

SEXUAL REPRODUCTION OF THE ALCYONACEAN CORAL *LOBOPHYTUM PAUCIFLORUM* IN SOUTHERN TAIWAN

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ABSTRACT

Sexual reproduction of the alcyonacean octocoral *Lobophytum pauciflorum* (Ehrenberg) in Nanwan Bay, southern Taiwan was studied by histological examinations of gonad development on monthly samples collected from tagged colonies between March 2001 and November 2002. A sample of 15 aggregations of *L. pauciflorum* in an area of 10 × 30 m was also examined in July 2002 to determine reproductive traits. *Lobophytum pauciflorum* is a gonochoric broadcast spawner and the sex ratio of the population is 1:1. *Lobophytum pauciflorum* often forms aggregations in which all of the colonies have the same sex. This suggests that the colonies in an aggregation are likely formed by asexual fission. Most (>50%) of the colonies in the female and male aggregations had gonads when their diameters were 10–15 and 5–10 cm, respectively. The average maximum fecundity was 16 eggs polyp⁻¹. Mature eggs were 400–870 μm in diameter. Oogenesis and spermatogenesis took about 12 mo. Spawning occurred from July–September during late summer to early autumn. This spawning season is consistent with the environmental conditions such as warmer water temperatures and new bare substrate created by typhoon disturbances that favor the survival and settlement of coral larvae.

Research on sexual reproduction of soft corals has increased enormously in the last two decades. These studies have revealed a wide variety of reproductive patterns among coral species and geographical regions. However, most studies have been concentrated in relatively few geographical locations, mainly the Red Sea (e.g., Benayahu, 1997a) and the Great Barrier Reef, Australia (e.g., Alino and Coll, 1989). Other regions with abundant soft corals, particularly the West Pacific islands, have received little attention. Research on soft coral reproduction in these areas is needed for a global perspective of life history patterns and a better understanding of the adaptive significance of reproductive traits in soft corals (Benayahu, 1997a).

The characteristics of sexual reproduction in soft corals are diverse. Benayahu (1997a) concluded that there are at least three modes of sexual reproduction in alcyonacean corals; i.e., broadcasting of gametes, external surface brooding, and internal brooding of planulae. The majority of tropical Alcyoniidae studied to date are gonochoric broadcast spawners with external fertilization and larval development (e.g., Alino and Coll, 1989; Benayahu, 1997a). Many broadcast spawning alcyonaceans have an annual spermatogenic cycle while their oogenesis is completed over a prolonged period with overlapping oogenic cycles (Yamazato et al., 1981; Alino and Coll, 1989; Benayahu, 1997a).

Broadcast spawning soft corals have been found to have short, seasonal, and synchronized spawning episodes (Alino and Coll, 1989; Benayahu, 1997a), similar to those of scleractinian corals (Harrison and Wallace, 1990). On the Great Barrier Reef, Australia, the soft corals spawn during the multispecies mass spawning event (Babcock et al., 1986; Alino and Coll, 1989). In contrast, the Red Sea soft corals ex-

hibit an extended reproductive season (Benayahu, 1997a), as do the scleractinian corals in that region (Shlesinger and Loya, 1985).

Lobophytum pauciflorum (Ehrenberg, 1834) is abundant and widely distributed in Indo-West Pacific reefs (Tursch and Tursch, 1982; Verseveldt, 1983; Benayahu, 1997b, 2002). It forms aggregations of physiologically discrete colonies (Fan, pers. obs.). The colonies encrust reef surfaces with low stalks and erect lobes. As is typical for this genus, polyps of *L. pauciflorum* are dimorphic with autozooids functioning as feeding polyps and bearing gonads. Little information is available on its reproductive biology other than that it is a gonochoric spawner and that it participates in a mass spawning event on the Great Barrier Reef (Alino and Coll, 1989). *Lobophytum pauciflorum* is one of the most abundant soft corals on coral reefs of southern Taiwan. The present study describes sexual reproductive characteristics of *L. pauciflorum* in southern Taiwan, including its sexuality, size structure, reproductive mode, spermatogenic and oogenic cycles, month of spawning, colony size at sexual maturity, and relationship between colony size and fecundity. The results are compared with reproductive data for *L. pauciflorum* from the Great Barrier Reef and other *Lobophytum* species.

MATERIALS AND METHODS

STUDY SITE.—This study was conducted on coral reefs in Nanwan Bay, southern Taiwan (21°55.950' N; 120°44.691' E) from March 2001–November 2002. All corals used in this study were collected monthly or bimonthly from the reef slope at 7–9 m depth.

SEXUAL REPRODUCTION.—Large colonies (>13 cm in diameter) of *L. pauciflorum* were randomly selected and tagged in March, April, and July 2001. Twenty-three female and five male colonies were identified after examination of spicules and gonads in these tagged colonies. Pieces, each 2 cm in diameter, were cut off at least 3 cm from the edge of tagged large colonies. To prevent excessive damage to the colonies, not all of the tagged colonies were sampled on each collection date. Each sample was placed in a plastic bag with a waterproof label. The color of eggs and sperm sacs of each sample was scored when they were alive. Then, the samples were fixed with 10% formalin in seawater for at least 24 hrs. Polyps were dissected by fine-point forceps under a binocular microscope. Wet preparations of their mesenteries were made and examined under a microscope. The sex of each colony was determined and the diameters of oocytes or sperm sacs were measured from each colony using a calibrated ocular micrometer. Only oocytes with apparent color and > 400 μm in diameter were scored as mature. Histological sections were used to confirm the developmental stage of oocytes and sperm sacs. For histological preparation, samples were fixed with 10% formalin in seawater for at least 24 hrs, rinsed in freshwater, decalcified in 8% formic acid, and stored in 70% alcohol. Tissue samples were dehydrated with increasing concentrations of alcohol, cleared with xylene, and embedded in Paraplast. Serial sections 6–8 μm thick were prepared and stained with Mayer's hematoxylin and eosin. These slides were examined for gamete development under a compound microscope at magnifications up to 1000 \times . The diameters of oocytes and sperm sacs were assigned to arbitrary size classes in 50 μm intervals (i.e., 0–49, 50–99 μm , etc.) to determine the size frequencies of gonads. The monthly variation in size frequencies for oocytes and sperm sacs of different size classes as well as the monthly variation in percentages of colonies containing mature gonads were used to determine the seasonal pattern of gametogenesis and spawning among colonies.

A sample of 15 aggregations of *L. pauciflorum* in an area of 10 \times 30 m was collected and examined before the predicted spawning month; i.e., in July 2002, to determine sex ratio, size structure of male and female colonies, and the relationship between colony size and reproductive traits such as sexual maturity and fecundity. In total, 146 colonies (78 female and 68

male) in the aggregation were measured and sampled. Two perpendicular diameters across the colony center were measured and their average was taken as the diameter of the colony. A piece ≥ 2 cm was collected from the center of each colony. All colonies in an aggregation were counted and sexed. The samples were fixed with 10% formalin in seawater for at least 24 hrs. Samples were examined at 64 \times magnification under a dissecting microscope. Colonies were considered sexually mature if oocytes or sperm sacs were visible under a dissecting microscope. Five polyps selected randomly from each female colony were dissected and the mean number of eggs per polyp was used to estimate polyp fecundity.

RESULTS

Histological sections revealed that all colonies of *L. pauciflorum* are gonochoric. Female and male gonads develop along mesenteries within polyp cavities in the autozooids of separate colonies. Autozooids bear gonads on up to six of the eight mesenteries, with early stage oocytes developing proximally and mature oocytes distally on mesenteries relative to the oral disc of polyps. Gonad maturation occurred synchronously within and between colonies. Maturation of oocytes was accompanied by a gradual color change from white to deep purple. Mature oocytes were first recorded around May 2001 and 2002, 3–4 mo prior to spawning. Maturation of sperm sacs was accompanied by a gradual color change from transparent to white. Mature sperm sacs were first recorded around June 2001 and 2002, 2–3 mo prior to spawning. The mature eggs and sperm sacs reached a diameter of 400–870 and 200–525 μm , respectively. The maturity of gonads before spawning was confirmed by histological sections. For mature eggs, the nuclei migrated toward the periphery of oocytes and became dented at one side. The mature sperm sacs had lumens. Spermatozoa were arranged with the heads located peripherally and the tails projecting toward the lumen.

GAMETOGENESIS.—Monthly variation of size-frequency distributions in oocyte diameters and the percentage of colonies containing mature eggs in *L. pauciflorum* from March 2001–November 2002 indicated a clear annual oogenic cycle (Figs. 1, 3A). Early oocytes appeared in mesenteries in March 2001, and continued to grow until September. Mature eggs with purple coloration appeared in May 2001 and 2002 (Fig. 3A). The color gradually deepened with time. All colonies ($n = 11$) had mature eggs on 4 September 2001 (lunar day 17, full moon phase) and had spawned, as evidenced by the disappearance of eggs in the tagged colonies when sampled on 21 September 2001 (lunar day 5, new moon phase). In 2002, all samples contained mature eggs in June ($n = 12$) and July ($n = 9$), 73% had mature eggs in August, 46% had mature eggs in September, and none of the samples had mature eggs in November. The sharp decline in colonies containing mature eggs in September 2001 as well as the gradual decline from July–September 2002 were probably the result of spawning.

Monthly variation in size-frequency distributions of sperm sac diameters and percentages of colonies containing mature sperm sacs also indicated a clear annual spermatogenic cycle (Figs. 2, 3B). Early sperm sacs appeared in mesenteries in April 2001, and continued to grow until August. All colonies ($n = 3$) had mature sperm sacs in June 2001, 75% had mature sperm sacs in September, and none of the samples had mature sperm sacs in November. The gradual decline in colonies containing mature sperm sacs from August–November 2002 was probably the result of spawning.

SEX RATIO.—The 15 aggregations in an area of 10 \times 30 m were composed of seven female and eight male aggregations. The number of colonies in each of the female

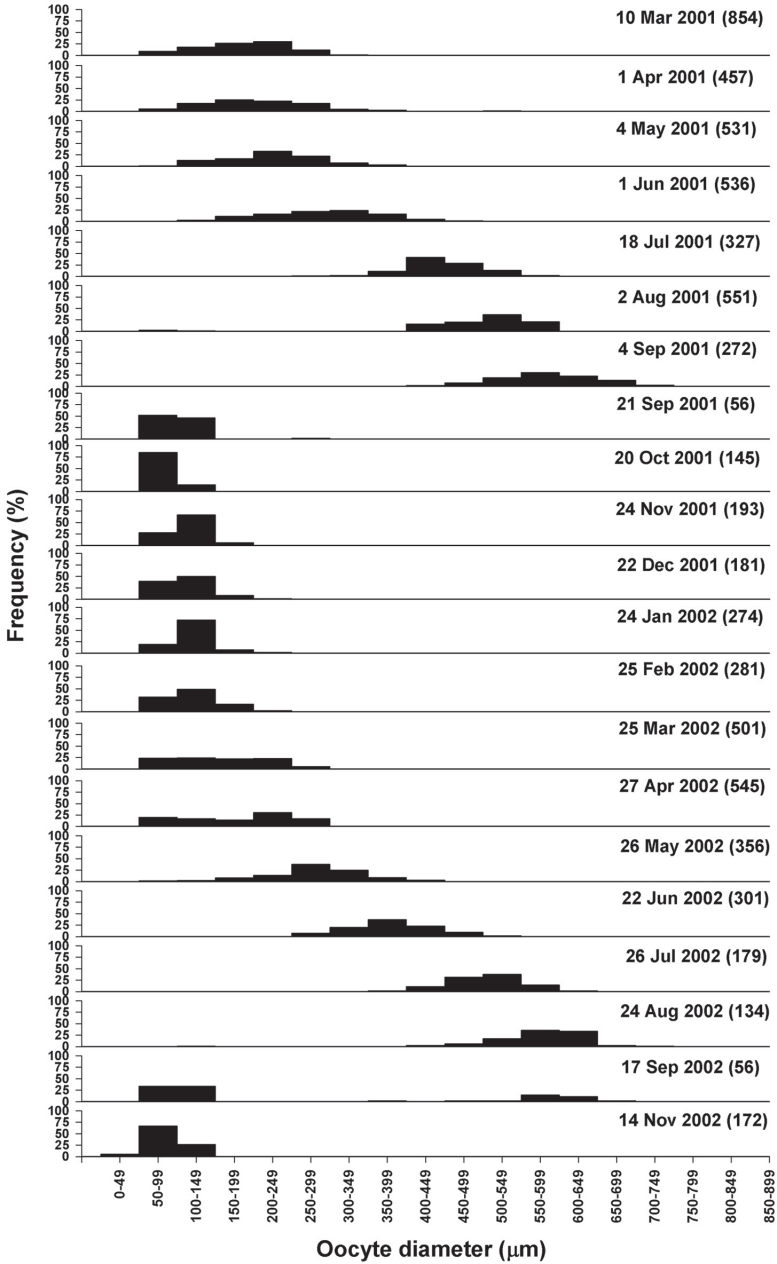


Figure 1. Monthly size-frequency distributions of oocyte diameters of *Lobophytum pauciflorum* in Taiwan. Numbers in parentheses indicate number of oocytes measured each month.

and male aggregations ranged from 2–49 and 4–20, respectively. All colonies in each aggregation were either of the same sex or lacked gonads. The total number of colonies belonging to the seven female and eight male aggregations was 92 (78 with eggs and 14 with no gonads) and 78 (68 with testes and 10 with no gonads) colonies, re-

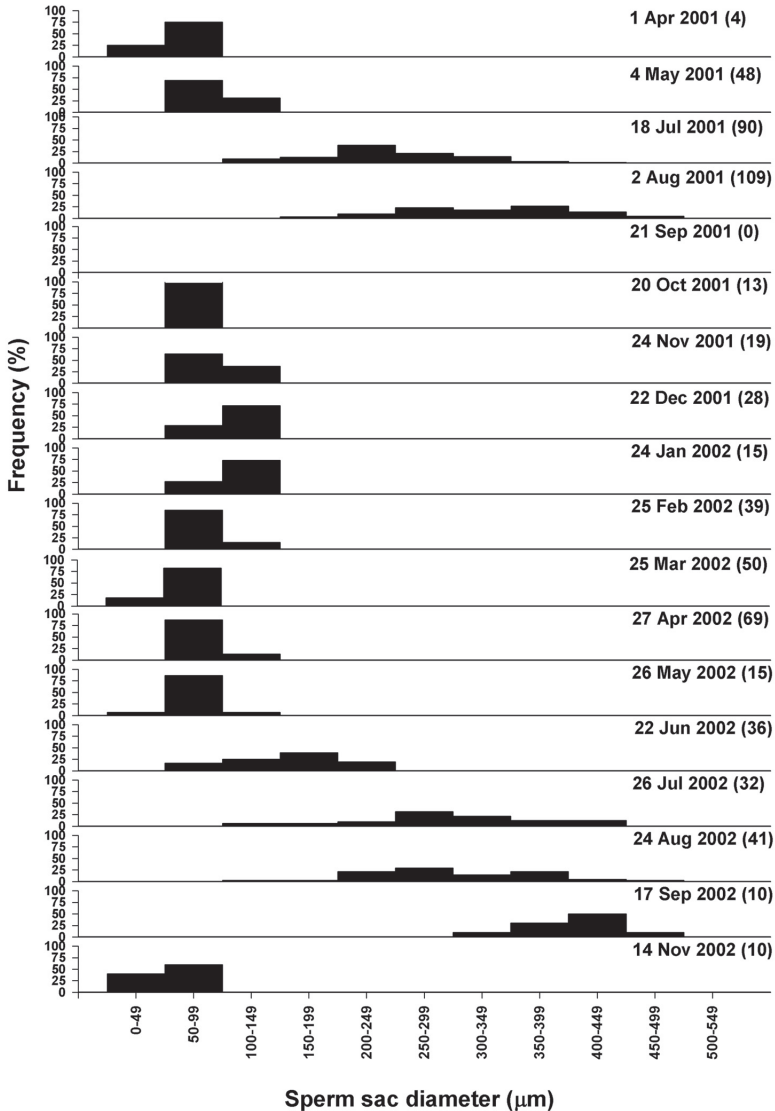


Figure 2. Monthly size-frequency distributions of sperm sac diameters of *Lobophytum pauciflorum* in Taiwan. Numbers in parentheses indicate number of oocytes measured each month.

spectively. The sex ratio did not differ from 1:1 for both aggregations ($\chi^2 = 0.07$, $P = 0.77$) and colonies (78: 68, $\chi^2 = 0.68$, $P = 0.41$).

SIZE STRUCTURE OF FEMALE AND MALE COLONIES.—The size-frequency distributions of female and male colonies in the 15 aggregations ranged from 9.5–57.5 and 6–42 cm in diameter with the modes at size class 15–20 and 20–25 cm, respectively (Fig. 4). The distributions of female and male colony sizes were similar ($\chi^2 = 16.95$, $P = 0.11$).

COLONY SIZE AT SEXUAL MATURITY.—Most (>50%) of the colonies in female aggregations bore gonads when they reached 10–15 cm in diameter or above, while those in male aggregations occurred at 5–10 cm in diameter (Fig. 5). The minimum

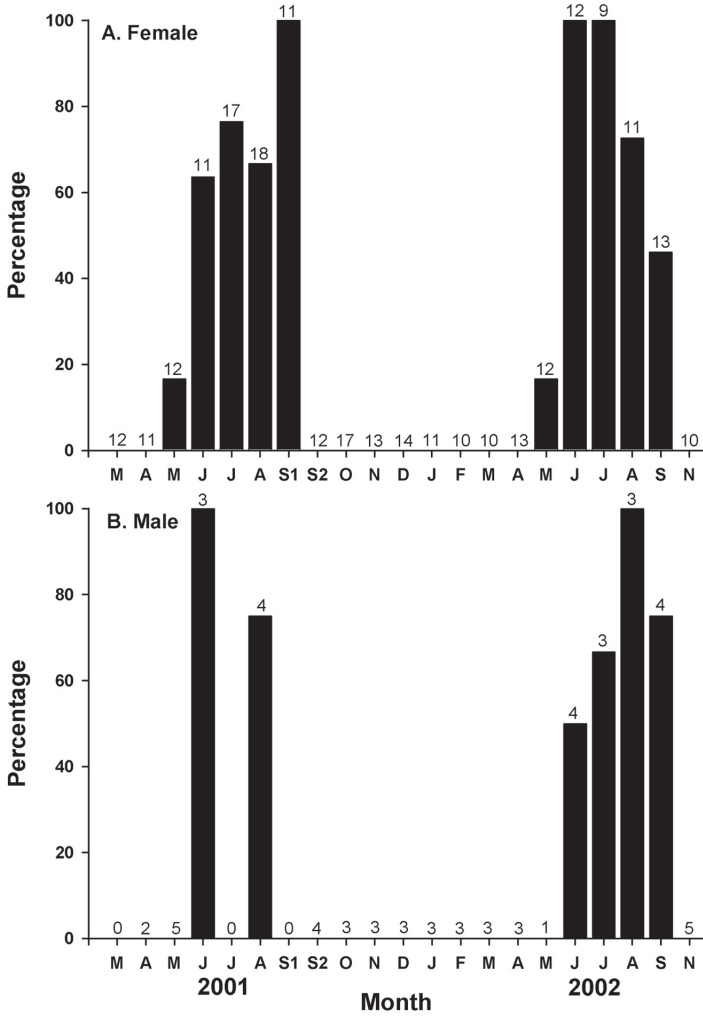


Figure 3. Monthly changes in percentage of colonies of *Lobophytum pauciflorum* containing mature gonads in (A) female colonies and (B) male colonies. Numbers above bars indicate number of colonies sampled. Letters refer to months; S1 and S2 indicate sampling at 4 and 21 September 2001, respectively.

colony size at sexual maturity was 8.0 and 5.5 cm in diameter for female and male colonies, respectively. Colonies < 5.0 cm in diameter were not found or examined in this study.

FECUNDITY.—Fifty-two female colonies ranging from 9.5–53.5 cm in diameter were examined. There was a positive relationship between colony size and the number of eggs per polyp (Fig. 6; $r^2 = 0.30$, $F = 21.8$, $P < 0.001$). An exponential equation ($y = 15.7(1 - e^{-0.05x})$) describes a curve increasing to an asymptote at a value of 15.7. Thus, the predicted average maximum fecundity was 16 eggs polyp⁻¹.

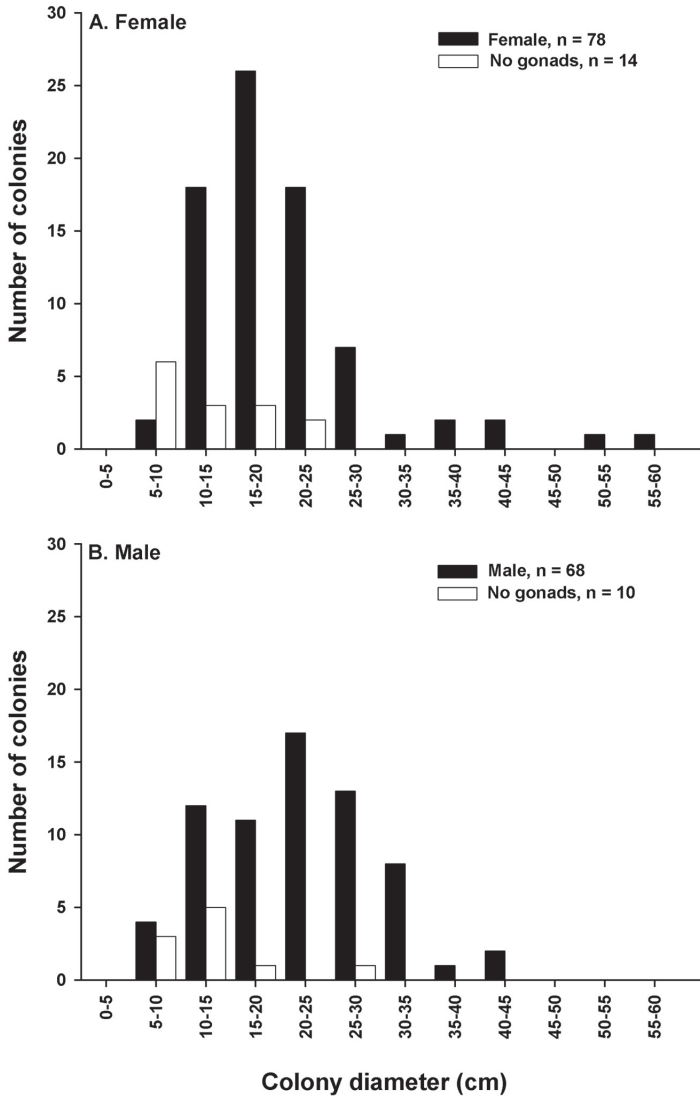


Figure 4. Size-frequency distribution of (A) female colonies and (B) male colonies from 15 aggregations of *Lobophytum pauciflorum* in an area of 10 × 30 m in southern Taiwan.

DISCUSSION

Similar to the other congeneric species, *Lobophytum pauciflorum* is a gonochoric broadcast spawner (e.g., Alino and Coll, 1989; Benayahu, 1997a; Table 1). Gonad structure of *L. pauciflorum* is also similar to that of other congeneric species from the Indo-Pacific reefs, such as *Lobophytum crassum* von Marenzeller, 1886 (see Yamazato et al., 1981) and *Lobophytum compactum* Tixier-Durivault, 1956 (see Michalek-Wagner and Willis, 2001). In these species, gonads are borne in all the mesenteries of a polyp except a pair of dorsal directives, with early stage oocytes developing

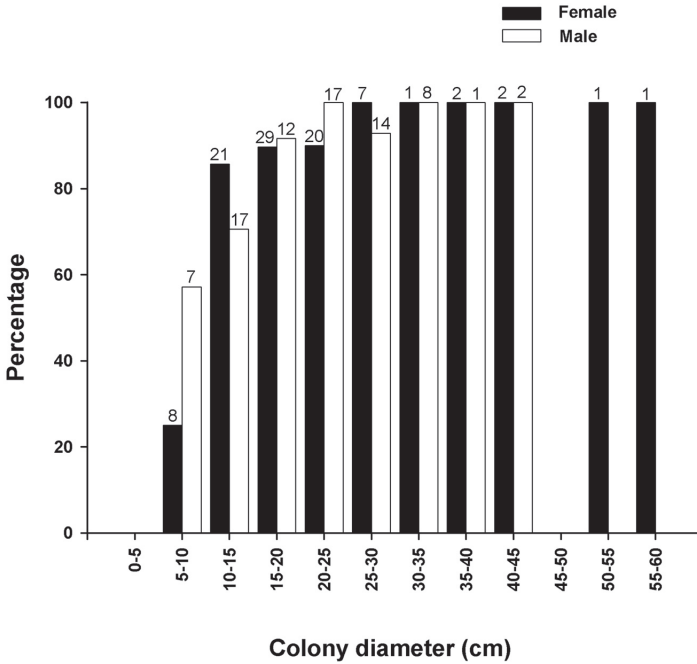


Figure 5. Percentage of colonies of *Lobophytum pauciflorum* with oocytes or sperm sacs per size class (mean colony diameter). Numbers above bars indicate number of colonies sampled.

proximally and mature oocytes distally on mesenteries relative to the oral disc of the polyp (Yamazato et al., 1981).

The oogenic cycle of *L. pauciflorum* in southern Taiwan requires 1 yr, while that of *L. pauciflorum* in the Great Barrier Reef, Australia and other *Lobophytum* species requires > 1 yr with large and small eggs, representing two cohorts, existing simultaneously within autozooids (Shinkarenko, 1981; Yamazato et al., 1981; Alino and Coll, 1989; Michalek-Wagner and Willis, 2001). It seems that the time required for oocyte maturation varies greatly in different alcyonacean species (Benayahu, 1997a).

Lobophytum pauciflorum produced larger mature eggs (400–870 μm in diameter) than did other *Lobophytum* species (Table 1). The greater egg size of *L. pauciflorum* may represent an increased investment in energy storage and survivorship of larvae (Sier and Olive, 1994; Fan and Dai, 1995). However, the fecundity of *L. pauciflorum* was lower (16 eggs polyp⁻¹) than that of *L. compactum* (23 eggs polyp⁻¹) and *L. crassum* (36 eggs polyp⁻¹). It may be regarded as a trade-off between egg size and fecundity in *L. pauciflorum*.

The coloration of the eggs seems to vary for a given soft coral species, even within the same colony on occasion (Alino and Coll, 1989). Mature colored oocytes of *L. pauciflorum* were found 3–4 mo before spawning. Mature oocytes of *L. compactum* appeared 2–3 mo prior to spawning (Michalek-Wagner and Willis, 2001). This is longer than that of most stony corals whose colored eggs appeared several weeks before spawning (Harrison and Wallace, 1990).

The length of the spermatogenic cycle of *L. pauciflorum* in southern Taiwan lasted about 11–12 mo, which resembles that of *L. pauciflorum* in the Great Barrier Reef, Australia (Shinkarenko, 1981) and *L. compactum* (see Michalek-Wagner and Willis,

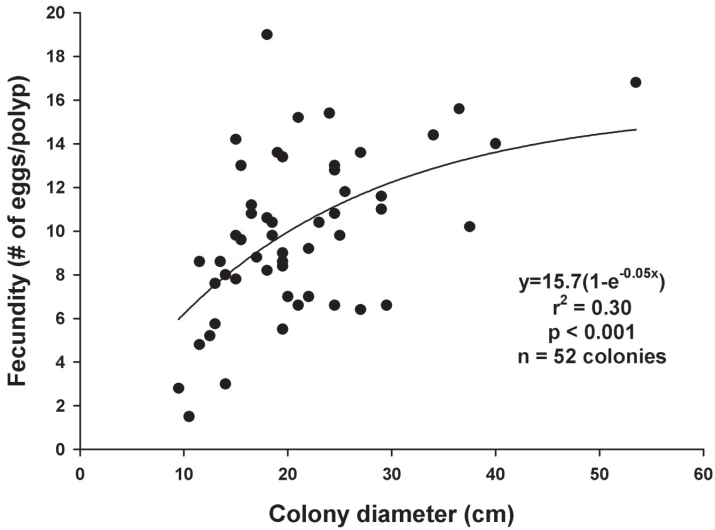


Figure 6. Relationship between polyp fecundity (number of mature oocytes polyp⁻¹) and colony size of *Lobophytum pauciflorum*.

2001), but is 2 mo longer than that of *L. crassum* (see Yamazato et al., 1981). Studies on gametogenic cycles of alcyonaceans have demonstrated that spermatogenesis is completed within 1 yr and is usually shorter than oogenesis (Benayahu, 1997a).

The colony size at sexual maturity of *L. pauciflorum* is smaller than that of *L. crassum* (25 cm, Yamazato et al., 1981). In addition, females of *L. pauciflorum* attain sexual maturity at a larger colony size (10–15 cm) than males (5–10 cm). A similar phenomenon was also found in *Sarcophyton glaucum* (Quoy & Gaimard, 1833) (see Benayahu and Loya, 1986) and *Parerythropodium fulvum fulvum* (Forsk., 1775) (see Benayahu and Loya, 1983).

The sex of colonies in an aggregation of *L. pauciflorum* was the same, indicating that small colonies may have been derived from fission of nearby large colonies. Further, *L. pauciflorum* tends to exist as many small colonies in dense aggregations instead of few large colonies (Fan, pers. obs.). This aggregation pattern of colonies may originate from the growth and fission of original founder colonies. McFadden (1986) demonstrated that colonies of an alcyonacean soft coral on the rocky shores from northern California to British Columbia can increase their rates of particle capture at high flow velocities by forming aggregations of small, clonally replicated colonies. In addition, alcyonaceans may increase their space acquisition by fission because relative growth rates of small colonies are greater than larger ones (Fabricius, 1995). Fission of *L. pauciflorum* may be a strategy to occupy a favorable substratum at faster rates than sexual recruits.

The reproductive season of soft corals in southern Taiwan is April–June for *Sarcophyton crassocaule* Moser, 1919 (see Chou, 2002), May and June for both *Sinularia scabra* Tixier-Durivault, 1970 and *Sinularia exilis* Tixier-Durivault, 1970 (see Wu, 1994), June–August for *Sarcophyton trocheliophorum* von Marenzeller, 1886 (see Chou, 2002), July and August for *Sinularia nanolobata* Verseveldt, 1977 (see Wu, 1994), and July–September for *L. pauciflorum*. The reproductive season of soft corals in the Red Sea also occurs in extended periods and this may lead to temporal

Table 1. Comparison of reproductive characteristics among *Lobophytum* corals. G: gonochoric. -: no data.

Species	Location	Sex	Length of oogenesis (mo)	Length of spermatogenesis (mo)	Egg size (μm)	Egg color	Fecundity (eggs/polyp)	Month of spawning	Size at sexual maturity (colony diam., cm)	Sources
<i>L. pauciflorum</i>	S Taiwan	G	12	11–12	400–870	Purple	16	July–September	10–15 for female 5–10 for male	1
	GBR	G	>12	12	462–693	White	11.5 \pm 1.3	October–February		2
	GBR	G	-	-	600	Green	-	November	-	3
<i>L. crassum</i>	Okinawa	G	24	9	573	-	36	June	25	4
	GBR	G	21	10–12	495–792	Pink, red	4.2 \pm 3.6	November–May		2
	GBR	G	-	-	650	Pink, purple	-	November	-	3
<i>L. compactum</i>	GBR	G	24	12	580–650	Purple, pink	23 \pm 0.6	November	-	3, 5
<i>L. hirsutum</i>	GBR	G	-	-	-	-	-	November	-	3
<i>L. microlobulatum</i>	GBR	G	-	-	600	White	-	November	-	3
<i>L. planum</i>	GBR	G	-	-	600	Green	-	November	-	3
<i>L. sp.</i>	Philippines	-	-	-	-	Pink, green	-	April–May	-	6

1: Present study; 2: Shinkarenko, 1981; 3: Aino and Coll, 1989; 4: Yamazato et al. 1981; 5: Michalek-Wagner and Willis, 2001; 6: Bermas et al. 1992.

reproductive isolation among alcyonaceans (Benayahu, 1997a). However, in contrast, alcyonaceans in the Great Barrier Reef spawn in multispecific spawning episodes (Alino and Coll, 1989). The geographic variation in reproductive timing seen in *L. pauciflorum* from southern Taiwan and the Great Barrier Reef is also found in the scleractinian corals *Echinopora lamellose* (Esper, 1795), *Merulina ampliata* (Ellis and Solander, 1786), *Mycedium elephantotus* (Pallas, 1766), and *Echinophyllia aspera* (Ellis and Solander, 1786). These coral species participate in the mass spawning during early summer in the Great Barrier Reef (Babcock et al., 1986), but delay spawning until the late summer and autumn in southern Taiwan (Fan and Dai, 1995, 1998; Fan 1996; Dai et al., 2000). The timing of reproduction may reflect environmental conditions favorable for the survival of larvae (Giese and Pearse, 1974). The possible advantage for these species of breeding near the end of seasonal disturbances (typhoons and heavy rainfalls) is to increase the substrate availability for settling larvae and to avoid high mortality caused by these disturbances, thus increasing their reproductive success (Shlesinger and Loya, 1985; Fan and Dai, 1995, 1998; Mendes and Woodley, 2002). The favorable environmental conditions for the survival of soft coral larvae during these months is supported by other sympatric alcyonaceans including *S. trocheliophorum* (see Chou, 2002) and *S. nanolobata* (see Wu, 1994), which also spawned during this period. Delay in the reproductive timing of these species in Nanwan Bay may be an adaptation to the local environment.

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