

Distribution and Sexual Reproduction of a Seagrass-bed-inhabiting Actinarian, *Phymanthus strandesi* (Cnidaria: Anthozoa: Actiniaria: Phymanthidae), at Hsiao-Liuchiu Island, Taiwan

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Ming-Doun Lin, Chaolun Allen Chen and Lee-Sing Fang (2001) Distribution and sexual reproduction of a seagrass-bed-inhabiting actinarian, *Phymanthus strandesi* (Cnidaria: Anthozoa: Actiniaria: Phymanthidae), at Hsiao-Liuchiu Island, Taiwan. *Zoological Studies* 40(3): 254-261. Distribution and sexual reproduction of the seagrass-inhabiting actinarian, *Phymanthus strandesi*, was investigated at Gerban, Hsiao-Liuchiu, Taiwan from July 1997 to June 1998. *P. strandesi* was distributed in the shallow intertidal zone of the reef flats with a mean density of 511 individuals/m². The distribution pattern of *P. strandesi* was contagious, and was significantly correlated with the presence of the seagrasses, *Thalassia hemprichii* and *Halodule uninervis*. *P. strandesi* is a small dioecious actinarian with a mean pedal disc diameter of 0.32 cm. A high proportion of the anemones were sexually indeterminate, whose sizes were significantly smaller than those of both males and females. The mean fecundity of females was 294 eggs/individual. The released eggs were 500 to 560 µm in diameter. Gametogenesis examined by paraffin section showed no distinct developmental pattern among monthly samples, suggesting that *P. strandesi* might reproduce continuously throughout the year. Although with a small body size and low fecundity, the large eggs, continual gametogenesis, and contagious aggregation in the seagrass bed might ensure the successful sexual reproduction of *P. strandesi*. <http://www.sinica.edu.tw/zool/zoolstud/40.3/254.pdf>

Key words: Actinarian, Sexual reproduction, Distribution, Gametogenesis, Seagrass bed.

Actinarians (sea anemones), which usually attach themselves to substrata by pedal discs, are one of the abundant sessile marine invertebrates in temperate and tropical benthic communities (for a review, see Shick 1991). Quantitative studies on benthic faunal communities have shown that availability of suitable substrata might affect the distribution pattern of actinarians. Distribution of *Zoalutius actius* on soft-bottom substrates is contagious and is correlated with patches containing solid objects, mostly tubes of polychaetes, as attachment surfaces (Fager 1968). Similarly, the distribution of the deep-sea actinarian, *Phelliactis robusta*, in soft sediment habitats was significantly associated with hard substrates (Vanpraët et al. 1990). In seagrass beds of

the Garden Island shore of Careening Bay, Western Australia, surface counts and core samples revealed relatively high abundance of *Heteractis malu*, and 3 rarer infaunal sea anemones (Peterson and Black 1986). Samples taken from 5 substrata showed that *H. malu* did not vary significantly with the presence or absence of seagrass, but was less abundant in shallow sand than in other substrata, whereas the average individual size of *H. malu* was smaller in areas with seagrass. This implies that larger *H. malu* tend not to occur in the substratum where seagrass is present.

Actinarian reproduction has primarily been studied in temperate regions (for a review, see Shick 1991). Most temperate sea anemones are dioecious

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and have an annual cycle of sexual reproduction correlated with seawater temperature (Jennison 1979, Wedi and Dunn 1983, Shaw 1989, for a review, see Shick 1991). The timing of spawning is probably determined by rising water temperature during the winter in *Sagartia troglodytes* (Shaw 1989), and those in *Anthopleura elegantissima* and *Urticina lofotensis* have been linked to maximum temperatures (Jennison 1979, Wedi and Dunn 1983). In contrast, limited information is available on species in tropical regions despite the high diversity of habitats, such as coral reefs, seagrass beds, and mangroves. Although annual reproductive cycles were observed in *Actinoporus elongatus* (Clayton and Collins 1992) and *Anthopleura dixoniana* (Lin et al. 1992), and a biannual reproductive cycle in *Bartholomea annulata* (Jennison 1981), a prolonged reproductive cycle was found in *Condylactis gigantea* and *Phymanthus crucifer* (Jennison 1981), indicating that the reproductive pattern in tropical sea anemones might be diverse in comparison to their temperate counterparts.

Phymanthus strandesi is a tropical actinarian occurring in the Indo-Pacific Ocean (Carlgren 1949). *P. strandesi* inhabits shallow-water intertidal reef flats covered by coral sands and the seagrasses, *Thalassia hemprichii* and *Halodule uninervis* at Gerban, Hsiao-Liuchiu Island, Taiwan. In this study, we first surveyed the distribution and estimated the density of *P. strandesi*. In particular, we tested for differences in spatial distribution of *P. strandesi* in seagrass beds and unvegetated areas. Second, gametogenesis and periodicity of sexual reproduction were investigated using histological examination, and characteristics of the distribution pattern and sexual reproduction of *P. strandesi* are discussed.

MATERIALS AND METHODS

Distribution

The field survey and collection of *Phymanthus strandesi* were conducted at Gerban, Hsiao-Liuchiu Island off the southwestern coast of Taiwan (120°21'10"E; 22°20'30"N). The site is an intertidal shelf of reef flats comprised of coral sand and rubble and vegetated by patches of seagrasses. The dominant species of seagrass are turtle grass, *Thalassia hemprichii*, and shoal grass, *Halodule uninervis*. In the period of tidal immersion, *P. strandesi* extends its sand-colored oral disc and tentacles upon the sediment surface, and is partially covered and uncovered as sand is moved by wave surges. While exposed to

the air at the lowest tides, *P. strandesi* is capable of retracting itself under the sediment surface, leaving cylindrical depressions dotting the sediment surface. To estimate the abundance and distribution pattern of *P. strandesi*, we performed visual counts during low tide in Mar. 1998. Two transect lines were laid out from the shore toward the sea, and were divided into 3 strata: shallow, intermediate, and deep, as referenced to Peterson and Black (1986). In each of the 3 strata, the number of sea anemones was counted in eighteen 15 × 15-cm² quadrats laid out haphazardly within a 2-m distance along the transect line. To determine whether the abundance of *P. strandesi* varied with the presence/absence of seagrass, we compared the number of sea anemones and the number of seagrass stems in 10 quadrats each laid out haphazardly in sand/coral rubble and seagrass beds, respectively.

Spatial patterns of the sea anemone population were analyzed using the Poisson distribution goodness-of-fit test (Zar 1999). Since the distribution of *P. strandesi* was Poisson rather than normally distributed, a 2-way model I analysis of variance (ANOVA) with a square-root transformation of counts was used (Zar 1999). To determine whether the abundance of *P. strandesi* varied between the seagrass bed and unvegetated area, the numbers of sea anemones within the quadrats were compared using student's *t*-test (Zar 1999). A linear regression analysis (Zar 1999) were then applied to determine the relationship between the number of sea anemones and the number of seagrass stems.

Relationship between wet weight and pedal disc diameter

Pedal disc diameter has been used as a conventional measurement for the size of actinarians (reviewed in Shick 1991). In order to use this parameter for our study, we tested whether pedal disc diameter (PDD) was correlated with wet weight. *P. strandesi* was collected and anesthetized using a solution of 7% magnesium chloride with seawater in a ratio of 1:1 for 2 h (Moore 1989). The PDDs of 211 individuals were measured individually as the mean of the largest and smallest pedal disc diameters. Then anemones were fixed in Bouin's fixative (Hopwood 1990) for at least 48 h. The wet weight (WW) of each specimen was then measured after excessive water was removed by blotting. The corresponding values of PDD and WW were plotted and were tested by linear regression analysis (Zar 1999).

Relationship between size and sex

To determine the relationship between size and sex, histological preparations of preserved specimens for which PDD and WW were recorded were examined to identify their sex using methods modified from Lin et al. (1992) and Chen et al. (1995). Specimens were washed with several changes of 50% ethanol and preserved in 70% ethanol (Hopwood 1990). A small piece of tissue containing gametogenetic mesenteries was embedded in paraffin, sectioned at 7 mm, and stained with basic fuchsin and picro-indigo-carmin (Clark 1980). The distributions of males, females, and sexually indeterminate individuals among 10 size classes were compared using the goodness-of-fit test (Zar 1999). Sexually indeterminate individuals were defined as individuals in which gametes were not observed in dissections under microscopic examination.

Gametogenesis, reproductive periodicity, and fecundity

To document reproductive periodicity, several individuals of *P. strandesi* were haphazardly collected between July 1997 and June 1998 at approximately monthly intervals. Histological sections were performed as above. Measurements of oocyte size and developmental stages of sperm followed methods modified from Lin et al. (1992) and Chen et al. (1995). Diameters of 50 oocytes containing nucleoli were measured for each female. The mean of the longest and shortest perpendicular diameters was used to indicate the diameter of irregularly shaped oocytes. The development of sperm was divided into 3 stages: stage 1, small groups of spermatogonia dispersed along the mesogloea or cysts containing spermatocytes only; stage 2, cysts with an outer layer of spermatocytes and an inner core of spermatids and sperm; and stage 3, cysts containing sperm only.

The sex of mature *P. strandesi* was determined in the field by the color and shape of the gonads, visibly apparent through the elongated transparent body

wall. Mature females contained green grape-shaped gonads, while males contained white spiral gonads. Fecundity of females was calculated from 5 mature individuals in May 1998, by counting the oocyte number from 2 gonads, and then multiplying this value by the number of gonads per individual.

RESULTS

Distribution

The mean density of *Phymathus strandesi* was 511 individuals/m². However, the distribution of *P. strandesi* in the intertidal was non-random (Poisson goodness-of-fit test, $p < 0.05$). A comparison of the variance and mean of samples indicated that *P. strandesi* showed a contagious distribution pattern (i.e., $s^2 > m$). Two-way ANOVA also revealed a significant difference in the distribution of *P. strandesi* among strata (Table 1, ANOVA, $F_{(2, 42)} = 14.462$, $p < 0.001$); but no differences between transect lines (Table 1, ANOVA, $F_{(1, 42)} = 0.211$, $p > 0.05$) or interaction between the transect line and stratum (Table 1, ANOVA, $F_{(2, 42)} = 0.4156$, $p > 0.05$) were observed. *P. strandesi* tended to occur on shallow stratum (Table 2) with a maximum density of 2841 individuals/m². In field observations, *P. strandesi* was always found attached to a stable substrate such as roots and rhizomes of seagrass or to the surface of a shell fragment or coral rubble. The number of *P. strandesi* in the seagrass bed quadrats was significantly higher than in unvegetated areas (student's $t = -2.831$, $p < 0.05$, $n = 20$). Furthermore, the occurrence of *P. strandesi* was significantly correlated with the occurrence of seagrass ($Y = -7.345 + 0.824 X$, $r = 0.95$, $p < 0.001$, $n = 11$).

Relationship between size and sex

A significant correlation was found between

Table 1. *Phymathus strandesi*. Two-way analysis of variance for the number of anemones in different strata at Gerban, Hsiao-Liuchiu

	df	MS	F value
Transect	1	0.464	0.211 ^{n.s.}
Stratum	2	31.827	14.462**
Transect X stratum	2	1.973	0.4156 ^{n.s.}
Residual	42	2.201	

n.s.: not significant; ** $p < 0.001$; df: degrees of freedom; MS: mean square.

Table 2. *Phymathus strandesi*. Fisher's PLSD for comparing the square root transformation of the number of anemones in shallow, intermediate, and deep strata at Gerban, Hsiao-Liuchiu

Source	Mean difference	Critical difference	p-value
Shallow vs. deep	2.556	1.116	< 0.001
Shallow vs. intermediate	2.749	1.116	< 0.001
Intermediate vs. deep	0.192	0.998	0.6994 ^{n.s.}

n.s.: not significant.

pedal disc diameter (x) and body weight (y) of *P. strandesi* ($y = 0.474x - 0.041$, $r = 0.609$, $p < 0.05$, $n = 221$) (Fig. 1). The average pedal disc diameter of *P. strandesi* was 0.32 ± 0.11 cm, and the average body weight (wet weight) was 0.111 ± 0.083 g. Of 199 sea anemones examined, 26 were male, 42 were female, and 131 were sexually indeterminate. No hermaphroditic individuals were found. There was no significant difference in body size between males and females, ($\chi^2 = 2.510$, $p > 0.05$), but sexually indeterminate individuals were significantly smaller than both females and males (with females, $\chi^2 = 22.951$, $p < 0.001$; with males, $\chi^2 = 26.783$, $p < 0.001$) (Fig. 2). However, the range of body size of sexually indeterminate individuals overlapped those of the sizes of females and males, indicating that some mature individuals may have released their gametes just prior to our monthly collection. This observation was confirmed by histological examination which revealed that empty vacuoles were present in the mesenteries of some individuals (data not shown).

Gametogenesis, reproductive periodicity, and fecundity

Gametogenesis in *Phymanthus strandesi* was similar to that described in other tropical actinarians (Jennison 1979, Jennison 1981, Lin et al. 1992). Oogonia were 18.9 ± 2.6 μm in diameter, and their nuclei measured 10 ± 1.5 μm ($n = 22$, in 5 individuals). Trophonema were present. During vitellogenesis, the germinal vesicle was located peripherally, and the yolk stained green with indigo-carmin.

Oocytes lacked zooxanthellae and had a maximum diameter of 494 μm in histological section. The diameter of a spawned oocyte was 500 to 560 μm ($n = 33$); it was light green, covered by microvilli, and contained zooxanthellae. The mean number of gonads in 5 female *P. strandesi* examined was 8.4 (ranging from 5 to 12), and mean fecundity was 294.4 oocytes (ranging from 40 to 475). Spermatogonia were 2.5 μm in diameter, and the cytoplasm stained blue with picro-indigo-carmin. Later in their development, spermatocytes stained red with basic fuchsin. Spermatids were concentrated in the center of sperm sacs. During the final stage of development, sperm sacs were full of mature sperm.

P. strandesi lacked a distinct reproductive cycle and probably reproduced continuously throughout the year. No peak in reproductively mature individuals was recorded during the 12-mo study. Size distribution among male, female, and sexually indeterminate individuals overlapped in several months (Fig. 3), and no distinct monthly cycle of gametogenesis was observed in histological sections. *P. strandesi* females exhibited a wide range of oocyte diameters, from 15.6 to 494 μm in collections of July 1997 and Apr. 1998 (Fig. 4a). However, collections in Oct., Nov., and Dec. 1997, and in Mar. and May 1998 yielded large proportions of small eggs (Fig. 4a). *P. strandesi* males were mature in Sept. 1997 and May 1998, but in the remaining monthly collections, they primarily showed stages I and II of spermatogonia (Fig. 4b). However, empty vacuoles appeared in the mesenteries of some individuals in each month based on histological examination (data not shown), indicating that gamete release by *P. strandesi* was continuous.

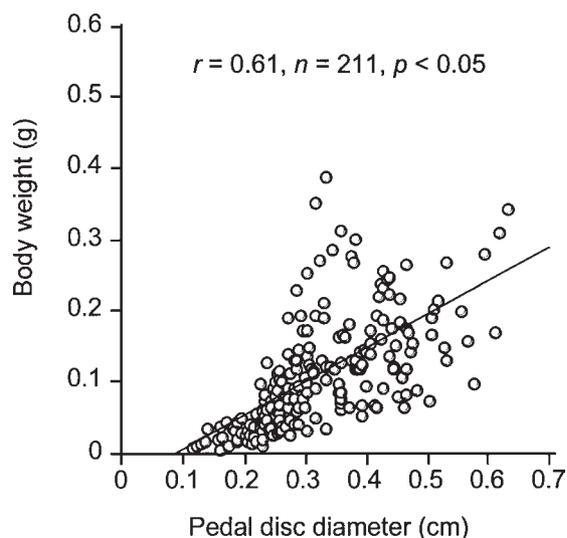


Fig. 1. Linear regression of pedal disc diameter and body weight.

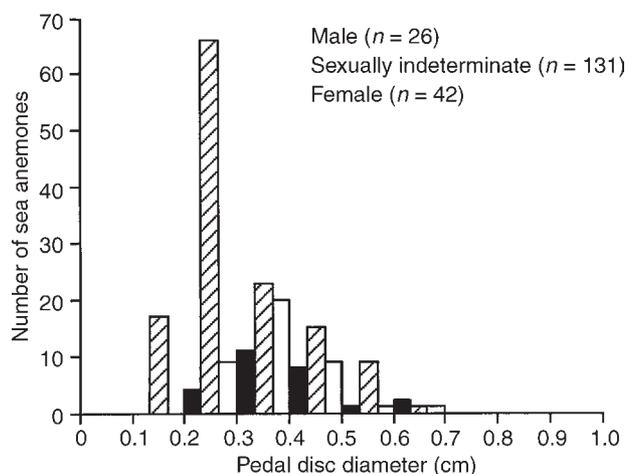


Fig. 2. Size frequency of male, female, and sexually indeterminate anemones.

DISCUSSION

A quantitative survey of *Phymanthus strandesi* in the intertidal zone off Hsiao-Liuchiu Island, Taiwan revealed that the infaunal assemblages of sea anemones in the seagrass bed were characterized by surprisingly high abundance. *P. strandesi* showed a contagious distribution and tended to occur in shallow intertidal areas where the seagrasses, *Thalassia hemprichii* and *Halodule uninervis*, were also abundant. At Careening Bay, Western Australia, *Heteractis malu* is the dominant infaunal actiniarian in seagrass beds (Peterson and Black 1986); however, correlation between the presence of seagrass and abundance of *H. malu* was not significant. On the other hand, individuals of *H. malu* found in the seagrass bed had significantly smaller body sizes (volume) than did those in unvegetated areas. This suggests that seagrass, although containing more potential prey, interferes with either light penetration (for photosynthesis of symbiotic algae in *H. malu*) or prey capture such that exposed positions on sand flats are better sites for *H. malu* (Peterson and Black 1986). Availability of prey is not a limiting factor for *P. strandesi*, as it showed little feeding response to food in an aquarium, and dissection indicated that no residue of large prey was found in the coelenteron (Lin 1999). Light penetration may play a small role in determining the distribution of *P. strandesi*, even though *P. strandesi* hosts endosymbiotic algae (zooxanthellae). *P. strandesi* tends to

occur on shallow substratum, and is a relatively small actiniarian (covering a surface circle of less than 2 cm in diameter when the tentacles are fully extended, pers. obs.) compared to *H. malu* (covering a surface circle of 4-6 cm in diameter, Peterson and Black 1986). Therefore, light penetrating among the seagrass leaves may be sufficient for the zooxanthellae to process photosynthesis in *P. strandesi*. Further examination of the photosynthetic physiology of zooxanthellae in *P. strandesi* should be provided to confirm this hypothesis. The other hypotheses, including stable substrates, refuge from predation, and reduced hydrodynamic energy enabling settlement of larvae (for a review, see Orth 1992), may explain the abundance of *P. strandesi* associated with seagrass. First, roots or rhizomes of seagrasses provide more-stable substrates than do coral sands or shell fragments on which an anemone can attach. Second, although predation on *P. strandesi* was not

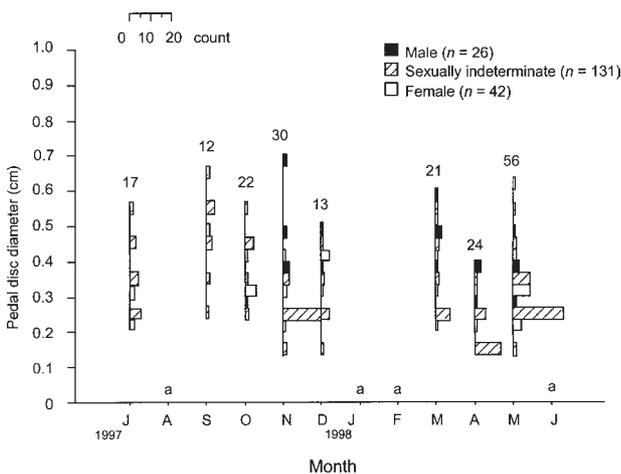


Fig. 3. Size profile of pedal disc diameter in *Phymanthus strandesi* female, sexually indeterminate, and male individuals for each month. Numbers above each bar indicate the sample size of sea anemones in each month. a: collection was not possible because of weather conditions.

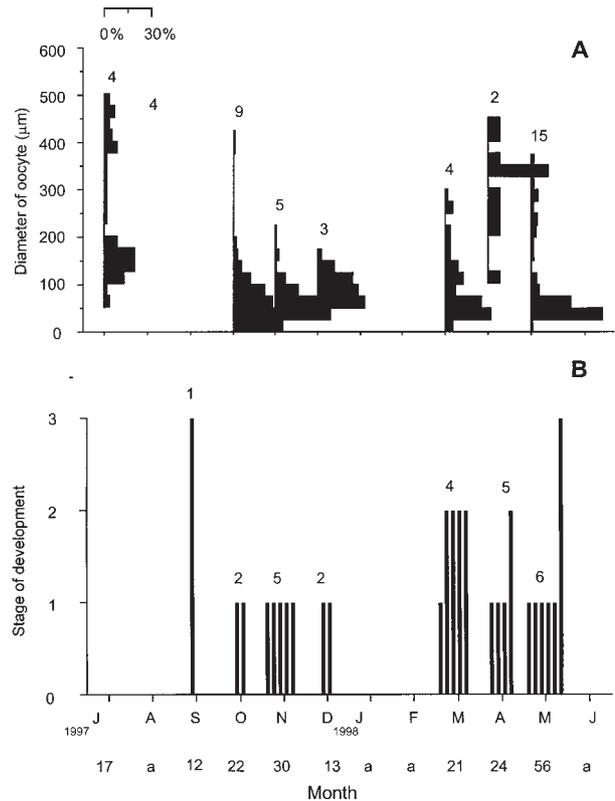


Fig. 4. Development of gametogenic cycles in *Phymanthus strandesi*. (A) Frequency distribution of oocytes. (B) Development stages of spermatogenesis; vertical bars represent the number of individuals of each stage of development. Numbers above each bar indicate the number of individuals observed each month; numbers under the axis indicate total number examined in each month. a: collection was not possible because of weather conditions.

observed in the field, fast retraction and the leaving of a distinct hole in the coral sands when disturbed indicate that roots or rhizomes can function as a refuge onto which *P. strandesi* can attach. Third, *P. strandesi* occurs in shallow intertidal substrata where hydrodynamic energy is relatively high. Since it is known that seagrasses can modify hydrodynamic processes (Fonseca et al. 1982, Ekman 1983 1987, Fonseca and Fisher 1986), they may play an important role in determining larval supply and settlement of *P. strandesi*. In addition to hydrodynamic modification, seagrasses may serve as an environmental cue for larval settlement in *P. strandesi*. In planulae of *Sagartia troglodytes*, metamorphosis occurs only if tubes of the polychaete *Sabellaria* are present (Riemann-Zürneck 1969). Planulae settlement and metamorphosis of *Urticina crassicornis* and *Cribrionopsis fernaldi* are facilitated by the presence of tubes of the polychaete, *Phyllochaeteopterus* (Chia and Spaulding 1972, Siebert and Spaulding 1976).

In tropical actinarians and corallimorpharians (a group of soft-bodied anthozoans resembling actinarians), reproductive periodicity varies among species. Actinarians examined in Malaysia and Florida exhibit patterns of brooding, hermaphroditism, and diffuse spawning over a long period each year (Jennison 1981, Dunn 1982). In contrast, an actiniarian, a corallimorpharian examined at Wanlitung, Taiwan (Chen et al. 1992, Lin et al. 1992), and a corallimorpharian examined at Eilat, Israel (Chadwick et al. 2000) indicate that polyps synchronously release gametes in mid-summer each year during the period of peak seawater temperature and day length. Although the seagrass-bed-inhabiting actiniarian, *P. strandesi*, at Hsiao-Liuchiu is suggested to reproduce continuously throughout the year based on the monthly plotting of size distribution among male, female, and sexually indeterminate individuals (Fig. 3), and on gametogenesis (Fig. 4), limitation of interpretation of our data should also be considered due to the lack of samples during 4 of the total 12 months. On the other hand, only immature spermaries and small oocytes were found during the winter period (Oct. to Feb.) in our study, suggesting that *P. strandesi* might have no mature gonads or release any gametes during the winter. If this is the case, the appearance of mature sperm and large eggs from Mar. to May would indicate that *P. strandesi* may spawn gametes only between Mar. and July, which is similar to the annual cycle of spring to summer gamete release found in other Taiwan anthozoans (Lin et al. 1992, Chen et al. 1995, Chen unpubl. data). Further complete data on the reproductive cycle of *P. strandesi* is needed to examine these 2 alternative

hypotheses.

It is believed that life history traits related to sexual reproduction and developmental patterns in sea anemones show phylogenetic conservatism at the congeneric level, but may diversify due to the influence of different ecological conditions (reviewed in Shick 1991). For example, sexual reproduction has been studied in 3 *Phymanthus* species so far, including *P. crucifer* (Jennison 1981), *P. loligo* (Lin 1999), and *P. strandesi* (this study). All 3 *Phymanthus* are dioecious and develop large eggs (ranging from 450 to 600 μm in diameter). However, fecundity is significantly lower in *P. strandesi* than in *P. loligo* (> 850 eggs per individual) (Lin 1999). This is probably due to the relatively small body size of *P. strandesi* among the 3 *Phymanthus* species. This implies that small body size, large eggs, and reduced fecundity are associated with brooding of young, and low fecundity may create a depressed potential for sexual recruitment (for a review, see Shick 1991). However, this is not the case in the evolution of the life history of *Phymanthus*. First, body sizes of *P. crucifer* and *P. loligo* are significantly larger than that of *P. strandesi*, but the former 2 are brooders with viviparous larval development (Jennison 1981, Lin 1999), while the latter is a spawner with oviparous larval development. Second, asexual reproduction was not observed in this study (Lin 1999); significantly high abundance of *P. strandesi* in the seagrass bed indicates that the local population may be composed of individuals recruited exclusively from sexual reproduction. Nevertheless, data are needed on population genetics and demography to support this hypothesis.

The diversification of reproductive traits within this genus may simply imply ecological adaptation by *Phymanthus* to different microhabitats. Both *P. strandesi* and *P. loligo*, for example, occur on shallow reef flats, but they occupy different microhabitats—the former aggregate themselves at high densities on seagrass beds, while the latter are usually scattered in holes of dead coral caves. *P. strandesi* has prolonged and continuous gametogenesis which may increase the probability for successful recruitment. Conversely, synchronous maturation of gametes peaked in Jan. for *P. loligo*, and brooding anemones occurred between Jan. and Apr. (Lin 1999). Young anemones found in the coelenteron of *P. loligo* (Lin 1999) suggest that larval development could occur under maternal protection, thus ensuring successful settlement after release.

In conclusion, *P. strandesi* is a small and dioecious actiniarian distributed contagiously in seagrass beds. The distribution of *P. strandesi* was signifi-

cantly correlated with the presence of the seagrasses, *Thalassia hemprichii* and *Halodule uninervis*. Gametogenesis examined by paraffin section showed no distinct developmental pattern among monthly samples, suggesting that *P. strandesi* might reproduce continuously throughout the year. Although with a small body size and low fecundity, the large eggs, continual gametogenesis, and contagious aggregation in the seagrass bed might ensure successful sexual reproduction in *P. strandesi*.

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小琉球產柱形瘤海葵之分布與有性生殖

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從 1997 年 7 月到 1998 年 6 月在小琉球蛤板海草床區研究柱形瘤海葵的分布與生殖。柱形瘤海葵分布在珊瑚礁岩盤的潮間帶，平均密度為每平方公尺 511 隻。柱形瘤海葵分布呈現聚集性且與泰來草與蝦草的出現成正相關。柱形瘤海葵為小型雌雄異體的海葵，平均足盤直徑為 0.32 公分。大部分的柱形瘤海葵為無法辨識性別的個體，其足盤直徑與雄性個體的足盤直徑顯著地小於雌性個體的足盤直徑。雌性個體的平均孕卵數為 294 個卵，而所釋放成熟卵的卵徑為 500 到 560 微米。組織切片檢查柱形瘤海葵每月配子之發育並無明顯的週期性，顯示柱形瘤海葵可能屬於全年生殖的海葵。雖然柱形瘤海葵的個體小且孕卵數低，可是聚集性的分布增加個體的密度，且全年性的配子發育，可以確保柱形瘤海葵有性生殖的成功。

關鍵詞：海葵，有性生殖，分布，生殖週期，海草床。

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