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Ecological and physiological differences between two colour morphs of the coral *Pocillopora damicornis*

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Abstract *Pocillopora damicornis* (Linnaeus) is a ubiquitous branching coral found throughout the Indo-Pacific region. Like many other species of coral, *P. damicornis* displays a large range of morphologies. At One Tree Island, it occurs as two distinct morphs that are easily distinguished by the presence or absence of pink pigmentation. The two colour morphs of *P. damicornis* were found to differ in their distribution and abundance in the One Tree Island Lagoon. The brown morph was more abundant than the pink morph in the shallows (<1 m), whereas the pink morph was more abundant at deeper sites (>3 m). The two morphs also differed physiologically. The brown morph tended to have a greater calcification rate than the pink morph, regardless of environmental conditions. However, the difference in the calcification rate between the two morphs became non-significant under shaded conditions (5% full sunlight), indicating some degree of physiological plasticity of the morphs. The pink colour in *P. damicornis* was due to a hydrophilic pigment with a major peak absorbance at 560 nm. The expression of pink pigment had both genetic and phenotypic components. The brown morph has a reduced genetic capacity to express the pigment relative to the pink morph. On the other hand, pigment expression could be induced by light in the pink morph. Although genetic differences ultimately determine the differences between the two morphs of *P. damicornis*, the extent of pigment expression is under some degree of environmental influence.

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Introduction

Reef-building corals are typified by taxa that often show a tremendous range of colours and colony morphologies within single species (Veron and Pichon 1976; Veron 1986). Colony shape may differ in branch thickness, spacing and geometrical arrangement, while colony colours may range from brown to pink within the one species (for review see Veron 1986). While intraspecific variability is increasingly being recognised as one of the hallmarks of the Scleractinia (Bradshaw 1965; Yonge 1968; Wijsman-Best 1974; Veron and Pichon 1976; Potts 1978; Foster 1979, 1980; Veron 1981; Willis 1985; Willis and Ayre 1985), the ecological and physiological ramifications of these differences remain largely unexplored.

The morphology of coral colonies has direct implications for physiological performance. Variation in colony shapes influence such aspects as the flow regime and local boundary-layer thicknesses outside colonies, and hence the gas and nutritional exchange that occurs across the surfaces of coral colonies (Patterson et al. 1991; Lesser et al. 1994). Colony shapes can also determine the availability and quality of tissue space for light capture, and hence the photosynthetic activity of resident zooxanthellae (Lesser et al. 1994). Colony morphology and the resulting physiological performance may play roles in determining the distribution of the different morphs of a species. To this end, a range of studies have correlated the occurrence of particular morphs with different environmental regimes (Dustan 1975; Foster 1979, 1980; Veron 1981; Potts 1984; Willis 1985; Gleason 1993). It is important to point out, however, that most of these studies do not distinguish whether variability in colony morphology determines distribution patterns or whether distribution determines colony morphology.

Colonies may also vary in the intensity and type of pigmentation. Two broad categories of colour are

associated with the tissues of corals. Zooxanthellae impart a brown colour to coral surfaces which may pale or intensify depending on local light conditions (Wethey and Porter 1976; Muscatine et al. 1984; Porter et al. 1984). The primary role of these pigments is in the harvesting of light, and changes in colony colour reflect changing photosynthetic strategies. Corals also have pigments that appear to be associated with the tissues of the host as opposed to the zooxanthellae (Kawaguti 1944; Shibata 1969). These compounds often bestow brilliant greens, reds and blues to the tissues of corals. While these compounds are a prominent component of the visual impact of a living coral reef (Fox and Pantin 1944), their role in the ecology and physiology of reef-building corals is completely undocumented. These compounds form the focus of the current study.

Pocillopora damicornis (Linnaeus) is one of the most widely distributed corals, and is typified by a broad range of morphologies and colours (Veron and Pichon 1976; Veron 1986). Various authors have classified the intraspecific variants of *P. damicornis* in different ways. Veron and Pichon (1976) associated the morphs of *P. damicornis* with the "biotopes" in which they were found, and Stoddart (1984a, b) showed that populations of *P. damicornis* could be distinguished on the genetic level. Furthermore, two morphs of *P. damicornis* are recognised in Hawaii, and they differ in the presence or absence of a yellow animal pigment, branching morphology, larvae releasing pattern, and larval longevity (Richmond and Jokiel 1984; Richmond 1987). *P. damicornis* from reefs associated with One Tree Island (southern Great Barrier Reef, Australia) is represented by two distinct morphs that can be distinguished by the presence or absence of a pink colour, and which are found occupying very similar habitats within the 8 km^2 lagoon. Preliminary studies have revealed that colony colour does not assort with common genetic loci (Hoegh-Guldberg, Benzie and Moreno unpublished data), but does correlate with some aspects of colony growth (Hoegh-Guldberg et al. 1994).

This study examines the distribution of the two morphs within One Tree Island lagoon and investigates the physiological correlates of colony colour. The results of a preliminary isolation of the factor responsible for the colour difference between the two morphs is also presented. The colour of the pink morph is due to a hydrophilic compound that absorbs maximally at 560 nm and whose expression is primarily controlled by the intensity of visible light falling on a colony.

Materials and methods

The experiments described in this study were performed on *Pocillopora damicornis* (Linnaeus) collected near One Tree Island Research Station at the southern end of the Great Barrier Reef, Australia (23° 30'S; 152° 06'E) between February and July 1994.

Collection and maintenance of corals

All corals used experimentally in this study were collected from similar environments (exposed to sun, ≃1 to 2 m in depth) in One Tree Island Lagoon. They were brought back to One Tree Island Research Station with minimum exposure to air, and were kept in flow-through aquaria until used. The tissue colour of colonies or nubbins was determined objectively using a standard colour chart (#26 to #40; 1993 Popular Colours, Dulux, Australia) and three people as independent assessors. The intensity of the pink pigment varied among colonies, from brown to intense pink. However, the colonies could generally be defined as of the "brown" morph (the paint card range #26 to #30 or the "pink" morph (the paint card range #31 to #40). These colour ranges corresponded to colours shown for the "highlight colour" in the Macintosh computer program (Control panels, Systems folder). The brown-morph range corresponded to a hue range of 500 to 7000, and a saturation range of 28453 to 65535 at the brightness of 4000, and the pink morph corresponded to a hue range of 60750 to 64000, and a saturation range of 28453 to 65535, also at the brightness of 4000. An underwater torch was used when coral colour was determined for in situ examination of colonies at depth.

Distribution of brown and pink colonies in One Tree Island Lagoon

The distribution of brown and pink colonies of *Pocillopora damicornis* was analysed within One Tree Island lagoon. To do this, the lagoon was divided into two general regions, "edge" and "centre" (Fig. 1). The edge was subjected to faster flows of water when the lagoon was connected with the ocean proper at incoming and ongoing tides, whereas the centre was calm with much reduced water flows (Frith 1981). Within each region, two microatolls were randomly chosen as replicate sites. The microatolls were divided into three habitats, forming horizontal adjacent belts around the outside periphery of the microatolls. The habitats were defined as top (the top surface of the crust of microatolls), slope (depths of 1 to 3 m), and bottom (sites at base of each microatoll; all deeper than 3 m). Within each habitat, five transects (1 m × 5 m) were placed haphazardly, and the number of brown and pink colonies of *P. damicornis* was counted within each transect. Within each site, the light intensity at each depth was measured using a light meter (LI 1000, LICOR) at times close to midday.

Calcification rates of brown and pink morphs under different environmental conditions

Small replicate subcolonies were made from three parent colonies (each ≃30 cm diam) of the brown and pink morphs. Coral colonies were broken into fragments (hereafter called nubbins) of 3 to 5 cm in length. The nubbins were glued onto numbered Perspex plates (30 mm × 30 mm × 3 mm) with marine epoxy (Vepox, Vessey Chemicals). The nubbins were held onto weighted plastic racks (IG051 mat, Nally).

Nubbins were grown in a number of different environments in the field to investigate the relative sensitivity of calcification in the two morphs to perturbed environmental conditions. Six nubbins from each colony were put into each of three replicated sites of four different treatments. Four different treatments were used (hereafter referred to as full sunlight, shade, channel, and calm bay). The nubbins for the full sunlight treatment were placed inside three randomly chosen replicate microatolls. The nubbins for the shade treatment were placed under the artificially constructed black mesh shades within another three randomly chosen replicate microatolls. The mesh shades cut off 93 to 94% of visible light at the surface of the water (measurements made at midday using a light meter, LI 1000, LICOR).

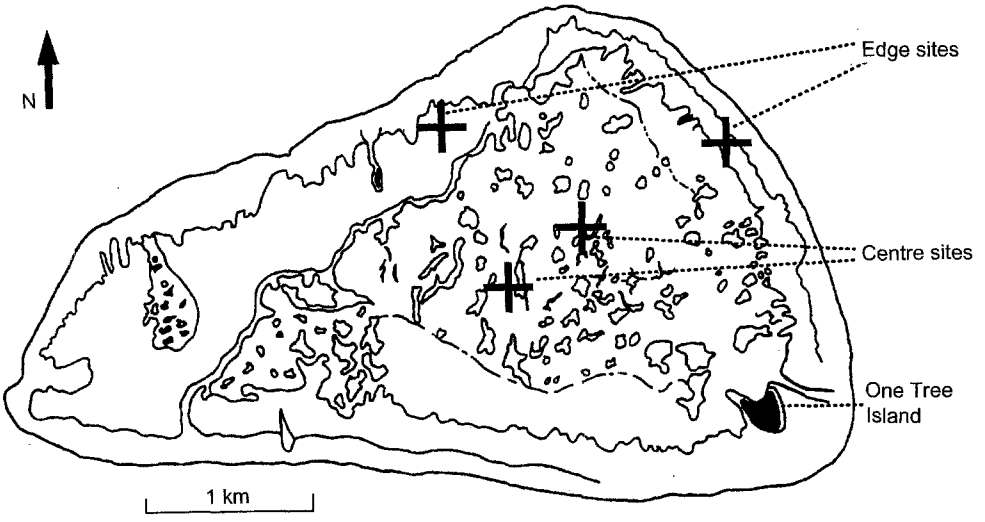

Fig. 1 Map of One Tree Island (southern Great Barrier Reef; 23° 30'S; 152° 06'E) showing two regions (*Centre* and *Edge*) in which distribution of the two morphs of *Pocillopora damicornis* were examined

The calcification rate of the nubbins was measured by the buoyant-weight technique (Jokiel et al. 1978), using an electric balance sensitive to 10 µg (A200S Analytic, Sartorius). Nubbins to be weighed were transported from the field submerged in plastic buckets. Epifauna and epiflora were removed from the Perspex base with a razor blade to exclude non-coral organisms from the measurements. After weighing, the nubbins were resecured to racks and returned to the field. The combined buoyant weight of the Perspex plate, epoxy, and the dead parts of the nubbin covered in epoxy was measured for each nubbin after the final measurement. This weight was then subtracted from both of the 2 and 4 mo buoyant-weight measurements of each nubbin, and the calcification rates were calculated as a proportion of the coral skeleton (that covered by living tissue) in each case.

The calcification rates of all six replicate nubbins were measured for the first time period (March to May, 1994). However, half of the replicate nubbins from the full sunlight and shade treatments were killed in order to analyse their physiological characteristics after the May measurement. Therefore, a maximum of three nubbins from full sunlight and shade habitats were available for calcification measurements between May and July. The influence of treatment, site, morph, and parent colony on the calcification rates of nubbins was analysed by a four-factor nested analysis of variance (ANOVA) and Student–Newman–Keuls (SNK) tests (GMAV5, Underwood and Chapman, University of Sydney) for data from each time period.

Number of zooxanthellae per surface area in brown and pink morphs under different environmental conditions

The density of zooxanthellae was measured for nubbins that had been subjected to the conditions described in the preceding subsection. Three replicate nubbins from each replicate site for full sunlight and shade treatments were analysed after the buoyant-weight measurements in May. The other three replicate nubbins from these treatments and four replicate nubbins from channel and calm bay treatments were analysed after their buoyant-weight measurements in July. All nubbins were placed in 10% formalin (diluted with sea water) at 04.00 hrs, when zooxanthellae from *Pocillopora damicornis* have their peak cell-division rates (Hoegh-Guldberg 1994). Nubbins were left in the formalin for 30 h and then transported to the University of Sydney. The number of zooxanthellae were standardized to surface area, which was measured for each fragment using a modification of the foil method of Marsh (1970).

Control of pigment expression: influence of light environment

The induction of the pink pigment was investigated using field experiments involving exposure of nubbins to a range of light conditions over 60 d. The aim of these studies was to determine whether the expression of the pink pigment in the tissues of *Pocillopora damicornis* was under genetic or environmental control.

Nubbins from three brown and three pink colonies of *Pocillopora damicornis* were made as described in earlier subsection, "Calcification rates of brown and pink morphs under different environmental conditions". Inner branches from both brown and pink colonies (low in pink pigment in both cases) were used in this experiment to make nubbins. Initial samples were taken to measure the concentration of pigment in the inner branches of both morphs at the beginning of the experiment. The original colours of the nubbins were recorded at the beginning and end of experiment as described in first subsection, "Collection and maintenance of corals".

Three nubbins from each colony were secured onto a weighted plastic rack with cable ties and distributed in each of three replicate sites (1 m depth at low tide) in each of three treatments. The three treatments used were full sunlight, shade (6 to 7% full sunlight), and full sunlight minus UV (wavelengths 200 to 360 nm excluded). For full sunlight minus UV treatment (hereafter called UV-less), nubbin racks were placed under a 6 mm-thick Perspex sheet (Plexiglas, Rohm), that was slightly larger in area than the rack, and which was supported by Perspex pillars at four corners. The Perspex sheet transmitted no UV light (200 to 360 nm), but was 90 to 95% transparent to the visible light (data not shown). The nubbins were left in the treatments for 60 d.

The colour and concentration of pink pigment in all nubbins were measured at the beginning and end of the experiment. Coral fragments (10 g wet wt) were extracted with 15 ml of 0.06 *M* phosphate buffer (pH = 6.65, made of 0.06 *M* KH_2PO_4 and 0.06 *M* K_2HPO_4) for 24 h. Preliminary studies revealed that this treatment was long enough to extract at least 95% of all pigment from the coral samples. The absorbance of extracts at wavelengths between 200 and 750 nm was measured using a scanning spectrophotometer (Phamacia Ultraspec III and Autofill III). Absorbance baselines were measured using extraction solvents as blanks. Details of the absorbance spectrum of the purified pigment are presented elsewhere (Dove et al. 1995).

The pigment extract has its peak absorbance at 560 nm. The concentration of pigment was calculated using absorbances at 560 nm for each sample using the extinction coefficient for the pink pigment which has been biochemically characterised by Dove et al. (1995; "pocilloporin", 34059 + 1635 $cm^{-1} M^{-1}$) . Pigment contents

were standardized to surface areas of each coral colony. Variation in concentration of pigment in the different morphs and treatments was analysed using a four-factor nested ANOVA followed by SNK tests (GMAV5, Underwood and Chapman, University of Sydney). Variation in the density of pocilloporin in the pink morph across light regimes was analysed separately using a three-factor nested ANOVA (GMAV5, Underwood and Chapman, University of Sydney).

Table 1 *Pocillopora damicornis.* Analysis of variance of density of brown and pink colonies (colonies 5 m^{-2}) in top, slope, and bottom habitats. Factors in parentheses are those in which preceding factors are nested (*r* region: *MS* mean square)

Source	*df*	*MS*	*F*	*p*
Top habitat: untransformed data, Cochran's test = 0.1683, NS				
region	1	13.225	1.18	0.3911
site (*r*)	2	11.225	8.89	0.0008
morph	1	81.225	38.22	0.0252
region × morph	1	34.225	16.11	0.0568
morph × site (*r*)	2	2.1250	1.68	0.2018
residual	32	1.2625		
total	39			
Slope habitat: untransformed data, Cochran's test = 0.2607, NS				
region	1	10.231	0.18	0.7127
site (*r*)	2	56.862	8.28	0.0013
morph	1	6.9128	0.44	0.5744
region × morph	1	34.568	2.21	0.2753
morph × site (*r*)	2	15.628	2.27	0.1192
residual	32	6.8705		
total	39			
Bottom habitat: log transformation, Cochran's test = 0.4407, $p < 0.05$				
region	1	3.5184	2.40	0.2614
site (*r*)	2	1.4653	1.09	0.3480
morph	1	14.286	97.3	0.0101
region × morph	1	0.0962	0.66	0.5033
morph × site (*r*)	2	0.1469	0.11	0.8967
residual	32	1.3429		
total	39			

Results

Distribution of brown and pink colonies in One Tree Island Lagoon

The density of all *Pocillopora damicornis* colonies did not differ between the edge and centre regions in any of the three habitats ($F_{1,2} = 1.18$; $F_{1,2} = 0.18$; $F_{1,2} = 2.40$, top, slope, and bottom, respectively, all $p > 0.05$; results of ANOVA given in Table 1). However, the relative proportion of brown and pink colonies varied greatly, depending on the atoll surveyed (variance indicated by standard error bars in Fig. 2). This difference was seen in the top and the slope habitats ($F_{2,32} = 8.89, p < 0.01$; $F_{2,32} = 8.28, p < 0.01$, respectively). There was a significantly greater number of brown colonies than pink in the top habitat ($F_{1,2} = 38.22, p < 0.05$; Fig. 2). The converse trend was seen in the bottom habitat ($F_{1,2} = 97.27, p < 0.01$; Fig. 2), while the numbers of brown and pink colonies did not differ significantly in the slope habitat ($F_{1,2} = 0.44, p > 0.05$; Fig. 2). The light intensities of the slope and bottom habitats were 71.3 ± 4.7% and 47.0 ± 7.5% of that of the top habitat, respectively.

Calcification rates of brown and pink morphs

Calcification rates of brown and pink colonies of *Pocillopora damicornis* from only two replicate sites within each treatment were used for statistical analyses (four-factor ANOVA), since all corals in one of the channel sites died sometime between the first and second weight measurements. Analysis of some factors was not directly possible, due to limitations in the experimental design. However, data could be pooled to obtain an approximate *F*-ratio for particular factors. This was

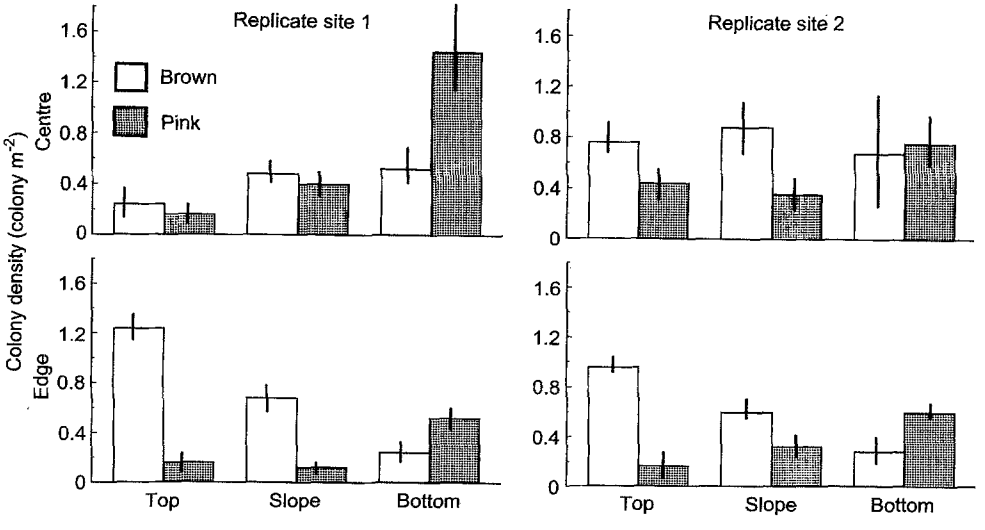

Fig. 2 *Pocillopora damicornis.* Population density (means ± SEM, $n = 5$) of brown and pink morphs in top, slope and bottom habitats in two replicate sites within centre and edge areas of One Tree Island lagoon

possible if one of the sources of variation involved in the factor had a p-value that was > 0.25 and thus could be eliminated from the mean-square estimate for the particular factors (M.G. Chapman, University of Sydney, personal communication).

The calcification rates of nubbins were significantly larger in the March to May period than in the May to July period [pooled data; time × site(treatment) eliminated; $F_{1,4} = 15.25, p < 0.05$; Fig. 3]. The following trends were shared by the calcification rates of corals in two time periods: (i) The calcification rates of corals in four treatments were very similar (Fig. 3), and differences among treatment means were only significant in the March to May period [pooled data, "site(treatment)" eliminated; $F_{3,12} = 18.54, p < 0.01$]. (ii) Judging by the mean calcification rates in four treatments, brown colonies tended to have greater calcification rates than pink colonies in all treatments (Fig. 3), although ANOVA of pooled data (as before) showed that morph effects were not significant ($F_{1,4} = 4.35$, $p > 0.05$ for March to May; $F_{1,4} = 4.02$, $p > 0.05$ for May to July). (iii) A large and significant variability between colonies was seen within both morphs ($F_{4,16} = 6.75$, $p < 0.01$ for March to May, $F_{4,16} = 6.23$, $p < 0.01$ for May to July).

There were differences in the outcomes between sampling periods. In the first time period, the interaction between morph and treatment was significant [pooled data; "morph × site(treatment)" eliminated; $F_{3,12} = 4.18, p < 0.05$], despite the morph being non-significant on its own [pooled data; "morph × site (treatment) eliminated; $F_{1,4} = 4.35, p > 0.05$]. However, interaction between the morph and treatment was not significant in May to July (similarly pooled data; $F_{12,3} = 2.77, p > 0.05$). In this case, a significant interaction between time period, treatment and morph was also found [pooled data, "time × treatment × colony (morph) " eliminated; $F_{1,2} = 12.7, p < 0.05$].

The density of zooxanthellae was analysed in two nubbins from each of two colonies of each morph within each of two replicate sites in each treatment after 4 mo (Fig. 4). Only the variation between colonies of each morph was significant. Pooling of data was not possible, since all factors whose F-ratios were obtained had a p-value that was > 0.25. Therefore, the significance of environment, morph or their interaction could not be analysed.

The density of zooxantheallae in nubbins in the light and shade treatments was analysed for each time period separately and comparatively between two time periods, using two replicates (independent data) from three colonies of each morph in three replicate sites per treatment for each time period. The density of zooxanthellae did not vary significantly between the two morphs after 2 or 4 mo of being left in light or shade (pooled data, $F_{1,4} = 0.41$, $p > 0.05$; $F_{1,4} = 0.08$, $p > 0.05$). However, the coral nubbins in the shade treatment had higher zooxanthellae densities than those in the light treatment (Fig. 5). Although such differences displayed only a statistically non-significant tendency after 2 mo, the differences became larger and statistically significant after 4 mo (Fig. 5). This was indicated by all three brown colonies and two of the three

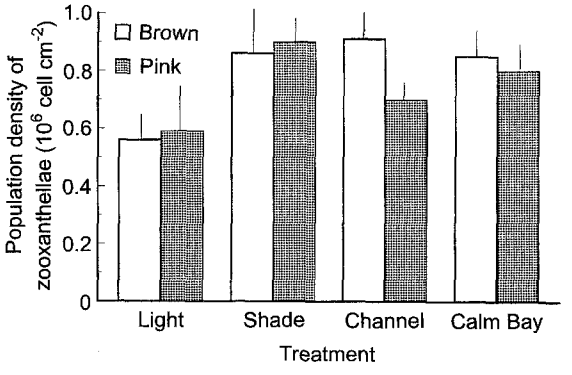

Fig. 4 *Pocillopora damicornis.* Mean densities of zooxanthellae (+ SEM) in tissues of brown and pink colonies in four treatments during two time periods (March–May and May–July 1994)

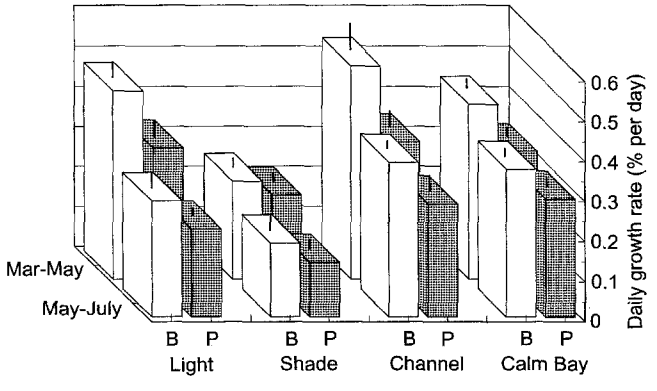

Fig. 3 *Pocillopora damicornis.* Mean calcification rates (+ SEM) of brown (*B*) and pink (*P*) colonies in four treatments during two time periods (March–May and May–July 1994)

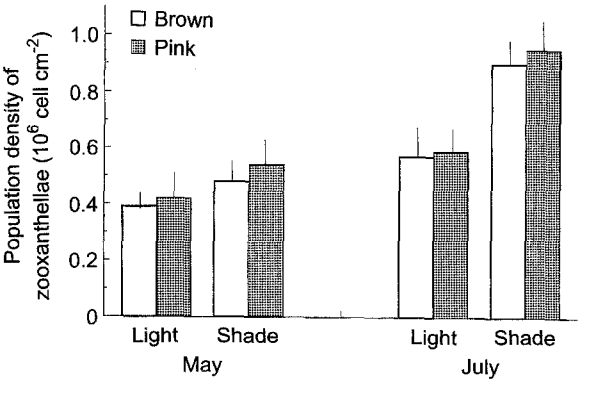

Fig. 5 *Pocillopora damicornis.* Mean densities of zooxanthellae (+ SEM) in tissues of brown and pink colonies in light (full sunlight) and shade (5% full sunlight) after 2 mo (May 1994) and 4 mo (July 1994)

pink colonies possessing significantly larger densities of zooxanthellae in the shade than in the light [$p < 0.01$; SNK test for treatment × colony(morph) with $p < 0.05$].

Control of pigment expression: influence of light environment

The extracts of the inner, brown parts of both brown and pink colonies had similar, low absorbances at 560 nm (Fig. 6). The absorption at 560 nm could not be converted to amount of pigment (pocilloporin) per surface area of corals because the surface area of the coral fragments was not measured. However, given that similar amounts of coral tissue were extracted ($\simeq 10$ g wet wt), it is clear that the brown inner branches from both morphs had a similar and low amount of pocilloporin in their tissues at the beginning of the experiment.

The concentration of pocilloporin was analysed at the end of 2 mo exposure to the three light regimes. Due to the death of some nubbins, and in order to have a consistent number of replicates in all treatments, data from two out of three replicate nubbins were used. After exposure to the three light regimes, the concentration of pocilloporin (pmol cm^{-2} coral tissue) was significantly higher in nubbins originating from pink colonies than in those originating from brown colonies [pooled data, morph × site(light regime) eliminated; $F_{1,4} = 45.9, p < 0.01$; Table 2 and Fig. 7]. Nubbins originating from brown colonies had similarly low concentrations of pocilloporin regardless of the light regime (Fig. 7), except in one case (Brown Colony #3) which produced a slightly greater ($p < 0.05$) amount of pocilloporin in full sunlight than in shade.

In contrast to brown colonies, the effects of colony ($F_{2,12} = 6.80, p < 0.05$, Table 2) and light regime [pooled data, site(light regime) eliminated; $F_{2,4} = 41.84$, $p < 0.01$, Fig. 7] on pocilloporin concentration were both significant in nubbins of the pink morph. All nubbins from pink colonies in full sunlight and UV-less treatments developed a pink colour. Interestingly, pocilloporin expression was not confined to the new tissue in the branch tips, but also developed in older tissues near the base of each nubbin. Nubbins originating from pink colonies that were incubated in the

Table 2 *Pocillopora damicornis.* Analysis of variance of pocilloporin concentration (pmol cm^{-2}) under three light regimes after 2 mo in brown and pink colonies and in pink colonies alone. Factors in parentheses are those in which preceding factors are nested (*l* light regime; *m* morph; *no test* cases where mean square estimates could not be compared with each other to obtain *F*-ratio)

Source	*df*	*MS*	*F*	*p*
Brown and pink colonies: data with arc-sine (%) transformation; Cochran's test = 0.1672, NS				
light regime	2	63.32	no test	no test
site (l)	6	4.476	2.89	0.0289
morph	1	271.5	no test	no test
colony (m)	4	5.911	3.82	0.0154
light regime × morph	2	24.40	no test	no test
light regime × colony(m)	8	6.317	4.08	0.0035
morph × site (l)	6	0.611	0.39	0.8752
colony (m) × site (l)	24	1.548	1.83	0.0329
residual	54	0.843		
total	107			
Pink morph: untransformed data; Cochran's test = 0.2456, NS				
light regime	2	25.31	no test	no test
site (l)	6	0.527	0.87	0.5437
colony	2	4.114	6.80	0.0106
light regime × colony	4	4.310	7.12	0.0035
colony × site (l)	12	0.605	1.62	0.1461
residual	27	0.375		
total	53			

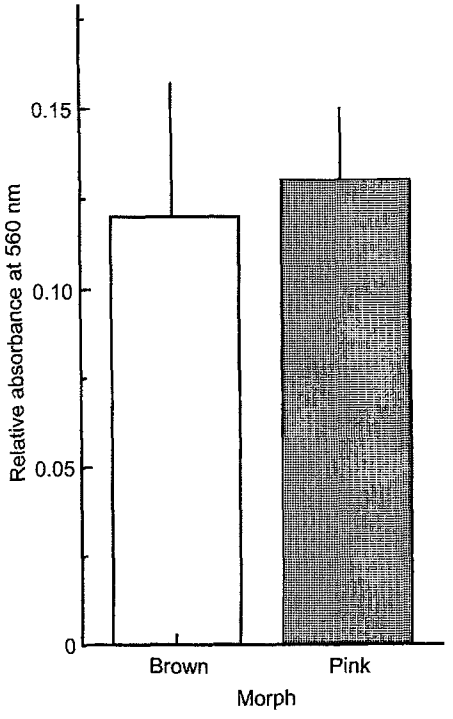

Fig. 6 *Pocillopora damicornis.* Absorbance (means + SEM, $n = 6$) of extracts of inner, brown branches of both brown and pink branches

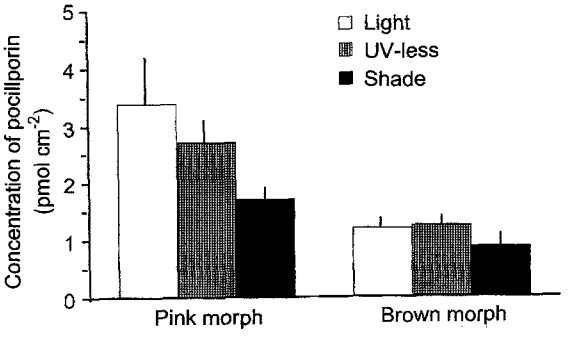

Fig. 7 *Pocillopora damicornis.* Concentration (means + SEM, $n = 9$) of pocilloporin measured in colonies of brown and pink morphs after 60 d exposure to three different light regimes

shade did not turn pink. The effect of the light regime was analysed separately for each pink colony because of the difference amongst colonies. All pink colonies had a significantly ($p < 0.05$) higher concentration of pocilloporin in full light than in shade after 2 mo of exposure (SNK test, Table 2). The difference in pocilloporin concentration between full light and UV-less treatments varied, depending on the colony. However, a significantly (at least $p < 0.05$) greater concentration of pocilloporin was seen in the UV-less treatment than in the shade treatment in 2 of the 3 pink colonies (Fig. 7).

Discussion

The results of this study revealed significant differences in the ecology and physiology of the two colour morphs of the coral *Pocillopora damicornis*. Not only did the distribution of the colour morphs differ with respect to depth, but differences were also apparent with respect to the rate of calcification and the expression of the pink pigment, pocilloporin. Preliminary isolation of the pigment revealed that it was hydrophilic, and was induced in tissues of the pink morph by visible light.

Differences in distribution and abundance of the two morphs in One Tree Island Lagoon

The distribution of the brown and pink morphs of *Pocillopora damicornis* overlapped at every site surveyed. Ideally, separate quadrats for counting colonies of each morph should have been used in order to maintain data independence. However, the density of colonies along the transects was relatively low (1 to 2 colonies m^{-2}) and consequently, it is unlikely that the density of one morph influenced that of the other. The relative abundances of the two morphs of *P. damicornis* did not vary between the two regions investigated in One Tree Island lagoon.

Variation in characteristics of coral colonies with depth is well known. Gleason (1993) found that the genetically distinct brown and green morphs of *Porites astreoides* differed in their distribution with depth. Gleason suggested that the green morph had a higher tolerance for UV radiation than did the brown morph, and hence was more abundant in the shallows. This mechanism has also been suggested with respect to the decrease in UV-screening compounds in corals with depth (Oliver et al. 1983). Colonies also tend to exhibit either more slender or flattened morphologies with increasing depth (Barnes 1973). The underlying cause of these changes with depth has been proposed to be due to the changing relationship between tissue and skeletal growth rates (Barnes 1973). The functional reasons for differences in skeletal morphology are complex. The selective advantages for adopting the globose form of several genera (e.g. *Goniastrea* spp., *Goniopora* spp. *Porites* spp.) have been speculated to be improved sediment drainage and light-harvesting efficiencies, and reduced wave resistance, while more arborescent colony shapes have been related to increasing feeding efficiencies (Dustan 1975).

Influence of colony morph and environmental conditions on calcification rates and zooxanthellae densities

The calcification rates of *Pocillopora damicornis* reported here are similar to those recorded for *Fungia* sp. (0.26% d^{-1}; Jokiel et al. 1978), *Porites* sp. (0.33% d^{-1}; Jokiel et al. 1978), and earlier measurements for *Pocillopora damicornis* (0.2 to 0.4% d^{-1}; Hoegh-Guldberg et al. 1994). The calcification rate of the brown morph of *P. damicornis* tended to be greater than that of the pink morph. This trend was consistent across all treatments, although it was only statistically significant in some treatments over the March to May period. Differences were often obscured by the enormous variability between the calcification rates of colonies of the same morph. The appearance of intramorphic variability of this magnitude is interesting in that many studies have assumed it to be negligible, and have often opted for single colonies (or nubbins made from single colonies) as replicates in experiments seeking to test the effect of different treatments (e.g. Muscatine et al. 1989).

Reduced light levels lead to reduced photosynthetic activity by the zooxanthellae, which are ultimately the source of the energy required for calcification (Pearse and Muscatine 1971; Chalker and Taylor 1978; Chalker 1981; Barnes 1982; Roth et al. 1982; Schonwald et al. 1987). Reduced calcification with reduced light has been observed before in *Pocillopora damicornis* (Roth et al. 1982) and many other species of hermatypic corals (Pearse and Muscatine 1971; Chalker and Taylor 1978; Chalker 1981; Barnes 1982; Schonwald et al. 1987). The observation that the relative skeletal growth rates of the two morphs of *P. damicornis* varied depending on the surrounding environmental conditions, suggests that there is a small degree of physiological plasticity within each morph. Lesser et al. (1994) also found that morphs of *P. damicornis* in Hawaii were correlated to different flow habitats, and showed plasticity in colony form. They concluded that corals maximised carbon delivery to the site of fixation by either having a suitable branching morphology for the surrounding flow regime or by changing the activities of enzymes such as antioxidant enzymes and ribulose bisphosphate carboxylase-oxygenase.

The zooxanthellae densities measured in this study were very similar to those measured in previous studies ($0.79 \pm 0.370\ 10^6$ cell cm^{-2} in *Pocillopora damicornis*,

Kinzie et al. 1984; $0.89 \pm 0.118\ 10^6$ cell cm^{-2} in *Stylophora pistillata*, Porter et al. 1984). Interestingly, the density of zooxanthellae did not differ significantly between the brown and pink morphs, with the exception of nubbins from the channel treatment where the density of zooxanthellae was much higher in the brown morph than in the pink morph (Fig. 5). This difference, however, must be treated with caution as the tissues in this one case were accidentally left exposed to air overnight, and hence may be in error. The density of zooxanthellae was higher in nubbins of both morphs that had been shaded for 2 mo. These results compare well with the shade adaptation of coral–zooxanthellae associations observed previously (Steele 1976; Zvanlinskii et al. 1980; Kinzie et al. 1984; Muscatine et al. 1984). The shade adaptation observed in the present study became more obvious as corals were acclimated to shade for longer periods (e.g. after 4 mo, Fig. 5).

The observation that brown and pink morphs have different growth rates yet similar densities of zooxanthellae suggests differences in the way that energy is partitioned within each morph. There are several possible explanations for this difference. The first is that the zooxanthellae of the pink morph may be different from those of the brown morph and may either photosynthesize less or translocate a lower proportion of the photosynthetic energy to the coral (Muscatine et al. 1984). Recent work on a number of symbiotic invertebrates has identified several host species where more than one species of zooxanthellae is involved (R. Rowan personal communication). So far, evidence suggests that zooxanthellae in the two morphs have similar photosynthetic rates (Hoegh-Guldberg and Moreno unpublished data). The second possibility is that the brown morph is a more active particle feeder and acquires extra energy by feeding and the uptake of dissolved organic nutrients (Jørgensen 1976; Falkowski et al. 1984). The last possibility is that the two morphs have the same amount of energy available for calcification but that the pink morph needs to allocate more energy than the brown to physiological functions other than skeletal growth. One key difference between the morphs is that the pink morph produces the pigment pocilloporin (Dove et al. 1995), while the brown morph does not. This extra pigment production may represent a significant energy sink and may be the basis for the reduced calcification rate of the pink morph.

Induction of pocilloporin: genetic and environmental controls

After 2 mo exposure to the three light regimes, pink colonies had an overall pigment (pocilloporin) concentration that was significantly higher than the brown colonies, which all had low pocilloporin densities in all treatments (Table 2 and Fig. 7). The nubbins of the pink morph in the light and UV-less treatments also showed significantly greater concentrations of pocilloporin than those in the shade for most colonies. Given that the nubbins had approximately the same levels of pocilloporin before exposure to the experimental light regimes (Fig. 6), two conclusions were made from these results. Firstly only those colonies defined as pink morph colonies in this experiment were able to produce pocilloporin to any tangible extent. This strongly suggests that the ability for expression of the pigment production is genetically controlled. The second conclusion was that pocilloporin production can be phenotypically induced by visible light in those colonies genetically capable of expressing significant amounts of pocilloporin (i.e. the pink morph). In the light and the UV-less treatments, pocilloporin was produced not only in the newly grown tip of the nubbins, but also in the old tissues that were originally brown. This suggests that the production of pocilloporin is not simply a feature of new tissues but that it can appear in older tissues that were presumably devoid of pocilloporin. The mean concentration of pocilloporin per surface area in pink-colony nubbins in the UV-less treatment was 72% of that in the full light treatment (Fig. 7). The difference between the full-light treatment and the UV-less treatment was significant in two pink colonies but not in one. This difference may have risen from the fouling of the Perspex sheets over time which resulted in up to a 30% reduction in visible light. There is also the possibility that UV light may enhance the production of pocilloporin. The converse of light stimulating pocilloporin expression was seen in the shade treatment. Nubbins from all three pink colonies that were transplanted into the shade treatment produced significantly less pocilloporin than those incubated in visible light.

The effect of visible light (and possibly UV light) on pocilloporin expression explains the distribution pattern of pocilloporin within pink colonies. Normally, only the outer tips are pink in pink colonies (Veron 1986), and it would appear that the shaded inner branches of *Pocillopora damicornis* colonies do not receive enough light for pocilloporin production. Given that pocilloporin does not act as a photoprotectant, UV-screen or photosynthetic accessory pigment (Dove et al. 1995), the functional explanation of why pocilloporin expression should be greatest on the outside of the colony is not clear. However, if pocilloporin has a role in protecting the coral from predation or in competitive interactions between itself and other corals, the presence of pocilloporin on the outside of a colony would make sense.

It is becoming increasingly apparent that species of reef-building corals represent diverse assemblages of physiological types. Understanding how these physiological types interact within coral communities is a goal for both experimental ecologists and physiologists. These results also have broader implications for experimental scientists working on reef organisms such as

corals. The high degree of variability between colonies of the one species (as in this study) makes it clear that studies that concern themselves with a narrow range of coral colonies potentially risk mistaking intraspecific differences as evidence of treatment effects.

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