Limnol. Oceanogr., 51(1), 2006, 30–37

Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: Implications for coral bleaching?

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Abstract

Experiments were conducted to determine the effects of colony pigmentation, irradiance, and flow on the temperature microenvironment that corals experience in shallow water. The warming of colony surfaces increased with increasing colony pigmentation (darker surfaces) and at high irradiance but was alleviated by higher water flow. Dark colonies were up to 1.5°C warmer than ambient seawater at high irradiance and slow flow. In contrast, very light colonies were similar in temperature to ambient water at all levels of flow and irradiance. The darkness of corals progressively increased along a gradient of decreasing water clarity from oligotrophic offshore reefs toward turbid high-nutrient reefs near the coast. The surface temperature of these darkly pigmented turbid-water corals was significantly greater than that of the paler corals in the clear-water environments at comparable seawater temperatures, light, and current conditions. The surface warming of darkly pigmented colonies in coastal environments is sufficiently high to exceed their bleaching threshold during warm, calm, and clear seawater conditions.

The term coral bleaching describes the loss or expulsion of endosymbiotic dinoflagellates from the coral host, often resulting in colony death or reduced growth and fecundity of the surviving colonies (Glynn 1993; Brown 1997; Podesta and Glynn 2001). Warmer-than-normal temperatures are widely accepted as the most important external trigger for mass coral bleaching (Glynn 1996; Brown 1997; Hoegh-Guldberg 1999). Corals live close to their upper thermal tolerance limit and start to bleach when local average summer temperature maxima are exceeded by 1–2°C for a number of days (Berkelmans and Willis 1999). Additionally, high irradiance, low flow, and low water turbidity have been identified as factors that can be responsible for coral bleaching, especially in combination with high water temperatures (Lesser et al. 1990; Glynn 1996; Nakamura and Van Woesik 2001).

Typically, the relationship between bleaching and temperature has been assessed on the basis of data obtained on seawater or sea surface temperatures. However, it is the temperature of the colony surface and of the boundary layer directly above it that determines physiological processes, which can deviate substantially from those of the larger body of surrounding seawater. This deviation of surface temperatures from ambient seawater temperatures is a function of several factors. Two main factors are the short-wave solar radiation incident on the surface and the proportion of the incident radiation absorbed by the surface (short-wave absorptivity); the latter factor itself is a function of the reflective and transmissive properties of the surface, defined by its darkness, orientation, and certain other material characteristics. The heat balance is maintained by losses from convection into the surrounding water (dependent on water flow and other surface characteristics involved in boundary layer formation), conduction into deeper surface layers, and emission of long-wave radiation. The goal of this study was to assess the effects and interactions of three of the factors involved in controlling the temperature microenvironment of coral colony surfaces, namely irradiance, flow, and colony darkness. True measures of short-wave radiation, absorptivity, and convection were not attempted in this study; instead, photosynthetically active irradiance was measured as a proxy for short-wave radiation, colony darkness (pigmentation) was used as a proxy for absorptivity, and water flow was manipulated to vary heat convection from the colony surfaces. The use of these variables helped relate the experimental results to in situ measurements, as irradiance, flow, and colony darkness are data that are readily available from underwater measurements in the field.

The study consisted of two laboratory and two field components. Under laboratory conditions, the temperature of standardized individual color chart fields submerged in seawater was determined at contrasting levels of flow and irradiance. The same laboratory setup was then used to measure the microtemperature environment around three corals, two massive and one branching species that varied in colony pigmentation from light to dark brown. In the field, the natural distributions of coral darkness were quantified on four reefs across the continental shelf, spanning from clear-water offshore to turbid coastal conditions. Finally, the surface warming of corals that varied in darkness was measured on inshore reefs at ambient flow speed and irradiance. The results show clear differences in the temperature microenvironment that corals experience at identical sea surface temperatures. These differences in surface warming may explain some of the observed differences in bleaching severity observed within and among colonies, sites, and regions.

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Acknowledgments

I thank Glenn De'ath for help with the statistical analyses and Craig Humphrey and Melanie Shaw for their contributions to the field and laboratory work. I also thank Janice Lough, Anke Klüter, Ulrike Siebeck, and Glenn De'ath for constructive comments on the manuscript. The University of Queensland developed and provided the ''Coral Health Charts.'' The research was funded by the Australian Institute of Marine Science (AIMS) and the Cooperative Research Center for the Great Barrier Reef World Heritage Area (CRC Reef Research).

Fig. 1. Differences in coral darkness, determined with a standardized color chart ('Coral Health Chart,' University of Queensland, Australia, www.coralwatch.org). Darkness can vary widely even within species, such as shown for *Acropora millepora* from a clear-water offshore reef (left, light pigmentation) and from a turbid inshore reef (right, dark pigmentation).

Methods

Two different methods were used to quantify the ''darkness'' (pigmentation) of colonies. First, in the first laboratory study and in the field, a standardized coral color chart printed on a thin, lightly textured plastic sheet was used (''Coral Health Chart,'' University of Queensland, Australia: www.CoralWatch.org; Siebeck et al. unpubl. data); the darkness of the six color fields of the color chart increases on a log scale from score 1 = near-white to score 6 = dark brown (Fig. 1); the six coral color chart fields in the C-series approximate those of the 5YR series in the established Munsell soil color chart (New York, Year 2000 Revised Washable Edition) as follows: 1 = white, 2 = 8/3, 3 = 7/5, 4 = 6/5, 5 = 4/4, and 6 = 3/3. Only the numeric information on the darkness of the coral color chart fields (scores 1–6) was used, with darkness recorded to the nearest half-score. Differences in hues (e.g., chroma, absorption of specific wavelengths) and fluorescent pigments produced by the animal host were ignored in this study, as they are expected to affect solar heating in a complex fashion (Salih et al. 2000; Coles and Brown 2003; Dove 2004); the four different series of hues on the coral color chart (series B–E) were therefore used only to facilitate the assignment of a darkness (color chart score). In multicolored colonies, the darkness and estimated proportions of each of the main colors were recorded and averaged. In the second laboratory experiments, coral darkness was determined by a second method, namely as background fluorescence, $F0$, using a pulse-amplitude modulated fluorometer (Mini-PAM, Walz). Preliminary measurements showed that within a given species, $F0$ was strongly and linearly related to the color chart readings ($r = 0.90$, $p < 0.0001$). This is because most visible pigments in corals are the fluorescing photosynthetic pigments of the endosymbionts: most corals turn white once their endosymbionts are lost and appear dark brown when endosymbiont densities and sizes are large. The advantage of using $F0$ was that the local darkness of the colony tissue could be determined at the exact measurement position of the temperature probe, which increased the accuracy for colonies in which darkness varied at scales of millimeters. One disadvantage of using $F0$ is that $F0$ is best used in dark-adapted colonies, decreasing at high irradiance; however, dark-adapted measurements were not possible with this experimental setup. $F0$ may also vary between species and even between different fibro-optical probes. Absolute values of $F0$ can therefore be compared only within rather than across different studies.

Temperatures were measured with AD590 semiconductor sensors connected to an ammeter with an accuracy of 4 digits. Constant voltage was applied to the temperature probes, and temperature changes were determined as changes in electric current. The sensors were calibrated against a reference quartz thermometer (model 2804 A, Hewlett Packard) in a large, well-insulated water bath. The two sensors tracked

within a few millidegrees between 25°C and 35°C, and the expected accuracy was 0.04°C (Quartz thermometer calibration accuracy). The 60-mm-long clear glass probe had a measurement tip that was ~1.5 mm in diameter. The tip was gently placed on the coral surface and kept there for 10–20 s before a reading was taken. After each surface measurement, the ambient water temperature was determined outside the boundary layer (away from the study object in the flow chamber, or 0.5 m above the reef in the field). Surface warming was therefore measured as the difference between colony surface temperatures and ambient water temperatures.

In the first laboratory experiment, the surface warming of the color fields of a submerged coral color chart was assessed at two levels of irradiance and flow. Measurements were taken outdoors in a flow chamber on the back deck of a research vessel at two levels of irradiance: around noon on a cloudless summer day (1,500–1,600 μmol m^{-2} s^{-1} surface irradiance; measured with a horizontal LiCor 1000 2π quantum sensor) and 1.5 h before dusk or after dawn (120–350 μmol m^{-2} s^{-1}). Unidirectional flow was created in the 12-liter flow chamber (consisting of four 15-cm-deep and 45-cm-long working sections) by altering the voltage for the propeller motor; the gentle rolling of the anchored 27-m-long research vessel (wave height, ~0.3–0.5 m) further added to the water motion. Flow speed was estimated by repeatedly timing particles traveling a fixed distance along the working section of the flow chamber and was set to approximately 2 and 5 cm s^{-1}. The body of the flow chamber was cooled in a 60-liter water bath, and fresh seawater was run through the flow chamber at 3.5 L min^{-1} to maintain a constant seawater temperature. At each flow speed and irradiance level, the temperature probe was placed two to three times on each of the 4-cm^2 color fields that increased in darkness and saturation values from near-white to dark brown (coral color chart scores 1–6). An additional treatment (scored as 0) was added by measuring the temperature of a submerged sheet of clear Perspex.

Surface warming was then determined for three species of corals that varied in pigmentation within and between colonies at two levels of irradiance and two or three levels of flow. The same flow chamber setup was used as for the first laboratory experiment. Five small heads each of the hemispherical corals *Favia matthai* and *Porites* sp. and 10 pieces of the digitate coral *Acropora millepora* were collected from shallow water (~3-m depth) at Fitzroy Island. They were kept in a 500-liter flow-through holding tank on the ship to recover from collection until experiments commenced 4 d later. Experiments were conducted 10 min after transfer into the flow chambers; hence, adjustment times for colony temperatures to the local conditions were limited. A longer preexposure may have led to greater warming through heat absorption and storage by the skeleton. After each temperature reading, the colony darkness was determined with a 2-mm fibro-optical probe connected to a pulse-amplitude–modulated fluorometer (Mini-PAM, Walz) at the exact position that was used for temperature measurement.

Mean coral darkness was determined on four reefs of the central Great Barrier Reef (GBR) that differed in mean turbidity and extent of terrestrial influences. These reefs were as follows: (1) High Island (17°9′S, 146°1′E; a turbid inshore reef with high water nutrient concentrations); (2) Fitzroy Island (16°55.5′S, 145°59′E; an inshore reef with greater water clarity and less exposure to terrestrial runoff from river flood plumes than High Island; Devlin et al. 2003); (3) Hastings Reef (16°31′S, 146°1′E; a mid-to outer-shelf reef, 71% relative distances across the continental shelf); and (4) Flynn Reef (16°44′S, 146°16.5′E; on the outermost edge of the continental shelf). Mean visibility across the continental shelf in the Cairns region has been estimated by spatial models as 5 m at High Island, 8 m at Fitzroy Island, 18 m at Hastings Reef, and 25 m at Flynn Reef (Fabricius and De'ath 2001). Concentrations of suspended solids also decrease across these reefs, from 2.7 ± 0.1 mg L^{-1} at High Island and 1.7 ± 0.3 mg L^{-1} at Fitzroy Island (N ~10 visits; Fabricius unpubl. data) to <0.5 mg L^{-1} for the offshore reefs off Cairns (Furnas et al. 2005). Similarly, chlorophyll concentrations decrease across the shelf in the Cairns region from 0.46 ± 0.4 and 0.41 ± 0.1 μg L^{-1} at High and Fitzroy Islands, respectively (N ~10 visits each; Fabricius unpubl. data), to 0.2 μg L^{-1} at the outermost edge of the continental shelf (Fabricius and De'ath 2004). Tissue darkness was measured in the first 40 scleractinian coral colonies that were encountered along six line intercept transects that run slope-parallel at the windward and leeward side at 4-, 8-, and 12-m depths. Hence, a total of 240 colonies were assessed on each reef, including all hard coral species. The measurements were conducted using self-contained underwater breathing apparatus (SCUBA) equipment for 4 d consecutively in January 2005, when sea surface temperatures were 28–29°C, and no signs of coral blanching or bleaching were observed.

Measurements of the temperature microenvironment around corals were conducted on inshore reefs to determine, in situ, the surface warming of cnidarians with contrasting darkness: the flat-encrusting stony coral *Montipora tuberculosa*, four other species of stony corals (including hemispherical, foliose and branching growth forms), two species of octocorals, and the zoanthid *Palythoa*. Additionally, surface warming was determined in the dark, thick, sediment-trapping turf algal mats on these inshore reefs. Measurements were conducted using SCUBA equipment at the leeward sides of the inshore reefs of High and Fitzroy Islands at 1.5–2-m water depth around noon during mostly cloudless periods in January 2004. Wind speed was ~20 km h^{-1}, wave height was ~0.2 m, water flow was 2–6 cm s^{-1}, and ambient water temperature was 29.5–30.3°C. On one windier day, a 2- × 2-m cage (1 m high) made of shade cloth loosely tied to a steel frame was used to reduce flow around the measured colonies. Downward irradiance at the level of each colony was measured with a 2π LiCor quantum sensor and averaged 400 ± 219 SD μmol m^{-2} s^{-1}. Surface darkness was measured with the coral color chart, temperatures were determined with a temperature probe attached to a 5-m-long cable that was brought to the dive boat, and local flow speed was estimated by tracking the speed of particles traveling 50 cm above the study site.

Linear models were used to assess the effects of darkness (numeric: expressed as $F0$ or color chart scores), flow (categorical), and irradiance (categorical) on surface warming. The initial models included linear effects in darkness and

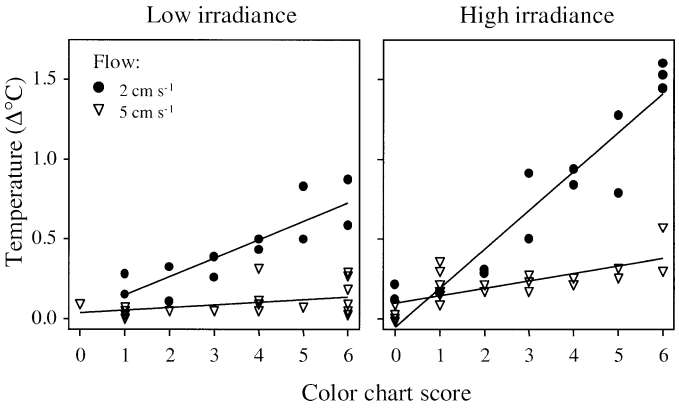

Fig. 2. Effects of flow, irradiance, and pigmentation (darkness) of color chart fields (scores 1–6, plus transparent Perspex = score 0) on the surface warming of color chart fields (deviation from ambient temperature). Measurements were conducted at flow speeds of 2 and 5 cm s^{-1} and at low irradiance (early morning) and high irradiance (noon) (Table 1).

interactions with flow, irradiance, and flow by irradiance. A backward-elimination technique ($p > 0.05$) was used to select the final models. Estimates of the relationship between darkness and surface warming were appraised using the final models. Linear models were also used to assess the effects of exposure to coastal influences (numeric: measured as ranked distance across the continental shelf), depth (categorical), and reef (categorical) on colony darkness. The darkness of the colony color was calculated as the mean color chart score per transect; the reef was treated as a random effect, and used as the error term for exposure; and depth was tested against the reef-by-exposure term. S-Plus was used for all statistical analyses (Statistical Sciences 1999).

Results

In the first laboratory experiment, the surface warming of the pigmented color chart fields significantly increased with the darkness of the color and irradiance and decreased with faster flow (Fig. 2; Table 1A). Very light surfaces were similar in temperature to the ambient water at all levels of flow and irradiance. With each darker color chart score, surface warming increased by 0.24°C (±0.01 SE) at high irradiance and slow flow, with temperatures of the darkest surfaces exceeding that of ambient water by 1.4°C (Table 1B). At low irradiance and low flow, surface warming increased from lightest to darkest fields by 0.7°C, and at high irradiance and faster flow, the warming was ~0.3°C. At low irradiance and faster flow, warming was <0.2°C, even on the darkest surfaces, and the pigmentation–surface warming relationship was nonsignificant ($p > 0.05$).

In the hemispherical coral *F. matthai*, the surface warming also increased with increased darkness and irradiance and decreased with faster flow (Fig. 3A; Table 2A). The warming of dark colony surfaces was 1.8°C at high irradiance and slowest flow, whereas light surfaces were 0.2–0.8°C above the ambient temperature. When color darkness (*F*0) was plotted against surface warming, the intercepts increased

Table 1. Relationship between the warming of color chart fields (deviation from ambient water temperature; Fig. 2) and their pigmentation (darkness) at varying levels of water flow (2 and 5 cm s^{-1}) and irradiance (noon = high and early morning = low). (A) Analysis of variance and (B) linear model output of the slopes (±SE) and their significance levels at the two levels of flow and irradiance.*

(A)	df	MS	*F*	*p*
Flow	1	3.008	199.9	<0.0001
Irradiance	1	0.445	29.53	<0.0001
Darkness	1	2.738	181.9	<0.0001
Flow : irradiance	1	0.0102	0.6775	0.414
Darkness : flow	1	1.992	132.3	<0.0001
Darkness : irradiance	1	0.292	19.41	<0.0001
Darkness : flow: irradiance	1	0.144	9.585	0.0029
Residuals	63	0.0150		

(B)	Flow (cm s^{-1})	Irradiance	Slope (SE)	*t*-value	*p*
	1	Low	0.116 (0.021)	5.585	<0.0001
	5	Low	0.016 (0.013)	1.252	0.215
	1	High	0.244 (0.014)	17.135	<0.0001
	5	High	0.048 (0.014)	3.527	0.0008

* MS, mean square.

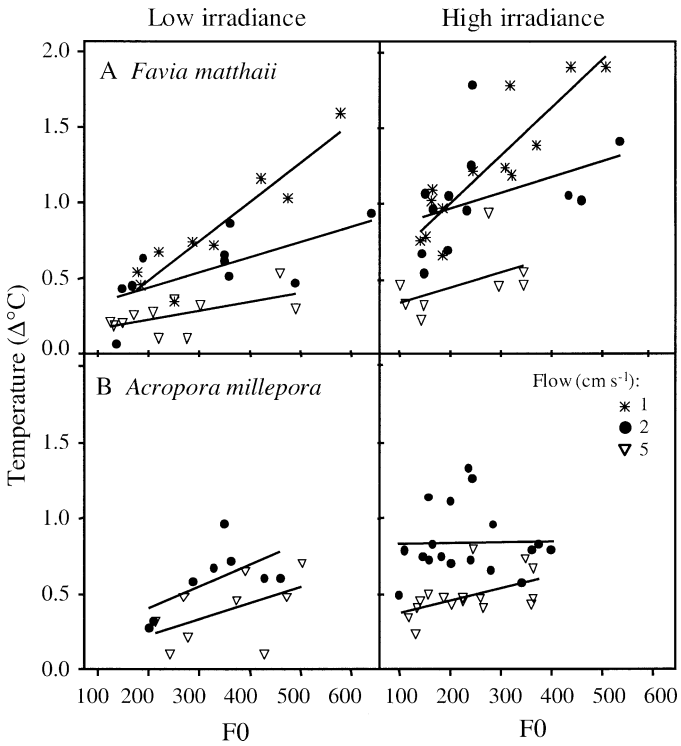

Fig. 3. Effects of flow, irradiance, and pigmentation (tissue darkness) on coral surface warming at high irradiance (noon) and low irradiance (early morning or late afternoon) in outdoor flow chambers (Table 2). Pigmentation was measured as background fluorescence, *F*0, determined with pulse-amplitude–modulated fluorometry. Warming is given as a deviation from the ambient water temperature (29.3°C). (A) Colonies of the hemispherical species *Favia matthai* at flow speeds of 1, 2, and 5 cm s^{-1}. (B) Colonies of the digitate species *Acropora millepora* at flow speeds of 2 and 5 cm s^{-1}.

Table 2. Relationship between coral surface warming (deviation from ambient water temperature) and colony pigmentation (darkness) at varying levels of water flow and irradiance in flow chambers. (A and B) *Favia matthai*, ANOVA and linear models output of slopes (±SE) and their significance levels at the three levels of flow (1, 2, and 5 cm s^{-1}) (Fig. 3A); (C) *Acropora millepora*, at 2 and 5 cm s^{-1} flow (Fig. 3b).*

(A)	df	MS	*F*	*p*
Flow	2	2.153	50.57	<0.0001
Irradiance	1	3.356	78.83	<0.0001
Darkness	1	2.141	50.29	<0.0001
Darkness : flow	2	0.3711	8.719	0.0005
Darkness : irradiance	2	0.1915	4.498	0.0156
Residuals	24	0.0426		

(B) Flow (cm s^{-1})	Slope (SE)	*t*-value	*p*
1	0.00290 (0.00036)	8.012	<0.0001
2	0.00103 (0.00031)	3.296	0.002
5	0.00073 (0.00043)	1.702	0.094

(C)	df	MS	*F*	*p*
Flow	1	1.246	34.13	<0.0001
Irradiance	1	0.3552	9.729	0.0031
Darkness	1	0.2215	6.067	0.0175
Residuals	47	0.0365		

* ANOVA, analysis of variance; MS, mean square.

with irradiance, whereas the slopes decreased with flow: at flows of 2 and 5 cm s^{-1}, the slopes of the relationship between these two parameters decreased to one-third and one-fourth the slopes at 1 cm s^{-1}, respectively, but surfaces still warmed up to 0.5°C above ambient temperatures. At low flow and low irradiance, the darkest surfaces warmed up to 1.5°C, whereas at higher flow, the lightest surfaces warmed to <0.2°C. Slopes of these relationships decreased with flow from 0.00290 at 1 cm s^{-1} to 0.00073 at 5 cm s^{-1} and were independent of irradiance. A similar darkness-related surface warming was also measured in flow chamber experiments in hemispherical massive *Porites* (data not shown). For the digitate colonies of the coral species *A. millepora*, surface warming of the small (mostly vertically oriented) branchlets also increased with irradiance and decreased with flow, while the effects of colony darkness (which had a narrower range than in *F. matthai*) were slightly weaker (Fig. 3B; Table 2B). Surfaces were 0.8°C warmer than ambient water at high irradiance and slow flow and 0.3–0.7°C warmer at lower flow and/or lower irradiance. In this species, the slope of the plot of color darkness (*F*0) against surface warming was 0.00075 (0.00032 SE; $t = 2.393$, df = 46, $p = 0.021$) and independent of flow and irradiance.

In the field, the darkness of corals varied widely between colonies and between reefs (Figs. 1, 4). Mean darkness per transect was independent of depth within the 4–12-m range investigated but changed across the continental shelf (Table 3): colonies were darkest on the most turbid inshore reef, High Island (mean = 3.5 ± 0.1 SE, $n = 6$), and their colors lightened with increasing water clarity and distance from the coast (Fitzroy, 3.2 ± 0.1; Hastings, 2.8 ± 0.1; and Flynn, 2.5 ± 0.1). The two darkest color scores (5 and 6) were found in 16% of the corals on the most turbid reef but in only 0.4% of the corals from the outermost reef, Flynn. Conversely, the lightest scores (1 and 2) were found in 35% of the corals at Flynn Reef but in only 5.4% of the corals at High Island (Fig. 1).

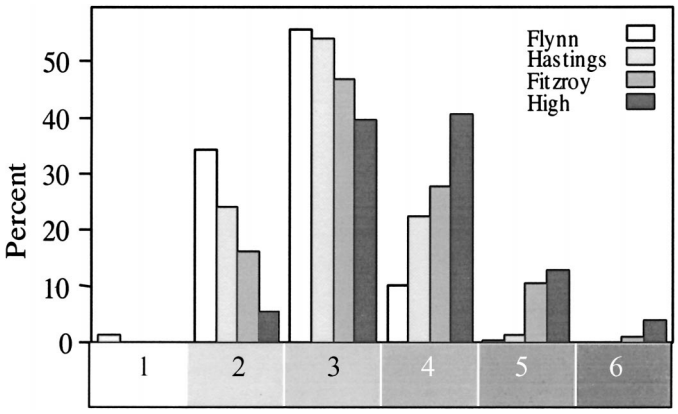

Fig. 4. Frequency distributions of coral colony pigmentation (tissue darkness) at four reefs with increasing exposure to coastal influences and decreasing water clarity (the offshore reef Flynn Reef having the clearest water, and the inshore reef High Island the most turbid water). Color darkness was measured in 240 colonies per reef with a scale from 1 to 6 using the coral color chart.

At inshore reefs at 1.5–2-m water depth, clear relationships between surface temperatures and surface darkness were also found at ambient irradiance and water flow. For example, dark colonies of the species *M. tuberculosa* were 0.4°C warmer than the ambient water, while lighter surfaces of the same species, including the few blanched colony surfaces found (color chart scores = 1–2), remained significantly cooler (Fig. 5A; Table 4A). The slope of the plot of color darkness against surface warming was 0.0400 (±0.0143 SE; $t = 2.791$, df = 17, $p = 0.013$). Similar darkness-related warming was found in a cross-section of 76 cnidarian colonies representing stony corals, octocorals, and a zoanthid at 1.5–2-m depth (Fig. 5B; Table 4B). The slope of the plot of color darkness against surface warming for these cnidarians at ambient flow and irradiance levels was 0.0363 (±0.0103 SE; $t = 3.513$, df = 74, $p = 0.0008$). The greatest surface warming was measured within turf algal mats, which exceeded the ambient water temperature by 0.8°C.

Table 3. ANOVA testing for differences in the darkness of coral colonies at four reefs across the continental shelf. Exposure to coastal and oceanic influences was estimated as the distance of the reefs to the coast (ranked); levels of depth were 4, 8, and 12 m.*

	df	MS	*F*	*p*
Exposure	1	3.179	581.6	0.00172
Reef/exposure	2	0.005		
Depth	2	0.0358	0.632	0.544
Exposure : depth	2	0.00678	0.120	0.888
Residuals	16	0.0567		

* ANOVA, analysis of variance; MS, mean square.

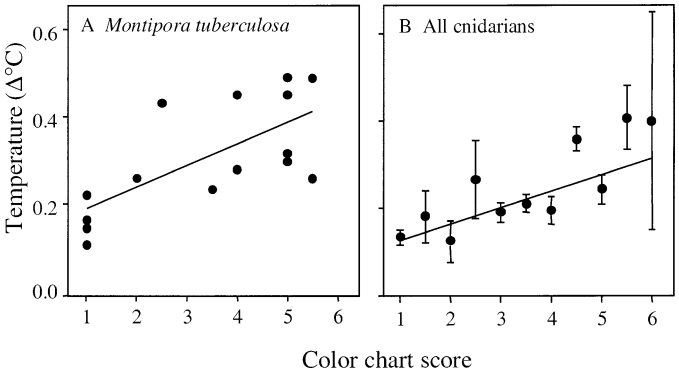

Fig. 5. In situ surface warming as a function of colony pigmentation (darkness) on two inshore reefs at 1.5–2-m depth at ambient flow and noon irradiance (Table 4). (A) The flat-encrusting species *Montipora tuberculosa.* (B) All cnidarian species combined.

Table 4. Relationships between the in situ coral surface warming (deviation from ambient water temperature) and colony pigmentation (darkness) at ambient levels of water flow and irradiance on two coastal reefs at 1.5–2 m depth. (A) The flat-encrusting coral *Montipora tuberculosa* (Fig. 4A) and (B) colony surfaces of 76 cnidarians with diverse growth forms (Fig. 4B)*

	df	MS	*F*	*p*
(A) *M. tuberculosa*				
Darkness	1	0.0870	7.7933	0.0125
Residuals	17	0.0112		
(B) All cnidarians				
Darkness	1	0.2030	12.3434	0.0008
Residuals	74	0.0164		

* MS, mean square.

Discussion

The present study showed that colony darkness, irradiance, and water flow can increase the temperature microenvironment around benthic organisms. While this relationship is not surprising per se, the extent of surface warming of up to 1.5°C above ambient seawater temperatures is physiologically significant for organisms such as corals that grow near their upper thermal tolerance limit. The results show that it is necessary to determine not only seawater temperatures but also benthos surface temperatures to adequately assess the thermal microenvironment, and hence temperature stress, in shallow-water organisms.

The surface warming measured in the laboratory and field experiments represents a conservative estimate of the extent of warming likely to be encountered in the field during calm weather conditions. For example, the field measurements were conducted at a wind speed of ~20 km h^{-1} and wave heights of ~0.2 m, and surface warming is likely to be greater during calmer conditions. In the laboratory experiments, the extent of surface warming measured in corals was similar to that of the thin plastic color chart sheets, despite the corals' much greater capacity for heat storage. Corals were preexposed to irradiance and flow for only 10 min before the measurements commenced, and it is likely that a longer preexposure would have warmed the corals more than the observed 1.5°C, through gradual thermal energy absorption and heat storage by the solid coral skeletons.

Darkness-related absorption of solar energy was previously described for the intertidal coral *Coeloseris mayeri.* This coral responds to subaerial exposure with extreme tissue retraction exposing its bare white skeleton, which results in a 10% reduction in the proportion of solar energy absorbed through increased albedo (Brown et al. 1994). Similar spectroradiometric studies on submerged corals would allow the identification and testing of other properties determining absorptivity (such as accessory pigments, colony orientation, and surface microstructures) that may determine the proportion of incident radiation absorbed. Interestingly, in the intertidal hemispherical corals *Goniastrea aspera,* no temperature differences were detected between the sun-facing surfaces and colony apices while the colonies were emerged from the water (Brown et al. 2002*b;* no data were given for the shaded sides); it remains to be determined whether evaporative cooling counteracted the solar heating during these times of emersion.

The results from this study have implications for the understanding of coral bleaching. Although high seawater temperature is widely accepted as the primary trigger of coral bleaching, irradiance is also known to trigger coral bleaching (Glynn 1996; Brown 1997; Hoegh-Guldberg 1999). The latter is evident from field observations showing that the onset of bleaching is often visible on the upper sides of colonies while their sides are still normally pigmented, that bleaching damage is often greater in shallow water and decreases with depth, and that high cloud cover appears to have prevented mass bleaching mortality during temperatures that normally incurred bleaching damage (Glynn 1996; Brown 1997; Mumby et al. 2001). Some studies have reported that high irradiance does not generally lead to bleaching during periods of nonelevated sea surface temperatures: high irradiance worsens coral bleaching at extreme temperatures but does not trigger a strong bleaching response during nonelevated temperatures (Coles and Jokiel 1978). High temperatures and irradiance both enhance the production of oxygen radicals, causing oxidative stress and damaging the photosystem II, which may explain why bleaching responses are most severe when high temperature and irradiance co-occur (Lesser 1996, 1997; Brown et al. 2002*a*). Other studies have suggested that irradiance on its own is responsible for coral bleaching (reviewed in Brown 1997; Fitt et al. 2001). These conclusions were based on experiments in which irradiance-exposed corals were generally kept in shallow water at low flow; since colony surface temperatures were not measured, it is possible that solar heating of the colony surfaces also contributed to triggering the observed bleaching in some of these studies.

These experiments have demonstrated that water flow substantially alleviated surface warming in corals by removing the warm boundary layer above colonies. This agrees with previous studies that concluded that flow-exposed reef environments, such as channels and reef flanks, will have lower coral bleaching susceptibility than flow-protected leeward reef sides or embayments (Nakamura and Van Woesik 2001; West and Salm 2003). Both in field surveys and experimen-

tally, corals survived high temperatures better at very fast flow (50–70 cm s^{-1}) than at low flow (2–3 cm s^{-1}), while no mortality occurred at <30°C at either flow speed (Nakamura and Van Woesik 2001). Improved removal of toxins (such as oxygen radicals) and passive gas diffusion have been suggested to be major mechanisms whereby water flow reduces bleaching susceptibility (Nakamura and Van Woesik 2001). The results from this study suggest that the convection of the warm boundary layer above the benthos is also an important mechanism, substantially cooling colonies and hence reducing temperature stress.

A better understanding of how irradiance, flow, colony pigmentation, and water quality affect the temperature microenvironment of corals may assist in interpreting some of the spatial and temporal variability observed in coral bleaching and in better predicting the bleaching resistance of locations. For example, coral bleaching was more severe near the coast than offshore on the GBR in the most severe mass bleaching events of 1998 and 2002 (Berkelmans and Willis 1999; Berkelmans et al. 2004). Inshore sea surface temperatures are commonly >1°C warmer than offshore reefs nearby due to a longer water residency time on the continental shelf and distance from cool-water upwelling (Wolanski 1994; Berkelmans et al. 2004). Because coastal corals are darkly pigmented, their colony surface temperature can further increase by up to 1.5°C through thermal absorption, exposing them to higher thermal stress than lighter offshore corals. Furthermore, suspended particles in turbid coastal waters on the GBR normally backscatter a proportion of the solar radiation, reducing the solar heating of the benthos. Many of the major large-scale coral bleaching events coincided with periods of unusually calm weather in the summer season (Glynn 1993; Brown 1997). Such periods are characterized by minimal wave-induced flow and extreme levels of irradiance due to minimal shading by clouds and lessened turbidity as particles sink and resuspension ceases. Such conditions lead not only to a warming of the seawater surface, but also to an enhanced warming of the darkly pigmented inshore corals. In contrast, offshore reefs on the wide continental shelf remained generally cooler than inshore reefs because of their proximity to cool upwelling water and eddy formation, which prevents thermostratification (Berkelmans et al. 2004); additionally, lighter coral pigmentation and higher swell-induced currents may have prevented a further surface warming of these colonies.

The color darkness of coral communities changes substantially along a gradient from coastal to offshore influences on the GBR, with corals being significantly darker toward the coast than offshore. Differences in pigmentation are more pronounced within species than across coral communities: for example, tissue darkness in massive *Porites* sp. changed by 3.4 color chart scores along a water quality gradient in the Central GBR that spans coastal to midshelf reefs (Cooper unpubl. data), whereas coral communities composed of numerous species changed by 1.0 score from coastal to offshore reefs. Colony darkness is largely a function of chlorophyll concentration in the coral tissue, which increases in response to elevated concentrations of nitrate and particulate nutrients and to shading (reviewed in Fabricius 2005). For example, chlorophyll concentrations increased by 50% and 70% in response to nitrate enrichment in two species of coral; this was due to 10% and 20% increases in the density of symbiotic dinoflagellates and a 40% increase in the amount of chlorophyll per dinoflagellate in both species (Marubini 1996; Marubini and Davies 1996). Similarly, a 28-d exposure to a slow-release fertilizer in the field resulted in a doubling in the numbers of symbiotic dinoflagellates and a significant colony darkening in two species of *Porites* (McClanahan et al. 2003), while a 60% light reduction increased the amount of chlorophyll per unit area in another species by 60% (Coles and Jokiel 1978). These experiments confirm that elevated levels of nutrients and turbidity are the major causes of the significant darkening of corals near the coast.

Temperature microenvironments have profound implications for benthic organisms, not only in the context of thermal stress but also by affecting many other temperature-controlled processes, such as metabolic and growth rates. For example, skeletons of massive *Porites* sp. are widely used as recorders of past and present temperatures. Their rates of linear extension increase by 27% of the mean values with each 1°C warming (Lough and Barnes 2000). Endosymbiont densities in corals vary spatially, as well as seasonally, more than twofold, being highest during cool months and visibly increasing tissue darkness (Stimson 1997; Brown et al. 1999; Fitt et al. 2000). Greater colony surface warming in winter than in summer due to seasonal increases in pigmentation may therefore dampen the temperature signal deposited in the coral skeleton compared with the seasonal variation in ambient seawater temperatures. In contrast, records of seawater temperature gradients along spatial gradients (e.g., from inshore to offshore conditions) may be exacerbated in coral skeletons due to the greater surface warming of dark inshore corals. The consideration of the temperature microenvironments around corals may further help in interpreting climate data derived from skeletons of massive *Porites* sp. along spatial or temporal gradients.

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Received: 1 February 2005
Accepted: 1 August 2005
Amended: 16 August 2005