UPV J. Nat. Sci. 1:39-58 (1996)

Some Aspects of the Population Biology of the Reef Coral, *Pocillopora damicornis* (Linnaeus), in Taklong Island, Guimaras

MARIE FRANCES J. NIEVALES[1]
Division of Biological Science, College of Arts and Sciences, U.P. in the Visayas, Miag-ao 5023, Iloilo, Philippines

PORFIRIO M. ALIÑO
Marine Science Institute, U.P. Diliman, Quezon City 1101, Philippines

ABSTRACT

Demographic parameters that included growth rate, reproduction, recruitment and mortality of the branching reef coral, *Pocillopora damicornis* Linneaus, in Kalirohan reef flat, Taklong Island, Guimaras were investigated from 1991 to 1992.

Radial colony growth averaged 20 mm per year regardless of initial size. Planulation was the predominant mode of reproduction. This occurred monthly throughout the year with peak larvae release between the new moon and first quarter. There was regular recruitment event of larval origin that corroborated monthly spawning. Size class specific mortality rates did not vary much but the largest size cohort had the least. Net larvae-derived recruitment surpassed depletion rate (natural mortality) of established colonies at the end of the study period. The observed demographic rates resulted in increased population size where more than half are recruits and maintained the left-skewed population size structure.

INTRODUCTION

Coral reefs are perhaps among the most endangered ecosystems in the world. In the Philippines, the proximity of coral reefs to the coastal area adds to their vulnerability to detrimental human activities. Management strategies have been conceived and implemented to avert the continued degradation of this ecosystem. Understanding how coral populations behave and persist through space and time is important in conceptualizing reef management strategies.

Pocillopora damicornis (Fig. 1) is a common species in the shallow waters of protected reefs in the Indo-Pacific region. It has been found to exhibit fast growth rate in an artificial reef and has been suggested as a potential material for coral farming for the aquarium and curio industry (Gomez et al 1985) and also as seed material for rejuvenating damaged reefs (Yap et al 1992). This is one of the illegally harvested coral species known as "white lace" in the coral trade (Ross 1984).

---

[1] Corresponding author.

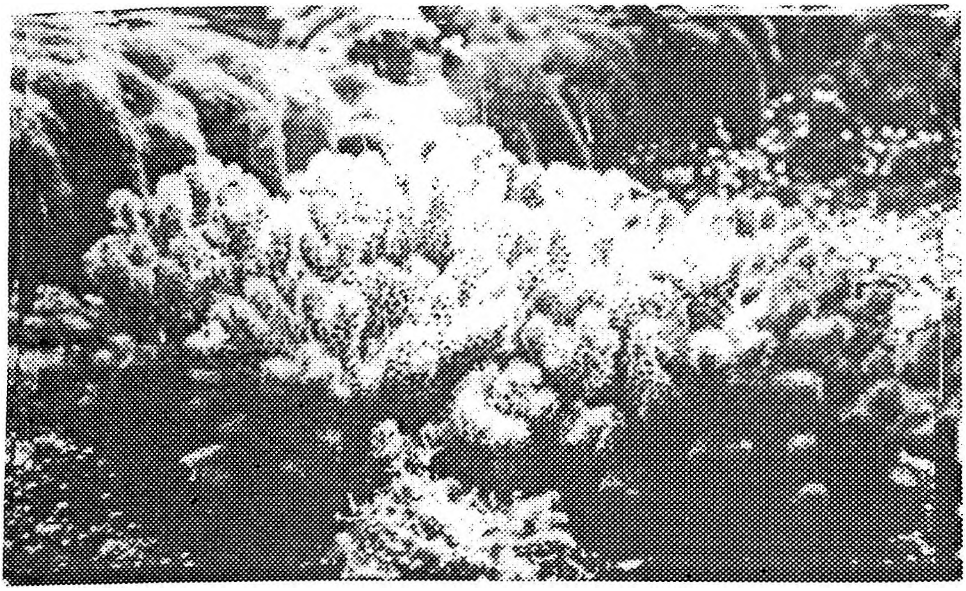

Fig. 1. ***Pocillopora damicornis*, Linnaeus.**

This study aims to describe some aspects of the population biology of the reef coral, *P. damicornis*, in a shallow reef flat in Taklong Island, Nueva Valencia, Guimaras, such as growth rate, reproduction, recruitment, and mortality rates. These demographic rates will elucidate the life history strategies of this population that enables it to survive and persist through time in the site. This life history information can be utilized further for modelling and predicting population trajectories.

MATERIALS AND METHODS

Study Site

The study was conducted in a reef flat some 150 m off the shoreline of Kalirohan Beach in Taklong Island, Nueva Valencia, Guimaras (122° E, 10° 22°N). The area is part of the Taklong Island National Marine Reserve (Fig. 2). The reef flat is shallow and water depth is a little over 2 m during spring high tides. Total live coral cover is estimated at 25% by individual count and cover estimate (Weinberg 1981) which is qualitatively considered a "fair" coral reef cover (Gomez and Alcala 1979).

Determination of Demographic Parameters

Density and dispersion

Four 20 m transects were established in the study site. The four transects were laid down parallel to the shore 10 m apart and all were within the inner reef flat zone

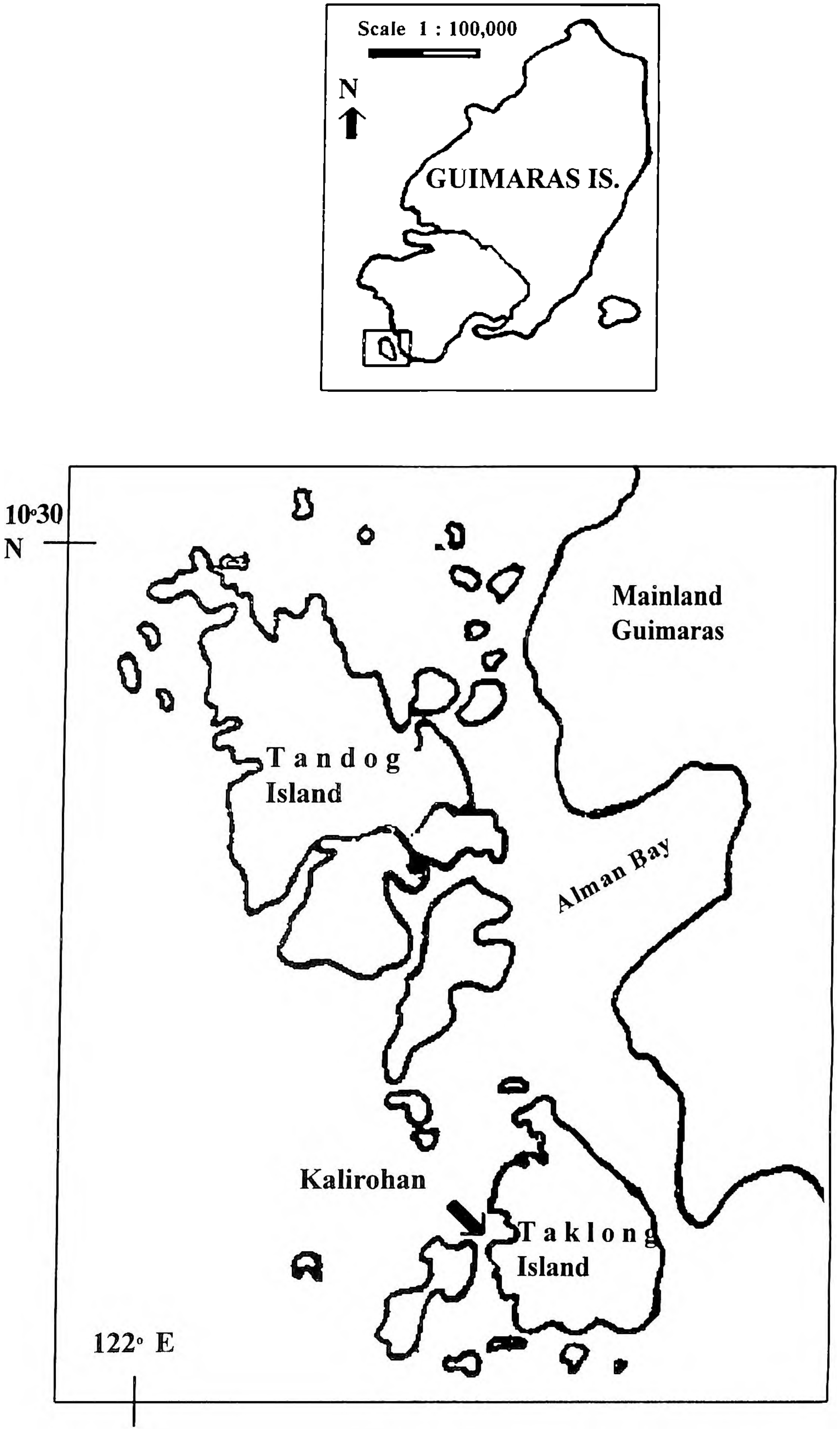

Fig. 2. Map showing the location of Kalirohan reef flat, Taklong Island, Nueva Valencia, Guimaras (see arrow).

on the same depth gradient. In each transect, 20 contiguous 1 sq m quadrats were laid down. Density of *P. damicornis* was estimated by counting the total number of colonies in each quadrat. Density was expressed as the number of colonies per sq m. To get its pattern of dispersion in the site, the occurrence and number of *P. damicornis* per quadrat were noted. From these data, the Coefficient of Dispersion (variance-to-mean ratio) was computed to determine departure from randomness (Fowler and Cohen 1990). The dispersion pattern of the colonies could give insights on how other demoghraphic processes such as recruitment and settement proceeds in the site.

Population size structure and coral colony radial growth

The population size structure in the site was evaluated by randomly choosing representative colonies of the species and measuring the size of each chosen colony. Sample colonies were selected using the point-centered quarter method (Weinberg 1981). All chosen samples were tagged with a coded plastic Dymo tape. The length (L) and width (W) of each colony were then measured with a caliper. Length (L) was defined as the longest diameter and width (W) the longest diameter perpendicular to the length axis. From L and W, the geometric radius, r, was computed as

$$r = \frac{(L \times W)^{1/2}}{2}$$ (after Polachek, 1978)

Each coral colony sampled was assigned to one of the following arbitrary size classes based on geometric radius, r:

Size Class I	: $r < 20$ mm
Size Class II	: $20 \text{ mm} \leq r < 40$ mm
Size Class III	: $40 \text{ mm} \leq r < 60$ mm
Size Class IV	: $60 \text{ mm} \leq r < 80$ mm
Size Class V	: $r \geq 80$ mm

Then, a size class frequency histogram was generated.

The size categorization used in this study was similar to that in Polachek (1978) on a related species, *Pocillopora meandrina*. Hughes (1984) used approximately the same size class widths as in this study for *P. damicornis*, except that his measurements were expressed in surface area (rather than r) and less size categories (three vs five) were employed. Ross (1984) also classified harvested colonies of *P. damicornis* from reefs in Central Philippines according to size, but the class width used was twice as broad.

Every quarter throughout the duration of the study, growth measurement of all colonies tagged at the beginning of the study were made using a caliper. Units of measurements were expressed to the nearest 0.5 mm. The absolute and radial growth rates of each tagged colony were computed as

$$\text{Absolute Growth Rate} = \frac{r_{t+1} - r_t}{\text{time}}$$

$$\text{Relative Growth Rate} = \frac{r_{t+1} - r_t}{r_t} \times 100$$

where r_t = the geometric radius at some initial time, and
r_{t+1} = the geometric radius after a time interval (every quarter or year).

In cases when some of the initial colonies disappeared or died after a quarter, new colonies (chosen through the point-centered quarter method) were tagged and measured. The mean annual absolute growth rate was determined at the end of the study.

Whole colony mortality

Tagged colonies were checked every quarter. Those that disappeared or died (wholly bleached with no polyps or completely overgrown with algae) were considered mortalities. The formula used in estimating mortality (M) was

$$M = \frac{\text{No. of dead colonies} + \text{missing at time, t+1}}{\text{no. of colonies sampled at time, t}} \times 100$$

Reproduction

Whole colonies located at the periphery of the study area were collected to establish the timing and regularity of larval release. Initially, collected colonies were limited to a size range following previous planulation experiments (i.e. $r > 50$ mm) (e.g. in Richmond and Jokiel 1984; Jokiel 1985; Richmond 1985). Peak release has always been found associated with lunar phase for this coral species (Fadlallah 1983; Richmond and Jokiel 1984; Jokiel 1985); however, geographical variations in the timing of release exist (Stimson 1978; Harriott 1983). So to establish the timing of peak release in the site, collection was timed with four lunar phases:

New Moon (NM) : between new moon and first quarter
First Quarter (FQ) : between first quarter and full moon
Full Moon (FM) : between full moon and last quarter
Last Quarter (LQ) : between last quarter and new moon

Colonies collected were measured for their individual length and width, then placed in buckets filled with seawater and transported to the laboratory in Taklong Island some 10 to 15 min away from the site. In the laboratory, each colony was placed in separate 2.5 l glass aquarium fully immersed in seawater and continuously aerated. Daily seawater changes were made if the colonies were kept for more than 24 h. The colonies were left for at least 12 h to a maximum of 38 h to planulate. Monitoring and recording of the number of planulae expelled by each colony was done every 2 h or more frequently when necessary. Between 3-6 colonies were used during each run. When colonies showed signs of stress (e.g. oversecretion of mucus, distinct foul smell and ejection of polyps), results from these colonies were excluded. All colonies were tagged and returned to the field afterwards. Two planulation runs per lunar phase were completed between January to March 1991. By then, the timing of peak release with the lunar phase was ascertained.

More planulation runs were performed to determine the regularity of spawning and the size range of colonies capable of spawning. Collections for these were synchronized with the lunar phase when the number of planulae released was greatest. Planulation experiments were undertaken in most months of the year to determine the regularity of spawning while smaller sized colonies were included in latter planulation experiments to determine which size cohorts were capable of releasing larvae. Sizes of colonies that were collected ranged from 40 mm - 95 mm in radius.

Recruitment

The four 20 sq m fixed plots established in determining population density and dispersion were the same plots observed to monitor influx and survival of visible recruits (dia ≥ 2 mm) (Bak and Engel 1979; Fitzhardinge 1988) in the study site. Every month beginning June 1991 up to March 1992, the position, origin, size, and fate (i.e. surviving, missing, dead) of each recruit were noted. The exact positions of visible recruits were recorded on an underwater slate. Origin (whether from larva or fragment) were recognized based on form and type of attachment (Richmond 1985). The average life-span of larvae-derived visible recruits was estimated based on life span of recruits that died or disappeared within the time frame of the study (i.e. before March 1992) despite possible underestimation. Average life span (X) was computed using the formula for deriving the average of grouped data (Fowler and Cohen 1990):

$$X = \frac{\Sigma fx}{n}$$

where: Σfx = the sum of frequency counts in all age classes (i.e. survival time, in months, after initial recruitment) of all recruits;
n = the total number of observations.

Abiotic Parameters

Abiotic parameters monitored in the study site included the minimum and maximum water temperatures, salinity, daylength, current speed and direction, and sedimentation rate.

Seawater temperature

A Taylor minimum - maximum thermometer was deployed at the bottom in the middle of the study site and left there throughout the duration of the study. Every month, the highest and lowest temperature readings were recorded.

Salinity

The weekly salinity level of surface water in the study site was determined using an Atago hand refractometer. The monthly salinity levels expressed in ppt were computed by taking the average of the weekly reading during each month.

Daylength

Daylengths were computed based on daily reports of sunrise and sunset times obtained from the Weather Bureau. The monthly daylength (in hour) was computed by getting the average of the daily daylength values.

Current speed and direction

Each month, the surface water current speed in the reef flat was monitored using drogues attached to calibrated strings. The drogue design is similar to that used by Hodgson (1989) except that the wing panels were made of flat G.I. sheets. Two drogues, about 10 m apart, were set out simultaneously by two persons in between tidal exchanges. Each person in a fixed position, would then slowly unroll the calibrated string attached to the drogue. Drogues were allowed to drift with the prevailing surface current for 10 min after which the distance each drogue traveled was measured based on the length of the unrolled calibrated string. The direction taken by each drogue was determined using a handheld compass. The average monthly current speed expressed in cm/s and the general current direction were recorded.

Sedimentation rate

Five pairs of silt traps made of PVC pipes were deployed within the study area. The dimensions of the silt traps followed the recommendation of Gardner (1980) with diameter to height ratio of 1:3 to avoid over- or undersampling. These traps were collected monthly and replaced with new sets. Contents were emptied and filtered. Residues were oven-dried at 60°C for five days then weighed to the nearest 0.01 g. Sedimentation rates were expressed in mg $cm^{-2}d^{-1}$.

The significance of association of some of these abiotic parameters with colony growth was tested using Pearson's product-moment correlation coefficient, r.

RESULTS

Density, Dispersion and Size Structure

The density of *P. damicornis* in the reef flat changed from 0.46 per sq m in March 1991 to 0.86 in March 1992. Fig. 3 shows an almost continuous density increase from March 1991 to January 1992 that began to decline in February.

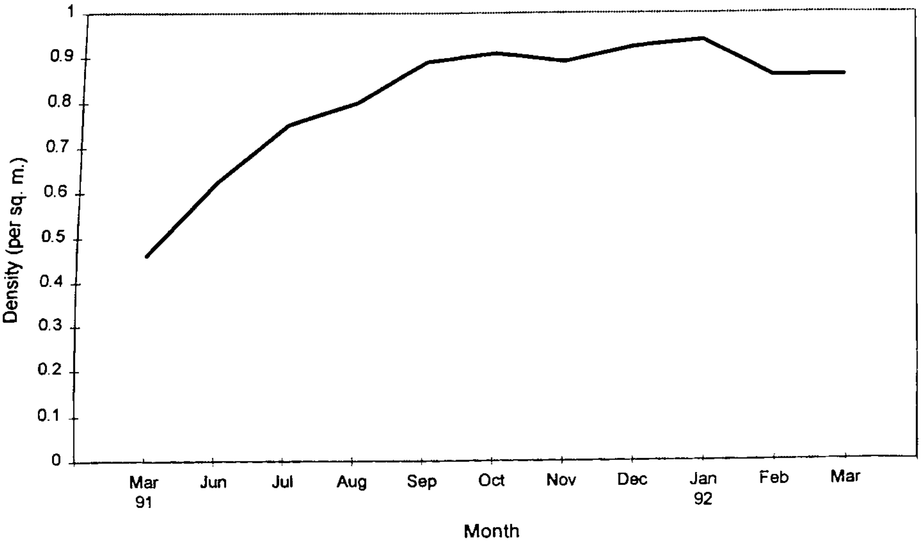

Fig. 3. Density changes over time in permanent plots.

Colony size ranged from r = 3.85 mm to 115.0 mm in the shallow waters but bigger colonies (r > 200 mm) were seen in the subtidal reef edges. Pocilloporid colonies tend to occur in clumps as suggested by the Coefficient of Dispersion (variance-to-mean ratio) value that was greater than 1.0. Considering the five arbitrary size classes, the size structure of the local population was skewed to the left. Smaller-sized colonies (r < 40 mm) consistently comprised almost two-thirds of the population on every quarterly assessment. Colonies with r > 80 mm never exceeded 7% of the total sampled population (Fig. 4).

Colony Growth

Radial growth rate of uninjured and space-unlimited colonies over a year averaged 20.3±1.45 (S.E.) mm while relative growth rate was 104.54±14.51% (Table 1a-b) regardless of size. Absolute radial growth is independent of initial size class ($r=-0.14$; $P>0.05$) while relative growth was negatively correlated with initial size ($r=-0.77$; $P<0.001$). Repeated monitoring of colonies every quarter revealed that radial growth was fastest in June to September 1991 (repeated measures MANOVA, $F<0.05$).

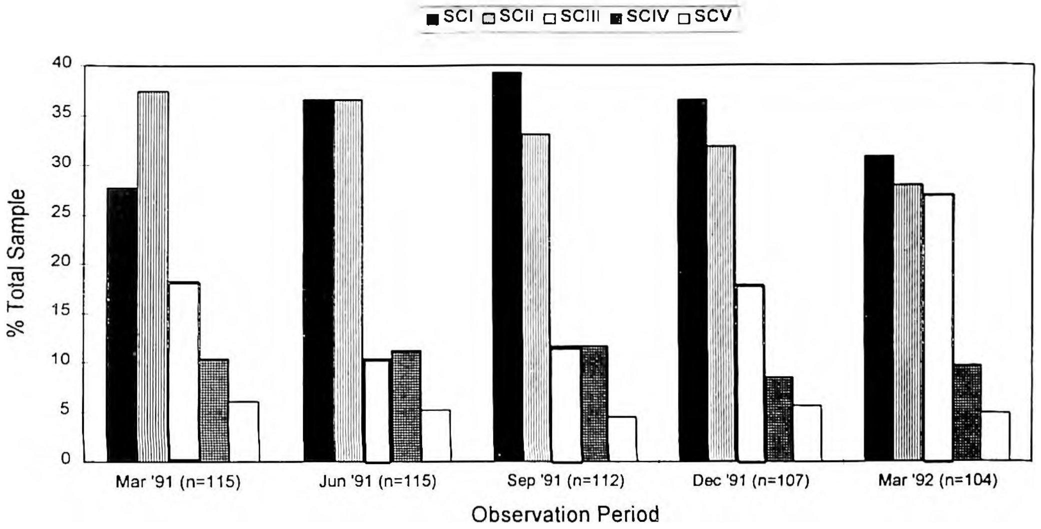

Fig. 4. Quarterly changes in size class structure of *P. damicornis* population in Kalirohan, Taklong Island.

Table 1a. Annual absolute growth rate (in mm) of "healthy", uninjured, yearlong surviving *P. damicornis* colonies.

Size Class	n	Mean	±S.E.
I (r < 20 mm)	12	22.72	2.16
II (r: 20-40)	10	18.26	2.09
III (r: 40-60)	6	20.66	3.73
IV (r: 60-80)	4	16.62	7.99
V (r > 80)	2	21.60	0.77
pooled Mean	(34)	20.26	1.45

Table 1b. Annual relative growth rate (in %) of "healthy", uninjured, yearlong surviving *P. damicornis* colonies.

Size Class	n	Mean	±S.E.
I (r < 20 mm)	12	201.97	17.28
II (r: 20-40)	10	72.64	8.96
III (r: 40-60)	6	42.87	8.87
IV (r: 60-80)	4	24.71	12.69
V (r > 80)	2	24.04	0.56

Considering the abiotic factors that were monitored (Table 2), faster radial coral growth was timed with relatively longer daylength and higher sedimentation rate (Fig. 5). Colony growth showed positive correlations with both daylength and sedimentation rate but were insignificant ($P > 0.05$).

Table 2. Abiotic conditions monitored from March 1991 to March 1992.

Month	Day-length (h)	Salinity (ppt)	Min T (°C)	Max T (°C)	ΔT	Sed. Rate ($mg\,cm^{-2}d^{-1}$)	Current Speed & Direction (cm/sec)
Mar-Apr '91	12.46	-	-	-	-	0.61	-
Apr-May	12.53	-	25.6	32.2	6.6	0.82	-
May-Jun	12.63	-	28.9	35.6	6.7	0.71	-
Jun-Jul	12.75	-	25.0	34.4	9.4	2.8	-
Jul-Aug	12.7	35	25.6	32.2	6.6	8.33	-
Aug-Sept	12.48	35	25.6	32.3	6.7	0.67	1.68 E-N-SW
Sept-Oct	12.18	35	26.7	33.9	7.2	1.16	3.8 NW
Oct-Nov	11.93	35	25.6	34.4	8.8	2.02	1.0 NW-NE
Nov-Dec	11.63	33.5	25.6	31.1	5.5	1.0	2.75 SW
Dec-Jan '92.	11.12	35	22.2	31.1	8.9	0.59	2.6 SW
Jan-Feb	11.57	35	25.0	31.1	6.1	0.24	1.74 SW
Feb-Mar	11.78	35	24.4	33.3	8.9	0.53	4.58 SW-NE
Dec-Jan '92	11.12	35	22.2	31.1	8.9	0.59	2.6 SW
Jan-Feb	11.57	35	25.0	31.1	6.1	0.24	1.74 SW
Feb-Mar	11.78	35	24.4	33.3	8.9	0.53	4.58 SW-NE
Range	11.12	33.5	22.2	31.1	6.1	0.24	1.0
	12.75	35.0	28.9	35.6	9.4	8.33	4.8

Reproduction

Pocillopora damicornis propagates by planulation and by fragmentation in the site with the former as the dominant mode of propagation. Mature colonies are brooders and release well-developed planktonic planulae that are ready to settle upon release (as early as within 2 h) under laboratory conditions. Planulae are pear-shaped, ciliated and brownish in color upon release due to the presence of symbiotic zooxanthellae. Planulae ranged in length from about 0.5 mm to 2.5 mm. In some cases, stressed colonies released bleached planulae.

There was regular production of planulae all year round (Table 3). Colonies in SC III to SC V ($r \geq 40$ mm) could planulate. Collectively, the reproductive cohorts easily comprised at least a third (33.4%) of sampled population (see also Fig. 4). Of the reproductive cohorts, those in SC IV released the most number of larvae per colony (Table 4). The larger proportions of colonies released their larvae during the new moon phase and least during the full moon phase (Fig. 6). Peak larvae production was synchronized with the new moon phase (Fig. 7).

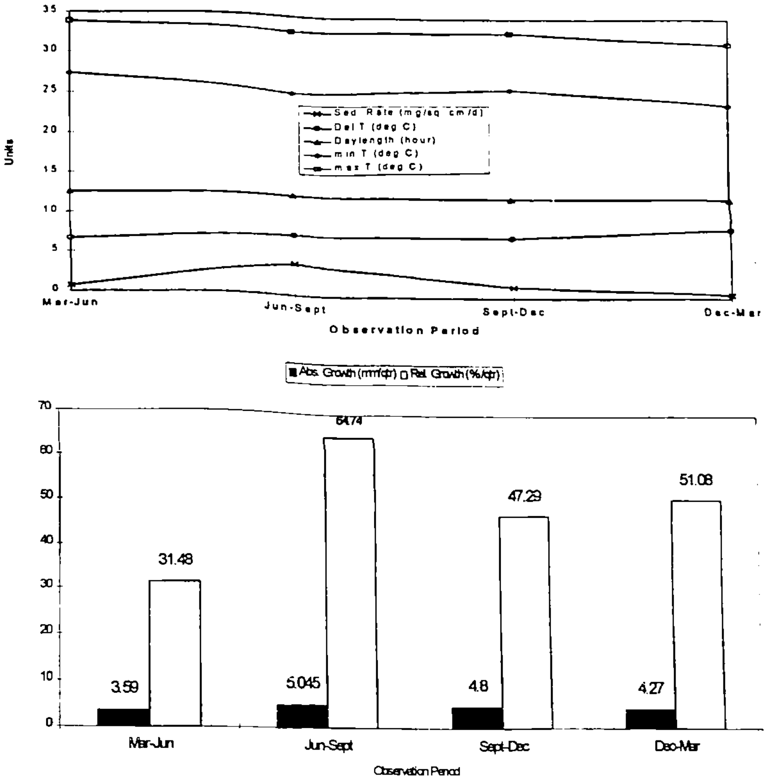

Fig. 5. Quarterly growth plotted against abiotic parameters.

Table 3. Relative availability of *P. damicornis* planulae (based on highest larval output per colony spawned in the laboratory) during the new moon phase unless indicated otherwise.

Month	Relative Abundance of Planulae
January 1991	+ full moon
(January 1992)	(+++)
February 1991	+++
(February 1992)	(+++)
March	+++ last quarter
April	+++
May	n.d.
June	+ first quarter
July	++
August	n.d.
September 1991	-
(September 1992)	(+++)
October	+ last quarter
November	+++
December	++

Legend: - none; + 1-10; ++ 10-50; +++ >50; n.d. no data

Table 4. Larvae production of *P. damicornis* colonies that spawned in the laboratory.

Size Class	n (no. of colonies observed)	Ave. no. of larvae released (per colony in 24 h)	approx. ratio among size classes
SC III	16	57	3
SC IV	21	120	6
SC V	1	21	1

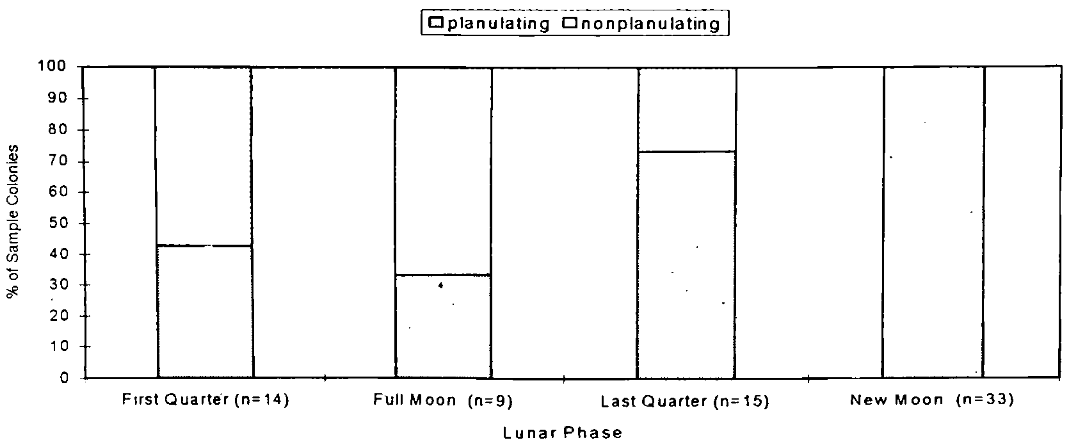

Fig. 6. Timing of planula release with lunar phase.

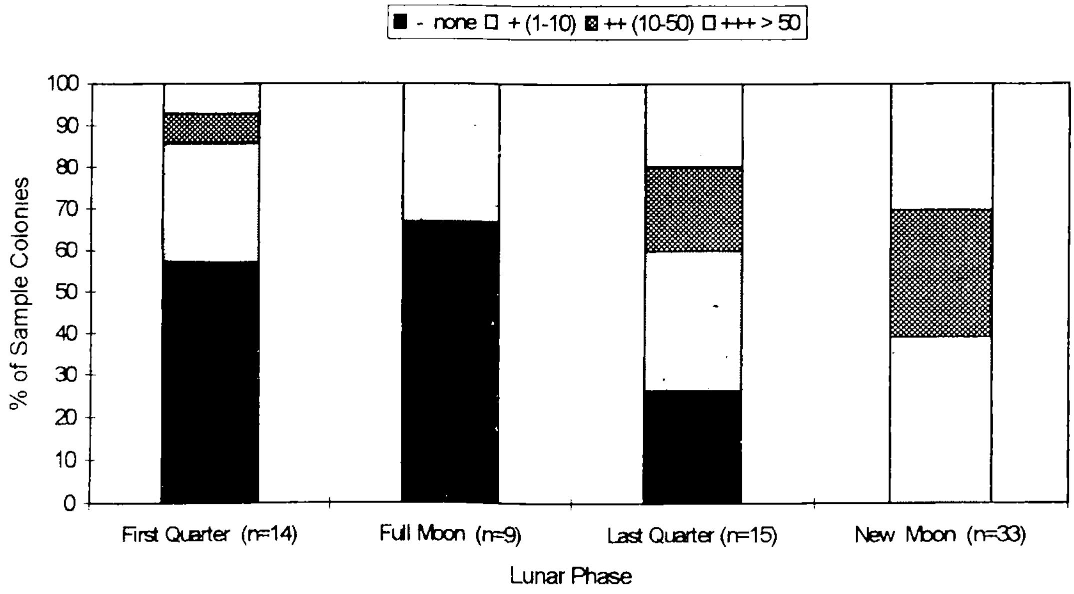

Fig. 7. Relative abundance of larvae production at different lunar phases.

Recruitment

Recruitment data strongly reflected the prevalent mode of reproduction. As revealed in Table 5, 88.1% (74) of the total recruits were larvae-derived "visible" recruits while only 15.9% (14) were fragment-derived. The origin of each recruit was verified based on the skeletal morphology of its base (Richmond, 1985).

Table 5. Monthly recruitment of *P. damicornis* in four 20 sq m plots in Kalirohan reef flat, Taklong Island, Nueva Valencia, Guimaras.

Observation Month (larvae)	new recruit (fragment)	new recruit (larvae)	surviving recruit (fragment)	surviving recruit (larvae)	dead/missing recruit (fragment)	dead/missing recruit (no. of recruits per 20 sq m)	AVE (n=4)
Apr-Jun '91	15						1.9
Jun-Jul	14	1	14		1		3.5 (3.8)
Jul-Aug	5	6	23	1	5		1.2 (2.8)
Aug-Sept	8	5	23	5	5	2	2.0 (3.2)
Sept-Oct	7		28	9	3	1	1.8
Oct-Nov	5		29	9	6		1.2
Nov-Dec	4	1	30	9	4		1.0 (1.2)
Dec-Jan '92	6	1	27	10	7		1.2 (1.8)
Jan-Feb	2		27	10	6	1	0.5
Feb-Mar	8		26	8	3	2	2.0
Total (after 11 mos.)	74	14	26	8	40	6	X= 1.7 (2.0)

(Note: values inside parentheses refer to combined larvae- and fragment-derived recruitment; without parentheses refer to larvae-derived recruitment only.)

There was an annual recruitment rate of 1.2 recruit per sq m. Larvae-derived "visible" recruits had initial radii ranging from 1.66 to 13.42 mm. On the other hand, fragment-derived recruits were larger ranging from 8.66 to 77.46 mm in radius.

The monthly presence of larvae-derived recruits in permanent fixed plots confirmed the periodic production of planulae. Fig. 8 shows that larvae-derived recruits were always present while fragment occurrence was episodic synchronized with high wave energy periods (between July to September 1991).

After 11 months, 26 of the 66 larva-derived recruits, fate of which was followed for at least a month, survived (Table 5, excluding Feb-Mar '92). This is equivalent to 39.4% survivorship. Recruits of larval origin were found to be generally short-lived

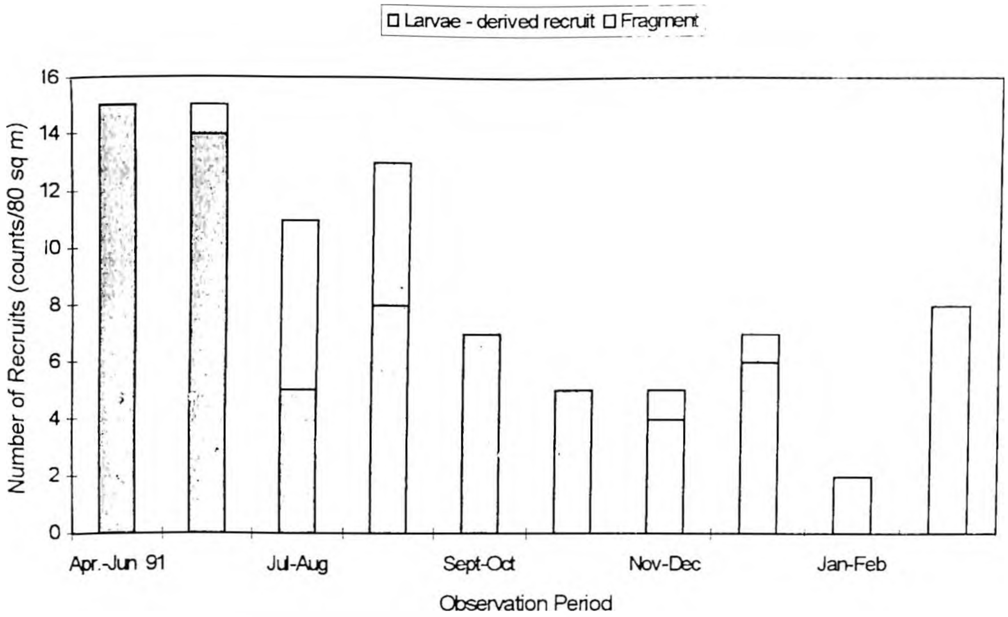

Figure 8. Recruit abundance in Kalirohan, Taklong Island.

Table 6. Life span frequency table of larvae-derived recruits.

Survival group (in months)	Frequency counts	f(x)
less than 1 (1)	14	14
1 to <2 (2)	8	16
2 to <3 (3)	7	21
3 to <4 (4)	7	28
4 to <5 (5)	3	15
5 to <6 (6)	3	18
6 to <7 (7)	2	14
7 to <8 (8)	1	8
	n= 45	Σf(x)=134
Ave. life span: Σf(x)/ n = 3 months		

with a life span of 3 months (Table 6). On the other hand, survivorship of fragment-derived recruits was higher (57.14%). However, many of these were observed to have shrunk in size over time

Colony Mortality

Over a larger spatial scale (~1500 sq m) the depletion rate was 47.3%. Mortality of established colonies was over 40% in all size classes except SC V (Table 7a). Over time, colony death per quarter (Table 7b) was highest in the first quarter (Mar-Jun 1991). This was closely followed by the second (Jun-Sept) and third quarter

Table 7a. Annual size-class specific mortality of *P. damicornis* in Kalirohan reef flat, Taklong Island, Guimaras.

Size Class	n (no. of colonies tagged)	d (no. of dead colonies)	Mortality (in %)
SC I	32	14	43.75
SC II	43	22	51.16
SC III	19	10	52.63
SC IV	12	5	41.67
SC V	6	2	33.33
Total	112	53	ave M = 47.32

Table 7b. Size-class specific mortality per quarter (Note: values inside parentheses refer to number of dead or missing colonies).

Size Class	n (no. initially tagged)	First Q Mar-Jun '91 % (counts)	Second Q Jun-Sept % (counts)	Third Q Sept-Dec % (counts)	Fourth Q Dec-Mar '92 % (counts)
SC I	32	18.75 (5)	7.69 (3)	10.17 (5)	5.41 (1)
SC II	43	18.60 (8)	31.71 (6)	38.99 (5)	16.13 (3)
SC III	19	10.53 (2)	17.65 (3)	12.50 (4)	33.33 (1)
SC IV	12	8.33 (1)	28.57 (3)	40.00 (0)	33.33 (1)
SC V	6	16.67 (1)	20.00 (1)	0.00 (0)	0.00 (0)
% M per Q		15.18 (17)	16.84(16)	17.72(14)	8.22(6)

(Sept-Dec) in decreasing order. There was least number of dead colonies observed in the last quarter (Dec-Mar 1992). In a smaller spatial scale (in four plots of total A= 80 sq.m.) mortality was lower (40.54%).

DISCUSSION

Colony Growth

The growth values obtained compared well with other growth studies conducted in the Philippines (e.g. Gomez et al 1985; Yap et al 1992) and matched well with growth rates reported for populations in Thailand (Phongsuwan 1991) and Hawaii (Polachek 1978). This shows that despite being widely separate in space and time, *P. damicornis* populations in the western Pacific exhibit narrow variations in growth rate. The growth rate established for this local population further confirms the slower growth of western Pacific populations *vis-a-vis* eastern Pacific populations (Richmond 1985; Richmond 1987). The insignificant differences in absolute growth rate of the different size classes establish the indeterminateness of coral growth (Polachek, 1978).

Pocillopora damicornis is considered as an opportunistic species (Maragos 1972; Connell 1973; Aliño et al 1985; Fitzhardinge 1988). The ability of small-sized colonies of this species to double their size (as shown by results on relative growth) within a short period gives them an edge in competing for space and consequently, access to critical resources like light and nutrients. Faster juvenile growth also implies that escape size from predation is reached sooner (Sebens 1982; Richmond 1985). Thus, it is proposed that investment of metabolic energy to somatic growth by small colonies is an adaptive strategy of opportunistic and brooding corals like *Pocillopora damicornis*.

Among the sufficiently monitored abiotic parameters, preliminary data showed that daylength and sedimentation rate are important on coral growth. Increasing daylength and higher sedimentation rates characterized periods when colony growth was faster. It is easy to relate faster growth with longer daylength considering that pocilloporids have light-requiring algal symbionts. These algal symbionts are found to translocate carbon to the coral host which the host then use to subsidize tissue growth (Muscatine 1991). On the other hand, heavy sediment load clogs polyps and limits light penetration which are detrimental to coral feeding, respiration, nutrient uptake, photosynthesis, and calcification. Inspite of this, *P. damicornis* showed better growth performance during a period of higher sedimentation rate. It should be noted that sedimentation levels observed in the site during the period ranged from 0.67 - 8.33 mg/cm^2/d. If monthly values were averaged for the quarter, the average would still fall within the "low" sedimentation regimes considered by Babcock and Davies (1991). It is generally believed that *P. damicornis* is resistant to high sedimentation as it is present in areas where the highest sedimentation rates have been recorded (Rogers 1990). Perhaps, *P. damicornis* colonies in Kalirohan reef flat are exposed to levels of sedimentation that they could tolerate.

Reproduction and Recruitment

The local population of *P. damicornis* are largely planulators, brooding then spawning fully-developed, ready-to-settle planulae. Colonies that planulated ($r \geq 40$ mm) are practically the same size groups that planulate in Hawaii (Holloran 1986; Martin-Chavez 1986). However, there is a need to sample a broader size spectrum (especially of the smaller ones) of pocilloporid colonies from the area before any conclusive statement regarding planulating size can be made.

In Kalirohan, Taklong Island, reproductive colonies have peak larval production between new moon and first quarter that is a similar planulation pattern observed for populations in Enewetak, Marshall Is. (Stimson 1978) and Lizard Is., Great Barrier Reef, Australia during austral summer (Harriott 1983). Why planular production relate to night irradiance is still largely unknown (Jokiel et al 1985). From planulation experiments in this study, larval release is likely to be monthly and takes place all year round as was likewise observed of populations in Palau, Hawaii, and Low Isles, Great Barrier Reef, Australia (var. authors in Fadlallah 1983).

Examinations of the skeletal morphology of the bases of pocilloporid colonies revealed that planulation could be the prevailing mode of propagation in the site. At the start of the study and in every quarterly assessment of colony growth and population size structure, majority (~97%) were found to have semicircular and flattened encrusting bases indicating that they were larvae-derived.

Asexual reproduction by fragmentation had augmented recruitment mostly during months when the Philippines generally experienced disturbance. It had been noted that Hawaiian populations of *P. damicornis* hardly resort to fragmentation as a reproductive strategy (Polachek 1978). In general, the same is true for populations in the western Pacific where recruitment via motile propagules seems to be more favored under conditions of unstable environmental conditions (Richmond 1985).

The recruitment rate in Kalirohan reef flat compared well with rates noted in Australian and Hawaiian reef flats with proportionate levels of live coral and pocilloporid cover (Fitzhardinge 1985; Harriott 1983). Although there was regular supply of recruits in the site all year round, most recruits were short-lived. Thus, there was fast turnover of new recruits every quarter. This demonstrates how important colony size is to survival. Small-sized recruits are more vulnerable to physical (e.g. dislodgement) and biological disturbance (e.g. predation, competition) than larger colonies (Polachek 1978; Richmond 1985; Hughes and Connell 1987; Hodgson 1990). Larger colonies have more polyps to "spare", so partial mortality due to grazing or breakage will not be likely fatal to the whole colony compared to coral juveniles. The absence of "crab protector" (Glynn 1988) in pre-three dimensional growth form (i.e. unbranched stage) may also exert some influence on recruit mortality.

Mortality

A comparison of the mortality rates in this study with those obtained by others on the same species reveals temporal and spatial variations in mortality trends. Perhaps, both environmental and biotic factors influence these variations. The mortality rate observed in Taklong Island, Guimaras was higher compared to the rate observed for this species in northern Philippines monitored in 1983 to 1984 (Yap et al 1992) that indicates interannual variations. Episodic death is suggested by differences in mortality but equal growth rates.

Environmental conditions may largely influence episodic death. These factors could include daylength and maximum temperature which were observed to have positive correlations with mortality trends of *P. damicornis* in the northern Philippine population (Yap et al 1992). A similar relationship exists in this study particularly with daylength. The greatest numbers of dead colonies were observed during the two quarters when daylengths were increasing and longest (Mar-Jun and Jun-Sept). Generally, these are also periods of high disturbance (strong SW monsoons and storm occurrence) in the country. This was the case in 1991 when 6 typhoons including a supertyphoon affected Panay and vicinity from March to August and may have been the major cause of death of many colonies in the site.

In this coral species, mortality appears to be size-related. Although all size cohorts had high mortality rates, the biggest size class had the lowest. Hughes and Connell

(1987) observed a similar but more evident trend for this same coral species in the reef crest zone in Australia. This trend is believed to indicate the existence of escape size against predation (Sebens 1982; Harriott 1983) or differential tolerance to certain environmental factors (Richmond 1985) that could be also size-related.

In Hawaii, Polachek (1978) got an opposite trend with higher mortalities in larger size classes. Although Polachek (1978) admitted that the actual cause of coral death was unknown, he hypothesized that mortality trend was a result of increased susceptibility to breakage or injury with size or age. It may then be useful to consider the significance of partial mortality on the eventual fate of the colony. In this study, many of the colonies that died within the year had some form of injury (breakage or dead portions) right at the start. Field studies demonstrated that the likelihood of injured colonies to progressively deteriorate and eventually die was high (Maragos 1972; Polachek 1978). The relative absence of pocilloporid predators in the site and its moderate competitive ability (Dai 1990; Nievales unpublished data) do not provide adequate explanations why there was such high mortality of established colonies during the study period. It may be necessary to evaluate mortality both over longer time scale and at shorter time intervals. In this way, both short-term and long term processes that affect colony survival can be well assessed.

Population Size Structure and Growth

The left-skewed population size structure is similar to the pocilloporid population in Hawaii (Polachek 1978) and in central (Cebu) Philippines (Ross 1984). Sebens (1983) suggested that the characteristic population structure of benthic organisms is a function of specific growth rate, recruitment patterns and mortality rate. He presented several events that could result to a left-skewed population structure. These would be: (1) if mortality is constantly high in all size classes; (2) if there is size-selective predation on large individuals; (3) immediately after an infrequent high recruitment event; and (4) during periods of high colonial fragmentation. Of these four possibilities, perhaps the likely reason is the continuous recruitment events that maintained a steady influx of new colonies into the smallest size class. Despite the fact that mortality appeared to be size-related with larger colonies having the highest survivorship, it seems that the recruitment rate is much higher than turnover to larger sized cohorts (i.e. few survive to become adult colonies). Further, it may be important to examine rate of growth transitions from one size cohort to another and the susceptibility to shrinkage (fragmentation) by the different cohorts. These may provide clearer explanations to the population structure aside from serving as useful empirical data for modelling population behavior over time.

Net recruitment surpassed mortality of established colonies thus resulting in positive population growth after a year. Estimates of population increase would vary between 61% to 80% depending on which mortality rate value is used. That the pocilloporid population indeed increased significantly from 1991 to 1992 is confirmed by density data. However, it must be emphasized that interannual variations in mortality and recruitment rates do exist and is beyond the scope of this study. Using the demographic rates obtained, in either case, the result is that more than half of the sampled population would be recruits. This shows the fast turnover rates in the local population and strongly reflects the fugitive life history strategy of this species.

ACKNOWLEDGMENTS

We thank the Fisheries Sector Program (FSP) for providing financial assistance to this project; Dr. Al Licuanan and two anonymous referees for giving valuable comments and suggestions to improve the manuscript; Mr. V. Basco for his assistance in the field;and the UPV Biological Sciences Division for allowing free access to its facilities in Taklong Island.

LITERATURE CITED

Aliño, P.M., V.V. Banzon, H.T. Yap, E.D. Gomez, J.T. Morales. 1985. Recovery and recolonization on a damaged backreef areas at Cangaluyan Island (Northern Philippines). In: Proceedings of the Fifth International Coral Reef Congress,Tahiti, 4:279-284.

Babcock, R.C. and P. Davies. 1991. Effects of sedimentation on settlement of *Acropora millepora.* Coral Reefs 9:205-208.

Bak, R.P.M. and M.S. Engel. 1979. Distribution, abundance and survival of juvenile hermatypic corals (*Scleractinia*) and the importance of life history strategies in the parent coral community. Mar. Biol. 54:341-352.

Connell, J.H. 1973. Population ecology of reef-building corals. In: Biology and Geology of Coral reefs 2. Bio. I. (eds. O.A. Jones and R.E. Endean), pp. 205-245. Academic Press, New York.

Dai, C. 1990. Interspecific competition in Taiwanese corals with special reference to interactions between alcyoonaceans and scleractinians. Mar. Ecol. Prog. Ser. 60:291-297.

Fadlallah, Y. 1983. Sexual reproduction, development and larval biology in scleractinian corals: A review. Coral Reefs 2:129-150.

Fitzhardinge, R.C. 1985. Spatial and temporal variability in coral recruitment in Kaneohe Bay (Oahu, Hawaii). In: Proceddings of the Fifth International Coral Reef Congress, Tahiti 4:373-378.

Fitzhardinge, R.C. 1988. Coral recruitment: The importance of interspecific differences in juvenile growth and mortality. In: Proceedings of the Sixth International Coral Reef Symposium, Townsville 2:673-678.

Fowler, J. and L. Cohen. 1990. Practical Statistics for Field Biology. John Wiley and Sons Ltd., England. 277 pp.

Gardner, W.D. 1980. Sediment trap dynamics and calibration: A laboratory evaluation. J. Mar. Res. 33:17-38.

Glynn, P.W. 1988. Predation on coral reefs: Some key processes and research directions. In: Proceedings of the Sixth International Coral Reef Symposium, Townsville 1:51-62.

Gomez, E.D. and A.C. Alcala. 1979. Status of Philippine coral reefs. In: Proceedings of the International Symposium in Marine Biogeography. S. Hem. Auckland, New Zealand 2:663-669.

Gomez, E.D. and A.C. Alcala. 1982. Growth of some corals in an artificial reef off Dumaguete, Central Visayas, Philippines. *Kalikasan,* Phil. J. Biol. 11:148-157.

Gomez, E.D., H.T. Yap, A.C. Alcala and P.M. Aliño. 1985. Growth studies of commercially important scleractinians. In: Proceedings of the Fifth International Coral Reef Congress, Tahiti 6:199-205.

Harriott, V.J. 1983. Reproductive seasonality, settlement and post-settlement mortality of *Pocillopora damicornis* (Linnaeus) at Lizard Island Great Barrier Reef, Coral Reefs 2:151-157.

Hodgson, G. 1989. Sedimentation of reef corals. Ph.D. Thesis, University of Hawaii. 38 pp.

Hodgson, G. 1990. Sediment and settlement of larvae of the reef coral, *Pocillopora damicornis,* Coral Reefs 9:41-43.

Holloran, M.K. 1986. The relationship between colony size and larva production in the reef coral, *Pocillopora damicornis* In: Coral Reef Population Biology (eds. P.L. Jokiel, R.H. Richmond and R.A. Rogers), Hawaii Inst. Mar. Biol. Tech. Rep. No. 37:167-169.

Hughes, T.P. 1984. Population dynamics based on individual size rather than age: A general model with a reef coral as an example. The Am. Nat. 123:778-795.

Hughes, T.P. and J.H. Connell. 1987. Population dynamics based on age or size? A reef coral analysis. The Am. Nat. 129:818-829.

Jokiel, P.L. 1985. Lunar periodicity of planula release in the reef coral, *Pocillopora damicornis* in relation to various environmental factors. In: Proceedings of the Fifth International Coral Reef Congress, Tahiti 4:307-312.

Jokiel, P.L., R.Y. Ito and P.M. Liu. 1985. Night irradiance and synchronization of planular release in the reef coral Pocillopora *damicornis.* Mar. Biol. 88:167-174.

Maragos, J.E. 1972. A study of the ecology of Hawaiian reef corals. Ph.D. Thesis University of Hawaii. 292 pp.

Martin-Chavez, E. 1986. Gametogenesis and origin of planulae in the hermatypic coral, *Pocillopora damicornis.* In: Coral Reef Population Biology (eds. PL Jokiel, R.H. Richmond and R.A. Rogers), Hawaii Ins. Mar. Bio. Bull. Tech. Rep. No. 37:193-205.

Muscatine, L. 1991. The role of symbiotic algae in Carbon and energy flux in reef corals. In: Coral Reefs. Ecosystems of the World (ed. Z. Dubinsky). Elsevier Science Pub., Amsterdam 26:75-87.

Phongsuwan, N. 1991. Recolonization of a coral reef damaged by a storm in Phuket Island, Thailand, Phuket Mar. Biol. Cent. Res. Bull. 56:76-83.

Polachek, T. 1978. The population biology of four common Hawaiian corals. M.Sc. thesis, University of Hawaii. 151 pp.

Richmond, R. 1985. Variations in the population biology of *Pocillopora damicornis* (Linnaeus). In: Proceedings of the Fifth International Coral Reef Congress, Tahiti 6:101-106.

Richmond, R. 1987. Energetics, competency and long distance dispersal of planula larvae of *Pocillopora damicornis.* Mar. Biol. 93:527-533.

Richmond, R.H. and P.L. Jokiel. 1984. Lunar periodicity in larval release in the reef coral, *Pocillopora damicornis* in Enewetak, Hawaii. Bull. Mar. Sci. 34:280-287.

Rogers, C.S. 1990. Responses of coral reef and reef organisms to sedimentation. A review. Marine Ecol. Prog. Ser. 62:185-202.

Ross, M.A. 1984. A quantitative study of the stony coral fishery in Cebu, Philippines. Mar. Ecol. 5:75-91.

Sebens, K.P. 1982. Competition for space, growth rate and reproductive output and escape in size. The Am. Nat. 120:189-197.

Sebens, K.P. 1983. Size structure and growth rates in populations of colonial invertebrates. In: The Ecology of Deep and Shallow Coral Reefs Undersea Research (ed. M.L. Reaka). NOAA Undersea Research Program Workshop on Coral Reef Ecol 1:9-15.

Stimson, J.S. 1978. Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. Mar. Biol. 48:173-184.

Vandermeer, J.H. 1981. Elementary Mathematical Ecology. A Wiley-Interscience Publications. 293 pp.

Weinberg, S. 1981. A comparison of coral reef survey methods. Bijdragen tot de Dierkunde 51:199-218.

Yap, H.T., P.M. Aliño and E.D. Gomez. 1992. Trends in growth and mortality of three coral species (*Anthozoa: Scleractinia*) including effects of transplantation. Mar. Ecol. Prog. Ser. 83:91-101.