north the more spawning peak was delayed. Peak spawning first started in late May 2004 in Sekisei Lagoon followed by Miyako Islands (late June), Kerama Islands (mid July), and Okinawa Island and Amami Ohshima (late July), the northernmost sites. In all cases, initiation of peak spawning was coincident with the elevated water temperature (ca. 28°C). Our data also indicated that the spawning period is longer at lower latitudes than at higher latitudes. It took almost three months before 80% of starfish were (3) “post-spawning” in Sekisei Lagoon, whereas it only took one month off Amami Ohshima (Fig. 3).

Discussion

We examined the timing of spawning of Acanthaster planci and its correlation with water temperatures at five latitudinally different areas in the Ryukyu Islands. A standardized, very simple method made it possible to sample and examine A. planci spawning at different sites separated by more than 700 km at the same time, making this a novel study. We are able to use our data to discuss (1) the relationship between water temperature and peak spawning period of A. planci, (2) methods for assessing the spawning peak in this species, and (3) applications to reveal larval dispersal of A. planci.

The relationship between water temperature and peak spawning period

The peak spawning of A. planci began when water temperature exceeded ca. 28°C throughout islands distributed across the Ryukyu archipelago. This threshold is in accord with what is known of the narrow temperature tolerance of the larval stages in this species. No cultured larvae develop beyond bipinnaria above 24°C and few reach the brachioralia stage at 26°C. Larvae die rapidly at 32°C (Lucas 1973). Thus, 28°C is a median temperature for larval survival (26–30°C). These temperature tolerance attributes also help explain our observation that the spawning period is short at higher latitude where suitable temperatures prevail for fewer months than at lower latitude. Indeed, previous studies on reproductive timing in A. planci (summarized in Table 2) have generally shown approximately synchronous gametogenesis at higher latitudes where seasonal fluctuation of water temperature is obvious (reviewed Birkeland & Lucas 1990). At lower latitudes in Guam, where water temperature is higher than 28°C for most of the year, gametogenesis is prolonged and less synchronized (Cheney 1974) whereas in Palau, spawning depends on monsoon when the water temperature exceeds 29–32°C (Ipip 2003).

It is also likely that the peak spawning period changes from year to year at each locality following inter-annual variation in water temperature. The peak of spawning off Okinawa main island was between 21 and 28 July in 2004, whereas in 2005 the peak was between 24 June and 11 July. In 2004, the water temperature first exceeded 28°C in mid July, but in 2005 temperature exceeded 28°C in early July, which likely explains spawning peak differences between the years and suggests that water temperature is the primary factor controlling the spawning of A. planci.

There are many other environmental factors that may influence the timing of spawning in echinoderms, viz. lunar cycle (Holothuria scabra (Jaeger), Mercier et al. (2000)), photoperiod (Coscinasterias muricata (Verrill), Georgiades et al. (2006), Pisaster ochraceus (Brandt), Pearse & Eernisse (1982), Asterias amurensis (Lüken), Byrne et al. (1997), Odontaster validus (Koehler), Pearse and Bosch (2002)), diet (Echinocardium cordatum (Pennant), Nunes & Jagoux (2004)), salinity (Allostichaster capensis (Perrier), Rubilar et al. (2005)) and temperatures (Stichopus japonicas (Selenka), Tanaka (1958), Holothuria atra (Jaeger), Holothuria edulis (Lesson), and Stichopus chloronotus (Brandt), Uthicke (1997)). In laboratory experiments, Lucas (1973) showed that lunar cycle does not influence the spawning of A. planci, but that it is regulated by either water temperatures and/or photoperiods. Subsequently, Lucas (1984) further confirmed that A. planci spawns regularly synchronizing with the water temperature fluctuation under an environment where there is no exposure to natural light or photoperiod. In the field observation, Babcock & Mundy (1992) reported that of A. planci demonstrated no clear evidence that lunar cycle or photoperiod are spawning cues. Other field observations also appeared to be any invariable tidal, lunar, or diel timing of spawning events (summarized in Birkeland & Lucas 1990). Our results further confirmed the importance of water temperature (28°C) for peak spawning of the species.

Then, what is the meaning of spawning around 28°C for
A. planci? Firstly in addition to the fact that it is the most suitable temperature for the A. planci larva itself, the impact of phytoplankton production in the coral reef area is greatest during the summer months when the water temperature is beyond 28°C in both Great Barrier Reef (Furnas et al. 1990) and Okinawa (Toda et al. 2003). Therefore, larval food for A. planci increases during summer and may assist growth and survival of A. planci larvae for their crucial life stage. Indeed, many other reef organisms spawn during the summer months (Johannes 1978) and enriched larval food natal reefs are suitable for growth and survival of such larvae (Furnas et al. 1990). Another possible reason is that summer is suitable for adult A. planci to spawn, because growth speed of corals is fastest in summer (Bak et al. 2009) and more abundant foods are available for adult A. planci during summer. With abundant food, adult A. planci may be able to invest a larger amount of energy in reproductive outputs.

Methods of assessing spawning peak in A. planci

Spawning periods of A. planci have been studied using different methods, i.e. gonad condition or histology, change in gonad index, field observation of spawning, change in oocytes size/frequency distribution and changing proportion of ripe and spent gonads (summarized in Birkeland & Lucas 1990). In this study, initiations of peak spawning were defined when more than half of each sex started spawning, because gonad index has been reported to decline dramatically once peak spawning is underway.
(Babcock & Mundy 1992). Gonad observation is very simple, and does not require special equipment or techniques. Although gonad observation is not as quantitative as the gonad index, the peak spawning periods estimated in this study gave results comparable to those of previous studies that utilized gonad indices (Branham et al. 1971, Cheney 1974, Yokochi & Ogura 1987, Babcock & Mundy 1992).

However, we should keep in mind that it is sometimes difficult without histological examination to distinguish a partially spawned gonad from developing gonads and redeveloping gonads. Relatively large gonads were found in the three samples (two female and one male) collected in late October off Miyako Islands. Given that (1) most of the specimens collected were spent by the end of September and (2) intense gametogenesis of *A. planci* generally occurs at 22°C or higher (Birkeland & Lucas 1990), these relatively large gonads might be due to redevelopment of gonads, whereby gametogenesis proceeds in parallel with spawning. Further studies including histological examinations will be required to assess possible minor spawning periods off the Ryukyu Islands in fall (October). However, both developing/redeveloping and partially spawning specimens have gonads slightly smaller than fully ripe ones. To avoid developmental stage misclassification, it is important to look for the presence of irregularly sized oocytes and an irregular distribution of gonads. Histological data show that starfish with partially spawned gonads have irregularly sized oocytes and an irregular distribution of gonads, whereas developing gonads have regular shapes (data not shown).

**Applications to reveal larval dispersal of *A. planci***

The spawning periods determined here will be useful for modeling studies in which the timing of larval release is a required input parameter for particle tracking in numerical simulations. Recent advances with the high resolution oceanographic simulation model JCOPE (Japan Coast Ocean Predictability Experiment) (Kagimoto et al. 2008) hold great promise in understanding larval dispersal and possible propagation of outbreaks across the southern Japanese islands.

The findings will also be useful in planning any larval sampling program designed to reveal the distribution of *A. planci* larvae. Although many researchers are aware of the importance of the larval ecology, attempts to carry out field programs on the planktonic phases of *A. planci* have had limited success because the larvae are rather patchy in time and space (Birkeland & Lucas 1990). The first prerequisite in a field survey to examine the distribution of *A. planci* larvae is prior information on the initiation of peak spawning period. This study demonstrated that the spawning peak of *A. planci* across the Ryukyu Islands is predictable by monitoring temperatures.

Our method of gonad observation is likely the simplest way for determining spawning peak in future studies elsewhere. By monitoring water temperature and using gonad observation, we can predict the best timing for larval sampling.

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