# CHAPTER 6. REPRODUCTIVE ISOLATION BETWEEN MORPHS?

## 6.1 Introduction

The identification of morphological variation within a species, raises the question of whether this represents intraspecific variation or species differentiation. The question is particularly relevant for groups such as corals, where taxonomic criteria are based primarily on morphological characteristics of the skeleton, which may be modified by a myriad of environmental influences. Lang (1984) has discussed a number of non-skeletal characters which may prove useful taxonomically. Reproductive characteristics, such as sexuality (hermaphroditism versus gonochorism) and sperm ultrastructure (Harrison, 1985), may prove to be one of the more important sources of systematic information at higher taxonomic levels. At the species level, a number of recent studies of corals have documented differences in reproductive characteristics between morphologically similar species. Van Moorsel (1983) used differences in seasonality of planulation, numbers of planula produced, and size at onset of reproductive maturity to separate *Agaricia agaricites* into *A. agaricites* and *A. humilis*. Similarly, Kojis (1986) identified two reproductively isolated species within the *Acropora palifera* group studied by Potts (1978), based on differences in breeding and planulating seasonality. Richmond and Jokiel (1984) reported evidence of reproductive isolation between two morphs of *Pocillopora damicornis* in a study of the periodicity of larval release. Differences in reproductive characteristics between morphologically similar species which spawn gametes have also been found. The breeding seasons of *Porites lutea* and *P. lobata* were found to be separated by approximately one month (Kojis and Quinn, 1982a). Studies by Kojis and Quinn (1981) and Babcock (1984, 1986) of *Goniastrea aspera* and *G. favulus* found that the mode of release of reproductive propagules and the buoyancy characteristics of eggs readily separated colonies of these two species.

Electrophoresis has also been used to separate taxonomically difficult species in other animal groups (Rollinson, 1980). The results of electrophoretic studies presented in Chapter 4 indicated that there were no significant differences in allelic frequencies between the convoluted and columnar morphs of *Pavona cactus* for the enzymes assayed. This suggests that the two morphs at Eclipse Island are part of the same interbreeding population. Therefore, further evidence of the taxonomic position of these two morphs was not sought. However, results for a small group of colonies of *Turbinaria mesenterina* showed consistent differences in gene and genotype frequencies between the plate and convoluted morphs, suggesting that two different populations or species had been sampled. Accordingly, evidence from reproductive characteristics was sought as additional information with which to assess the taxonomic position of these two morphs. The ability of individuals or populations to interbreed has been widely accepted as the primary method of defining a species biologically. However, in the absence of any information on sexual reproduction in *T. mesenterina*, it was first necessary to ascertain the mode and timing of reproduction in this species. In this chapter, the gametogenic cycles and reproductive strategies of *T. mesenterina* are examined for evidence of reproductive isolation between the two morphs. The period of gamete development and the timing of release of reproductive products were compared to determine the likelihood of temporal barriers to interbreeding. The age of reproductive maturity, polyp fecundity, and sex ratios were compared for evidence of divergence in reproductive strategies, which might suggest a lack of interbreeding.

Early work on the seasonality of reproduction in tropical marine invertebrates suggested that breeding was continuous, in response to the characteristically slight fluctuations in seasonal environmental parameters at these latitudes (Giese and Pearse, 1974). In Chapter 2 it was shown that seasonal temperature variation is in the order of 10°C at Magnetic Island and Eclipse Island, despite being at a tropical latitude (19°). Correspondingly, recent research on coral reproduction on the Great Barrier Reef has shown that breeding is highly seasonal for spawning species at this latitude (Babcock, 1984, 1986; Harrison *et al.*,

1984; Heyward and Collins, 1985; Oliver, 1985; Wallace, 1985; Willis *et al.*, 1985; Babcock *et al.*, 1986), and at latitudes both 5° higher (Harriott, 1983a, Babcock *et al.*, 1986) and 4° lower (Kojis and Quinn, 1981, 1982a, 1982b; Kojis, 1986; Bothwell, 1982). Moreover, approximately one-third of the scleractinian species on the Great Barrier Reef spawn together during a one-week period in a highly synchronized, mass spawning event (Harrison *et al.*, 1984; Willis *et al.*, 1985; Babcock *et al.*, 1986). Spawning is restricted to the spring and summer months in all hermatypic species so far studied on the Great Barrier Reef. Therefore it was of interest when observations of gametogenic development in *Turbinaria mesenterina* indicated that it spawned in autumn, 4-6 months out of phase with other spawning species. A further objective of the present chapter is to document the reproductive strategy of a coral species whose breeding seasonality is unique on the Great Barrier Reef, looking for clues that will help to elucidate the proximate and ultimate factors controlling gametogenesis and breeding in corals.

## 6.2 Materials and Methods

### 6.2.1 Gametogenic Cycles

Samples were collected from 12 colonies of *Turbinaria mesenterina* from Nelly Bay, Magnetic Island (Figure 8, Chapter 2), at approximately 6 week intervals between March 1981 and June 1982. The 12 colonies sampled included 3 female and 3 male colonies of each of the convoluted and plate morphs. They also included the 10 colonies sampled for growth analysis in Chapter 5 (Section 5.2.2). A further 46 mature colonies in the vicinity of these core colonies were tagged and sampled haphazardly for determination of population synchrony in breeding. All colonies sampled on a regular basis

were greater than 1m in diameter. Samples were fixed in 10% seawater formalin, decalcified in a solution of 3-6% formic acid and 5% formalin, and stored in 70% ethanol once specimens had been dissected.

Oocyte volumes, determined from polyp dissections according to methods described in 6.2.2, were used to follow the course of gametogenic development in the 3 female colonies of the 2 morphs throughout the one year period. Sperm squashes and broken sections of live colonies from the larger pool of tagged colonies were examined for evidence of gamete maturity (Harrison *et al.*, 1984) on sampling dates between October 1981 and June 1982. Male and female colonies of both forms were collected every 6-12 days between 16 October and 24 November 1981 (*i.e.* the period of mass spawning on the Great Barrier Reef), and between 3 March and 22 May 1982 (following observations of motile sperm in many colonies). Colonies were transported to outdoor aquaria, supplied with seawater from a recirculating system. Plankton mesh filters over inlets and outlets were designed to trap eggs in aquaria. Aquaria were monitored daily for the presence of eggs.

Portions of representative samples from all stages of the gametogenic cycle, were prepared for histology, and sections examined to verify interpretations made in dissections. Samples were processed with an automatic tissue processor, using a schedule of 40 minutes in each solution in the dehydrating, clearing and wax impregnating series (Winsor, 1984). Final wax impregnation was accomplished using a vacuum infiltrator. Infiltrated tissues were oriented in individual embedding moulds so that polyps were sectioned both transversely and longitudinally. Blocks were trimmed at 10$\mu$ and sectioned at 6$\mu$ using a rotary microtome. Ribbons were floated on a warm water bath, mounted on a microscope slide with albumen, and dried at 60°C for 24 hours. Sections were stained using Winsor's modification of the Gomori trichrome stain (Winsor, 1984).

Specimens of mature testes for electron microscopy were fixed for 2 hours in 2% glutaraldehyde at ambient temperature, postfixed in 1% $OsO_4$ for 1 hour at 4°C, and embedded in Spurr's resin.

Sections were stained with uranyl acetate and lead citrate, and photographed on a Siemens Elmiskop 102 transmission electron microscope.

### 6.2.2 Polyp Fecundity and Reproductive Effort

Following decalcification, three polyps, located at least 4cm from the colony edge (*i.e.* beyond the immature zone, see section 6.3.1), were dissected from each female colony. Polyps were teased from the surrounding coenenchyme and a longitudinal incision made from the stomodaeum to the base of the mesenteries. The mesenteries, which contain the eggs, were gently separated and the total number of eggs in all mesenteries counted. Mean polyp fecundity at each sampling date was calculated from egg counts for 9 polyps of each morph, except where indicated in Figures 36 and 37.

The length, width and depth of 6 eggs from each polyp were measured using a dissecting microscope with an ocular micrometer. Random numbers were used to select the mesenteries and eggs for measurement. As the fixed eggs maintained the shape imposed by the skeletal architecture of the corallite, and were cuboidal in shape even after decalcification, egg volumes were calculated as the product of the 3 egg dimensions measured. Mean egg volumes were calculated from measurements of 54 eggs for each morph at each sampling date. The mean volumes, lengths, widths, and depths, of mature oocytes at the beginning of the breeding season (April 1981), were compared between morphs with t tests (sample variances pooled to estimate population variance (Winer, 1962)).

Reproductive effort is usually determined as the ratio of weight or calorific content between gonads and somatic tissue (Hirshfield and Tinkle, 1975). However, determination of these values is difficult for organisms which are heavily calcified.

Instead, total oocyte volume per polyp was used as an 'index of reproductive effort' (R.E.) per colony unit, and calculated as:

$$R.E. = \bar{v} \times n$$

where $\bar{v}$ was the mean volume per egg, and n was the total number of eggs per polyp. The mean number of polyps per $cm^2$ of colony was calculated from counts of polyps in 10 one $cm^2$ squares for each of the 6 colonies used in polyp fecundity measurements, in order to determine reproductive effort per $cm^2$ of colony surface.

The change in polyp fecundity with increasing distance away from the colony edge was documented for one plate colony. Polyp fecundity and mean oocyte volume were calculated for 3 polyps at each of 9 distances (polyp rows 1-5, 7, 8, 10 and 12). The mean distance from the colony edge was measured for the 3 polyps in each of these rows, and polyp ages estimated from growth rate data in Chapter 5.

### 6.2.3 Size at Reproductive Maturity and Sex Ratio

A survey of the reproductive status of 340 colonies in different size classes was carried out in January 1982, prior to the spawning period of *Turbinaria mesenterina*. Size classes were based on 4cm increments in colony diameter, corresponding approximately to the annual increase in diameter for this species (Chapter 5, Section 5.3.1). Between 15 and 20 colonies of the 2 morphs were sampled from each size group. Two 100m tape measures were laid along the 1m and 4m depth contours (the depths corresponding to the peaks in abundances of the convoluted and plate morphs respectively, Chapter 2). The first 15 to 20 colonies in each size class encountered within 1m of the tapes were sampled. It was necessary to swim on a compass bearing beyond the tape measures to collect adequate numbers of colonies in the larger size classes. Two diameters at right angles were measured using a flexible tape laid along the contours of the colony, and the mean used in analyses. Samples were prepared for dissection as described in 6.2.1. The presence or absence, and sex of gonads were recorded. The mean size at reproductive maturity

was determined as the size at which 50% of the colonies sampled contained gonads. Size classes were converted to estimated colony age, using the rates of linear extension calculated for year 2 in Section 5.3.1. Year 1 rates were assumed to be abnormally low because of the bleaching event that occurred during the time period (Chapter 5).

Of the colonies sampled for size class analysis, 90 colonies of the convoluted morph and 87 colonies of the plate morph were reproductively mature. The sex of each colony was determined from dissections, and the ratio of males to females compared between morphs in a $X^2$ homogeneity test. A $X^2$ goodness-of-fit test was also used to test for departures from a 1:1 sex ratio in the samples from each morph.

## 6.3 Results

### 6.3.1 Gonad Structure and Arrangement

*Turbinaria mesenterina* is gonochoric, all polyps within a colony being either male or female. One exception to this pattern of sexuality was found, where one colony of the 235 examined had polyps containing both eggs and testes.

No difference in gonad arrangement was found between the polyps of convoluted and plate colonies. In both cases gonads developed within the mesenteries. Figure 32B shows a chain of young oocytes developing within the mesogloea of the mesenteries. There are commonly 12 mesenteries per polyp, but the number may vary between 10 and 20. Gonads were found in all, regardless of the number of mesenteries present. Figure 33B shows a transverse section of a male polyp with mature testes in all 12 mesenteries. Both ovaries and testes extended the entire length of mesenteries

## FIGURE 32

Oogenesis in *Turbinaria mesenterina*.

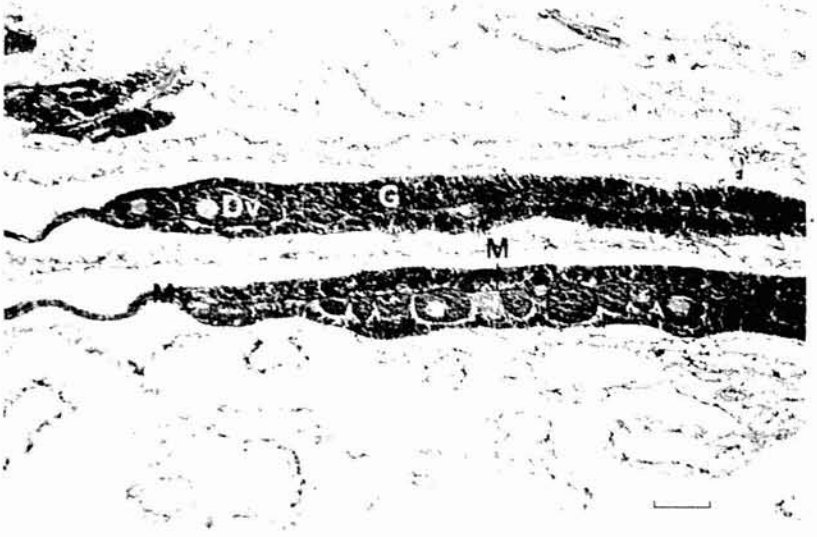
**A** Longitudinal section through portions of four female polyps showing chains of cuboidal, full-sized, primary oocytes and the overlap of ovaries between polyps. Convoluted colony, sampled 7 May 1982. Scale bar represents 0.5mm.

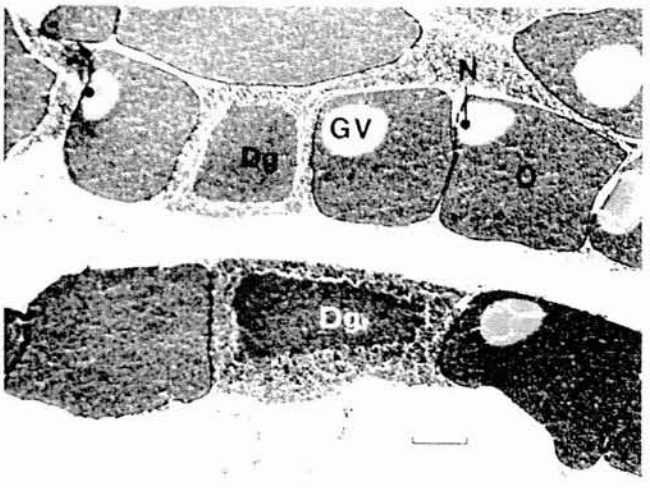
**B** Longitudinal section through a young ovary showing primary oocytes developing within the mesogloea of a mesentery. Plate colony, sampled 31 May 1982. Scale bar represents 0.1mm

**C** A section of a mature ovary containing full-sized primary oocytes with peripheral germinal vesicles. Two oocytes are in the process of degenerating. Plate colony, sampled 7 May 1982. Scale bar represents 0.05mm.

Dg - degenerating oocyte; Dv - developing oocyte: G - gastrodermis GV - germinal vesicle; M - mesogloea; My - mesentery; O - oocyte; S - stomodeum.


S
O


GV
G
M


N
GV
Dg
O
Dg

## FIGURE 33

Spermatogenesis in *Turbinaria mesenterina*

**A** Longitudinal section through a male polyp showing testes overlapping those of the adjacent distal polyp. Testes contain mature loculi. Plate colony, sampled 7 May, 1982. Scale bar represents 0.5mm.

**B** Transverse section through a male polyp showing mature testes in all 12 mesenteries. Convoluted colony, sampled 7 May 1982. Scale bar represents 0.1mm.

**C** Longitudinal section through several loculi of a mature testis, showing tails of spermatozoa projecting into central lumen of each loculus. Immature spermatocytes from the 1982-83 gametogenic cycle are also present. Plate colony, sampled 7 May 1982. Scale bar represents 0.05mm.

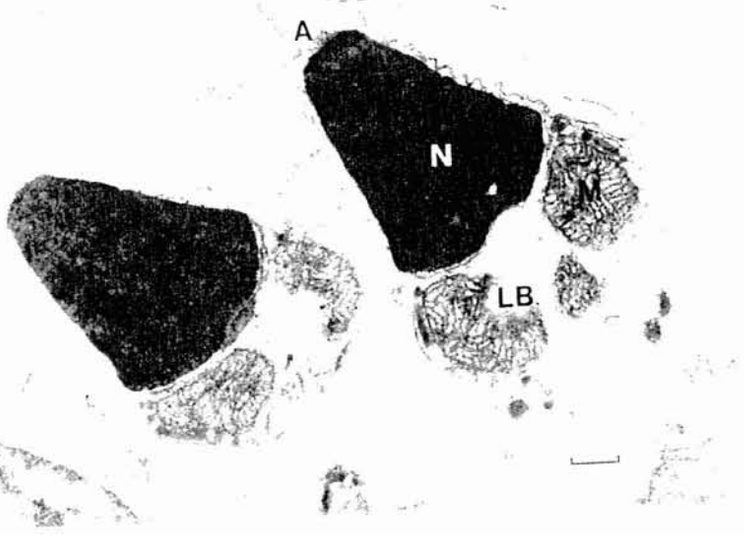
**D** Electromicrographs of a mature spermatozoa, showing conical nucleus and start of long anterior process. Convoluted colony, sampled 31 May 1982. Scale bar represents 0.5$\mu$m.

A - anterior process; C - coelenteron; Lu - lumen; LB - lipid body; M - mitochondria; MF - mesenterial filament; N - nucleus; S - spermatocytes; SH - sperm heads; St - stomodeum; T - testes.


SL
T


MF
T
C


SH
Lu
Sy


A
N
M
LB

in long chains of oocytes or loculi. Gonads of more distal polyps generally extended underneath those from adjacent proximal[1] polyps (Figures 32A and 32B). This arrangement reflects the budding pattern in colony growth of *T. mesenterina*. New polyps arise from near the base of peripheral polyps, on their lateral, distal surfaces. Polyps extend for a short distance in the plane of colony growth, and then bend perpendicularly so that the stomodeal area is raised above the base of the polyp. Therefore parent polyps overlap daughter polyps in their basal portions.

A zone of reproductively immature polyps (=sterile zone of Wallace, 1985) was found at the edge of colonies in both forms. Figure 34 shows that this zone was less than 2cm in length for one plate colony, and contained all polyps that were less than 1 year old. Polyps approximately 1.2cm from the edge were able to produce oocytes in the lower halves of mesenteries *i.e.* in the portions that overlapped the adjacent year-old polyps. As measurements of oocyte volume were made just prior to spawning in 1982, this may be interpreted as meaning that all polyps that were not present at the initiation of gametogenesis in 1981 were unable to produce gonads. However, if budding was underway, the lower portions of the mesenteries (the oldest portion of the polyp according to these observations) were able to produce gonads. Polyps that were between 1 and 2 years in age produced gonads but these had reduced fecundity in comparison with older polyps. Polyp fecundity and reproductive effort reached a maximum and thereafter remained constant for polyps greater than 4cm from the colony edge, or greater than 2 years in age.

### 6.3.2 Gametogenic Cycles and Breeding Seasonality

A single cycle of gametes developed annually in both the convoluted and plate morphs of *Turbinaria mesenterina*. Oogenesis

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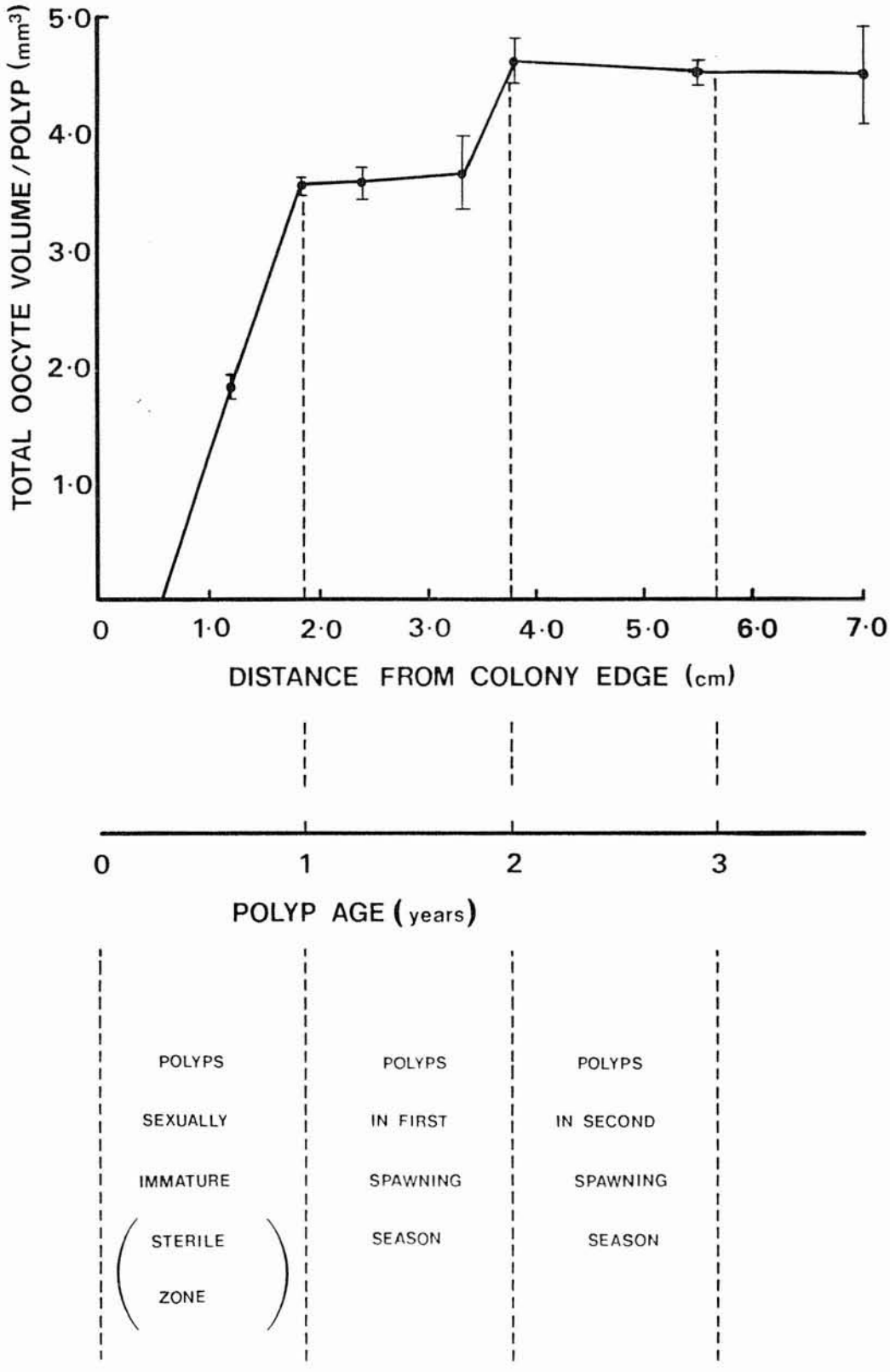
[1]Proximal and distal refer to the location of the polyp with respect to the centre of the colony.

FIGURE 34

Total oocyte volume versus polyp age in *Turbinaria mesenterina*

Shown are the mean total oocyte volumes per polyp (± S.E.) of a representative colony (plate morph), just prior to spawning (3 March 1982). The distance of polyps from colony edge was converted to polyp age using linear extension rates calculated in Chapter 5. N=3 polyps for each sample.


TOTAL OOCYTE VOLUME / POLYP (mm³)
5·0
4·0
3·0
2·0
1·0
0
1·0
2·0
3·0
4·0
5·0
6·0
7·0
DISTANCE FROM COLONY EDGE (cm)
0
1
2
3
POLYP AGE (years)
POLYPS SEXUALLY IMMATURE (STERILE ZONE)
POLYPS IN FIRST SPAWNING SEASON
POLYPS IN SECOND SPAWNING SEASON

began in early autumn in the 1981-82 cycle, and spawning occurred over a protracted period 10-14 months later (Figures 35 and 36). Thus gametogenic cycles of consecutive years overlapped for a period of up to two months. Although breeding was not actually observed, it is assumed that gametes were released for external fertilization, because of the absence of embryos or larvae in dissections or histological sections, and the presence of loculated testes with mature spermatozoa throughout the period of oocyte release. The high polyp fecundity also suggested that embryos were not brooded (Connell, 1973). • The lack of spawning in aquaria was probably due to suboptimal conditions associated with a recirculating seawater system, as samples of colonies at the end of each observational period still had gametes.

Changes in mean oocyte volume followed similar patterns throughout oogenesis in the two morphs (Figures 35, 36). Mean oocyte volume increased gradually for the first 4 months as oocyte numbers rose, increased rapidly over the next 4-5 months of vitellogenesis, and fluctuated between 2.1-2.8 x $10^{-2}mm^3$ for the last 5-6 months of their cycles. Oocytes had large, peripheral germinal vesicles throughout this latter stage, suggesting that an extended 'waiting' period followed oocyte maturation. Because the last release of oocytes did not occur until 14 months after the initiation of the cycle, small, developing oocytes from the 1982-83 cycle were intermingled on the same mesentery with mature oocytes of the 1981-82 cycle for a period of 2 to 3 months (Figure 37). Table 27 shows that although oocyte volumes at maturity were not significantly different, each of the 3 dimensions were significantly different between the 2 morphs. Oocytes from convoluted polyps were significantly longer than oocytes from plate polyps, but significantly smaller in both width and depth.

Although the initial number of oocytes produced per polyp was similar for the two morphs, the number of oocytes reaching maturity differed markedly between them. The mean number of oocytes rose rapidly in both convoluted and plate colonies to 210 and 250 per polyp, respectively, in the first 3-4 months of gametogenesis. Most of the oocytes developed through to maturity in the plate form (in the order of 200 oocytes per polyp, Figure 35). However, in the convoluted form, only 50% of the initial number

## FIGURE 35

Seasonal variation in oocyte volume and polyp fecundity in the plate morph of *Turbinaria mesenterina*.

Shown are the means ± S.E. N=54 for each oocyte volume sample, unless indicated otherwise over the error bar. N=9 for each fecundity sample, unless indicated otherwise over the error bar.

●——● Mean oocyte volume

O---O Mean polyp fecundity (No. oocytes per polyp)

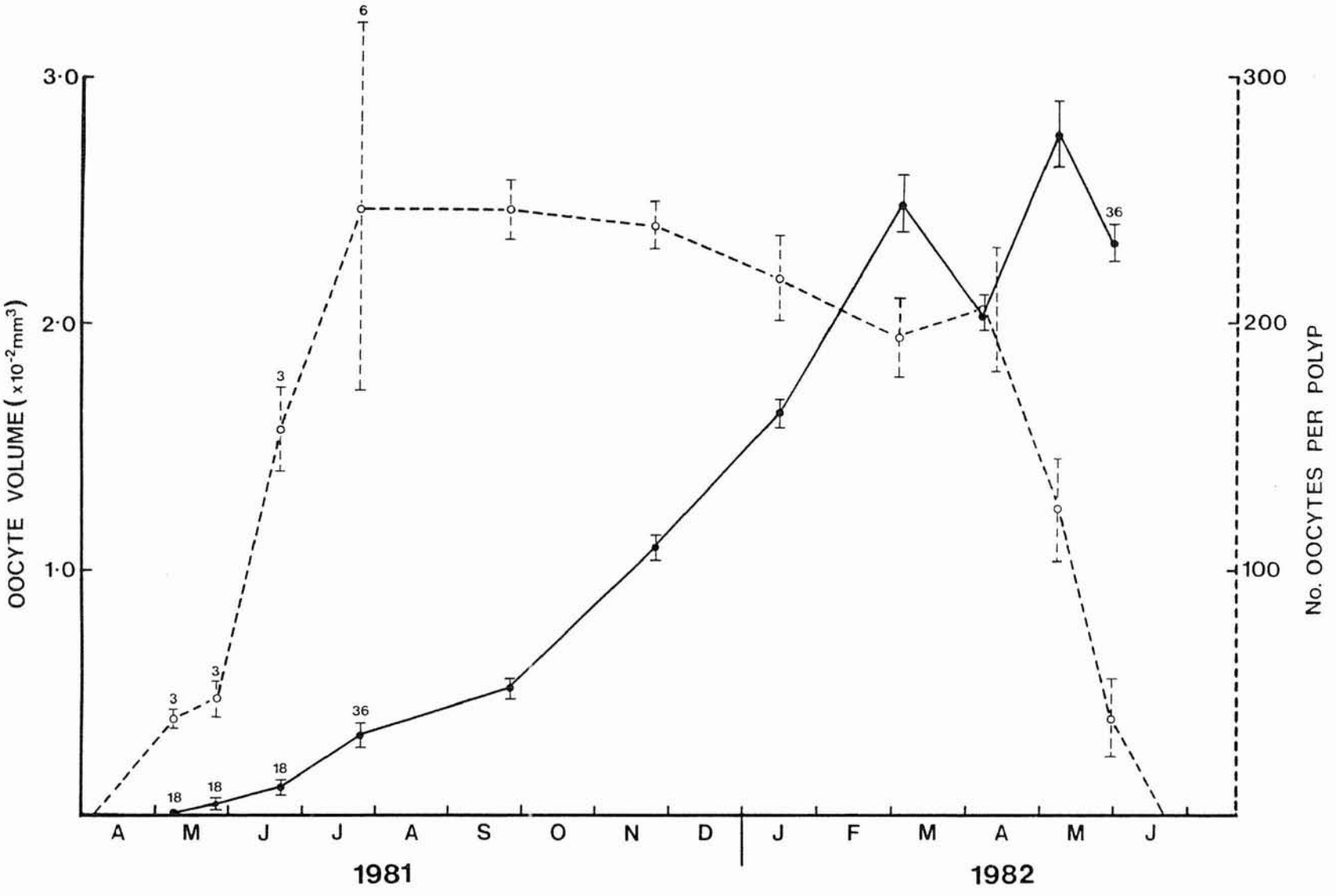

OOCYTE VOLUME (x10⁻²mm³)
No. OOCYTES PER POLYP
3·0
2·0
1·0
300
200
100
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1981
1982
6
3
3
3
18
18
18
36
36

FIGURE 36

Seasonal variation in oocyte volume and polyp fecundity in the convoluted morph of *Turbinaria mesenterina*.

Shown are the means ± S.E. N=54 for each oocyte volume sample, unless indicated otherwise over the error bar. N=9 for each fecundity sample, unless indicated otherwise over the error bar.

●——● Mean oocyte volume

O---O Mean polyp fecundity (No. oocytes per polyp)

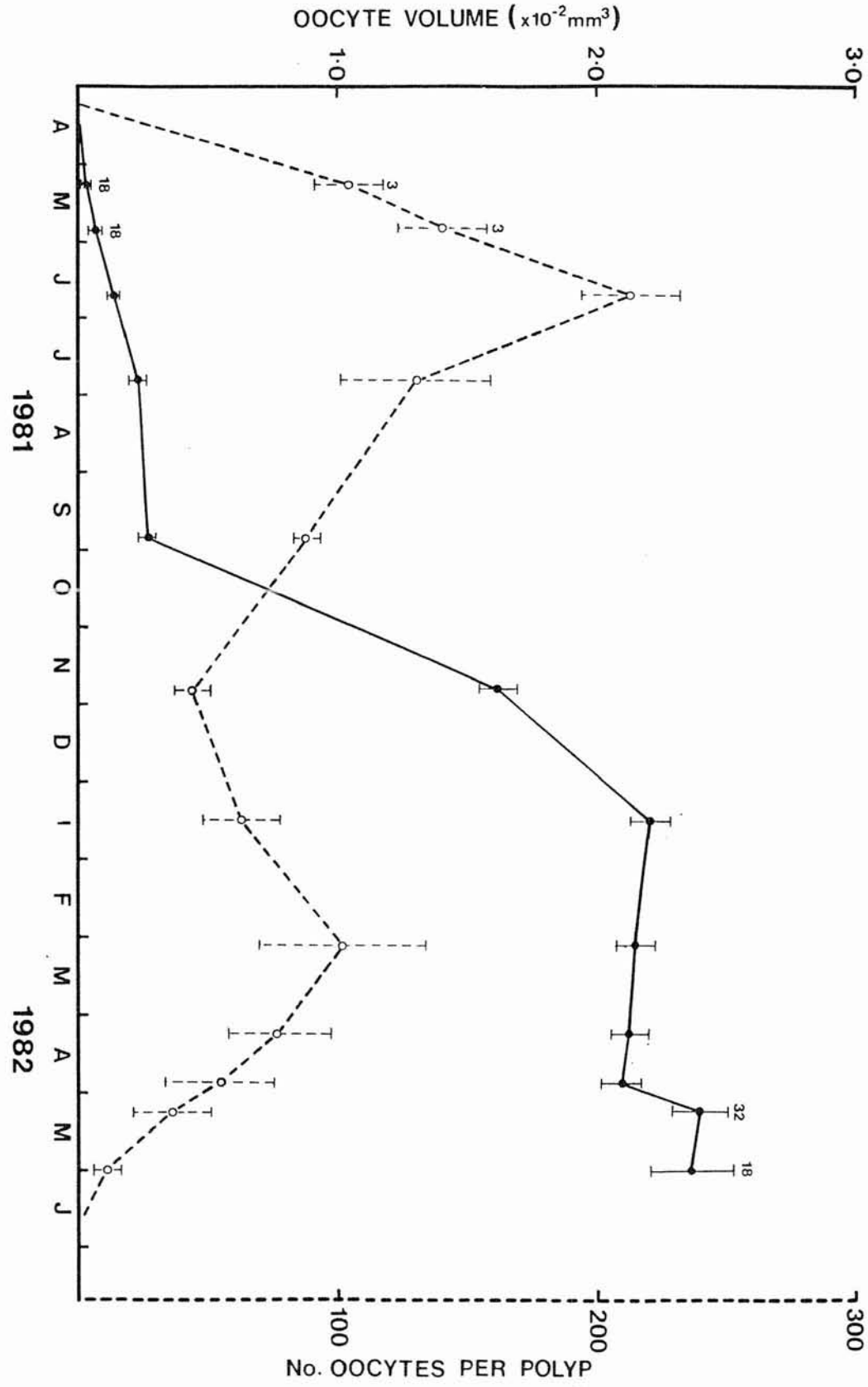

OOCYTE VOLUME (x10⁻²mm³)
1·0
2·0
3·0
A
M
J
J
A
S
O
N
D
I
F
M
A
M
J
1981
1982
18
18
3
3
32
18
100
200
300
No. OOCYTES PER POLYP

FIGURE 37

Seasonal variation in 'reproductive effort' per polyp for the convoluted and plate morphs of *Turbinaria mesenterina*.

Shown are the means ± S.E. N=9 polyps for each sample, unless indicated otherwise over the error bars. (See text for method of calculating total oocyte volume per polyp.)

| | |
|---|---|
| ● | Plate morph |
| O | Convoluted morph |
| _____ | 1981-82 gametogenic cycle |
| _._._. | 1980-81 gametogenic cycle |
| _ _ _ _ _ | 1982-83 gametogenic cycle |

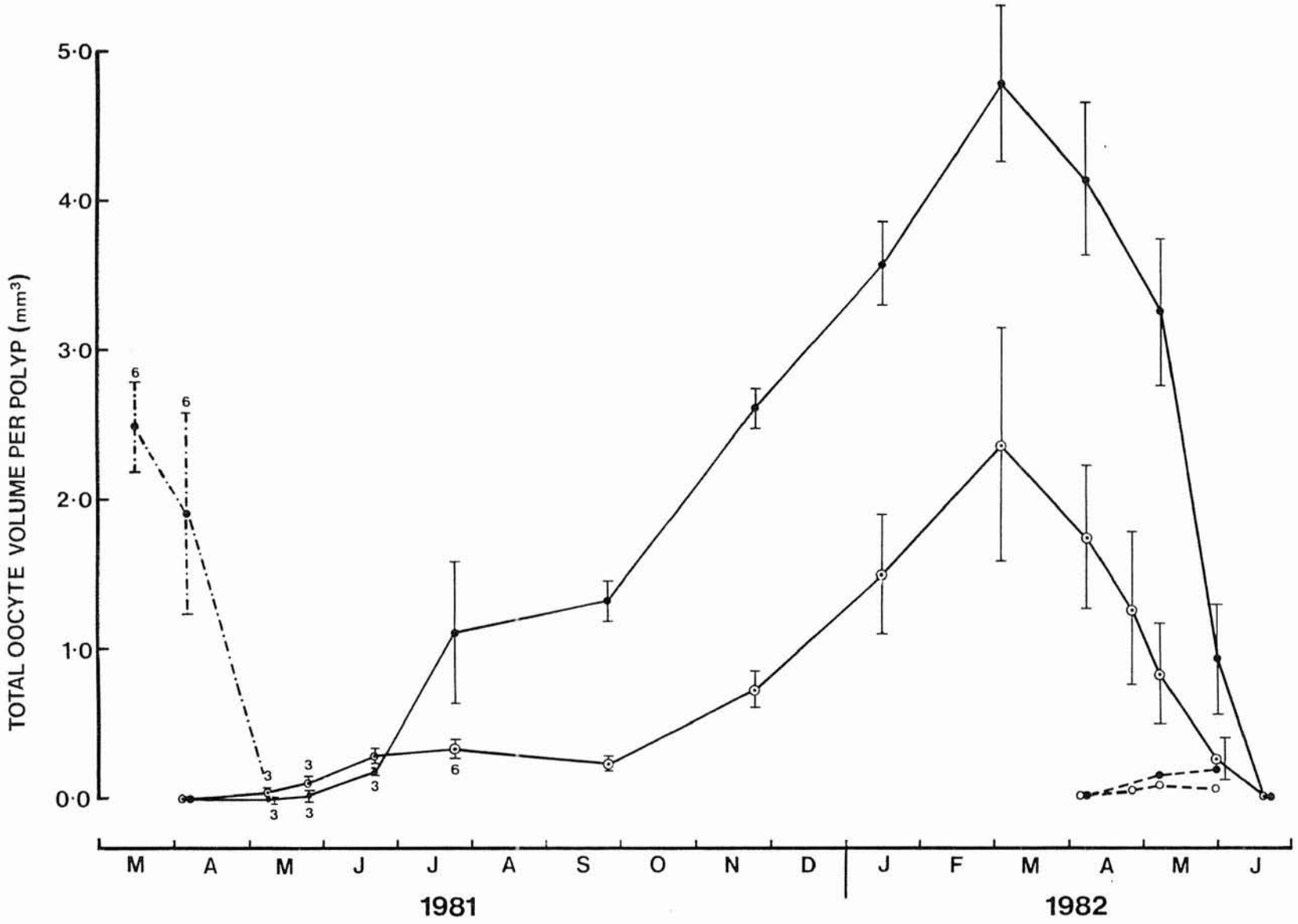

TOTAL OOCYTE VOLUME PER POLYP (mm³)
5·0
4·0
3·0
2·0
1·0
0·0
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1981
1982

**TABLE 27.** Comparison of volume and linear dimensions for mature oocytes from convoluted and plate colonies. Data are the mean ±95% confidence limits. T tests were used to compare means. T statistics (t) and associated probability levels (P) are given. N = 54 for each sample.

| | PLATE COLONIES | | CONVOLUTED COLONIES | | | |
|---|---|---|---|---|---|---|
| **VARIABLE** | Mean | 95% C.L. | Mean | 95% C.L. | t | P |
| Volume | **0.0204** | ±0.0013 | 0.0213 | ±0.0014 | 0.94 | >0.2 |
| Length | 0.36 | ±0.025 | 0.50 | ±0.020 | 8.73 | <<0.001 |
| Width | 0.36 | ±0.016 | 0.28 | ±0.016 | 6.51 | <<0.001 |
| Depth | 0.17 | ±0.009 | 0.15 | ±0.007 | 12.35 | <<0.001 |

matured (Figure 36). It is assumed that the reduction in oocyte numbers in the early part of the gametogenic cycle was due to the degeneration of the oocyte membrane followed by resorption of the ooplasm (eg. Figure 32C). No evidence of ooctye fusion was observed in dissections or histological sections. The rapid increase in mean oocyte volume occurred at least 2 months after the greatest decrease in oocyte number, also suggesting that resorption rather than fusion of oocytes occurred. The large error bars on mean oocyte numbers during the first 4 months of the cycle reflect a degree of asynchrony within the population during the period of rapid rise in oocyte numbers.

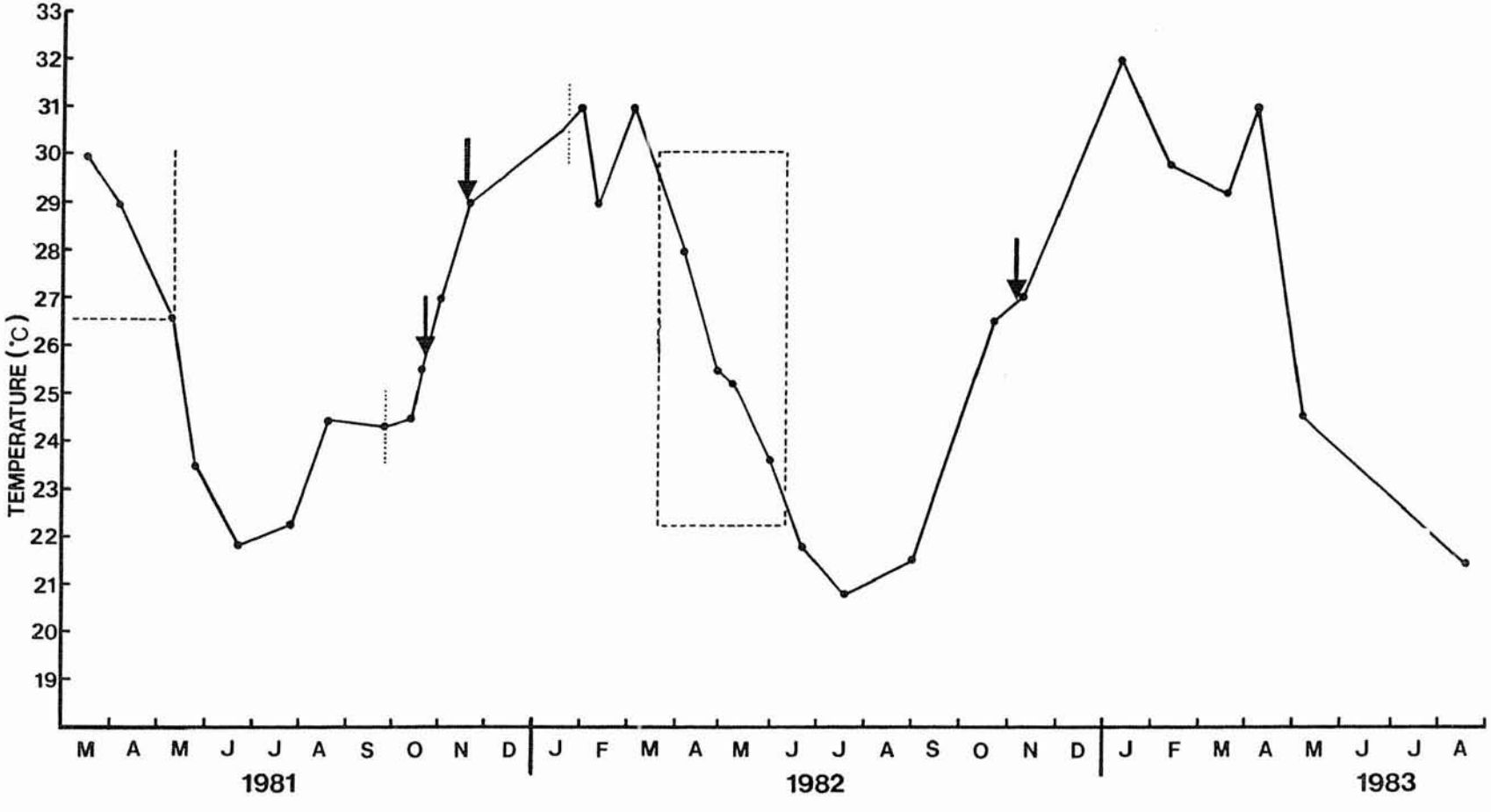
The decline in oocyte numbers from March through to June in convoluted colonies and from April through to June in the plate colonies, indicates that spawning occurred over a protracted period in both morphs. Protracted breeding was found at the level of the individual colony as well as at the population level. The large error bars on mean oocyte numbers during this period reflect differences among colonies in the rate at which oocytes were released. The rate of release, in both forms, tended to be more synchronized among polyps from the same colony than among polyps from different colonies.

The decrease in oocyte numbers coincided with the start of the autumn drop in sea temperatures in 1982 (Figure 38). Throughout the next 3 months of spawning, sea temperatures continued to fall towards the winter minimum. Although the data

FIGURE 38

Spawning seasonality in relation to seawater temperatures (at 4m) for *Turbinaria mesenterina* at Nelly Bay, Magnetic Island.

Dashed lines indicate periods of protracted spawning found for the Nelly Bay population of *T. mesenterina*. Dotted lines indicate the period of rapid oocyte growth. Broad arrows indicate dates of mass spawning of other coral species at Magnetic Island in the families: Acroporidae, Faviidae, Oculinidae, Pectinidae, Mussidae and Poritidae (Harrison *et al.* 1984; Babcock *et al.*, 1986).


TEMPERATURE (°C)
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1981
1982
1983

are incomplete for the 1980-81 cycle, oocyte volumes per polyp also indicate that spawning began in the vicinity of the annual fall in sea temperatures.

Spermatogenesis also took place over a 12 to 14 month period, and testes were mature well before the breeding season. Motile spermatozoa were observed in sperm squashes from both morphs from January through to May. Ultrastructurally, spermatozoa had a conical nucleus surmounted by a long anterior process which greatly increased the length of the sperm head (Figure 33D). The mid-piece contained mitochondria, and various other vesicles which correspond to the 'pro-acrosomal' vesicles of othe cnidarian sperm (Hinsch and Clarke, 1973).

### 6.3.3 Reproductive Effort

Combining the mean oocyte volume with the mean number of oocytes per polyp produced an estimate of reproductive effort. Figure 37 shows that reproductive effort was very similar for the two morphs in the first 3 months of their cycles. However, throughout the remaining stages of the gametogenesis, polyps of plate colonies consistently produced approximately double the oocyte volume of polyps of convoluted colonies. The divergence in total oocyte volume per polyp between the two morphs coincided with the decrease in oocyte numbers through resorption in polyps of convoluted colonies. The failure of up to 50% of oocytes to develop through to maturity in this form may be due, in part, to space constraints imposed by the convoluted morphology of these colonies. The mean number of polyps per $cm^2$ ($\pm$ 95% confidence limits) in colonies sampled for fecundity analysis, was higher for the convoluted colonies (11.5 $\pm$ 1.027) than for the plate colonies (8.5 $\pm$ 0.401). Although polyps were closer together in convoluted colonies, reproductive effort per $cm^2$ was still lower in these colonies than in plate colonies ($27.2 mm^3 cm^{-2}$ versus $40.6 mm^3 cm^{-2}$).

### 6.3.4 Size at Reproductive Maturity and Sex Ratio

The mean size at reproductive maturity (for 50% of colonies within a size class) corresponded to an approximate diameter of 24cm for convoluted colonies and 27cm for plate colonies (Figure 39). Using the growth rates calculated in Chapter 5, these diameters were equivalent to 7.8 years of age for the convoluted and 7.5 years of age for the plate colonies. Although the convoluted colonies were smaller in diameter at reproductive maturity, their slower growth rates in the lower size clases suggested that the two morphs reached reproductive maturity at roughly equivalent ages.

The smallest colonies found to contain gonads were between 12 and 16cm in diameter in both forms, or approximately 4 years in age. Both male and female colonies were found in this size class, indicating that both sexes reach reproductive maturity at approximately the same time. All colonies sampled in the 32-36cm and larger size classes contained gonads, indicating that all colonies were reproductively mature by their 9th or 10th year of growth.

The ratio of male to female colonies (Table 28) did not differ statistically between the two morphs ($X^2$=0.127 with d.f.=1, P>0.5). In both samples there was a slight excess of females but the sex ratio did not differ significantly from 1:1 for either morph (convoluted colonies: $X^2$=1.344 with d.f.=1, P>0.1; plate colonies: $X^2$=0.184 with d.f.=1, P>0.5).

**TABLE 28.** Sex ratios for the plate and convoluted morphs of *Turbinaria mesenterina*. Samples were collected from Nelly Bay, Magnetic Is., along transects at depths of 1m and 4m.

| Morph | No. of Female Colonies | No. of Male Colonies |
|---|---|---|
| Convoluteds | 51 | 39 |
| Plates | 46 | 41 |

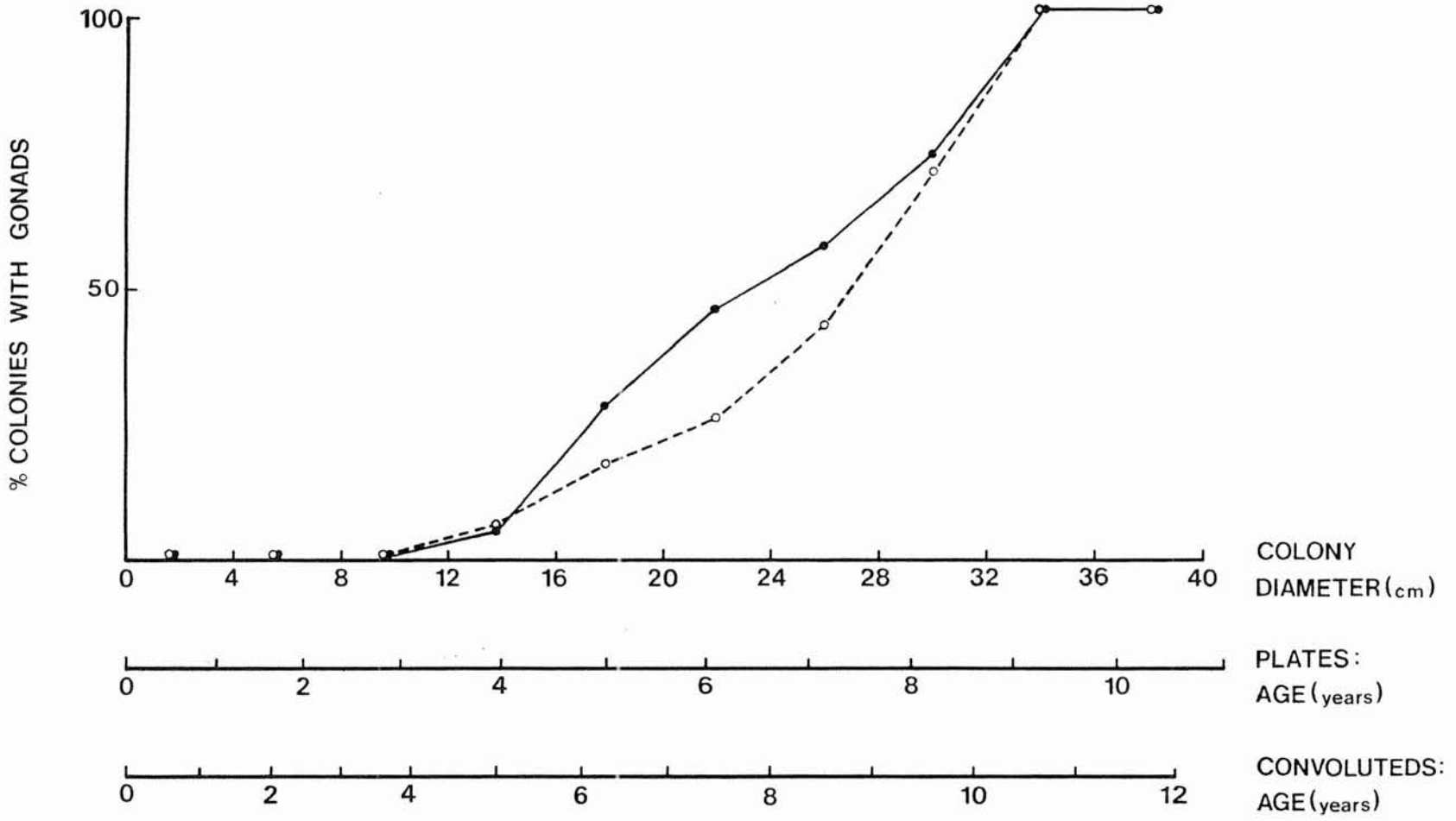
FIGURE 39

Comparison of size and estimated age at reproductive maturity between the convoluted and plate morphs of *Turbinaria mesenterina*.

The percent of colonies with gonads prior to spawning (January 1982) is shown for each 4cm size class. N ranged between 15 and 20 for each size class sample of each morph. Colony diameter was converted to age using linear extension rates calculated in Chapter 5.

O---O Plate morph

●——● Convoluted morph


% COLONIES WITH GONADS
100
50
0
4
8
12
16
20
24
28
32
36
40
COLONY
DIAMETER (cm)
0
2
4
6
8
10
PLATES:
AGE (years)
0
2
4
6
8
10
12
CONVOLUTEDS:
AGE (years)

## 6.4 Discussion

Recently, studies of reproductive characters have been successfully used to clarify the taxonomic position of closely related or problematic species of corals. Differences in the seasonality of the breeding period have been particularly important in this respect (Van Moorsel, 1983; Kojis and Quinn, 1982a; Kojis 1986). Differences in the onset of reproductive maturity (Van Moorsel, 1983) and in the buoyant properties of eggs (Kojis and Quinn, 1981; Babcock, 1984) have also been documented between closely related, sympatric species. In the present study no evidence of reproductive isolation through temporal barriers to interbreeding was found between the convoluted and plate morphs of *Turbinaria mesenterina*. For both, the timing of the onset of oogenesis and spermatogenesis, period of oocyte growth, and the length and seasonality of the breeding period were identical. Similarly, there was no evidence of divergent sexual strategies, with respect to gonad structure and arrangement, size and age at reproductive maturity, or sex ratio, which might suggest that the two morphs represented reproductively isolated populations.

Polyp fecundity and reproductive effort were the only reproductive characters found to differ between the colonies of the two morphs sampled. When reproductive effort was measured as the total oocyte volume per polyp, polyps of plate colonies more than doubled the reproductive effort of those from convoluted colonies. Measured as volume per $cm^2$, the difference in reproductive effort between the two morphs was reduced, because polyps in convoluted colonies are more closely packed than those in plate colonies, particularly in concave areas caused by folding of the laminae. However, reproductive effort, even when calculated on an area basis, was still lower in the convoluted morph. As individual oocyte volumes at maturity were equal, the lower reproductive effort of the convoluted morph was due entirely to lower egg numbers. The length of the mesentery governed the number of eggs developing, and is itself limited by the distance between polyps in *T. mesenterina*. Thus, the reduced polyp fecundity of convoluted colonies is

partially explained by the reduced distance between polyps. An examination of the relationship between tissue and skeleton revealed a second way in which colony morphology of the convoluted form reduced the space available for egg development. The cuboidal shape of fixed oocytes suggested that skeletal structures determined shape, and that egg dimensions would reflect space availability within the corallite. Although oocyte volumes at maturity were the same in the two morphs, ocytes were smaller in width and depth in the convoluted morph, but greater in length. These differences may be interpreted in light of the greater thickness of corallite structures in the convoluted morph (Veron and Pichon, 1980; Chapter 2). Heavier calcification of skeletal structures in this morph reduced the available space between septa for egg growth in 'width' causing eggs to increase in 'length' to maintain the volume. The greater length of eggs in convoluted colonies further reduced the number able to develop per mesentery.

It is also possible that energy allocation to reproduction differed between the two morphs in response to varying growth requirements associated with colony morphology. Linear extension rates were not significantly different between adult colonies of the two forms (Table 22, Chapter 5), despite the greater thickness of corallite structures in convoluted colonies. Therefore, energy allocated to reproduction in plate colonies may have been diverted to thickening the skeleton at the expense of oocyte maturation in convoluted colonies. However, egg numbers increased rapidly in the first three months of gametogenesis to a maximum which was similar for both morphs, indicating that polyps from both colony types experienced similar controls on the initial process of oogenesis. The fact that similar numbers of oocytes developed initially, and that mature oocytes were equal in volume, further supports the conclusion that genetic differences at the species level do not exist between these two morphs. There are several possible explanations for the subsequent resorption of oocytes in the convoluted form. It is possible that differences in the amount of energy available for reproduction between morphs were not manifested until the period of rapid oocyte growth. Evidence that space availability within the corallite determines fecundity was documented, but it is also possible that other external factor(s),

such as nutrition or an environmental parameter, limited the number able to mature in the convoluted form.

Kojis and Quinn (1984) found that fecundity decreased with depth for *Acropora palifera* at Salamaua, and attributed the decrease to reduced light intensity and water movement in the deeper water habitat. In Chapter 2, differences in light intensity and water movement were the major differences documented between the shallow and 'deep' habitats of the convoluted and plate morphs, respectively, of *T. mesenterina*. However, as the inverse relationship between fecundity and depth was found for *T. mesenterina*, it is suggested that light and water movement differences in habitat were not responsible for the lower fecundity of the convoluted morph. It is equally unlikely that the higher light intensities experienced by convoluted colonies, either in the visible or UV range, were a source of stress (cf. Coles and Jokiel, 1978; Delvoye, 1982; Jokiel, 1980), as oocyte resorption took place during the winter months. Sedimentation rates, which have also been implicated in the reduction of fecundity (Kojis and Quinn, 1984), were higher in the shallow habitat (Chapter 2). However, the increased water movement at the shallow site would have effectively reduced the need for energy expenditure in sediment removal (cf. Johannes, 1975). Equivalent growth rates for adult colonies of the two morphs, for the June to November period of oocyte resorption in the convoluted morph (Figure 27, Chapter 5), suggests that the shallow water habitat was not stressful. However, Jokiel and Guinther (1978) have shown that reproductive activity may be affected by suboptimal conditions when growth rates are unaffected, so growth may not be as sensitive an indicator of suboptimal conditions as reproduction. The fact that the largest colonies of *T. mesenterina* at Nelly Bay were convoluted colonies in shallow water, and that the abundance of colonies in shallow water was equal to or greater than that in deeper water (Chapter 2), argues against the shallow water habitat being suboptimal in general. It is concluded that space and possibly energy constraints, caused by differences in colony morphology, were more likely to have regulated polyp fecundity in the convoluted morph than either environmental factors or genetic differences equivalent to species differentiation.

The protracted autumn breeding period of *Turbinaria mesenterina* is unique among the reproductive strategies found to date for hermatypic corals on the Great Barrier Reef (Kojis and Quinn, 1981, 1982a, 1982b; Kojis, 1986; Bothwell, 1982; Harriott 1983a, 1983b; Babcock, 1984, 1986; Harrison *et al.*, 1984; Oliver, 1985; Heyward and Collins, 1985b; Wallace, 1985; Willis *et al.*, 1985; Babcock *et al.*, 1986). Because of this difference in strategy, and the number of comparative reproductive studies available from the region, it was of interest to document the reproductive ecology of this species to further elucidate proximate and ultimate factors controlling gametogenic development and breeding in corals. There is much correlative evidence which indicates that seasonal changes in seawater temperature synchronize reproduction in marine animals (Orton, 1920; reviewed in Kinne, 1963; Giese and Pearse, 1974). However, Clark (1979) pointed out that confusion has arisen in discussions of proximate factors, because environmental parameters may operate in two ways to synchronize breeding. He distinguished between environmental conditions necessary for gonad maturation and breeding (eg. temperature and food availability), and specific environmental signals which trigger physiological events in animals leading to breeding (eg. light regimes, tides, temperature changes). Lunar periodicty and photoperiod cues appear to be the proximate factors inducing synchronized spawning for most corals on the Great Barrier Reef (Kojis and Quinn, 1981, 1982a, 1982b; Harriott, 1983a; Harrison *et al.*, 1984; Willis *et al.*, 1985; Babcock *et al.* 1986). For these species, spawning appears to occur on the first appropriate cue after maximum oocyte size has been reached. The autumn spawning period of *T. mesenterina*, was four to six months out of phase with these species[2] and commenced shortly after seawater temperatures began to fall towards the winter minimum. As mature egg sizes and motile spermatozoa were observed in January, but spawning was delayed until March, it is possible that the seasonal change in temperature pattern was the trigger for the onset

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[2]Three other inshore species in the same genus (*Turbinaria bifrons, T. peltata, and T. radicalis*) also spawn in winter (unpublished data). Two free-living, ahermatypic species of coral (*Heteropsammia cochlea and Heterocyathus aequicostatus*), the former from the same family (Dendrophyllidae), spawn in autumn or early winter (Fisk, 1981).

of the spawning period. However, the spawning season was protracted, both for individual colonies and for the population in general, and continued throughout the annual decrease in temperature. Protracted breeding seasons have been found for the free-living scleractinians *Heteropsammia cochlea* and *Heterocyathus aequicostatus* (Fisk, 1981), the actinian *Anthopleura elegantissima* (Ford, 1964) and the gorgonians *Muricea californica* and *M. fruticosa* (Grigg, 1979), and correlated with decreasing temperatures in each case. Although decreasing temperatures may lead to spawning, the protracted length of the spawning season in these species suggests that falling temperatures do not provide as clear a signal for breeding synchronization as lunar and photoperiod cues. This interpretation for *T. mesenterina* must be treated with caution as more detailed observations of spawning are required before the possiblity of lunar periodicity of gamete release throughout the extended breeding season can be excluded. The late summer/early autumn mass spawning of corals in the Dampier Archipelago (Western Australia) is also 4 to 5 months out of phase with the mass spawning of corals on the Great Barrier Reef (Simpson, 1985). Although mass spawning in Dampier occurs shortly after the summer maximum in sea temperature, the cues inducing spawning appear to be similar to those on the Great Barrier Reef *i.e.* lunar periodicity, photoperiod changes and possibly tidal cycles.

Although the temperature pattern throughout the breeding season of *T. mesenterina* was the inverse of the temperature pattern at the time of the mass spawning at Magnetic Island, the initiation of oogenesis in this species occurred at approximately the same time (April-May) as has been documented for most other spawning corals on the Great Barrier Reef[3]. The period of rapid growth of oocytes for

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[3]Magnetic Island: April to May - *Goniastrea aspera, Platygyra sinensis* (Babcock, 1984, 1986). May - *Montipora digitata* (Heyward and Collins, 1985b). February - *Acropora formosa, Fungia fungites* (Oliver, 1985). January or February - *Goniastrea favulus* (Babcock, 1986).
Big Broadhurst Reef: Between February and June - *Acropora hyacinthus, A. loripes, A. nobilis, A. valida* (Wallace, 1985).
Lizard Island: April to June - *Porites lutea, P. australensis* (Harriott, 1983a). Between January and April - *Lobophyllia corymbosa* (Harriott, 1983a). Between June and August - *Favia favus* (Harriott, 1983a).

*Turbinaria mesenterina* coincided with the rapid increase in average temperature at Nelly Bay. The same pattern of rapid oocyte growth during rising temperatures has been observed in other species where oocyte dimensions have been measured on a monthly or bimonthly basis (Babcock, 1984, 1986; Oliver, 1985a; Fadlallah, 1985; Heyward and Collins, 1985b). Thus the physiological requirements for gonad development may be temperature dependent in corals. As many of the same species spawn at the same time at Heron Island and Lizard Island, despite temperature differences of approximately 2°C (Harriott, 1983a, unpubl. data), the requirement appears to be for an increase in temperature rather than for an absolute temperature. The importance of temperature in controlling gametogenesis in corals is further supported by the one month difference in the mass spawning of corals at Magnetic Island and offshore reefs (Harrison *et al.*, 1984; Willis *et al.*, 1985; Babcock *et al.*, 1986). Because these species appear to spawn on the first appropriate cue following gamete maturation, the later spawning of many of the same species at offshore reefs reflects the one-month delay in the temperature rise on these reefs (Babcock *et al.*, 1986). Years of split spawning within populations when the full moon falls early in the potential period of breeding (Willis *et al.*, 1985) further implicates the importance of temperature in gamete maturation. It is suggested that rising sea temperatures are a 'necessary environmental condition' (*sensu* Clark, 1979) for gonad maturation in corals, but not necessarily for the initiation of breeding which may be triggered by a variety of cues.

Discussions of the ultimate factors determining the synchronization (Babcock *et al.*, 1986) and seasonality of breeding in corals must be largely speculative, but the large number of corals known to breed during late spring on the Great Barrier Reef suggests that environmental conditions at this time, are optimal for both breeding and larval settlement and survival in most reef habitats in this region. Differences in the timing of mass spawning

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Heron Island: April to May - *Favites abdita* (Kojis and Quinn, 1982b). March - *Goniastrea favulus* (Kojis and Quinn, 1981). May or June - *Leptoria phrygia* (Kojis and Quinn, 1982b). August to September - *Porites lobata, P. lutea, P. andrewsi* (Kojis and Quinn, 1982a).

between the Great Barrier Reef and Western Australia indicate that the ultimate causes for breeding seasonality in corals may vary between geographic locations. Simpson (1985) has suggested that the seasonal change in the wind current patterns are the ultimate causes of the late summer/early autumn mass spawning on Western Australian reefs. *T. mesenterina* is so far unique in the Great Barrier Reef region in maintaining mature oocytes for an extended period and then spawning in autumn. It is possible that the inshore habitat of this species holds the clue to understanding the selective pressures leading to such a strategy. *T. mesenterina* is one of the few coral species largely restricted to nearshore, turbid reefs characterized by the seasonal presence of large macroalgae. At Nelly Bay, species of the genus *Sargassum* dominate the reef flat and upper reef slope areas during the summer months but are reduced to short basal holdfasts by May (J. Hart, pers. comm.). A similar pattern has been observed at Geoffrey Bay, Magnetic Island (Morrissey, 1980) and on other inshore fringing reefs in the region (Cribb, 1973). Competition with *Sargassum* spp. for settlement sites and for light is therefore high between November and April, the period when coral larvae from the annual mass spawning are settling and initiating colony growth. The much lower recruitment rates found at Nelly Bay in comparison with offshore reefs (Wallace, pers. comm.) may indicate that conditions for larval settlement and/or juvenile survival following mass spawning on this inshore reef are not optimal. However, this source of competition is greatly reduced during the period of settlement and early growth of *T. mesenterina*. Observations of numerous juveniles throughout the study area indicate that *T. mesenterina* recruits successfully following sexual reproduction. Furthermore, line transect studies of Bull (1977) indicted that it was one of the three most abundant species in terms of percent cover in three bays around Magnetic Island. It is speculated that the seasonality of breeding in *T. mesenterina* optimizes survival of larval recruits through the avoidance of spatial competition with seasonally abundant algae particularly *Sargassum*.

In summary, *Turbinaria mesenterina* is a stable gonochoric species and spawns gametes over a protracted breeding season in autumn. No evidence of reproductive isolation between the

convoluted and plate morphs was found. However, differences in polyp fecundity between morphs were related to space constraints associated with colony morphology, and possibly to differential energy allocation between growth and reproduction. The reproductive mode described here for *T. mesenterina* does not support Fadlallah's (1982) predicitions of brooding for the scleractinian family, Dendrophyllidae, but supports Harrison's (1985) prediction that systematic patterns in sexuality may be more consistent than patterns in the mode of reproduction at higher taxonomic groupings. Colonies first attain reproductive maturity at ages between 4 and 10 years, with 50% of the population being mature in their 7th year of growth. These are probably underestimates of the true age at each stage, as rates of colony growth in the first few years are much lower than rates in later years (cf. Babcock, 1985). The sex ratio in the Nelly Bay population was approximately 1:1. Oogenesis and spermatogenesis required 12 to 14 months for completion, but overlap in adjacent cycles maintained an annual gametogenic rhythm. Sperm have a long, pointed anterior process, supporting emerging trends in sperm ultrastructure between hermaphroditic and gonochoric families (Harrison, 1985). The autumn breeding period, in contrast to the spring mass spawning in the region, suggests that different proximate factors synchronize breeding in corals. If falling temperatures provide the cue for spawning in *T. mesenterina*, then temperature changes do not synchronize spawning in populations to the same extent as lunar and photoperiod cues. Nevertheless, rising temperatures appear to be a necessary environmental condition for gonad maturation in broadcasting species of coral in the region. The reduction of spatial competition with seasonally abundant macroalgae on inshore reefs may provide the selective pressure for the autumn breeding period of *T. mesenterina*.

# CHAPTER 7. CONCLUDING DISCUSSION

The success of scleractinian corals in colonizing shallow, tropical marine environments has often been attributed, in part, to their morphological variability (Yonge, 1940, 1963). This same variability has created many problems for taxonomic studies within the order (eg. Veron and Pichon, 1976). Partly because of these difficulties, most biogeographical and evolutionary studies of corals have resolved patterns only to the level of genera (Vaughan and Wells, 1943; Wells, 1956; Stehli and Wells, 1971; Rosen, 1981; Veron, 1985), despite the fact that studies at the species level reveal much more about evolutionary processes (Potts, 1985). Before biogeographical or evolutionary studies of corals can be advanced further, a clearer understanding of the species concept, as it applies to the Scleractinia, is required. It is equally important to determine the sources of intraspecific morphological variation in corals before the significance of this variation can be assessed (Chapter 1).

In this project, morphological variation was studied in two inshore species of scleractinian corals, firstly to clarify the taxonomic relationship between morphological variants identified as belonging to the same species through traditional skeletal-based taxonomic studies (Veron and Pichon, 1980). Secondly, the basis of the morphological variation was investigated to determine whether the variation represented phenotypic plasticity or genetic polymorphism. Thirdly, the relationship between growth and colony morphology was explored to elucidate the mechanisms by which variation in colony morphology is achieved in corals.

Electrophoretic evidence presented in Chapter 4 indicated that the convoluted and columnar morphs of *Pavona cactus* at Eclipse Island were part of a single, interbreeding population. Studies of linear extension rates and corallite structures in actively growing regions (Chapter 5) supported this conclusion. In contrast, an electrophoretic study of a small sample of convoluted and plate

colonies of *Turbinaria mesenterina* (Chapter 4), suggested that two reproductively isolated populations had been sampled. However, no evidence of temporal barriers to interbreeding could be found when gametogenic cycles and breeding seasonality were compared (Chapter 6). Comparisons of other reproductive characteristics failed to reveal any divergence in strategies which would suggest that the two morphs represented reproductively isolated populations (Chapter 6). The similarity in morphology between all immature colonies throughout the sampling area (Chapter 5), the continuous nature of the morphological variation in adult colonies (Chapter 2), and the convergence in form between transplanted and resident colonies (Chapter 3) also suggested that one morphologically variable species had been studied. Comparisons of linear extension rates between morphs (Chapter 5), further supported this interpretation. The gene and genotype frequencies determined in the electrophoretic survey were based on a small sample size and may not be representative of the population. A more extensive survey of electrophoretic genotypes of the two morphs has been undertaken to clarify these results (Ayre and Willis, in prep.). Inter-morph breeding trials would provide the ultimate proof that the two morphs represented one biological species, but verification of fertile progeny is clearly difficult for a species whose mean age at first reproduction is seven years. Evaluation of the available evidence indicates that the convoluted and plate morphs are morphological extremes of a single species, *Turbinaria mesenterina*. Thus a variety of techniques have upheld previous taxonomic conclusions based on skeletal morphology for these two species (Veron and Pichon, 1980).

A major finding of the present study is that morphological variation has evolved via different pathways in two species of coral. Both species inhabit inshore fringing reef biotopes and are foliaceous in form. However, colonies of *Turbinaria mesenterina* were phenotypically plastic when transplanted between sites within their normal environmental range, whereas colonies of *Pavona cactus* were phenotypically stable in a parallel study (Chapter 3). Additional electrophoretic and histocompatiblity studies suggested that colony morphology is genetically determined in *Pavona cactus*. All colonies of each asexually replicated genotype exhibited the same growth form, despite large distances between colonies (Chapter

4). Abnormal or stunted growth forms of *P. cactus* were produced in extreme conditions, but stress-induced, non-adaptive responses were not considered to be part of the general phenomenon of phenotypic plasticity. The present distribution of morphs of *P. cactus* at Eclipse Island (Chapter 2) may represent active, behavioural selection at the settlement stage, or historical differences in overall patterns of settlement and mortality. As discussed in Section 2.6, the lack of identifiable environmental differences separating the distributions of convoluted, intermediate and columnar morphs favours the latter explanation. In conclusion, although both species are highly variable in growth form, variation in *T. mesenterina* represents plasticity in the phenotypic expression of colony morphology in response to environmental variation, whereas variation in *P. cactus* represents genetic polymorphism.

Recently, a model has been proposed by Potts (1983, 1984b, 1985) to explain the selective pressures which have led to the lack of speciation and concomitant high levels of morphological variation in corals, which implicitly assumes that variation in corals is genetic in origin. The model suggests that corals have experienced evolutionary disequilibrium through frequent sea level fluctuations. Given the long-lived nature of most corals, Potts suggests that speciation has been prevented because too few generations have elapsed since the recolonization of the shallow continental shelves from remnant reef slope populations. Also, the relaxation of natural selection during the recolonization, coupled with a dispersive larval stage and the persistence of old genotypes, have prevented populations from differentiating and maximized the expression of intraspecific variability. Potts (1983, p. 621) states that "at least part of the variation seems to be genetically determined", but all of the mechanisms that he described require that the variation be, in fact, primarily genetic in origin.

Although Potts' model has provided a useful focus for discussions of the evolutionary ecology of corals, assumptions about high genetic variablity in coral species are largely unfounded. Present knowledge of the genetic structure of coral populations extends only to Western Australian populations of one species of coral (Stoddart, 1984a, 1984b). Although *Pocillopora damicornis* is

highly variable in morphology (Veron and Pichon, 1976), Stoddart (1984a) concluded that the genetic structures of these populations "showed no unique features which might have led to a remarkable diversity of phenotypes" and suggested that phenotypic plasticity mediated the expression of genotypes in this species. As reviewed in Section 3.4, very little is known about the extent to which either phenotypic plasticity or genetic polymorphism is employed as a morphological strategy by corals. It is clearly premature to speculate on which strategy is more important in explaining morphological variation in corals. It is clear that before models of evolutionary processes in corals can be further developed or verified, much more must be known about the nature and extent of genetic variation in corals. The present study emphasizes that morphological variation in coral species may reflect either underlying genetic differences or plasticity in the phenotypic expression of colony form. If phenotypic plasticity is found to be the more common strategy, this could explain the high intraspecific variability in corals without the need to invoke high levels of genetic variation. It would also help to explain the lack of speciation in corals, as directional selection is retarded when the variation is not directly heritable (Bradshaw, 1984).

Analysis of the relationship between colony growth and morphology in *T. mesenterina* suggests that growth form variation represents a photoadaptive response by the colony to control the exposure of photosynthetic tissues to light. All small colonies (<10cm in diameter) were identical in form, implying that initial colony growth is genetically controlled. However, differences in colony morphology between deep and shallow colonies, became progressively greater as colony size increased, suggesting that the phenotypic expression of growth form is subsequently modified by the environment (Chapter 5). Analyses of differences in morphology before and after colonies were transplanted to the reciprocal depth, indicated that changes in the angle of growth led to differences in growth form expression (Chapter 3). The high correlation between growth form and depth in this species (Chapter 2) may be interpreted as meaning that the angle of corallite addition responded to a depth-related factor. Evaluation of environmental factors found to vary with depth (light, water motion, and sedimentation, Chapter 2)

suggests that variation in light intensity probably controls the angle of polyp addition, although other aspects of colony morphology may be influenced by differences in water motion (*eg*. thickness of coralla and corallite structures), or rate of sedimentation (*eg*. general hemipherical outline of convoluted colonies). In addition to considerations outlined in Chapter 2 in support of this interpretation, it is difficult to envisage how an abrupt change in growth angle following transplantation to a new depth could be precipitated by differences in either water motion or sedimentation. It is suggested that polyp budding along the periphery of the colony is coordinated to enhance the display of photosynthetic tissue to light. Budding in high light regimes occurs at angles which introduce self-shading of colony components and increase canopy development within the colony. Hence the utilization of high light energy is maximized. In contrast, budding in low light regimes is restricted to more horizontal angles to optimize the exposure of photosynthetic tissues to light. Thus the colony response of *T. mesenterina* to light is similar to the multilayer versus monolayer strategies of plants, adopted in high and low light regimes respectively (Horn, 1971). The effect of light on colony growth is not mediated by photosynthetically-linked differences in rates of calcification between depths, as has been proposed for colony variation with depth in *Montastrea annularis* (Goreau, 1963; Barnes, 1973). The observed changes in growth angle represent direct photoadaptive responses to light and are akin to phototropic responses.

The determination of colony morphology in *Pavona cactus* appeared to be related to a different set of controlling factors and physiological constraints. Differences in the thickness and spacing of fronds reflected differential allocation of resources to primary and secondary calcification between the convoluted and columnar morphs (Chapter 5). Skeletal structures of corallites were the same in actively extending tip regions of colonies. However, in older portions of colonies, secondary calcification was directed primarily towards infilling the spaces between septo-costae in the convoluted form, but towards increasing the 'height' of septo-costae and inserting new corallites, as well as infilling in the columnar form. Thus bifacial fronds of convoluted colonies became denser but increased only marginally in thickness. In contrast, columnar

fronds became thicker and more rounded, or multifacial, with age. As columnar fronds also became denser, a large proportion of energy allocated to growth is directed towards secondary calcification in this morph. Patterns in the allocation of resources to primary calcification also differed between the two morphs. Fronds extended linearly along both their distal edges and lateral margins in convoluted colonies, whereas fronds in columnar colonies extended only along their distal edges, and often bifurcated, further minimizing the length of growing margin to be supported. Thus proportionally more of the total energy available for growth is directed towards primary calcification in the convoluted form. It is suggested that these differences in the allocation of resources to primary and secondary calcification are determined genetically in *P. cactus*.

Although the present study provides some evidence that genotypes of phenotypically plastic species have greater fitness throughout the range of environmental conditions tolerated by the species than phenotypically stable genotypes, it also illustrates how irreversible morphologies may disadvantage individual colonies in changed conditions. Given that both strategies have led to intraspecific variation in corals, when is plastic control superior to genetic determination? Bradshaw (1965) argued that, although disruptive selection, due to variation in selective pressures either spatially or temporally, may lead to genetic polymorphism or phenotypic plasticity, there are situations where the latter strategy is more adaptive for plants. For example, in long-lived sessile organisms, genetic mechanisms do not enable individuals to adapt to environmental changes through time. Furthermore, when spatial heterogeneity occurs over very small scales (as light regimes do from the top to the bottom of large coral colonies), phenotypic plasticity provides the only significant mechanism for individuals to respond to such variation. In reviewing discernible patterns in variation within plant populations, Sarukhan *et al.* (1984) suggested that environmental influences exert greater control on variation in plants than genetic influences. As discussed previously (Chapter 1), corals resemble plants in many ways. Resolution of the mechanisms used to attain a diversity of forms in coral species, will provide further insights into the selective pressures operating on coral populations.