

Spatial Variability of Size and Sex in the Tropical Corallimorpharian *Rhodactis* (= *Discosoma*) *indosinensis* (Cnidaria: Corallimorpharia) in Taiwan

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(Accepted October 21, 1994)

Chao-Lun A. Chen, Chang-Po Chen and I-Ming Chen (1995) Spatial variability of size and sex in the tropical corallimorpharian *Rhodactis* (= *Discosoma*) *indosinensis* (Cnidaria: Corallimorpharia) in Taiwan. *Zoological Studies* 34(2): 82-87. Spatial variability in size and sex and sexual expression in the tropical corallimorpharian *Rhodactis* (= *Discosoma*) *indosinensis* Carlgren, 1943, were studied at Wanlitung in southern Taiwan (120°41'E; 22°01'N). *Rhodactis indosinensis* formed three bowl-like aggregations in the study site. The mean body sizes of *R. indosinensis* individuals were significantly larger in the middle of an aggregation than at the margin. Females were located in the middle of each aggregation, and males were scattered around the margins. When mature females were transplanted from the middle of the aggregation to the margin, they had significantly decreased in size and changed into males by eight months later. When reproductively inactive polyps were transplanted from the margin of the aggregation to the middle, they had increased in size and developed into males by eight months later. This positional separation of the sexes may result from different environmental factors which exist between the middle and the margin of an aggregation.

Key words: Sex change, Size variability.

Many anthozoans exhibit unequal spatial distribution of gamete development within clones or colonies. This phenomenon occurs in some clonal sea anemones and hard corals (Francis 1973a,b 1976, Chornesky and Peters 1987, Soong and Lang 1992). For example, within aggregations of the gonochoristic sea anemone *Anthopleura elegantissima*, most polyps located at the interclonal border are small and infertile and have low fission rates. In contrast, polyps in the center of the clone are typically larger and fertile (Francis 1976). In the hermaphroditic hard coral, *Porites asteroides*, fertility decreases gradually from the center to the margins of the colony (Chornesky and Peters 1987). This pattern implies that polyps at the margin of a clone or colony may be younger or that they

receive more stress, either abiotic, biotic or both, than those in the center, giving rise to an unequal spatial distribution of gametogenesis in these sea anemones and hard corals.

Sexual determination in sea anemones has been suggested to be genetically strict gonochoristic with unisexuality of individual clones, and absence of observed sex changes in individuals over time (for review, see Fautin 1990, Shick 1991). However, some hermaphroditic species, e.g., *Epiactis prolifera*, show an environmental role in the determination of sex (Dunn 1975, Fautin and Chia 1986; for review see Fautin 1990, Shick 1991). *E. prolifera* first mature as females, and then grow and become hermaphrodites, suggesting that sexual expression in *E. prolifera* is closely

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correlated with size (Dunn 1975).

Rhodactis indosinensis is an aggregative tropical corallimorpharian closely related to sea anemones and hard corals, and is distributed in shallow waters of eastern Asia (Carlgren 1943). *R. indosinensis* is gonochoristic, females being larger than males, and it spawns annually in May to June (Chen et al. 1995). Using *R. indosinensis* as subjects in this study, we examined two theses: Does the spatial distribution of polyp size and gamete development occur in this corallimorpharian, and is sexual expression in *R. indosinensis* determined environmentally?

MATERIALS AND METHODS

This study was conducted at Wanlitung, southern Taiwan (for description, see Chen et al. 1995). *R. indosinensis* formed three large, bowl-like aggregations in the low tide zone of the study site. The three aggregations were irregular in outline and were labelled A, B, and C, moving seaward from the shore (Fig. 1). The longest and shortest diameters of each aggregation were measured. Dimensions of aggregation A were 4.2 m × 2.5 m, of B were 2.5 m × 1 m, and of C were 2.4 m × 1 m. The depth of water at each bowl-like aggregation varied as tides fluctuated, but approximate low-tide water depth at aggregation A was

66 cm, at B was 60 cm and at C was 56 cm.

Size distribution within aggregations

The oral disc diameter of *R. indosinensis* was used as a parameter of size (Chen et al. 1995). Transects were established along the short and long axes of each aggregation (Fig. 1). By definition, "middle" was where the two transect lines crossed, and "margin" was the terminal end of each transect line (Fig. 1). Six quadrats (28 cm × 24 cm), three at the middle and three at the margin, were established in each aggregation. The oral disc diameters of polyps within these quadrats were measured monthly from May 1989 to April 1990. The mean sizes of polyps in the middle and margin quadrats were compared within and between aggregations by three-way ANOVA (Sokal and Rohlf 1981).

Sexual distribution within aggregations

Sexes of *R. indosinensis* polyps were determined in the field by the color and shape of gamete bundles (Chen et al. 1995). Those polyps which had no visible gametes were classified as reproductively inactive and this was confirmed microscopically.

In May 1990, six quadrats (three middle and three margin) were randomly established in each aggregation. All polyps in the 18 quadrats were dissected in situ to check their sexes. The sex ratio of polyps within each quadrat was calculated and tested for departure from parity using a Chi-square test (Sokal and Rohlf 1981).

Transplantation experiments

Transplantation experiments were conducted to test whether sexual expression in *R. indosinensis* polyps is dependent on location within an aggregation. *R. indosinensis* firmly attaches itself to dead coral skeleton. Pieces of coral skeleton with attached *R. indosinensis*, were chiseled off and transplanted to the middle and margin of each aggregation. The pieces of coral skeleton were fixed by use of nails and wires to prevent washout from wave action. The sex of each transplanted polyp was determined by the presence of gamete color. All transplanted polyps were individually checked monthly to confirm their presence and condition. The oral disc diameters of all transplanted polyps were measured at the beginning and at the end of each experiment.

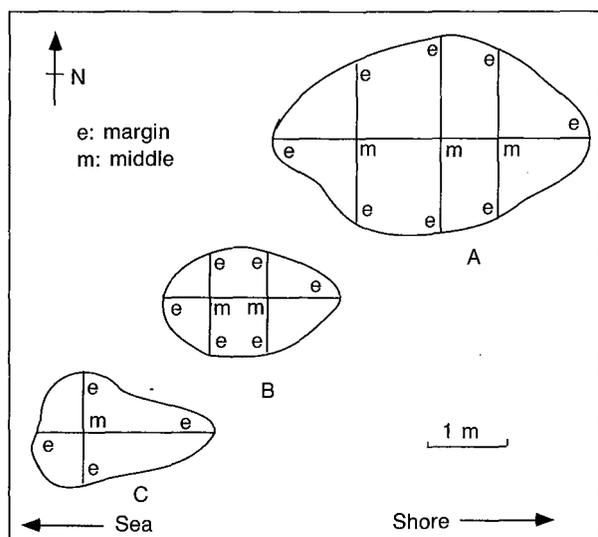


Fig. 1. Position of the three monitored aggregations (A, B and C) along the coastline of Wanglitung, southern Taiwan. Transect lines were established along the axes and quadrats were set at the margins (e) and middle (m) of each aggregation.

In April 1988, 20 females from the middle of each aggregation were transplanted to the landward margin of that aggregation. In their new location, they were occasionally exposed to the air during some spring low tides. During the next spawning period, i.e., twelve months later, they were removed and their gamete development was examined histologically.

In August 1989, the same experiment was repeated for a period of eight months. In addition, 20 reproductively inactive polyps that were located initially at the margin of each aggregation were transplanted to the spaces where females had been removed earlier. Sexes of these polyps were examined histologically at the end of the experiment in April 1990. A student *t*-test was used to determine any size changes of the transplanted polyps before and after transplantation (Sokal and Rohlf 1981).

RESULTS

Size distribution within aggregations

The mean body sizes of *R. indosinensis* (Table 1) were significantly larger in the middle of an aggregation than at the margin (ANOVA, $F(1,969) = 62.46$, $p < 0.05$, Table 2). In addition, there were correlated relations between size and particular aggregations and locations (ANOVA, $F(2, 969) = 12.03$, $p < 0.05$, Table 2) and locations and months (ANOVA, $F(11, 969) = 6.90$, $p < 0.05$, Table 2). Overall, size differences of polyps showed the same trends in these three aggregations. All middle polyps were significantly larger than those on the margins during the monthly surveys (ANOVA, $F(22, 969) = 1.97$, $p < 0.05$, Table 2).

Sex-distribution within aggregations

The sex-ratios of *R. indosinensis* in each quadrat were significantly different from parity ($p < 0.05$, χ^2 -test, Table 3). Only females occurred in the middle of each aggregation. In contrast, the sex-ratio in the margin quadrats was biased toward males, but females did occasionally occur there (Table 3).

Transplantation experiments

In April 1989, all 46 survivors of the 60 transplanted females had changed to males. Histological examination of these transplanted female polyps

showed that male gametes had developed to the same stage as those of neighboring untransplanted males. In the second experiment in 1989, of the 40 surviving originally female polyps, 30 had changed to males, while ten were reproductively inactive. The body sizes of survivors were significantly smaller than before transplantation ($t = 7.39$, $n = 100$, $p < 0.05$, Fig. 2).

In April 1990, 33 survivors remained from the 60 transplanted reproductively inactive, marginal polyps and now consisted of 30 males and three reproductively inactive polyps. The body sizes of these survivors had significantly increased compared to before transplantation ($t = 2.03$, $n = 93$, $p < 0.05$, Fig. 2).

DISCUSSION

This study has revealed two phenomena pertaining to *R. indosinensis*. First, spatial heterogeneity of size and sexual distribution exists within an aggregation, and second, a change in size and sexual expression occurs after transplantation of polyps.

Body size in sea anemones has been shown to be dependent on many different factors in-

Table 1. The mean and standard deviation (sd) of polyp size (mm) at the margin or middle of each aggregation

Aggregation	Margin (mean \pm sd)	Middle (mean \pm sd)
A	43.8 \pm 11.9	47.5 \pm 14.6
B	43.1 \pm 9.7	44.9 \pm 14.8
C	40.0 \pm 13.2	50.9 \pm 13.2

Table 2. Three-way analysis of variance for the mean size of polyps

Source of variation	df	MS	F value
Aggregation	2	172.88	0.095n.s.
Location	1	9,425.81	62.46**
Month	11	438.92	0.42n.s.
Aggregation X Location	2	1,815.5	12.03**
Aggregation X Month	22	281.08	0.94n.s.
Location X Month	11	1,040.77	6.90**
Aggregation X Location X Month	22	297.89	1.97**
Error	969	150.92	

n.s.: not significant; **: $p < 0.01$; df: degrees of freedom; MS: mean square.

Table 3. Total number of polyps, number of males, number of females, and sex-ratio from each quadrat at two different positions within each of the three monitored aggregations in May 1990. Number of sexual indeterminate polyps is not given

Position	Middle				Margin				
	Aggre.	Total	Male	Female	ratio**	Total	Male	Female	ratio**
A		16	0	11	0:11	15	12	0	12:0
		17	0	15	0:15	19	15	2	7.5:1
		20	0	17	0:17	19	12	4	3:1
B		18	0	15	0:15	20	12	5	2.4:1
		17	0	17	0:17	13	7	0	7:0
		17	0	15	0:15	15	9	3	3:1
C		16	0	14	0:14	15	10	0	10:0
		17	0	12	0:12	16	9	1	9:1
		16	0	10	0:10	18	14	2	7:1
Total		154	0	126	0:126	150	100	17	5.9:1

** : sex-ratio significantly biased from 1:1 (χ^2 -test, $p < 0.01$).

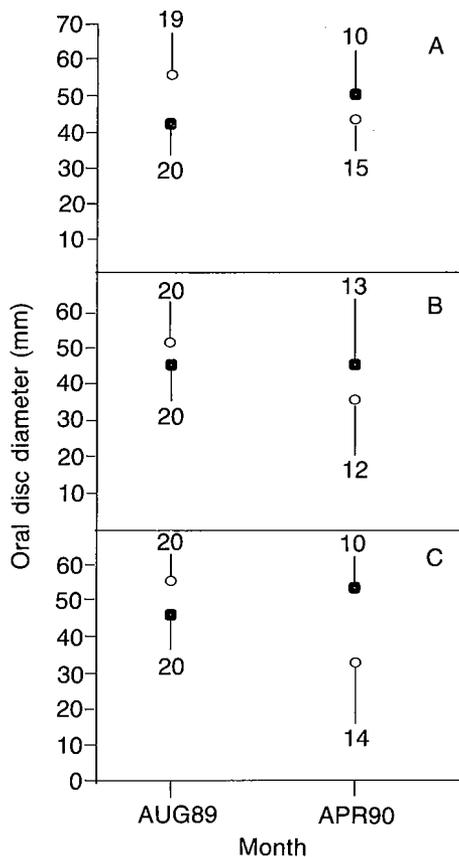


Fig. 2. Size change of transplanted polyps between August 1989 and April 1990 in each aggregation. The point is the mean value and the vertical bar indicates + or - 1 SD of oral disc diameter. The sample size is shown either above or below the bars. Open dot: females transplanted from the middle to margin. Black dot: reproductively inactive polyps transplanted from the margin to the middle.

cluding feeding, exposure to water and temperature (for review, see Shick 1991, Lin et al. 1992). Due to the similarity in body form between sea anemones and corallimorpharians (both are skeletonless anthozoans), we suggest that the growth of corallimorpharians is also indeterminate, and body size may be influenced by environmental factors. Polyps of *R. indosinensis* are small when they occur around the periphery of aggregations where they are exposed to the air more frequently than those in the middle of the aggregation. Thus, the small size of marginal polyps might be due to exposure to stressful conditions. In *R. indosinensis*, males are smaller than females. This result is congruent with the evidence in *Epiactis prolifera* that sex is closely correlated to size (Dunn 1975).

Spatial heterogeneity of sexual distribution within aggregations is characteristic in *R. indosinensis*. However, spatial heterogeneity of fertility occurs in other anthozoans. The reproductively mature and brooding polyps of a Caribbean coral, *Porites asteroides*, are located in the center of the colony (Chornesky and Peter 1987). In nine species of Panamanian corals (Soong and Lang 1992) and ten coral species of the Great Barrier Reef (Wallace 1985, Willis 1987), infertile polyps are located at the margins (sterile zone) of the colony (Wallace 1985) and fertility decreases gradually from the center to the margin. In these cases, it has been proposed that polyps adjacent to the sterile zone are younger than ones in other areas of colonies (Wallace 1985, Willis 1987, Soong and Lang 1992). The results of manipulations, simulating natural wounds in three massive corals

have provided evidence that the location of polyps within a colony determines fertility (Soong and Lang 1992). Fertile polyps are concentrated in the center of clones of the sea anemone *Anthopleura elegantissima*, while marginal polyps are specialized for aggression toward members of other clones (Francis 1973a,b 1976). In *R. indosinensis*, the fact that size changes exhibited patterns both from larger to smaller and smaller to larger provides strong implication for our hypothesis that it is the polyp's relative position within the aggregation that influences size and sex maturation rather than the polyp's age.

R. indosinensis is a "true sex changer" as defined by Policansky (1982) in that the same organism may function as one sex during one breeding season and as the other sex during another. Genetic or environmental factors both can mediate sexual expression in various animals (Charnov 1977 1982) and plants (Freeman et al. 1980, Policansky 1982). For the sea anemone *Actinia tenebrosa* sex is genetically fixed so that translocation does not change the gender of polyps (Ayre 1988). In contrast, the change from female to male in transplanted polyps of *R. indosinensis* indicates that sexual expression in this corallimorpharian is labile and environmentally mediated.

We infer that the sex change of *R. indosinensis* fits the size-advantage model developed by Ghiselin (1969) in which natural selection should favor sex change over dioecy when a polyp's reproductive success as a male or a female is closely related to age or size, and where the relationship is different for each sex (for a review, see Charnov 1982). For example, although natural sex change from male to female in *R. indosinensis* polyps was not observed in this study, selection may cause a *R. indosinensis* polyp to function as a male when small, but as a female when it becomes larger. In this study, the body size of females decreased sharply after transplantation, suggesting that sexual expression in *R. indosinensis* favors the "cheaper" or "less costly" gender under energetically less favorable conditions (Charnov 1982, Frank and Ian 1988). We also suggest that the relationship between size, sex and location of polyps within aggregations could be simply that location determines size, and then size determines sex. Based on this, the marginal polyps transplanted to the middle of an aggregation could have grown enough to develop into females, given enough time.

Generally, a clone has only one sex, as in the corallimorpharian *Corynactis californica* (see Holts and Beauchamp 1993) or one mode of asexual

reproduction, as in the sea anemone *A. elegantissima* (see Francis 1976). Since polyps of *R. indosinensis* within an aggregation are gonochoristic, and have three different asexual reproductive modes (Chen et al. 1995), the clonality of the aggregations is questionable. Assuming that an aggregation of *R. indosinensis* is a clone and the sex of polyps can change in either direction, the spatial heterogeneity of sexual distribution may occur in the following scenario. When a larva settles on the substratum, it develops as a male when it is small in size (Chen et al. 1995) and exposed to disturbance and spatial competition with other sessile organisms. After extending the area of the aggregation via asexual reproduction, the larger polyps, now in the center of the aggregation, become females. The marginal polyps still remain small-sized males. If size decreases via asexual reproduction, relocation of polyps, physical wave action or cyclones, then females change to males. In contrast, assuming that an aggregation of *R. indosinensis* is formed by more than one clone, (i.e., random settlement of larvae from sexual reproduction), size-mediated sexual expression may still cause larger polyps to become females in low-stress positions within the aggregation, while smaller polyps at the margin of the aggregation remain males. Further information regarding the genotypes of individuals belonging to an aggregation is required before these alternative scenarios can be evaluated.

Sex change of the corallimorpharian *R. indosinensis* is related to the location and size of polyps. This paper provides the first reported case of this phenomenon for the gonochoristic anthozoans. Flexibility in the expression of gender depending on location within an aggregation may be an adaptive strategy for efficient investment in sexual reproduction evolved by the sessile corallimorpharian *R. indosinensis*.

Acknowledgements: We thank Drs. D. G. Fautin, J. L. Simon, K. Soong, L. L. Liu, and L. S. Fang for encouragement and reviewing the manuscript; Dr. B. L. Willis, Ms. G. Brodie, B. J. Norris, L. Chen, Mr. B. Stobart, K. Martin-Smith, P. Spencer (James Cook University, Australia) and Dr. N. E. Chadwick-Furman (Israel) for final revision and Ms. M. L. Chang-Lai for helping with field collection. Thanks also to Dr. D. G. Fautin for her advice on the species name. Special thanks are due to Ms L. Chen for typing and correcting the manuscript. This paper is adapted from a thesis submitted to the National Sun Yat-sen University by C. A. Chen

in partial fulfilment of the requirements for a MSc degree.

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臺灣產印支圓盤擬珊瑚海葵之個體大小及性別之空間變異

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本研究報導在台灣南部萬里桐淺水海域，印支圓盤擬珊瑚海葵的個體大小及性別的空間變異。印支圓盤擬珊瑚海葵在研究地點形成 3 個「碗狀」的大群集。位於群集中央的個體顯著的大於群集邊緣的個體。雌性個體位於群集的中央，而雄性個體則散布在群集的邊緣。個體遷移實驗顯示，位於群集中央的雌性個體在搬遷到群集邊緣 8 個月後，個體顯著變小，且發育成雄性。而位於群集邊緣性別不可辨的個體，在搬遷到群集中央 8 個月後，個體顯著變大，發育為雄性。我們推測印支圓盤擬珊瑚海葵在其空間分布中之某些環境因素，為其個體大小及性別表現的決定因子。

關鍵詞：性轉換，大小變異。

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