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Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific

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Symbiotic reef corals occupy the entire photic zone; however, most species have distinct zonation patterns within the light intensity gradient. It is hypothesized that the presence of specific symbionts adapted to different light regimes may determine the vertical distribution of particular hosts. We have tested this hypothesis by genetic and *in situ* physiological analyses of the algal populations occupying two dominant eastern Pacific corals, over their vertical distribution in the Gulf of California. Our findings indicate that each coral species hosts a distinct algal taxon adapted to a particular light regime. The differential use of light by specific symbiotic dinoflagellates constitutes an important axis for niche diversification and is sufficient to explain the vertical distribution patterns of these two coral species.

Keywords: corals; niche diversification; symbiont diversity; light gradient; specificity; zooxanthellae

1. INTRODUCTION

Hermatypic—reef-building—corals maintain mutualistic symbioses with photosynthetic dinoflagellates in the genus *Symbiodinium*, commonly known as 'zooxanthellae' (Trench 1993). Symbiotic corals depend on the photosynthesis of their algae, as it may cover the entire metabolic needs of the host and it has been implicated in the high $CaCO_3$ deposition rates of these organisms (Muscatine & Porter 1977). Although symbiotic corals are distributed over the entire photic zone, where they are exposed to a depth-mediated light gradient spanning several orders of magnitude, most individual coral species have limited vertical distributions along this gradient (Wellington 1982; Jackson 1991; Knowlton & Jackson 1994), resulting in vertical zonation patterns. The genus *Symbiodinium* is a diverse and divergent assemblage comprising several distantly related subgeneric clades, each consisting of an unknown number of 'types' or species (Rowan & Powers 1991*a*; Trench 1997; LaJeunesse 2001, 2002). When cultured under identical conditions, isolates exhibit broad differences in photosynthetic responses (Chang *et al.* 1983; Iglesias-Prieto & Trench 1994, 1997*a*,*b*). The existence of such physiological diversity underpins the argument that certain algal types have adaptations to particular light regimes. The establishment of specific symbioses between *Symbiodinium* adapted to different light regimes and distinct host species may result in habitat and resource partitioning for the holosymbiont along depth-mediated light gradients (Iglesias-Prieto & Trench 1997*b*). Here, we test this hypothesis using genetic and *in situ* physiological analyses of the symbionts from two dominant scleractinean species in the eastern Pacific along their entire depth range. The vertical distribution patterns of the eastern Pacific coral reef communities have been extensively documented (Glynn 1976; Wellington 1982; Reyes-Bonilla & López-Pérez 1998). In general, shallow environments are occupied by different species in the genus *Pocillopora*, whereas in deeper habitats most of the available space is occupied by different species of the genus *Pavona*. In the Gulf of California in particular, shallow environments (0–6 m) are typically dominated by *Pocillopora verrucosa*, whereas deeper ones (6–14 m) are dominated by *Pavona gigantea* (Reyes-Bonilla & López-Pérez 1998). The distinctive zonation pattern of these corals was previously explained by a combination of physical and biological factors affecting the coral host, including selective predation by fishes (Glynn 1976; Wellington 1982). The simplicity of the community structure and the sharply defined zonation patterns at the study site, provided an excellent opportunity to test the role of symbiont specificity on the vertical distribution patterns of corals along their entire depth range.

Our results indicate that the presence of host-specific symbionts, adapted to two different light climates, is sufficient to explain the patterns of vertical distribution of these two species. These results reinforce the importance of niche diversification as a factor in the maintenance of coral reef diversity (Connell 1978).

2. MATERIAL AND METHODS

(a) *Collection of corals*

We conducted our research between September 1998 and July 2001 at La Gaviota Island, located in La Paz Bay in the southern

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part of the Gulf of California, Mexico, 24°17′ N, 110°20′ W. We surveyed a 1250 m^2 section of reef. Corals at the study site are distributed along a 30° slope spanning from the subtidal (0.5 m) to 14 m in depth. Coral samples ($n = 10$ for each species) were collected along their entire vertical distribution range with a hammer and chisel. Samples for DNA analyses were preserved in dimethyl sulpho oxide (DMSO) buffer (Rowan & Powers 1991*b*).

(b) *Fluorescence determinations*

Fluorescence measurements were performed with two underwater pulse amplitude modulated fluorometers (diving-PAM). We carefully selected fully pigmented vertically oriented tips (light-exposed) of *Po. verrucosa* and upper parts of *Pa. gigantea* colonies. We recorded the maximum light-dependent reduction of the effective quantum yield of photosystem II ($\Delta F/Fm'$) at noon on cloudless days relative to its maximum at dusk (Fv/Fm). We defined the maximum excitation pressure over photosystem II as: $Q_m = 1 - [(\Delta F/Fm'$ at noon$)/(Fv/Fm$ at dusk$)]$. The measurements made with 1 min dark adaptation, to completely relax photochemical quenching, were realized at local apparent noon ±15 min between September 1998 and June 1999. Dark adaptation was achieved after attaching an opaque polyvinyl chloride fibre optics holder to the colonies. For the measurements without dark adaptation on 14 July 2000, fluorescence determinations were made with two diving-PAMs at local noon ±40 min. To prevent any bias as a result of changes in the solar declination angle during this 80 min window, the two diving teams operating the fluorometers covered the entire depth profile in opposite directions. Reference maximum Fv/Fm values were determined over the entire depth range at dusk ±15 min. Fv/Fm values for *Po. verrucosa* were 0.591 ± 0.056, $n = 61$, and 0.629 ± 0.047, $n = 39$ for *Pa. gigantea* (averages ± s.d.). The vertical extinction coefficient K_d of the water was obtained with the photosynthetic active radiation sensor of the diving-PAM previously calibrated against a Li-Cor cosine-corrected light sensor.

(c) *Genetic analyses*

Algal cells were isolated from coral tissue by a flow of pressurized filtered seawater, 5 mM ethylene diamine triacetic acid (EDTA). Algal cells were ground in liquid nitrogen and resuspended in 1 ml DNA extraction buffer to isolate DNA as described (Rowan & Powers 1991*b*). Nuclear small subunit ribosomal RNA genes were amplified using specific primers and their restriction length polymorphism (RFLP) patterns after *Taq*I digestion were compared with standards obtained from cultured algae of known clade type (LaJeunesse & Trench 2000). Polymerase chain reaction (PCR)–denaturing gradient gel electrophoresis (DGGE) fingerprinting of the faster-evolving internal transcribed spacer region 2 (ITS-2) was conducted as previously described (LaJeunesse & Trench 2000). The symbionts from these corals were compared with standards made from commonly occurring *Symbiodinium* species (LaJeunesse 2001). 5.8S genes were amplified with ITS flanking primers targeting the entire spacer region (LaJeunesse 2001) and cycle-sequenced using the ABI prism big dye terminator cycle sequencing ready reaction kit (PE Applied Biosystems). The sequences presented in this paper have been deposited in the GenBank database (accession numbers AF 411413–411416). Phylogenetic analyses were conducted on aligned data using ClustalW. Bootstrap analysis was performed on the neighbour joining tree to assess the relative support of each branch (Felsenstein 1985).

(d) *Coral transplants*

To distinguish whether the associations between coral species and symbiont types were the result of the prevailing environmental conditions or symbiont specificity, we performed reciprocal transplantation experiments beginning in September 1998. Whole branches of *Po. verrucosa* were detached by hand and fragments of *Pa. gigantea* (15 cm diameter) were collected with a hammer and chisel. Specimens of *Po. verrucosa* collected at 3.0 m were relocated to a site with 10.0 m depth, whereas specimens of *Pa. gigantea* collected at 10 m were moved to a 2.7 m depth. Corals were attached to the rock substratum at their new location with construction cement.

3. RESULTS

The depth-dependent variations of Q_m for *Po. verrucosa* and *Pa. gigantea* colonies after 1 min dark adaptation are shown in figure 1*a*. Q_m is negatively correlated with depth for both species ($r^2 = 0.77$, $p < 0.05$ and $r^2 = 0.88$, $p < 0.005$ for *Po. verrucosa* and *Pa. gigantea*, respectively). A comparison of excitation pressures indicates that the symbionts of each coral species respond differently to variations in the light fields associated with depth. The algae inhabiting *Po. verrucosa* colonies growing at 2.5 m are exposed to four times higher irradiances than the algae of *Pa. gigantea* at 9.5 m; however, both experience similar maximum excitation pressures on photosystem II. Minimum Q_m values at the intercepts of the regression lines with the abscissa (7 and 13 m) coincide with the lower limits of distribution for both species. The results suggest that the differential capacity of the algal symbionts to adjust their photosynthetic apparatus to sub-saturating light intensities determines the lower limits of distribution of their respective hosts. Although the slopes of the regression lines are similar, the intercepts with the pressure axis are significantly different (0.273 ± 0.040 and 0.638 ± 0.085 for *Po. verrucosa* and *Pa. gigantea*, respectively). Excitation pressures as calculated here are correlative with the non-photochemical quenching coefficient (R. Iglesias-Prieto, unpublished data), a common measurement of the amount of excess energy dissipated as heat under a particular light intensity. The results indicate that symbionts inhabiting *Pa. gigantea* would experience more than twice the excitation pressure at the surface relative to the symbionts of *Po. verrucosa*.

We further characterized the relationship between Q_m and irradiance by measuring $\Delta F/Fm'$ at noon without a period of dark adaptation. Although photochemical quenching was not fully relaxed, this alternative procedure allowed more readings to be taken during times of peak irradiance. The results indicate similar trends to the dark-adapted dataset, with negative relationships between Q_m and depth ($r^2 = 0.65$, $p < 0.0001$, $n = 98$ and $r^2 = 0.79$, $p < 0.0001$, $n = 155$ for *Po. verrucosa* and *Pa. gigantea*, respectively). The slopes of the regression lines indicate that the algae in *Po. verrucosa* exhibit a larger reduction of Q_m with depth than those in *Pa. gigantea* (-0.0487 ± 0.0030 and -0.0403 ± 0.0015, respectively). The symbionts of *Pa. gigantea* consistently exhibit higher Q_m values than the symbionts of *Po. verrucosa* over the entire light gradient (figure 1*b*). The intercept with the pressure axis indicates that the algae in *Pa. gigantea* would experience 32% higher light pressures than those in *Po. verrucosa* at

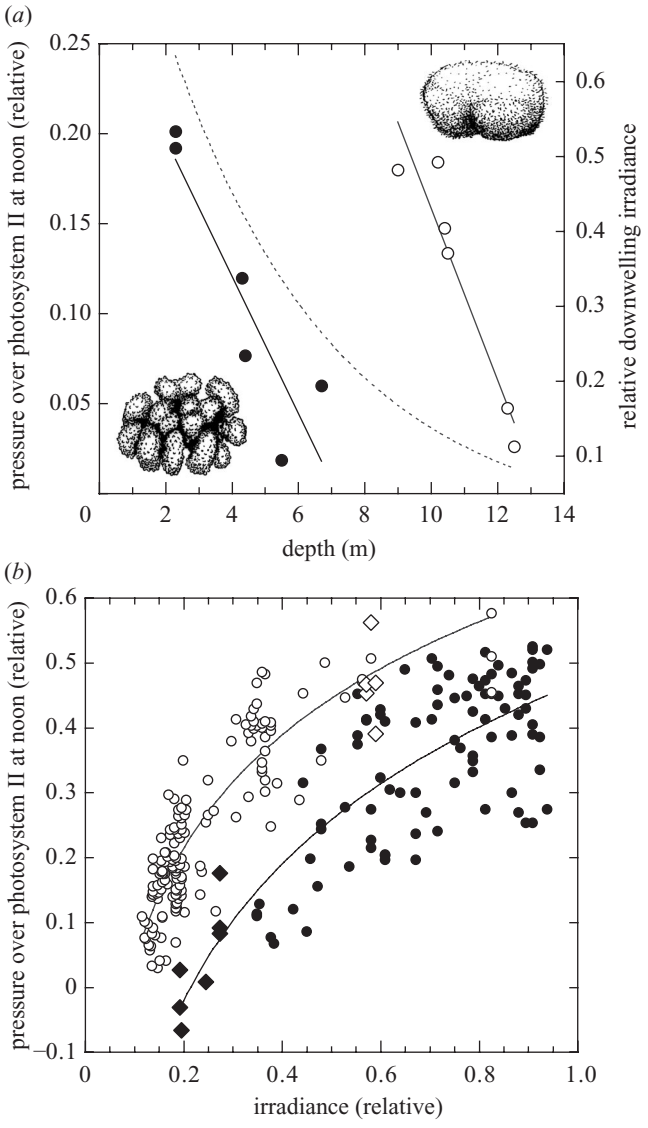

Figure 1. Maximum pressure over photosystem II at noon. (*a*) Depth-dependent variations of Q_m for *Pocillopora verrucosa* (dark circles and scheme at the lower left corner) and *Pavona gigantea* (open circles and scheme at the upper right corner) after 1 min of dark adaptation. Data were collected between September 1998 and June 1999. Relative downwelling irradiance (dashed line) corresponds to a K_d of 0.20 m^{-1}. The average water temperature at the study site for this period was 22.3 ± 2.0 °C. (*b*) Variations in Q_m as a function of irradiance for *Po. verrucosa* (filled circles) and *Pa. gigantea* (open circles). Transplants of *Pa. gigantea* (open diamonds) and naturally detached colony fragments of *Po. verrucosa* (filled diamonds). The data were collected on 14 July 2000. Seawater temperature was 27.8 ± 2.0 °C and K_d was 0.16 m^{-1}.

the surface. Analyses of photo-physiological performance indicate that algae present in *Po. verrucosa* exhibit responses consistent with 'sun-loving' species whereas algae in *Pa. gigantea* appear to be 'shade-adapted' (*sensu* Björkman 1981).

To test the possibility that two different species of symbionts account for the observed differences in photophysiology, we incorporated several molecular methods to examine their genetic identity. RFLPs resulting from *Taq*I digest of the small subunit ribosomal RNA gene (SSUrRNA) identified two distinct algal types. In this region of the eastern Pacific, *Po. verrucosa* harbours a symbiont from clade 'D' (Baker 1999; LaJeunesse 2001) and *Pa. gigantea* possesses a type from clade 'C' (Rowan & Powers 1991*a*). DGGE of the internal ITS-2 was then used to assess the genetic identity of these algal populations at resolutions approximating the ecological species level (LaJeunesse 2001, 2002) and to detect the presence of multiple symbiont types within a coral colony (Rowan *et al.* 1997). PCR–DGGE analyses revealed that each coral possessed a particular symbiont type occupying each coral along its entire range of vertical distribution (figure 2*a*,*b*). Type D1 occurred within *Po. verrucosa*, whereas type C1c was found within *Pa. gigantea*. A phylogenetic reconstruction based on sequences of the 5.8S ribosomal gene from both algal species (figure 2*c*), confirms that these *Symbiodinium* species are distantly related. Subsequent surveys in the region, involving hosts in nine genera, identify C1c symbionts only in the *Pavona* spp. Symbionts 'type' D1 and a clade C 'type' different from C1c are exclusive to the *Pocillopora* spp. (T. C. LaJeunesse and H. Reyes-Bonilla, unpublished data).

Initially, we transplanted three *Pa. gigantea* colonies from 10.0 to 2.7 m and three *Po. verrucosa* specimens from 3.0 to 10.0 m. Q_m values (figure 3*a*) for the *Po. verrucosa* colonies, 24 h after transplantation, were 0.015 ± 0.005 indicating the amount of light present in the environment was well below that required to saturate their photosynthetic apparatus. For these colonies, the values of $\Delta F/Fm'$ at noon and Fv/Fm at dusk were not statistically different. Under this condition, the energy balance of the colonies would be negative, placing the symbiosis outside its limits of tolerance (Spencer-Davies 1991).

Pavona gigantea transplants responded to their new light environment by developing very large Q_m values (0.627 ± 0.021) consistent with photoinhibition. By March 1999, the three *Po. verrucosa* colonies died attached to the substratum. Only one *Pa. gigantea* colony survived for 20 months attached to the substratum. Q_m values showed reductions in the surviving *Pa. gigantea* colony, to 0.540 in March and 0.530 in June 1999, presumably by acclimatization. After eight months, exposure to the new light conditions, the upper surfaces of the transplanted *Pa. gigantea* colony exhibited Q_m values more than three times higher than those observed in the upper surfaces of *Po. verrucosa* colonies growing at the same depth. The Q_m values obtained from the transplants can be described by a regression line similar to the one obtained from the natural samples (figures 1*a* and 3*a*), indicating that the symbiont of *Pa. gigantea* has a limited ability to acclimatize to the high irradiance environment found at 3.0 m. Genetic analysis of the symbionts from the surviving *Pa. gigantea* colony indicated that it maintained its association with symbiont C1c after 20 months exposure to high light (figure 2*b*, lane 9).

We then transplanted five more colonies of *Pa. gigantea* from 10.0 to 3.0 m and analysed several colonies of *Po. verrucosa* found naturally detached from their substratum at depths between 8.0 and 10.0 m in July 2000. Q_m values for *Pa. gigantea* colonies (0.469 ± 0.025, $n = 5$) 24 h after transplantation were significantly higher (Student's *t*-test: $p < 0.05$; figure 1*b* open diamonds) than those from *Po. verrucosa* (0.318 ± 0.024, $n = 18$) growing at comparable

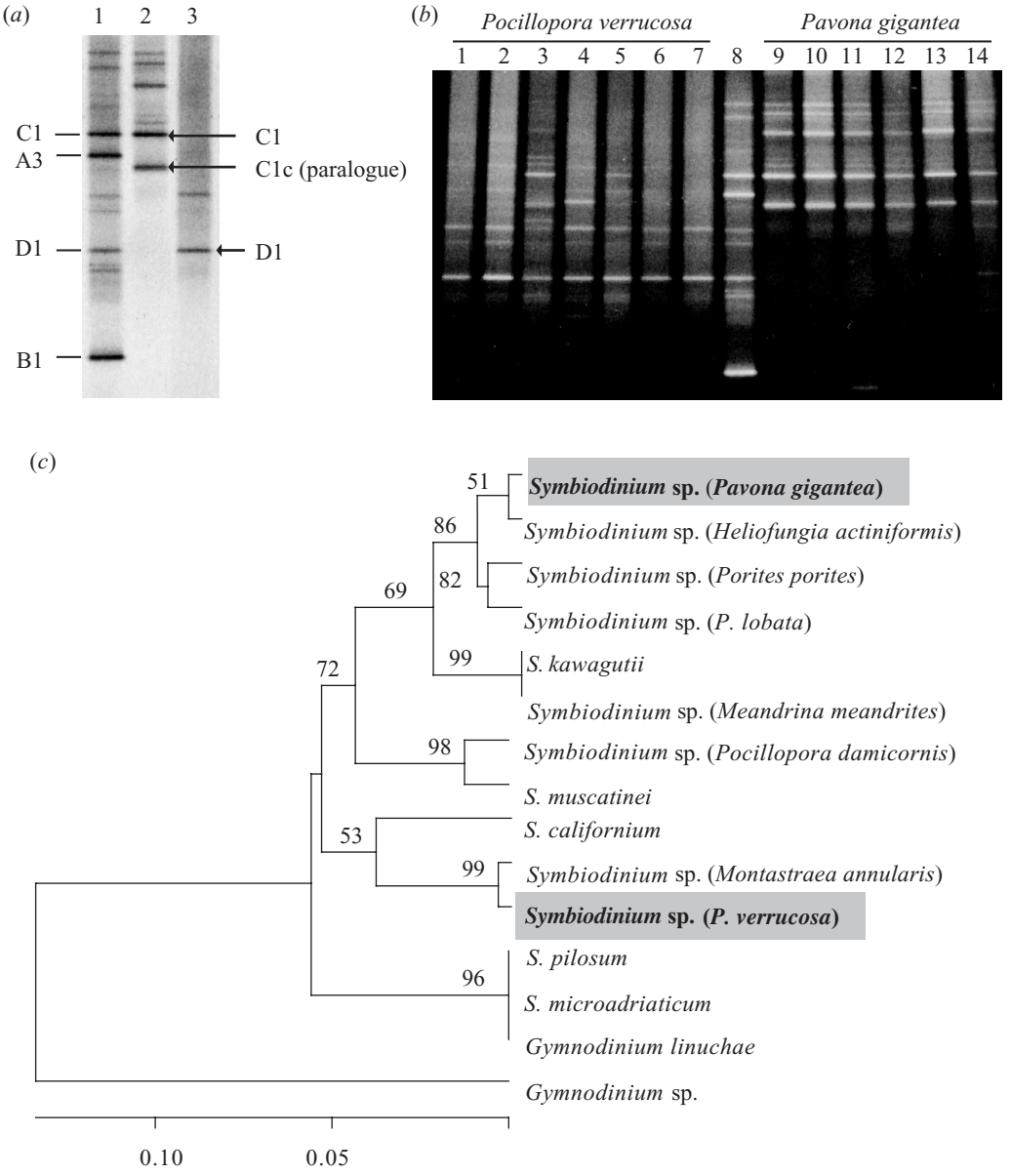

Figure 2. Symbiont characterization. (*a*) PCR–DGGE profiles of 'C1c' species from *Pavona gigantea* (lane 2) and type 'D1' from *Pocillopora verrucosa* (lane 3). ITS-2 fingerprints are the result of fixed intragenomic variation within the ribosomal gene array. Lane 1 consists of standards made by pooling ITS-2 amplifications of C1-, A3-, D1- and B1-type *Symbiodinium* (LaJeunesse 2002). (*b*) PCR–DGGE fingerprinting of the ITS-2 of symbionts collected from different *Po. verrucosa* colonies growing at 1.0, 1.5, 2.0, 3.0, 3.0, 3.6 and 7.0 m depths (lanes 1–7, respectively), markers as in (*a*) (lane 8). Lane 9 algae from the *Pa. gigantea*-transplanted colony (deep to shallow) and lanes 10–14, symbionts from *Pa. gigantea* colonies growing at 7.0, 7.2, 7.5, 8.0 and 12.0 m, respectively. (*c*) Phylogenetic reconstruction of the *Symbiodinium* lineage using the 5.8S ribosomal genes; the numerals above the lines indicate bootstrap support based on 500 replicates. Scale bar: number of substitutions per site.

depths (3–4 m) (figure 1*b*). After 1 year, the transplanted *Pa. gigantea* colonies retained their original symbionts (figure 3*b*). Colonies of *Po. verrucosa* found detached from the substratum exhibit significantly lower Q_m values (0.041 ± 0.034, $n = 7$; figure 1*b* closed diamonds) than those measured for *Pa. gigantea* colonies (0.219 ± 0.022, $n = 13$) in the same depth range (Student's *t*-test: $p < 0.05$). Although we do not know for how long these *Po. verrucosa* colonies were exposed to low light intensities, their low Q_m values suggest that the contribution of the symbionts to their metabolisms would be negligible, compromising their long-term survival. This interpretation is supported by the observation that the substrate at depths greater than 10 m is littered with numerous detached fragments of dead *Po. verrucosa* colonies.

4. DISCUSSION

The vertical distribution of certain symbiont types has been correlated with depth, but their physiological attributes were never directly measured (Rowan & Knowlton 1995; Rowan *et al.* 1997). In this study, for the first time, to our knowledge, the *in situ* physiological performance of the symbionts from each coral was determined by measuring the amplitude of the diurnal light-dependent reduction of the effective quantum yield of photosystem II ($\Delta F/Fm'$)

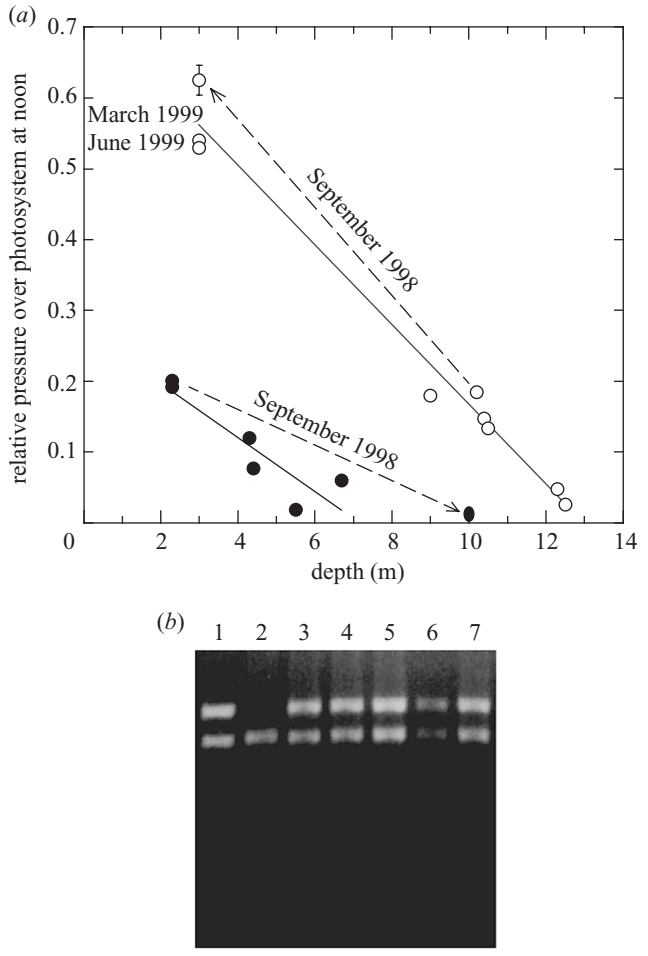

Figure 3. Transplant experiments. (*a*) Depth-dependent variations of Q_m for *Pocillopora verrucosa* (closed circles) and *Pavona gigantea* (open circles) after 1 min of dark adaptation. Broken arrowed lines indicate the origin and destination of the relocated colonies. The regression line for *Pa. gigantea* including the data collected from the transplants during 10 months ($r^2 = 0.978$, $p < 0.0001$) is very similar to the one obtained from the natural samples. (*b*) *Taq*I digestion of SSUrRNA genes. Clade 'C' standard (lane 1); clade 'D' standard (lane 2); algae from different *Pa. gigantea* colonies transplanted from 10 to 3 m after 1 year (lanes 3–5); algae from *Pa. gigantea* found at 1.2 m depth (lane 6); and at 13.0 m depth (lane 7).

at noon, relative to the maximum quantum yield at dusk (*Fv*/*Fm*) on cloudless days. Primary producers, including hermatypic corals, exhibit a typical diurnal oscillation in the quantum efficiency of photosystem II (Brown *et al.* 1999; Hoegh-Guldberg & Jones 1999; Gorbunov *et al.* 2001). This oscillation results from the induction of several photoprotective pathways competing with photochemistry for the deactivation of chlorophyll *a* excited states, when the rate of light absorption exceeds that of photochemistry, and/or from light-dependent damage of photosystem II. Q_m as employed here is a variation of the excitation pressure concept introduced by Maxwell *et al.* (1995). In its original formulation, excitation pressure over photosystem II was defined as: $Q = 1 - qP$, where qP represents the photochemical fluorescence quenching coefficient. To calculate the quenching coefficients, accurate determinations of absolute fluorescence yields in the dark and under actinic illumination are required (Ting & Owens 1992; Maxwell & Johnson 2000). Absolute fluorescence yields can be obtained in the field by maintaining a constant optical geometry between the samples and the fluorometer throughout a 24 h period (Gorbunov *et al.* 2001). Unfortunately this procedure can realistically be applied to very few specimens. Employing the method introduced here, based on relative fluorescence yield determinations, we were able to record the amplitude of the diurnal changes in $\Delta F/Fm'$ from hundreds of individual coral colonies along an entire environmental gradient. As defined here, maximum excitation pressure or Q_m is a useful descriptor of physiological performance of the algae as symbionts. Values that are close to zero indicate that even during periods of the maximum irradiance most of the reaction centres II remain open, suggesting that photosynthetic rates are light-limited. However, values close to 1.0 indicate that under maximum irradiance most of the reaction centres II are closed, suggesting photoinhibition.

Two competing hypotheses may explain the association between the vertical zonation of each coral species, the physiological characteristics of each symbiont type and their host distribution. In the absence of specificity, the observed distribution of symbionts may result from the habitat selection process by the algae so as to infect hosts located close to their optimal light requirements, or a post-settlement selection by the host for algae optimally adapted to the prevailing local light conditions (Trench 1988; Rowan & Knowlton 1995). Therefore, the observed association between algal taxon and host species would be a consequence of the different vertical distribution patterns of the corals. Alternatively, if the associations between algal and host species are determined by biological compatibility and not exclusively by the environmental conditions, the observed differential vertical distributions of the corals could be the result of the differential light-use abilities of their specific symbionts (Iglesias-Prieto & Trench 1994, 1997*a*,*b*). The results of the reciprocal transplantation experiments presented here are consistent with the existence of specificity.

Contrary to the prevailing idea that most reef corals have flexible associations with their symbiont communities, and are capable of reshuffling symbionts in response to environmental changes (Rowan & Knowlton 1995; Rowan *et al.* 1997; Baker 2001, 2003), our data indicate that these two dominant coral species exhibit a high degree of symbiont specificity, independent of the environmental conditions. Although we did not detect coral bleaching in the area during this study, both species suffered significant bleaching and mortality in the summer of 1997 (Reyes-Bonilla 2001). In this context, the view that coral bleaching—the loss of symbiotic algae—can promote a rapid response to environmental change by allowing corals to modify their symbiont populations (Buddemeier & Fautin 1993; Baker 2001, 2003) may not apply to these two species.

Geographical and local selection pressures might also influence specific interactions between hosts and symbionts. Consistent with our findings, preliminary analyses of *Pa. gigantea* colonies of the Panamanian coast (A. C. Baker and T. C. LaJeunesse, unpublished data) identified C1c. Finding the same symbiont in locations separated by a wide latitudinal range would indicate that this symbiosis is stable throughout the eastern Pacific. However,

Pocillopora species from these more equatorial regions associate with several different symbionts including C1c. Paradoxically, in the western and central Pacific, C1c is highly specific to *Pocillopora*, not *Pavona*. Pavonids from these same regions associate with particular clade C types (e.g. C1, C3h, C27 (LaJeunesse *et al.* 2003, 2005) but not C1c). This geographical mosaic in host–symbiont specificity demonstrates the capacity for a symbiont to be specialized for one particular host in one region, but display variations in specificity over wide geographical ranges (Thompson 1994). Clearly, differences in environmental (e.g. temperature and irradiance) and biotic factors (e.g. both host diversity and abundance, and symbiont diversity and abundance) from region to region probably modulate the specificity expressed between certain partners.

In principle, the limits of vertical distribution of a particular coral species may depend largely on the acclimatization capabilities of its symbionts. Some coral species (25–30%) examined so far associate simultaneously with more than one symbiont type, whereas the rest appear to maintain symbioses with only one algal type (Baker 1999; LaJeunesse 2002). In corals associating with more than one symbiont, changes in the relative abundance of each algal taxon have been correlated with irradiance gradients (Rowan & Knowlton 1995; Rowan *et al.* 1997). These changes presumably allow the host taxon to extend its depth range while remaining ecologically dominant. The underlying assumption for this interpretation is that each different symbiont–host combination has a different environmental optimum along the irradiance gradient. By contrast, hosts harbouring monotypic populations of symbionts may have limited vertical distribution patterns within the acclimatization constrains of their specific symbiont. The evolution of specific symbiotic associations between algae adapted to different light climates and individual coral species would result in zonation and reduced competition for space along an irradiance gradient (Muscatine & Porter 1977; Iglesias-Prieto & Trench 1994, 1997*b*). Symbiont specificity in this context would constrain the acclimatization capabilities of individual coral species to rapid environmental variations. For example, after a coral-bleaching episode, corals harbouring multiple algal types may experience temporary changes or shifts in relative abundances among their compatible specific symbionts (Baker 2001), but not by forming 'new' host–symbiont associations (Hoegh-Guldberg *et al.* 2002). The evidence presented here indicates that the presence of specific symbionts adapted to different light regimes is sufficient to explain the vertical distribution patterns of the two dominant species analysed. Collectively, our results indicate that the differential use of light by specific symbiotic dinoflagellates constitutes an important axis for niche diversification, controlling the abundance and distribution of hermatypic corals.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.