Reproductive ecology of *Diaseris distorta* (Michelin) (Fungiidae) in the Galápagos Islands, Ecuador

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**ABSTRACT**

The sexual reproduction of *Diaseris distorta* is described from a population at Devil’s Crown, Floreana Island, Galápagos Islands, Ecuador. Gametogenesis is classified in four developmental stages for each gender. Individuals are gonochoric and most likely broadcast spawners. Gametogenesis was active during the warm, wet season from at least February to June, peaking at the end of April. Mature female gametes were abundant around full moon with lesser numbers present around new moon. Synapticicular spaces were replete with eggs or spermaries in all stages of development. It is likely that gametes develop continuously during the breeding season. Studies of fecundity of female individuals yielded estimates of 7,894-13,000 mature eggs cm⁻² live surface tissue per cycle. Total egg volume was approximately 4.90-8.86 mm³ per cycle with 4-8 spawning cycles yr⁻¹ (19.6-64.5 mm³ eggs yr⁻¹). The sex ratio of the study population was highly skewed toward males, approximately 5:1. Individuals as small as approximately 240 mm³, or approximately 1.75 cm in diameter, were sexually active. Asexual fragmentation is important locally. The potential for sexual reproduction is high, but its effectiveness locally or in establishing new, more distantly located populations is unknown.

**Keywords** *Diaseris*, Mushroom coral, Coral reproduction, Eastern Pacific.

**Introduction**

Although there have been relatively few studies on fungiid coral reproduction, some aspects of their sexual and asexual reproductive biology are known (Abe 1937, Krupp 1983, Yamashiro and Nishihira 1998). In Palau, *Fungia actiniformis* [formerly *Heliofungia actiniformis*] was reported to be a hermaphroditic brooder (Abe 1937), however, Willis et al. (1985) observed this species to be a gonochoric broadcaster on the Great Barrier Reef. In Hawaii, studies by Krupp (1983) demonstrated that *Fungia scutaria* was a gonochoric broadcast spawner. Although some spawning behavior has been reported (Oliver 1985, Willis et al. 1985), patterns of gamete development are virtually unrecorded, with the exception of Krupp (1983). Our work is the first to document gametogenic cycles in an eastern Pacific fungiid coral and its progression throughout the calendar year.

The study population of *Diaseris distorta* is highly sexually active, although it is unclear if it is benefiting significantly from autochthonous sexual recruitment. Understanding the sexual reproductive ecology of *Diaseris distorta* is obscured by its high rate of specialized fragmentation (Yamashiro and Nishihira 1998), which is dominant. Sexual reproduction is probably its predominant means of geographic dispersal, although our results do not confirm that this seemingly isolated population at Floreana Island sexually recruits successfully.

**Methods**

Individuals of *Diaseris distorta* were collected near Devil’s Crown (Corona del Diablo), off Floreana Island, Galápagos Islands, Ecuador (Fig. 1). Thirty-two collections were made, at 13-15 m depth, from 1989 to 1998. Three to five polyps were histologically processed for each date. Sample size ranged from 5 to 59 individuals yr⁻¹ (N=171). Fixation, decalcification, infiltration and embedding were performed according to techniques described in Glynn et al. (1994, 1996). Two pieces of each polyp were embedded for cross sectional and/or longitudinal viewing. One slide of serial sections was taken from each of three areas: oral, middle, and aboral. Sections were cut and stained following procedures described in Glynn et al. (1994).

Development of ova and spermaries was divided into 4 stages, which are described below. One section on each slide was scored for each developmental stage and data were plotted with Sigmaplot 5.0 as in Glynn et al. (1996). Chi-square analyses of seasonal and lunar trends were performed according to Glynn et al. (1996).

Egg diameters (Stage IV eggs) were randomly selected (N=10) from one section per sample (N=10 samples). Eggs are located in mesenteries that are not uniform in morphology, i.e. with respect to depth within the polyp. Histological preparations of longitudinal slices of polyps showed meandering masses of eggs from which several finger-like projections extended. These were not consistent in shape or size and were located between spaces created by the dissolution of the synapticicular during processing.

Due to variations in egg distribution, the number of mature eggs cm⁻² surface area of polyp was estimated as follows. The mean number of mature eggs was calculated from one delineated cm² of tissue sliced between the oral and aboral surface for N=4 female samples (slides). Mean numbers of mature eggs also were determined for areas of whole slices cut through both oral and aboral planes (N=2). These one dimensional egg counts were adjusted volumetrically for a 2.8 mm (N=4) tissue depth. Two independent estimates resulted from this method (7,894 and 13,000 eggs cm⁻²).

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One size series collection was made during the peak of the yearly breeding season to determine the approximate size of individuals at gametogenesis. Twenty-four individuals were sampled, ranging from 150-1980 mm² in planar area. One sexual recruit in the size series data was identified by its completely circular shape and a lack of mature fragmentation grooves or slits. The septal array in this individual was spoke-like, whereas in regenerating polyps, regenerating segments develop septae at abrupt angles to the original fragment. In daughter fragments, i.e. asexually generated individuals (Yamashiro et al. 1998), the initial orientation often approximates a teardrop, with irregular tissue portions attached.

**Results**

Gonadal development and gametocyte classification

**Ova**

Most of the eastern Pacific scleractinian coral species studied in our laboratory display distinct color changes during egg development. We did not observe this in *Diaseris distorta*, nor were texture changes obvious. Therefore, egg stages were generally distinguished by size and nuclear migration (Fig. 2A). Stage I ova were oval, 12-20 μm in diameter and located in the mesenterial gastrodermis, often resting near the mesoglea. Usually a thin layer of yellow cytoplasm enveloped a light beige nucleus and dark pink nucleolus. Stage II ova had migrated into the mesoglea and ranged from 22-62 μm, but usually were not greater than 53 μm. The cytoplasm was yellow and occasionally light pink. The nucleus was now white and granular with a dark yellow nucleolus. Stage II ova had migrated into the mesoglea and ranged from 22-62 μm, but usually were not greater than 53 μm. The cytoplasm was yellow and occasionally light pink. The nucleus was now white and granular with a dark yellow nucleolus. Stage III ova increased in size and changed slightly in color. At 64-85 μm, they were generally dark and were often blotchy or mottled. Stage IV ova were 88-140 μm. Although the cytoplasm granularity increased, no color change was noted. They were distinguished by the position of the nucleus, which had migrated peripherally, and now appeared flattened against the plasma membrane. Although all four stages of ova were present in most female samples, no spawned ovaries were identified.

**Spermaries**

Approximately seven light gray or lavender cells within the mesenterial mesoglea comprised Stage I spermaries. They formed a cluster 15-22 μm in diameter. Stage II spermaries ranged from 24-40 μm in diameter (Fig. 2B). Cells were generally lightly stained. In rare cases, these cells were well defined. Stage III spermaries were 40-82 μm and were darker pink or more purple. Often they contained a lumen and were more organized than at Stage II. Stage IV spermaries were usually larger than 84 μm. A reduction in cell size denoted the beginning of this stage, when primary spermatocytes divided into brownish secondary spermatocytes, starting from the interior and progressing peripherally. A second division into smaller purple spermatids also took place. Mature Stage IV spermaries were shaped as funnels or teardrops and stained from light purple to dark magenta with gold-tailed spermatozoa bunched to one side. Since only four samples were found with spawned spermaries, this category was also included in Stage IV scoring. They were deflated with a few spermatozoa within the shrivelled gastrodermis.
Reproductive Condition

Gamete development was gonochoric, no hermaphrodites were found. Approximately half (56%) of the 171 polyps examined harbored gametes, however, males dominated the population 5.4:1 (81 males and 15 females). Chi-square analysis revealed a significant difference from the expected ratio of 1:1 (p<0.001). All four stages of gametocyte development were usually present in male or female polyps and were intermingled along each reproductive mesentery. Gametes were concentrated in the mid-region of the polyp tissue. Sclerospectae are bridged by numerous calcareous synapticulae. Consequently, mesenterial tissues must fit into these partitioned areas and around the skeletal components themselves. No embryos or planulae were observed in tissues or gastrovascular cavities.

Most samples included in the size series collection (27 April 1991) were found to be reproductive (16 of 24). Of the ten smallest individuals (150-483 mm²), only 4 contained gametes (238 mm², 272 mm², 306 mm², 483 mm²). One of these (306 mm²) was identified as a sexual recruit and harbored early stages of male gametes as well as mature spermatozoa. The other three appeared to have previously separated from a parent polyp. Those with the beginnings of thin, non reproductive, regenerating tissue bands (30-40 mm² or greater), were presumably separated recently from the parent and harbored gametes in the original fragment portion of approximately 100 mm².

We examined the possibility of sex change associated with size. Within the size series collection, only one female was present (1190 mm²). Since several smaller (238-1088 mm²) and larger (1260-1980 mm²) males were collected and two males were the same size as the female, no correlation between size and sex was evident.

Seasonality

Reproductive activity of Diaseris distorta predominantly occurred from late February to June at Devil’s Crown (Fig. 3A). Activity increased during the month of March (the warm, wet season) and decreased in late May (beginning of the cool, dry period). Although this result coincided with the most concentrated sampling, Chi-square analyses of gamete Stages I-IV showed a significant seasonal trend (p<0.025). Since most samples of both sexes contained all stages of gonadal development, the presence of mature gametes followed a similar significant (p<0.01) trend (Fig 3B). Gametogenic activity during the sparsely sampled remaining months was low and there was little indication of maturation of both sexes. Males were highly productive throughout the breeding season, while females were most plentiful and most often mature during the latter half of April (Fig. 3A and B). Spawned spermaries were found in collections made on 8 May 1989, 27 April 1991, 18 March 1992 and 25 February 1994.

Lunar Periodicity

Although the fourth quarter of the lunar cycle (days 22-28, new moon=day 0) was more sparsely sampled, male polyps harbored gametes throughout the month. Gamete development in female individuals was found only in samples taken around new and full moon phases (Fig. 3C). Since female samples contained most gametocyte stages, the presence of Stage IV gametocytes followed similar trends (Fig. 3D). Chi-square analysis showed no significant lunar trends in reproductive activity or gamete maturity. Since female samples harbored at least three stages of development (usually including Stage IV ova), ova graphs may reflect a biased sampling effort (72% collected during new/full moon quarters). Spawned male gonads were also detected in only new and full moon samples (lunar days 0, 3, 14 and 15, N=4). Mature spermaries alone were found in one sample (lunar day 14, one day before full moon) and two others (lunar days 9 and 25) had only earlier male stages.

Fecundity

Mean mature egg diameter in Diaseris distorta was approximately 103 μm (Table 1), measured from the 10 polyps containing Stage IV eggs. Mean volume per mature egg was 6.2 mm³ x 10⁻⁴. The average number of mature eggs cm⁻² polyp surface was estimated between 7,894 and 13,000 eggs cm⁻². Since most female polyps displayed all four stages of gametogenesis and the breeding season lasts for at least four months (late February – early June) we assume that egg maturation occurs at least monthly. Therefore, we multiplied the mean number of eggs cm⁻² by four to estimate yearly spawning output per polyp. This results in the production of approximately 31,580-51,800 mature eggs cm⁻² yr⁻¹. If split spawning is part of the Diaseris reproductive pattern (evident in Fig. 3, C and D), these numbers would also reflect this scenario, assuming 1 monthly spawning per polyp. If maturation and spawning occur in individuals bimonthly, then 63,150-104,000 could be the yearly yield. This would produce a mean egg volume of 4.90-8.06 mm³ cm⁻² per cycle (Table 1), 19.6-32.1 mm³ cm⁻² for 4 cycles or a split spawning event, and 39.2-64.5 mm³ cm⁻² for bimonthly activity.
Fig. 3  Seasonal and lunar scattergrams of gametogenesis at Devil’s Crown, Galápagos Islands, based on 32 collections and a total of 171 polyps examined (1989-1998). Annual plots: (A) % polyps with gametocyte Stages I-IV (male polyps {M} in upper panel, females {F} lower); (B) % gonads with Stage IV gametocytes. Lunar plots: (C) % polyps with gametocyte Stages I-IV; (D) % gonads with Stage IV gametocytes. Full moon occurs near lunar day 15. An asterisk (*) denotes spawned spermaries were present.

Table 1.  Mature egg size (Stage IV oocytes), volume egg⁻¹, no. of mature eggs cm⁻² polyp surface tissue and estimates of mean mature eggs and egg volume cm⁻² yr⁻¹ at Devil’s Crown, Galápagos Islands. All measurements from histological sections. Egg volume was calculated from the mean egg diameter (±SEM) by using the formula for a sphere.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Value</th>
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<tbody>
<tr>
<td>Mean egg diameter</td>
<td>103.7 ± 2.2  (eggs, polyps) (6-10,10)</td>
</tr>
<tr>
<td>Mean volume egg⁻¹</td>
<td>6.2 ± 0.4 (mm³ x 10⁻⁴ ± SEM) (eggs, polyps) (6-10,10)</td>
</tr>
<tr>
<td>Mean no. eggs (cm⁻² ± SEM)</td>
<td>7,894 ± 957 (per cycle)</td>
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<td>13,000 ± 343 (polyps) (6)</td>
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<tr>
<td>Mean no. eggs (cm⁻² yr⁻¹)</td>
<td>31,580-51,800 (4 cycles yr⁻¹)</td>
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<td>63,150-104,000 (8 cycles yr⁻¹)</td>
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<tr>
<td>Total egg volume (mm³ cm⁻² yr⁻¹)</td>
<td>19.6-32.1 (4 cycles yr⁻¹)</td>
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<td>39.2-64.5 (8 cycles yr⁻¹)</td>
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Discussion

Life History and the Reproductive Condition

Emphasis has been placed on the asexual reproduction of fungiid corals by disc detachment (Motokawa et al. 1987, Yamashiro and Yamazato 1987) and their unique fragmentation methods (Yamashiro and Nishihira 1998). The newly metamorphosed polyp of fungiiids, believed to be derived from a settled planula, generates a stalk on which the polypoid disc (anthocaulus) is attached and supported, hence the name “mushroom coral”. The disc, as it grows, eventually separates from the stalk by dissolution of the stalk skeleton (Wells 1966, Hoeksema 1988). The dislodged polyp lives freely on the bottom and the stalk is free to regenerate another disc.

An unusual method of asexual fragmentation also occurs in Diaseris. Yamashiro and Nishihira (1998) and Yamashiro et al. (1989) described separation and release of daughter fragments by slit formation at the periphery of the polyp skeleton in Diaseris distorta and Diaseris fragilis, respectively. This likely occurs by dissolution of the skeleton, whereby daughter fragments eventually are released or drop off, grow a new mouth and regenerate a complete polyp.

It was previously not known if individuals originating from fragments were able to develop gonads (Hoeksema 1989). In this study, regenerating polyps of Diaseris distorta, 238 mm² in size, were already reproductive. However, once the original sexually-derived polyp is diminished by fragmentation it is difficult to determine if the remaining fragment originated from sexual or asexual reproduction. Therefore, determining age by size is extremely problematic. Daughter fragments (presumably recently separated) with thin non-reproductive regenerating tissue bands contained gametes in the
original fragment portion of approximately 1 cm². Thus, the relationship of size and sexuality before and after fragmentation is critical to the study of the reproductive ecology of this species.

It appears that sexual recruits of 306 mm² (17x18mm) are already sexually active. Although no growth measurement data were reported herein, sexual maturity most likely occurs at an early age, perhaps much earlier than other reported funguids. Size at first reproduction reported for *Fungia concinna* and *Fungia fungites* was 6 cm or 4 yr of age (Harrison and Wallace 1990). *Heliofungia actiniformis* of 8 cm (10 yr old) released planulae (Abe 1937, Connell 1973).

Skewed sex ratios are often a result of fragmentation (Harrison and Wallace 1990). This has the advantage of producing large numbers of replicants with locally adapted genotypes (Richmond and Hunter 1990). Like *Diaseris* (5.4:1), populations of *Fungia concinna* and *Fungia fungites* were also reported to contain skewed sex ratios in favor of males, between 2.5:1 to 5.5:1 (Oliver 1985). High numbers of males may be advantageous, since egg fecundities are large.

**Seasonality**

In general, eastern Pacific corals prefer warmer waters for gamete production than the cooler seasons or conditions of upwelling (Glynn et al. 1994, 1996, 2000). *Diaseris distorta* is reproductively most active in the Galápagos from at least February to June. The massive eastern Pacific coral, *Pavona clavus* in the Galápagos region, follows the same reproductive seasonality as *Diaseris distorta* (Glynn et al. unpublished). Additionally, both species show evidence of at least some low level reproductive activity during the months of October through December.

Other fungiid species have similar seasonal preferences. *Fungia fungites* and *Fungia concinna* on the Great Barrier Reef and *Fungia scutaria* were also reported to spawn during the warm months (Krupp 1983, Oliver 1985, Willis et al. 1985). *Fungia scutaria* also has a narrow breeding season, spawning once per lunar cycle spanning a few months in Hawaii.

**Lunar Periodicity**

Although no lunar pattern can be determined with confidence, spawned male gametes were detected around new and full moon. Since various generations of gametes are present within most polyps throughout the lunar cycle, and time to maturation is unknown, these results may indicate a staggered maturation within the population (split spawning), or perhaps gametes mature more than once per month. Evidence of bimonthly activity in eastern Pacific corals has already been demonstrated for several reef-building species (Glynn et al. 1991, 1994, 2000). Abe (1937) described planulae release on several days around the new moon from September to April in Palau (Wells 1966).

**Fecundity**

Mean annual fecundities (eggs cm⁻² yr⁻¹) of 3,822 and 6,316 were extrapolated by Harrison and Wallace (1990) for *Fungia concinna* and *Fungia fungites*, respectively, from values presented in Oliver (1985). The extrapolated annual volumes (mm³ cm⁻²) were 31.3 and 51.7, respectively. Oliver (1985) reported a 250 μm mature egg diameter for live eggs (190 μm when reduced 25% for tissue processing) and 1 spawning cycle per year. Although eggs cm⁻² per spawning cycle and yearly egg volumes are similar to those of *Diaseris*, annual egg production of *Diaseris* is potentially much greater by about 10 to 20-fold (Table 1). This is most likely a function of the small egg size and the greater number of cycles reported, however, estimates of eggs per cycle of *Diaseris* reported here are greater by a factor of two. Egg abundances cm⁻² are comparable with values reported by Harrison and Wallace (1990) for broadcast species of *Porites* which have comparably small eggs. *Pavona gigantea* in the Galápagos, reported to be one of the most fecund scleractinian corals (Glynn et al. 1996), has small eggs (104 μm) and produces 10,280-30,800 eggs cm⁻² yr⁻¹. Egg production is similar but slightly lower than that reported for *Diaseris*.

**Recruitment**

Extensive searches throughout the Galápagos Archipelago have not turned up any other living populations of fungiid corals. Numerous skeletons of both *Diaseris distorta* and *Cycloseris curvata* occur near the small island Xarifa, in Gardner Bay, Española Island approximately 88 km upstream of the study population. Therefore, *Diaseris* at Devil’s Crown may have previously had a source of new recruits and potentially another gene pool with which to interact.

Very few sexual recruits were identified from the study population. The observation of skewed sex-ratios, perhaps associated with high rates of fragmentation and local geographic isolation, suggest that there is limited dispersal potential of *Diaseris distorta*.

Gametes released at Devil’s Crown may be swept away by strong oceanic currents into deeper water to produce larvae with a slim chance for settlement. Currents measured in the fungiid community often attained high velocities. Feingold (1995) reported mean values of 9.0 cm sec⁻¹ in a WNW direction. Glynn and Wellington (1983) observed current velocities of 12.9-25.7 cm sec⁻¹ toward the north. It is possible, therefore, that larvae may reach Isabela Island, approximately 75 km away (downstream), however, if settlement does not occur within a few days of fertilization, they may be swept out to sea. Krupp (1983) described planulae of *Fungia scutaria* that were highly active, but most easily found creeping along the bottom of their holding aquaria for 9-10 days. He also reported small (84 μm) negatively buoyant eggs. Perhaps the potential for self-seeding may be greater than...
first expected, but in 9-10 days, planktonic planulae in equatorial currents could be hundreds of kilometers away. *Diaseris distorta* and *Cyclloseris curvata* are found throughout the Indo-Pacific (Veron 2000) and a few scattered populations are found in the eastern Pacific in Mexico and Costa Rica (H. Reyes-Bonilla, J. Cortés pers comm), and in the Galápagos Islands (sampled in this study). This suggests that these fungiids are capable of long-distance dispersal, but may become locally isolated.

Regardless of the conditions, sexual recruitment in fungiids appears to be low. Nishihira and Pourg-In (1989) suggested that populations of *Diaseris fragilis* in the Gulf of Thailand were asexually maintained, among thousands examined no anthocauli scars were ever found. Yamashiro et al. (1989) did not find stalked specimens or detachment scars on *Diaseris fragilis* as small as 5 mm. They concluded that new individuals were produced exclusively by asexual autotomy. Fisk (1983) suggested that *Diaseris distorta* actually bypasses the sexual phase.

While it is possible that sexual recruits may not be present in some fungiid populations, it is more likely that the stalked phase of the life cycle is very cryptic or not found in the same location as the free living disc. *Fungia scutaria* anthocauli (about 1 mm diameter) were detected in aquaria attached to coralline rubble about 3 weeks after the first spawn (Krupp 1983), however, Krupp also surmized that sexual recruitment was rare. In a survey at Devil’s Crown, 29 of 541 individuals (5.4%) showed no evidence of previous fragmentation. These possibly sexual recruits had radii ranging from 2.5–25 mm and possessed rounded tubercle attachment scars, indicative of anthocauli origins. Hoeksema (1989) reported that in the majority of species detachment scars heal completely, complicating assessment of the relative contributions of sexual versus asexual propagation.

It has already been suggested that some corals in the eastern Pacific region successfully reproduce by asexual means exclusively and were derived from pulses of larvae dispersed from populations in the central Pacific (Richmond 1985). Information on larval behavior and competency period of this gonochoric broadcast spawner in relation to current advection will be necessary to relate gamete production to successful sexual recruitment.

**Dedication** This paper is dedicated to Florence Zelden Colley.

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**References**


