Environmental Limits to Coral Reef Development: Where Do We Draw the Line?[1]

JOAN A. KLEYPAS,[2]* JOHN W. MCMANUS,† AND LAMBERT A. B. MEÑEZ†

*National Center for Atmospheric Research, P.O. Box 3000 Boulder, CO 80307-3000
†ICLARM, MCPO Box 2631, 0718 Makati City, Philippines

SYNOPSIS. Understanding how reefs vary over the present ranges of environmental conditions is key to understanding how coral reefs will adapt to a changing environment. Global environmental data of temperature, salinity, light, carbonate saturation state, and nutrients were recently compiled for nearly 1,000 reef locations. These data were statistically analyzed to (1) re-define environmental limits over which reefs exist today, (2) identify "marginal" reefs; i.e., those that exist near or beyond "normal" environmental limits of reef distribution, and (3) broadly classify reefs based on these major environmental variables. Temperature and salinity limits to coral reefs, as determined by this analysis, are very near those determined by previous researchers; but precise nutrient levels that could be considered limiting to coral reefs were not obvious at the scale of this analysis. However, in contrast to many previous studies that invoke low temperature as the reef-limiting factor at higher latitudes, this study indicates that reduced aragonite saturation and light penetration, both of which covary with temperature, may also be limiting. Identification of "marginal" reef environments, and a new classification of reefs based on suites of environmental conditions, provide an improved global perspective toward predicting how reefs will respond to changing environmental conditions.

INTRODUCTION

Coral reefs have long been considered stenotolerant ecosystems, confined by a relatively narrow range of environmental conditions. Reefs are broadly recognized as being limited to warm, clear, shallow, and fully saline waters. Achituv and Dubinsky (1990) reviewed the environmental limits to coral reefs with respect to light, temperature, salinity, sedimentation, "hydromechanic" factors, and ocean circulation, with most of these limits having been determined from site to site measurements and laboratory experiments. Recently available global data of both marine environmental conditions and reef distribution now allow us to extend our analysis of what affects reef distribution to the global scale. This paper is not a strict assessment of coral reef environmental tolerances everywhere, but it

does address three broad goals with respect to global reef distribution. First, a data-based assessment of environmental limits to coral reef development is presented. Second, "marginal" reefs are identified based on their proximity to environmental limits. Third, a broad environmental classification of reefs is proposed.

We focused on five major physico-chemical factors: temperature, salinity, nutrients, light availability, and aragonite saturation state (Table 1), because we consider these to be *first-order determinants of reef distribution at the global scale*. Many other factors can ultimately determine both location and extent of reef development, such as hydrodynamic conditions (e.g., waves, currents, storm frequency) and biological variables (e.g., larval sources, diversity, disease), but because these usually operate at the regional scale of reef distribution, we consider them second-order determinants.

The quality of data used in this evaluation is a function of both temporal and spatial resolution. Temporally, data would ideally be resolved to the same scale that each

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[2] E-mail: kleypas@ncar.ucar.edu

TABLE 1. *Physico-chemical environmental variables that potentially affect reef distribution.*

Variable	Reef limits	Temporal scale	Notes
Min. temp.	18	"annual minima"	too many references for coral
°C	18	"prolonged"	and reef temp. tolerances to
	16	"short-term"	list here; for a review, see
	15	"few days expos."	Coles and Fadlallah, 1991
	15–16	"long-term limit"	
	18	1–2 wk. cont. exp.	
	11.5–14.0	2–30 days	Arabian Gulf
Salinity	25–42	continuous	see Coles and Jokiel, 1992 for
PSU	20	<1 day exposure	extensive review
Light	50–450		range of I_k for individual corals;
$\mu E\ m^{-2}\ s^{-1}$			I_k is measure of coral adapta-
			tion to light (Chalker, 1981)
	30–40% of surf.	Limits reefs	see Achituv and Dubinsky, 1990
	10% of surf.	Limits corals	
Arag. saturation	not established		Function of $[Ca^{2+}]$, $[CO_3^{2-}]$,
Ω-arag			temp., sal.
Max. nutrients	0.5–3.0 NO_3?		No limits established for NO_3 or
$\mu mol\ liter^{-1}$	0.1–2.0 PO_4?		PO_4; see Szmant, 1997

particular variable affects a reef. For example, the "lethal dose" of low temperature to corals is a function of both duration and severity of the cold water event (see Table 1). To capture such short-term events, the data would require daily resolution. A global analysis at this resolution is currently impractical, so one must make the assumption that daily fluctuations are not significantly different between locations having the same weekly average temperature.

Spatially, data resolution would ideally match reef size. Again, this is currently impractical, as individual reefs are usually 1–100 sq. km in size, while most global data sets have scales of 10,000 sq. km (1° × 1°). The mismatch of reef-scale to data-scale is important in areas where the environment changes rapidly over short distances, such as where restricted water circulation (*e.g.,* a lagoon) can result in sharp temperature differences.

One final consideration of scale is the time period over which data were collected. Many data sets used here are based on over 100 years of ocean observations. Others, particularly the satellite-based data, were collected over only a few years time and may not represent a true climatology.

Scale is therefore an important issue in this analysis and results should be interpreted cautiously. If one keeps this in mind,

however, these data present a unique opportunity to synoptically examine some important global controls on reef distribution today, and also provide a baseline for examining how changes in environmental conditions might affect coral reefs in the future.

METHODS

The recent compilation of a database of worldwide reef distribution (ReefBase, 1996) has finally enabled a direct comparison between reef distribution and major oceanographic environmental conditions. ReefBase provided an original number of 6,451 reef locations. These were analyzed onto a 1° × 1° global grid, which resulted in a total of 968 grid cells having reefs. Forty-seven of these include only non-reef coral communities, as described either in ReefBase or other sources (*e.g.,* Solitary Islands: Harriott *et al.,* 1994; Easter Island: DiSalvo *et al.,* 1988; Kermadec Islands: Schiel *et al.,* 1986; St. Lucia Marine Reserve: Riegl *et al.,* 1995; Japan: Iryu *et al.,* 1995; Veron, 1993). Coral communities are usually distinguished from coral reefs on the basis of their inability to accumulate a buildup of calcium carbonate (Buddemeier and Smith, 1999). These locations were removed when analyzing the global limits to

reef development, but were retained in the reef classification procedures.

Environmental conditions were compiled for each 1° × 1° location, and statistical methods were used to evaluate the range of conditions over which coral reefs are found today. Temperature, salinity, nutrient, and carbonate saturation data sets are publicly available and each is briefly described below. Calculation of light availability was more complicated and is described in greater detail below. A summary of data sets used is presented in Table 2.

Minimum, maximum and mean temperature data were calculated from NOAA's AVHRR-based sea surface temperature (SST) data records. These are provided as weekly averages for the globe, and incorporate both remotely sensed and ship-board measurements (Reynolds and Marsico, 1993). Minimum and maximum monthly salinity values were derived from Levitus (1994); and phosphate and nitrate surface measurements were obtained from Levitus et al. (1993). All Levitus data were available at 1° × 1° resolution. Surface aragonite saturation (Ω-arag) was calculated from a 2° × 2° global grid of [CO_3^{2-}] (Archer, 1996). These data were extrapolated from GEOSECS ocean chemistry data (Takahashi et al., 1980) and have an accuracy of about ±10 μmol kg⁻¹. Ω-arag was calculated from [CO_3^{2-}] according to Mucci (1983), and using annual average temperature (Reynolds and Smith, 1994) and salinity (Levitus, 1994).

Light penetration limits how deep a reef will grow. Light that is available to a reef is a function of three major variables: (1) light reaching the ocean surface, which is a function of sun angle and atmospheric attenuation; (2) its attenuation (K) with water depth, which is a function of water clarity; and (3) reef depth. For this exercise, light penetration at a reef site was determined by combining photosynthetically available radiation (PAR) at the surface with the attenuation coefficient of light of wavelength 490 nm (K_{490}) (Kleypas, 1997; see also Bosscher and Schlager, 1992; Bosscher and Southam, 1992). Monthly-averaged 3-hourly estimates of PAR were obtained from an inference model that uses global satellite measurements of both top of the atmosphere radiation and cloud cover (Pinker and Laszlo, 1992a, b). Maximum 3-hourly PAR values were extracted as an estimate of monthly average PAR at noon (PAR_{noon}). Likewise, seven years of monthly K_{490} values from the Coastal Zone Color Scanner archives were averaged to produce a monthly climatology. Using these two monthly climatologies (PAR_{noon} and K_{490}), and assuming that the minimum PAR necessary for reef growth is 250 μE m⁻² s⁻¹ (Kleypas, 1997), monthly average depth of maximum light penetration (Z_{noon}) was calculated according to the formula:

$$Z_{noon} = \frac{\ln(PAR_{min}/PAR_{noon})}{K_{490}}$$

where

PAR_{min} = minimum PAR necessary for reef growth, 250 μE m⁻² s⁻¹

PAR_{noon} = maximum daily PAR at sea surface, μE m⁻² s⁻¹

K_{490} = diffuse extinction coefficient of light (λ = 490 nm), m⁻¹

Reefs are only briefly exposed to noon-day light intensity, so the calculated Z_{noon} values are actually deeper than expected reef development. Twelve monthly values of Z_{noon} were calculated for each site, from which minimum, maximum, and average Z_{noon} values were derived.

The above environmental data were compiled for each ReefBase location and statistics were used to describe the limits of reef development. Statistical analyses included basic data analyses, principal component analysis, and cluster analysis (agglomerative nesting based on dissimilarities). Principal component and cluster analyses were performed using S-PLUS© version 3.3.

RESULTS

Environmental limits to reef growth

The range, average and standard deviation of environmental variables for all reef sites are summarized in Table 3. A correlation matrix of variables (Table 4) indicates that some variables are strongly correlated, notably temperature and Ω-arag (r^2

TABLE 2. *Environmental data used to evaluate ReefHab locations.*

Parameter & source	Units	Spatial	Temporal	Period of collection
Sea surface temperature				
Reynolds and Marsico, 1993	°C	1 deg	weekly	1982–present
Salinity				
Levitus, 1994	PSU	1 deg	monthly	1900–present
Nutrients				
Levitus *et al.*, 1993	μmol liter⁻¹	1 deg	overall avg.	1900–present
PAR				
Pinker and Laszlo, 1992a	Wm⁻²	2.5 deg	monthly	Jul 1987–Dec 1989
Water transparency				
(CZCS attenuation coeff.)				
Austin and Petzold, 1981	K₄₉₀	18 km	monthly	Nov 1978–Jun 1986
Carbonate ion [CO₃²⁻]				
Archer, 1996	μmol kg⁻¹	2 deg	overall avg.	July 1972–Apr 1978

= 0.43–0.76), and nitrate and phosphate (r^2 = 0.30). "Marginal" reefs and coral communities are identified by their proximity to the minima or maxima of each variable (Table 5).

Temperature. Minimum weekly temperature for reefs is 16°C, recorded from the northern Persian Gulf (Kubbar and Taylor Rock). Outside the Persian Gulf, minimum reef temperature is 17.3°C, at Elizabeth Reef off southeast Australia. The analysis did not indicate that Red Sea reefs experience weekly average temperatures less than 18°C. Maximum weekly temperature on any reef site was 34.4°C, at Bahrain in the Persian Gulf. High temperature reefs are uncommon outside semi-enclosed seas. The Andaman Islands (Bay of Bengal), however, experience temperatures to 31.7°C. Other locations with high temperatures include the Philippines (31.4°C), Spratly Islands (31.3°C), north Australia (31.2°C), and Laccadive Islands (31.2°C).

Salinity. The salinity range among all reef sites was 23.3–41.8 PSU, which is close to the 25–42 range reported by Coles and Jokiel (1992). Lowest monthly salinity occurs at Moscos Island off Burma. All locations having monthly average salinity greater than 38 are in the Red Sea and Persian Gulf. Among reefs outside of these two areas, Abrolhos Reef off Brazil has the highest salinity (37.2).

Nutrients. The modal value for both nitrate and phosphate among all reef locations is 0.0 μmol liter⁻¹, (which indicates an immeasurable level). Ninety percent of all locations have less than 0.60 μmol liter⁻¹ nitrate and 90% have less than 0.20 μmol liter⁻¹ phosphate. Highest concentrations of both nutrients occur in the equatorial upwelling region of the eastern Pacific, near the Galápagos Islands (up to 5.61 μmol liter⁻¹ nitrate, and 0.54 μmol liter⁻¹ phosphate). Reefs in the Strait of Hormuz also experience high nutrients, while Arabian Sea reefs have disproportionately high phosphate to nitrate ratios.

Aragonite Saturation. Aragonite saturation state (Ω-arag) is determined by the equation

TABLE 3. *Statistically derived environmental averages and extremes among reef sites (does not include non-reef coral communities).*

Variable	Min	Max	Avg	SD
Temperature (°C)				
average	21.0	29.5	27.6	1.1
minimum	16.0	28.2	24.8	1.8
maximum	24.7	34.4	30.2	0.6
Salinity (PSU)				
minimum	23.3	40.0	34.3	1.2
maximum	31.2	41.8	35.3	0.9
Nutrients (μmol L⁻¹)				
NO₃	0.00	3.34	0.25	0.28
PO₄	0.00	0.54	0.13	0.08
Aragonite saturation (Ω-arag)				
average	3.28	4.06	3.83	0.09
Max Depth of Light Penetration (m)				
average	−9	−81	−53	13.5
minimum	−7	−72	−40	13.5
maximum	−10	−91	−65	13.4

$$\Omega\text{arag} = \frac{[Ca^{2+}][CO_3^{2-}]}{K_{sp}}$$

TABLE 4. Matrix of least squares linear regressions (r²) for environmental variables.*

	Tmin	Tmax	Smin	Smax	Zavg	Zmin	Zmax	NO₃	PO₄	Ω-arag
Tavg	.87	.48	.08	.08	.03	.05	.01	–	.02	.76
Tmin		.18	.09	.12	.11	.14	.08	–	.04	.62
Tmax			.01	–	03	.02	.04	–	–	.43
Smin				.70	.03	.04	.04	–	.03	–
Smax					–	–	–	–	–	–
Zavg						.93	.94	–	.15	.03
Zmin							.79	–	.16	.05
Zmax								–	.13	.02
NO₃									.30	–
PO₄										–

* Regression coefficients less than 0.01 are not shown, and those greater than 0.3 are underlined.

where K_{sp} is the stoichiometric solubility product of aragonite. Values of Ω-arag less than 1.0 indicate undersaturation, while values greater than 1.0 indicate supersaturation. The entire surface ocean is supersaturated with respect to aragonite, but the degree of saturation varies with latitude (Ω-arag = 4.1 at the equator, to 1.5 at the poles). Higher saturation in the tropics is due primarily to higher temperatures. Among reef locations, Ω-arag varies between 3.3 (Elizabeth Reef) and 4.1 (Solomon Islands; Red Sea). Reefs that experience lowest saturation are those in upwelling regions (e.g., Galápagos Is.) where deeper, CO_2-enriched waters reach the surface; or at high latitudes. Coral communities occur where Ω-arag is as low as 3.1.

Light. Light penetration varies along two gradients: latitude and distance from shore. Open ocean atolls located away from the equatorial upwelling zone receive the most light. Many reefs and coral communities receiving the least amount of light occur at high latitudes, where light penetration (250 $uE\ m^{-2}\ s^{-1}$) can seasonally be less than 10 m (e.g., coral communities of mainland Japan and northern Florida). However, many low latitude coastal reefs appear to suffer from equally low light levels, probably due to high turbidity (e.g., Tunku Abdul Rah of Borneo). Indeed, few light-limited reefs in Table 5 would be described as "thriving," and some may actually be non-reef coral communities.

Identification of reefs in "marginal" environments

Both reefs and non-reef communities occur near the accepted limits of each envi-

ronmental variable (Table 5). However, the "line" between coral communities and coral reefs is confounded by the covariance of temperature, aragonite saturation and light (Fig. 1). Some coral communities (e.g., eastern Pacific locations) are obviously limited by some factor other than those examined here, such as isolation from larval sources, but most communities occur at 25–35° latitude, consistent with sharp changes in temperature, aragonite saturation, and light. Minimum temperatures are high near the equator and drop off precipitously outside 20° latitude (Fig. 1A). Many but not all of the high-latitude coral communities occur below the 18°C line.

Aragonite saturation covaries with temperature, from maximum values near the equator, to lowest values outside 20–30° latitude (Fig. 1B). The reef to coral community transition occurs near Ω-arag = 3.4 and only a few reefs occur where saturation is less than this. These include the Houtman Abrolhos reefs off Western Australia, and open ocean reefs off southeast Australia (including Lord Howe Island), which also experience fairly high light penetration in winter. In contrast, waters surrounding the Ryukyu Islands have higher Ω-arag values (3.6–3.7). Highest Ω-arag occurs in the Red Sea and from Papua-New Guinea through the Solomon Islands (4.1). Highest Ω-arag in the Caribbean (3.9) occurs along a belt from Cuba through the Bahamas.

Minimum monthly light penetration is greatest (70 m) at 15° north and south of the equator, but shallows to less than half that (30 m) outside the tropics (Fig. 1C). Unlike minimum temperature, light pene-

tration varies widely within these limits, so that low-light reefs occur t ighout the tropics. Locations that receive ast light year round are not high latit fs but rather those of turbid coasts .g., Papua-New Guinea). Most of these are identified as reefs, but there may be some bias toward identifying tropical non-reef coral communities as reefs. For example, the coral communities of Broad Sound, a turbid region of the Great Barrier Reef, do not develop true reefs (Kleypas, 1996).

Several high latitude coral communities have apparently not formed reefs even though they occur in waters above the "lower limits" of light, aragonite saturation and temperature, and are not associated with unusually high nutrient values. The Solitary Islands (Australia) and the St. Lucia reefs (South Africa) are two such communities; both have community structures similar to nearby reefs, but do not form reefs themselves. This suggests that either some other factor prevents these communities from building reefs (e.g., competition, storm frequency, geologic history), or that they are cumulatively stressed by a combination of low temperature, light and saturation state.

An environmental classification of reefs

Principal component analysis of the suite of variables at the 968 locations revealed that 55% of the variance in the data was explained by light, temperature and aragonite saturation state. Nitrate and salinity explained little of the variance, and phosphate only slightly more. Clustering analyses (dissimilarity indices) were performed on many combinations of all variables, but the best separation of sites was achieved with clusters based on Tmin, Tmax, Zmin, Zmax, and Ω-arag.

When all sites were clustered according to temperature (Fig. 2A) or Ω-arag (Fig. 2B), there was a strong latitudinal segregation of reefs and non-reef coral communities. When reefs were grouped according to light, however, the clustering reflected distance from shore (Fig. 2C). When all three variables were used, the classification grouped reefs and non-reef communities according to their cumulative "marginality"
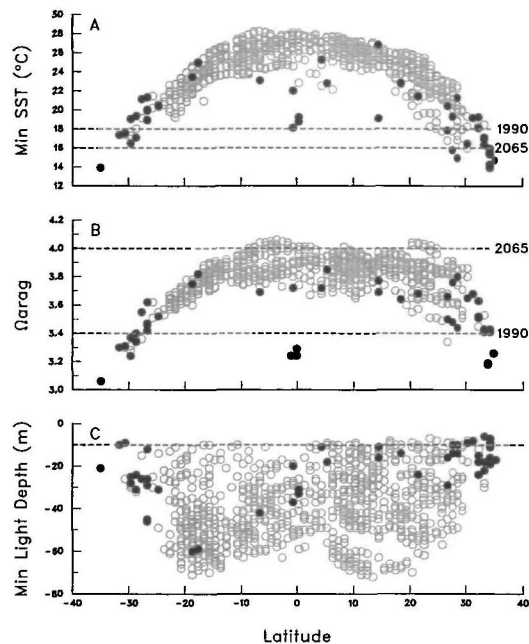

FIG. 1. Distribution of reefs as a function of latitude and (A) minimum sea surface temperature; (B) aragonite saturation state; and (C) minimum monthly noon-day light penetration. Open circles represent reefs; filled circles represent non-reef coral communities. Approximate present-day (1990) environmental limits to coral reefs are shown versus estimated position of those limits for the year 2065 (based on temperature and CO_2 projections). No significant change in light penetration is expected.

to environmental limits (Fig. 3). Four main classifications arose from the clustering: (1) low-temperature and/or low-Ω reefs (42% are non-reef coral communities); (2) low-light reefs (18% non-reef); (3) moderate-light reefs (7% non-reef); and (4) "no worries" reefs (2% non-reef) which are apparently free from any marginal conditions. No coral reefs were classified as low-temperature, low-Ω and low-light.

DISCUSSION

Using environmental variables to help draw the line around coral reef distribution is useful when defining absolute limits, but within those limits, there obviously are additional lines that define the differences between reef types. This analysis has attempted to examine reef distribution at the global scale, and ignores environmental variation beyond the spatial scale of 1 degree, and

TABLE 5. *Examples of reefs that exist within "marginal" environmental conditions.**

Low temperature reefs (minimum weekly SST <18°C)

Min temp	Reef
13.9	[New Zealand: Bay of Islands]
13.9–17.1	[Japan mainland]
15.0–17.8	[Gulf of California: Playa d Carmen; Guaymas; 1 Espiritu Santo; La Paz]
16.5	[Florida: Panama City Beach; Hog I]
16.5–17.1	[Kermadec Is]
16.0–17.8	Northern Persian Gulf
17.3–17.7	SW Pacific: Elizabeth and Middle Reefs; Acacia Plateau; Lord Howe I
17.9	[Taiwan: Yenliao Bay]
17.9	Hawaiian Is: Kure and Midway Atolls

High temperature reefs (maximum weekly SST >31.5°C)

Max temp	Reef
33.6–34.4	Persian Gulf (maximum at Fasht Adhm, Bahrain)
34.2	Strait of Hormuz
31.6–33.9	Gulf of Oman
31.7–32.9	Southern Red Sea
32.1	[Gulf of California: Concepcion Bay]
31.8	Gulf of Aden: Maskali; Musha
31.5–31.8	Central Red Sea
31.6–31.7	Andaman Is

Low salinity reefs (monthly minimum <30 PSU)

Min salinity	Reef
20.7	[Gulf of Guinea: Elobey Grande]
23.3	Burma: Moscos Is
27.0	Bay of Bengal: St Martins I
27.0–29.9	Eastern Pacific: Ensenada de Utria; Isla de Gorgona
28.9–29.3	Central GBR: Cairns; Murray; Low Wooded Is; Fitzroy I
29.7	Gulf of Thailand: Sichang Is; Ko Lan; Ko Sak; Khao Sam Roi Yo

High salinity reefs (monthly maximum >40 PSU)

Max salinity	Reef
41.8	Gulf of Aqaba
41.8	Gulf of Suez
41.2–41.8	Northern Red Sea
40.0–41.2	Central Red Sea
40.3–40.9	Persian Gulf

High nitrate reefs (average >2 μmol liter^{-1})

NO$_3$	Reef
3.24–5.61	[Galápagos Is]
3.34	Strait of Hormuz
2.50–2.76	N Honduras: Guanaja; Laguna de Guaymoreto
2.69	Gulf of Oman: Clive Rock
2.15–2.65	Mid Pacific: Marquises, Phoenix; Baker; Starbuck; Kiritimati; Malden
2.00–2.23	Micronesia: Gilbert Is

temporal scale of a month. However, the results offer a broad view of how reef distribution is controlled by the environment, and provide a basis for designing smaller scale examinations. The major environmental variables that correlate with the basic global pattern of reef distribution are temperature, light, and carbonate saturation state, and these three variables are discussed in detail below. Reefs apparently can occur in a wide range of nutrient levels, and our failure to identify either phosphate or nitrate as an important control on reef distribution is interesting. However a definitive statement that reef distribution is independent of nutrient concentration would be premature for several reasons: (1) global nutrient data are only available as annual averages, and seasonal variations are not resolved; (2) primary production in many open ocean regions may be limited by iron rather than by nitrate or phosphate (Martin

TABLE 5. *Continued.*

High phosphate reefs (average >0.4 μmol liter⁻¹)

PO₄	Reef
0.41–0.54	[Galápagos Is]
0.40–0.54	Arabian Sea: Wadi Zead; Masirah I; [Kuria Muria]
0.40–0.49	Mid Pacific (eq): Marquises, Phoenix Is; Starbuck; Kiritimati; Malden
0.43	Strait of Hormuz
0.40	Gulf of Oman: Clive Rock
0.40	Gulf of California: Cabo Pulmo; El Pulmo; [Isla Espiritu Santo; La Paz]
0.40	French Polynesia: Pukarua; Reao

Low aragonite saturation reefs (Ω-arag <3.5)

Ω-arag	Reef
3.06	[New Zealand: Bay of Islands]
3.18–3.43	[Japan mainland]
3.24–3.34	[Kermadec Is]
3.24–3.49	[Galápagos Is]
3.28–3.35	SW Pacific: Middleton, Elizabeth, Middle Rfs; Acacia Plat, Lord Howe I
3.30–3.31	[Western Australia: Rottnest I; Perth]
3.34–3.49	[Gulf of California: Playa d Carmen; I Espiritu Santo; La Paz; Guaymas]
3.37–3.47	[SE Australia: Solitary Is]
3.36	Western Australia: Houtman Abrolhos
3.42	[SW Pacific: Easter I]
3.46	S French Polynesia: Rapa, Marotiri
3.50	Taiwan: N Coast, Yenliao Bay

Low light reefs (minimum depth of light penetration >−15 m)

Depth	Reef
−6−−19	[Japan mainland]
−9	[Florida: Panama City Beach; Hog I; Crystal River; Captiva I; Sanibel I]
−9−−10	[Western Australia: Perth; Rottnest I]
−10	Borneo: Tunku Abdul Rah
−10−−16	[Gulf of California: Guaymas; Concepcion B; I Espiritu Santo; La Paz]
−11	India: Gulf of Kutch
−11	[Gulf of Thailand: Sichang I]
−11−−18	[Gulf of Guinea: Elobey Grande; Cape Three Points]
−12	[SE Australia: Brisbane]
−13	China: Hainan
−14	[East Florida Coast: St Lucie Nearshore Region; Jacksonville]
−14	[Arabian Sea: Kuria Muria]
−14−17	Persian Gulf: Mudayrah; Naval Base and Twin Reefs; Kubbar; Taylor Rk
−15	Central GBR Inner shelf: Bowden Reef
−15	Southern Red Sea: Al Qunfudahah; Jazirat as-Siqalah
−15	West Yucatan: Campeche
−15	[Georgia: Gray's Reef]

* Non-reef coral communities are in brackets.

et al., 1994), yet iron is rarely measured; (3) nutrient excess probably limits reefs indirectly by enhancing macroalgal competition for space (Lapointe *et al.,* 1997), phytoplankton competition for light (Hallock and Schlager, 1986), and bioerosion (Hallock, 1988).

An interesting result of the analysis was that Bermuda was the only "low-temperature and/or low-Ω" reef of the Caribbean and western Atlantic. This might indicate that Caribbean/western Atlantic reefs are more stenotolerant than Indo-Pacific reefs.

Alternatively, it indicates that some other factor limits these reefs more than elsewhere (*e.g.,* storm frequency, low diversity, substrate control).

Another look at temperature

The relative effects of temperature versus aragonite saturation on coral reef development remain uncertain. Temperature remains a good proxy for drawing the latitudinal limits to distribution, but it is not the only physical variable that correlates with the transition from coral reef to non-
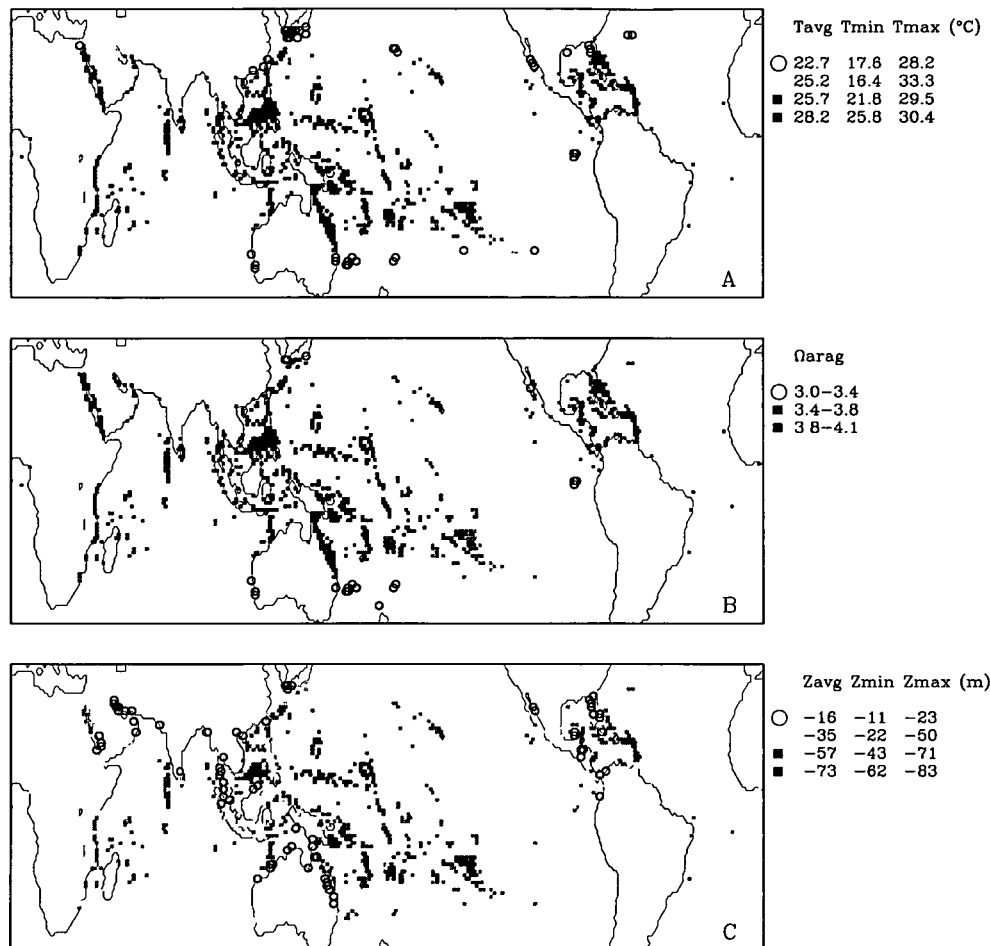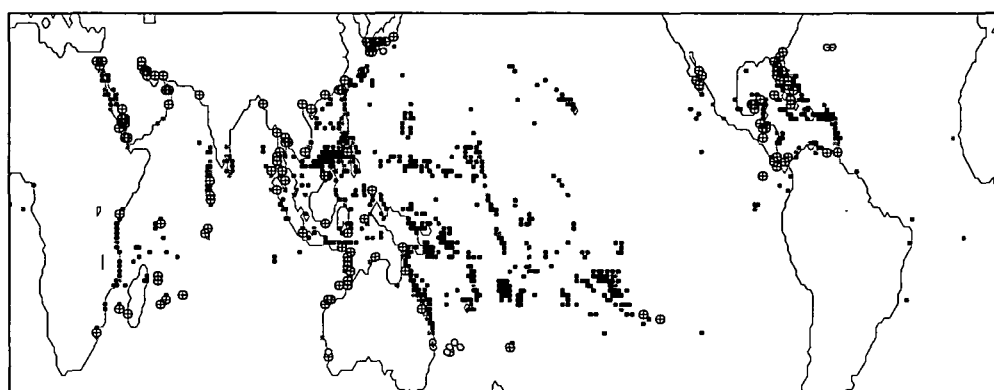
FIG. 2. Clustering of reefs on the basis of (A) sea surface temperature (Tavg = average temperature, Tmin = minimum, Tmax = maximum); (B) aragonite saturation state (Ω-arag); and (C) monthly average depth of noon-day light penetration (Zavg = average depth, Zmin = minimum, Zmax = maximum).

reef coral community. At the latitudinal limits for reef development, it is impossible to determine from the data if temperature per se is the limiting factor, or whether aragonite saturation state and/or light level, which covary with temperature, are also limiting. Most reef-building corals can not withstand temperatures below 18°C. Those which tolerate the coldest winter temperatures (Persian Gulf corals) also exist under high saturation conditions. Their increased temperature tolerance is generally attributed to adaptive mechanisms, but the possibility that both temperature and saturation state affect these corals should be considered.

A closer look at aragonite saturation

Carbonate saturation state has been proposed as a major control on carbonate sedimentation rates (Opdyke and Wilkinson, 1993). Buddemeier (1994) stated that carbonate saturation was very likely a significant factor in the control of calcification and photosynthesis, and Smith and Buddemeier (1992) estimated that a doubling of present-day atmospheric CO_2 would reduce surface ocean aragonite saturation in the tropics from 340 to 240%. Aragonite saturation has been largely neglected in terms of reef distribution, probably because of the paucity of carbonate saturation measure-

	Tmin	Tmax	Ω	Zmin	Zmax	
☉	18.1	27.1	3.4	−28	−72	low Temp, low Ω
⊕	22.3	30.3	3.8	−14	−31	low Light
▨	23.4	30.3	3.8	−22	−52	mod Light
■	25.0	30.1	3.8	−47	−73	"no worries"

FIG. 3. Clustering of reefs on the basis of temperature (Tmin, Tmax), aragonite saturation state (Ω-arag), and depth of noon-day light penetration (Zmin, Zmax). Marginal reefs are classified according to limiting variables, while a "no worries" classification indicates those that fall well within the temperature, saturation state and light limits to reef development.

ments. In fact, $[CO_3^{2-}]$ data of this analysis were extrapolated from high quality data but relatively few measurements. Still, Buddemeier's (1994) suggestion that carbonate chemistry is at least as important as temperature is supported by the results presented here. The complexity of this relationship are exemplified by the geographic comparisons below.

Laboratory-derived calcification rates of corals and algae decline significantly as aragonite saturation state is reduced (Gattuso et al., 1998). Langdon et al. (1998) also measured a 30% drop in community calcification of the BIOSPHERE 2 coral reef mesocosm as Ω-arag was reduced from 5.0 to 3.2. Unfortunately, few field data are available to test these findings. Our analysis indicates that Red Sea reefs should have the highest calcification rates and eastern Pacific reefs should have the lowest. Gross carbonate production at Aqaba, Red Sea (Ω-arag = 3.9), is in fact higher than that of Hawaiian Reefs (Ω-arag = 3.6) at the same latitude (Heiss, 1995), despite having similar light and temperature regimes. Galápagos reefs (Ω-arag = 3.2) however, are thin accretions (Macintyre et al., 1993) that

are sometimes considered coral communities rather than reefs. Carbonate production at the Galápagos is relatively low (net community production = 8–16 kg m^{-2} y^{-1}, Glynn, 1988), although low temperature (Glynn et al., 1996) and high bioerosion rates (Reaka-Kudla et al., 1996) also seem to affect net calcification. Low aragonite saturation state may also explain the observation by Cortés (1997) that eastern Pacific reefs tend to be poorly cemented. Data from high latitude reefs are somewhat confusing. Crossland (1988) noted that Houtman Abrolhos corals were lightly calcified, but at the same location, Smith (1981) measured extremely high calcification rates (although the summer rate was nearly four times that of winter). In the current data analysis, attempts to further correlate aragonite saturation state with reef calcification are limited by: 1) covariance of temperature and light with saturation state; 2) lack of field-measured calcification rates; and 3) extrapolation of oceanic GEOSECS measurements to shelf areas, where decreased circulation and/or higher organic production may affect saturation state (S. V. Smith, personal communication).

The broad effects of light

Depth of light penetration has never been quantitatively analyzed as a control on reef distribution, due primarily to the lack of light data for the ocean surface. The data used here are only satellite-based estimates of light penetration. Nevertheless, these data indicate that light penetration varies more than any environmental factor of this analysis. Reduced growth rates at higher latitudes are often attributed to low temperatures, but the evidence here indicates that, just as light attenuation explains reduced reef calcification with depth, seasonally low light penetration at high latitudes may limit reef calcification to shallower depths than in the tropics (Grigg, 1982).

In terms of a reef's ability to cope with environmental change, adaptations to varying light conditions are the most obvious. Many studies (not discussed here) document the photoadaptive mechanisms of corals, from morphological plasticity to zooxanthellae density, to either optimize or cope with available light. These mechanisms allow many coral species to maintain metabolic functions over a broad light range. Photosynthesis : irradiance curves show that most corals function uniformly across a range of light intensity, then decline rapidly outside that range (Chalker, 1981). Even though corals receive less light at high latitudes, acceptable light levels can still be found in shallow waters, and the metabolic functions of those corals should be similar to those that receive more light in the tropics. This could explain why metabolic studies performed on shallow reef flats show little variation with latitude (although see Pichon's [1997] discussion of high metabolic variability as a function of community composition, season and reef type).

Despite the adaptions to changing light levels, coral reefs do have minimum light requirements. As light penetration decreases outside the tropics, depth of reef growth shallows accordingly. Active reef growth at high latitude is restricted to relatively shallow depths (e.g., Lord Howe Island, Harriott et al., 1995; Ryukyus, Kan et al., 1995, and Iryu et al., 1995; Kermadec Islands,

Schiel et al., 1986). Many light-limited coral communities listed in Table 5 (e.g., Gulf of Thailand, Gulf of Guinea) are not marginal in terms of the other variables. Of course, low light at some locations is due to high suspended sediment, which itself is limiting to reef growth.

Does environmental classification reflect reef function?

Previous reef classification schemes have been based on geomorphology (e.g., atolls, barrier, fringing etc.). These are useful in terms of historical reef development, particularly with respect to sea level change and substrate control. Over shorter time periods, and as we enter a century of rapid global change, an environment-based reef classification should be useful for predicting reef response if the classification reflects reef function (metabolism, nutrient cycling, calcification). Reef function appears to be uniform across the latitudinal distribution of reefs (see review of Kinsey, 1985), then declines rapidly at the poleward threshold of reef distribution (Hopley, 1989). Likewise, temperature, light and saturation state remain fairly uniform in the tropics, then also decline rapidly at this threshold (Fig. 1).

An environment-based reef classification allows one to compare coral reef distribution with coral reef function. For example, if light is important to overall reef function, then the wide range of light regimes across the global distribution of coral reefs indicates that reef function varies across a continental shelf as much as it does from tropics to high latitudes. Hopley (1989) pointed out that numbers of coral species, coral growth rates, and reef framework decreased much more rapidly across continental shelves than across latitudinal zones. Likewise, the strong correlation of aragonite saturation state with reef distribution compels us to more closely examine this variable in terms of overall reef function. This environment-based classification will be least useful at sites which are affected by some other, overriding factor; for example, reefs which are geographically isolated (eastern Pacific, Cortés, 1997; Brazilian coastline, Carannante et al., 1988), or which suffer frequent storm damage (e.g., Buck Island

Bar, Macintyre and Adey, 1990). However, such variables can certainly be used to refine the classification.

Coral reef response to global change

Estimating how reefs will respond to global change, relies on our understanding of how reefs are distributed relative to the environment. Of the three major variables addressed in this paper, large-scale shifts in light distribution are not likely, but global shifts in aragonite saturation and SST are probable. The IPCC (Houghton *et al.*, 1996) predicts that by the middle of next century, atmospheric CO_2 concentration will reach twice the preindustrial level, and atmospheric temperatures will increase by about 2°C. Surface ocean uptake of CO_2 will reduce aragonite saturation state by about 30% (Gattuso *et al.*, 1999), and the current Ω-arag isoline of 3.5 will shift equatorward by at least 15 degrees latitude (Fig. 1). Alternatively, a 2°C increase in SST will move the 18°C isotherm poleward about 5 degrees latitude (Fig. 1). In the simplest analysis, if reefs are restricted by temperature, then we would expect an expansion of reefs poleward; but if reefs are restricted by saturation state, then we would expect a constriction of reefs equatorward. The dichotomy of this prediction will only be resolved through closer examination of these two controls.

In a more complicated analysis, the transition from coral reefs to non-reef building coral communities at high latitudes is often attributed to biological factors such as decreased coral diversity, increased competition with macroalgae, and increased bioerosion. We considered these factors to be secondary at the global scale. However, where coral reefs are limited by competition with adjacent communities, their future may be determined more by response of the competing community to global change, than by environmental changes alone.

CONCLUSIONS

When analyzing ecological distributions, researchers naturally use data that are readily available or easy to measure. Temperature is probably the most widely measured ocean variable, and since the initial obser-

vation of Vaughan (1919) that coral reefs are restricted to waters where annual minimum temperature is greater than 18°C, it has remained a good environmental proxy for drawing the line around reef distribution. However, with respect to future studies of reef response to global change, this study emphasizes the need to investigate variables that are less well understood but which may play a role in determining the fate of reefs in a rapidly changing world. In particular, this attempt to define the environmental limits to reef development points to two major areas for further investigation. First, as pointed out by Smith and Buddemeier (1992) and Buddemeier (1994), the role of aragonite saturation state in limiting coral reef distribution needs to be defined. Second, although light has always been recognized as an important control on coral growth, this relationship needs to be quantified at the level of coral communities and reefs. This exercise has not drawn a distinct line around coral reef and coral community limits, but it does enable one to approach the question "where do we draw the line" with more information at hand.

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