

Reproductive patterns of fungiid corals in Okinawa, Japan

Yossi LOYA^{1,*}, Kazuhiko SAKAI², and Andrew HEYWARD³

¹ Department of Zoology, Tel Aviv University, Tel Aviv, Israel

² Tropical Biosphere Research Center, Sesoko Station University of the Ryukyus, Okinawa, Japan

³ Australian Institute of Marine Science, Perth, Australia

* Corresponding author: Y. Loya

E-mail: yosiloya@post.tau.ac.il

Communicated by Makoto Tsuchiya

Abstract The reproductive modes of corals in the family Fungiidae are relatively poorly known. In this study we document the findings over five years of observations of various reproductive traits and seasonal reproductive patterns of 12 species of mushroom corals from northern Okinawa. We provide new records with respect to sexuality and mode of reproduction for six species: *Ctenactis crassa*, *Fungia paumotensis*, *F. scruposa*, *F. granulosa*, *Halomitra pileus* and *Sandalolitha dentata*. Furthermore, we indicate two new species that change sex (*C. crassa* and *F. scruposa*), as well as identify *F. fungites* in Okinawa as a gonochoric brooder. We estimate the reproductive effort of *C. echinata*, *C. crassa* and *F. repanda* for the months of July and August of the years 2007–2009, discuss their diurnal rhythms, degree of spawning overlap and the potential for hybridization vs. temporal reproductive isolation in these species. We conclude by highlighting the fungiids as ideal model organisms for studies of reproductive ecology, larval development and the evolution of life-history traits.

Keywords coral reproduction, Fungiidae, sex change, reproductive isolation, life-histories, hybridization

Introduction

Despite intensive studies and increasing knowledge over the last three decades of the various reproductive modes in scleractinian corals (see reviews in Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990; Baird et al. 2009), we are still far from recognizing the large variety of this group's reproductive traits.

Observations of coral reproduction have seen a progression in perspective, from the classic presumption of internal fertilisation followed by release of planulae larvae (Hyman, 1940), through a renaissance during the 1980s in which broadcast spawning of gametes became the most common pattern observed (Harrison et al. 1984; Schlesinger and Loya 1985; Babcock et al. 1986; Heyward et al. 1987; Hayashibara et al. 1993; Schlesinger et al. 1998), to the present, in which diversity of reproductive modes, including sex reversal and various methods of asexual propagation, have all been observed as part of the modern reproductive vista in many coral communities (Loya and Sakai 2008; Baird et al. 2009).

In southern Japan, Yamazato's early observations (Yamazato et al. 1975, 1981) of seasonal breeding and likely external fertilisation in the soft coral *Lobophytum crassum* and stony coral *Goniopora* sp., ushered in a renewed focus on coral reproduction in that region, which led to

the documentation in 1987 of broadcast spawning in 18 species of corals at Sesoko Island, in northern Okinawa (Heyward et al. 1987). Subsequent assessment of corals over summer at the Kerama Islands, beginning in 1989, extended the list of Japanese broadcast spawning corals to more than 85 species and confirmed the pattern of summer broadcast spawning in the region (Hayashibara et al. 1993). The Acroporiidae and Faviidae, dominant and sub-dominant components of most Okinawan reefs, were well represented in the original and subsequent research. However, reproduction in some Families, including the Poritiidae, Agariciidae, Mussiidae and Fungiidae, was documented with scant information, often limited to single observations on 1–2 species (see Heyward et al. 1987; Hayashibara et al. 1993; Richmond and Hunter 1990).

The decline in the abundance and diversity of corals on the fringing reefs of Okinawa over the subsequent two decades, attributed to *Acanthaster* predation, elevated turbidity and bleaching (Nishihira and Yamazato 1972; Nishihira 1987; Yamaguchi 1986; Yamazato 1981; Loya et al. 2001) has been reflected in a significant local loss of originally abundant coral species and in some cases entire coral communities.

In northern Okinawa today it seems that many of the long-term survivors of these environmental changes are species from those families that received the least attention in the pioneering studies of coral reproduction. The Fungiidae (mushroom corals), long known to demonstrate tolerance to thermal stress and sedimentation (e.g. Hoeksema 1991), are a notable example and remain abundant on many northern Okinawan reefs, where other taxa have greatly declined or became locally extinct (see Loya et al. 2001).

Fungiids are solitary, largely single-polyped, “free-living” species, which differentiates them from the majority of scleractinians, which are sessile, colonial species. They are commonly regarded as synchronous spawners that depend on external fertilization for sexual reproduction (see reviews by Fadlallah 1983; Richmond and Hunter 1990; Harrison and Wallace 1990; Baird et al. 2009).

The reproductive modes of corals in the family Fungiidae are relatively poorly known (Abe 1937; Krupp 1983; Kramarsky-Winter and Loya 1998; Loya and Sakai 2008). They are a globally distributed group of stony

corals that lend themselves to experimental manipulation, due to their resilience, and ease of non-destructive collection and handling. In this study we document, the findings over multiple years of observation, pertaining to the reproductive traits of 12 species of mushroom corals from northern Okinawa. The study seeks to add to the basic biological knowledge of this important stony coral group, and also to demonstrate their utility for future research into coral reproduction and life-histories.

Materials and methods

During the initial stages of the research, and as part of a wider research scope aimed at studying reproductive strategies in the Fungiidae, in June 2004 we haphazardly collected 10–20 individuals of 12 fungiid species belonging to 5 genera (see Fig 1a, b) from a patch reef near Sesoko, Okinawa, Japan, (26.395°N; 127.522°E). The site is inhabited by tens of thousands of specimens densely distributed between 3–16 m depth (Loya and Sakai 2008). The fungiid species were transferred to the laboratory and placed in five 2 m³ running seawater containers. Each sampled coral was tagged individually with a numeric plastic tag attached to it by a nylon fishing cord inserted through a thin hole drilled at the edge of the coral skeleton with a portable dental drill. No adverse effects on the corals were observed due to the tagging procedures. After two weeks of acclimation in the large running-seawater containers, each coral was placed in an individual 40 × 20 × 20 cm aquarium, all of which were then placed in the large containers. The study started on 3 July, 2004 (full moon). We began nightly observations of the corals for possible spawning from 17:00 until a few hours after dawn, for eight consecutive nights (after closing the sea water supply and lowering the water level in the large containers to approximately 5 cm below the aquaria level, thus isolating each individual coral in a separate aquarium).

We recorded the sex of each individual coral by noting the unique shape of the shed gametes. Aquaria with opaque, cloudy water contained males and those with numerous tiny “granules”, creating a foamy-like surface after 3–4 hours, contained females. Aquaria with trans-

parent water contained corals that did not release gametes (see photos in Loya and Sakai 2008). We verified our observations using microscope preparations of the gametes. In the morning we renewed the running-sea-

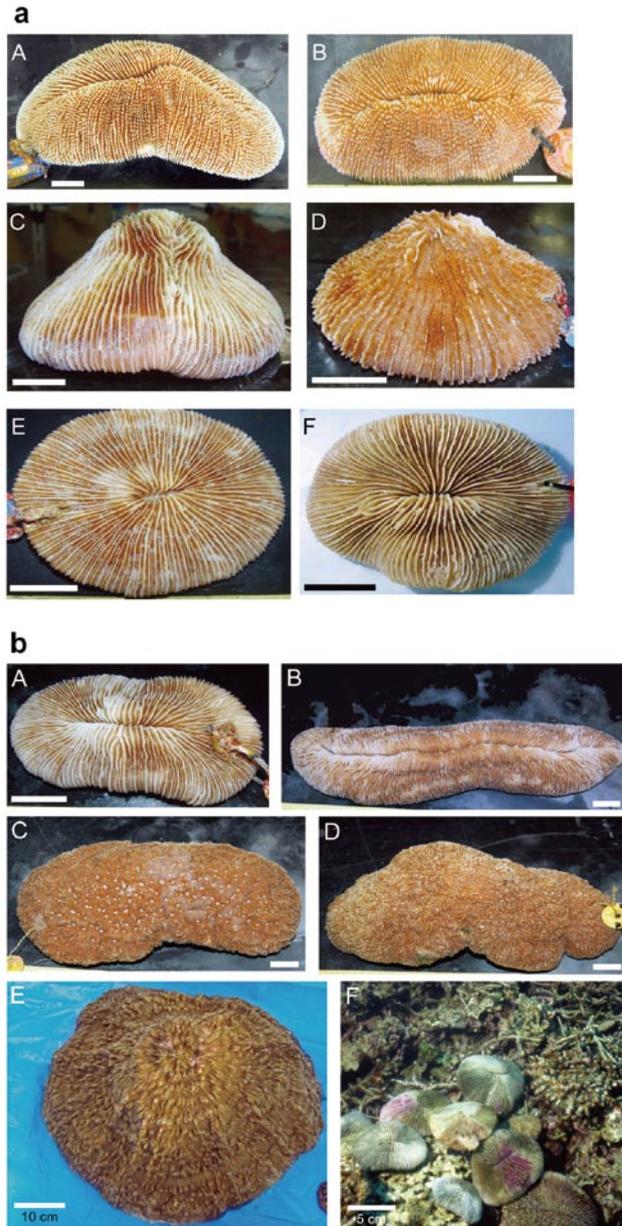


Fig. 1 Photographs of the fungiid species studied during 2004–2009 at Sesoko, Okinawa, Japan. In all photos the scale bar = 2.5 cm unless otherwise indicated. **a** (A) *Ctenactis echinata*, (B) *C. crassa*, (C) *Fungia repanda*, (D) *F. scruposa*, (E) *F. concinna*, and (F) *F. granulosa*. **b** (A) *Fungia paumotensis*, (B) *Herpolitha limax*, (C) *Sandalolitha dentata*, (D) *Sandalolitha robusta*, (E) *Halomitra pileus*, and (F) an aggregation of *Fungia fungites* at 5 m depth, Sesoko, Okinawa

water supply. Similar procedures and observations were repeated during August 2006, June–August, 2007, July and August 2008 and June and July, 2009. The fungiid species observed during these periods were *Ctenactis echinata*, *C. crassa*, *Fungia repanda*, *F. scruposa*, *F. concinna*, *F. granulosa*, *F. paumotensis*, *F. fungites*, *Sandalolitha robusta*, *S. dentata* and *Halomitra pileus* (Fig. 1a, b). Species identification was mainly based on Hoeksema (1989), as well as on Veron and Pichon (1980) and Veron and Stafford-Smith (2000).

As a result of the sex change exhibited by *Fungia repanda* and *Ctenactis echinata*, first observed during their breeding period of August 2006 (Loya and Sakai 2008), we subsequently increased the sample sizes of these species and in addition that of *C. crassa* and *F. scruposa*, due to their relatively high abundance in the study area, in order to test the possibility of sex change in these species as well. After each annual set of observations the tagged corals were transferred back to their natural habitat and retrieved in June or July of the following year (i.e. ca. 2 weeks before the breeding season).

After the initial observations during 2004, we continued sampling and observing the spawning patterns of all 12 species, following the full moons of 2007 (30th June, 30th July), 2008 (18th July, 17th August), 2009 (7th July). No observations were carried out in August 2009. In addition, because virtually no spawning occurred during the 10 nights after the full moon (NAFM) of June 2004, 2006 and 2007 during subsequent years we concentrated on monitoring the corals after the full moons of July and August.

Results

Distribution and life-history traits

All the fungiids studied reside side by side on the reef in a patchy spatial distribution. Among these, *F. fungites* distinctly inhabits mainly the shallow reef flat to a depth of 4 m, and *H. pileus* the deeper, sandy bottom of the reef at 16–18 m depth. All other fungiid species have a similar depth distribution (3–16 m depth). Some individuals were observed in narrow crevices with low illumination, while others resided in well-illuminated areas of the reef; some

were partially buried in sand, some were situated upside down, and a few were partially injured, but the majority of individuals appeared healthy. While many other coral species had died at this reef site during the 1998 catastrophic bleaching event in Okinawa (Loya et al. 2001), most fungiiids had survived.

Table 1 summarizes information on life-history traits of the fungiid species studied. It provides new records with respect to sexuality and mode of reproduction for six species: *Ctenactis crassa*, *Fungia paumotensis*, *F. scruposa*, *F. granulosa*, *Halomitra pileus* and *Sandalolitha dentata*. Moreover, it provides two novel observations indicating that:

- (1) *F. fungites* in Okinawa is a gonochoric brooder (Loya et al. unpublished), hence it exhibits a mixed mode of reproduction (i.e. releases gametes in the GBR and brood planulae in Okinawa, see Table 1). Baird et al. (2009) report that only 13 of a total of 111 scleractinian genera, for which records exist, contain species that both brood and spawn.

- (2) In addition to *C. echinata* and *F. repanda* which were reported for the first time in stony corals to change sex (Loya and Sakai 2008), *F. scruposa* and *C. crassa* also exhibit protandrous sex change, with the latter also displaying bidirectional sex change. This unique reproductive trait, so far reported to occur only in mushroom corals, is analogous to that of plants, which exhibit labile sexuality in response to energetic and/or environmental constraints.

Reproductive effort and spawning overlap

We estimated the reproductive effort (RE) (i.e. percentage of individuals releasing gametes at a particular month of a given year based on the total number of individuals releasing gametes in that year) of *C. echinata*, *C. crassa* and *F. repanda* for the months of July and August of the years 2004–2009. However, here we present the data only for 2007–2009 (Table 2), since the relatively small sample sizes observed in previous years did not allow for conclusive results. All three species

Table 1 Summary of information on life-history traits of fungiid corals observed during 2004–2009. Numbers in parentheses indicate the reference

Species	Colonial or solitary	Reproductive mode	Sexuality	Direction of Sex change
<i>Ctenactis echinata</i> (Pallas, 1766)	solitary	s (1)	g (1)	protandry, bidirectional (1)
<i>C. crassa</i> (Dana, 1846)	colonial	s (2)	g (2)	protandry, bidirectional (3)
<i>F. concinna</i> Verrill, 1864	solitary	s (4)	g (4)	
<i>F. fungites</i> (Linnaeus, 1758)	solitary	s (4)	g (4)	
<i>F. fungites</i> (Linnaeus, 1758)	solitary	b (5)	g (4)	
<i>F. paumotensis</i> Stutchbury, 1833	solitary	s (2)	g (2)	
<i>F. repanda</i> Dana, 1846	solitary	s (6)	g (1)	protandry (1)
<i>F. scruposa</i> Klunzinger, 1879	solitary	s (2)	g (2)	protandry (3)
<i>F. granulosa</i> Klunzinger, 1879	solitary	s (2)	g (2)	
<i>Halomitra pileus</i> (Linnaeus, 1758)	colonial	s (2)	g (2)	
<i>Herpolitha limax</i> Esper (1797)	colonial	s (7)	g (7)	
<i>Sandalolitha dentata</i> Quelch, 1884	colonial	s (2)	g (2)	
<i>S. robusta</i> (Quelch, 1886)	colonial	s (7)	g (7)	

s=Spawn gametes; b=Brood planulae; g=Gonochoric; (1) Loya and Sakai (2008); (2) this study; (3) Loya and Sakai (unpublished); (4) Willis et al. (1985); (5) Loya et al. (unpublished); (6) Baird et al. (2003); (7) Babcock et al. (1986).

spawned mainly 4–8 nights after the full moon (NAFM) of July and August, exhibiting various RE (Table 2).

C. echinata. This species exhibited high predictability (i.e. low variability, see Table 1) in its spawning time. In general, high RE values were recorded during the 5th and 6th NAFM of both months and all years (with one notable exception of the 6th NAFM of August 07, when a minimum RE of 4.6% was recorded). Highest RE was recorded during the 6th NAFM of July in the years 07, 08, 09 (65.1%, 57.1% and 40.4%, respectively). In 2008, during the 5th and 6th NAFM of July, *C. echinata* peaked with 54.7% and 57.1% reproduction, respectively.

C. crassa. This species greatly resembles *C. echinata*, except in its possessing multiple mouths. High RE were

recorded during the 6th NAFM of August 07 (72.2%) and July 08 (41.7%) and the 7th NAFM of July 08 (47.2%). Interestingly, whereas in July 07, during the 5th, 6th and 7th NAFM *C. crassa* did not release any gametes whatsoever, during the following year (2008) and at the same NAFM in July, its RE peaked during the 5th and 6th NAFM (see Fig. 2).

F. repanda. This species exhibited a clear preference to reproduce during the month of August with much lower RE during July. Thus, during the 5th and 7th NAFM of August 07 its RE peaked at 45.8% and 54.2%, respectively. Interestingly, during the 6th NAFM it dropped to 8.3%. During the 5th and 6th NAFM of August 08 its RE peaked at 48.1% and 37% and dropped to nil on the 7th

Table 2 Reproductive effort - RE_x* (i.e. percent individuals spawning in July or August based on the total number of **new** individuals spawning in both months) of *Ctenactis echinata*, *C. crassa* and *Fungia repanda* during 4–7 nights after the full moon (NAFM) of July and August of 2007, 2008 and 2009

Fungiid species	No. of NAFM	Reproductive effort (RE _x)					Av.	SD
		Jul 07	Aug 07	Jul 08	Aug 08	Jul 09		
<i>C. echinata</i>	4	2.3	13.9	0	11.9	46.8	15.0	18.8
<i>C. crassa</i>	4	11.1	2.7	0	22.2	64.5	20.1	26.3
<i>F. repanda</i>	4	0	18.8	0	3.7	8.3	6.16	7.8
<i>C. echinata</i>	5	34.8	30.2	54.7	33.3	51.1	40.8	11.2
<i>C. crassa</i>	5	0	5.5	19.4	16.7	35.5	15.4	13.8
<i>F. repanda</i>	5	0	45.8	0	48.1	4.2	19.6	25.0
<i>C. echinata</i>	6	65.1	4.6	57.1	52.4	40.4	43.9	23.7
<i>C. crassa</i>	6	0	72.2	41.7	33.3	16.1	32.7	27.3
<i>F. repanda</i>	6	2.4	8.3	33.3	37.0	29.2	13.4	15.6
<i>C. echinata</i>	7	30.2	18.6	7.1	11.9	0	13.6	11.5
<i>C. crassa</i>	7	0	27.7	47.2	8.3	3.2	17.3	19.9
<i>F. repanda</i>	7	8.3	54.2	3.7	0	20.8	17.4	22.0
<i>C. echinata</i>	n _x , N	33,43	24,43	23,42	24,42	47,47		
<i>C. crassa</i>	n _x , N	27,36	22,36	20,36	23,36	31,31		
<i>F. repanda</i>	n _x , N	10,48	45,48	10,27	21,27	24,24		

* RE_x = Reproductive effort in a given month (x); RE_x = n_x/N × 100. n_x = Number of individuals releasing gametes in July or August. N = Total number of new individuals releasing gametes in both months; i.e., individuals that spawned in both months were counted only once, thus n_x (< or = N); Av. = Average; SD = Standard deviation.

NAFM. During the 4th to 7th NAFM of July, throughout 2007–2009, *F. repanda* exhibited negligible RE (0–8%) except for the 6th and 7th NAFM of July 09 (29.2% and 20.8%, respectively).

Diurnal rhythms

Spawning overwhelmingly occurred during the night for nearly all species. During night observations, the general assemblage of fungiid species could be relied on

not to commence spawning for several hours after sunset. The earliest *F. repanda* and *C. echinata* colonies spawned was at 21:00 hrs; however, this was atypical and involved very few individuals. Major spawning activity for *C. echinata* and *C. crassa* was generally recorded in the period 22:00–00:30 hrs and most notably during the hour 22:30–23:30. *C. crassa* demonstrated very high intercolony synchrony, with a precise spawning time amongst separate individuals, while *C. echinata* tended to have a

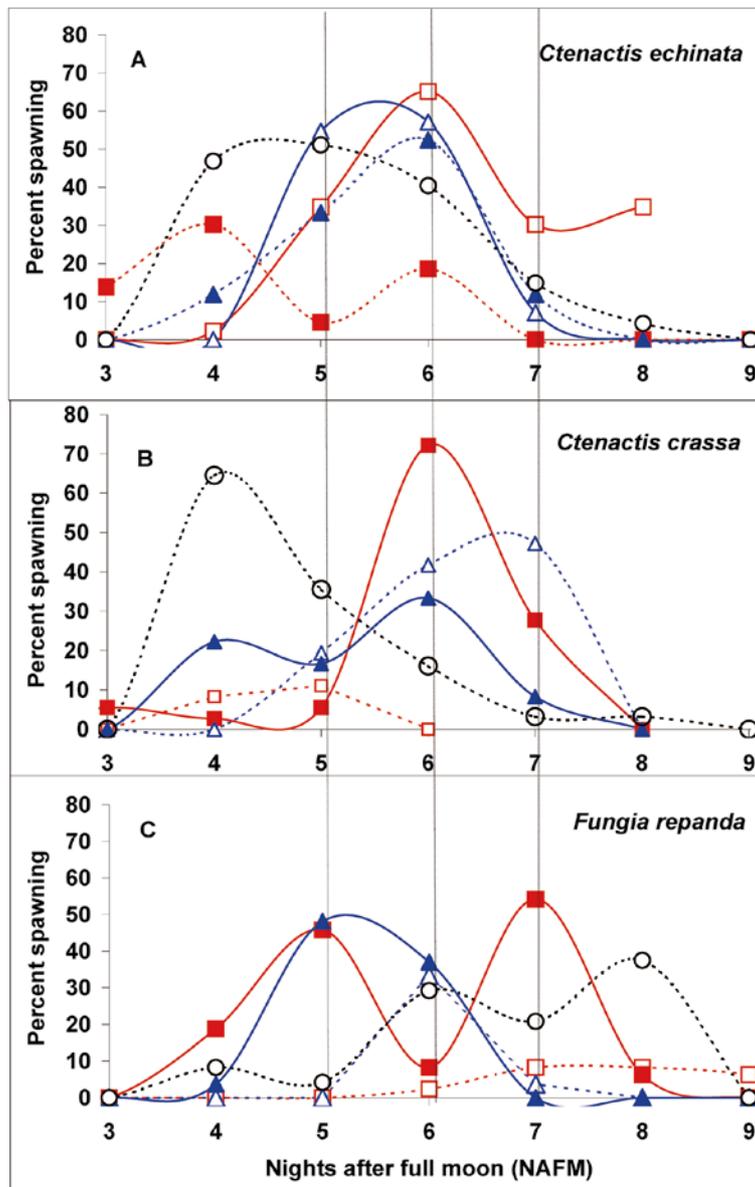


Fig. 2 Average percent spawning of the fungiid species: (A) *Ctenactis echinata*, (B) *C. crassa* and (C) *Fungia repanda* during 3–8 nights after full moon (NAFM) of July (full marks) and August (empty marks) of 2007 (red lines), 2008 (blue lines) and 2009 (black line)

broader spawning peak across more than an hour. Observations during 2007 and 2008 recorded a secondary peak of gamete release between 01:00–02:00 hrs in *C. echinata*. Although a few colonies of *F. repanda* did spawn earlier in the night, around the same time as the *Ctenactis* species, the major gamete release period was several hours later. In 2007 the major peak in spawning of *F. repanda* was ca. 05:00 hrs. In August 2008 *F. repanda* again displayed peak spawning activity in the early hours of the morning, mostly around 03:00 hrs. Effectively, *F. repanda*'s major spawning was temporally isolated from the two *Ctenactis* species.

In the three species with the largest sample sizes (*C. echinata*, *C. crassa* and *F. repanda*, see Table 2) spawning was observed over successive nights in both July and August. A few individual colonies of *C. echinata* were recorded spawning on up to four successive nights, although typically 15–35% of the cohort spawned on two successive nights and a single night of gamete release per individual was most common. The timing of gamete release largely overlapped the periods of reduced tidal flow, particularly during the initial spawning nights, closest to the full moon, when tidal range was greatest (see Fig. 3). For *C. echinata* and *C. crassa* the spawning

activity peaks were at or near the top of the tide, while for *F. repanda* the major spawning event occurred towards low tide (Fig. 3). Nonetheless, this association with periods of slack water became less pronounced during subsequent nights as tidal range decreased.

In *C. echinata*, within the cohort of tagged colonies there was increasing variation in the timing of spawning between individuals over three successive nights. During the 2007 and 2008 spawning seasons, the time of spawning in up to one third of the *C. crassa* individuals appeared to become later on each successive night. In essence, corals that spawned over two successive nights were recorded to spawn at 22:00–23:00 on the first night, while on the second night they released gametes as late as 03:00

Discussion

While the vast majority of scleractinian corals are out-crossing, simultaneous hermaphrodites, (Harrison and Wallace 1990; Hayashibara et al. 1993), all the species whose reproduction has been studied within the family Fungiidae (Table 1) have been reported to express only one sex throughout their life; thus these corals are either

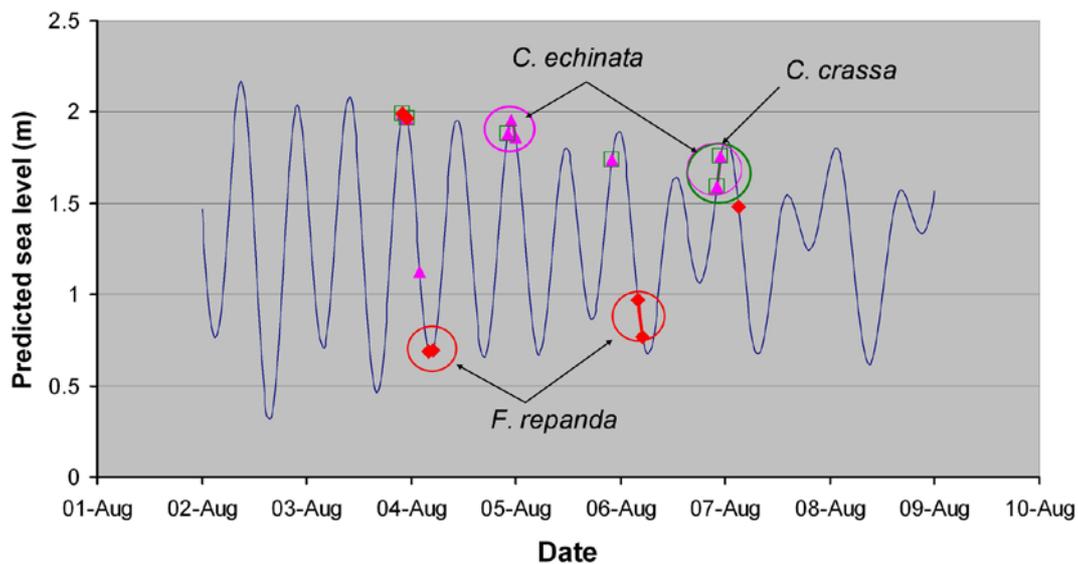


Fig. 3 Timing of major spawning nights for three fungiid species in August 2007 in relation to tide: *C. echinata* (purple triangles), *C. crassa* (green open squares) and *F. repanda* (red diamonds). Full moon was on July 30 (i.e. Aug. 1st was 2 NAFM, etc.). Circles indicate the time of the major spawning activity for each species. Predicted tidal heights were produced for the nearby port of Toguchi, according to methods of Pawlowicz et al. (2002)

male or female (i.e. gonochoric=dioecious) (Fadlallah 1983; Krupp 1983; Babcock et al. 1986; Harrison and Wallace 1990; Kramarsky-Winter and Loya 1998; this study). Some of these studies confirmed their conclusions by means of histological studies, verifying that in neither of the fungiids studied were male and female gonads found together prior to spawning (Krupp 1983; Kramarsky-Winter and Loya 1998; Loya and Sakai 2008). This observation rules out the possibility of cyclical hermaphroditism, as reported for three species of the deep-sea ahermatypic coral *Caryophyllia* (Waller et al. 2005).

Successful fertilization relies largely on a tight synchronization of conspecific gamete release. Asynchrony between species and discrete, narrow spawning times (synchrony) within species may be under strong selection to reinforce prezygotic reproductive isolation and reduce the likelihood of heterospecific gamete mixing, leading to hybridization (Gardner 1997; Fukami et al. 2003; Levitan et al. 2004). Overlapping spawning times, on the other hand, facilitate interspecific hybridization.

The extent of synchrony in gamete release during a spawning event could exert a major influence on population dynamics and population genetic structure through its effects on gamete and/or zygote dispersal, as well as on the genetic constitution of the gamete pool available for fertilization. Thus, for species complexes in which sibling species have extensive sympatric distributions, it can also play an important role in ongoing reproductive isolation and/or speciation.

Temporal reproductive isolation appears to be a matter of degree between fungiid species spawning in July and August at Sesoko. It is most clear between *F. repanda* and the two *Ctenactis* species (see Fig. 2), with major spawning peaks often separated by a matter of hours (e.g. Fig. 3). This is not to say that no overlap was observed, as particular individuals of *F. repanda* did have minor spawning periods simultaneously with *Ctenactis*, and even the temporal separation between major spawning periods was reduced to less than an hour in some years (data not shown). However, significant levels of fertilization are likely to require high levels of gamete concentration, favoring success between synchronously spawning nearest neighbors. Laboratory observations on broadcast spawning *Acropora* species (Heyward unpublished data), where

eggs and sperm were mixed together *in vitro* for varying periods after spawning, suggest that significant fertilization occurs within the first 10–15 minutes, and possibly even sooner as in the case of fungiids that do package their gametes at spawning. Consequently, even without factoring any possible recognition/compatibility constraints on hybridization, the tendency for conspecifics to aggregate and spawn in close synchrony suggests that during minor spawning overlaps between species there is a lower probability of success than cross-fertilization. These factors may particularly come into play with the two *Ctenactis* species. Our observations over multiple years indicate that *C. echinata* has a major spawning period in July, but the level of spawning in August is still significant. In some years there was temporal separation of spawning between *C. echinata* and *C. crassa*, achieved by a major spawning of one or the other species happening on different nights or in different months, e.g., *C. echinata* 6 NAFM Jul 07 and *C. crassa* 6 NAFM Aug 07, or *C. echinata* spawning on its own on the 5th and 7th NAFM in Jul 07, etc. Nonetheless, there were plenty of significant spawning events of both species on the same nights, such as on 6 NAFM of Jul and Aug 08 and 4 NAFM in Jul 09 (see Table 2). Figure 3 shows overlap in spawning between *C. echinata* and *C. crassa* on all four nights in August 07, but for the first three nights this overlap involved only a single spawning colony of *C. crassa*, with up to 13 colonies of *C. echinata* spawning in synchrony on one of those nights. Effectively, August 4th, the 5th night after the full moon, was a major spawning event for *C. echinata*, with little potential for hybridization from *C. crassa*. Nonetheless, during some nights there was a high level of temporal overlap with the peak spawning time of *C. crassa* and *C. echinata*, such as recorded on August 6th (see Fig. 3). Consequently, there would appear to be a high potential for hybridization between these two congeners. To some extent the very tight spawning synchrony exhibited by *C. crassa* may favour successful cross fertilization, but further research is required in order to assess the potential for hybridization between these two species, along with their spawning behavior and spatial distribution in the field.

In this respect, one should note the study of Gittenberger et al. (2006), who analyzed DNA samples from

fungiid corals in order to reconstruct the phylogeny of the Fungiidae. Although their molecular phylogeny reconstructions largely reflected that based on morphological characters by Hoeksema (1989), they did find some distinct differences. Noteworthy is *C. crassa*, which appears in various cladograms, based on different markers, in separate positions away from its congeners. Gittenberger et al. (2006) suggest that this may have been caused by one or more bottleneck events in the evolutionary history of this species, which resulted in a much faster average DNA mutation rate in *C. crassa* as compared to the other fungiid species.

Sequential spawning on 2–4 nights and over multiple months, together with the strong association of gamete release with minimal tidal flows, may be particularly important for these species. The males appear to produce large volumes of sperm, like *Acanthaster planci* (Babcock et al. 1994), which has been shown in the field to achieve high levels of fertilization at a distance of 8 m, and significant fertilization at several tens of meters separation. For the Okinawan fungiid corals used in the present study, high volume sperm release, in combination with the tendency to aggregate and the high degree of synchrony exhibited by both males and females, should ensure significant fertilisation success.

Unlike most hermaphroditic broadcast spawning species, which release gametes as strongly buoyant packages, the gonochoric fungiids release their gametes as a cloud. The eggs, which in the present study typically ranged in diameter between 100–150 μm , are smaller than the oocytes measured for most other coral families (e.g. Babcock et al. 1986). Perhaps as a consequence of size or due to differences in lipid content, the fungiid eggs exhibited little or only very weak positive buoyancy. Small oocyte size with weak or even negative buoyancy has also been reported for other fungiids (see Krupp 1983). They were easily mixed into the water column and consequently would be unlikely to form surface slicks.

In the field, released fungiid eggs and sperm are both likely to slowly mix throughout the water column, with concentrations being initially highest near the seabed in the immediate vicinity of the spawning adults. Laboratory evidence for hermaphrodite coral spawners indicates that the highest levels of fertilization success require an order

of 10^5 – 10^6 sperm per ml (e.g. Oliver and Babcock 1992), with an exponential decrease in fertilisation success as sperm concentration decreases to 10^4 /ml or less. It seems clear in corals and other broadcast-spawning species that gamete dilution is an important factor in the field during natural spawning. Selection for high gamete concentrations would favour high levels of spawning synchrony and timing of release at periods of reduced water movement. Both of these attributes are demonstrated by the fungiids, but with some differences between the species. *C. echinata* tended to spawn closest to slack high water and demonstrated good intercolony synchrony, but in this study it also exhibited spawning over 3–4 nights and broader spawning windows each night than *C. crassa* and *F. repanda*. Both the latter had a tighter window of intercolony spawning synchrony and one or two main nights of activity in July or August. During a particular lunar cycle each species had one or two nights that were the major spawning time, but spawning did occur at other times on the same or different nights for smaller numbers of individuals, and overlap of spawning did occur between species. Oliver and Babcock (1992) noted for other broadcast spawning coral species that on nights when only small numbers of corals spawned, the fertilization potential was much lower than on major spawning nights. A similar situation is also likely to occur in the field with the Okinawan fungiids, in which minor spawnings and inter-specific overlap in timing result in reduced fertilization or potential hybridization, and cross-fertilization success is principally achieved during the key periods of major spawning for each species.

In summary, fungiid corals exhibit a large array of biological traits that make them ideal model organisms for studies of reproductive ecology, larval development and the evolution of life-history traits: they are a globally-distributed group of stony corals that lend themselves to easy experimental manipulation, due to their hardiness and ease of non-destructive collection and handling; they demonstrate predictable spawning cycles and ontogenic pathways typical of broadcast-spawning corals and relative plasticity of sexual reproduction (e.g. the ability of some species to repeatedly change sex), which is similar to some dioecious plants displaying labile sexuality in response to energetic and/or environmental constraints,

as well as their ability to reproduce asexually; and the potential occurrence of hybridization and/or recent reproductive isolation, as well as sibling species, all provide a range of intriguing questions for future research. Many questions remain, but a critical mass of research in several areas (reproductive ecology, spawning mechanisms, molecular markers, and population genetics) is generating the tools and the conceptual basis necessary for future advances in our understanding.

Acknowledgments

This paper is dedicated to the late Professor Kiyoshi Yamazato, our *sen sei*, colleague and most of all very dear friend. This work was supported by a fellowship to Y.L. and A.H. from the Japanese Ministry of Science, Education, Culture and Sports (Foreign Visiting Professor) at the Tropical Biosphere Research Center-Sesoko Station, University of the Ryukyus. We thank the Director Professor M. Nakamura for providing the opportunity and facilities to carry out the research. The assistance of the staff is greatly appreciated, especially that of S. Nakamura, Y. Nakano, A. Takemura, and C. Uchima. We are grateful to N. Namizaki and H. Yamamoto for their invaluable help during the first stages of this project and thank C. Steinberg at AIMS for tidal analysis. We thank all the students participating in the TBRC 2007 COE International Summer Course, for help in the field and aquaria, especially to O. Bronstein, J. Ceh, D. Combosch, R. Elahi, S. Harii, N. Isomura, P. Mardnui, M. Nakamura, R. Suwa, A. Wahyun and C. Yoffe.

References

- Abe N (1937) Post larval development of the coral *Fungia actiniformis* var. *palawensis* Doderlein. *Palao Trop Biol Sta Stud* 1: 73–93
- Babcock RC, Bull GD, Harrison L, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Mar Biol* 90: 379–394
- Babcock RC, Mundy CN, Whitehead D (1994) Sperm diffusion models and in situ confirmation of long-distance fertilization in the free spawning asteroid *Acanthaster planci*. *Biol Bull* 186: 17–28
- Baird AH, Guest J, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annu Rev Ecol Evol Syst* 40: 551–571
- Baird AH, Mundy CP, Babcock RC (2003) Habitat selection by larvae influences the depth distribution of six common coral species. *Mar Ecol Prog Ser* 252: 289–293
- Fadlallah, YH (1983) Sexual reproduction, development and larval biology of scleractinian corals. A review. *Coral Reefs* 2: 129–150
- Fukami H, Budd AF, Levitan DR, Jara JA, Kersanach R, Knowlton N (2004) Geographic differences in species boundaries among members of the *Montastraea annularis* complex based on molecular and morphological markers. *Evolution* 58: 324–337
- Gardner JPA (1997) Fertilization in the sea. *Adv Mar Biol* 31: 1–78
- Gittenberger A, Reijnen BT, Hoeksema BW (2006) Chapter 3: A molecular analysis of the evolutionary history of mushroom corals (Scleractinia: Fungiidae) and its consequences for taxonomic classification. In: The evolutionary history of parasitic gastropods and their coral hosts in the Indo-Pacific. PhD thesis, National Museum of Natural History, Leiden, pp 35–56
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Ecosystems of the world. Coral reefs*. Elsevier, Amsterdam, pp 133–207
- Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. *Science* 223: 1187–1189
- Hayashibara T, Shimoike K, Kimura T, Hosaka S, Heyward A, Harrison P, Kudo K, Omori M (1993) Patterns of coral spawning at Akajima Island, Okinawa, Japan. *Mar Ecol Prog Ser* 101: 253–262
- Heyward AJ, Yamazato K, Yeemin T, Minei M (1987) Sexual reproduction of corals in Okinawa. *Galaxea* 6: 331–343
- Hoeksema BW (1989) Taxonomy, phylogeny, and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zool Verh* 254: 1–295
- Hoeksema BW (1991) Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. *Mar Ecol Prog Ser* 74: 225–237
- Hyman L (1940) *The Invertebrates; Protozoa through Cteno-*

- phora. Vol 1. McGraw-Hill, New York.
- Kramarsky-Winter E, Loya Y (1998) Reproductive strategies of two fungiid corals from the northern Red Sea: environmental constraints? *Mar Ecol Prog Ser* 174: 175–182
- Krupp DA (1983) Sexual reproduction and early development of the solitary coral *Fungia scutaria* (Anthozoa: Scleractinia). *Coral Reefs* 2: 153–164
- Levitan DR, Fukami H, Jara J, Kline D, McGovern TM, McGhee KE, Swanson CA, Knowlton N (2004) Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. *Evolution* 58: 308–323
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sembali H, and van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4: 122–131
- Loya Y, Sakai K (2008). Bidirectional sex change in mushroom corals. *Proc Roy Soc Biol B* 275: 2335–3343
- Nishihira M, Yamazato K (1972) Brief survey of *Acanthaster planci* in Sesoko Island and its vicinity, Okinawa. *Sesoko Mar Sci Lab Techn Rep* 1: 1–20
- Nishihira M (1987) Natural and human interference with the coral reef and coastal environments in Okinawa. *Galaxea* 6: 311–321
- Oliver J, Babcock R (1992) Aspects of fertilisation ecology of broadcast spawning corals: sperm dilution effects and *in situ* measurements of fertilization. *Biol Bull* 183: 409–417
- Pawlowicz R, Beardsley B, Lentz S (2002) Classical tidal harmonic analysis including errors in MATLAB using T-TIDE. *Comput Geosci* 28: 929–937
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: Comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Mar Ecol Prog Ser* 60: 185–203
- Schlesinger Y, Loya Y (1985) Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. *Science* 228: 1333–1335
- Schlesinger Y, Goulet TL, Loya Y (1998) Reproductive patterns of scleractinian corals in the northern Red Sea. *Mar Biol* 132: 691–701
- Veron JEN, Stafford-Smith M. (2000) Corals the world (3 volumes). Australian Institute of Marine Science, Townsville, Australia.
- Veron JEN, Pichon M (1980) Scleractinia of Eastern Australia. Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae. *Aust Inst Mar Sci Monogr Ser* 4
- Waller RG, Tyler OA, Gage JD (2005) Sexual reproduction in three hermaphroditic deep-sea *Caryophyllia* species (Anthozoa: Scleractinia) from the NE Atlantic Ocean. *Coral Reefs* 24: 594–602
- Yamaguchi M (1986) *Acanthaster planci* infestations of reefs and coral assemblages in Japan: a retrospective analysis of control efforts. *Coral Reefs* 5: 23–30
- Yamazato K (1981) A note on the expulsion of zooxanthellae during summer, 1980 by Okinawan reef-building corals. *Sesoko Mar Sci Lab Tech Rep* 8: 9–18
- Yamazato K, Oshiro M, Oshiro E (1975) Reproductive biology of a scleractinian coral, *Goniopora queenslandiae decima*. *Abstr 13th Pac Sci Congr* 1: 135
- Yamazato K, Sato M, Yamashiro H (1981) Reproductive biology of an alcyonacean coral, *Lobophytum crassum* Marenzeller. *Proc 4th Int Coral Reef Symp* 2: 671–678

Received: 30 September 2009

Accepted: 22 October 2009

© Japanese Coral Reef Society