Zentrum für Marine Tropenökologie

EFFECTS OF RECENT WARMING EVENTS ON CORAL REEF COMMUNITIES OF COSTA RICA (CENTRAL AMERICA)

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To my parents,
Luis and Emmy,
for giving me all the sun
nested in their hearts

“Guano Happens”

-**Brian Fagan**, introducing the catastrophic consequences
of the El Niño episodes of the 1800’s on
the Peruvian Guano-extracting operations.
Floods, Famines and Emperors, 1999

***“And even till this day the same nature
has remained in corals so that they harden when exposed to air”***

-**Ovid**, after celebrating the hero Perseus who cut off Medusa’s head,
describing how seaweeds, hardened by contact with the monsters’ severed head,
were scattered by rascally sea-nymphs throughout the seas.
Metamorphoses, Book IV, 1 A.D.

***“There is perhaps
the real point where life rises obscurely from the sleep of a stone,
without detaching itself from the rough point of departure”***

-**Professor Pierre Aronnax**, meditating on the nature
of corals and their skeletons.
Jules Verne, 20000 Leagues under the Seas, 1869

Coral Garden

Darkness...

There was a small cave by the sea. A small beach of grey sand inside, blue rippling water, blue rippling reflection on the ceiling. Blue light playing with my mind. Waves of light playing on my skin. Stranded in this hollow world.

This twilight will last forever...

I wail, I thrush my tail on the sand. I push with my hands the sand, I need the coolness. Heat. My mind reels. What strange wave threw me here? Someone called me in my sleep. When did the colours disappear? All white. Bones, stones, Death. My body is dying, bright, hot air. Someone said once “how would it be to walk on land, to float in the air”, but my thought has a tail, my words have fins...

Swim away then, if you can...

Blue light, blue water, blue thought – what am I? Serpents of delirium. Pale white skin, grey-green fin. Storm and tempest, whirlwind and rain, take my hand, take the hand with the sea-coloured fingers and these thin membranes, I can wear no ring. I am not a woman, this blue hair with the silver strands belong to the Lord of the sea. He gives no rings. Come, save me my Lord! Your sister is stranded on a small, grey beach in a vaulted cave. Where are the coral gardens? Lord, are you stranded too? Did we part yesterday, or was it eons ago? Why have you left the ocean to die?

Eons Little time for a creation...Lean close, feel the heat rise as I lift my palms. Watch, as I bend my small finger to burn the armies of cold rushing across the sky. This is the day of Becoming. Becoming Another.

How long have I been lying here? Do cities still stand, twinkling in the night like vast sheets of white flames? Are the sea kingdoms still thriving? Has my Lord left the seas, has he shed his tail and fins? Storm and tempest. I wish I could summon the lesser winds to cool the world. Colours fading to startling white, the palaces of the deep have turned to marble.

Now, Here the World I change. Furious. The end of silence is approaching with a roar. Uplifting shores and rocking mountains. Ash and glory. I unfurl my wings. Hiding the moon. Unleashing another age. Armies of angels fill the skies. Is this the end of the world? Alone I defeat the dragon’s claw with a single breath from my lips.

Light? Lord, it is blinding me – has the sun risen on the sea? No, it is fading again.
My tail is turning to stone. I feel I could break into pieces if I move it again- Am I a thousand years old? In my heart you can find dust settled in other ages. But now I am fragile, made of blue glass.

Fragile, yes...

Lord! A small child is walking towards me. And while he is approaching, he is growing, his eyes blinding me, becoming a man. My Lord! My Lord, it is you! Save me!
You are saved, he says.
But I cannot move my tail, it is breaking.
He sits beside me, strokes my hair.
Ask the waves to take me back, oh Lord, save me.
You are saved, he repeats calmly.
If you believe, then you are saved.
No Lord, no.
The cave falls on me and I shatter into a thousand pieces.

And finally night fell...

Chrystalla Thoma

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SUMMARY

EFFECTS OF RECENT WARMING EVENTS ON CORAL REEF COMMUNITIES OF COSTA RICA (CENTRAL AMERICA)

This thesis documents bleaching, mortality and recovery of corals in a time period (1991-2001) when three warming events affected coral reef communities at the Pacific and Caribbean coast of Costa Rica, Central America. The study sites (six in the Pacific and two in the Caribbean) are very important because of their coral abundance, diversity, presence of rare species, and reefs´ structural complexity. The condition of these coral communities is deteriorating rapidly due to a combination of natural and anthropogenic disturbances. The effects of the warming events were assessed at regional scale by surveying broad portions of the coast (dozens of kilometers) and on the local scale, by determining the percentages of affected or healthy coral colonies and changes in coral cover using the transect method. On the individual scale, monitoring of tagged colonies during the onset and demise of the warming events was used to determine individual responses to the stress. The evolution of the warming events was characterized by in situ measurements of temperature and meteorological variables (sun hours, rainfall) and complemented with historical records of surface seawater temperature (1982-2001).

During the 1982-2001 time period, four El Niño episodes affected the coral reef communities at the Pacific coast of Costa Rica. Another warming event in 1995 took place in the Caribbean with negative consequences for the reef corals of the area. Warmings at the Pacific coast tend to precede or coincide with the Caribbean warmings, perhaps linking seemingly unrelated environmental crises to bleaching events. During all mass bleaching events (1982-2001) in Costa Rica, doldrum-like weather (long spells of sunny, dry days together with calm, clear waters) prevailed and was coincidental with the warm water excursions. These conditions are highly conducive to bleaching due to an increase of solar radiation reaching the corals together with the thermal stress, suggesting that the association between environmental parameters and bleaching is more complex than has been suspected. Tagged colonies had different bleaching levels and recovery capabilities, and the bleaching in one species was related to zooxanthellar densities and not to changes in pigments concentration. Overall mortality of entire colonies and live cover during the warming events were low (ca. 6% and ca. 35% respectively), particularly during the 1997-98 El Niño. This is remarkable given the strength and duration of the warming period. The least affected area was the Golfo de Papagayo, where upwelling events reduced the strength of the warming. The strongest El Niño episodes not always resulted in the highest tissue mortality, suggesting that selective processes (more thermal tolerant coral genotypes and zooxanthellae clades) and local oceanographic settings may be interacting and decreasing the warming impact. These results suggest that the responses of coral reef communities to warming episodes, such as El Niño, are complex and dynamic, and site and species-specific factors are interacting to a degree that precludes casual generalizations. Furthermore, there is evidence of localized positive effects on coral reproduction, recruitment and growth during warming events. The dictum that El Niño episodes are absolutely detrimental to coral reef communities has to be revised. However, the negative impact of mass bleaching events upon corals is clear, and the prospect of an increase in frequency and intensity will have detrimental consequences for the future of these wonderful marine ecosystems.

The stable isotopic (δ^{13}C and δ^{18}O) signature of the 1997-98 El Niño in the coral *Pavona clavus* (at Bahía Culebra and Islas Murciélagos, three depths) and *Gardineroseris planulata* (Islas Murciélagos, one depth) is currently investigated. Preliminary results suggest that seasonal average amplitude of the δ^{18}O records of both species, follows the seasonal changes in surface seawater temperature accurately. However, mean δ^{18}O, during the peak of the 1997-98 El Niño, was highly inconsistent between colonies, depths, localities and the two studied species. We believe that the attenuated δ^{18}O signal corresponding to the highest El Niño warming (between March and November1997) indicates that the coral growth has diminished. Mean δ^{13}C, and its seasonal amplitude, were different between all colonies and depths, though it tends to be slightly more constant at 12 m depth and in colonies collected at the Islas Murciélagos. Monthly δ^{18}O values from six colonies were strongly correlated with seawater temperature (7 m depth), sunlight, wind speed, and rainfall. These preliminary results indicate that *P. clavus* from the study area may be a reliable surrogate of environmental conditions, and hence may render the study of past climate variations possible.

ZUSAMMENFASSUNG

AUSWIRKUNGEN KLIMATISCHER ERWÄRMUNGSPHASEN AUF KORALLENRIFFE IN COSTA RICA (MITTELAMERIKA) ZWISCHEN 1991-2001

Die vorliegende Arbeit dokumentiert und analysiert das Bleichen und Absterben von Steinkorallen sowie deren Wiederbesiedlung während dreier Phasen erhöter Wassertemperatur in den Jahren 1991-2001 an der pazifischen und karibischen Küste von Costa Rica. Die Untersuchungsgebiete (sechs im Pazifik und zwei in der Karibik) sind gekennzeichnet durch eine hohe Korallendichte, das Vorkommen seltener Arten und eine komplexe Riffmorphologie. Der Zustand der Korallengemeinschaften verschlechtert sich zusehends durch eine Kombination natürlicher und antropogener Störungen. Um die Auswirkungen der Warmphasen zu untersuchen wurden zunächst Riffe entlang der Küste aus dem Flugzeug geortet und anschliessend mit ‚rapid-assessment'-Methoden in situ auf Veränderungen unter-sucht. Das Verhältnis von gesunden zu geschädigten Korallen wurde mit Transekt-Methoden quantifiziert, die prozentuale Korallen-Bedeckung ermittelt und über die Jahre verfolgt. Einzelne Kolonien wurden markiert und über den gesamten Verlauf der Warmphase beobachtet, um die individuellen Reaktionen der Korallen auf den Temperaturstress zu verfolgen. Der Verlauf der Wassertemperatur, der Sonnenscheindauer sowie des Süßwassereintrages durch Niederschläge wurde gemessen und Satellitenaufzeichnungen der Meeresoberflächentemperatur (1982-2001) ergänzt.

Zwischen 1982-2001 beeinträchtigten vier El Niño-Phasen die Korallenriffe an der Pazifikküste Costa Ricas und 1995 schädigte eine außerordentliche Wassererwärmung die Korallenriffe längs der karibischen Küste Costa Ricas. Die pazifischen Warmphasen gehen dabei für gewöhnlich den karibischen voraus oder fallen mit ihnen zusammen. Während aller Ereignisse des Massenbleichens von Korallen in Costa Rica (1982-2001), herrschten extrem lang anhaltende Phasen von hoher Sonneneinstrahlung, Windstille und klare Sichtverhältnisse unter Wasser vor (‚Doldrums'-Wetterlage). Dies legt die Vermutung nahe, dass Umweltfaktoren und Korallenbleichen sehr viel enger zusammenhängen als bisher vermutet wurde. Die untersuchten Arten blichen unterschiedlich stark aus und zeigten eine unterschiedliche Regenerationsfähigkeit. Das Bleichen einer Art erfolgte nachweislich durch die Verringerung der Zooxanthellendichte und nicht durch eine Abnahme der zellspezifischen Pigmentdichte. Die Sterberate ganzer Kolonien (ca. 6%) sowie der Bedeckungsgrad mit Korallen (35%) waren während der Warmphasen relativ niedrig, was insbesondere für den sehr starken und lang anhaltenden 1997-98 El Niño

erstaunlich ist. Es waren auch nicht unbedingt die stärksten Erwärmungen, die die höchste Korallensterblichkeit zur Folge hatten. Daraus folgt, dass andere Gründe, wie z.B. die Existenz verschiedene hitzetoleranter Korallen-Genotypen oder Zooxanthellen-Stämme oder lokale Strömungsverhältnisse eine Rolle spielen. Meine Ergebnisse zeigen, dass Korallen sehr vielfältig und dynamisch auf Erwärmungsereignisse, wie den El Niño, reagieren und hierbei die Wechselwirkung verschiedener Faktoren, wie die innerartliche Variabilität und die Standortbezogenen Umweltbedingungen eine bedeutende Rolle spielen, die eine Verallgemeinerung der Kausalzusammenhängen verbieten. Außerdem konnte ich nachweisen, dass Warmphasen sogar Fortpflanzung, Aufwuchs und Wachstumsraten positiv beeinflussen können. Daher muß die verbreitete Auffassung, dass El-Niño Ereignisse grundsätzlich verheerende Auswirkungen auf Korallenbestände haben revidiert werden. Andererseits betätigen meine Untersuchungen, dass Massen-Bleich-Ereignisse Korallenriffe zerstören können-insbesondere, wenn man davon ausgehen muß, dass El-Niños zunehmend häufiger und stärker werden.

Die Verteilung stabiler Isotopen (δ^{13}C and δ^{18}O) im Kalkgerüst der Korallen *Pavona clavus* (at Bahía Culebra and Islas Murciélagos) und *Gardineroseris planulata* (Islas Murciélagos) während des 1997-98 El Niño werden zur Zeit analysiert. Erste, vorläufige Ergebnisse zeigen, dass die jahreszeitlich schwankende Durchschnittsamplitude des δ^{18}O-Gehaltes beider Arten sehr schön den Schwankungen der Oberflächentemperatur folgt. Andererseits wies der durchschnittliche δ^{18}O-Gehalt während des Höhepunktes des 1997-98 El Niño-Ereignisses hohe Schwankungen zwischen Kolonien, Wassertiefen, Standorten und den beiden untersuchten Arten auf. Meines Erachtens bedeutet das verminderte δ^{18}O-Signal während der höhesten El Niño Erwärmung (zwischen März und November 1997) nahezu eine Unterbrechung des Korallenwachstums. Der durchschnittliche Gehalt an δ^{13}C und seine saisonale Schwankung unterschieden sich zwischen allen Kolonien und Tiefen, wobei dieser Wert in 12 m Tiefe, sowie in Proben von der Islas Murciélagos generell konstanter war. Monatliche δ^{18}O-Werte von sechs Kolonien waren stark mit der Wassertemperatur (in 7m Tiefe), der Sonneneinstrahlung, der Windgeschwindigkeit und dem Niederschlag korreliert. Diese Ergebnisse lassen vermuten, dass *P. clavus* ein zuverlässiger Indikator für die vorherrschenden Umweltbedingungen im Untersuchungsgebiet ist und damit die Untersuchung weiter zurückliegender Klimaveränderungen ermöglicht.

ACKNOWLEDGEMENTS

The story presented in this thesis, is the product of a long process whose prelude was in March 1982. During my first SCUBA diving experience, one grey and rainy afternoon at the Caribbean coast of Costa Rica, I saw how the octocorals performed a primeval dance, slowly fanning the arrogance of huge, massive brain and star corals, in consortium with the stylish elkhorn and staghorn corals. A multicolored entourage of other smaller coral members flattered the gargantuan brutes by emerging in a solemn petrified pomp. Very different was the spectacle that I witnessed in mid 1983, during the first dive of a weeklong diving-safari to the same reef. The dive was performed under a magnificent blue sky and in clear, warm (too warm) waters. Almost immediately, I noticed that the former vibrant and multicolored coral assemblage was different and looked strange to me. Many huge massive corals were splattered by white or pale brown patches. Some colonies were entirely white. Others green, because algae started to colonize the colonies' dead surfaces. I remember how the clean white finger corals looked as if they were porcelain figures attached to the bottom. All the immersions that we did in shallow waters were an unpleasant experience due to the high seawater temperature. To the naive observer that I was, the uncanny spectacle was a mere curiosity. It was as if it had snowed on top of the corals, while the water temperature was like in a bath tub. Obviously, something wrong was happening, but I was unaware of what was causing these changes in the coral colors. Three months later, in October 1983, during my last visit of that year to the Caribbean reefs, I saw how the colors that originally captured my attention started to show again, mainly because the white and pale tonalities receded. The water was significantly cooler than during the previous visits and diving was again enjoyable. It was unknown to me that the waning of the catastrophic 1982-83 El Niño episode had begun.

Since then, I have been allured by the study of how coral reef communities fare during El Niño protean swings of mood. During my evolution in the process of learning and studying the subject, many colleagues, friends and institutions have provided advice, support, feedback and all kinds of unconventional help. For the planning and accomplishment of this doctoral thesis, I was very lucky to have met Matthias Wolff, who, with his overwhelming pragmatism and expertise on the El Niño, every time provided the proper advise and the strategy to follow. I really thank you Matthias, also for always having (or making) the time to discuss with me and for never losing your smile or enthusiasm no matter how complicated the situation was.

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In Costa Rica, I have to thank Alberto León “Beto”. (He instructed me on that very first dive in 1982.) You have always been the omnipresent friend during the lean seasons and during the years of plenty. There are still many reef islands and Little Ice Ages to unveil. Gracias Beto. I also have to acknowledge the support given by Eleazar Ruíz “Gaspa”, who, in 1994, unconditionally decided to come onboard to join me in the coral reef adventure. Another stowaway was Carlos “Buzo” Gamboa. Thanks to both of you.

And you Fernando, eternal poet of forgotten forests, mystical seas, and primeval creatures, your stories are still remembered by the stars captured in the morning dew. Forever yours is the sea, where corals dream of the fire and the blood of sunsets. Your death is a dream that you would not remember.

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1 INTRODUCTION

The end of the twentieth century was marked by the most dramatic bleaching and subsequent mortality of corals ever recorded. From summer 1997 to autumn 1998, thousands of reefs in the Indian and Pacific Ocean, and the Caribbean, NW Mediterranean and Red Sea were affected to a different extents (ISRS 1998, Metalpa et al. 2000, Wilkinson 2000a, b). Some reefs, unscathed by previous bleaching events, bleached extensively, and their recovery from the concomitant loss of coral cover will take several decades in the most optimistic scenarios (Wilkinson et al. 1999). Coral reefs in Belize, for example, have probably never suffered bleaching and mortality comparable to the 1997-98 event at least over the last 3,000 years (Aronson et al. 2000).

Unprecedented as well was the scientific coverage of the exceptionally strong increase of sea temperature, which was directly or indirectly liable for the mega-bleaching event. This warm episode, El Niño 1997-98, is considered the strongest on record by some measures (McPhaden 1999a, b, Enfield 2001). The warming became apparent in early spring 1997 and lasted until autumn 1998, abruptly interrupted by a drop in temperature signaling the onset of the 1999-2000 La Niña episode. Localized coral mortality was last recorded in spring 1999 (Wilkinson et al. 1999).

The 1997-98 bleaching event gave us a measure for the effects that natural disturbances can have upon the world’s coral reef communities. Corals have adapted and evolved within a wide range of disturbances on the geological and ecological time scales (Pandolfi and Jackson 1997, Greenstein et al. 1998). What seems to be new to the corals, and certainly to the scientific community, is the scale and frequency at which bleaching and warming episodes (e.g. El Niño) have occurred since the 1970s (Glynn 1996, Hoegh-Gouldberg 1999, Trenberth and Stepaniak 2001, Tudhope et al. 2001).

In this section, the oceanographic and meteorological framework of the El Niño, La Niña, the Southern Oscillation and some responses of the marine communities to the warming events, as well as the essence of coral bleaching will be reviewed.

1.1 *EL NIÑO, LA NIÑA AND THE SOUTHERN OSCILLATION*

El Niño is the consequence of complex ocean-atmosphere interactions that spawn a general warming in superficial water of the tropical eastern Pacific. The name originally referred to the warm current that flows south of the Ecuador and Peruvian coast in late December to early January and it is accompanied by torrential rains. The arrival time is around Christmas and epiphany, and the name celebrates the birth of the Christ Child. The term was first mentioned in technical reports during the late nineteenth century (Carranza 1891, Eguiguren 1894, Carillo 1892). There is no written mention in colonial testifying to any earlier use of the term (Caviedes 2001).

For about the last 40 years, it has been known that the South American El Niño warming is actually a regional manifestation of an ocean-atmosphere complex interaction on large scale (Bjerknes 1966a, b). During El Niño, a general warming in superficial water of the tropical eastern Pacific is initiated and is characterized by strong perturbations in the currents and thermal stratification of the water masses (Endfield 1981, Philander 1989). These changes in circulation of the sea are prompted by alternating wind systems blowing above it, the Southern Oscillation (SO), which is considered the atmospheric counterpart to El Niño (Philander 1990). The SO was early recognized as a seesaw-like interannual variation of barometric pressures (Walker 1923, Walker and Bliss 1932). Originally, the SO was described with pressure records from Darwin (Australia) and Santiago (Chile); nowadays the records from Darwin/Djakarta and Tahiti are used.

Basically, the SO consists of a low atmospheric pressure cell in the vast Indonesian region that is inversely correlated with the high pressure cell in the southeast Pacific (Fig. 1), setting the transport of air masses from the subsidence regions (high pressure) to the convective regions (low pressure) (Fig. 2a). This equatorial transport of air masses from east to west is known as the Walker circulation (Bjerknes 1969). The system is fed back by the presence of cool surface waters resulting from the divergence of surface water by the easterly Trade Winds. There is little evaporation from these cool waters and little transfer of caloric energy from ocean to atmosphere; such conditions promote long lasting droughts in areas near the Peruvian coast (Merriman 1955, Enfield 1981, Caviedes 2001). In this phase of the SO, the upwelling and the westward transport of superficial water are intensified. While the thermocline is brought up in the east, it is

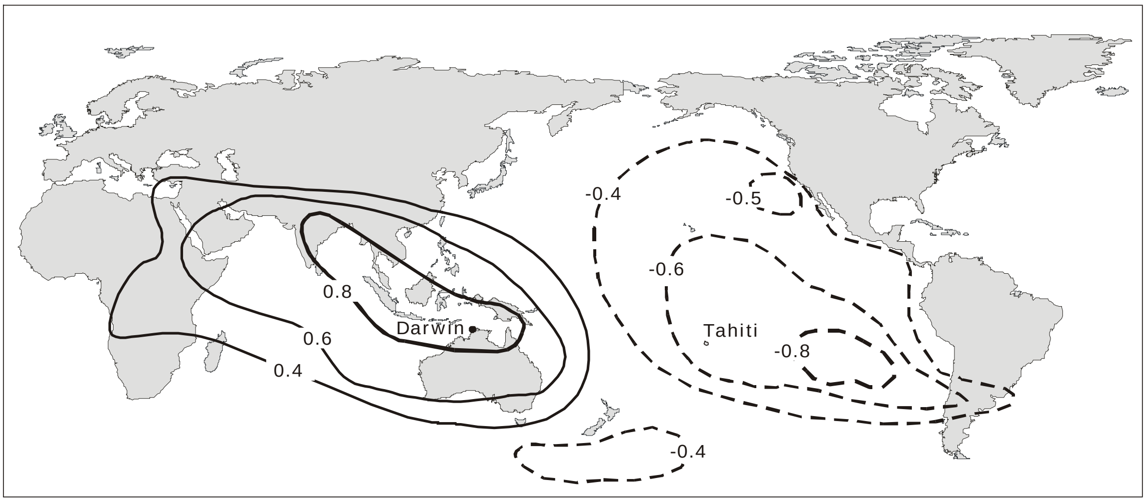

Figure 1 The two components of the Southern Oscillation (SO). Solid lines show positive correlations or air pressures with Darwin/Djakarta in the eastern extreme of the SO. Broken lines show negative correlations with Tahiti in the western extreme (i.e. if the pressure is high at Darwin/Djakarta, it is low at Tahiti or Eastern Island and vice versa). Redrawn from Rasmusson (1984), Glantz (2001), and Caviedes (2001).

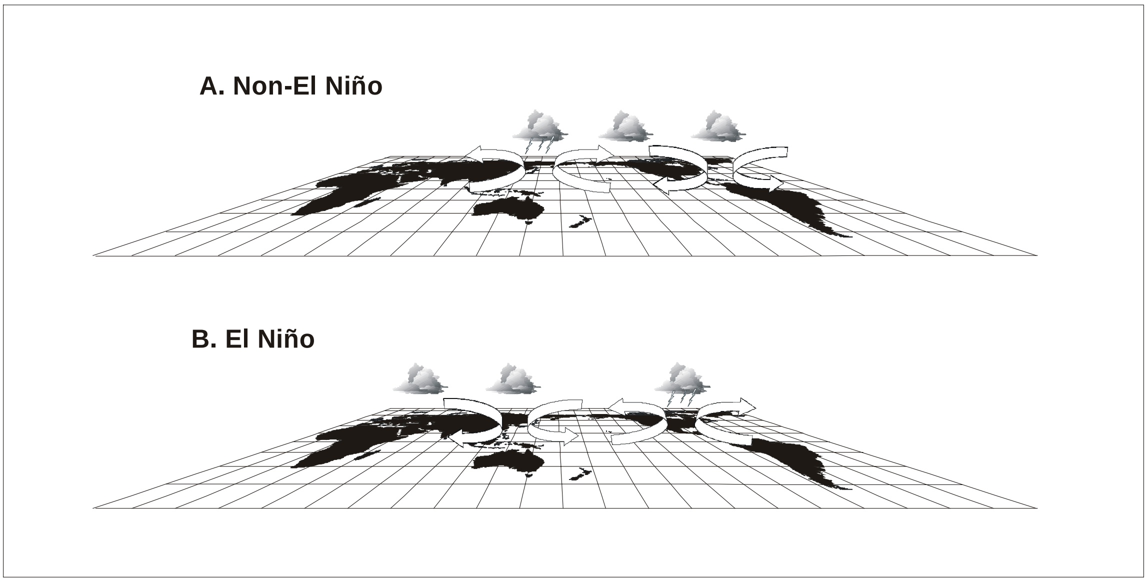

Figure 2 Walker circulation during non-El Niño (A) and El Niño (B) stages. Arrows show the predominant flow directions of the air masses along the equatorial Pacific. Torrential downpours are indicated by the clouds and lines. Based on Cavides (2001).

deepened in the western Pacific as warm water accumulates transferring water vapor to the atmosphere.

When the cell system is reversed (Fig. 2b) by a sudden collapse (or slackening) of the Trade winds, the accumulated warm water returns eastward to the central Pacific and eventually to the South American coast, causing the thermocline to be depressed (Rassmusson and Wallace 1983, McPhaden 1999a). In addition, the hot and humid air masses accompanying the warm waters and the setting of the low convective zone install torrential rains in the otherwise arid coast (Sears 1895, Merriman 1955). This is the El Niño signature in the coastal zone, where fluvial sediments evincing catastrophic floods have recorded the devastation brought by past episodes (Sandweiss et al. 1996, Rodbell et al. 1999). While this eastward phase propagation has been more common in recent El Niños (Wang 1995), previous descriptions emphasized a westward propagation of the warming, and it was regarded as the canonical El Niño episode (Rasmusson and Carpenter 1982). Currently, it is known that the warming along the Peruvian coast can precede the warming in the central Pacific, and sometimes it follows it (Trenberth and Stepaniak 2001). The horizontal advection of warm waters as a well-defined low salinity front (Picaut and Delcroix 1995), is caused by the development of Kelvin waves in the upper 100 m of the water column. However, other types of waves, such as the westward-moving Rossy waves, are known to be generated (McPhaden 1994, Fedorov and Philander 2000). Non-El Niño conditions are reassumed, when the thermocline depths begin to move eastward in response to a weakening in eastward wind speed. Coastal and equatorial upwelling begin to strengthen, as the westward winds intensify (Nicholls 1987), and the SO shifts to another phase, as the regular Walker circulation is reassumed.

Before extending further to characterize the other phase of the SO, which typifies La Niña, it is important to consider how the SO swings have been linked to the warm and cold episodes. The differences between the centers of the SO pressure system (Tahiti minus Darwin) have been expressed into an index, the Southern Oscillation Index (SOI) (Fig. 3). Berlage (1957) was the first one to note a strong correlation between SOI anomalies and the sea surface temperatures (SST) in Perú, and a low phase coinciding with El Niños. A high (positive) SOI implies a predominance of easterly winds and cooler conditions in the Pacific (La Niña), while a low (negative) SOI means a weakening or absence of the easterlies torrential downpours at the Peruvian coast and warm ocean waters (El Niño).

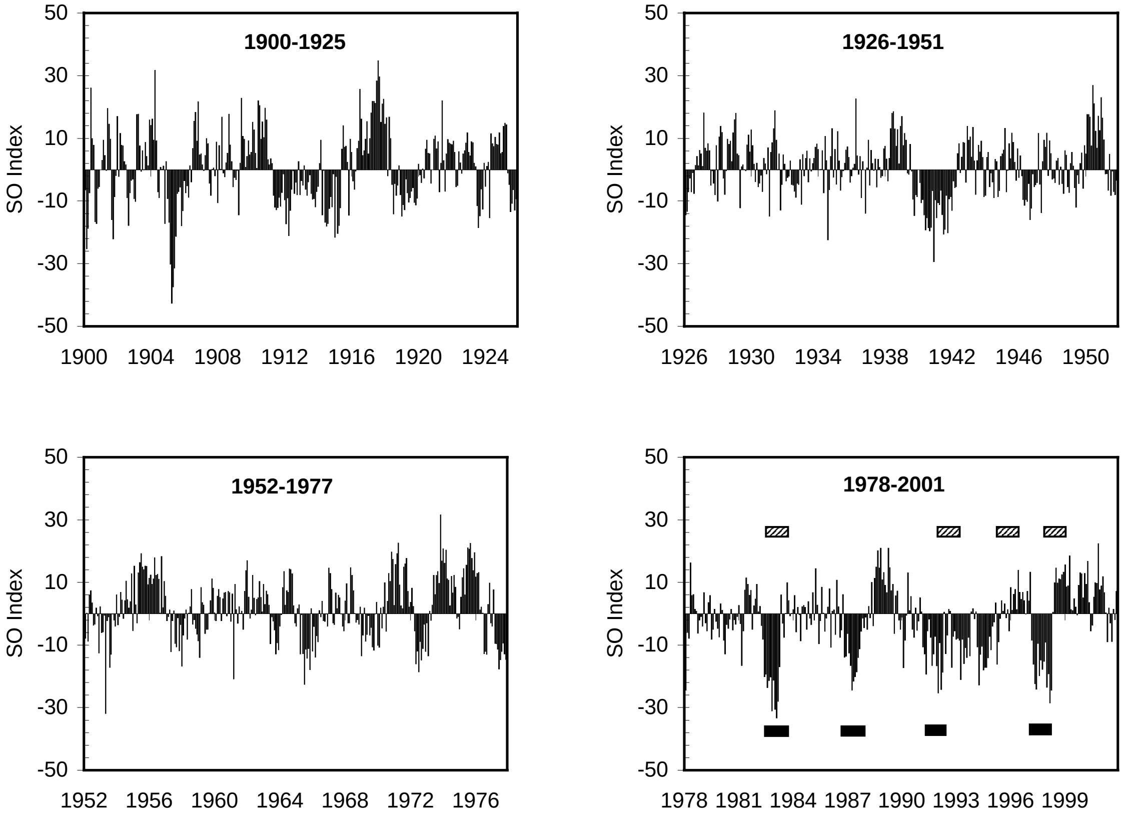

Figure 3 Monthly averages of the Southern Oscillation Index (SOI), 1990-2001. The SOI indicates the difference of sea level pressure (Tahiti minus Darwin). Major bleaching events in Costa Rica are indicated by black (Pacific coast) and stripped (Caribbean coast) horizontal bars. Averages obtained from the Bureau of Meteorology, Australia (www.bom.gov.au/climate/current/soihtml1).

Not all depressions in the SOI are accompanied by warming of the tropical Pacific, and only the occurrence of both constitutes a true El Niño. For example, one of the most pronounced dips of the SOI during the last century occurred in 1904-05 (Fig. 3) and was not accompanied by an El Niño (Caviedes 2001). However, it has been pointed out that depressions in the SOI are accompanied by conditions similar to El Niño, even though a fully developed El Niño does not occur (Bacastow et al. 1980).

Pronounced peaks in the SOI (cold phase of the SO) are related to a very strong South Pacific high pressure cell and strong, constant southeast Trade winds in the tropical Pacific. Consequently, a strengthening of the upwelling along the South American coast and the equatorial belt is observed (Caviedes 1973, Philander 1989). When these conditions prevail for several months and the SSTs are below monthly minima, further shoaling of thermocline at the Southern American coast and concomitant deepening in the western Pacific signal the onset of a La Niña episode. Before the 1997-98 El Niño and the 1998-2000 La Niña episodes, it was considered that normal years, when the El Niño was absent, included La Niña (Wyrtky 1982). Today, it is recognized as another phase of the SO and distinct from normal years.

The different evolution of each El Niño, with significant departures from the scenarios outlined before, shows the complexity of the interacting processes influencing the SO and El Niño. It is not known whether these departures are due to intrinsic properties of the warming itself, or to the ongoing climate change (Fedorov and Philander 2000, Cole 2001, Trenberth and Stepaniak 2001).

Since when have El Niño episodes been occurring? It is highly probable that the proper oceanographic and atmospheric conditions needed for the initiation of major El Niño episodes started at the time of the closure of the Central American seaway. There is evidence of a steady circulation of warm water from east to west and vice versa before the closure (Colgan 1990, Marincovich 2000), precluding El Niño-like events. With the seaway interrupted, the particular circulation patterns of the Pacific Ocean, and the physical conditions necessary for an El Niño, were initiated (Colgan 1990, Smolka 1991). However, there is a strong debate on the veracity of early Holocene episodes of El Niño, as evinced by flood sediments and shell middens (Sandweiss et al. 1996, 2001, DeVries et al. 1997, Rodbell et al. 1999).

The El Niño-related weather disturbances outlined above have direct and indirect consequences for different ecosystems, ranging from sea-bottom dwelling communities to tropical rain forests (Tarazona et al. 1996, Pounds et al. 1999). It is futile to attempt to pin point which ecosystem undergoes the most dramatic changes due to El Niño episodes, as it is frequently done in the media. For example, how can one gauge which is more detrimental to the environment: whether the millions of hectares of forest lost due to fires during El Niño-related droughts (Siegert et al. 2001), or the virtual elimination of coral formations in some areas of the eastern and Indo Pacific (Reaka-Kudla et al. 1996, Wilkinson 2000a)? The temporal scale of those changes is seldom considered, i.e. weeks vs. decades, either reversals in the net result of the disturbance (positive to negative and vice versa), or the disastrous synergistic effects of El Niño when combined with certain human activities such as logging (Curran et al. 1999).

With the exception of stunning greening and flowering of desert plains, and dramatic crop failures and droughts in the eastern Pacific regions influenced by El Niño (Caviedes 1973, 1975, Dillon and Rundel 1990, Arntz and Fahrbach 1991), few other terrestrial effects of the warming episodes were thoroughly studied before the 1990s. However, a recent published review (Holmgren at al. 2001) indicates that the El Niño effects are currently investigated on plant and animal populations from a wide range of terrestrial environments. The best documented effects of El Niño on ecosystems are those in marine habitats. It was the devastation wrought by El Niño 1972-73 upon the coastal ecosystems of South America, the first comprehensive and regional-scale documentation of El Niño-related population fluctuations, and changes in the community structure of organisms (Caviedes 2001). When the next very strong El Niño episode of 1982-83 struck the marine ecosystems, a multifarious group of scientists was ready to document the fate of a wide range of marine and terrestrial environments, together with the physical and oceanographical evolution of the event. [See Glynn (1990), and Arntz and Fahrbach (1991) for comprehensive reviews of the ecological consequences of the 1982-83 El Niño.]

The catastrophic declines of seabirds, marine mammals, commercially targeted fish species, and mass bleaching and mortality of reef corals, are all negative consequences considered to epitomize El Niño (e.g. Glantz 2001). Even though these negative impacts seem to be accompanying features of the most violent El Niño episodes, there are, however, other effects which are less publicized and can be regarded as positive, at least, for some organisms. For example, diversity and biomass of macrobenthic invertebrates in Peruvian waters showed significant positive fluctuations in response to an increase in dissolved oxygen during the 1982-83 and 1991-92 El Niño episodes (Tarazona et al. 1988, 1996). At Ecuador and Colombia, several crustacean species multiplied in large numbers and expanded their distribution to Perú and Chile, during the 1972-73 and 1982-83 episodes (Arntz and Fahrbach 1991, Caviedes 2001).

One of the best documented positive El Niño effects on marine invertebrates is the explosive population growth experienced by the Pacific scallop (*Argopecten purpuratus*) in Perú, and, to a lesser extent, in Chile (Wolff and Mendo 2001). During the1982-83 El Niño, an increase in *A. purpuratus* population biomass from 100 metric tons to ~30,000 metric tons within a few months was documented in Independence Bay, southern Perú (Wolff 1985). Such a spectacular proliferation, favored by El Niño conditions, is thought to be the result of several factor which include: (1) enhanced growth rates; (2) shorter larval phase and concomitant mortality; (3) increase of mortalities of the scallop predators; (4) increase of reproduction and recruitment; and (5) lessening of competition pressure from other filter feeders (Wolff and Wolff 1983, Wolff 1987, Wolff and Mendo 2001). Although scallop fishing in the area of Independence Bay is practiced regularly, it is during El Niño years that harvest of this species reaches unprecedented levels. The 1982-83 El Niño-associated bonanza resulted in the construction of several processing plants (Wolff 1987). During the 1997-98 warming episode, *A. purpuratus* population growth was again intensified, but the harvest was significantly lower (Wolff and Mendo 2001). The extraction of non-reproductive juveniles, together with an increase of the fishing fleet up to an order of magnitude, soon led to the depletion of the banks and collapse of the fisheries (Wolff and Mendo 2001). Finally, the presence of ancient shell middens (some ~4000 years old) along the Peruvian coast, where distinct strata of *A. purpuratus* are intercalated with others of mollusks species that thrive and dominate during non-El Niño conditions, suggests that similar *A. purpuratus* enormous population explosions were common during past El Niños (Arntz and Farbach 1991, M. Wolff pers. comm. 2001). Certainly, the ancient coastal inhabitants benefited of the positive effect of El Niño on the scallop populations, as it is observed today.

1.2 CORAL BLEACHING

The term “bleaching” was originally coined by Vaughan (1911) to describe the condition of the upper surfaces of massive coral colonies periodically exposed during low tides. He pointed out that on the bleached colonies, the rapid tissue death and decay resulted in areas of bare white skeleton. Yonge and Nicholls (1931) also described the change of color, i.e. paling, resulting from experimental changes of light and food. Today, the term is used to describe the loss of color in corals and other symbiotic reef invertebrates that harbor autotrophic dinoflagellates (zooxanthellae) within their endodermal cells (Williams and Bunkley-Williams 1990, Glynn 1993, 1996, Brown 1997a, b, Hoegh-Guldberg 1999, Fitt et al. 2001).

The symbiosis between scleractinian corals and the zooxanthellae has endured ca. 210 million years, since the late Triassic (Stanley and Swart 1995), and has facilitated reef building by enhancing coral calcification (Barnes and Chalker 1990) and providing photosynthetically fixed carbon to the host (Muscatine 1990, Muller-Parker and D'Elia 1997). The algal-coral partnership seems to be complex and mutable in the light of the new findings of several symbiont clades in some coral host (Rowan 1991, Rowan et al. 1997, Glynn et al. 2001, Kinzie et al. 2001). Several clades can be differently distributed in a single coral colony in response to microscale environmental conditions (Rowan et al. 1997). This new perspective, of a more dynamic and complex relationship between the coral host and the zooxanthellae, departs significantly from the original conception of one single algal species for the cnidarians (Taylor 1974), and has given rise to the Adaptive Bleaching Hypothesis (Buddemeier and Fautin 1993). It posits that different algal partners within the coral host can shift in spatial and temporal scales, resulting in partnership complexes of many combinations. Under certain environmental conditions, warming events for example, some combinations will prove more functional than others, and the symbiotic partnership will respond by changing the algal guild composition. The implications of this hypothesis are very important due to the recurrent bleaching events witnessed during the last 20 years. For example, during the 1997-98 El Niño, corals hosting a determinate algal clade were more resistant to bleaching than others with another clade (Glynn et al. 2001). What will be crucial to document in situ, after a mass bleaching event, is the acquisition, by bleached corals, of more thermally resistant algal clades and the subsequent substitution of the guild.

The coral bleaching itself is commonly referred to as the reduction in the density and/or pigment content of the symbiotic zooxanthellae (Coles and Jokiel 1978, Hoegh-Guldberg and Smith 1989). However, mass bleaching has never been reported as solely due to the loss of photosynthetic pigments (Hoegh-Guldberg 1999), as sometimes occur under extreme experimental conditions (e.g. Lesser 1996). The mechanism of zooxanthellae loss are still not well identified and most probably there are different scenarios depending on the nature and intensity of the disturbance, and the host itself. Nevertheless, several bleaching mechanisms have been reported such as the discharge of entire zooxanthellae into the host coelenteron (Gates et al. 1992, Ralph et al. 2001), degradation of the symbionts in situ (Brown et al. 1994), release of entire coral endodermal cells containing zooxanthellae (Brown et al. 1994, Le Tissier and Brown

1996), and necrosis of coral tissue with subsequent algal degeneration (Glynn et al. 1985).

The physiological responses of the zooxanthellae and the coral to bleaching vary significantly and some are species-specific. Damages to the photosynthetic mechanisms of the zooxanthellae are known to be caused by bleaching at high temperatures and /or solar irradiance (Iglesias-Prieto and Trench 1994, Fitt and Warner 1995, Brown 1997a, Hoegh-Gouldberg 1999, Hoegh-Gouldberg and Jones 1999), irreversibly impairing the photosynthetic activity of the symbionts. However, Ralph et al. (2001) found photosynthetically active zooxanthellae after been expulsed during experimentally induced bleaching. Bleached corals, on the other hand, experience reduced skeletal growth (Goreau and MacFarlane 1990, Vargas-Ángel et al. 2001), reproductive failures (Glynn and D'Croz 1990, Ward et al. 1999), decreased capacity to repair tissue damage (Mascarelli and Bunkley-Williams 1999), and an increased susceptibility to diseases (Glynn 1993, Kushmaro et al. 1996, Goreau et al. 1998).

These relatively non-lethal responses of corals to bleaching mentioned above, seem to be species-specific and can also be determined by the intensity of the bleaching, and the nature of the stressor that originally caused it. For example, while preying on reef fish, sharks can break coral colonies and disturb several square meters of reef (Jiménez 1996), and the affected colonies show localized bleaching at the broken branches. Earthquakes can destroy thousands square meters of reef formations (Cortés et al. 1992, Jiménez and Cortés 1994), and the surviving corals bleached extensively. Localized bleaching was also observed during low salinity conditions (Goreau 1964), low water temperature (Glynn and D'Croz 1990, Jiménez 2001a), extreme low tidal exposures (Glynn 1976), and increased solar radiation and/or water temperature (Williams and Bunkey-Williams 1990, Glynn 1993, Brown et al. 1994, 2000). These examples are from specific factors which may trigger coral bleaching, which, in turn, may affect only individual colonies or limited sections of the reef (e.g. shallow flats), or at least, some reefs within particular regions.

Mass bleaching events, on the contrary, affect many coral species from wide geographical regions (thousands of kilometers), and can last from one to two years (Williams and Bunkey-Williams 1990). Events of such magnitude have been only recently reported, with the first observation being in 1979 (Coffroth et al. 1990). Since that date, over 70 major coral bleaching events have been documented (Glynn 1984, 1990, 1993, 1996, Coffroth et al. 1990, Williams and Bunkey-Williams 1990, Brown 1997a, Hoegh-Gouldberg 1999). This is unprecedented in the scientific community, since the 1960s and 1970s were years of active coral reef research and no major bleaching was observed. Furthermore, not even underwater film makers, who worked extensively during those years, recorded any major coral bleaching (Hoegh-Gouldberg 1999). The absence of observations suggest that the increased bleaching frequency observed since the early 1980s is genuine, though it can also be the result of an increase in the number of observers (Glynn 1993, 1996). But the 1970s also landmark a general change in the world's climate and the occurrence of El Niño episodes (Timmermann et al. 1999, Cole 2001, Trenberth and Stepaniak 2001, Tudhope et al. 2001). This is highly suggestive of a link between the frequency of bleaching events and the global warming, particularly due to the strong correlation between mass bleaching and high sea temperatures (Glynn 1993, 1996, Goreau and Hayes 1994). If that turns out to be true, a grim scenario for coral reef communities can be drawn, where all the sub-lethal effects of bleaching will be more common and coral mortality will increase. Furthermore, prognosis of changes in the atmospheric CO_2 concentrations suggests significant alterations of the acidity of the oceans and in consequence, a decrease in the calcification rate of corals and other organisms (Gattuso et al. 1999). Kleypas et al. (2001) argue quite convincingly that this reduction in calcification has already begun.

Finally, bleaching is regarded as a sign of stress, and the accompanying changes in the coral coloration are convenient indicators for a researcher. But as Fitt et al. (2001) have noted, loss of algal symbionts may have occurred weeks to months before the human eye detects any signal, suggesting that bleaching as an indicator of stress limits (e.g. temperature) is not an appropriate parameter. Nevertheless, in particular situations, unequivocal bleaching responses are triggered in a short period of time after the abnormal conditions begin, such as the warming events studied in this thesis, and the start of the bleaching event can be match to the disturbance evolution. This is facilitated by the constant monitoring of reefs and their physical environment, which together with further field and experimental studies, will improve the understanding of the causal factors of coral bleaching.

2 FOCUS OF THIS THESIS

Documenting the trajectory of coral reef communities in the course of disturbances such as the 1997-98 warming event, and the disturbances history as well, improves our understanding of coral resilience and recovery dynamics. This is important due to the heralded global warming scenario with more frequent and stronger El Niño episodes (Timmermann et al. 1999). This thesis documents coral bleaching, mortality and recovery in a time period (1991-2001) when three warming events affected coral reef communities in the Pacific and Caribbean coast of Costa Rica. Additionally, changes in skeletal stable isotope composition ($\delta^{18}O$ and $\delta^{13}C$) of the coral *Pavona clavus*, related to El Niño 1997-98, are currently investigated.

Our working hypotheses, derived from our previous research in the 1980s, were:

- Coral reef communities responses to warming events affecting Costa Rica (1991-2001) are different, and dependent on the species assemblage, physical environment (Caribbean vs. Pacific), and local-specific evolution of the warming.
- Coral reef communities recovery, as expressed by the total percentage of live tissue, is highly dependent on environmental factors affecting the corals (e.g. sedimentation, pollution, seasonal upwelling), the species composition and the growth rates of the coral.
- Individual coral colonies show different responses to the warming events, and they are evinced in the susceptibility to bleach, to recover (tissue damage repair), in the coral symbionts densities, and in the variability in stable isotope composition (oxygen and carbon) of the skeleton.
- Seasonal variations in skeletal stable isotopes ($\delta^{18}O$ and $\delta^{13}C$) of the coral *Pavona clavus* are attributed to environmental conditions during the time of calcification.

3 MATERIALS AND METHODS

3.1 SELECTION OF THE STUDY SITES

The Pacific and Caribbean coast of Costa Rica have been visited on a regular basis in order to gather information on the distribution and abundance of coral reef communities. Surveillance of the littoral is done by low-altitude flights in order to photograph potential study sites, which are later ground-checked by SCUBA, snorkeling, and Manta Tows. The latter implies towing from a boat one or two divers who make observations of the coral communities. As a result, eight localities (Fig. 4) were chosen to follow the fate of corals during heralded warming events. They are distributed within the upwelling area of Golfo de Papagayo, and the more thermally stable waters of the central Pacific coast and Golfo Dulce, and in the southern Caribbean coast of the country.

3.2 CORAL REEF COMMUNITIES IN THE STUDY SITES

In this section, the most important characteristics of the study sites are summarized. More detail information about the Costa Rican Pacific and Caribbean coral reef communities is presented in Cortés and Jiménez (2002a, b).

3.2.1 GOLFO DE PAPAGAYO

Located in the least rainy region of the country, Golfo de Papagayo (Fig. 4) harbors important coral reef communities consisting of 17 species of reef-building corals (Cortés and Jiménez 2002a, Jiménez 2001a). Reefs constructed by massive corals such as *Pavona clavus*, *Pavona gigantea* and *Gardineroseris planulata* are found at Islas Murciélagos and Bahía Culebra. Unique to this area, is the presence of a small population of the free-living mushroom coral *Fungia* (*Cycloseris*) *curvata* and a rare *Leptoseris papyracea* patch reef. This is the only known population of *F. curvata* in Costa Rica and the only live stand *of L. papyracea* in the eastern Pacific region (Jiménez 1997, 2001a). Branching corals (*Pocillopora* spp.) are also important reef builders in the area. Certainly, the seasonal upwelling of Papagayo and the concomitant increase in dissolved nutrients and planctonic organisms in the water are important factors influencing coral community structure on the physiological and ecological level. For instance, reef frameworks structurally built by *P. clavus* and *P. gigantea* are found at depths (>10 m) were temperature can be below 14°C for several hours during major upwelling episodes (Jiménez 2001b). In contrast, *Porites lobata*, a species less tolerant

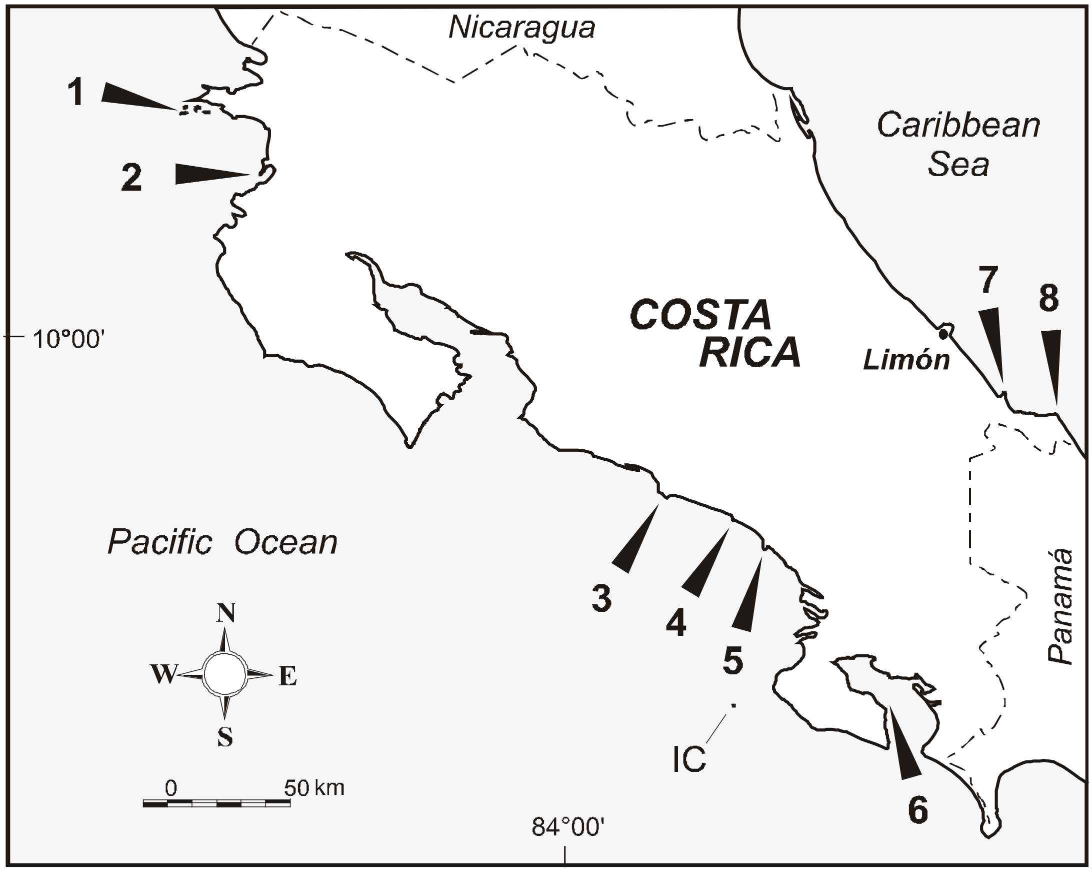

Figure 4 Location of the coral bleaching study sites on the Pacific and Caribbean coast of Costa Rica distributed in four regions: Golfo de Papagayo (1. Islas Murciélagos, 2. Bahía Culebra), Central Pacific (3. Parque Nacional Manuel Antonio, 4. Punta Cambutal, 5. Parque Nacional Marino Ballena), Golfo Dulce (6. Sándalo), and Southern Caribbean (7. Parque Nacional Cahuita, 8. Refugio Nacional de Vida Silvestre Gandoca-Manzanillo). Also mentioned in the text: Limón, and Isla del Caño (IC). Bleaching in the Pacific coast corresponded to the El Niño episodes of 1991-92 (weak) and 1997-98 (by some accounts the strongest of the 20th century). The 1995-96 warming at the Caribbean was not directly associated to any major El Niño.

to low water temperature, is dominant in the warmer waters off the central and south sections of the coast (Cortés and Jiménez 2002a). Additionally, growth rates of three species, that have been studied elsewhere in the eastern Pacific, are highest at Papagayo and this may be the result of increased heterotrophic feeding during the upwelling season (Jiménez and Cortés 2002). Threats to the coral reef communities of the Papagayo area are the building of coastal infrastructure, uncontrolled tourism activities and coral extraction for the curio trade (Cortés and Jiménez 2002a).

3.2.2 CENTRAL PACIFIC COAST

Relatively few coral communities are found in the central section of the Costa Rican Pacific coast (Fig. 4), and this is mainly due to high runoff and sediment loads from rivers, and abundant high-energy sandy beaches. Several large rocky outcrops sustain most of the reef communities, where nine species of reef-building corals have been reported (Cortés and Guzmán 1998). Coral reef communities consist mainly of *P. lobata*, some *Pavona* spp. and few pocilloporid corals. Two of the studied localities (Manuel Antonio and Ballena, Fig. 4) are National Parks and our research there (Jiménez and Cortés 2001, 2002, Cortés and Jiménez 2002a) is the first comprehensive picture of the coral reef communities of this part of the coast. During the last decade, an increase in sediment loads, associated with road constructions and deforestation of the watersheds, have affected coral communities in the area.

3.2.3 GOLFO DULCE

Bordered by the Península de Osa, Golfo Dulce (Fig. 4) is an interesting study site due to its tectonic origin and enclosed embayment with a 60 m depth sill and 200 m depth in its inner parts (Hebbeln et al. 1996). Ten species of reef-building corals have been reported for the outer and inner littorals of the Península de Osa and Golfo Dulce (Cortés and Jiménez 1996, Cortés and Guzmán 1998). The inner sections of Golfo Dulce have low coral cover (mainly *P. lobata*), while the outer sections show a marked increase in cover and diversity (Cortés 1990). The study site of Sándalo (Fig. 4) is one of the reefs with higher coral cover and diversity in the gulf (Cortés 1992). This reef has deteriorated seriously during the last ten years (Cortés and Jiménez 2002a) and, like other reef communities in Golfo Dulce, live cover and growth have been reduced as a result of recent terrigenous sedimentation, since the area has been extensively deforested (Cortés 1990, Cortés et al. 1996, pers. obs.).

3.2.4 SOUTHERN CARIBBEAN COAST

The most diverse and structurally complex coral reefs of the country are found at the Caribbean coast. Fringing and patch reefs, carbonate banks and algal ridges have been recognized (Cortés and Jiménez 2002b). More than 40 species are known for shallow areas and the exploration of deep offshore reefal environs will increase these number (Jiménez and Cortés in prep.). One of the study sites (Parque Nacional Cahuita, Fig. 4) is the largest fringing reef of the country, with well-developed spurs and grooves dominated by massive (*Siderastrea siderea*, *Diploria* spp., *Montastraea* spp.), foliaceous (*Agaricia* spp.) and branching (*Acropora palmata*, *Porites* spp.) corals intermingled with hydrocorals (*Millepora* spp.). These species are also present at the second study site (Refugio Nacional de Vida Silestre Gandoca-Manzanillo, Fig. 4), though reef complexity in shallow waters is less remarkable than in Cahuita. The deep offshore fronts of the carbonate platform of Gandoca-Manzanillo run parallel to the coast to a depth of 40 m, hosting an interesting deep-water coral communities and spectacular barrel sponges (Jiménez and Cortés in prep.). Dramatic changes in live coral cover and community structure have been observed at several reefs of the region (Cortés 1994, Cortés and Jiménez 2002b, Jiménez in prep.), and are attributed to a combination of increased terrigenous sediment influx (watershed deforestation and banana plantations), and natural disturbances. For example, mass mortality events of the sea fan *Gorgonia flabellum* and the black sea urchin *Diadema antillarum* were reported in the early 1980s (Guzmán and Cortés 1984, Murillo and Cortés 1984). In April 1991, a magnitude 7.5 earthquake uplifted the coastal zone and caused the death of ca. 5,000 m^2 of coral reefs at Cahuita (Cortés et al. 1992). A few months after the earthquake, a massive arrival of logs, debris and heavy swells during the rainy season caused high destruction in the uplifted platforms and surviving colonies in shallow waters (Jiménez and Cortés 1994). Lastly, high concentrations of heavy metal pollution of anthropogenic origin have been found in coral skeletons in the two studied sites (Guzmán and Jiménez 1992), and the mechanical properties of the skeletons seem to be different to other reefs in the area (Jiménez and Cortés 1993).

The selected coral reef communities in the present study can be considered coastal “Hot-Spots” due to their importance as coral species reservoirs, high diversity, reef structural complexity, and source (direct or indirect) of economic income to the human populations in the vicinities. Although these coral reef communities are under several management policies (e.g. National Parks, Conservation Areas), deterioration has not been deterred and this is mainly due to the combination of human activities and natural disturbances.

3.3 BLEACHING AND SEA WARMING EPISODES

Coral reef communities responses to increases in sea temperature were studied on a regional and local scale. For example, several kilometers of coast were surveyed to different depths (normally 1 to 15 m, occasionally to 30 m) at each area in order to provide an all-encompassing view of the warming event and its consequences upon the corals. This involved intensive dives with SCUBA and the previously mentioned Manta Tows. The magnitude of coral bleaching and mortality was determined by counting the proportion of affected colonies, the percentage of coral live cover, following the fate of distinct colonies, and counting symbiotic zooxanthellae and measuring chlorophyll pigments. An overview of these methods and the portrayal of the warming events will be presented in this section.

3.3.1 BLEACHING AND MORTALITY OF COLONIES

The percent of pigmented, bleached and dead coral colonies was determined at different depths by counting the number of colonies of each species in a transect (measuring tape) positioned parallel to the shore line and haphazardly across the studied sites. Transect length and width were according to the size and extension of areas occupied by corals. In the Golfo de Papagayo, a 100 m-long X 4 m-wide transect was utilized at each surveyed site. At the central Pacific coast, several 300 to 500 m X 3 m and 600 X 2.5 m transects were used. At Golfo Dulce and the Caribbean coast, coral communities were assessed in 50 m X 2 m and 150 m X 2 m transects respectively. A colony was scored bleached if more than 5% of the colony surface area was white or pale, and dead if it was recently overgrown by algae.

3.3.3 CORAL COVER

The percentage of live and dead coral cover was determined with a 10 m long chain (1.1 cm link^{-1}) along five to seven transects parallel to the shore line and across the bottom areas occupied by corals. The number of links corresponding to each category of substrate (live or dead coral) was translated to a percentage with respect to the total number of links in the chain.

3.3.4 SINGLE MASSIVE CORAL COLONIES

Changes in bleached surfaces in massive colonies of *Porites lobata*, *Pavona clavus* and *Pavona gigantea* were measured from nails marking the limits of bleaching areas and monitored during 6-9 mo after the warming events. Tagged colonies were inspected for as long as 1-2 yrs, until tags were overgrown by tissue.

3.3.5 ZOOXANTHELLAR DENSITIES AND CHLOROPHYLL CONCENTRATIONS

One fragment of eight bleached and eight fully pigmented colonies of *P. lobata* was sampled to determine the zooxanthellar density and chlorophyll pigments (*a* and *c*) at three different localities off the central Pacific coast of Costa Rica. All samples (24) were analyzed with standard procedures described in publication I (Jiménez and Cortés 2001).

> Coral bleaching and mortality were assessed at regional scale by surveying broad portions of the coast. On the local level, percentages of affected or healthy colonies and changes in coral cover were determined by transect methods. At the individual scale, monitoring of tagged colonies was used to determine how they fared during the peak and demise of the warming episodes.

3.3.6 SEAWATER TEMPERATURE AND METEOROLOGICAL DATA

Hobo-Temp and Stow-Away (Onset Computer Inc.) underwater temperature data loggers were used to monitor subsurface seawater temperature on one of the study sites (Bahía Culebra, Fig. 4). The thermistors were attached to corals with plastic cable-ties and set to record every 36 min. The units were replaced every month to avoid fouling organisms on the submersible case. Additionally, short-term temperature recordings in the water column (0-30 m depth) were made by SCUBA with a calibrated mercury thermometer at all study sites. Additionally, sea surface temperature (SST) and cloudiness for the 1982-2001 time period were utilized to characterize the warming event itself and the weather during the event. The SST and cloudiness data are monthly averaged global gridded analysis from the Reynolds NCEP optimal interpolation analysis (Reynolds and Smith 1994) and the NCEP-NCAR reanalysis (Kalnay et al. 1996) respectively. Both data sets are a blend of in situ observations and bias-corrected satellite data. Rainfall and sun hours from the nearest meteorological stations to the study sites were provided by the Costa Rican Instituto Meteorológico Nacional.

> The warming events were characterized by *in situ* measurements of subsurface seawater temperature and meteorological variables, and complemented with historical records of surface seawater temperature (1982-2001).

3.4 El Niño Isotopic signature on Coral Skeletons

The stable isotopic ($\delta^{13}C$ and $\delta^{18}O$) signature of the 1997-98 El Niño in the coral *Pavona clavus* (at Bahía Culebra and Islas Murciélagos, three depths) and *Gardineroseris planulata* (Islas Murciélagos, one depth) is being currently investigated. The purpose of this study is to evaluate these coral species as surrogates to reconstruct the history of past El Niño episodes in the upwelling area of the Golfo de Papagayo. *P. clavus*, in particular, may prove to be an excellent candidate for climate reconstruction studies, due to morphology of the colonies, size, growth rate and abundance in the study area.

3.4.1 CORALS, EL NIÑO AND ENVIRONMENTAL VARIABLES

The stable isotope composition of *P. clavus* at Bahía Culebra is currently investigated in six colonies (4 m depth), which were annually stained with Alizarine red**,** during the interval 1995 to 1999. The staining lines provided the datum marks that orientated the sampling for isotopes (12-14 samples yr^{-1}). Six other colonies**,** at 7 and 12 m depth, were drilled**,** and the resulting twelve cores sub-sampled for isotope composition during the last five years (1995-2000). Two *P. clavus* and two *G. planulata* colonies at Islas Murciélagos were also stained in October 1997, during the peak of that year coral bleaching and mortality, and their isotope composition will be compared to the corals at Bahía Culebra. Additionally, we are evaluating how representative is the isotope seasonal trend of *P. clavus* of the environmental conditions during non-El Niño years. For this purpose, six other colonies (7 m depth) were cored on a monthly basis (13 months, 1999-2000) and the individual isotope averages (4 samples mo^{-1}) between colonies compared. The pooled monthly mean isotope composition of all colonies (24 samples mo^{-1}) is compared to monthly averaged environmental variables (seawater temperature, salinity, rainfall, sun hours and wind speed).

3.4.2 ANALYSIS FOR ISOTOPE COMPOSITION

Coral cores were cut with a rock saw, and the slabs (5-8 mm thick) X-rayed. Positive prints were used to identify the corallites' axis, where the carbonate powder for the analysis of isotopes was collected (12-14 samples yr^{-1}). Drilling of slabs was done with a low-speed drill using 0.8 mm diameter bits. The skeletal carbonate powder was homogenized, and the stable oxygen and carbonate isotopes of these samples (80-90 μg) were measured with a Finnigan MAT251 mass spectrometer, coupled with an automatic carbonate preparation device.

The stable isotopic (δ^{13}C and δ^{18}O) signature of the 1997-98 El Niño is currently investigated in *Pavona clavus* and *Gardineroseris planulata* coral species at Bahía Culebra (4, 7, and 12 m depth) and Islas Murciélagos (4 m) .

Monthly stable isotope values from six *P. clavus* colonies at Bahía Culebra, are compared with environmental variables is order to evaluate this species as a proxy indicator for environmental conditions at the study area.

4 Results and Discussion

The general results of the five papers (Jiménez 2001c, Jiménez and Cortés 2001, Jiménez et al. 2001, Jiménez and Cortés submitted, and Jiménez et al. in prep.) will be reviewed in this section in order to provide a comprehensive view of the recent warming events which have affected coral reef communities in Costa Rica. A characterization of the sea temperature rise in the three main areas of study, circumscribed to the 1982-2001 time period, will be presented first, followed by the observed responses of the corals during the warming episodes.

4.1 THE WARMING EVENTS

The Pacific and Caribbean coasts of Costa Rica have experienced several episodes of sea temperature rise of different magnitude and duration throughout the time period 1982 to 2001 (Fig. 5a). Four of these events (1982-83, 1986-87, 1991-92 and 1997-98), can be ascribed to local manifestations of the El Niño episodes in the eastern Pacific. Coral bleaching and mortality were observed during the onset and peak of the events. The Caribbean episode of 1995-96 occurred in the absence of a concomitant warming period in the Pacific. However, this episode started after the prolonged unstable period of 1991-1995 in the eastern Pacific which is controversial in terms of defining an El Niño event (e.g. Trenberth and Hoar 1996, Latif et al. 1997). Although the oceanographic and meteorological characteristics of this warming episode have yet to be studied in detail (e.g. Alfaro 2000). Alfaro and Jiménez (in prep.) have found a correspondence between sea temperature rise in the Caribbean and the Pacific coast of Costa Rica. An increment of temperature in the former is preceded by six months in the latter (Fig. 6). This correspondence is also significant to time lags of one and zero, suggesting that, during severe El Niño episodes, the Caribbean responses are synchronous. These findings suggest a higher interdependence between oceanographic and atmospheric processes in the eastern Pacific and the western Caribbean than previously thought (e.g. Enfield and Mayer 1997, Enfield and Alfaro 1999). However, it is clear that the Caribbean basin is affected by other processes than El Niño, and eastern Pacific disturbances are only part of the oceanographic story of Caribbean waters.

Between 1982-2001, five major sea warming episodes occurred in Costa Rica. Only one, the 1995 Caribbean episode, took place in the absence of an El Niño event in the eastern Pacific.

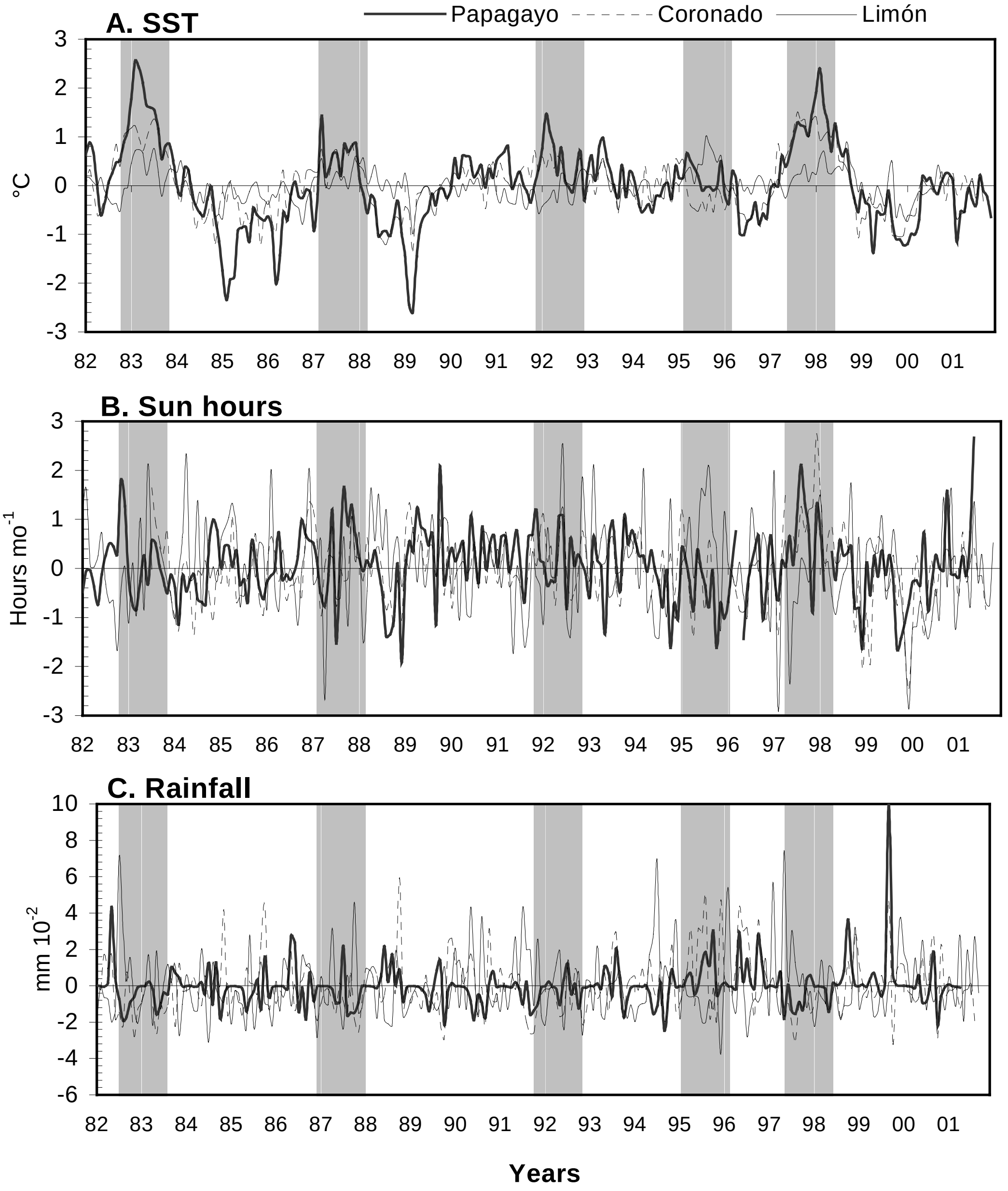

Figure 5 Comparison of monthly anomalies of sea surface temperature (SST), sun hours and rainfall at the Golfo de Papagayo (northern Pacific coast), Bahía de Coronado (central Pacific, in front of study site number 5, see Fig. 4) and Limón (Caribbean). Anomalies were calculated by subtracting monthly means derived for the period 1982-2001 from individual months. The vertical shading shows the approximate timing of bleaching and mortality of corals in the study areas. Bleaching events of 1982-83 and 1987 are discussed by Cortés et al. (1984), Guzmán et al. (1987), and Guzmán and Cortés (2001).

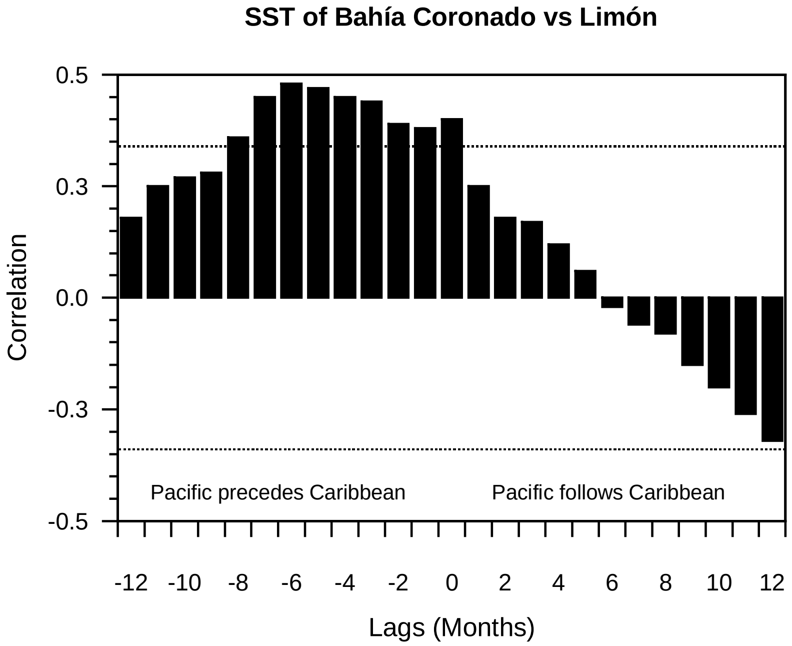

Figure 6 Cross correlation of normalized sea surface temperature (SST) anomalies from Bahía Coronado (Pacific) and Limón (Caribbean). Dotted lines denote 95% significance levels. Lags are expressed in months. From Alfaro and Jiménez, in prep.

4.2 WEATHER PATTERNS DURING THE WARMING EVENTS

Patterns in the meteorological conditions during the warming events can be drawn from monthly sun hours and rainfall anomalies (Fig. 5b, c). Prolonged spells of stable weather accompanied the climate shifts, producing sunny, dry days that extended for weeks and months in the Pacific coast. Less consistent were the conditions at the Caribbean, where the opposite trend (cloudy and rainy spells) also occurred. This general pattern is thought to be the result of the intensification in the summer Trade winds over the Caribbean during El Niño events, disrupting the normal progress of the rainy season by producing a protracted mid-year low in runoff (known as Veranillos de San Juan), and setting dry spells which can develop in to droughts of different intensities (Fernández and Ramírez 1991, Amador and Alfaro 1996, Waylen et al. 1996a, b). The most dramatic manifestations of these unusual weather are translated into the off-season intensification of north-eastern winds over the Golfo de Papagayo area. This region is characterized by the seasonal upwelling of cold waters during most of the dry season. Wind gusts of more than 100 km hr^{-1} were recorded in September-October

1997, months corresponding to the height of the rainy season during non-El Niño years, triggering short-lived strong upwelling events (Jiménez et al. 2001). The 1995-96 Caribbean warming, although not directly connected to any major El Niño episode, was accompanied by similar doldrum-like weather (Jiménez 2001c), with sunny and dry spells setting off the conditions for a mass-bleaching event (see next section).

Weather conditions during major warming events tend to be expressed in long spells of sunny, dry days, setting drought-like interludes of variable extent. This trend is more pronounced in the Pacific than in the Caribbean.

4.3 MASS-BLEACHING AND MORTALITY EVENTS

Whenever the weather conditions favored the onset of doldrum-like weather coincidental to an abnormal rise in sea temperature, a mass bleaching event was triggered in the Pacific or Caribbean coast of Costa Rica. The long, dry and sunny spells in association with calm and more transparent waters (due to a decrease in runoff and concomitant sediment loads), facilitates light penetration in the water column, increasing irradiance levels reaching corals. The increase in solar radiation is known to produce photochemical damage, disrupting the biochemical pathways within the symbiotic zooxanthellae (Glynn 1996, Hoegh-Guldberg 1999, Hoegh-Guldberg and Jones 1999, Brown at al. 2000, Dunne and Brown 2001, Fitt et al. 2001), and this negative effect is exacerbated at temperatures higher than normal (Coles and Jokiel 1978), which are the El Niño trademark. In Costa Rica, the five large scale coral bleaching and mortality episodes of the 1982-2001 period (Fig. 5) were linked to protracted sea warming and climate conditions such as described above. The 1982-83, 1991-92, 1997-98 El Niño episodes bleached and killed corals at both coasts of the country (Cortés et al. 1984, Guzmán et al. 1987, Jiménez and Cortés 2001, 2002, Jiménez et al. 2001, Cortés and Jiménez 2002a, b); the episode of 1986-87 is known to have affected corals only at the Pacific coast (Guzmán and Cortés 2001, Jiménez and Cortés 2002), and the 1995-96 warming had an effect only on Caribbean reefs (Jiménez 2001c). The on-going 2002 El Niño was initially felt in the Papagayo area in August-September 2001 (Jiménez et al. unpub. data), probably due to the arrival of the first set of Kelvin waves that crossed the eastern Pacific basin. The one to two degrees increase in water temperature at 7 m depth lasted several weeks and coral bleaching was observed by the end of September, when weather conditions favored clear skies and a drop in precipitation occurred.

Common to all five mass-beaching events (1982-2001) in Costa Rica was the doldrum-like weather which settles during the excursions of warm water in the region.

Other proposed explanations for such large-scale bleaching and mortality of corals deal with the rates of sea warming and/or duration of high sea temperature above a critical threshold (Glynn et al. 1988, Gleeson and Strong 1995, Podestá and Glynn 1997, 2001, Fong and Glynn 2001). Our field observations suggest a much more complex interaction of environmental and biological factors responsible for bleaching events. For example, the 1997-98 warming, which was recorded in situ by submersible data-loggers, had two warming phases, one in the second half of 1997, and a second in the first half of 1998 (Jiménez et al. 2001). Large-scale coral bleaching was observed for most of the Costa Rican coast in the first phase of the warming, and it was nearly absent in the second (it was limited to a *Pocillopora* spp. stand in Bahía Culebra). Thermal attributes can not satisfactorily explain the absence of extensive bleaching in 1998, when the warming rate and elevated temperatures were both higher and of similar duration to those of 1997 (Fig. 7). However, mass bleaching of corals was indeed coincidental with sunlight positive anomalies in the first warming phase and doldrum-like weather that persisted for weeks. This observation suggests that it is inadequate to explain large-scale bleaching events without consideration of the role of solar radiation, and it is becoming clear that biological and ecological factors may be participating as well. For example, different thermal-thresholds are given by genetic variability of coral and algal symbionts (Edmunds 1994, Brown 1997b, Buddemeier and Fautin 1993, Rowan et al. 1997, Glynn et al. 2001), physiological photoprotective defenses (Dunne and Brown 2001), coral community structure (Marshall and Baird 2000), and possible by the selective effects of El Niño episodes on the survivorship of more tolerant colonies or clones (Jiménez et al. 2001). All this factors may interact to produce a highly dissimilar response to warming events.

It is highly suggestive that the 1997 mass-bleaching event in Papagayo was triggered when high solar radiation was coincidental with accelerated warming rates.

The association between environmental parameters and bleaching events is, therefore, more complex than has been suspected, and further field observations and monitoring of variables are needed.

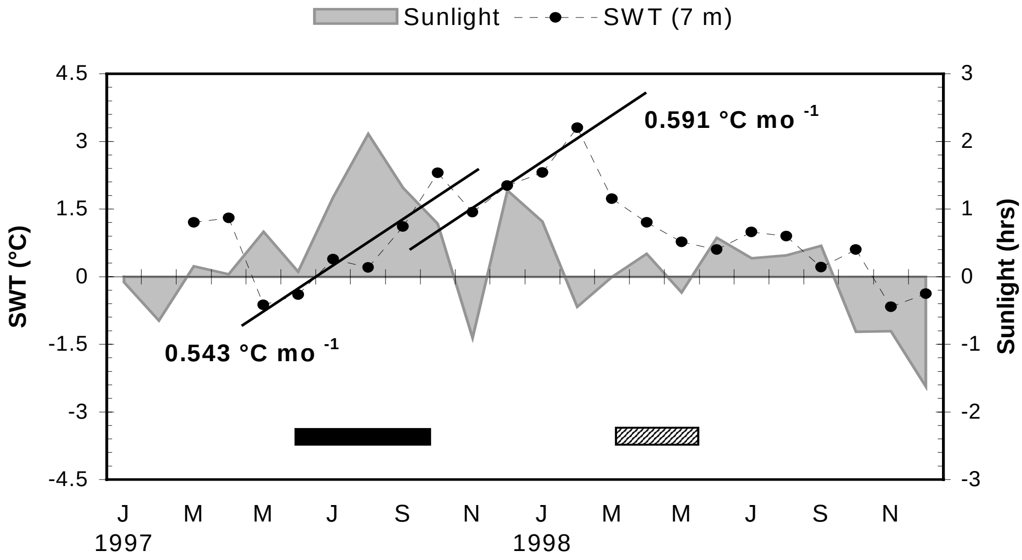

Figure 7 Seawater temperature (SWT) and sunlight monthly anomalies for the 1997-98 period. The slopes (solid lines) of the two warming phases and the rate of warming (°C mo^{-1}) are indicated. Anomalies were calculated as in Fig. 5. The horizontal bars show the approximate timing of mass-scale (black) and limited (dashed) bleaching and mortality. The 1998 bleaching was observed only at Bahía Culebra and in one small *Pocillopora* spp. stand (10 m^2).

4.4 CORAL REEF COMMUNITIES RESPONSES

Although the present thesis comprises observations of several warming events and a wide-range of geographical locations in Costa Rica, it is difficult to produce a definite picture of the coral reef communities responses to the warming events, mostly because there are temporal and spatial components that cannot be avoided. Additionally, there are confounding factors which may act on a local scale and are site and species-specific. However, several inferences from our studies certainly contribute to the understanding of how corals fared during warming events.

4.4.1 RESPONSES OF INDIVIDUAL MASSIVE CORAL COLONIES

Zooxanthellar densities between normally pigmented and bleached *P. lobata* colonies were invariably higher in the former than in the latter (Fig. 8a). While symbiont densities were similar in the three study sites for normally pigmented colonies, they varied significantly in bleached corals. Pigment concentrations of the symbionts, on the other hand, generally did not show differences between bleached and pigmented colonies or between study sites (Fig. 8b, c). Only at one locality, Ballena, Chlorophyll-*a* concentrations were higher in pigmented than in bleached corals (Fig. 8b); this may be the result of site-specific oceanographic conditions and not the bleaching event itself (Jiménez and Cortés 2001).

These results are important in the light of controversial, and some times contradictory, evidence of why the coral tissue pales. Bleaching due to changes in zooxanthellar symbionts has been reported for several coral species (e.g. Hoeg-Guldberg and Smith 1989, Jones 1997). However, bleaching of corals due to pigment loss is also known to occur (Kleppel et al. 1989, Brown et al. 2000).

Our results suggest that the observed bleaching in colonies of the massive coral *Porites lobata* during the 1991-92 El Niño, was related to zooxanthellar densities and not to changes in pigment concentrations.

Tagging of massive coral colonies during El Niño episodes of 1991-92 (*P. lobata*) and 1997-98 (*P. clavus* and *P. gigantea*) provided the opportunity to track changes in specific members of the reef community. Bleached colonies of *P. clavus* and *P. gigantea* in the Golfo de Papagayo, generally fared better than *P. clavus* at the central Pacific coast. While colonies from Papagayo completely overgrew the dead areas in seven months, this process took one to two years in the central Pacific (Jiménez and Cortés 2001). Similar slow recovery was observed in *P. lobata* colonies affected by the 1997-98 El Niño (Jiménez and Cortés submitted). Colonies of this species still exhibited partial tissue mortality in January 2001, almost three years after the warming event. Finally, since it was possible to identify individual colonies during the recovery time, we found high variability between colonies of the same locality in recovering and retaining the zooxanthellar densities.

Monitoring of tagged colonies of massive species permitted to recognize how variable are recovery rates (how fast dead areas in the colonies were completely overgrown by tissue) between individuals and localities.

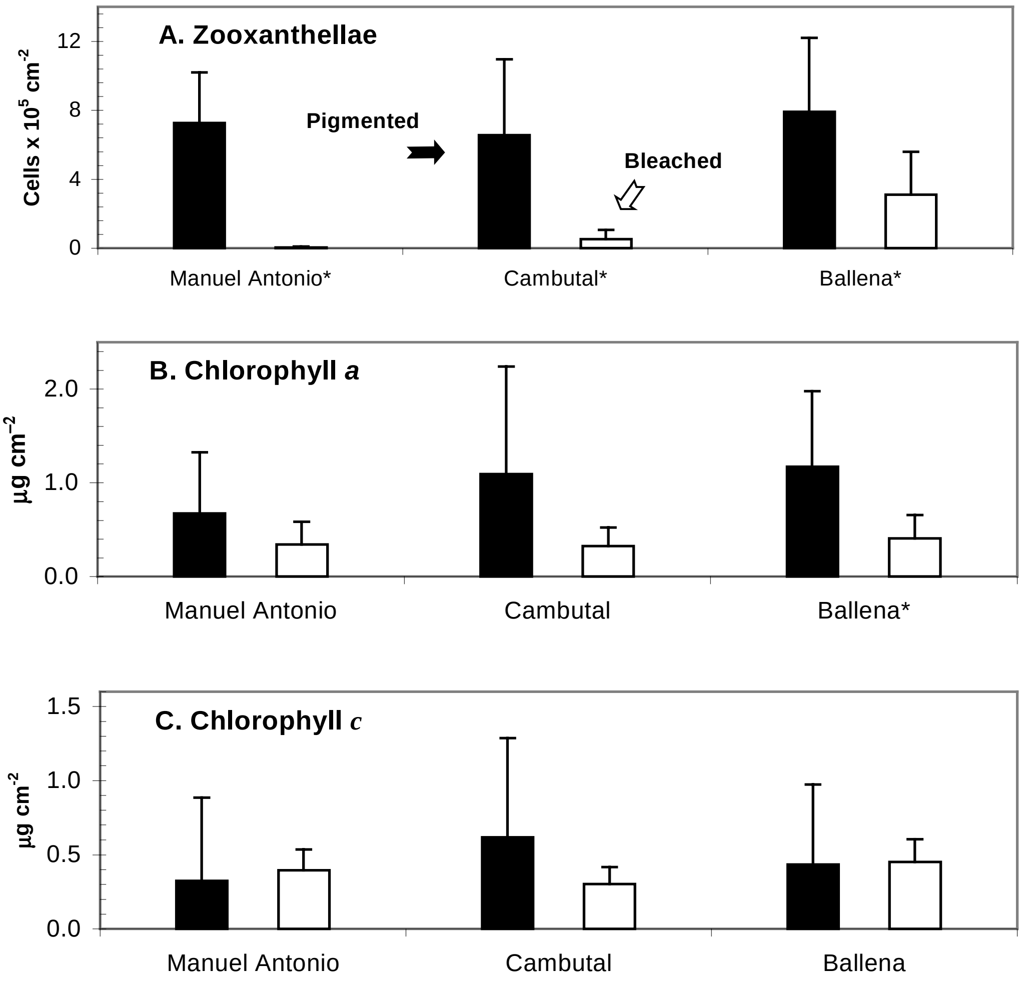

Figure 8 Comparison of mean zooxanthellar densities (A) and chlorophyll *a* (B) and *c* (C) in normally pigmented (black bars) and bleached (white) *Porites lobata* colonies in the central Pacific coast during the 1991-92 El Niño. * Significant differences (Student's t-Test, $P<0.05$). See Fig. 4 for sites location.

One of the most important contributions of this section is the acknowledgement of the high variability of individual responses to the warming itself and the subsequent recovery. This extents to coral from different sections of the reef and localities within a given area. Moreover, different parts of the same colony can be distinctly affected by the warming, cautioning against simplistic explanations and careless generalizations of coral responses to stress. To illustrate further the importance of this point, let us briefly consider the variability noted in six conspecific coral colonies thriving under the same environmental conditions. Studying the El Niño 1997-98 signature in skeletal stable isotopes ($\delta^{18}O$ and $\delta^{13}C$) of *P. clavus* colonies from Bahía Culebra, Jiménez et al. (see section 4.4.5, page 36) found dissimilar patterns for each colony during the peak of the mass-bleaching period in 1997 (Fig. 9). The corals were collected within 1 m^2 in the reef,

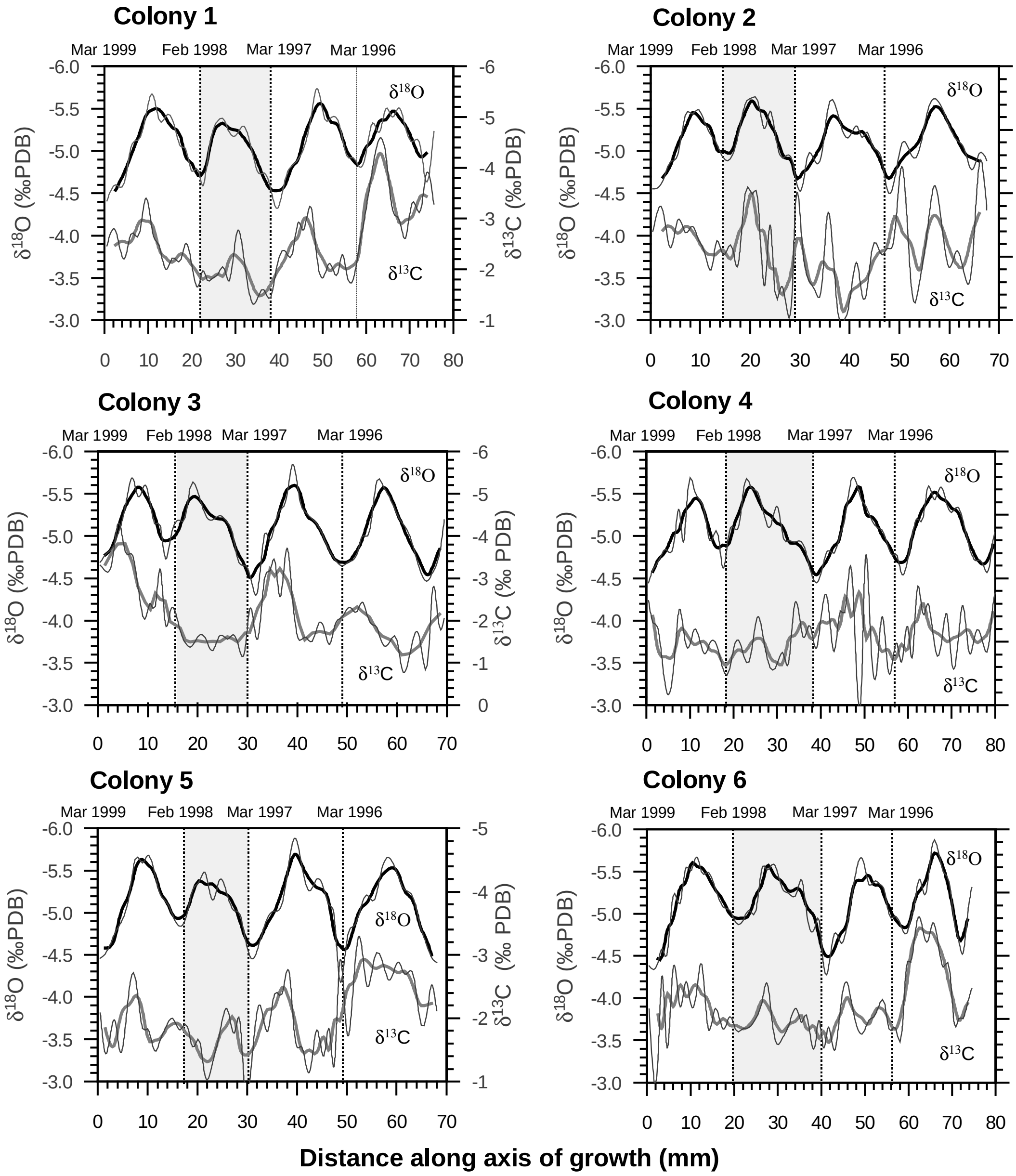

Figure 9 Skeletal stable isotope records ($\delta^{18}O$ and $\delta^{13}C$) of six *Pavona clavus* colonies, Bahía Culebra, collected at 4 m depth. Thick lines are 3-point running averages. Scales are inverted to follow the temperature pattern. Vertical dashed lines indicate Alizarine red staining dates. The vertical shading indicates when first phase of the 1997-98 El Niño episode occurred and large-scale coral bleaching was observed. Samples were taken along the maximum axis of growth starting from the tissue (0 mm) and throughout the datum staining lines in the skeleton.

therefore, the same environmental conditions can be expected. If the goal is to characterize the 1997-98 episode based on the isotopes derived from these colonies, six different interpretations may arise, evidencing the need to consider variability at the individual level.

> Individual colonies of the coral *P. clavus* had dissimilar isotopic signatures tracing the 1997-98 El Niño episode, cautioning against generalizations derived from the study of one single colony.

4.4.2 TEMPORAL AND SPATIAL SCALES

Based only on the counting of coral colonies, the most affected areas by the warming events were the central and south Pacific, and the Caribbean coast (Fig. 10). In these regions, more than 55% of all coral colonies bleached. Death of entire colonies varied from 6 to nearly 9%. Although percentage of dead colonies in the Golfo de Papagayo and Golfo Dulce was similar (~6%), more colonies retained their symbionts in the former (~60%) than in the latter (~36%). It is surprising that mortality of colonies associated to the 1997-98 was remarkably low, given the strength and duration of the warming. These observations draw attention to the different biological and physical processes that may interact at different magnitudes in each locality, and which could be site-specific. For example, off-season upwelling in the Golfo de Papagayo may ameliorate the effect of the warming events as observed for the Golfo de Panamá, where corals remained unscathed during the 1997-98 warming (Glynn et al. 2001). On the other hand, site-specific oceanographic conditions may amplify the rise in sea temperature, as observed in small, shallow coves of Costa Rica (Jiménez and Cortés 2001, Jiménez et al. 2001).

In summary, a wide-spectrum of species-specific responses to the warming episodes and differences in their abundance within areas are surely contributing to the degree of bleaching and mortality at the regional scale. Caribbean coral reef communities, for example, differ to a great extent from their Pacific counterparts in species composition, structure of the coral assemblages, genetic background, symbiotic zooxanthellae, and oceanographic settings. All these features need to be considered, if comparisons among localities are to be made.

Mortality of entire coral colonies attributable to warming events during the 1991-98 time period was unexpectedly low, given the strength and duration of the rise in sea temperature, particularly during the 1997-98 episode.

The least affected area was the Golfo de Papagayo where the warming was weakened or temporarily interrupted by the occurrence of upwelling episodes.

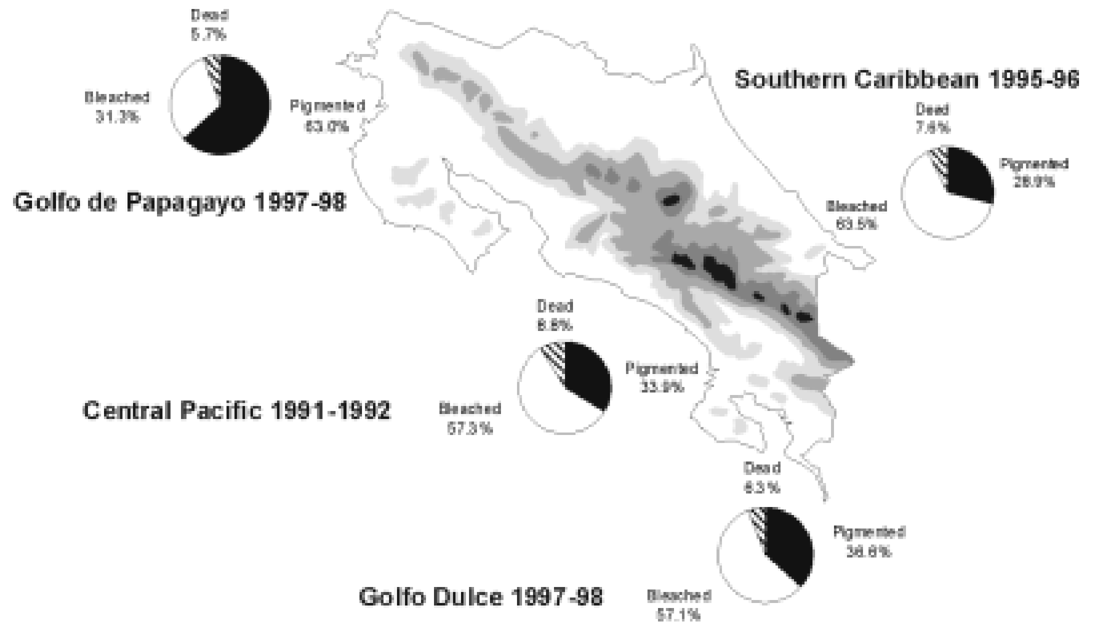

Figure 10 Status of coral colonies during warming events and distributed according to the studied areas. Pie charts represent proportion of colonies which lost (bleached) or retained (pigmented) their symbiotic dinoflagellates and/or pigments. The 1995-96 warming was not coincidental with an El Niño episode in the eastern Pacific. See Fig. 4 for specific sites location.

4.4.3 CHANGES IN CORAL COVER

Measuring changes in coral cover (i.e. tissue mortality) is another method of assessing the impact of warming events and the recovery of coral communities from disturbances (e.g. Connell et al. 1997). In Costa Rica, the extent of coral tissue mortality attributed to El Niño episodes varied significantly among study sites and warming events (Fig. 11). Bahía Culebra, in the Golfo de Papagayo, seems to be the most heavily impacted locality with more than 80% mortality during the 1997-98 episode (Jiménez et al. in prep.). However, ~90% of the tissue loss corresponded to the species *L. papyracea* and *P. clavus*. Likewise, the high mortality (>60%) at Isla del Caño during the 1987 episode resulted from the startling mortality of one species, *P. lobata* (Guzmán and Cortés 2001). Additionally, it is clear that there are confounding factors linked to the site or are species-specific, which may lead to wrong statements. Bahía Culebra was indeed the locality where tissue loss was most severe during the 1997-98 El Niño, though this is true for only two corals of the reef community and where the transects were made. These observations caution against generalizations of El Niño effects over spatial and temporal scales based only on coral cover data and without a clear reference of the species contribution to that mortality.

> Coral cover changes are practical means to measure the impact of natural disturbances such as El Niño, and the subsequent recovery of the coral reef communities. However, it is crucial to avoid generalizations based only on cover changes without categorizing the contribution of every coral species to that mortality.

Interestingly, when comparing localities where coral cover loss was repeatedly measured during El Niño episodes (Fig. 11), tissue mortality at Cambutal was significantly higher in 1991-92 than in 1997-98. This is remarkable because the magnitude and extent of the 1997-98 warming surpassed to a great extent any documented El Niño during the last century (Enfield 2001). The same was observed at Isla del Caño (Guzmán and Cortés 2001), where tissue mortality due to the 1997-98 episode was meager compared with the impact of previous warming events (Fig. 11). The coral community structure at these sites hasn’t change significantly in the several years respite between the warming events, namely, there have been the same species and abundance. Only at Cambutal, *Psammocora stellata* was extirpated after the 1997-98 El Niño. This strongly suggests that, since the occurrence of the 1982-83 El Niño, coral reef communities in certain localities of the Pacific coast of Costa Rica may have been through a selection process mentioned before, together with a limited ability to acclimatize (Jiménez et al. 2001). As a final point, we cannot rule out the possible influence of site-specific oceanographic conditions which might have lessened the warming impact.

> For a given El Niño episode, tissue loss varied significantly between localities, and this may be the consequence of site and/or species-specific factors.
>
> For a given locality, the strongest El Niño episodes not always resulted in the highest tissue mortality. Selective mechanisms and local oceanographic settings may be interacting and curtailing tissue mortality.

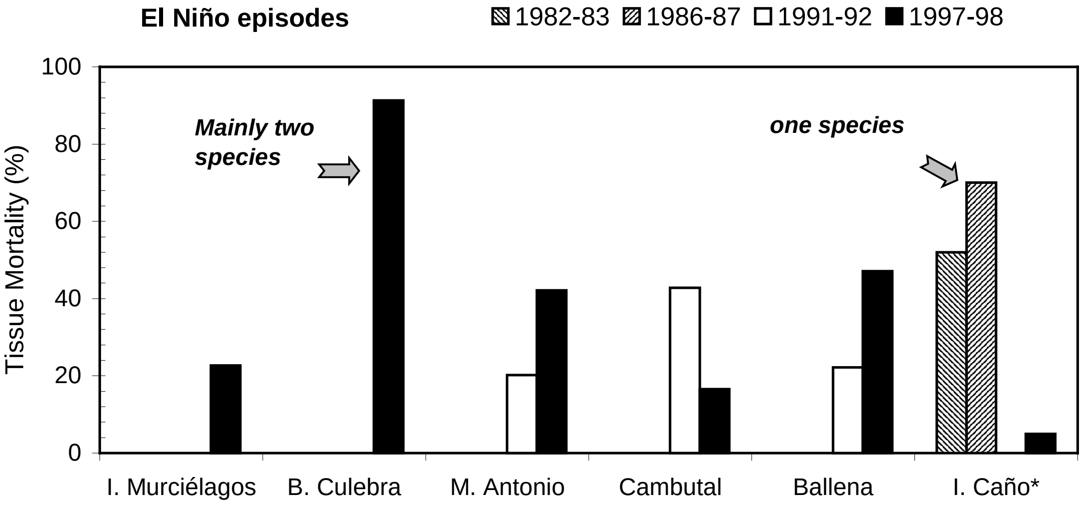

Figure 11 Comparison of tissue mortality associated to El Niño episodes at several localities of the Costa Rican Pacific coast. Isla del Caño data from Guzmán et al. (1987), and Guzmán and Cortés (2001). See Fig. 1 for sites location.

4.4.4 LONG-TERM CONSEQUENCES OF WARMING EVENTS

A comparison of tissue and colony mortality in all warming events which have affected Costa Rica since 1982 is presented for the first time (Fig. 12), though there are several aspects which need to be clarified. These data set is highly heterogeneous, because it includes coastal and insular localities, different depths and oceanographic settings, site-specific assemblages and abundance of species (Caribbean vs. Pacific), and several biological features which differ between localities (e.g. growth, recruitment, bioerosion, competition, diseases).

With these considerations in mind, a limited picture of the coral communities responses, i.e. mortality of tissue and entire colonies during the last five warming events, can be disclosed. At first glance, the 1982-83 El Niño stands by itself in terms of high percentage of mortality and range of species and localities affected, though quantitative data is limited to one locality (Isla del Caño). The effects of this warming were observed in the Golfo de Papagayo area and several Caribbean coral reefs as well (Cortés et al. 1984, pers. obs.), but no quantification of the impact (e.g. death of entire colonies) was made. Nevertheless, fishermen and divers tell of high numbers of previously healthy massive colonies (>1.5 m diameter) in several reefs of the Papagayo and central Pacific areas which were found dead after the 1982-83 warming (Jiménez 1998). These colonies can still be observed and they may provide a rough estimation of how severe was the impact of this El Niño episode on massive coral species (Fig. 12).

Better documented on a geographical scale, the 1997-98 El Niño-related mortality varied considerably among localities and species, but average mortality was not much different from the 1982-83, 1991-92 and 1995-96 (Caribbean) warming events. Furthermore, mortality of colonies was lower during this El Niño than the 1991-92, 1995-96 episodes, and dramatic decrease (>70%) in live cover of particular species was also reported during the 1986-87 El Niño (Fig. 12). Therefore, there is no clear cut trend in the responses of the Costa Rican coral reef communities in the Pacific coast (expressed as bleaching and mortality) to the recent El Niño warming episodes. This is probably the result of several confounding factors, such as a short, limited interval of observations and data gathering, changes in the background biotic properties (e.g. selection processes to more temperature resistant genotypes), and site and species-specific conditions (see previous section).

The observations presented in this section suggest that the expected relation between warming events intensity and the negative impacts upon coral reefs is far from being a mathematical singularity. The response of coral reef communities to warming episodes such as El Niño cannot be fully understood with the limited temporal, spatial and biological perspective currently available.

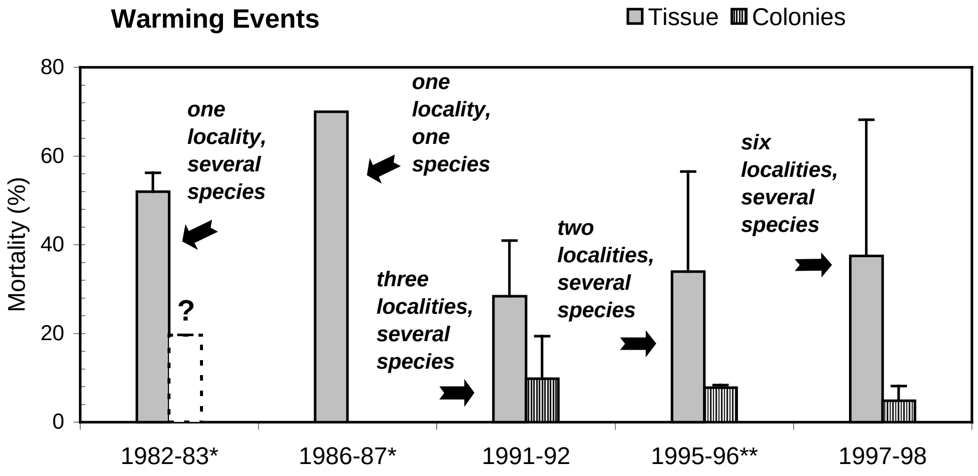

Figure 12 Comparison of overall tissue and colony mortality associated to warming events at the Pacific and Caribbean coast of Costa Rica. Coral colony mortality attributed to the 1982-83 El Niño episode is a rough estimation from anecdotal information provided by fishermen and sport divers and in situ counting of dead colonies in the late 1980s and early 1990s (Jiménez 1998, Cortés and Jiménez 2002a). * Isla del Caño, from Guzmán et al. (1987), and Guzmán and Cortés (2001). **Caribbean data of tissue mortality from Jiménez in prep.

4.4.5 Isotopic Composition (Preliminary Results)

In general, the $\delta^{18}O$ monthly values derived from *P. clavus* colonies show a fair correspondence with the sea surface temperature (SST) during the study time period (Fig. 13). Enrichment of the oxygen signal follows the seasonal occurrence of the Papagayo upwelling during the dry season (December-April), and depletion follows the establishment of the rainy season, when seawater temperature is higher (May-November). Corals from different depths had the same seasonal trends, although there were small differences in the amplitude. The $\delta^{13}C$ fluctuations between colonies and years did not show a clear seasonal trend, suggesting that physiological processes may be interacting and producing changes in the $\delta^{13}C$ composition. Several factors may affect and change $\delta^{13}C$ levels and they comprise: (1) photosynthesis rates of zooxanthellar symbionts (McConnaughey 1989, Muscatine et al. 1989, Grottoli and Wellington 1999); (2) coral heterotrophy (Grottoli and Wellington 1999); and (3) sun light (McConnaughey 1989, Muscatine et al. 1989, Carriquiry et al. 1994, Wellington and Dunbar 1995, Grottoli and Wellington 1999).

> Isotopic oxygen values of six *P. clavus* colonies show a clear seasonal trend, which follows the characteristic sea surface temperature fluctuations of the study area at the Golfo de Papagayo. In contrast, $\delta^{13}C$ had no clear seasonal trend, suggesting that other factors may be interacting and modifying the carbon. isotopic signal.

During the 1997-1998 El Niño, individual colony $\delta^{18}O$ depletion values of *P. clavus* and *G. planulata* were higher or similar to other years. The lowest oxygen isotope values should be expected between March and December 1997 (the peak of the warming event), not during 1996-97 or 1998-99. From the pooled means (Fig. 13) and individual $\delta^{18}O$ values (Fig. 9, section 4.4.1, page 29), it is observed that $\delta^{18}O$ depletion was highest either before or after the period during which it would theoretically be expected, or it was not much different. To reject the possibility of the samples not having been well homogenized, the analyses were repeated twice for all samples within the 1997 and 1998 interval, and for all six colonies. The resulting differences between measurements were within instrumental error, and within the intrinsic colony variability, validating the results. Similarly attenuated $\delta^{18}O$ signals have been found in other coral

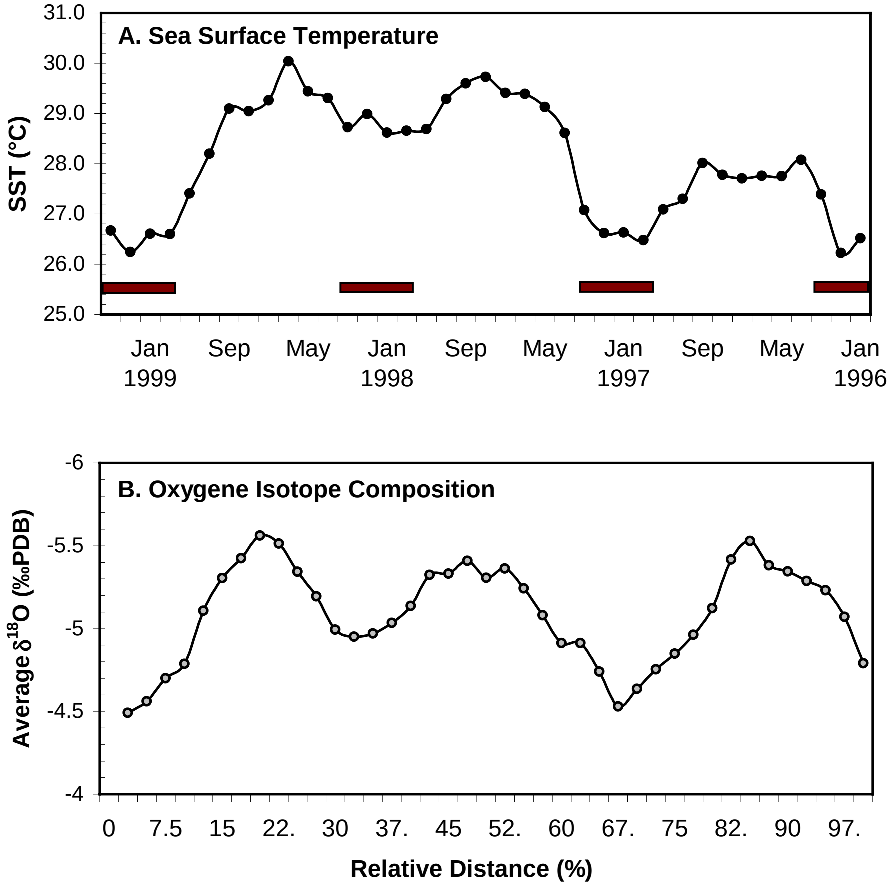

Figure 13 Comparison of (A) sea surface temperature (SST) and (B) oxygen isotope composition derived for six *Pavona clavus* colonies (4 m depth). SST X-axis is inverted to follow the relative distance of the d18O averages, which in turn had the Y-axis inverted to follow the SST seasonal trend. Due to differences in annual growth rates between the colonies, the 233 isotope measurements referring to the six corals were normalized with respect of sampling length along the slab (*sensu* Brey et al. 1999), pooled and sorted into 16 intervals of relative core length (0-2.5%, 2.5-5%,….95-97.5%, 97.5-100%). 0% corresponds to the coral tissue layer from which the sampling was initiated. SST are monthly averaged global gridded temperature readings from the Reynolds NCEP optimal interpolation analysis (Reynolds and Smith 1994). Horizontal black bars indicates the approximate timing of the seasonal upwelling of Papagayo. Note that the intensity of the 1997-98 upwelling was significantly reduced due to the El Niño episode of that year.

species (e.g. Linsley et al. 1994, 1999, Wellington and Dunbar 1995). We believe that the attenuated $\delta^{18}O$ signal corresponding to the highest El Niño warming (between March and November1997) indicates that the coral growth has diminished. Corals may have accreted less skeleton for several months, and the signal in the sample might be obscured by the rest of the carbonate material analyzed for isotope composition.

Mean $\delta^{18}O$, during the peak of the 1997-98 El Niño, was highly inconsistent between colonies, depths, localities and the two studied species. The period of the highest warming during the El Niño episode did not coincide with the highest depletion in skeletal $\delta^{18}O$. Slow growth rates during that period may explain the attenuated $\delta^{18}O$ signal during the 1997-98 El Niño.

The $\delta^{18}O$ and $\delta^{13}C$ for the six *P. clavus* colonies sampled on a monthly basis displayed similar seasonal trends, with the lowest values between April and December, corresponding to the beginning and end of the rainy season respectively (Fig. 14). There was major within-colony variability of $\delta^{18}O$ in several colonies, during the interval between July and October, with the highest standard deviation of both isotopes in September, the peak of the rainy season. Similar inter- and intra-colony $\delta^{18}O$ variability has been found elsewhere for other coral species (Guzmán and Tudhope 1998, Linsley et al. 1999), and it has been suggested that biological mediated processes (vital effect) are responsible for the isotopic difference.

Monthly $\delta^{18}O$ and $\delta^{13}C$ values of six *P. clavus* colonies displayed consistent seasonal trends. However, there was major inter- and intra-colony variability. These preliminary results suggest that caution must be exercised when reconstruction of environmental variables is based on a single coral colony.

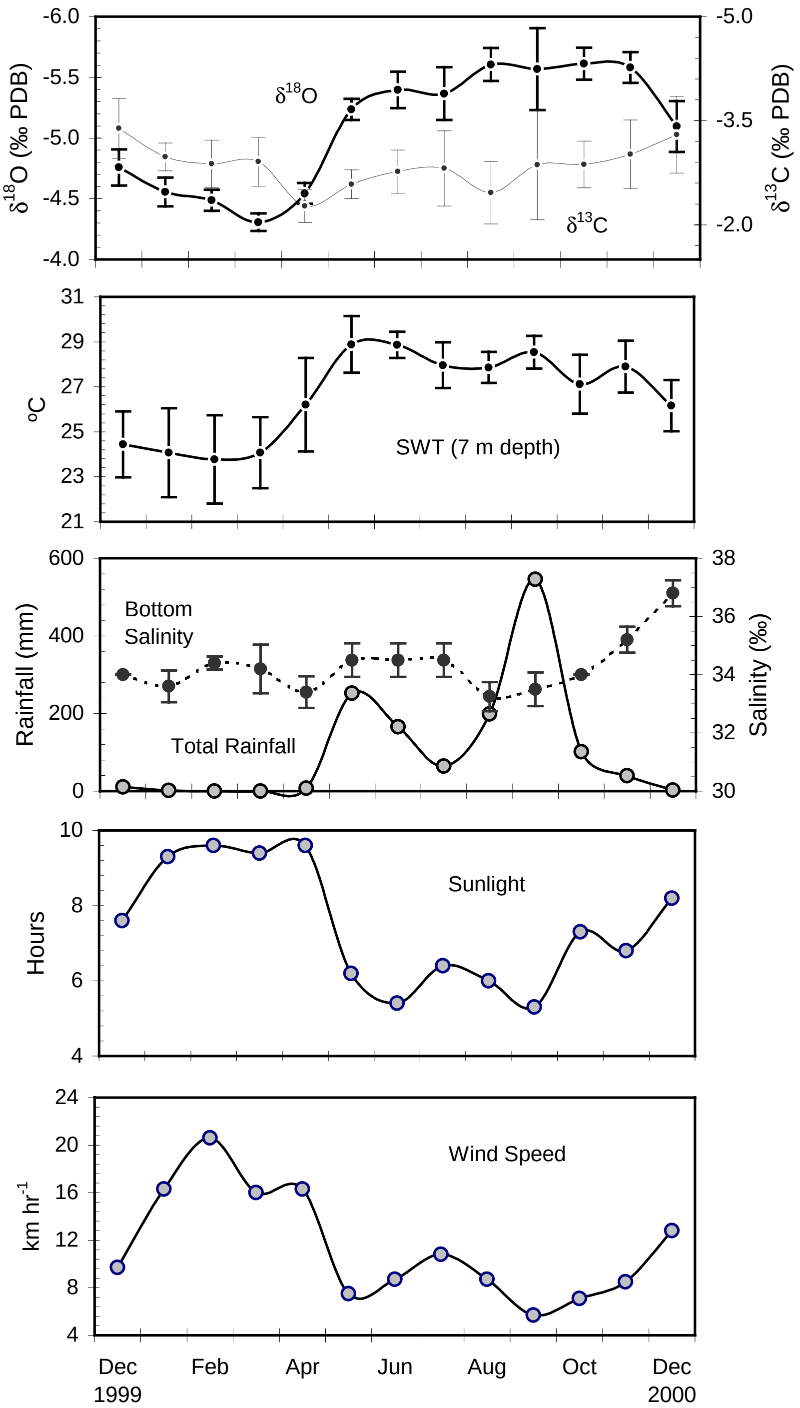

Figure 14 Averaged monthly values of δ^{18}O and δ^{13}C (24 samples per month), seawater temperature (SWT) and salinity (7 m depth), and three meteorological variables. Bars mark 1 standard deviation. Only δ^{18}O values were strongly correlated with SWT, sunlight, and wind, and fairly correlated with rainfall.

In order to explore the possible causal factors for the seasonal δ^{18}O and δ^{13}C trends, the combined isotope records were compared against environmental variables (Fig. 14). For these averaged data, δ^{18}O is strongly correlated with temperature, sunlight, and wind, and fairly correlated with rainfall. On the other hand, δ^{13}C was not significantly correlated with any of the variables (including δ^{18}O). The δ^{18}O results indicate that the environmental variables are well correlated to each other, reflecting the dominant seasonal pattern in the Papagayo area. For example, during the onset of the dry season (clear skies, strong winds, zero precipitation), the upwelling of Papagayo (drop in sea temperature) is triggered (Jiménez 2001a). The δ^{18}O high correlation with four of the five environmental variables suggests that δ^{18}O derived from *P. clavus* skeletons can be used as a proxy for environmental reconstruction in the study area.

The strong *P. clavus* δ^{18}O correlation with environmental variables, such as seawater temperature, sunlight, wind speed and rainfall, suggests that this species can be used as a proxy record of environmental conditions in the Golfo de Papagayo.

The preliminary results outlined above are the first step in providing a comprehensive evaluation of the capacity of massive colonies of *P. clavus* from the Papagayo area, for the recording of environmental parameters. This coral species has been used before for reconstructing some environmental variables (Shen et al. 1992, Dunbar et al. 1994, Wellington and Dunbar 1995, Grottoli and Wellington 1999). We will expand these preliminary analysis by monitoring for the δ^{13}C and δ^{18}O of seawater from samples collected directly above the corals at the Pavona reef, in Bahía Culebra. The sampling stations are the same utilized to collect the corals for the skeletal isotope analysis. The objective is to track seawater δ^{13}C and δ^{18}O during a complete seasonal cycle (rainy and dry season, upwelling and non-upwelling conditions), and to correct the skeletal isotope concentration for seawater effects. Finally, with the corrected values and the seawater temperature, we intend to produce an equation that describes the relation between those parameters (i.e. paleotemperature equation).

With these preliminary results, we initiated the process of evaluating the reliability of *P. clavus*, at the Golfo de Papagayo, to be used in climate reconstruction studies. Currently, we are complementing the study of coral isotopes by monitoring the δ^{13}C and δ^{18}O of seawater, and, thus, relating the coral isotope composition to that of the water. This is a very important aspect, which is not commonly done with water samples and corals of the same study site.

5 Concluding Remarks

After the general review of the principal results of the five papers that comprise this thesis, several concluding remarks can be postulated. These remarks underline the complexity of studying the impact of warming events upon coral reef communities. Conceivably they may contribute to set directions for future research on corals and warming events.

- Not all major warming events can be unambiguously related to catastrophic mass bleaching and mortality of corals. Spatial and temporal differences exist which may be related to biological processes other than the warming itself, though oceanographic settings do have a role as well. Furthermore, there is evidence of enhanced coral reproduction and recruitment during warming events. The dictum that El Niño episodes are detrimental to coral reef communities has to be revised, due to evidence of dissimilar effects upon coral communities.

- Baseline data must be produced during years without any abnormal rise in sea temperature. Live coral cover, status of individual colonies and monitoring of zooxanthellar densities during “normal” conditions will prove extremely valuable when bleaching events are triggered. Ancillary information derived from satellites (sea temperature, solar radiation, cloudiness) is accessible almost on a daily basis and can assist to typify these periods, when the field work and observations are conducted.

- Doldrum-like weather by itself does not pose great danger to corals in the studied areas of Costa Rica, as evinced from the absence of mass-bleaching during such conditions (though in shallow, reef flats minor bleaching has been observed). Although a rapid rise of sea temperature is known to have triggered bleaching and mortality of corals elsewhere, our studies suggest that it is the interaction between both factors that had a negative effect on Costa Rican coral reef communities.

- Another bleaching event and concomitant mortality of corals occurred in August-September 2001 in the Papagayo area, in conjunction with calm spells. Only colonies of branching corals were affected, and they were interspersed among fully pigmented colonies. These telltale occurrences strengthen the point made throughout this review, that the mechanisms for mass-bleaching of corals are more complex than previously thought, and their implications for the entire coral reef community are highly dependent on the combination of community structure, algal symbiont clades and stress history.

- Is the impact of warming events on Costa Rican coral reef communities properly gauged, either by percentages of tissue loss or mortality of colonies? Our results indicate that both parameters are needed, but may well provide a wrong depiction of the impact if they are restricted to the bleaching period. Mortality does not end with the demise of the warming episode, it may continue for months after the thermal stress has subsided. Therefore, monitoring of the status of coral communities and symbiont densities should continue, even though the oceanographic settings have returned to normality.

- Is it necessary to continue monitoring and documenting the fate of Costa Rican coral reef communities during forthcoming warming events? Research, as the one conducted here, is important, because manifestations of mass bleaching and mortality of corals may not have always been engrained in historical El Niño and the Southern Oscillation rhythms. The strong El Niño episodes of 1957-58 and 1972-73 passed without any known concomitant mass mortality of corals. (The 1960s and 1970s was a period of active coral reef research and any geographical-scale bleaching event could not have gone unnoticed.) It is crucial, therefore, to document and study any bleaching and mortality events that may occur to ascertain whether the apparent increase in bleaching frequency since the 1980s is a real trend or an artifact caused by the increase in the numbers of observers.

- During the years between warming episodes, the coral reef communities in Costa Rica have shown variable capabilities to recover. At some localities, live cover and the abundance of important species have not yet attained pre-warming values. This trend may certainly be aggravated by the ever increasing anthropogenic impacts and any increase in the frequency and strength of warming events.

- Our preliminary results on the isotopic ($\delta^{13}C$ and $\delta^{18}O$) composition of *Pavona clavus* suggest that these species is suitable to be utilized in environmental reconstruction studies in the Golfo de Papagayo area. However, two other results have important implications for paleoclimatic reconstructions. First, we found significant inter and intra-colony isotopic variations, and second, El Niño signature of very strong episodes can be attenuated. These observations suggest that climatic reconstructions based on reef corals should contemplate the analysis of several cores instead of one from a single colony. Obviously, this is a trade off between budget, time, and human resources, but the benefits may well worth the effort.

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PUBLICATIONS

This thesis consists of four manuscripts already published in reviewed scientific journals, or in the process of been reviewed by external referees of the journal, and a fifth manuscript, which is the preliminary results of an ongoing study on coral skeletal isotopes. The manuscripts, arranged in chronological order depending on the warming event that they documented, are mentioned in the list below.

PUBLICATION I

Effects of the 1991-92 El Niño on scleractinian corals of the Costa Rican central Pacific coast

Published as:

Jiménez, C. and J. Cortés. 2001. Effects of the 1991-92 El Niño on scleractinian corals of the Costa Rican central Pacific coast, *Rev. Biol. Trop*. 49 (Supl. 2): 239-250.

The original idea for this study was developed by the two authors. The first author conducted the field and laboratory work, data analysis and wrote the first version of the manuscript. The last version was achieved with the cooperation of the second author.

PUBLICATION II

Bleaching and mortality of reef organisms during a warming event in 1995 on the Caribbean coast of Costa Rica

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Jiménez, C. 2001. Bleaching and mortality of reef organisms during a warming event in 1995 on the Caribbean coast of Costa Rica, *Rev. Biol. Trop*. 49 (Supl. 2): 271-275.

The author was responsible for all phases of the study.

PUBLICATION III

Coral bleaching and mortality associated with the 1997-98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica)

Published as:

Jiménez, C., J. Cortés, A. León and E. Ruíz. 2001. Coral bleaching and mortality associated with the 1997-98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica), *Bull. Mar. Sci*. 69: 151-169.

The concept and initial idea for this publication were elaborated by the first author, who conducted and coordinated the field work; this last activity together with the second author. The fourth author collaborated in all phases of the expeditions. Monitoring of temperature was done by the first author in collaboration with the third author. Data analysis and first version of the manuscript were the responsibility of the first author. The final version was prepared by the first author together with the second, and improved with the cooperation of the other co-authors.

PUBLICATION IV

Coral cover change associated with El Niño, central Pacific coast of Costa Rica, 1992-2001

Submitted as:

Jiménez, C. and J. Cortés. Coral cover change associated to El Niño, central Pacific coast of Costa Rica, 1992-2001

The original concept for this contribution was elaborated by the first author and discussed with the second. The first author conducted the field work, the analysis of data, and the first version of the manuscript. The last version was prepared with the cooperation of the second author.

PUBLICATION V

Stable Isotopic (δ^{13}C and δ^{18}O) Composition in the eastern Pacific coral *Pavona clavus*: Seasonal and Intraspecific Variation and Response to Environmental Variables

In preparation:

Carlos Jiménez, Andreas Mackensen, Thomas Brey, Matthias Wolff, Alberto León and Jorge Cortés

The original concept for this contribution was elaborated by the first author and discussed with the other co-authors. Field work was done by the first author in collaboration with the fifth and sixth co-authors. The first two authors did all laboratory work. The first author is currently analyzing the data and preparing preliminary versions of the contributions to be discussed with the other collaborators.

EFFECTS OF THE 1991-92 EL NIÑO ON SCLERACTINIAN CORALS OF THE COSTA RICAN CENTRAL PACIFIC COAST

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ABSTRACT

Coral communities on the central Pacific coast of Costa Rica were affected during the 1991-92 El Niño warming event. More than 57% of all observed colonies at three localities (Parque Nacional Manuel Antonio, Punta Cambutal, and Parque Marino Ballena) were bleached. Mortality during this El Niño was much lower (~9%) than in previous events. *Psammocora* spp. accounted for ~66% of dead corals, while massive (*Porites lobata*, *Pavona* spp.) and branching (*Pocillopora* spp.) for ~34%. Our results suggest that the observed bleaching in *P. lobata* was related to zooxanthellar densities and not to changes in pigment concentrations: only chlorophyll *a* varied between normally pigmented and bleached colonies at one locality (Ballena). Site differences in zooxanthellar densities or their pigment concentrations, may not be the result of the bleaching event itself, because a percentage of dead corals and zooxanthellar densities of bleached colonies seems to follow a trend with the exposure to tidal regimes and currents at each site. Local oceanographic conditions can be influencing the zooxanthellar densities and their response to the warming, together with intrinsic differences between colonies as well. The impact of this event can be considered serious given the short period of time that elapsed between El Niño related mortalities and the slow reefs recovery, the mode of reproduction of reef building species, and the anthropogenic-originated disturbances which affect the coral communities and reefs of the Costa Rican central Pacific coast.

Key words: El Niño, ENSO, bleaching, corals, Costa Rica, zooxanthellae, eastern Pacific

INTRODUCTION

The 1990s are considered the warmest years on record (Vogel and Lawler 1998) and included the strongest El Niño event of the century (McPhaden 1999). This decade has also witnessed coral bleaching and mortality events worldwide at unprecedented scale (Anonymous 1998, Wilkinson *et al*. 1999). Whether this bleaching events are the result of a large scale global warming and/or a combination of physical and biological factors acting locally, coral reefs of the world are facing rapid deterioration (Bryant *et al*. 1998). Therefore, it is important to record all bleaching events regardless of their magnitude or extent, in order to find patterns, if any, and to relate this to the coral’s health. As a baseline, a detailed account of bleaching events (such as the one described here) will assist in understanding the history and fate of coral communities and reefs of the Pacific coast of Costa Rica, which are under heavy pressure by anthropogenic and natural disturbances (Cortés and Jiménez in prep.).

The unusual period of extended warmth, observed in the tropical Pacific Ocean in the early 1990s, appears to be different from what was observed in previous decades (Goddard and Graham 1997, Zhang *et al*. 1998), and the nature of this warming has been of ample debate: Is it a forced global warming, expressed as a single 1990-95 El Niño event, or just decadal variability? (see Trenberth and Hoar 1996, 1997, Latif *et al*. 1997, Rajagopalan *et a*l. 1997). In any case, the 1991-92 warming event began in September 1991 with a dramatic relaxation of the easterly trade winds (Janowiak 1993), peaked in March-April 1992 , and returned to cold sea-surface temperature (SST) by August 1992 (Kousky 1993, Kessler and McPhaden 1995). However, it is considered to have lasted until 1993, with a briefer warming in March-April 1993 (Kessler and McPhaden 1995). It is suggested that, after the 1991 Pinatubo eruption, the 1991-92 warming seemed to have greatly increased (amplified) (Self *et al*. 1997).

The 1991-92 event reduced the primary productivity (Barber *et al*. 1996), the ocean-atmosphere CO_2 flux (Feely *et al*. 1995), and the carbon and nutrient concentrations (Wanninkhof *et al*. 1995) in the equatorial Pacific, and produced significant community changes on bottom macrobenthos at the central Peruvian Coast (Tarazona *et al*. 1995). Manifestations at mid-latitudes ranged from coherence with the north Atlantic Oscillation (Huang *et al*. 1998), to heavy rainfall in California (McPhaden *et al*. 1998), and to nutrients depletion and warming off the North American coast (McPhaden 1994, Chavez 1996).

Coincidental with the mature phase of this warming event, we recorded coral bleaching and mortality at the central Pacific coast of Costa Rica. Bleaching is the disruption of the symbiosis between the coral and photosynthetic zooxanthellae by stressors such as exposures to extremes in temperature, ultraviolet radiation, salinity, oxygen, pollutants and bacterial infections (Glynn and D'Croz 1990, Szmant and Gassman 1990, Gates *et al*. 1992, Kushmaro *et al*. 1996, Jones 1977a, Hoegh-Guldberg 1999), resulting in loss of zooxanthellae and/or its pigments and the subsequent paling or bleaching of the colony. Although it is not always possible to identify the source of stress (Brown 1987), this loss of coloration is present in other natural or experimentally stressed invertebrates (Jokiel 1980, Muscatine *et al*. 1991). There is evidence that, when the zooxanthellae photoinhibition sensitivity is impaired or lowered, coral bleaching is produced (Hoegh-Guldberg and Jones 1999), particularly under conditions of higher than normal temperatures. There are a number of cellular mechanisms which reduce zooxanthellar densities in bleached corals. These are degeneration of cells *in situ*, and release of zooxanthellae from mesenterial filaments and within host cells (Gates *et al*. 1992, Brown *et al*. 1995). The zooxanthellae chlorophyll pigments allow light absorption, and corals or sections of colonies with higher concentration of pigments seem to be more efficient in capturing light (Muller-Parker and D'Elia 1997).

Here we present an account of the coral bleaching and mortality, zooxanthellae loss and pigment concentration at three localities of the Pacific coast of Costa Rica during and after the 1991-92 El Niño.

MATERIALS AND METHODS

Study sites: Coral communities were observed for bleaching at three localities of the central Pacific coast of Costa Rica (Fig. 1): in Parque Marino Ballena (Ballena) during four day field trips from May to November 1992, and Parque Nacional Manuel Antonio (Manuel Antonio) and Punta Cambutal (Cambutal) in June and November 1992. Patch reefs of *Porites lobata* Dana 1846 are common in protected coves and near sandy beaches of Manuel Antonio (Jiménez and Cortés submitted). Dead *Pocillopora* frameworks are overgrown with live colonies of *Pocillopora elegans* Dana 1846, *Pocillopora damicornis* Linnaeus 1748, and *Psammocora* spp. Live coral coverage (LCC) is relatively high (33.7 ± 19.3%, range 9.2–81%) (Jiménez and Cortés submitted). Coral communities upon basalt or sand of Punta Cambutal are located at a semi enclosed cove and have a LCC of 24.8 ± 11.6% (range 6.6-36.4%) dominated by *P. lobata*. Pacht reefs and coral communities of Ballena consist mainly of the massive species *P. lobata*, *Pavona gigantea* Verrill 1869 and scarce *Pocillopora* spp. (Jiménez and Cortés submitted). LCC is low (7.6 ± 2.0 %, range 1.1-19%) but increases at the submerged banks and islets of the park.

Coral bleaching observations: The occurrence of bleaching and mortality were determined by diving along four transects in Manuel Antonio (500 x 3 m long; 2-4 m depth), one at Cambutal (300 x 3 m; 2-4 m depth), and four at Ballena (600 x 2.5 m; 0.5-6 m). A colony was considered normal if it had no signs of bleaching; bleached if it showed more than 5% of the colony area white; dead if it was recently overgrown by algae. In order to monitor the condition of several large (1-1.5 m diameter) colonies of a massive coral, *P. lobata*, tags were driven with steel nails into six colonies per study site (2-4 m depth, June 1992), recording the coral's appearance at the moment of tagging. Additionally, water column temperature was recorded several times during dives utilizing a calibrated bulb thermometer (0.05 °C accuracy). On subsequent visits during 1993 (April, May) and 1994 (June), only general observations on the state of the communities were made.

Zooxanthellar densities and chlorophyll concentrations: On 13 June 1992, one fragment was sampled from eight normal and eight bleached colonies of *P. lobata* from Ballena (2-4 m depth) and Cambutal (3-4 m), and the following day from Manuel Antonio (2-4 m). All coral fragments were frozen and transported (5 hr) to the laboratory packed in ice. Within one month, tissues were removed from the skeletons utilizing an Airbrush (*sensu* Szmant and Gassman 1990). The zooxanthellar density was determined in the tissue homogenate from eight replicate grids per sample using a hemacytometer. Zooxanthellae were normalized to the homogenate volume and area of the coral fragment. For zooxanthellar chlorophyll (chl) *a* and *c* analysis, coral fragments were placed in 10 ml acetone 90% for 24 h at 5°C (Lorenzen and Jeffrey 1978). Samples (10 ml) were then centrifuged for 10 min at 3000 rpm, and the absorbances of the supernatant were read on a Schimadzu UV-160A spectrophotometer. The equations of Jeffrey and Humphrey (1975) were used to calculate chl-*a* and chl-*c* concentration which were normalized with the fragment's area and expressed as μg cm^{-2}. The Barlett and Hardy test was used to evaluate the normality of data and the Cochran test to evaluate the heterogeneity of variances (Underwood 1997), and the data were analyzed using Student's *t*-test and ANOVA to compare normal and bleached colonies and localities respectively.

RESULTS

Coral bleaching observations: The first reports of bleaching along the central Pacific coast of Costa Rica during the 1991-92 El Niño event were in mid March 1992 from Manuel Antonio (B. Hedges, pers. com. 1992) and in April from Ballena (C. Gamboa, pers. com. 1992). Other bleaching reports in Costa Rica were in April at the southern Península de Osa (M. Nagy, pers. com. 1992), Isla del Caño (Guzmán and Cortés in press), and Isla del Coco (M. Montoya, pers. com. 1992). In May 1992, coral bleaching was still wide spread in Ballena, and in June and November in Manuel Antonio and Cambutal. Although no new bleached corals were observed during the November survey (some bleached colonies indeed started to recover their pigments by then, see further down), some previously bleached corals died.

Seawater temperature (SWT), measured by the park rangers at 0-2 m depth in Ballena, was between 33 and 34°C during doldrum conditions which prevailed for several days in March-April 1992 (peak of the warming event). This corresponded to an increase in SWT of ~4-6°C from the COADS (Woodruff *et al*. 1987) monthly mean (28.5 ± 0.7°C, range 26.3-30.3°C) calculated for the zone (grid centered at 9°N 84°W) during the warm, dry season (December/March). During the aftermath of the 1991-92 El Niño event, mean SWT continued to be above 29°C at all three localities in June 1992 (Table 1), but in November it cooled below 28°C.

During our surveys, starting in May 1992, coral bleaching was recorded down to a depth of 8 m and it was not possible to observe a definite bleaching pattern in the affected colonies: massive colonies (*P. lobata*, *Pavona clavus* Dana 1846, *P. gigantea*) bleached indistinctly at the tops, flanks or sides in gradual or discrete patches; branching corals (*Pocillopora* spp.) and *Psammocora* spp. bleached whole or at certain branches which started to be colonized by filamentous algae. Pink pustules surrounding bleached sections of massive colonies were abundant at all localities and depths. It was also common to observe normally coloured or pigmented colonies interspersed with neighboring bleached or dead colonies.

The incidence of normal, bleached and dead colonies varied considerably among coral species and locality (Fig. 2). At Manuel Antonio, *Psammocora* spp. was the most affected coral with ~40% of all colonies dead, while more than 60% of all *Pocillopora* spp. colonies were bleached (Fig. 2a). At Cambutal, 38 km south of Manuel Antonio (Fig. 1), the situation was inverse: *Pocillopora* spp. had the highest percentage of dead colonies (20%), and *Psammocora* spp. of bleached colonies (~80%) (Fig. 2b). Interestingly, colonies of *P. gigantea* at this locality remained pigmented and showed no signs of any discoloration or dead portion in the tissue. At Ballena, approx. 50 km south from Manuel Antonio (Fig. 1), *Pocillopora* and *Psammocora* were again the most affected species, with the highest percentage of dead (~18%) and bleached (88%) colonies respectively (Fig. 2c). *P. lobata* was another species which showed differences among localities, having in Manuel Antonio and at Cambutal the highest percentage of dead and bleached colonies respectively (Fig. 2).

Grouping all coral species per study site (“Total” in Fig. 2), it is easier to identify Manuel Antonio as the most affected locality during the 1991-92 El Niño event: the percentages of bleached (~60%) and dead (~4%) colonies were similar at Cambutal and Ballena respectively, whilst Manuel Antonio had the highest percentage of dead corals (~21%).

Considering all coral species from the three localities, ~57% of all observed colonies (n= 1849) bleached during the 1991-92 El Niño event, and mortality was ~9%. *Psammocora* spp. accounted for ~66% of dead corals, and massive and branching corals for ~33%. Comparing these results with the impact of the 1997-98 El Niño on corals of the northern Pacific coast of Costa Rica (Jiménez *et al*. in press), bleaching and mortality were lower in 1997-98 (~32 and ~6% respectively). *Pocillopora* spp. accounted for ~84% of the total mortality, and massive corals and *Psammocora* spp. for ~16%.

The tagging in June 1992 of large colonies of *P. lobata* (six at each locality), helped to notice changes (if any) in the condition of individual colonies that occurred until our last survey in November 1992 (Table 2). The six fully pigmented colonies (“normal”) showed no change, including the one with the pink pustules. From 12 colonies which had bleached either at their tops, flanks or all over, four remained bleached and had tissue partial mortality (TPM), six changed to a pale tan coloration with TPM (except for colony 17), and two acquired a dark brown or mustard coloration (considered normal) with TPM (one had also purple pustules).

By November 1992, as mentioned earlier, no further noticeable bleaching was observed. The remaining bleached colonies were the ones observed before (June), and mortality (mostly TPM in massive corals) was still recorded. Small stands of *Psammocora* spp. were completely overgrown by a mat of brown algae in Manuel Antonio and Cambutal. At Ballena, in several medium sized *P. lobata* colonies, territorial damselfish were observed with expanded algal mats over the corals' TPM areas colonized by algae. At all localities, mortality of whole colonies was noticed to have been more common in *Pocillopora* spp., *Psammora* spp. and small (<20 cm diameter) *P. lobata*, particularly at 1 to 3 m depth.

The sites were visited twice in 1993 and once in 1994. Some of the corals previously bleached had overgrown the TPM sections which were formerly invaded by filamentous algae. More commonly, sponges, coraline algae, barnacles and polychaetes thrived at the spots were the TPM was observed. No large *P. lobata* colonies were found dead, and some of the former bleached corals had overgrown the TPM and the tags, preventing further individual identification.

Zooxanthellar densities and chlorophyll concentrations: When comparing zooxanthellar densities between localities (Fig. 3a), normal pigmented colonies of *P. lobata* had no significant differences ($p>0.05$, df=2, F= 0.23, ANOVA) and ranged from 6.5 to 7.9 cells 10^5 cm^{-2}. On the other hand, zooxanthellar densities in bleached colonies varied significantly ($p<0.01$, df=2, F= 10) according to locality, being the lowest in Manuel Antonio (0.04 ± 0.04 cells 10^5 cm^{-2}) and the highest at Ballena (3.1 ± 2.5 cells 10^5 cm^{-2}) (Fig. 3a). Normally pigmented colonies had significantly higher zooxanthellar densities (Student's *t*-test, df=7) than bleached colonies at all localities (Manuel Antonio $p<0.01$, t=2.36; Cambutal $p<0.01$, t=2.36; Ballena $p<0.05$, t=2.2). For example, at Manuel Antonio, mean zooxanthellar density was more than 150 times higher in normal than in bleached colonies, while at Cambutal and at Ballena was 12.7 and 2.5 times respectively.

Pigments' concentration (chl-*a*, chl-*c*, Fig. 3b, c) had no significant differences ($p>0.05$) among localities in either normal or bleached colonies. Additionally, only at Ballena the concentration of one of the pigments, chl-*a*, was significantly higher ($p<0.05$, df=8, t= 2.54) in normal (1,1 ± 0,8 μg cm^{-2}) than in bleached (0,4 ± 0,2 μg cm^{-2}) colonies.

DISCUSSION

A vast majority of mass coral bleaching (on a geographical scale) have been associated with warmer than normal SWT (Glynn 1993, 1996, Hoegh-Guldberg 1999). In 1991, a mass bleaching event occurred in almost all coral reef regions of the world (Goreau and Hayes 1994) and it was coincidental with the onset and development of the 1991-92 El Niño (Glynn 1996). It was not until May of 1992 that extended bleaching occurred in the eastern Pacific, specifically at the central Pacific coast of Costa Rica. During May 1992, a small and localized bleaching event was also reported in the Caribbean Sea (Winter *et al*. 1998). Subsequent bleaching events were reported in 1994 and 1995, non-ENSO years (Glynn 1996).

The 1991-92 El Niño effects in Costa Rica were restricted to the central and southern coast. Other localities were visited in the north of the country, Bahía Culebra (27-28.IV.1992) and Sámara (24-26.IV and 17.VII.1992) (Fig. 1), but no evidence of coral bleaching or recent mortality that could be attributed to the on-going warming event was observed. In contrast, the 1982-83 warming event affected corals at widely separated localities along the Pacific coast: Bahía Culebra, Sámara, Isla del Caño, Manuel Antonio and several areas around Ballena (Cortés *et al*. 1984, Guzmán *et al*. 1987). At Manuel Antonio, no live corals were seen in November 1983, and at Ballena, bleached corals were noticed, though no evidence of massive mortalities was found during the short survey. At those localities, branching corals (*Pocillopora* spp.) and *Psammocora* spp. were more affected than massive species (Cortés *et al*. 1984), as we noted during the 1991-92 El Niño. At Isla del Caño, live coral cover was reduced by approximately 40% during the 1982-83 El Niño (Guzmán *et al*. 1987). Live coral cover was unaffected by the 1991-92 event, and reduced by 5% after the 1997-98 El Niño (Guzmán and Cortés in press).

Although on a regional scale the 1991-92 El Niño was not as severe as the 1982-83 event (less than 9% coral mortality in 1991-92 vs. 50-90% in 1982-83), its impact was far from negligible because the coral communities affected were recuperating from previous events. For example, in 1987-88, coral bleaching and mortality were observed by divers at Manuel Antonio (J. Cruz, pers. com. 1992) and at Cambutal (H. Sánchez, pers. com. 1992), coincidental with a strong El Niño event (Kessler and McPhaden 1995). The impact of both events could explain the abundance of large, dead massive colonies of *P. lobata* and *P. clavus*, and stands of *Pocillopora* spp. and *Psammocora* spp. in Manuel Antonio, Cambutal and Ballena.

Our results indicates that *P. lobata* response to the 1991-92 El Niño related bleaching was mainly the expulsion of zooxanthellae without a significant change in pigment concentration. Bleached colonies had reduced zooxanthellar densities compared to full pigmented colonies, and in all sites but one (Ballena, chl-*a*), they did not have a generalized decrease in the zooxanthellar specific pigments, as noted in other bleached corals (e.g. Hoegh-Guldberg and Smith 1989, Le Tissier and Brown 1996, Jones 1997b). Although a lowering of chlorophyll's concentration in bleached corals have been reported (Kleppel *et al*. 1989, Brown *et al*. 2000), there are no reports of bleaching exclusively due to pigments loss (Hoegh-Guldberg 1999), and the reasons for that remains unclear (Jones 1997b). Additionally, given also the presence of chl-*a* in the endolithic green algae hosted in the coral skeleton (Kleppel *et al*. 1989), we can not rule out their potential interference with our analysis. In general, chlorophyll concentrations are known to vary considerably depending on the species, the depth of collection, light exposure, and degree of photosynthetically active radiation and ultraviolet light (Dustan 1979, Titlyanov 1981, Kinzie *et al*. 1984, Hoegh-Guldberg and Smith 1989, Brown *et al*. 2000). Furthermore, it has been found that concentration of a particular pigment can be higher or lower than another (e.g. Titlyanov 1981, Kinzie *et al*. 1984), and this calls for caution when searching for a pattern between pigmented and bleached colonies. Whether the concentrations reported here for the normal pigmented colonies are typical for *P. lobata*, is a topic that needs to be studied in more detail.

Zooxanthellar densities reported here varied from 6.5 to 7.9 cells 10^5 cm^{-2}, which are in the range documented for other scleractinian corals: between 5 and 200 cells 10^5 cm^{-2} (Hoegh-Guldberg and Smith 1989, Brown *et al*. 1995, 2000). These broad variations can be related to seasonal changes in population densities of zooxanthellae (Fagoonee *et al*. 1999) and inherent differences between colonies and species (Jones 1997a), which can make the sampling of similar symbionts densities difficult when comparing colonies in space and time. Although these changes may account for the small observed variations in normal corals, the zooxanthellar densities in bleached colonies appear to follow a geographical gradient according to exposure level to tidal regimes and currents of the study site. Surveyed coral communities at Manuel Antonio, showed the lowest zooxanthellar densities and they are located in more enclosed and protected coves than in the other two sites. The enclosure nature of Manuel Antonio probably facilitates the entanglement of water by eddies formation reducing water exchange with open waters, which in its turn may amplify the thermal stress due to the warming event. In a lesser extent, Cambutal is a semi enclosed cove but with much more water exchange during tidal fluctuations than at Manuel Antonio. Although eddies and entanglement of phytoplankton blooms have been observed in Ballena (Cortés and Jiménez in prep.), corals are more exposed to surge and open waters than at the other study sites.

If *P. lobata* loses its symbionts, but pigment concentration do not change significantly, the coral metabolic functions may not be impaired, and they may probably continue at a lower level. The latter has been related to the lowering of growth rates, healing and shedding of sediments capacities, and the higher susceptibility to diseases of bleached *vs*. pigmented corals (Goreau and MacFarlane 1990, Glynn 1993, Meesters and Bak 1993, Mascarelli and Bunkley-Williams 1999). The implications are important as many new epizootic diseases have been observed to be concurrent with bleaching related damage (Goreau *et al*. 1998).

At a local scale, during the 1991-92 warming event, corals were commonly observed to differ in their tendency to bleach and to exhibit a gradation of discoloration intensity, as reported by many authors (Hoegh-Guldberg 1999 and references therein). This was also observed in Costa Rica during one bleaching event coincidental with the 1997-98 El Niño (Jiménez *et al*. in press). Several factors can be responsible for such a variability: light intensity reaching the corals, genotypes of the zooxanthellae and the corals, zooxanthellar cell size, and micro-scale environments (Edmunds 1994, Glynn 1996, Rowan *et al*. 1997, Jones 1997a, Hoegh-Guldberg 1999). Additionally, there is apparently a threshold limit for some corals which defines the level of zooxanthellae loss required for the colonies to discolor. For example, *Acropora formosa* Dana 1846 begin to discolor when they have lost more than 50% of the algal standing stock (Jones 1997b). It is not known if there is any such threshold for *P. lobata*. Studies focused on the zooxanthellae dynamics and responses to periodic El Niño related warmings are needed, particularly concentrating on the main reef building corals in the eastern Pacific.

To summarize, the 1991-92 El Niño related coral mortality in the coral communities of the central Pacific coast of Costa Rica, was less severe than the 1982-83 event, but it affected coral communities that were still recovering. This is a serious problem because they show slow recovery rates from impacts due to the combination of factors such as the main mode of reproduction (asexual), low recruitment, high rates of bioerosion, anthropogenic-generated coastal sedimentation, and phytoplankton blooms (Glynn 1990, Guzmán 1991, Cortés and Jiménez, in prep.). Nevertheless, given appropriate conditions (e.g. absence of catastrophic El Niño events, massive coral mortalities, and management of marine and terrestrial areas), recovery of Costa Rican coral reefs and communities is feasible in the long term (10-14 yr.), as observed in the protected reefs of the national park Isla del Caño (Guzmán 1999, obs. pers.).

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TABLE 1

In situ water temperature (°C) statistics at the three studied sites during the aftermath of the 1991-92 El Niño event.

Date	Locality	Mean	Standard deviation	n	Max.°C	Min.°C	Depth Range (m)
15-16.V.92	Ballena	31.2	0.4	13	32.0	31.0	0-5
12.VI.92	Ballena	29.8	0.3	12	30.5	29.5	0-5
13.VI.92	Cambutal	30.1	0.8	4	31.0	29.5	0-2
14.VI.92	M. Antonio	30.2	0.6	8	31.0	29.5	0-4
13-14.XI.92	Ballena	27.9	0.4	18	28.5	27.9	0-5
14.XI.92	Cambutal	27.7	0.3	6	28.0	27.5	0-2
15.XI.92	M. Antonio	28.0	0.8	8	29.0	27.0	0-3

Monthly mean SST (1971-1987) from April to January is 28.2 ± 0.45°C (Woodruff et al. 1987). n= number of temperature readings

TABLE 2

Condition of the tagged *Porites lobata* colonies at the three study sites during the 1991-92 El Niño aftermath.

Locality	Colony	June 1992	November 1992
Manuel Antonio	1	Bleach at top and flanks	Normal with purple dots, TPM
	2	Bleach mostly at the top	Pale tan coloured
	3	Normal	Normal
	4	Normal	Normal
	5	Normal	Normal
	6	Bleach all over	Bleach, TPM
Cambutal	7	Normal	Normal
	8	Bleach at top and flanks	Pale tan coloured, TPM
	9	Bleach all over	Bleach, TPM
	10	Bleach at top and flanks	Normal, TPM
	11	Bleach mostly at the top	Pale tan, TPM
	12	Bleach mostly at the top	Bleach at the top, TM
Ballena	13	Bleach mostly at flanks	Pale tan coloured, TPM
	14	Bleach all over	Pale tan coloured, TPM
	15	Normal with purple dots	Normal with purple dots
	16	Normal	Normal
	17	Bleach at top and flanks	Pale tan coloured
	18	Bleach all over	Bleach, TPM

Bleach= more than 5% of colony area white coloured. TPM= tissue partial mortality with overgrowing algae

FIGURE CAPTIONS

Figure 1. Study sites at the Costa Rican central Pacific coast. 1. Parque Nacional Manuel Antonio (Manuel Antonio in the text and other figures); 2. Punta Cambutal (Cambutal); 3. Parque Marino Ballena (Ballena). Other localities mentioned in the text: Bahía Culebra (B.C.), Sámara (SA.), Isla del Caño (I.C.) and Península de Osa (P.O.).

Figure 2. Percentage of normal (black bars), bleached (white) and dead (stripped) coral colonies at the three studied sites during May, June and November 1992. PL= P. lobata, PO= Pocillopora spp., PC= P. clavus, PG= P. gigantea, PS= Psammocora spp. n= number of colonies.

Figure 3. Mean (bars) ± standard deviation of (a.) zooxanthellar density; (b.) Chlorophyll-a, and (c.) Chlorophyll-c in normal (black bars) and bleached (white) P. lobata colonies (8 per locality), sampled in June 1992 at the three studied sites. *Differences between normal and bleached colonies are significant ($p<0.05$).

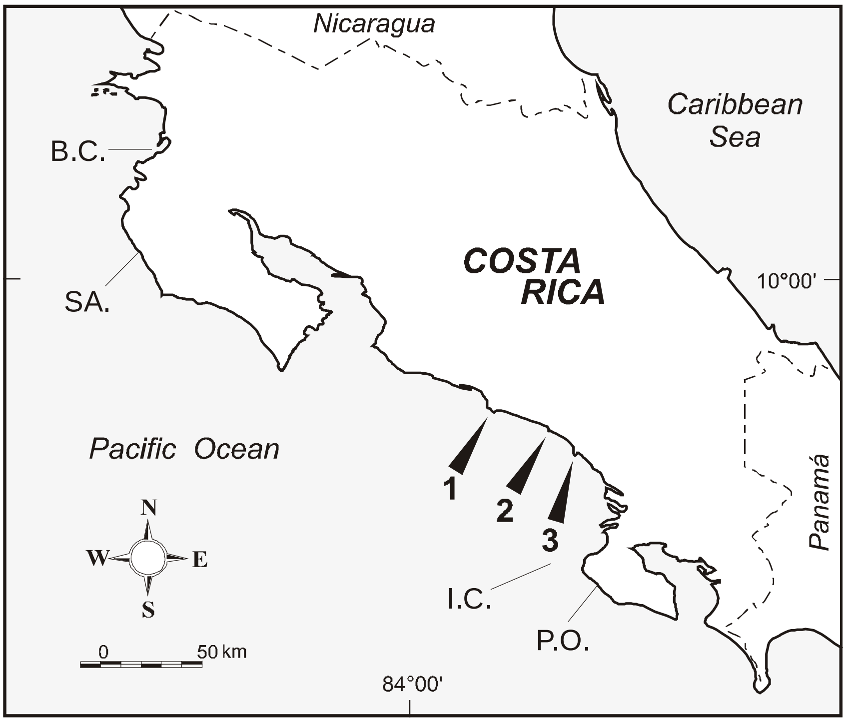
Nicaragua
Caribbean Sea
B.C.
SA.
COSTA RICA
10°00'
Pacific Ocean
1
2
3
N
W
E
S
I.C.
P.O.
0
50 km
84°00'
Panamá

Figure 1

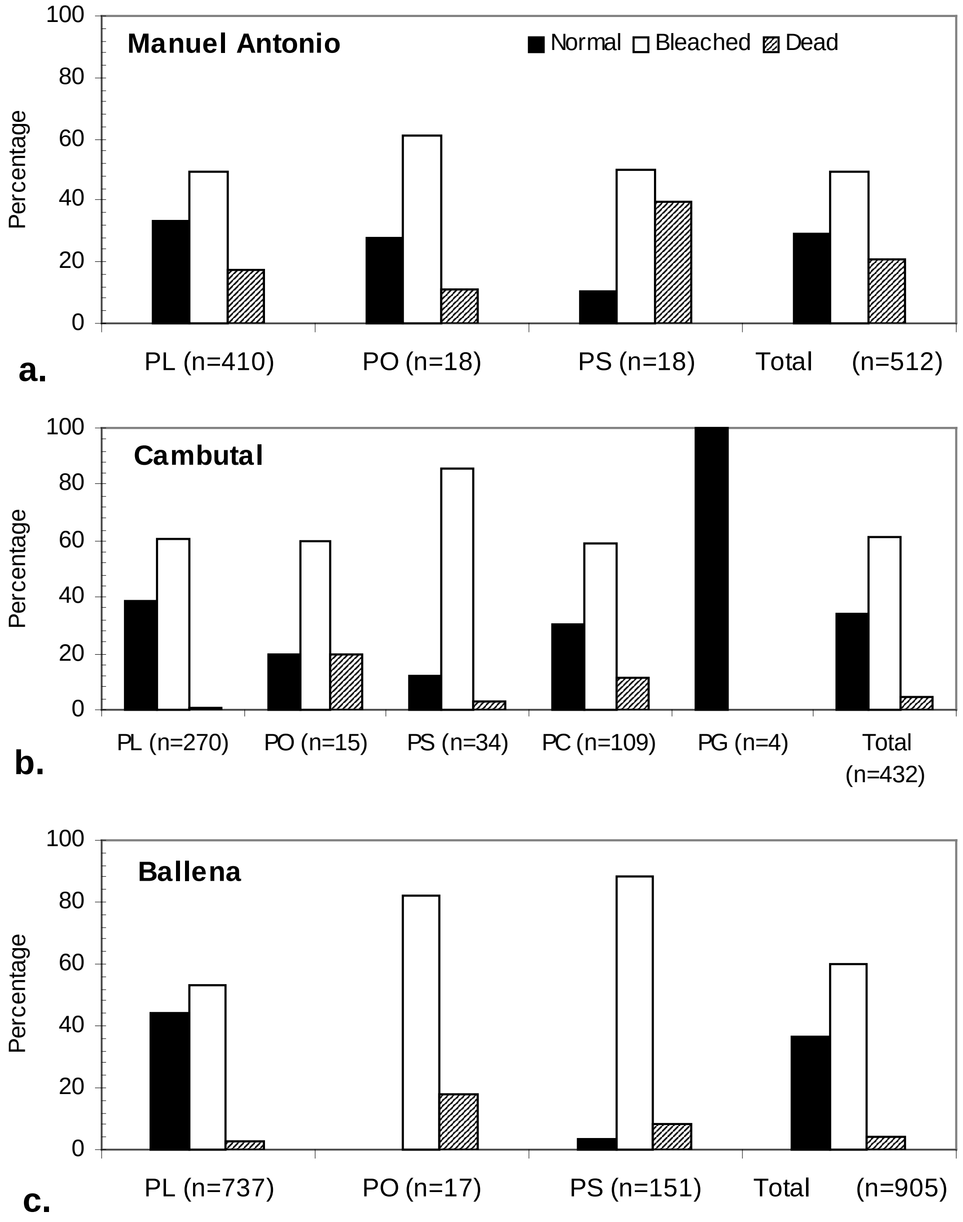
a.
Manuel Antonio
■ Normal □ Bleached ▨ Dead
Percentage
0
20
40
60
80
100
PL (n=410)
PO (n=18)
PS (n=18)
Total (n=512)
b.
Cambutal
Percentage
0
20
40
60
80
100
PL (n=270)
PO (n=15)
PS (n=34)
PC (n=109)
PG (n=4)
Total (n=432)
c.
Ballena
Percentage
0
20
40
60
80
100
PL (n=737)
PO (n=17)
PS (n=151)
Total (n=905)

Figure 2

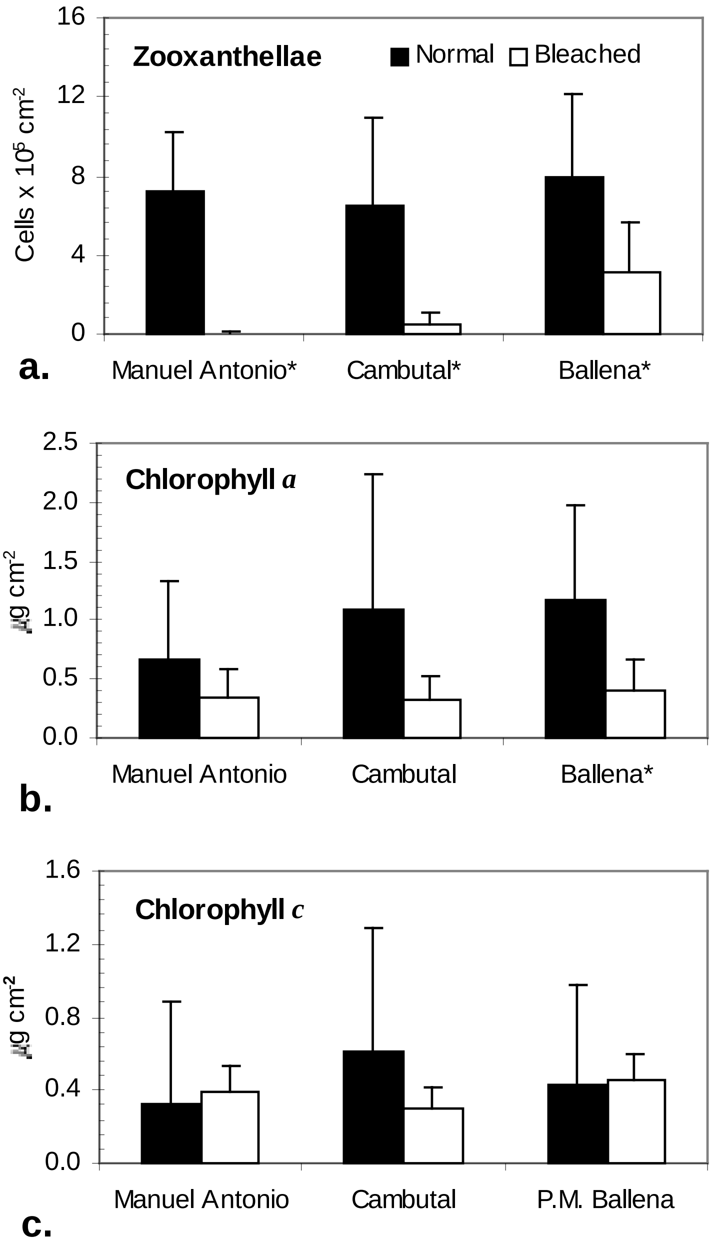
16
12
8
4
0
Cells x 10^5 cm^{-2}
Zooxanthellae
■ Normal ☐ Bleached
a.
Manuel Antonio*
Cambutal*
Ballena*
2.5
2.0
1.5
1.0
0.5
0.0
µg cm^{-2}
Chlorophyll *a*
Manuel Antonio
Cambutal
Ballena*
b.
1.6
1.2
0.8
0.4
0.0
µg cm^{-2}
Chlorophyll *c*
Manuel Antonio
Cambutal
P.M. Ballena
c.

Figure 3

BLEACHING AND MORTALITY OF REEF ORGANISMS DURING A WARMING EVENT IN 1995 ON THE CARIBBEAN COAST OF COSTA RICA

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ABSTRACT

Coral reefs at the Caribbean coast of Costa Rica were affected during a bleaching event associated with the 1995 warming of the Western Caribbean. During doldrum weather in late August 1995, reef organisms at Parque Nacional Cahuita were 62% and 7.4% bleached and dead respectively, whilst 67.6% bleached and 8.2% died in the Refugio Nacional de Vida Silvestre Gandoca-Manzanillo. However, Cahuita had the highest mean number of bleached (257 ± 51.1) and dead (30.5 ± 5.6) colonies in the surveyed transects, and bleaching was observed down to a depth of 20 m. The most affected species (>10% of dead colonies) were the hydrocoral *Millepora complanata* and the scleractinian corals *Montastraea* spp. at Cahuita, and *Porites furcata*, *Porites porites* and *M. complanata* at Gandoca-Manzanillo. Mean seawater temperature was between 30.5 and 31.1°C (0-18 m depth) during four days of observation at the end of August 1995. Coral reefs of the Costa Rican Caribbean coast have shown a rapid decline during the last 20 years due to natural and anthropogenic disturbances. The effect of the 1995 warming added more pressure to the already deteriorated reefs.

Key words: Coral reefs, bleaching, warming, coral mortality, Costa Rica, Caribbean.

NOTE

The bleaching of coral reef organisms has been observed during the last years with an unprecedented scales in almost all coral reef regions of the world (Glynn 1993, 1996, Hoegh-Guldberg 1999). Higher than normal seawater temperature (SWT) has been pointed out as the triggering factor in mass bleaching events (Goreau and Hayes 1994, Glynn 1996, Brown 1997, Hoegh-Guldberg 1999). In the Caribbean region, mass bleaching events have been observed since at least 1940, as a consequence of the impact of Hurricane Flora on Jamaica (Goreau 1964). Thereafter, coral bleaching was reported in the 1980’s in different parts of the Caribbean (e.g. Cortés *et al*. 1984, Williams *et al*. 1987, Williams and Bunkley-Williams 1990), and on a larger scale during the1990’s (Wolfgang 1995, Glynn 1996, Hoegh-Guldberg 1999, Quinn and Kojis 1999), although not all were related with anomalous increase in SWT (e.g. Atwood *et al*. 1992).

In the late summer of 1995, one of the bleaching events occurred throughout the western Caribbean (Rowan *et al*. 1995, Wolfgang 1995, Anonymous 1997, Guzmán and Guevara 1998, Winter *et al*. 1998), with coral bleaching reported for the first time along the Belizean barrier reef (Glynn 1996). At the southern Caribbean coast of Costa Rica, we observed coral bleaching and mortality during 25-28 August 1995 in the Parque Nacional Cahuita and the Refugio Nacional de Vida Silvestre Gandoca-Manzanillo (Fig. 1). The occurrence of bleaching was determined by diving along a 150 m transect parallel to the shore line, and recording bleached and dead coral species within two meters on either side of the transect. At Cahuita (1.5-8 m depth), three transects were laid on the outer reef crest and lagoon, and one on the inner crest (Fig. 1). At Gandoca-Manzanillo (2-10 m), three transects were laid around the reef bordering the town of Manzanillo, and one at the eastern end of the fringing reefs (Fig. 1). A colony was considered bleached when it had more than 5% of the colony area white, and dead when it had been overgrown by algae. SWT was recorded in the water column down to a depth of 18 m with a calibrated bulb thermometer.

Bleaching and mortality were observed in sixteen scleractinian coral species, one hydrocoral and one zooanthid (Table 1). Corals were pale or white, and bleaching pattern was often in small patches. In shallow waters entire colonies were pale, and only in small size corals whole-colony bleaching was observed. At Cahuita, affected colonies were observed down to a depth of 20 m. In the transects, more than 60% of all colonies were bleached and general mortality was around 7% (Table 1). The most affected species were Millepora complanata and Montastraea spp. (>10% of their colonies died).

At Gandoca-Manzanillo, affected colonies were observed down to a depth of 15 m, and bleaching and mortality were around 67% and 8% respectively (Table 1); Porites furcata, Porites porites and M. complanata being the three most affected species, each with more than 10% of dead colonies.

The occurrence of bleaching and mortality was not randomly distributed in the surveyed sites (Chi-square, p<0,001 in all cases). At Cahuita, the highest incidence of bleaching (7.60% of all colonies in the transect) and dead organisms (7-9%) was in the transects II to IV (Fig. 2a), that is, in the northeastern sections of the outer barrier and in the inner small barrier (Fig. 1). At Gandoca-Manzanillo, transects around the town (V, VI, Fig. 1) had the highest percentage of bleaching (~69%) and mortality (8-10%) (Fig. 2b). Significant differences were found only in the mean number of bleached and dead colonies when comparing all transects in both surveyed sites (Fig. 2c). Cahuita had significantly more bleached (257 ± 51.1 colonies, p<0.01 Student’s t-test) and dead (30.5 ± 5.6 p<0.01) colonies than at Gandoca-Manzanillo. These differences in bleaching and mortality incidence could be related to biological and physical factors within and between sites. For example, local oceanographic settings which may create completely different physical environments, are suspected to be acting with a higher than expected genetic variability in zooxanthellae strains and coral colonies (Edmunds 1994, Glynn 1996, Brown 1997, Muller-Parker and D’Elia 1997, Rowan et al. 1997, Winter et al. 1998)

Mean SWT in the water column was between 30.5 and 31.1 °C during the four days of observation at the end of August 1995 (Table 2), and on one opportunity it was 29,5 °C at 15 m depth at Cahuita. Local divers and fishermen in the towns of Cahuita and Manzanillo, indicated that SWT was warmer during doldrum weather conditions (when waters are clear and calm) which lasted almost two weeks prior to our surveys, when they observed changes in the coral’s coloration. Warm SWT and doldrum weather extended until the end of September 1995 (R. Smikle, pers. com. 1996), though it is not known if further bleaching and mortality occurred at the surveyed sites.

At a first glance, the mortality recorded here (7-8% of all colonies) could be taken as minimal, particularly if it is compared with the effects of the 1995 warming on the coral reefs of Cayos Cochinos, Honduras (Guzmán and Guevara 1998). There, affected colonies were recorded down to a depth of 28 m, and mortality ranged from 6 to 86% in scleractinian corals (mainly *Montastraea* spp.) and 74% for the hydrozoan *M. complanata*. Furthermore, a high infection rate of the Black Band Disease or BBD (Antonious 1981) observed in those reefs in 1996, seemed to have been triggered by the 1995 bleaching event, increasing partial mortality of the surviving colonies (Guzmán and Guevara 1998). Whereas in subsequent visits to Cahuita during 1996, surviving colonies showed extensive tissue partial mortality (overgrown by calcareous and fleshy brown algae), few dead whole-colonies were observed. Additionally, only two *Siderastrea siderea* and one *Diploria clivosa* colonies were infected by the BBD. Therefore, the extent of the 1995 bleaching and mortality in the two Caribbean localities of Costa Rica, is comparable to what was observed in Puerto Rico (Winter *et al*. 1998), where few corals died during the same warming event. Also, to the same area of Cahuita during a previous warming event in June 1983, when moderate bleaching and death of reef organisms were observed when SWT along the Caribbean coast of Costa Rica was between 29 and 35°C (Cortés *et al*. 1984).

What makes the observed mortality during the 1995 warming event relevant to the coral reefs of the Caribbean coast of Costa Rica? To answer this, we have to consider the actual situation of those reefs and the processes which are influencing them. The Costa Rican Caribbean reefs are under the negative impact of increased terrigenous sediment loads (Cortés and Risk 1984, 1985, Hands *et al*. 1993, Cortés 1992, 1994, Cortés *et al*. 1998), chemical and solid pollution (Cortés and Guzmán 1985, Mata *et al*. 1987, Guzmán and Jiménez 1992, Rojas *et al*. 1998, Cortés and Jiménez 2002), punctuated uplift of the coast (Cortés *et al*. 1992, 1994, Denyer 1998), mass mortalities of reef organisms (Guzmán and Cortés 1984, Murillo and Cortés 1984), and tourism related activities (Cortés 1994, Cortés and Jiménez 2002, Jiménez, unpublished). All this factors acting in combination have been associated with a significant deterioration of the reefs. Not only near-shore reefs are affected, even offshore submerged banks were observed to have been reached by heavy loads of silt (Cortés and Jiménez 2002). The consequence is a rampant deterioration of the reefs and it explains the observed decrease in live coral cover from 40% in the 1980’s to less than 10% in the 1990’s at Cahuita (Cortés 1994), and from 12 to 7% in less than six years in the northwestern reefs at Gandoca-Manzanillo (Cortés and Jiménez 2002).

Given the poor condition of the coral reefs at the Caribbean coast of Costa Rica, due to the factors cited above, a small to moderate bleaching and mortality could have severe repercussion on the whole reef. That is, the corals which seem to be faring well despite the environmental degradation and which are contributing more to the percentage of live coral cover (Risk *et al*. 1980, Cortés and Risk 1985, Cortés 1994, Cortés and Jiménez 2002), will be affected significantly by any rate of mortality, such as the one reported here. This will be expressed as a general reduction in live coral cover, which, in its turn, will give algae a chance to flourish and to outcompete corals for substrate and light, as has been recorded in several plots at Cahuita (Jiménez unpublished). Hence the need to implement land management policies in the coastal zone and the protection and study of these reefs.

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TABLE 1. Number of affected coral colonies according to species at Cahuita (1,5-8 m depth, 27-28.VIII.1995) and Gandoca-Manzanillo (2-10 m, 25-26.VIII.1995).

Species	Cahuita			Manzanillo		
	Normal	Bleach	Dead	Normal	Bleach	*Dead*
AGARICIA AGARICITES	34	102	11	6	51	2
Agaricia tenuifolia	29	28	1	--	--	--
Acropora palmata	33	38	2	3	6	0
Acropora cervicornis	2	2	0	--	--	--
Siderastrea siderea	37	69	3	12	32	1
Siderastrea radians	44	55	6	11	35	2
Stephanocoenia intercepta	3	1	0	--	--	--
Porites furcata	92	94	13	6	23	6
Porites porites	31	86	6	23	58	10
Porites astreoides	33	103	13	9	54	3
Colpophylia spp.	2	3	0	2	3	0
Diploria strigosa	32	70	7	5	7	0
Diploria clivosa	32	68	8	19	43	3
Favia fragum	9	60	3	7	21	2
Montastraea spp.	5	10	0	--	--	--
Montastraea cavernosa	1	12	2	2	3	0
Millepora complanata	54	182	46	41	76	22
Palythoa caribbea	35	45	1	4	7	0
Total	508	1028	122	150	419	51
Percent per locality	30.6%	62.0%	7.4%	24.2%	67.6%	8.2%

TABLE 2. Seawater temperature (°C) statistics at Cahuita and at Gandoca-Manzanillo, Caribbean coast of Costa Rica. SD= standard deviation; n= number of temperature readings.

Date	Locality	Mean	SD	n	Max.°C	Min.°C	*Depth Range (m)*
25.VIII.1995	Manzanillo	30.5	1.5	26	32.4	28.0	0-15
26.VIII.1995	Manzanillo	30.5	1.3	23	32.4	27.5	0-18
27.VIII.1995	Cahuita	31.1	1.0	28	32.4	29.5	0-15
28.VIII.1995	Cahuita	30.8	1.2	19	32.4	28.0	0-12

FIGURE CAPTIONS

Figure 1. Study sites at the Caribbean coast of Costa Rica and location of transects (Roman numbers): Parque Nacional (P.N.) Cahuita and Refugio Nacional de Vida Silvestre (R.N.V.S.) Gandoca-Manzanillo.

Figure 2. Percentage of normal (black bars), bleached (white) and dead (stripped) colonies according to transects (T) at (a.) Cahuita and (b.) Gandoca-Manzanillo. (c.) Mean number (bars) and standard deviation (line) of normal, bleached and dead colonies at Cahuita (black) and at Gandoca-Manzanillo (white).

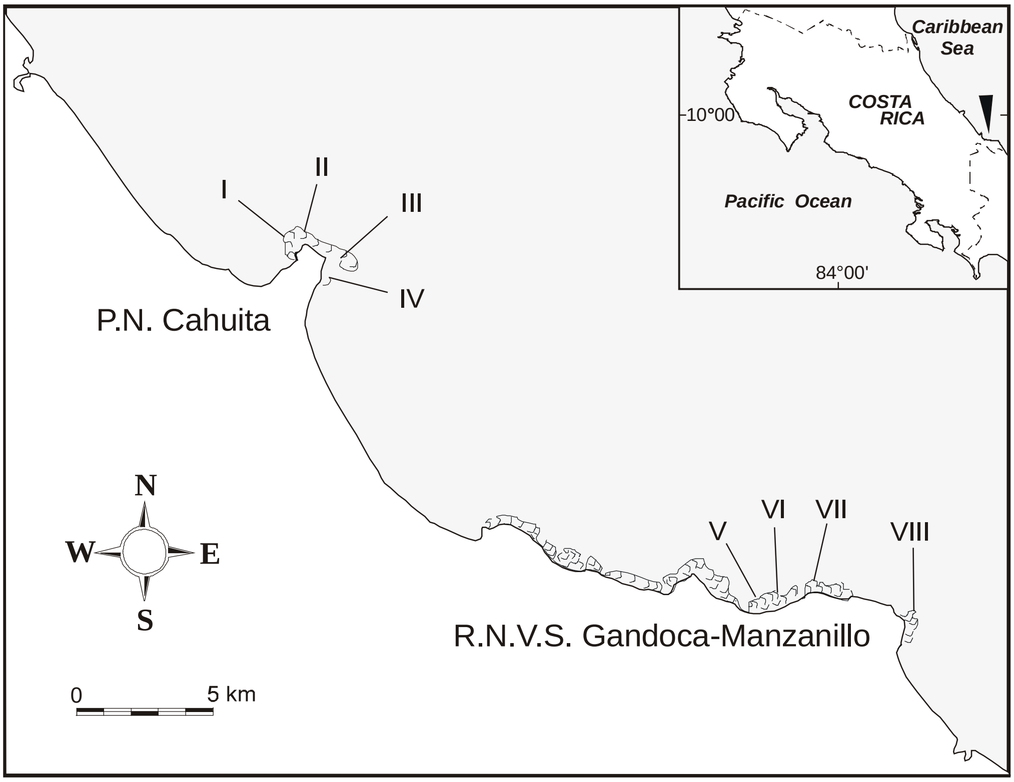
Caribbean Sea
COSTA RICA
10°00
Pacific Ocean
84°00'
I
II
III
IV
P.N. Cahuita
N
W
E
S
0
5 km
V
VI
VII
VIII
R.N.V.S. Gandoca-Manzanillo

Figure 1

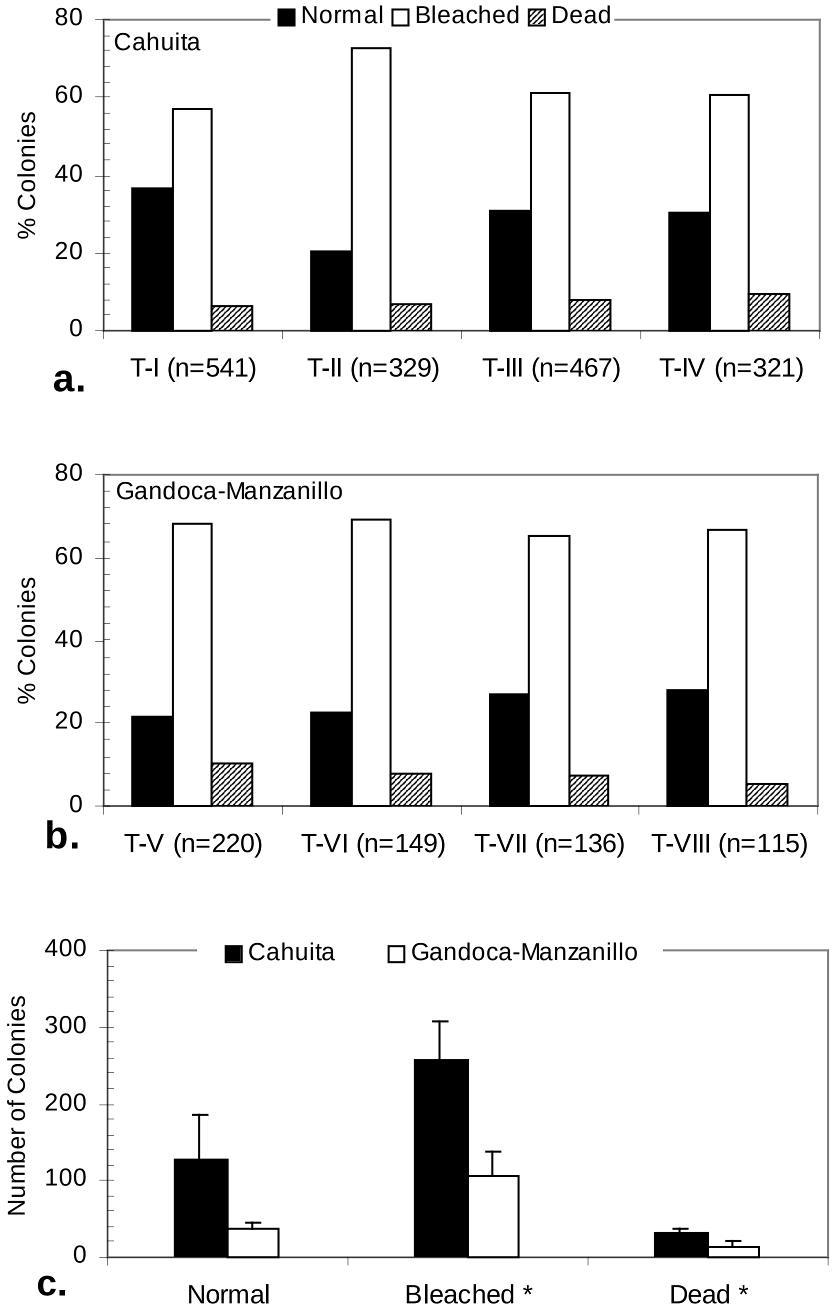
■ Normal □ Bleached ▨ Dead
Cahuita
% Colonies
0
20
40
60
80
T-I (n=541)
T-II (n=329)
T-III (n=467)
T-IV (n=321)
a.
Gandoca-Manzanillo
% Colonies
0
20
40
60
80
T-V (n=220)
T-VI (n=149)
T-VII (n=136)
T-VIII (n=115)
b.
■ Cahuita □ Gandoca-Manzanillo
Number of Colonies
0
100
200
300
400
Normal
Bleached *
Dead *
c.

Figure 2

CORAL BLEACHING AND MORTALITY ASSOCIATED WITH THE 1997-98 EL NIÑO IN AN UPWELLING ENVIRONMENT IN THE EASTERN PACIFIC (GULF OF PAPAGAYO, COSTA RICA)

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ABSTRACT

Coincidental with the 1997-98 El Niño, overall coral bleaching (32.4% of all colonies) and mortality (5.7%) were observed on the Pacific coast of Costa Rica, in the seasonally cool waters of the Gulf of Papagayo and in the more thermally stable waters of Golfo Dulce. At a *Pavona clavus* reef (Culebra Bay, Gulf of Papagayo), mean seawater temperature at 7 m depth ranged from 0.2º to 3.9ºC warmer than in previous years for nearly all months during 1997 and 1998. Water column temperature to 25-30 m depth was above 29ºC for several days, which exceeded the long term average. Even though mortality was low for most coral species, it was severe (>90% decrease in live cover) in a small population of *Leptoseris papyracea* known only at Culebra Bay. *Pocillopora* spp. accounted for more than 60% and 80% of all bleached and dead colonies, respectively. Other coral species regained their normal pigmentation by the beginning of 1998 with little evidence of tissue mortality. The El Niño event of 1997-98 is considered the strongest on record by some measures, but coral mortality on the Pacific coast of Costa Rica was much less than in previous events, drawing attention to El Niño disturbance variability on local scales.

INTRODUCTION

Increases in seawater temperature (SWT) associated with El Niño warming events cause high mortalities in many benthic organisms, especially reef-building (zooxanthellate) corals (Glynn, 1984; 1990; Robinson, 1985). At specific sites in the tropical eastern Pacific, unusually high SWT (≥30ºC) can persist for weeks or months during a warming event (Podestá and Glynn, 1997), exceeding the physiological thermal tolerance limits of corals (Jokiel and Coles, 1977; Glynn and D'Croz, 1990). Coral mortalities of 50-100% were associated with the 1982-83 El Niño in the eastern Pacific (Glynn et al., 1988), interrupting 300 years of reef accretion (Colgan, 1990; Glynn and Colgan, 1992), and reducing populations of some coral species to near extinction (Glynn, 1997).

The impact of recent El Niño warming events has been studied at several localities in Costa Rica. Extensive coral bleaching and mortality were observed during the 1982-83 event (Cortés et al., 1984), resulting in about 50% mortality at Caño Island, off the south coast of Costa Rica (Guzmán et al., 1987), and up to 90% at offshore Cocos Island (Guzmán and Cortés, 1992). Coral bleaching associated with the 1991-92 El Niño was observed at Caño Island (30-80% of all colonies, Guzmán and Cortés, this issue) and at three localities off the central Pacific coast of Costa Rica (>50% of all colonies, Jiménez and Cortés, 2001).

The recent 1997-98 El Niño warming event, considered the strongest on record by some measures (Chavez et al., 1999; McPhaden, 1999a; Enfield, this issue), caused an estimated $33 billion in damage and 23,000 deaths worldwide (Kerr, 1999). This event modified oceanographic features such as sea level in the eastern Pacific (Nerem at al., 1999), current dynamics in the South China Sea (Yin et al., 1999), and day length (Dickey et al., 1999). The mass coral bleachings of 1997-98, coincident with the 1997-98 El Niño, are believed to be the most severe on record (ISRS, 1998). Coral reefs were severely affected in the Indian Ocean with shallow reef coral mortalities of up to 90% (Wilkinson et al., 1999), and on the Australian Great Barrier Reef where the dominant acroporids suffered over 70% mortality at Orpheus Island (Baird and Marshall, 1998). In Costa Rica, the warming event affected corals as early as May 1997, peaked during August-October of that year and continued on a lesser scale until the first half of 1998.

This study documents coral bleaching and mortality associated with the 1997-98 El Niño at Culebra Bay and in the Murciélagos Islands (Fig. la,b), areas known locally as Papagayo. This region, also known as The Gulf of Papagayo, experiences seasonal upwelling (Stumpf and Legeckis, 1977). Observations were also made at a small reef at Sándalo, Golfo Dulce, a nonupwelling site off the south coast of Costa Rica (Fig. la).

MATERIALS AND METHODS

Study sites: The Murciélagos Islands (Fig. 1a) support well developed coral communities (Cortés, 1996-1997). Twelve coral species are known from this area, with *Pocillopora* spp. and *Pavona* spp. being the most abundant taxa. Coral bleaching observations were restricted to the leeward side of San José, Cocineras, San Pedrito (hereafter *Pocillopora* spp. reef) and Golondrina islands. (In this paper, coral reefs refer to structural reefs, i.e. to formations of living corals that accrete onto dead modern skeletal frameworks.) The small *Pocillopora* spp. patch reef (~0.3 ha) has low topographic relief, low diversity and high live coral cover (LCC) (47.5 to 95.2%; pocilloporid corals account for ~62% of the total live cover). Various coral communities formed of mixed assemblages of species are found in Culebra Bay, south of the Murciélagos Islands (Fig. 1). Twenty coral species have been reported from the Culebra Bay area (Jiménez, 2001b). Monitoring for bleaching was conducted in coral communities on basalt or sand substrates located around Palmitas, Viradores and Pelonas islands (Fig. lb, ~19-21% LCC mainly *Pocillopora* spp.) and on two patch reefs (Fig. lb), one constructed by *Pavona clavus* (hereafter *Pavona* reef; 0.8 ha, ~57% LCC) and the other by *Leptoseris papyracea* (hereafter Leptoseris reef 2.5 ha, ~58% LCC). Other coral species are present at both reefs, but their contribution to LCC is <30%. The patch reef at Golfo Dulce, Sándalo (hereafter Golfo Dulce, Fig. la) has relatively low LCC (~29%), low topographic relief, moderate extension (4 ha), and is built mainly by *Porites lobata*, *Pocillopora damicornis* and *Pocillopora elegans* (Cortés, 1992; pers. obs.).

Subsurface Seawater Temperature: Four Hobo-Temp and Stow-Away (Onset Computer Inc.) underwater temperature data loggers (± 0.5°C accuracy) were used to monitor SWT at 7 m depth in Culebra Bay (Fig. 1). The thermistors were deployed on the *Pavona* reef from May 1997 to December 1998, and on the *Leptoseris* reef from August 1997 to December 1998. The data loggers were placed among coral colonies 10-20 cm above the bottom and set to record every 36 min. The units were replaced every month. Short-term temperature recordings (1-6 days) were also made at the Murciélagos Islands (7 and 12 m depth, *Pocillopora* spp. reef) and Golfo Dulce (5 m, *Porites lobata/Pocillopora* spp. reef) during the bleaching event of 1997. In addition, SCUBA divers at Culebra Bay (May 1997 to March 1998) and at Murciélagos Islands (October 1997) recorded temperatures with a calibrated mercury thermometer (0.1 ^{o}C precision) to a depth of 20-30 m. The Bartlett and Hardy test was used to evaluate the normality of data and the Cochran test the heterogeneity of variances (Underwood, 1981, 1997). When non-normality and heterogeneity of variances were significant p< 0.05), the square root transformation was applied (Sokal and Rohlf, 1995). These results were compared with temperature data for the same localities and dates (Jiménez, 1998, 2001a) from previous years (1995-96), using Statistica ver. 5 analytical software. To identify the source of significant variation between months, a *post hoc* group analysis (Tukey HSD test) was utilized.

For waters ~65 km from the study area, weekly mean sea surface temperatures (SST) during the 1982-83 and the 1997-98 El Niño events were compared utilizing Reynolds NCEP optimal interpolation analysis data sets (1 x 1 degree grid centered on 10.5^{o}N, 86.5^{o}W). These data are based on SST fields blended from buoys, ships and bias-corrected satellite data (Reynolds and Smith, 1994).

Coral Bleaching Observations: Coral communities were monitored for bleaching by diving at the study sites 3-4 days per month from 1997 to 1998 (Culebra Bay), two days in July 1997 (Golfo Dulce), and six days in October 1997 (Murciélagos Islands). Bleaching was quantified at Culebra Bay (4-12 m depth) and in the Murciélagos Islands (4-8 m) by counting the number of colonies of all species in a 100 meter-long by 4 meter-wide transect positioned haphazardly across the study sites. At Golfo Dulce (3-6 m), coral communities were assessed in a 50 m x 2 m transect laid across the study site. A colony was scored as bleached if more than 5% of the colony surface area was white or pale, and dead if it was recently overgrown by algae. Changes in bleached surface areas in two massive *Pavona clavus* (2.5 and 10 m diameter approx.) and seven *Pavona gigantea* (0.25-0.60 m diameter) colonies were measured from nails marking the limits of bleaching from July to December 1997. At the *Leptoseris* reef in Culebra Bay, high mortality of this very small coral occurred during the onset of the El Niño warming event (May 1997). The percent of live and dead *L. papyracea* was recorded in April and May 1996, June 1997, and February 1998 with a 10 m long chain (1.1 cm/link) laid parallel to the shoreline and across the study site (15 m depth). Additionally, live cover loss was monitored with the aid of iron rods driven into the periphery of the assemblage in May 1996 (Jiménez, 1998). Percent coral cover was transformed (arcsine) before statistical testing.

RESULTS

Seawater Temperature: Subsurface water temperatures at the *P. clavus* reef were significantly warmer for nearly all months during the study period (May 1997 to December 1998) when compared with the available temperature data from previous years (Table 1). Only April 1998 was not significantly different from April 1995 (Tukey, p>0.05). Subsurface temperatures were colder in May 1996 and 1997 than in May 1995 and 1998 (Tukey, p<0.05). Monthly mean temperatures were higher during the first two thirds of 1998, with differences in the range of 0.2º to 2.9°C, than in previous years. The largest temperature difference occurred in February 1996, usually the time of year with the lowest monthly average temperature *(*25.5º ± 1.8°C, Table 1). From December 1997 to April 1998 (upwelling months), water temperature was 1.0º to 2.9°C higher than in previous years.

The last third of 1997 (September – December) was the warmest period with mean differences from 1998 in the range of 0.9º to 2.4°C. September and October of 1997 had the highest monthly mean temperatures (30.0º ± 0.5°C and 29.9º ± 0.1ºC, respectively, Table 1), with the lowest mean temperature (May) 2ºC higher than the lowest temperature in 1998 December. The number of days with mean temperatures above 29ºC for September and October in 1997 was 54 (Fig. 2), compared with 17 for the same period in 1998. Furthermore, water temperature was above 30ºC for 32 consecutive days from 17 September to 20 October 1997. In general, 1997 had higher mean monthly temperatures (0.9-2.4ºC) than in 1998 and, considering all shared months (May to December), it was a significantly warmer year (29.1º ± 1.0ºC, t=28.26, p<0.0001, df=15180) than 1998 (28.6º ± 1.6ºC).

Monthly mean SWT at 7 m depth at the *P. clavus* and *L. papyracea* reefs was significantly warmer at the latter site during four months of the comparison period (Table 2). The greatest differences (0.30º-0.66ºC) were observed in August, October and November of 1997. Although mean monthly temperatures at both reefs followed similar patterns, there were significant daily variations according to the tidal regime and exposure of the reefs to upwelling pulses.

Mean SWT at the Murciélagos Islands and Golfo Dulce, as measured by data loggers, was high during our visits in 1997. At the Murciélagos Islands, approximately 40 km North of Culebra Bay (Fig.1), SWT was significantly warmer (29.2º ± 0.2ºC, t= 21.21, p<0.0001, df= 827) at 7 m depth than at 12 m (28.9º ± 0.3°C) during six days in October

1997. The lowest temperature (28.4°C at 12 m) was recorded during the initiation of an off-season upwelling event. At Golfo Dulce (Fig. 1), water temperature at 7 m was 29.9º ± 0.3°C (range 29.3º -30.6°C) during two days in July 1997.

Culebra Bay was warmer (30.3º ± 0.5ºC, t= 36.6, $p<0.0001$, df= 663) than the Murciélagos Islands area and slightly less warm (29.3º ± 0.4°C, t= 17.73, $p<0.0001$, df= 300) than Golfo Dulce for the corresponding periods of time.

Temperature readings made by divers at different localities around Culebra Bay, recorded values above 29°C to depths of 25 - 30 m from August to October 1997 (Table 3). In November 1997, water temperature was still around 28.8°C at 21-25 m. Variation in SWT was slight (<0.5ºC) between 10-15 m depth, and below 21 m from September to November 1997. In January and February 1998, the variation in temperature was 0.7ºC, and in March it was 1.9ºC. In the Murciélagos Islands, water temperatures above 28ºC were recorded at relatively shallow depths (Table 3); SWT was 25.5º –26.0ºC at 26-30 m depth. The difference between the mean temperatures at 10-15 m and deeper was 0.5ºC. In general, mean water column temperature at the Murciélagos Islands (27.6º ± 0.8ºC) was significantly lower than at Culebra Bay (29.8º ± 1.1ºC, t= 10.07, $p<0.0001$, df= 43) in October 1997.

A comparison of weekly mean Reynolds SSTs in the Gulf of Papagayo during the 1982-83 and 1997-98 El Niño events reveals SSTs ≥ 29ºC for 33 consecutive weeks in 1983, with 14 weeks above 30ºC (Fig. 4a). In contrast, two prolonged warming periods occurred in 1997-98, the first over 28 consecutive weeks in 1977 and the second for 26 weeks (two weeks above 30ºC) the following year. In situ SWT at Culebra Bay (*Pavona* reef) during the 1997-98 El Niño showed marked deviations from the Reynolds SST data for the corresponding period (Fig. 4b). While both temperature records exhibited a roughly similar trend, Reynolds SSTs were more uniform, not showing the abrupt thermal swings and extremes that occurred at 7 m depth on the reef.

Coral bleaching: The first signs of bleaching and mortality at the *Leptoseris* reef in Culebra Bay (Fig. 1) were documented during the first visit of the year in mid May 1997. Dead and bleached colonies of *L. papyracea* were observed at 15 m depth and bleached *Fungia (Cycloseris) curvata* individuals at 12 m. However, it was not until June 1997 that severe bleaching and mortality were observed in *L. papyracea,* and six other coral species, at several reefs and coral communities to a depth of 15 m (Table 4). In general, affected pocilloporid species showed almost complete bleaching along the bathymetric range at which they occur in Culebra Bay (1 - 10 m). Bleached massive corals had discolored or white patches on both their upper surfaces and shaded bases, covering more than two-thirds of each colony. No additional bleaching was observed in *Pavona clavus* and *Pavona gigantea* colonies marked with nails in July 1997, or in any other colonies. By August, the bleached patches and nails were covered with filamentous algae. However, in September 1997 the living coral tissue started to advance, overgrowing the sediment-coated, dead areas completely by January 1998. These bleached colonies were interspersed among normal appearing colonies of smaller dimensions, which did not bleach during the bleaching episode or in subsequent months.

The occurrence of bleached colonies at Culebra Bay peaked during August-October 1997 when mean daily SWT (7 m depth) was above 29°C. This period coincided with doldrum-like weather conditions and sparse cloud cover. Such conditions prevailed for almost 40 days, until the end of October (Fig. 3). The most commonly bleached corals (>50% of colonies) were *Pavona varians*, *Porites lobata* and the azooxanthellate coral *Tubastraea coccinea* (Table 4). Mortality was observed in eight species and ranged between 0.7 to 11% (Table 4). *Leptoseris papyracea* (not shown in Table 4 because its colonies were not counted, but instead measured by the chain transect method) suffered the highest mortality at Culebra Bay, with a decrease of 94.7% in live cover relative to a previous survey in April 1996 (Jiménez, 1997; Fig. 5). Mortality in *Leptoseris* continued until June 1997. In February 1998, the percentage of live coral cover was similar to that recorded in June 1997 (t=0.492, p=0.6400, df=8), indicating, as previously suggested, that further significant mortality did not occur. In February 1998, the average distance between the reef periphery in May 1996 and the remaining live *Leptoseris* colonies was 1.0 ± 0.15 m (range 0.73 to 1.25 m, n= 11), showing the extent of contraction of this assemblage.

By February and March 1998, almost all of the coral colonies at Culebra Bay had recovered their normal coloration and further bleaching was not observed. However, in April 1998 a small patch (10 m^2) of *Pocillopora* spp., located on the peninsula in front of the Pelonas Islands (Fig. lb), bleached and remained in this condition for five consecutive months. This patch regained its normal appearance by September 1998 with no partial or total mortality of colonies evident.

Coral bleaching and mortality at the Murciélagos Islands were observed in October 1997, particularly in shallow sections (4-8 m) of one *Pocillopora* spp. reef (San Pedrito Island). Totally bleached corals were surrounded by normally-pigmented colonies, as was observed in Culebra Bay. Seventy-five percent of the colonies of *Pocillopora inflata,* a recently described species (Glynn, 1999) with a limited distribution in the eastern Pacific, were bleached (Table 4). Mortality of *P. inflata* was not observed at the time of the survey. Other affected species with more than 20% of bleached colonies were *Pocillopora damicornis, Porites lobata* and *Pocillopora eydouxi* (Table 4). Coral mortality in the Murciélagos Islands was less than in Culebra Bay and occurred only in *Pocillopora elegans* (~3%), *P. damicornis* (~2%) and *Pavona gigantea* (~1%) (Table 4). One massive colony of *Gardineroseris planulata* (~1.5 m in diameter) had discolored or bleached patches colonized by filamentous algae alternating with normally pigmented areas (the same mortality pattern observed in two massive *Pavona clavus* colonies at Culebra Bay, see above).

At Golfo Dulce, more than 300 km south of Culebra Bay (Fig. 1), coral bleaching was observed in five coral taxa (Table 4). The most affected were *Psammocora* spp. (~75%), *P. elegans* (~63%) and *P. damicornis* (~61%). Only *P. damicornis* and *P. elegans* experienced mortality (~12% and ~5% respectively) at the time of the survey in July 1997. Branching colonies bleached in a pattern similar to that observed in Culebra Bay and the Murciélagos Islands. Almost all sampled colonies of massive species *(Pavona clavus* and *Porites lobata)* showed complete tissue bleaching.

Branching corals *(Pocillopora* spp.) had the highest percentage of bleached colonies in Golfo Dulce and the lowest in the Murciélagos Islands (Fig. 6a). Massive species *(Pavona clavus, Pavona gigantea, Porites lobata, G. planulata)* were more affected in Culebra Bay than in the Murciélagos Islands, and although bleaching was high in Golfo Dulce (~30%), no mortality was observed (Fig. 6b). For crustose *(Pavona varians, Porites panamensis*), nodular *(Psammocora* spp.), free-living *(Fungia curvata)* and cryptic (*Tubastraea coccinea)* coral species pooled (Fig. 6c), bleaching was highest in Golfo Dulce (~76%). In general, the highest mortality occurred in branching corals, while bleaching was prevalent in crustose, nodular, free-living, cryptic, and branching colonies. Bleaching and mortality were relatively low in most massive species (Fig. 6d).

Considering all coral species (excluding *L. papyracea,* which was quantified using the chain transect method) from the three study localities, only 32.4% of all colonies (n= 5409) bleached during the 1997-98 ENSO event, and overall mortality was 5.7% (Fig. 7a). Branching species comprised more than 80% of the dead corals. They formerly contributed 40 to 90% of the total live coral cover (Jiménez 2001b). Comparing these results with the impact of the 1991-92 ENSO event (Fig. 7b) on corals along the central Pacific coast of Costa Rica (Jiménez and Cortés, 2001), it is evident that bleaching and mortality were higher during the earlier disturbance (57.3% and 8.8%, respectively). The abundant massive corals *(P. lobata, P. clavus)* and the nodular *Psammocora* spp. accounted for 28.8% and 66.3% of the total mortality, while the less common *Pocillopora* spp. suffered only 4.9% mortality (Fig. 7b).

DISCUSSION

During the onset of the 1997-98 El Niño warming event, coral bleaching and mortality were observed as early as May 1997, when large stands of *L. papyracea* bleached at 15 m in Culebra Bay. But it was not until June 1997 that other coral species started to bleach, showing partial or total mortality to a depth of 12 m. The extent of *L. papyracea* bleaching and mortality in May, and the thick carpet of algae and sponges growing over the dead colonies, suggest that mortality occurred 1-2 mo before our survey. Suspected mortality of *L. papyracea* in March-April is coincident with the arrival in the eastern Pacific of the first set of ENSO-generated Kelvin waves in December 1996/January 1997 (Chavez et al., 1998; McPhaden and Yu, 1999), which reached the Central American coast by February (Yu and Rienecker, 1998). The bleaching and mortality response may have occurred sometime after the initial temperature rise, as has been observed in experimentally heated corals (Berkelmans and Willis, 1999) and under natural conditions (Winter et al., 1998). Differences in monthly sea temperatures between the *Leptoseris* and *Pavona* reefs indicate that these areas are subjected to different microscale oceanographic conditions, and that one site can be warmer than the other during the same period. Therefore, it is possible that the warming at the *Leptoseris* reef was greater or occurred earlier than at the other reefs in Culebra Bay, which had experienced no coral bleaching as of May 1997.

The warming in Culebra Bay started during the Papagayo upwelling season (December-April), when corals at 12 m are normally exposed to temperatures as low as 12^{o}C for a few hours and to 20^{o}C for several days (Jiménez, 2001a). It is possible that corals such as *L. papyracea,* typically found in deep and cool waters (Dinesen, 1980), are seasonally acclimatized to lower temperatures during the upwelling season. A limited, possibly seasonal, thermal acclimatization has been observed in other coral species (Coles and Jokiel, 1978; Brown, 1997; Berkelmans and Willis, 1999). It may be the case that *Leptoseris* has a bleaching threshold that is lower during the upwelling season than that present in other coral species inhabiting shallow areas, which are not exposed to such low temperatures. Additionally, *L. papyracea* was shown to be very sensitive to temperature changes in all attempts to repopulate dead *Leptoseris* reefs at Culebra Bay (Jiménez, 1998).

For other coral species, bleaching and mortality were observed at Culebra Bay during 6 mo beginning in June 1997, and peaked after a rapid temperature increase, when SWT at 7 m depth exceeded 29^{o}C for 97 days. During this period El Niño developed rapidly, setting record high temperatures in the eastern equatorial Pacific (McPhaden, 1999b). Doldrum-like weather conditions lasted for more than 50 consecutive days and were coincidental with the peak months (September-October) of the coral bleaching and mortality. Water column temperature was above 30^{o}C to a depth of 25-30 m for several days. An unusual continuation of the mid-year (usually June) decrease in precipitation and doldrum-like weather, known as "Veranillo de San Juan" in Costa Rica, also occurred during the 1982-83 El Niño event (Ramírez, 1983). Doldrum-like weather, when coastal waters are clear and calm, facilitate light penetration, increasing the irradiance levels reaching corals. In 1997, water visibility (>25 m) and light penetration increased during the doldrum-like weather conditions over Culebra Bay, while the year 1998 had very few days with clear waters (less than 10 m visibility, see below). Bleaching has been observed when high water temperatures, and the likely synergistic effect of increased irradiance (Goreau and Hayes, 1994; Glynn, 1996), increase the sensitivity of zooxanthellae to photoinhibition (Hoegh-Guldberg and Jones, 1999). Bleaching also has been observed after sudden temperature increases during the normally warmest months of the year (Winter et al., 1998). Calm weather conditions preceded and accompanied the progression of the bleaching event at Culebra Bay, as has been observed on the Australian Great Barrier Reef (Harriot, 1985), in the Florida Keys (Causey, 1988), French Polynesia (Drollet et al., 1994), and the Caribbean coast of Costa Rica (Cortés et al., 1984; Jiménez, 2001c). Despite this, calm spells have not accompanied other bleaching events, such as the 1993 episode in the US Virgin Islands (Quinn and Kojis, 1999). Worthy of note, the two bleaching episodes in Culebra Bay (from August to October 1997, and from April to August 1998, Fig. 3) also occurred in the Gulf of Chiriquí, Panamá (Glynn et al., this issue) and at Gorgona Island, Colombia (Vargas-Angel et al., this issue). Although the timing of bleaching was not identical at these widely separated localities (3º to 11º N), the height of each bleaching episode corresponded closely with the local maximum sustained sea temperatures.

Except for *L. papyracea,* coral mortality during 1997-98 was generally low at the three study localities and was concentrated mostly in Culebra Bay (>90% of the total mortality). We consider this mortality pattern valid, despite the different observation times at the three localities in 1997 (>30 days at Culebra Bay, 6 days at Murciélagos Islands, and 2 days at Golfo Dulce). Additional coral mortality was not observed at the Murciélagos Islands in February, April, or from June to October 1998 (G. Bassey, pers. com. 1999), nor during a visit to this site in May 1999. This suggests that most mortality at the Murciélagos Islands occurred during the few months before our visit in October 1997, and decreased thereafter. Similarly, coral mortality was observed mainly before November 1997 in Culebra Bay, but not afterwards. Although our surveys at Golfo Dulce were conducted during July 1997, additional coral mortality was not observed in subsequent visits in 1998 (E. Ruiz, pers. observ.).

The relatively high percentage of coral mortality at Culebra Bay could be attributed to local oceanographic conditions, which can change the rate of warming. For example, the 1997 off-season occurrence of upwelling in June (Culebra Bay, Fig. 3) and October/November (Murciélagos Islands), due to an unusual intensification of Trade Wind strength at that time of year (IMN, 1998), may have interrupted sea warming, thus lowering the impact of high temperature stress on corals. Intensification of the Trade Winds over the northern Costa Rican Pacific coast has been observed during other El Niño warming events (Fernández and Ramírez, 1991; Amador and Alfaro, 1996), and this occurs in the second half of years during ENSO events. Mean SWT at 7 m and throughout the water column was significantly lower (0.8º and 2.2°C, respectively) at the Murciélagos Islands area than in Culebra Bay during October 1997. The former area is more exposed to oceanic conditions and Papagayo upwelling than the latter (A. Gutiérrez, pers. comm. 1997), thus lessening the impact of the warming event there. In addition, upwelling was absent at Culebra Bay during the doldrum-like weather, which occurred after June 1997.

Although coral colonies recovering from mass coral reef bleaching events elsewhere have suffered moderate to heavy mortality (Williams and Bunkley-Williams, 1990), the majority of colonies at Culebra Bay recovered their normal pigmentation by the beginning of 1998 with only slight tissue mortality. Tissues in large *P. clavus* and medium-sized *P. gigantea* colonies completely overgrew the dead areas in 7 mo. Even though bleaching strongly compromises tissue damage repair (Mascarelli and Bunkley-Williams, 1999), it has been suggested that large colonies have more energy available for regeneration (Loya, 1976; Bak, 1983). That large colonies often have sizeable areas of healthy tissue (with apparently normal densities of symbiotic zooxanthellae) directly surrounding bleached patches, tissue regeneration may be accelerated by the translocation of energy (Mascarelli and Bunkley-Williams, 1999). This would lead to a more rapid recovery of damaged areas (Meesters et al., 1997). It is also important to consider that partial bleaching may result from physiological and/or genetic variation in different parts of the same host colony (Brown, 1997) or differences in the environmental tolerances of zooxanthella strains within a colony (Muller-Parker and D'Elia, 1997; Rowan et al., 1997; Glynn et al., this issue). These same factors may also contribute to differential responses among and within coral colonies.

We cannot rule out the possible selective effects of the 1982-83 and 1991-92 El Niño events on the survivorship of more tolerant colonies or clones to elevated temperature stress, together with a limited ability of corals to acclimatize. Branching corals, severely impacted during the 1982-83 El Niño event in the eastern Pacific (Glynn, 1984, 1990; Guzmán et al. 1987; Guzmán and Cortés, 1993), with mortalities greater than 80%, fared quite well during the 1997-98 event, with only 8% mortality at the three sites investigated here. Similar conclusions can be drawn when comparing coral mortality in the Gulf of Panamá, another upwelling area in the eastern Pacific. Total coral mortality was ~85% during the 1982-83 warming event, and this was associated with the normally lower, more variable temperatures in the Gulf of Panamá (Glynn et al., 1988). We report here less than 6% overall coral mortality on the Pacific coast of Costa Rica coincident with the 1997-98 El Niño event, despite sustained temperatures ≥ 30ºC that resulted in 51% overall coral mortality at Caño Island, Costa Rica in 1983 (Glynn et al., 1988). However, the fact that some coral reefs have bleached repeatedly during every major ENSO event suggests that there have been no major shifts in reef community structure in favor of heat tolerant taxa (Hoegh-Guldberg, 1999). This possibility needs to be investigated at local scales or on specific reefs where coral responses to warming stressors demonstrate varied patterns.

It is particularly surprising that the 1982-83 El Niño was more detrimental to eastern Pacific coral reefs than the 1997-98 event because the latter event appears to have been as strong as (or stronger than) the former (Chavez et al., 1999; McPhaden, 1999a; Enfield, this issue). While the intense phase of the 1982-83 ENSO was fairly short (4 months), peaking in April-May 1983 (Hansen, 1990), the intense phase of the 1997-98 El Niño was much longer, from spring 1997 to spring 1998 (Chavez et al., 1999;

McPhaden, 1999a b; Enfield, this issue; Podestá and Glynn, this issue). This suggests that physical factors alone may not determine the bleaching response of coral reefs to thermal stress (Williams and Bunkley-Williams, 1990; Brown et al., 1994; Glynn, 1996; Hoegh-Guldberg, 1999). This conclusion is supported by the observation (documented in reports to NOAA's Coral Health and Monitoring Program) that reefs in the far eastern Pacific showed significant variation in their affected species, degree of bleaching and eventual mortality. Local differences in oceanographic conditions that affect the length and rate of warming (Glynn et al., 1988; Glynn, 1993, 1996; Fong and Glynn, this issue) are likely to play a role in explaining the incidence and severity of bleaching at particular sites. The differences between nearshore SWTs at Culebra Bay and the more exposed Murciélagos Islands (both measured in situ on the study reefs) validate this notion. Similarly, warming events may act very differently at local scales depending on the population structure of the reefs concerned. Historical patterns of thermal stress, combined with genetic variation within and between different species of coral host (Edmunds, 1994; Knowlton and Jackson, 1994; Brown, 1997) and/or algal symbionts (Buddemeier and Fautin, 1993; Rowan et al., 1997; Glynn et al., this issue) will contribute to bleaching variability. Taken together, these observations indicate that bleaching thresholds are most likely site and time dependent (Winter et al., 1998). This perspective cautions against predictions of bleaching incidence and severity over larger spatial and temporal scales without an appreciation of the physical and biological factors that interact during bleaching.

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TABLE 1. Monthly temperature (ºC) means (standard deviation) at 7 m depth, *Pavona* reef, Culebra Bay. Square root transformations were performed before statistical testing. df, degrees of freedom; F and t, statistical descriptors; p, probability. Data for 1995 and 1996 from Jiménez (1998, 2001a).

Month	1995	1996	1997	1998	df	F	t	p
Jan	26.6 (0.2)	--	--	27.8 (0.8)	908	--	11.3	<0.0001
Feb	--	25.5 (1.8)	--	28.4 (1.2)	1947	--	41.6	<0.0001
Mar	--	26.0 (2.5)	--	27.6 (2.3)	2467	--	16.7	<0.0001
Apr	28.3 (0.7)	27.4 (2.6)	--	28.5 (1.6)	2	93.43		<0.0001
May	28.9 (0.7)	28.1 (1)	28.1 (0.8)	29.5 (0.8)	3	525.87	--	<0.0001
Jun	--	--	28.8 (2.1)	29.8 (0.4)	2434	--	17.1	<0.0001
Jul	27.8 (1.3)	--	28.9 (0.6)	29.5 (0.4)	2	1546.71	--	<0.0001
Aug	28.2 (0.6)	--	28.9 (0.6)	29.5 (0.5)	2	1391.55		<0.0001
Sep	--	--	30.0 (0.5)	29.1 (0.7)	3435	--	41.4	<0.0001
Oct		--	29.9 (1.1)	28.2 (0.6)	2555	--	45.2	<0.0001
Nov	--	--	28.8 (0.3)	26.7 (1.2)	4078	--	79.6	<0.0001
Dec	--		28.5 (0.4)	26.1 (1.6)	1359	--	54.2	<0.0001

TABLE 2. Differences in mean monthly temperatures (ºC) at 7 m depth in *Pavona clavus* and *Leptoseris papyracea* reefs, Culebra Bay. Data were transformed utilizing the square root function. df, degrees of freedom; F and t, statistical descriptors; p, probability; N.D., no data due to unit failure.

Month	*Pavona*	*Leptoseris*	Difference	df	t	p
1997						
Aug	28.82	29.48	-0.66	291	10.41	<0.0001
Sep	30.00	29.95	0.05	3418	3.07	0.0021
Oct	29.87	29.51	0.36	1708	10.92	<0.0001
Nov	28.78	29.08	-0.30	3404	33.34	<0.0001
Dec	28.55	28.43	0.12	2691	8.81	<0.0001
1998						
Jan	27.84	27.71	0.13	1698	3.24	0.0012
Feb	28.38	28.40	-0.02	2255	0.44	0.6585
Mar	27.63	27.61	0.02	2457	0.13	0.8978
Apr	28.52	28.58	-0.06	2397	0.90	0.3663
May	29.48	29.40	0.08	2333	2.33	0.0200
Jun	29.85	N.D.	--	--	--	--
Jul	29.52	29.55	-0.03	2392	2.36	0.0183
Aug	29.53	29.59	-0.06	2478	3.68	0.0002
Sep	29.10	28.96	0.14	2353	4.54	<0.0001
Oct	28.24	28.08	0.16	2364	5.15	<0.0001
Nov	26.73	26.70	0.03	2368	0.63	0.5335
Dec	26.05	26.15	-0.10	2381	1.46	0.1442

TABLE 3. Subsurface water temperature (ºC), ± 1 standard deviation, measured by divers at Culebra Bay and Murciélagos Islands. n= number of measurements.

Location Month	10-15m	16-20m	21-25m	26-30m
Culebra Bay				
1997				
May	26.9± 1.9 n=16	26.2± 1.6 n=4	26.0± 1.6 n=8	25.7± 1.5 n=3
Jun	24.7 ± 2.9 n=17	24.6 ± 3.9 n=7	25.7 ± 3.6 n=6	22.1 ± 3.8 n=6
Jul	28.6 ± 1.1	25.6 ± 1.2 n=21	25.0 ± 0.9 n=3	-- n=3
Aug	30.9 ± 0.9 n=19	28.8 ± 1.0 n=3	28.8 n=1	--
Sep	30.3 ± 1.3 n=17	30.2 ± 1.2 n=5	30.6 ± 0.9 n=12	--
Oct	30.0 ± 1.4 n=16	29.4 ± 0.6 n=11	30.0 ± 0.1 n=3	30.0 n=1
Nov	29.0 ± 0.6 n=25	28.7 ± 0.2 n=4	28.8 ± 0.2 n=2	--
Dec	28.7 ± 05 n=26	27.5 ± 0.1 n=4	--	--
1998				
Jan	27.6 ± 0.4 n=18	26.9 ± 0.2 n=7	--	--
Feb	27.0 ± 1.0 n=26	26.2 ± 0.6 n=7	26.3 ± 0.3 n=3	--
Mar	28.1± 1.3 n=17	26.7 ± 05 n=9	26.2 ± 03 n=2	--
Murciélagos Is.				
1997				
Oct	28.0 ± 0.4 n=16	27.6 ± 0.6 n=9	27.2 ± 0.5 n=16	25.7 ± 0.3 n=4

TABLE 4. Percentage of affected coral colonies (number of colonies) by species at the three sites examined in 1997. N= normal, B= bleached, D= dead.

Species	Culebra Bay 4-12 m, June-October			Murciélagos Islands 4-12 m, October			Golfo Dulce 3-6 m, July		
	N	B	D	N	B	D	N	B	D
Pocillopora elegans Dana 1846	61.3	31.5	7.2	84.3	13.0	2.8	32.6	62.8	4.7
	(449)	(231)	(53)	(91)	(14)	(3)	(14)	(27)	(2)
Pocillopora damicornis (Linnaeus 1748)	54.0	35.0	11.0	70.8	27.2	2.1	26.7	61.4	11.9
	(881)	(570)	(179)	(276)	(106)	(8)	(27)	(62)	(12)
Pocillopora eydouxi Milne Edwards & Haime 1860	74.8	25.2	0	79.3	20.7	0	-		
	(77)	(26)		(23)	(6)				
Pocillopora meandrina Dana 1846	50	47.9	2.1	-	-	-	-		
	(24)	(23)	(1)						
Pocillopora inflata Glynn 1999	-	-	-	25	75	0	-		
				(6)	(18)				
Pavona clavus Dana 1846	58.7	37.4	3.9	88.4	11.6	0	75	25	0
	(254)	(162)	(17)	(107)	(14)		(9)	(3)	
Pavona gigantea Verrilll869	59.8	33.7	6.5	86.1	13	0.9	-		
	(55)	(31)	(6)	(192)	(29)	(2)			
Pavona varians Verrilll864	41.4	58.6	0	100	0	0	-		
	(12)	(17)		(13)					
Psammocora spp.	60.2	36.3	3.4	80.4	19.6	0	24.2	75.8	0
	(350)	(211)	(20)	(86)	(21)		(8)	(25)	
Porites lobata Dana 1846	50	50	0	76.2	23.8	0	68.6	31.4	0
	(23)	(23)		(16)	(5)		(24)	(11)	
Porites panamensis Verrill 1870	58.1	40.1	0.7	87.3	12.7	0	-	-	-
	(81)	(55)	(1)	(62)	(9)				
Gardineroseris planulata (Dana 1846)	100	0	0	96.7	3.3	0	-	-	-
	(2)			(87)	(3)				
Fungia (Cycloseris) curvata (Hoeksema 1989)	46.1	43.6	10.3	-	-	-	-	-	
	(18)	(17)	(4)						
Tubastraea coccinea Lesson 1829	45	55	0	85.3	14.7	0	-	-	
	(18)	(22)		(64)	(11)				

FIGURE CAPTIONS

Figure 1. Locations of the coral bleaching study sites (a) at the Pacific coast of Costa Rica, and the in situ temperature recorders (b) at Culebra Bay. 1. Murciélagos Islands, 2. Culebra Bay, 3. Golfo Dulce (Sándalo).

Figure 2. Number of days the daily mean seawater temperature (7 m depth) was above 29°C at the *Pavona* reef site, Bahía Culebra. Temperature recorders were installed in mid May 1997.

Figure 3. Daily mean seawater temperature at the *Pavona* reef (7 m depth), Bahía Culebra, from 15 May 1997 to 31 December 1998. Horizontal shaded blocks denote periods of coral bleaching and mortality.

Figure 4. Comparison of weekly mean sea surface temperature (SST) (Reynolds NCEP optimal interpolation analysis) ~ 65 km offshore of the study area during the 1982-83 and 1997-98 El Niño events (a). In situ *Pavona* study reef temperature records at 7 m compared with Reynolds SSTs, 1997-98 (b).

Figure *5. Leptoseris papyracea* percent cover (chain transect method) at 15 m depth, Culebra Bay.

Figure 6. Percent normal (black bars), bleached (open) and dead (stripped) coral colonies at three study sites. Branching colonies= *Pocillopora* spp.; Massive colonies = *P. clavus, P. gigantea, P. lobata* and *G. planulata;* Other colony morphologies = *P. varians, P. panamensis, Psammocora* spp., *F. curvata* and *T coccinea.*

Figure 7. Percent normal (black), bleached (white) and dead (stripped) coral colonies observed during the 1997-98 (a) and 1991-92 (b) El Niño events on the Pacific coast of Costa Rica. Coral species colony morphologies as in Fig. 6.

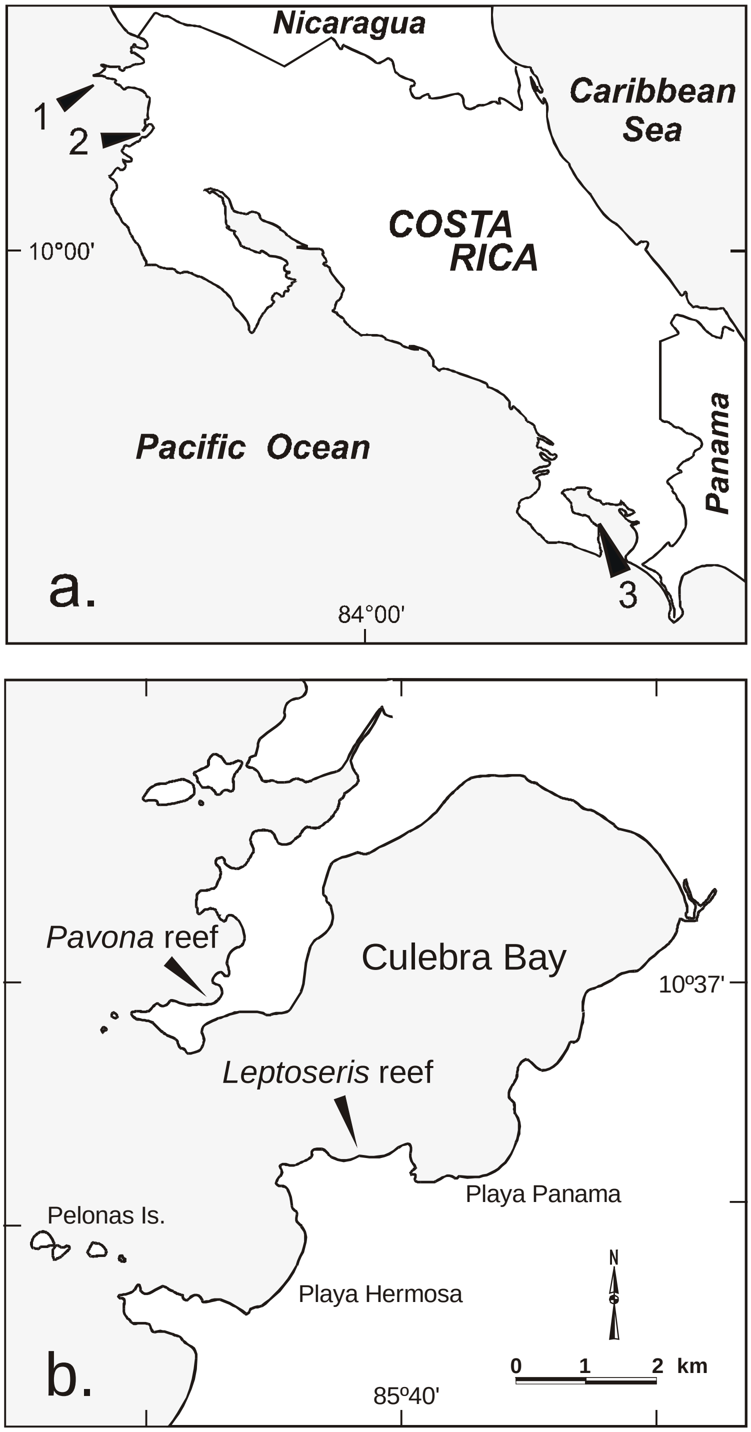

Nicaragua
Caribbean Sea
1
2
COSTA RICA
10°00'
Pacific Ocean
Panama
a.
84°00'
3
Pavona reef
Culebra Bay
10º37'
Leptoseris reef
Playa Panama
Pelonas Is.
Playa Hermosa
N
0 1 2 km
b.
85º40'

Figure 1

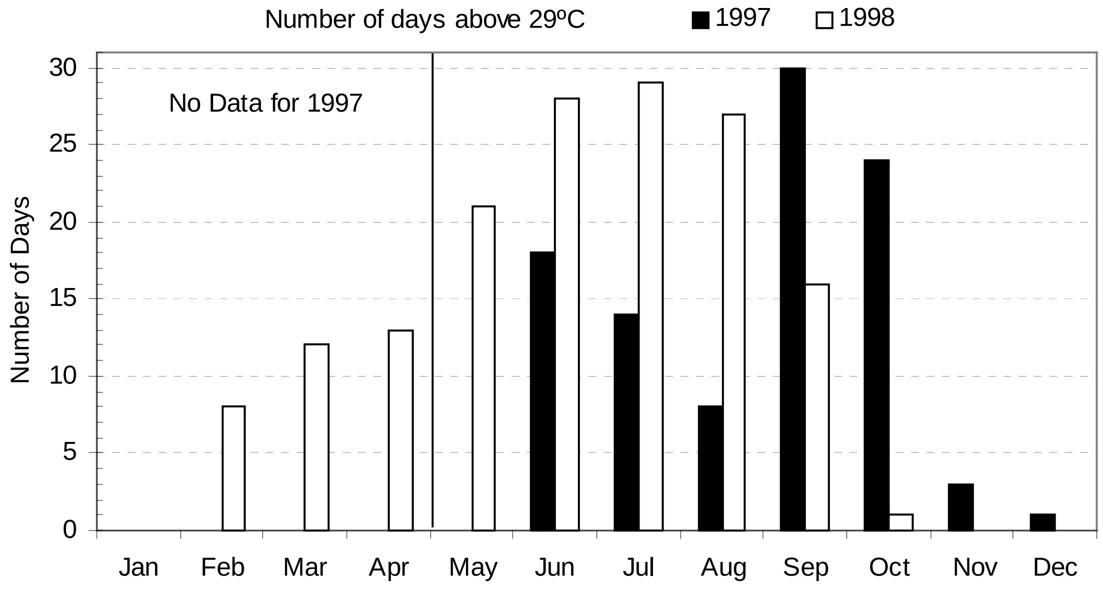


Figure 2

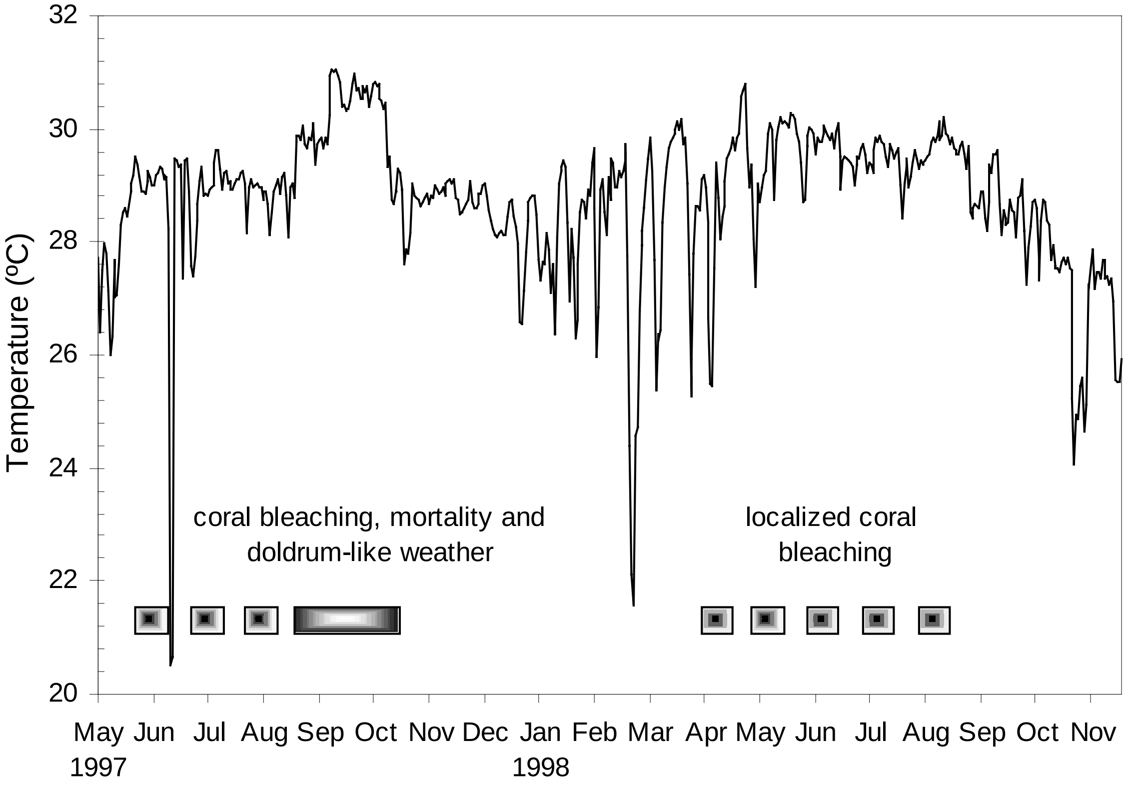


Figure 3

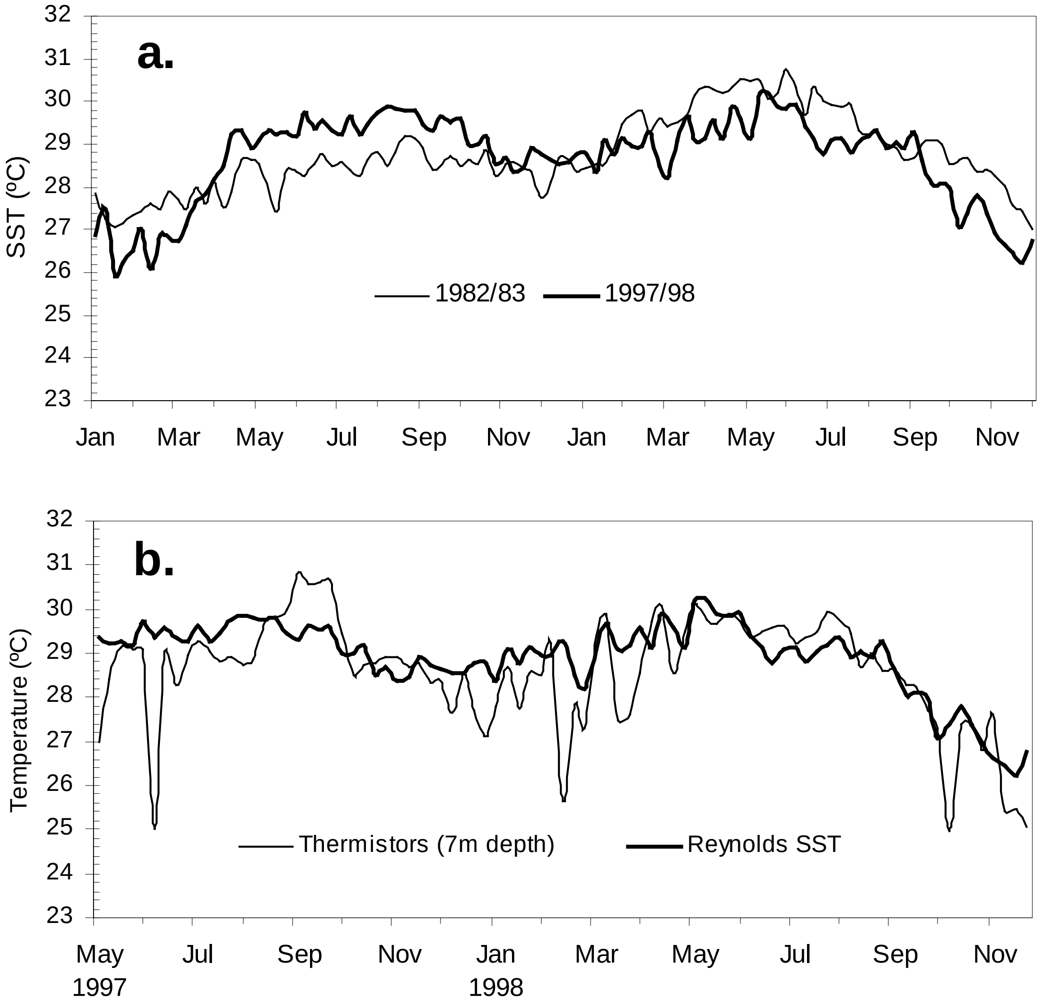

a.
SST (ºC)
32
31
30
29
28
27
26
25
24
23
1982/83
1997/98
Jan
Mar
May
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
b.
Temperature (ºC)
32
31
30
29
28
27
26
25
24
23
Thermistors (7m depth)
Reynolds SST
May
1997
Jul
Sep
Nov
Jan
1998
Mar
May
Jul
Sep
Nov

Figure 4

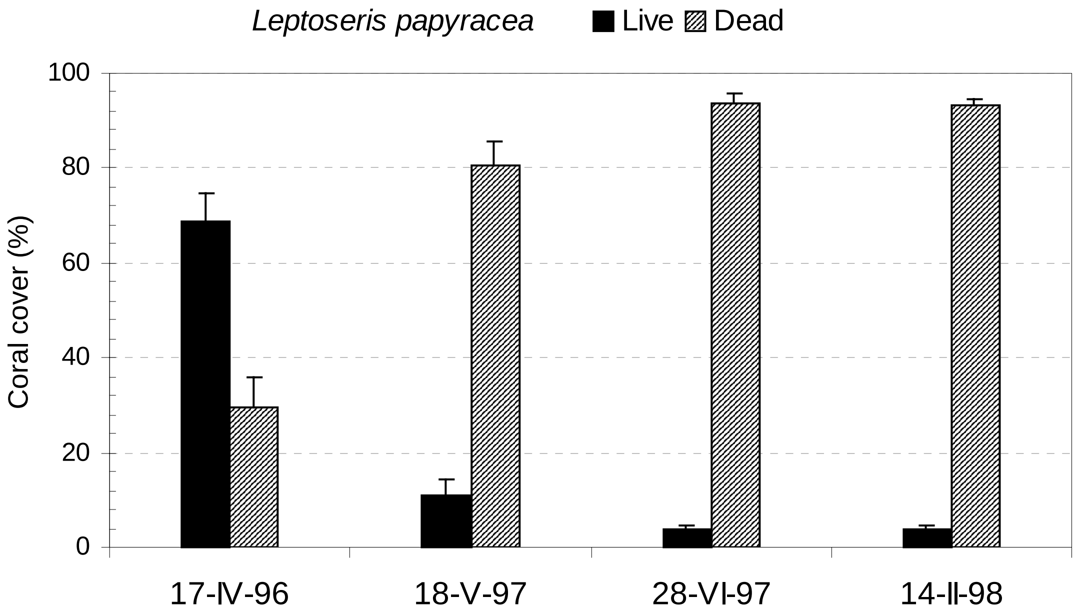

Leptoseris papyracea
■ Live ▨ Dead
100
80
60
40
20
0
Coral cover (%)
17-IV-96
18-V-97
28-VI-97
14-II-98

Figure 5

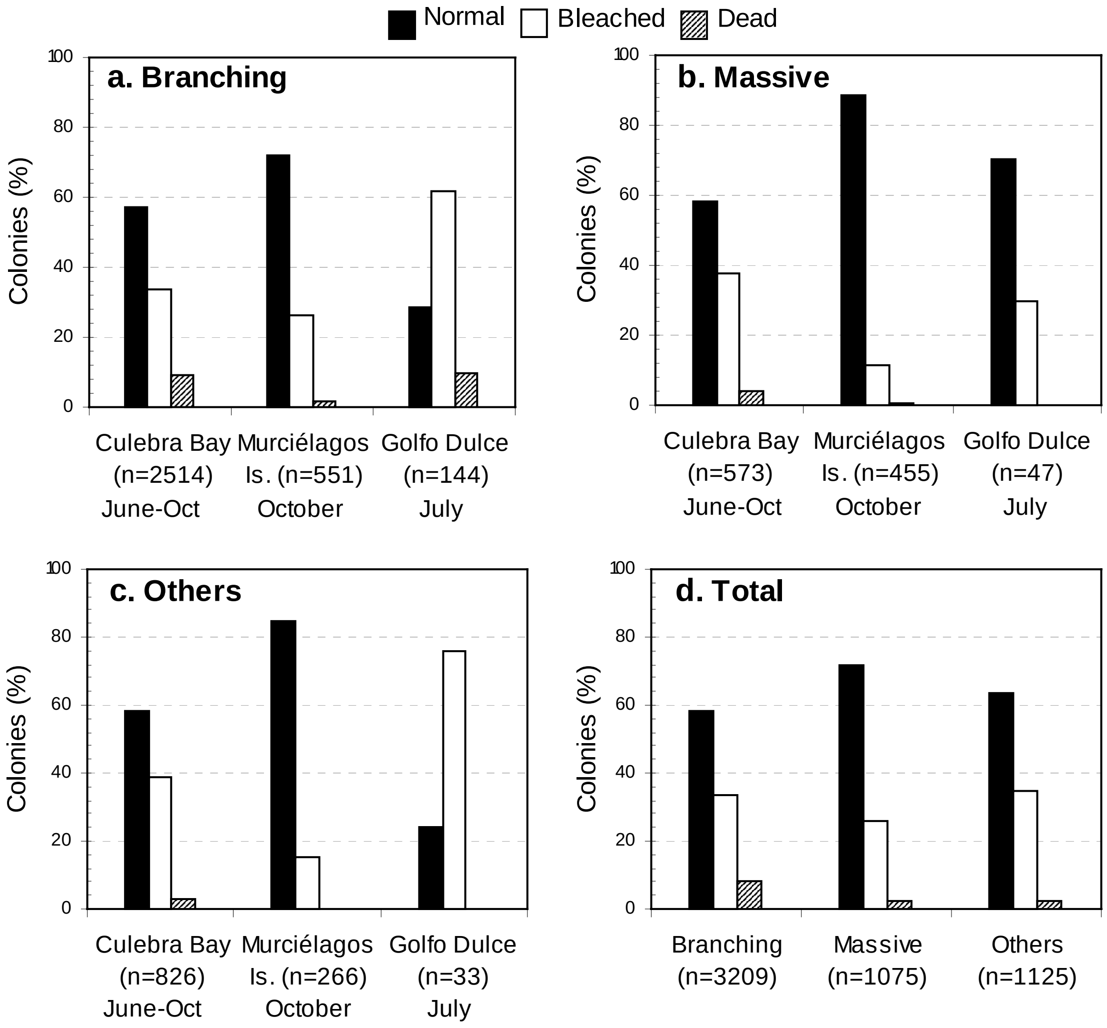
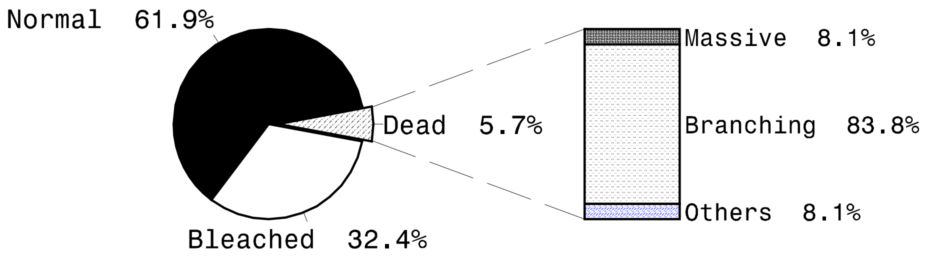

■ Normal
☐ Bleached
▨ Dead
a. Branching
b. Massive
c. Others
d. Total
Colonies (%)
0
20
40
60
80
100
Culebra Bay (n=2514) June-Oct
Murciélagos Is. (n=551) October
Golfo Dulce (n=144) July
Culebra Bay (n=573) June-Oct
Murciélagos Is. (n=455) October
Golfo Dulce (n=47) July
Culebra Bay (n=826) June-Oct
Murciélagos Is. (n=266) October
Golfo Dulce (n=33) July
Branching (n=3209)
Massive (n=1075)
Others (n=1125)

Figure 6

a. ENSO 1997/98



b. ENSO 1991/92

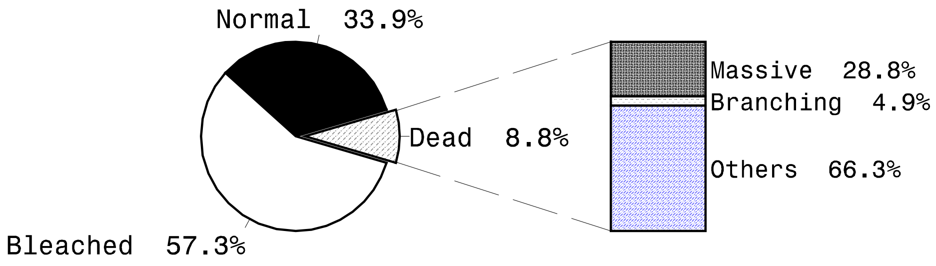


Figure 7

CORAL COVER CHANGE ASSOCIATED TO EL NIÑO, CENTRAL PACIFIC COAST OF COSTA RICA, 1992-2001

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ABSTRACT

Changes in the live and dead coral cover were documented at three localities off the Costa Rican central Pacific coast first in 1992 during the aftermath of the 1991-1992 El Niño; again in the period between 1994 and 1995, and last in January 2001. Recovery of coral communities after the 1991-1992 El Niño was expressed by a significant increase (~40%) in 1994 of live coral cover at one locality (Manuel Antonio). A subsequent decrease (~50%) in response to the very strong 1997-1998 episode was recorded at Manuel Antonio and Ballena, mainly due to partial tissue mortality of branching (*Pocillopora* spp.) and massive (*Porites lobata*) corals. Remarkably, mortality of entire colonies associated to that event was scarce and confined to branching and nodular (*Psammocora stellata*) corals. This species was not found at one locality (Cambutal) in the 2001 survey and it is presumed locally extirpated. The recovery of this coral and others will depend on recruits from surviving colonies in deeper waters and other coral communities in the vicinities. Within sites at a given locality, contrasting results in live coral cover variability were found, and it is partially due to distinct coral assemblages, coral growth, physical exposure to tidal regime, and related with the last one, variable duration and intensity of the warming event. In general, predominant meteorological conditions at the studied area are more conducive to solar radiation stress during El Niño years and are related to changes in the atmosphere-ocean interactions in response to the warming events.

KEY WORDS: Coral, El Niño, ENSO, bleaching, eastern Pacific, Costa Rica

INTRODUCTION

Coral reef communities are subjected to unpredictable natural disturbances, ranging from catastrophic events such as cyclones or earthquakes to limited perturbations such as scrapings by crustaceans. In the eastern Pacific region, natural disturbances known to have affected coral reefs communities include dinoflagellates blooms (Guzmán et al. 1990), low tidal exposure (Eakin and Glynn 1996; Cortés and Jiménez 2002), storms (Robinson 1985, Guzmán 1986, Glynn et al. 1998, Lirman et al. 2001, Cortés and Jiménez 2002), fresh water (Cortés et al. 1994), and low sea water temperature during the Little Ice Age (Glynn et al. 1983). But El Niño is perhaps the most important source of natural disturbance exerting an important control over coral communities in the eastern Pacific, on the ecological and geological scales (Glynn 1990, Glynn and Colgan 1992). For example, at the Islas Galápagos, following the 1982-1983 event, reef recovery failed and coral reef structures were virtually eliminated (Reaka-Kudla et al. 1996).

Even though El Niño effects on eastern Pacific marine ecosystems were first described during the 1972-1973 episode (Caviedes 2001), it was not until the 1982-1983 event that its consequences on coral reefs were first documented (Glynn 1984). In Costa Rica, between 50% and 90% reduction of live coral cover attributable to the 1982-1983 event was recorded at insular coral reef communities (Cortés et al. 1984, Guzmán et al. 1987, Guzmán and Cortés 1992). The 1986-1987 El Niño caused no major mortality, although interruptions in massive corals at the northern coast suggest extensive partial mortality associated with this event (Jiménez and Cortés 2002). It was during the 1991-1992 episode that bleaching and mortality of corals were reported again at the central Pacific coast (Guzmán and Cortés 2001, Jiménez and Cortés 2001). Surprisingly, the 1997-1998 event, the strongest in recorded history (Enfield 2001), caused low reduction of live cover and relatively scarce mortality of entire colonies in the north and south of the country (Guzmán and Cortés 2001, Jiménez et al. 2001).

This study documents coral cover variability in a time period (1992 to 2001) when two El Niño warming events affected coral communities at the Manuel Antonio National Park, Punta Cambutal, and Ballena Marine National Park (Fig. 1), localities here referred as the Costa Rican central Pacific coast.

MATERIALS AND METHODS

STUDY SITES: Manuel Antonio National Park (hereafter Manuel Antonio) (Fig. 1) has ~55,000 ha of marine area and consist of a mixture of islands, coves, rocky headlands and sandy beaches. Manuel Antonio has various coral communities upon basalt or sand substrates and a few small (< 0.1 ha) patch reefs (Cortés and Jiménez 2002). *Pocillopora* spp., *Porites lobata* and *Psammocora stellata* are the most abundant taxa. Thirty-eight kilometers south-east of Manuel Antonio, at a semi-enclosed cove in Punta Cambutal (hereafter Cambutal) (Fig. 1), a small coral community dominated by *Porites lobata* is found. Large colonies (>1.5 m diameter) of *P. lobata* are intermingled with medium-sized (~1 m) *Pavona clavus* and *Pavona gigantea* colonies. Abundant coral communities consisting mainly of *P. lobata* and *P. gigantea* are found in Ballena Marine National Park (hereafter Ballena), south from Cambutal (Fig. 1). Ballena has more than 5,000 ha of marine area comprising several islands, islets, submerged banks, rocky headlands, and sandy and rocky beaches. Mixed assemblages of solitary corals and octocorals dominate the deep water (> 15 m) communities (Cortés and Jiménez 2002).

SEA SURFACE TEMPERATURE (SST) AND METEOROLOGICAL DATA: The environmental data used to examine possible factors affecting coral cover, are monthly averaged global gridded analysis of SST (1° x 1° grid centered on 9.5°N, 84.5°W) from the Reynolds NCEP optimal interpolation analysis (Reynolds and Smith 1994), and cloudiness (2.5° x 2.5° grid centered on 8.57°N, 84.37°W) from the NCEP-NCAR reanalysis (Kalnay et al. 1996). Both data sets are a blend of in situ observations, ships, aircraft and bias-corrected satellite data. Rainfall (1984-2001) and sun hours (1983-2001) data from the nearest meteorological stations to the Manuel Antonio study area (Quepos, 09°26'N, 84°09'W and Damas, 9°29'N, 84°12'W), were provided by the Costa Rican Instituto Meteorológico Nacional. For the Cambutal and Ballena areas, the nearest meteorological station, Palmar Sur (8°67'N, 83°28'W), has a fragmentary record of rainfall and sun hours missing several months of the 1991-1992 and 1997-1998 El Niño years. A comparison of this station with the Quepos and Damas during the 1980s and 1990s (Fig. 2), showed no major differences in the seasonal patterns or amount of monthly rain (t-Test t= 0.25, P= 0.799, df= 288) or sun hours (t= 0.32, P= 0.745, df= 222). Therefore, the Quepos and Damas stations are considered representative for the entire study area. Monthly anomalies of SST and meteorological data were calculated by subtracting monthly means derived for the period 1982-2001 from individual months.

CORAL COVER TRANSECTS: Surveys to quantify coral cover were undertaken in November 1992 at Manuel Antonio (five sites), Cambutal (one) and Ballena (four) where corals were mostly affected by the 1991-1992 El Niño (Jiménez and Cortés 2001). They were repeated at

Cambutal and Ballena in June 1994, Manuel Antonio in April 1995 (non-El Niño years), and at all localities in January 2001 (after the very strong 1997-1998 event). The mid 1990s is a time period which some categorize as the 1990-1995 El Niño (Trenberth and Hoar, 1996). However, the SST data for the study area presented in this paper (see below) do not show a consistent pattern of high SST during that period of time. Therefore we consider 1994 and 1995 as non-El Niño years (see Latif et al., 1997 for the 1990s' warming debate). The percentage of live and dead coral cover was determined with a 10 m long chain (1.1 cm link^{-1}) along five to six transects parallel to the shoreline and across ten study sites presenting very different characteristics (Table 1). The number of links corresponding to each category of substrate was translated to a percentage with respect to the transect total number of links. Statistical comparisons utilizing the number of links, not the percentages, were performed after testing for normality and heterogeneity of variances (Underwood 1997). To identify the sources of significant variation between years, a post hoc group analysis (Tukey HSD test) was utilized. Data among sites of a given locality were not analyzed statistically due to dissimilar characteristics that make them not comparable (Table 1).

RESULTS

SEA SURFACE TEMPERATURE (SST) AND METEOROLOGICAL DATA: Mean monthly anomalies of SST and meteorological data are compared in Fig. 3. Four distinct warming events occurred in the waters off the study area during the 1982-2000 time period, when positive anomalies above 0.4 °C were the norm for several consecutive months (Fig. 3A). These warm periods correspond to El Niño events which varied in intensity from weak (1991-1992), and moderate (1986-1987) to very strong (1982-1983 and 1997-1998). Therefore, the study area is sensible to local manifestations of El Niño events in the eastern tropical Pacific.

Given the occurrence of four El Niño events revealed from the SST record, several generalities in the meteorological data can be seen (Fig. 3B-D). For example, during the El Niño episodes, it is less cloudy and drier than in other years, and the number of sun light hours per month tend to be higher. A noteworthy exception is the 1986-1987 El Niño, when anomalies of cloudiness and sun hours varied considerably. Compared with the 1991-1992 El Niño, the 1997-1998 event had the most prominent anomalies in all variables.

CORAL COVER TRANSECTS: Percentage of live (LCC) and dead (DCC) coral cover were examined in relation to years, localities, and species within localities. A total of seven coral species were encountered in the transects during the three surveys (Table 2). The highest number of species (six) at one location was found at Manuel Antonio, decreasing to four at Ballena. The species *P. lobata* contributed more than any other coral to the total live cover at all localities and years. Its percentage of cover tended to be higher during non-El Niño years (1994, 1995), though it was statistically significant only at Ballena (F= 3.82, P=0.027, df= 2), where the 2001 (post-El Niño) cover of this coral showed a ~50% reduction with respect of 1994. In the last survey in January 2001, the tops of nearly all colonies of *P. lobata* at Manuel Antonio were dead and had become colonized by filamentous algae or covered with sediments. The periphery of these dead areas is being overgrown by coral tissue forming a conspicuous ridge. The same mortality and regeneration patterns were observed on a lesser extent at Ballena and Cambutal.

The cover of three other species was significantly lower in 2001 than in previous years, with *P. elegans* (F= 5.52, P= 0.006, df= 2) and *P. damicornis* (F= 4.48, P= 0.015, df= 2) at Manuel Antonio, being less affected than *P. stellata* at Cambutal where this coral was completely absent in the last survey. Mean cover of *P. stellata* (~1.3%) was not significantly different during 1992 and 1994. Cover of the other species did not vary considerably between surveyed years (P > 0.05). In general, no coral species analyzed individually showed any significant increase in cover, i.e. recovery, during the time period between the two El Niño episodes.

Percentage of live and dead coral cover showed large variability among studied sites of a given locality and year (Fig. 4). At Manuel Antonio, LCC and DCC varied significantly only at two sites, where LCC was higher in 1995 than in 1992 and 2001 (P < 0.05, Tukey), and DCC was lower in 1995 than in 2001 (P < 0.05, Tukey). During the last survey in 2001, numerous dead *Pocillopora* spp. and *P. stellata* colonies covered with algae were recorded in the transects at one site (2), while extensive partial tissue mortality on *P. lobata* colonies was very common at another site (5). Only one site was surveyed at Cambutal and even though percentage of cover for most species declined during the 2001 survey (Table 2), mean LCC (~23%) and DCC (~47%) did not vary significantly between sampling years (Fig. 4). At Ballena (Fig. 4), LCC at one site (9) was lower in 2001 than in 1994 (P < 0.01, Tukey); DCC was considerably higher at three sites for the 2001 survey (P < 0.001, Tukey).

Changes of total LCC (all species pooled) and DCC at each locality over the study time period are presented in Fig. 5. Mean LCC (~39%) was found high at Manuel Antonio and low (~20%) at Ballena (Fig. 5A). For both localities, the 1994 and 1995 surveys (between El Niño events) had the highest LCC percentages of the studied period. At Manuel Antonio, LCC in 1995 differed significantly from the 1992 (P < 0.01, Tukey) and 2001 (P <

0.05, Tukey) surveys, both performed during an El Niño and post-El Niño years respectively. In contrast, the 1994 LCC at Ballena differed only with the 2001 survey (P < 0.05, Tukey). Mean DCC was highest at Cambutal (~48%) and lowest (~24%) at Ballena (Fig. 5B). It was significantly higher in 2001 than in previous years at Manuel Antonio and Ballena. At these localities, DCC was not significantly different during El Niño and non-El Niño years (1992 vs. 1994-1995) (P > 0.05 in both cases, Tukey).

DISCUSSION

El Niño warming events in the eastern Pacific are evident in the central Pacific coast of Costa Rica as demonstrated in this paper. During the 1982-1983, 1986-1987, 1991-1992 and 1997-1998 episodes, sea temperature rose to and remained above the normal seasonal temperature cycle for several consecutive months. Also shown is the co-occurrence of climate shifts resulting in prolonged sunny and dry spells. Although cloud cover was less consistent during the 1986-1987 episode (overcast periods with clear interludes), the SST, rainfall and sun hours anomalies showed similar trends to other El Niño years. The general pattern observed in the environmental data is the result of the intensification in the summer trade winds over the Caribbean during El Niño years, producing a protracted mid-year low in runoff and setting drought-like conditions along the Pacific coast of Costa Rica (Fernández and Ramírez, 1991, Waylen et al., 1996). Due to this marked decrease in cloud cover and runoff, the calm coastal waters are clear, facilitating light penetration and thus heightening the irradiance levels reaching the corals. The increase in solar radiation is known to produce damage by disrupting the biochemical pathways within the zooxanthellae (Glynn 1996, Hoegh-Guldberg 1999; Hoegh-Guldberg and Jones 1999, Brown at al. 2000, Dunne and Brown 2001, Fitt et al. 2001), and this negative effect is exacerbated at temperatures higher than normal (Coles and Jokiel 1978) which are the El Niño trademark.

In Costa Rica, coral bleaching and mortality in 1992 and 1997 coincided with prolonged warm water excursions and doldrum-like weather on the Pacific coast (Jiménez and Cortés 2001, Jiménez et al. 2001), and in 1995 on the Caribbean coast (Jiménez 2001a). Other mass-bleaching events have been documented elsewhere during similar oceanographic and climatic conditions (Glynn 1996, Brown 1997, Hoegh-Guldberg 1999, Fitt et al. 2001), but not so in the Virgin Islands where bleaching was not accompanied by doldrum-like weather (Quinn and Kojis 1999). The paucity of bleaching and mortality in the study area in 1987 despite sea temperature anomalies similar to or higher than in other years in which bleaching and mortality occurred, may have been the result of the higher cloud cover and runoff which, in combination, decreased solar radiation stress. Similar atmospheric conditions during 1998 may explain the considerably small number of corals that bleached that year in the upwelling area of Golfo de Papagayo (Jiménez et al. 2001). Few corals bleached, even though sea temperature anomalies were higher than in autumn 1997 when widespread bleaching and mortality of corals were first documented. Likewise, Mumby et al. (2001) attribute the scarcity of bleaching at the Society Islands during the 1998 warming event to high cloud cover. Finally, an interesting explanation for the nearly absence of coral bleaching at the Andaman Sea during the 1998 warming, is given by Dunne and Brown (2001). They propose that elevated solar radiation prior to sea-temperature maxima may protect corals from bleaching, by priming the coral and algae photoprotective defenses. Clearly, the association between environmental parameters and bleaching events is more complex than has been suspected, and further field observations and monitoring of variables are needed.

Surveys to quantify coral cover in Manuel Antonio, Cambutal and Ballena were carried out in a time period when two of the most recent El Niño occurred, with one of them, the 1997-1998 episode, considered the strongest event on record (McPhaden 1999, Endfield 2001). Although mortality of entire coral colonies associated with this event was remarkably low in Costa Rica, < 6% (Jiménez et al. 2001), partial tissue mortality was high in massive corals resulting in a decrease in live cover at Manuel Antonio and Ballena. We relate this partial mortality to the 1997-1998 El Niño. During the January 2001 survey, dead patchy areas were still evident in the majority of *P. lobata* and *P. clavus* colonies. While regeneration of tissue over similar dead surfaces required less than 8 mo elsewhere (Jiménez et al. 2001), at Manuel Antonio, Cambutal and Ballena dead areas were still covered with sediments and filamentous algae more than three years after the warming episode. Similar long recovery time, 2 to 3 yrs, has been reported for massive corals in Colombia (Vargas-Ángel et al. 2001). Although fast regeneration of tissue in experimentally bleached corals has been associated with colony size (Mascarelli and Bunkley-Williams, 1999), slow growth rates may retard the healing process. Growth rates of *P. clavus* and *P. lobata* in the study area, as determined by X-rays of cores (Jiménez and Cortés, unpublished data), are 8 to 10 mm yr^{-1} which is considerably lower than 10 to 20 mm yr^{-1} shown in Bahía Culebra (Jiménez and Cortés 2002).

Coral species composition throughout the study period did not change drastically and only one coral species, *P. stellata*, disappeared at one locality (Cambutal) after the 1997-

1998 warming event. Previously, during the 1991-1992 El Niño, this coral was greatly affected at Manuel Antonio with ~40% of all colonies dead (Jiménez and Cortés, 2001); at Cambutal and Ballena, however, mortality was lower (<15%). The disappearance of *P. stellata* at Cambutal did not have an effect on the percent of total cover which was not significantly dissimilar to previous years. Interestingly, this species was not affected in Mexico by the 1997-1998 warming episode (Carriquiri et al. 2001), endorsing the geographical complexity of coral responses to thermal-stressors such as El Niño. Local extirpation of other coral species in relation to El Niño has been observed in the eastern Pacific. One hydrocoral and two scleractinian species were not found shortly after the 1982-1983 and 1997-1998 episodes (Glynn et al. 2001). Similar species losses were also reported from the Maldives (McClanahan 2000).

At Manuel Antonio, more than 60% of *P. elegans* and *P. damicornis* were bleached and circa 15% were dead or with partial tissue mortality after the 1991-1992 El Niño (Jiménez and Cortés 2001). By 1995, *Pocillopora* spp. cover was similar to 1992 despite high growth rates, between 32 and 45 mm yr^{-1} (Guzmán and Cortés, 1989; Jiménez and Cortés 2002), which may suggest fast recovery rates from partial mortality. However, after the 1997-1998 El Niño, live cover of *P. damicornis* and *P. elegans* declined by 50% and 70% respectively. Eastern Pacific pocilloporid corals are very sensitive to increments in temperature (Glynn and D'Croz 1990) and mortalities greater than 80% at Isla del Caño were attributed to the 1982-1983 El Niño warming (Guzmán et al. 1987). Such high mortality rates during warming events may drive *Pocillopora* spp. populations to very low levels, impairing recovery and recruitment. This is critical at localities such as Manuel Antonio where pocilloporids are not abundant and have limited recovery capabilities. Interestingly, *P. elegans* cover was not significantly reduced at Cambutal and Ballena. Similarly, conspecific corals elsewhere have shown differences in susceptibility to bleach, mortality rates and recovery capabilities (Brown 1997, Hoegh-Gouldberg 1999, Marshall and Baird 2000, Fitt et al. 2001, Glynn et al. 2001). This has been interpreted as the result of corals' adaptation to local conditions, different warming intensities at each locality, thermal acclimation, and presence of several clades of symbionts.

Recovery (i.e. total live cover higher than 1992 values) of coral communities in the studied area was shown to vary greatly among localities. Only at Manuel Antonio, during the 3 yrs between 1992 to 1995, live cover surpassed 1992 percentages, while in 1994 there was a tendency (not statistically significant) at Cambutal and Ballena of slight recovery. This suggests that longer periods between disturbances are needed at those localities in order to regain pre-disturbance levels. This can be the result of spatial differences in the extent of coral mortality (entire colonies), regeneration of damaged colonies (tissue partial mortality), recruitment, growth, bioerosion, and frequency and intensity of other disturbances such as siltation. Biotic and environmental factors that may influence dispersal, colonization and resilience of corals in the eastern Pacific are reviewed by Glynn and Ault (2000). Our observations suggest that more stressful abiotic environments at Cambutal and Ballena are due to high input of sediment loads from road construction and coastal development (Cortés and Jiménez 2002).

It is becoming clear that climatologically driven stressors such as the El Niño events are extremely important factors structuring coral communities in the eastern Pacific (Glynn and Colgan 1992, Glynn 1990, 1996, 2001, Glynn and Ault 2000). In a 16 yr study at Isla del Caño (Fig. 1), Guzmán and Cortés (2001) documented the trajectory of coral reef communities in the course of several natural disturbances. They found large changes in adult populations and in recruitment. This kind of study provides a better understanding of recovery processes that may be acting. Similar research are needed in other coral communities, along with the documentation of the disturbance history, if we ought to be able to improve the environmental and ecological understanding of coral communities dynamics and resilience under scenarios of more frequent and stronger El Niño episodes (Timmermann et al. 1999, Tudhope et al. 2001). In addition, we have to consider that, while severe El Niño episodes are disastrous if coral populations are driven to the edge of local extinction by dramatic mortalities of coral taxa, moderate events, however, with non-lethal rise in temperature, may have a positive effect on coral reef communities. For example increases in growth rates, reproductive activity and recruitment pulses have been observed after some El Niño episodes (Glynn et al. 1991, 1994, Feingold 1995, Guzmán and Cortés 2001, Vargas-Ángel et al. 2001, Jiménez and Cortés 2002), drawing attention to documenting other aspects of the corals’ physiology and metabolism.

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TABLE 1. Description of the sampling sites at the three surveyed localities. n, total number of transects.

Locality	Site number	Depth range (m)	Predominant Substrate	Degree of Turbulence
Manuel Antonio (n= 20)	1	1-3	Basalt-Sand	Medium
	2	1-4	Basalt-Sand	Low
	3	2-4	Sand	High
	4	3-5	Sand-Basalt	Low
	5	2-8	Basalt-Sand	Medium
Cambutal (n= 6)	6	2-6	Basalt-Sand	High
Ballena (n= 20)	7	2-3	Sand-Basalt	Medium
	8	2-3	Sand-Basalt	High
	9	2-6	Basalt	High
	10	3-6	Basalt-Sand	High

TABLE 2. Percentage of cover (standard deviation) by species and year at the three study sites. n= number of transects where the species was present.

Species	Manuel Antonio			Cambutal			Ballena		
	1992	1995	2001	1992	1994	2001	1992	1994	2001
Pocillopora elegans Dana 1846	7.6 (6.5) n=15	7.8 (6.5) n=18	2.3 (1.4) n=14	1.1 (0.8) n=4	2.5 (1.6) n=2	0.2 (0.1) n=2	1.1 (0) n=1	0.3 (0.1) n=6	0.5 (0.3) n=4
Pocillopora damicornis (Linnaeus 1748)	2 (2.1) n=10	2.2 (2.1) n=15	1.1 (0.4) n=4	--	--	--	--	--	--
Pavona clavus Dana 1846	3.8 (1.9) n=4	3 (2.1) n=9	1.9 (1.1) n=6	3.6 (2.9) n=6	5.1 (3.4) n=5	1.9 (2.1) n=6	--	0.3 (0.1) n=2	0.2 (0.2) n=2
Pavona gigantea Verrill 1869	--	--	--	2.1 (0.9) n=4	2.1 (1.4) n=3	1 (1.7) n=4	--	--	--
Psammocora stellata (Verrill 1860)	6.2 (5.1) n=9	8.9 (8.9) n=15	4.7 (5.7) n=15	1.5 (1.2) n=3	1.1 (0.2) n=2	--	0.6 (0.6) n=3	0.5 (0.5) n=10	0.8 (0.6) n=5
Porites lobata Dana 1846	29.6 (19.6) n=16	38.5 (20.7) n=18	28.3 (18.5) n=17	16.6 (8.9) n=6	18.2 (10.7) n=6	18.1 (9.5) n=6	20.3 (17.9) n=20	26.7 (13.8) n=19	13.3 (6.2) n=20
Tubastraea coccinea Lesson 1829	7.2 (0) n=1	6.6 (2.5) n=3	2.3 (1.3) n=3	--	--	--	--	--	--

FIGURE CAPTIONS

Figure 1. Location of the coral cover transects (numbers) on the central Pacific coast of Costa Rica (insert). Other localities mentioned in the text: Islas Murciélagos (IM), Bahía Culebra (BC), Isla del Caño (IC) and Golfo Dulce (GD).

Figure 2. Comparison of monthly data from the Palmar Sur meteorological station: rainfall (A) during 1980-1995, and sun hours (B) during 1983-1995 with the Quepos and Damas stations.

Figure 3. Mean monthly anomalies of sea surface temperature (A), cloudiness (B), rainfall (C) and sun hours (D) at the study area for the 1982 to 2001 time period. The vertical shading shows the approximate timing of El Niño events.

Figure 4. Percent (and SE) of live (A) and dead (B) coral cover according to the studied sites organized from north to south as in Fig. 1. Manuel Antonio (1 to 5); Cambutal (6); Ballena (7 to 10). ANOVA $^*P < 0.05$; $^{**}P < 0.001$.

Figure 5. Percent (and SE) of total live (A) and dead (B) coral cover at the three studied localities. ANOVA $^*P < 0.05$; $^{**}P < 0.001$.

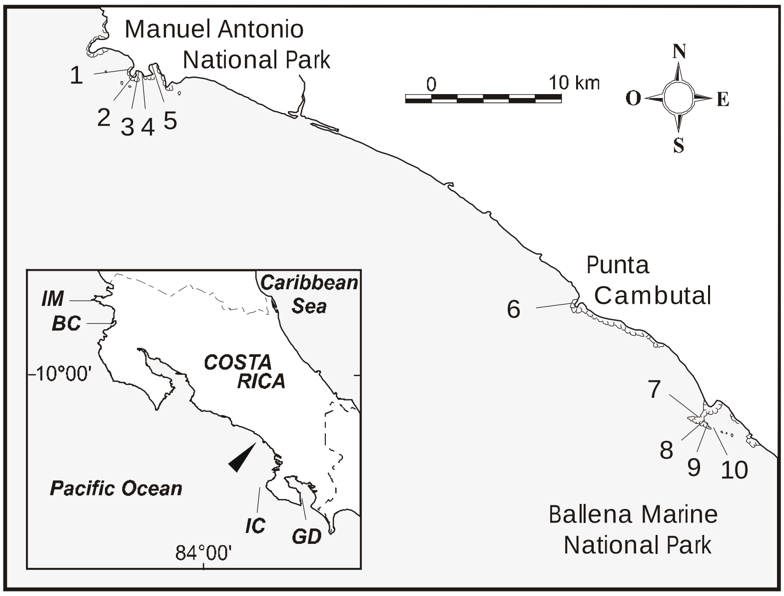
Manuel Antonio
National Park
1
2
3
4
5
0
10 km
N
O
E
S
Punta
Cambutal
6
7
8
9
10
Ballena Marine
National Park
IM
BC
Caribbean
Sea
COSTA
RICA
10°00'
Pacific Ocean
IC
GD
84°00'

Figure 1

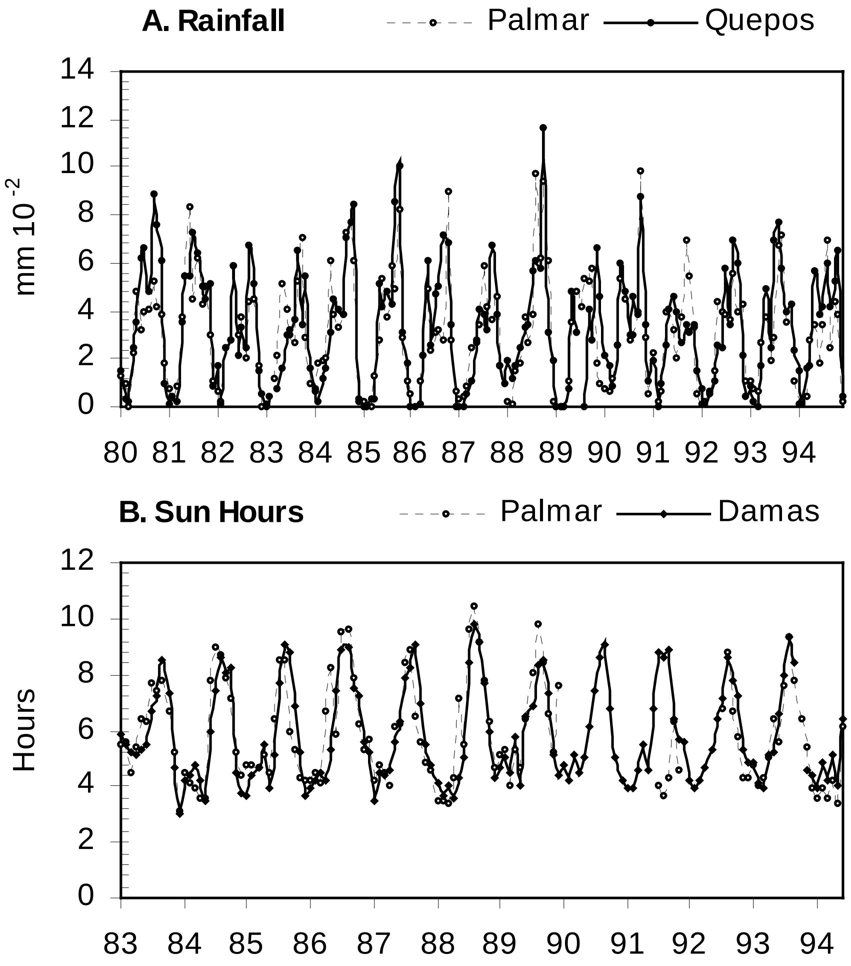
A. Rainfall
Palmar
Quepos
mm 10 $^{-2}$
14
12
10
8
6
4
2
0
80 81 82 83 84 85 86 87 88 89 90 91 92 93 94
B. Sun Hours
Palmar
Damas
Hours
12
10
8
6
4
2
0
83 84 85 86 87 88 89 90 91 92 93 94

Figure 2

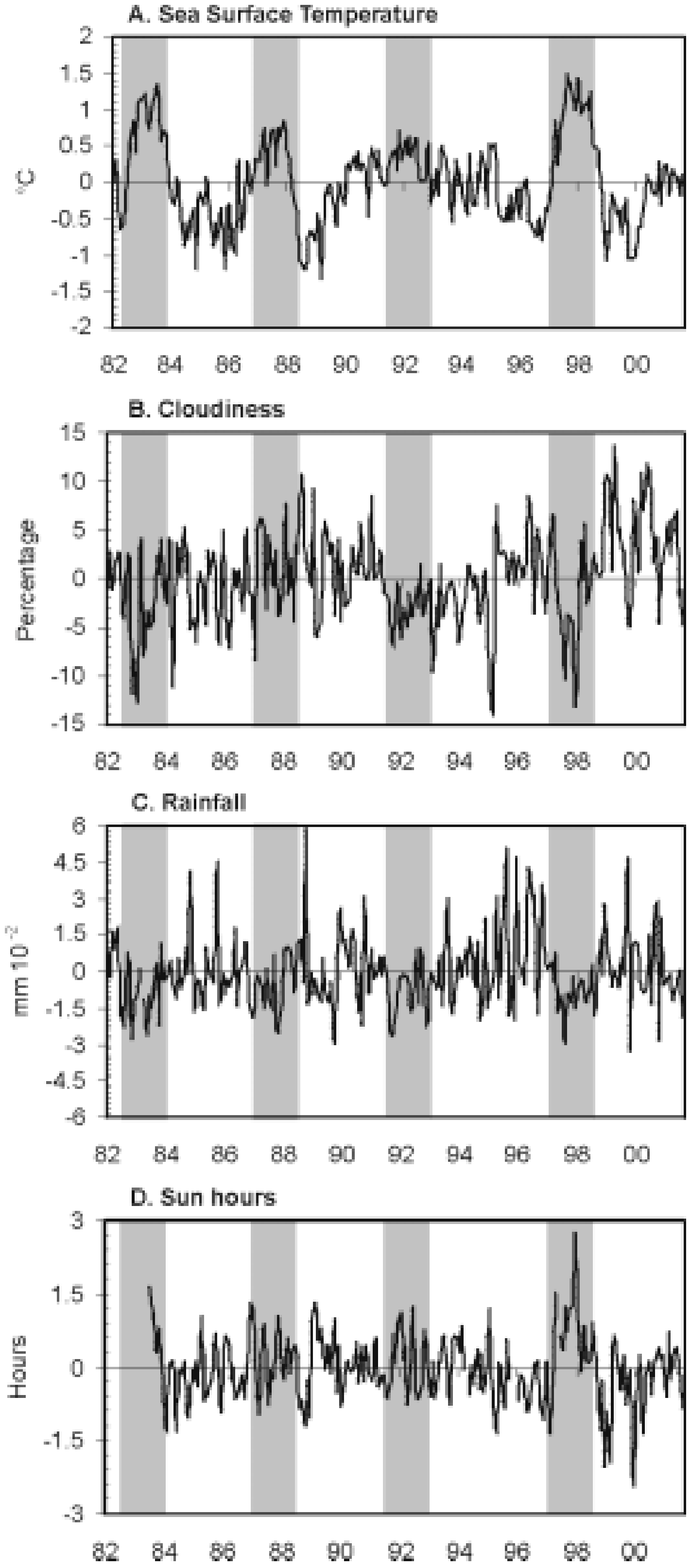
A. Sea Surface Temperature
°C
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
B. Cloudiness
Percentage
15
10
5
0
-5
-10
-15
C. Rainfall
mm 10^{-2}
6
4.5
3
1.5
0
-1.5
-3
-4.5
-6
D. Sun hours
Hours
3
1.5
0
-1.5
-3
82
84
86
88
90
92
94
96
98
00

Figure 3

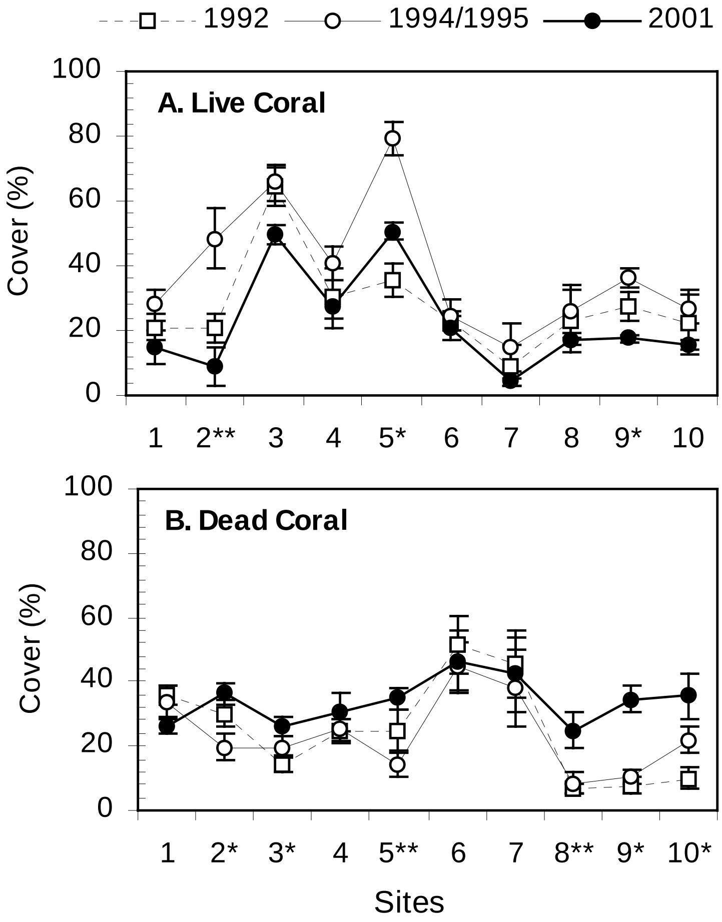
1992
1994/1995
2001
A. Live Coral
Cover (%)
0
20
40
60
80
100
1
2**
3
4
5*
6
7
8
9*
10
B. Dead Coral
Cover (%)
0
20
40
60
80
100
1
2*
3*
4
5**
6
7
8**
9*
10*
Sites

Figure 4

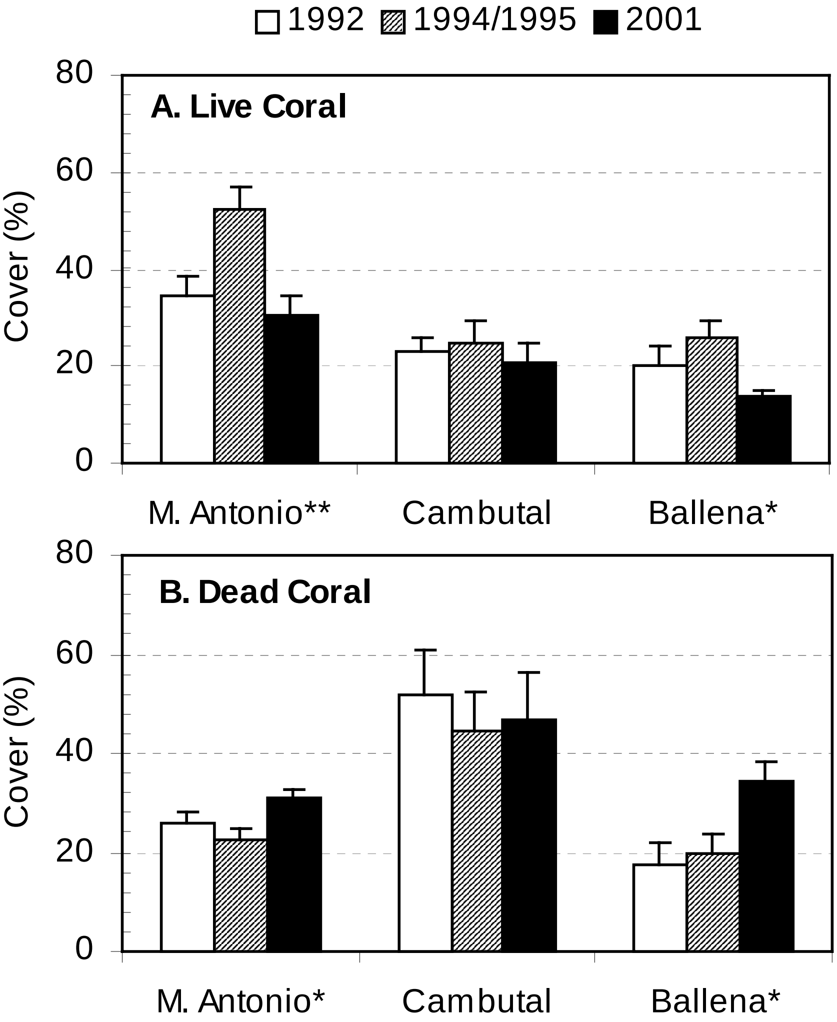
□ 1992 ▨ 1994/1995 ■ 2001
A. Live Coral
Cover (%)
80
60
40
20
0
M. Antonio**
Cambutal
Ballena*
B. Dead Coral
Cover (%)
80
60
40
20
0
M. Antonio*
Cambutal
Ballena*

Figure 5

ONGOING STUDY ON:

STABLE ISOTOPIC ($\delta^{13}C$ AND $\delta^{18}O$) COMPOSITION IN THE EASTERN PACIFIC CORAL PAVONA CLAVUS: SEASONAL AND INTRASPECIFIC VARIATION AND RESPONSE TO ENVIRONMENTAL VARIABLES

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In preparation

ABSTRACT

The variation of the skeletal stable isotopic ($\delta^{13}C$ and $\delta^{18}O$) composition in the eastern Pacific coral *Pavona clavus* is currently investigated by means of several approaches: (1) by comparing the isotopic records, at a monthly resolution, of six colonies closely spaced; (2) by associating the seasonal variation of the isotopic composition to environmental variables of six colonies, which were sampled at one month intervals over a 13 mo experimental period; (3) by comparing the isotopic records of colonies taken from three different depths (4, 7 and 12 m); and (4) by contrasting the isotopic records of *P. clavus* colonies from different localities (Bahía Culebra and Islas Murciélagos), as well as with another massive species (*Gardineroseris planulata*). All these studies will assist in the evaluation of *P. clavus* as a surrogate to reconstruct environmental conditions in the upwelling area of the Golfo de Papagayo (northern Costa Rica).

Preliminary results suggest that seasonal average amplitude of the $\delta^{18}O$ records is fairly constant among closely spaced colonies, and follows closely the seasonal changes in surface seawater temperature (SST). However, there is a discrepancy between the $\delta^{18}O$ depletion spikes and in situ sea water temperature (SWT) measurements (7 m depth). Mean $\delta^{18}O$, during the peak of the 1997-98 El Niño, was highly inconsistent between colonies, depths, localities and the two studied species. Although the period of the highest warming during the El Niño episode did not coincide with the highest depletion in skeletal $\delta^{18}O$, the seasonal oxygen composition amplitude was a good indicator of the warming. Slow growth rates or alterations in the skeletal deposition pattern (evidenced by the irregular skeletal density), during that period, may explain the attenuated $\delta^{18}O$ signal during the 1997-98 El Niño. Mean $\delta^{13}C$, and its seasonal amplitude, were different between all colonies and depths, though it tends to be slightly more constant at 12 m depth and in colonies collected at the Islas Murciélagos. Monthly $\delta^{18}O$ values from six colonies were strongly correlated with SWT, sunlight, wind speed, and rainfall. These preliminary results indicate that *P. clavus* from the study area may be a reliable surrogate of environmental conditions, and hence may make the study of past climate variations possible.

Currently, we are expanding these studies and the monitoring, of seawater $\delta^{18}O$ and $\delta^{13}C$, in order to better explain the seasonal isotope trends of *P. clavus* in the Golfo de Papagayo area.

INTRODUCTION

Isotopic composition of layered materials has been widely recognized as a surrogate to reconstructing environmental conditions. Urey (1947), who studied the relation between oxygen isotopes on the shells of marine organisms and the surrounding water, proposed the first application of isotope geochemistry to determine past environmental temperatures. Since then, the technique has been successfully applied to other marine organisms that accrete skeletons, recording important information of ambient conditions.

Corals incorporate in their skeletons chemical elements from the sea water, reflecting the oceanographic and climatic conditions during the calcification. In addition, corals can live for centuries, and, hence, they are considered excellent proxy indicators of environmental variability (Barnes and Lough 1990). Through the analysis of coral skeleton trace elements and isotopic composition, it has been possible to study local variation in sea temperature, salinity, precipitation, nutrients, volcanic eruptions, river discharge, global changes in temperature, and the historical influence of human activities (pollution), just to cite a few topics (see reviews in Buddemeier and Kinzie 1976, Dodge and Vaišnys 1980, Dunbar and Cole 1993 for environmental and climate changes).

In the eastern Pacific region, coral skeletal stable isotopic composition has been effectively used for reconstruction of environmental variability at different time scales. For example, massive death of Costa Rican corals 300-400 years ago was associated to the cooling during the Little Ice Age (Glynn et al. 1983). Moreover, based on $\delta^{18}O$ composition, decadal and century-scale temperature and rainfall variability has been studied from corals collected at Costa Rica (Carriquiry et al. 1988, 1994, Wellington and Dunbar 1995), Panamá (Dunbar and Wellington 1981, Druffel et al. 1990, Linsley et al. 1994, Wellington and Dunbar 1995), Galápagos (Shen et. al. 1992, Dunbar et al. 1994, Wellington and Dunbar 1995, Wellington et al. 1996), and Clipperton Atoll (Linsley et al. 1999, 2000). In all these papers, skeletal $\delta^{18}O$ composition is the stable isotope linked to seawater temperature, though, it is also influenced by variations in seawater isotopic composition due to evaporation or rainfall. The rationale behind the use of the oxygen isotope is that coralline aragonite exhibits a temperature relation, such that $\delta^{18}O$ decreases by ~2‰ for every 1°C increment in seawater temperature (Epstein et al. 1953). Coral skeletal $\delta^{18}O$ is precipitated out of isotopic equilibrium with the seawater (Weber and Woodhead 1972, McConnaughey 1989), and this offset is constant for conspecific corals.

The $\delta^{13}C$ skeletal composition has proven to be more difficult to link to environmental variables because of physiological processes that produce changes in the isotope composition. For example, photosynthesis rates of zooxanthellar symbionts are known to change $\delta^{13}C$ levels (McConnaughey 1989, Muscatine et al. 1989, Grottoli and Wellington 1999). Coral heterotrophy also affects $\delta^{13}C$ values, due to the low carbon isotope content of zooplankton (Grottoli and Wellington 1999). Additionally, light is another factor that affects skeletal $\delta^{13}C$ levels in corals (McConnaughey 1989, Muscatine et al. 1989, Carriquiry et al. 1994, Wellington and Dunbar 1995, Grottoli and Wellington 1999). The implications for environmental reconstruction include changes in irradiance (i.e. cloud cover) and zooplankton availability, and hence productivity (Grottoli and Wellington 1999).

Why study the isotopic composition of *Pavona clavus* in the upwelling area of Papagayo? This coral species has several attributes, which indicate that it could be used as a convenient proxy or surrogate for reconstructing environmental parameters. These attributes consist of: (1) hemispherical or lobular growth forms which facilitate the drilling of large, massive colonies; (2) high growth rates in the Papagayo area (>20 mm yr^{-1}, Jiménez and Cortés 2002), which allow sampling for isotope composition on a weekly or monthly resolution; and (3) wide distribution and abundance at the Golfo de Papagayo.

The objectives of this on-going study are: (1) to evaluate if *P. clavus* skeletal $\delta^{18}O$ isotope composition accurately recorded the 1997-98 El Niño; (2) to identify the $\delta^{13}C$, $\delta^{18}O$, and skeletal density seasonal trends, and to explore if they are influenced by the Papagayo upwelling; (3) to quantify $\delta^{13}C$ and $\delta^{18}O$ variability between and within colonies from two different localities; (4) to assess if *P. clavus* from the upwelling region of Papagayo can be used as a reliable tracer of environmental variables, and hence to facilitate the implementation of an environmental reconstruction for the area.

MATERIALS AND METHODS

Seawater Temperature and environmental data: Hobo-Temp and Stow-Away (Onset Computer Inc.) underwater temperature data loggers (± 0.5°C accuracy) were used to monitor SWT at 4, 7 and 12 m depth in Culebra Bay (Fig. 1). The data loggers were placed among coral colonies 10-20 cm above the bottom and set to record every 36 min. The units were replaced every month. Salinity was measured on a monthly basis with an optical refractometer, during 2-3 days at five permanent monitoring stations across Bahía Culebra. Water samples for the salinity determination were collected directly above the coral colonies. Rainfall, sunlight hours and wind speed from the nearest meteorological station to Bahía Culebra (Llano Grande de Liberia, 10°06'N, 85°53'W) were provided by the Costa Rican Instituto Meteorológico Nacional.

Staining: In March 1995, six colonies of *P. clavus* were collected at the *Pavona* reef (4 m depth), and stained for 9-10 h in plastic boxes (110 l) with aerated seawater and re-located within 1 m^2 plot at the same depth of collection. All colonies were cemented to the bottom utilizing Portland II cement mix with plaster (3:2). The same colonies were stained again in February-March of 1996, 1997, 1998 and finally collected in 1999. Therefore, the alizarin marks provided the datum lines used as reference for the isotopic sampling and to determine the coral annual growth increments. A similar procedure was utilized for the staining of *P. clavus* (October 1996 and 1997) and *G. planulata* (October 1997) colonies at the Islas Murciélagos (Fig. 1). The corals were collected in May 1999. After collection, all stained colonies were rinsed in running freshwater to remove coral tissue and then sun dried.

Drilling of colonies and slabs: Healthy *P. clavus* colonies at 7 and 12 m depth were cored parallel to the main axis of growth, using an underwater pneumatic drill. The cores (25 cm length, 5 cm diameter), and the stained colonies, were cut with a rock saw, and the slabs (5-8 mm thick) X-rayed. Positive prints were used to identify the corallites' axis, where the carbonate powder for the analysis of isotopes was collected. Drilling of slabs was done with a low-speed drill using 0.8 mm diameter bits. Growth rates of *P. clavus* in the study area are high (>20 mm yr^{-1}, Jiménez and Cortés 2002), thus, samples taken at approximately 1 mm intervals are adequate to provide a monthly resolution of the isotopic records.

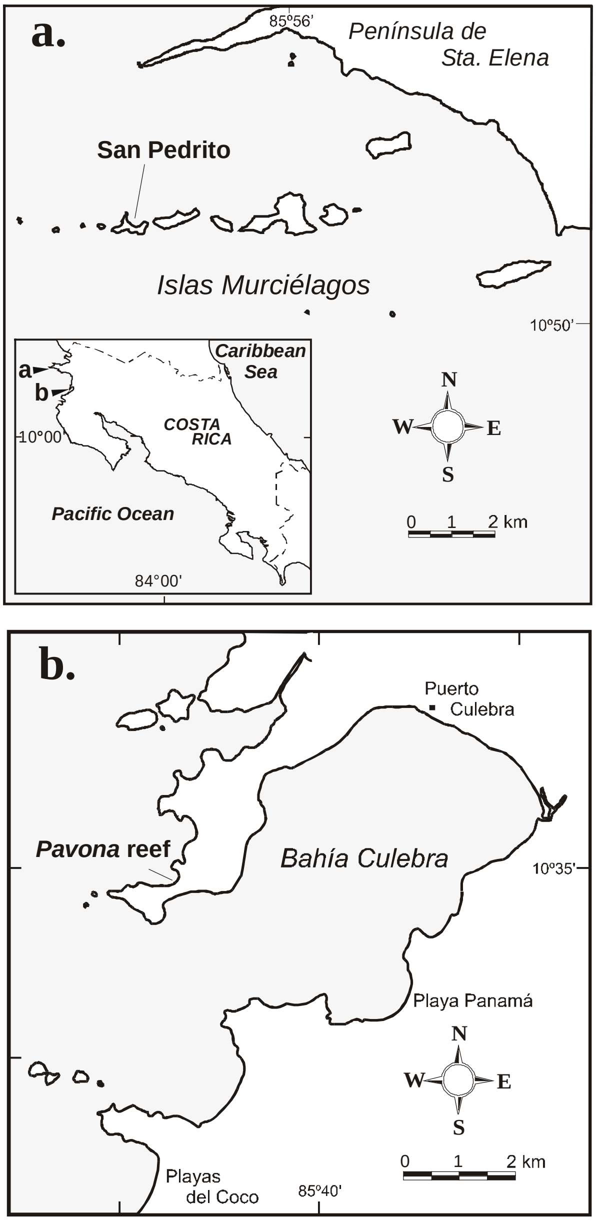

Figure 4 Locations of the isotope study sites (A) at the San Pedrito reef, Islas Murciélagos, and (B) at the *Pavona* reef, Bahía Culebra. Both study sites are located within the area known as Golfo de Papagayo. Corals were stained at Islas Murciélagos in 1996 (*Pavona clavus*) and 1997 (*P. clavus* and *Gardineroseris planulata*) and collected in 1999. At Bahía Culebra, six colonies of *P. clavus* were stained every year from 1995 to 1998, and collected in 1999.

Monthly coring of *P. clavus*: In October 1999, six healthy, large (>2.5 m diameter) *P. clavus* colonies were selected at 7 m depth at the *Pavona* reef, and sampled on a monthly basis from December 1999 to December 2000. The cores (15 mm diameter, 20 mm length) were carefully collected from the top area of each colony using a stainless steel plug-borer, and a cement plug was used to fill the hole. *P. clavus* tissue regeneration at the study area is fast (see Jiménez et al. 2001), and the plug was normally covered in 3-5 mo. Samples were at least 15 cm apart. Cores were rinsed and cut with the same procedures mentioned above. Four samples for isotope analysis were taken from the outer 0.5-0.8 mm of the core by approaching the drill bit to the skeleton. The carbonate powder was lightly crushed and homogenated.

Deposition of high and low density bands: To relate the isotopic composition with the annual deposition of growth bands (low and high density), we utilized optical densitometry measurements derived from the X-rays of cores and slabs. The radiographic prints were scanned using a Lumiscan 85/IMG LAB v.3 device and analyzed with the sofware MATLAB v.5.3. From each scanned print, one rectangular area (80 mm-length x 2.7 mm-width) was chosen for the light absorbency analysis to obtain a profile of optical densities. The program performs an average of the density values of approximately three corallites, and it is presented as a new light intensity beam, expressed in percent of absorbed light (100% correspond to the densest material). The resulting profile matches the transect where the samples for isotope concentrations were taken.

Isotopes measurements: The skeletal carbonate powder was homogenized, and the stable oxygen and carbonate isotopes of these samples (80-90 µg) were measured with a Finnigan MAT251 mass spectrometer, coupled to an automatic carbonate preparation device. The precision of measurement is ±0.08‰ for $\delta^{18}O$ and ±0.06‰ for $\delta^{13}C$, based on routine measurements of a laboratory working standard. All measurements are reported relative to the Pee Dee belemmite (PDB) reference standard.

PRELIMINARY RESULTS AND COMMENTS

Isotopic records of stained corals at the *Pavona* reef: The δ^{18}O monthly values derived from the six *P. clavus* colonies show a close correspondence with the sea surface temperature (SST) during the study time period (Fig. 2). Enrichment of the oxygen signal follows the seasonal occurrence of the Papagayo upwelling during the dry season (December-April), and depletion follows the establishment of the rainy season, when seawater temperature is higher (May-November). However, δ^{18}O depletion values between 1996-97 are higher or similar to 1997-98 and 1998-99, respectively (Fig. 2B). Although the seasonal δ^{18}O amplitude (lowest 1998 value minus lowest 1997 value) indicates a warming in that period, the monthly record suggests otherwise. Based only on the monthly records, we would have considered the period 1997-98 as a cool year, compared to 1996-97, and that was not the case (Fig. 2A).

Considering the isotopic records derived from individual colonies (Fig. 3), all stained colonies, in general, displayed similar δ^{18}O seasonal trends. The δ^{18}O was enriched around the datum staining lines, which approximately correspond to the coldest months of the upwelling season. On the contrary, δ^{13}C had not a clear seasonal trend and was very different between colonies (Fig. 3). However, in some colonies, δ^{13}C depletion tended to occur during the warmest months of the year, as observed for the oxygen isotope.

A comparison of weekly mean temperature derived from waters ~65 km offshore from the study site (utilized in Fig. 2A), and the sea water temperature (SWT) recorded in situ by the thermistors (7 m depth), shows that there is a discrepancy between both data sets (Fig. 4). While both temperature records exhibited a roughly similar trend, SSTs were more uniform, not showing the abrupt thermal swings that were affecting the stained corals. Therefore, regardless of the moderate agreement between the δ^{18}O values and the SST (Fig. 2), the lowest oxygen isotope values should be expected between March and December 1997, not during 1998-99. From the pooled means (Fig. 2) and individual δ^{18}O values (Fig. 3), it is observed that δ^{18}O depletion was highest either before or after the period when theoretically it would be expected, or it was not much different (colonies 2 and 4, Fig. 3). To rule out the possibility that we were analyzing a poorly homogenous carbonate sample, and, therefore, missing the El Niño δ^{18}O depletion spike, we repeated the analysis twice, for all samples within the May 1997 and February 1998 interval, and for all six colonies. The resulting differences

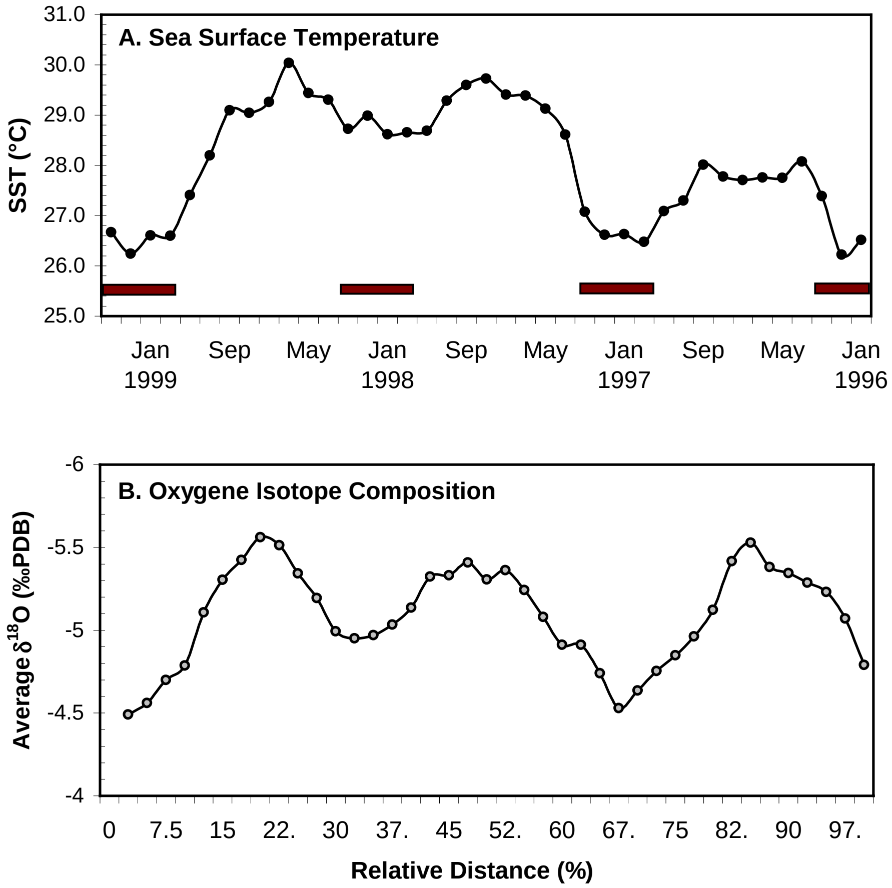

Figure 2 Comparison of (A) sea surface temperature (SST) and (B) oxygen isotope composition derived for six *Pavona clavus* colonies (4 m depth). SST X-axis is inverted to follow the relative distance of the δ^{18}O averages, which in turn had the Y-axis inverted to follow the SST seasonal trend. Due to differences in annual growth rates between the colonies, the 233 isotope measurements referring to the six corals were normalized with respect of sampling length along the slab (*sensu* Brey et al. 1999), pooled and sorted into 16 intervals of relative core length (0-2.5%, 2.5-5%,….95-97.5%, 97.5-100%). 0% corresponds to the coral tissue layer from which the sampling was initiated. SST are monthly averaged global gridded temperature readings from the Reynolds NCEP optimal interpolation analysis (Reynolds and Smith 1994). Horizontal black bars indicates the approximate timing of the seasonal upwelling of Papagayo. Note that the intensity of the 1997-98 upwelling was significantly reduced due to the El Niño episode of that year.

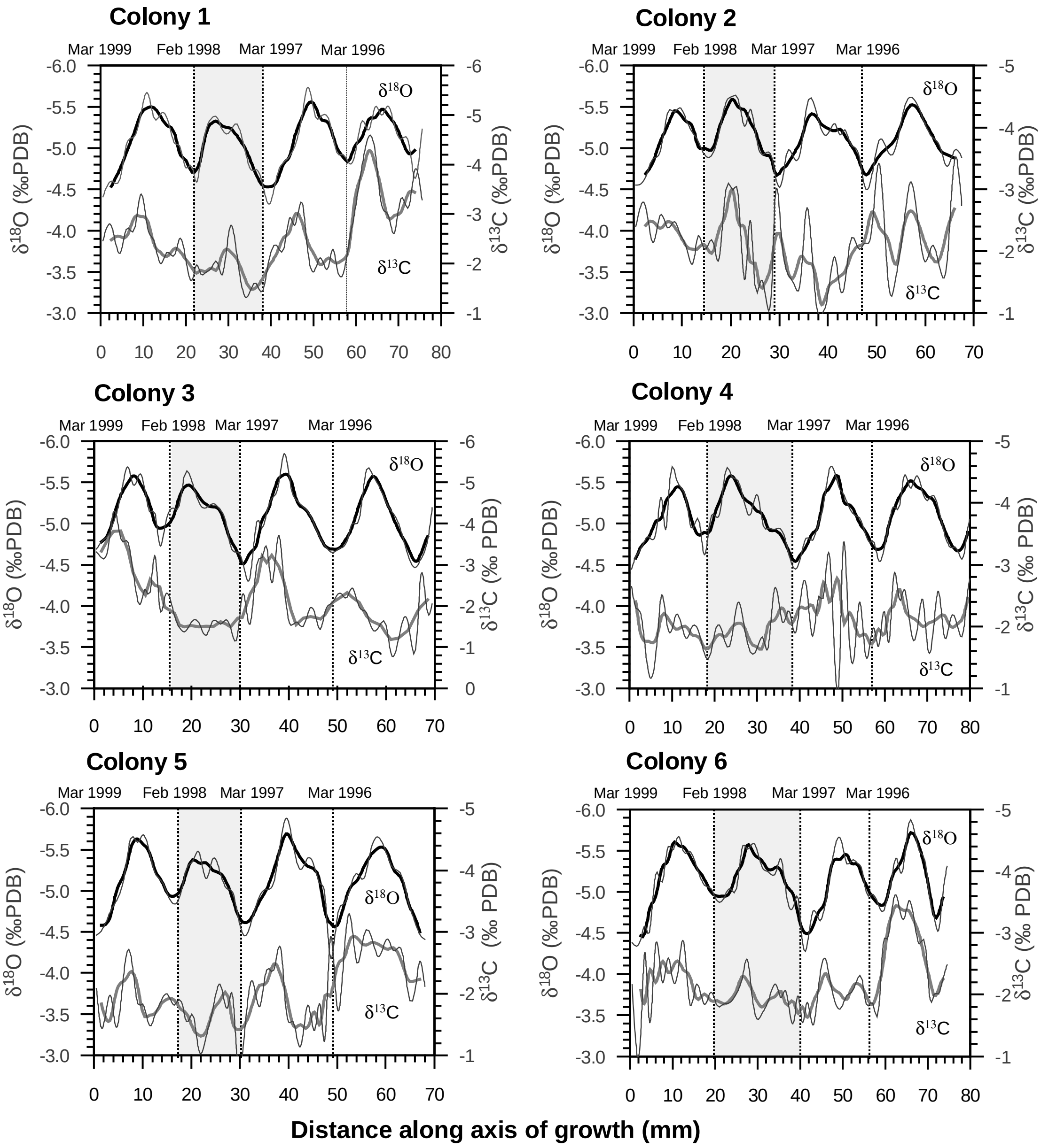

Figure 3 Skeletal stable isotope records (δ^{18}O and δ^{13}C) of six *Pavona clavus* colonies, Bahía Culebra, collected at 4 m depth. Thick lines are 3-point running averages. Scales are inverted to follow the temperature pattern. Vertical dashed lines indicate Alizarine red staining dates. The vertical shading indicates when the first phase of the 1997-98 El Niño episode occurred and large-scale coral bleaching was observed. Samples were taken along the maximum axis of growth starting from the tissue (0 mm) and throughout the datum staining lines in the skeleton. Pooled means from these results are shown in Fig. 2.

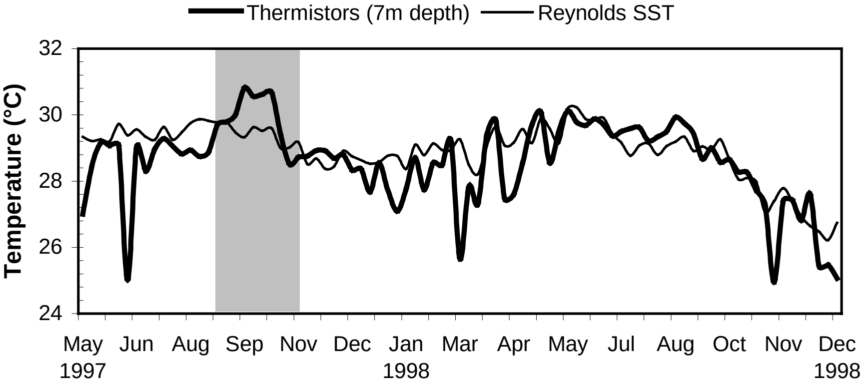

Figure 4 Comparison of weekly mean sea surface temperature (Reynolds SST) with in situ Pavona study reef temperature records at 7 m depth, May 1997 to December 1999. Reynolds SST are derived for waters ~65 km offshore of the study area. The vertical grey shading indicates the approximate timing of the 1997-98 El Niño episode, which lasted more than five weeks.

between measurements, were within instrumental error, and within the intrinsic colony variability.

The isotope composition in the datum lines was compared among colonies by analyzing four continuous carbonate replicate samples per line on each colony. The results show that there were significant discrepancies of δ^{18}O enrichment only in March 1996 and March 1999 (Fig. 5). This suggests that most *P. clavus* colonies underwent similar enrichment and the δ^{18}O signal was more consistent.

Isotopic records of corals from different depths: The isotopic records derived from six colonies at 7 m and six at 12 m (Fig. 6, 7) show similar patterns, for *P. clavus* colonies at 4 m depth as described above. Due to the lack of any datum lines, we consider that the lowest δ^{18}O values indicate the coldest months of the upwelling (February-March). As a consequence, it was possible to match the oscillations of the δ^{18}O values with the seasonal thermal amplitude emblematic of the area, as shown above. While δ^{13}C values from colonies at 7 m are inconsistent with the values from colonies at 4 m, δ^{13}C from colonies at 12 m tend to be more constant to a seasonal cycle and is generally more depleted than at any other depth (Fig. 7).

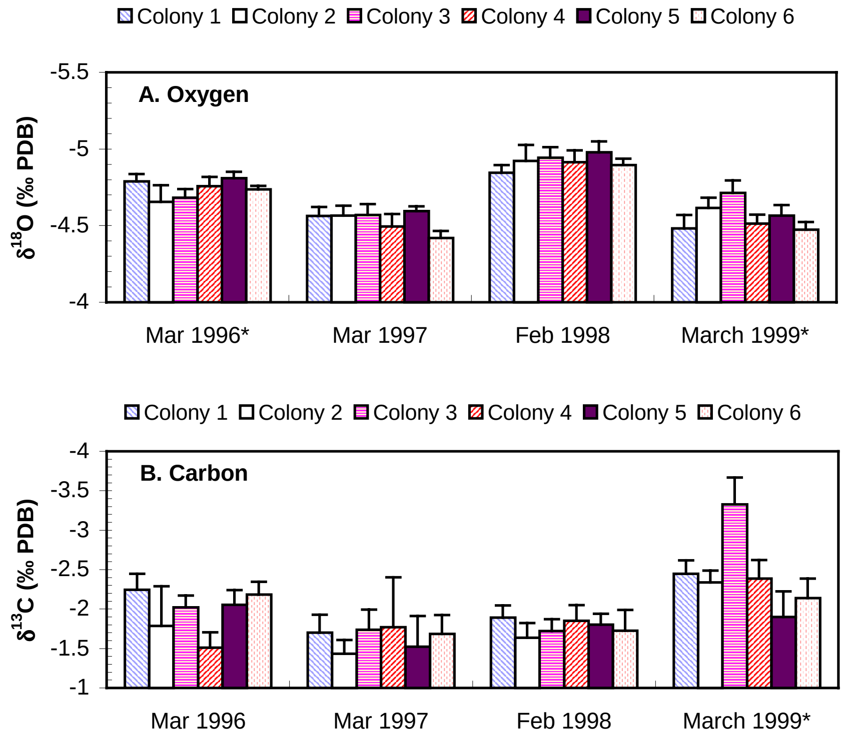

Figure 5 Comparison of δ^{18}O and δ^{13}C isotope composition of four contiguous replicate samples collected along each Alizarine datum lines. Error lines correspond to 1 SD. Oxygen isotope means significantly different (*) in March 1996 (One-way ANOVA, P<0.05) and March 1999 (P<0.001). Carbon isotope means different only in March 1999 (P<0.001).

Interestingly, δ^{18}O depletion values corresponding to the 1997-98 interval are similar or lower than other years, mainly 1996-97 (Fig. 6, 7), repeating the same pattern observed in colonies from 4 m. The δ^{18}O records corresponding to the 1995-97 interval are quite irregular for colonies collected at 12 m depth (Fig. 7), suggesting that water temperature at 12 m was lower than at 4 and 7 m depth, and that these conditions prevailed in 1996-97. Colder conditions at 12 m were previously recorded, namely in April 1996, during an upwelling event (Jiménez 2001). While sea temperature was below 14 °C at 12 m depth, at 7 m it was always above 20 °C. Continuous records of SWT at 7 and 12 m (Fig. 8), confirms the thermal regime of the deeper section of the reef. Monthly maximum temperature are generally higher at 7 m than at 12 m depth (Fig. 8A), and lower temperatures are more pronounce at 12 m (Fig. 8B).

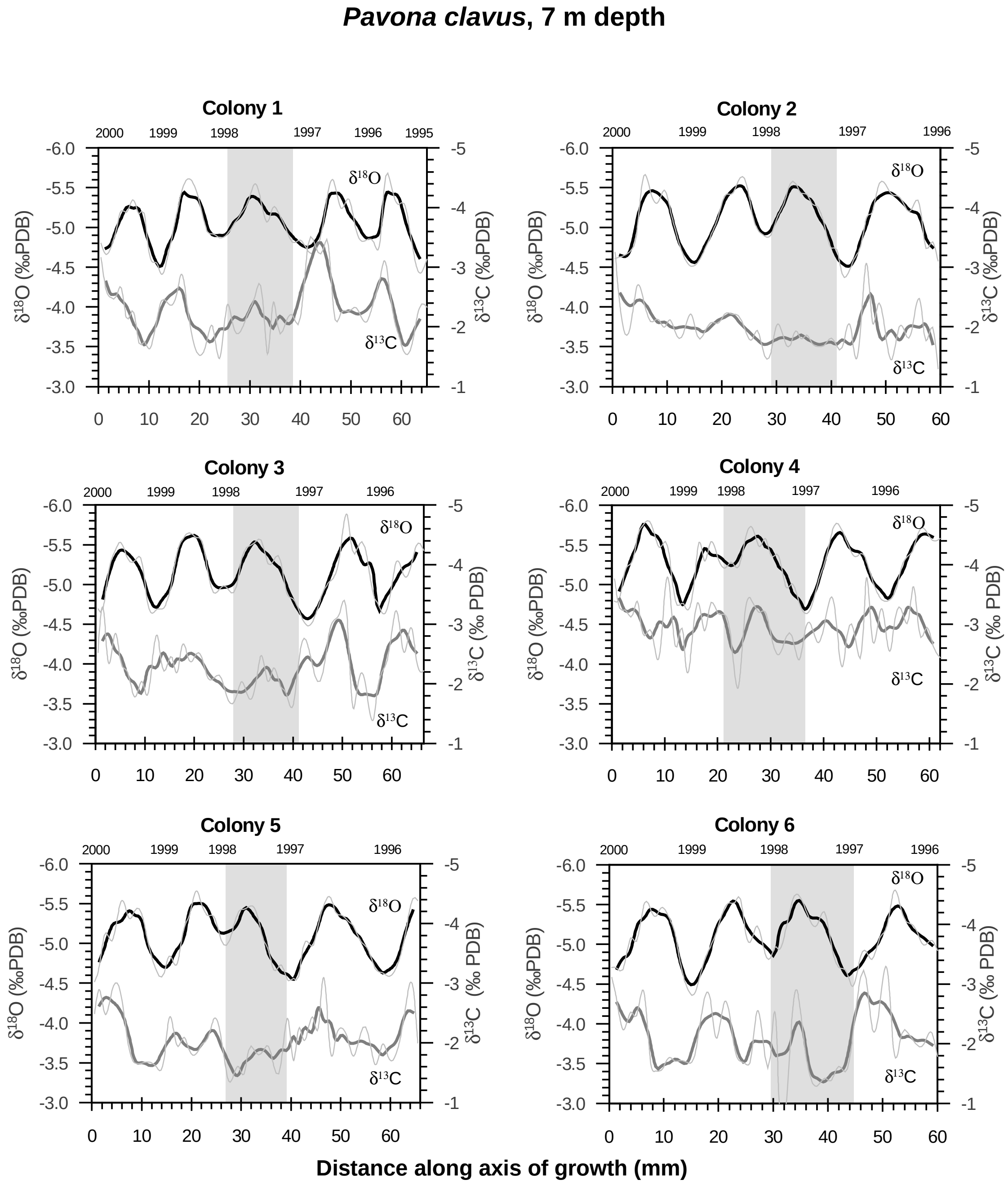

Figure 6 Skeletal stable isotope records ($\delta^{18}O$ and $\delta^{13}C$) of six *Pavona clavus* colonies, Bahía Culebra, collected at 7 m depth. Thick lines are 3-point running averages. Scales are inverted to follow the temperature pattern. The vertical shading indicates when the first phase of the 1997-98 El Niño episode occurred and large-scale coral bleaching was observed. Samples were taken along the maximum axis of growth starting from the tissue (0 mm).

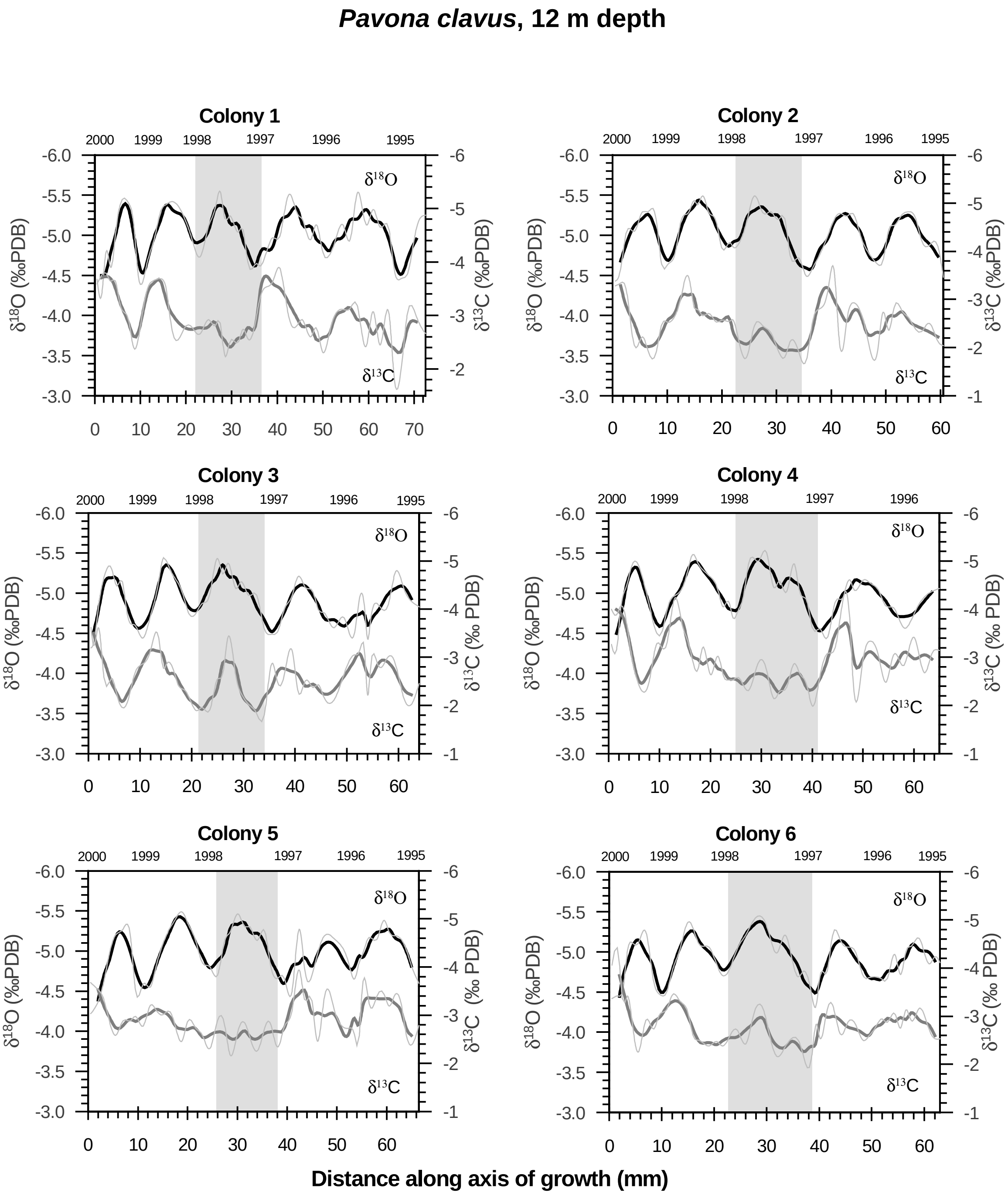

Figure 7 Skeletal stable isotope records ($\delta^{18}O$ and $\delta^{13}C$) of six *Pavona clavus* colonies, Bahía Culebra, collected at 12 m depth. Thick lines are 3-point running averages. Scales are inverted to follow the temperature pattern. The vertical shading indicates when the first phase of the 1997-98 El Niño episode occurred and large-scale coral bleaching was observed. Samples were taken along the maximum axis of growth starting from the tissue (0 mm).

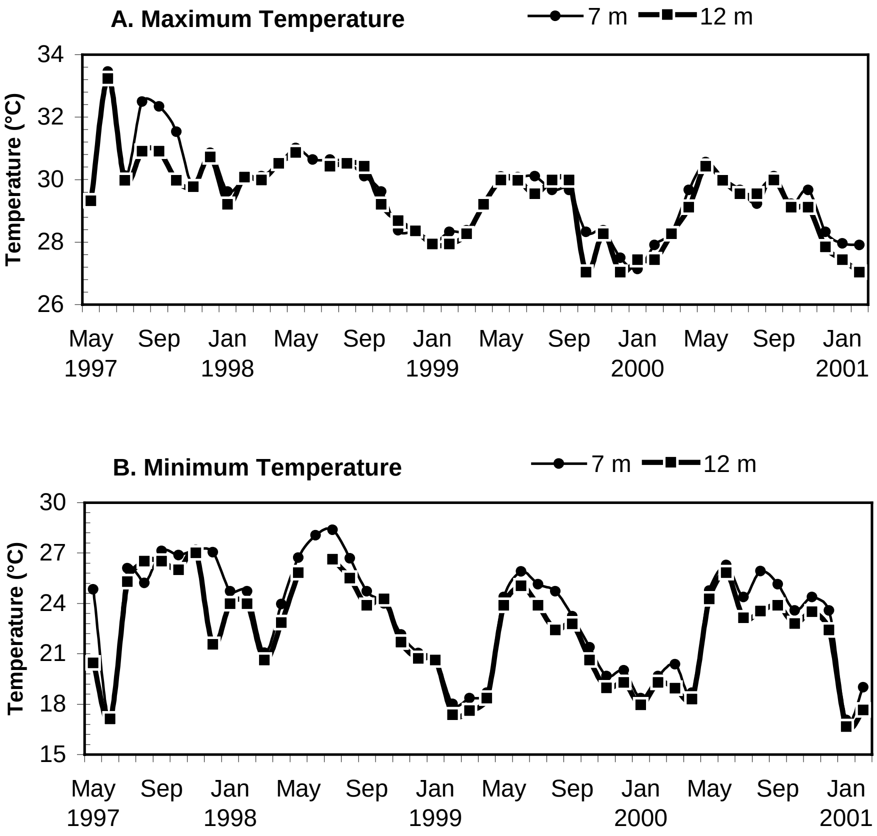

Figure 8 Comparison of monthly (A) maximum and (B) minimum in situ seawater temperature (7 and 12 m depth) at the Pavona reef study site, Bahía Culebra, from May 1997 to January 2001. Interruption in the 12 m temperature record due to thermistor's failure.

Isotopic records of corals from Islas Murciélagos: With the isotope seasonal records derived from *P. clavus* and *G. planulata* collected at the Islas Murciélagos, we confirmed that the peculiar $\delta^{18}O$ records during the 1997-98 interval were not limited to the *Pavona* reef at Bahía Culebra. Both species show 1997-98 $\delta^{18}O$ values lower (less depleted) or similar to other years (Fig. 9). This is puzzling, because the 1997 datum line corresponded to the peak of coral bleaching and sea warming, both related to the 1997-98 El Niño. We are confident about matching the dips of the $\delta^{18}O$ trend to the February-March interval, due to the datum lines made by the Alizarine red and the correspondence between the $\delta^{18}O$ and the SWT at

Bahía Culebra. Therefore, possible mistakes in assigning dates are minimized in these data set.

The δ^{13}C seasonal trends are very different between corals from Islas Murciélagos and Bahía Culebra. At the former, δ^{13}C fluctuations closely match those of δ^{18}O (Fig. 9), that is, for both isotopes, depletion or enrichment occurred during the rainy season. Corals at Bahía Culebra had no such correspondence between both isotopes. At Islas Murciélagos, correlations between δ^{13}C and δ^{18}O are highly significant in both, *G. planulata* (colony 1, r= 0.63 $P<0.001$; colony 2, r= 0.74 $P<0.001$) and *P. clavus* (colony 1, r= 0.64 $P<0.001$; colony 2, r= 0.42 $P<0.01$).

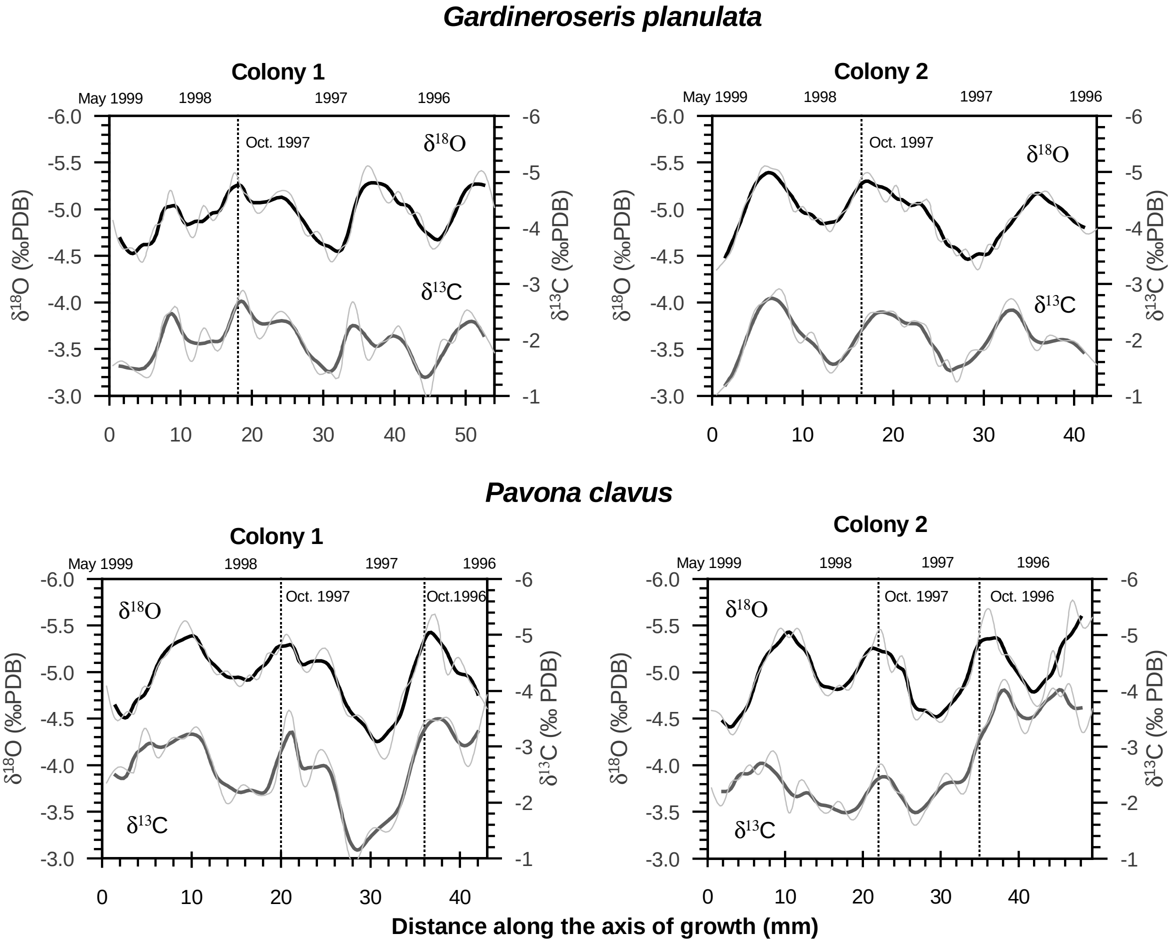

Figure 9 Skeletal isotope records (δ^{18}O and δ^{13}C) of *Gardineroseris planulata* and *Pavona clavus* colonies from Islas Murciélagos. Thick lines are 3-point running averages. Vertical dashed lines indicate Alizarine red staining dates. Scales are inverted to follow the temperature pattern. Samples were taken along the maximum axis of growth starting from the tissue (0 mm).

Monthly isotopic records: The $\delta^{18}O$ and $\delta^{13}C$ for each of the six *P. clavus* colonies sampled on a monthly basis and for the combined records are presented in Fig. 10. There were significant between-colony differences only in values of $\delta^{13}C$ over the study period (13 months). In general, all colonies displayed similar seasonal $\delta^{18}O$ and $\delta^{13}C$ trends, with the lowest values between April and December, corresponding to the beginning and end of the rainy season respectively. However, there was major within-colony variability of $\delta^{18}O$ in several colonies (2, 3 and 4, Fig. 10) during the interval between July and October, with the highest standard deviation of both isotopes in September, the peak of the rainy season.

In order to explore the possible causal factors for the seasonal $\delta^{18}O$ and $\delta^{13}C$ trends, the combined isotope records are compared against environmental variables in Fig. 11. For these averaged data, $\delta^{18}O$ is strongly correlated ($P<0.001$) with temperature ($r= -0.86$), sunlight ($r= 0.88$), and wind ($r= 0.87$), and weakly but significantly correlated ($P<0.05$) with rainfall ($r= -0.58$). These results indicate that the environmental variables are well correlated to each other, reflecting the dominant seasonal pattern on the Papagayo area. For example, during the onset of the dry season (clear skies, strong winds, zero precipitation), the upwelling of Papagayo (drop in sea temperature) is triggered. Therefore, the dry season and the upwelling are closely related to the each other. The $\delta^{18}O$ is correlated with four of the five variables, and, thus, with the seasonal cycle. For that reason, $\delta^{18}O$ derived from *P. clavus* skeletons can be used as a proxy for environmental reconstruction. On the other hand, $\delta^{13}C$ was not significantly correlated with any of the variables (including $\delta^{18}O$). These preliminary results suggest that $\delta^{13}C$ from *P. clavus* skeletons is not a good tracer of environmental variables in Bahía Culebra.

Deposition of high and low density bands: The seasonal $\delta^{18}O$, $\delta^{13}C$, and skeletal density trends of colonies from 4 m depth are compared in Fig. 12, 13. (We are still elaborating the optical densitometry graphics of corals from 7 and 12 m depth, and from Islas Murciélagos.) In general, all colonies displayed irregular seasonal trends in skeletal deposition, with the lowest density values either before or after the datum lines. High density values might be bimodal within a single year. If unimodal (for example colony 2, 1997-99 interval), they match $\delta^{18}O$ seasonal depletion during the rainy season (Fig. 12). In contrast, low density values seem to be coupled with $\delta^{13}C$ enrichment (Fig. 13). These

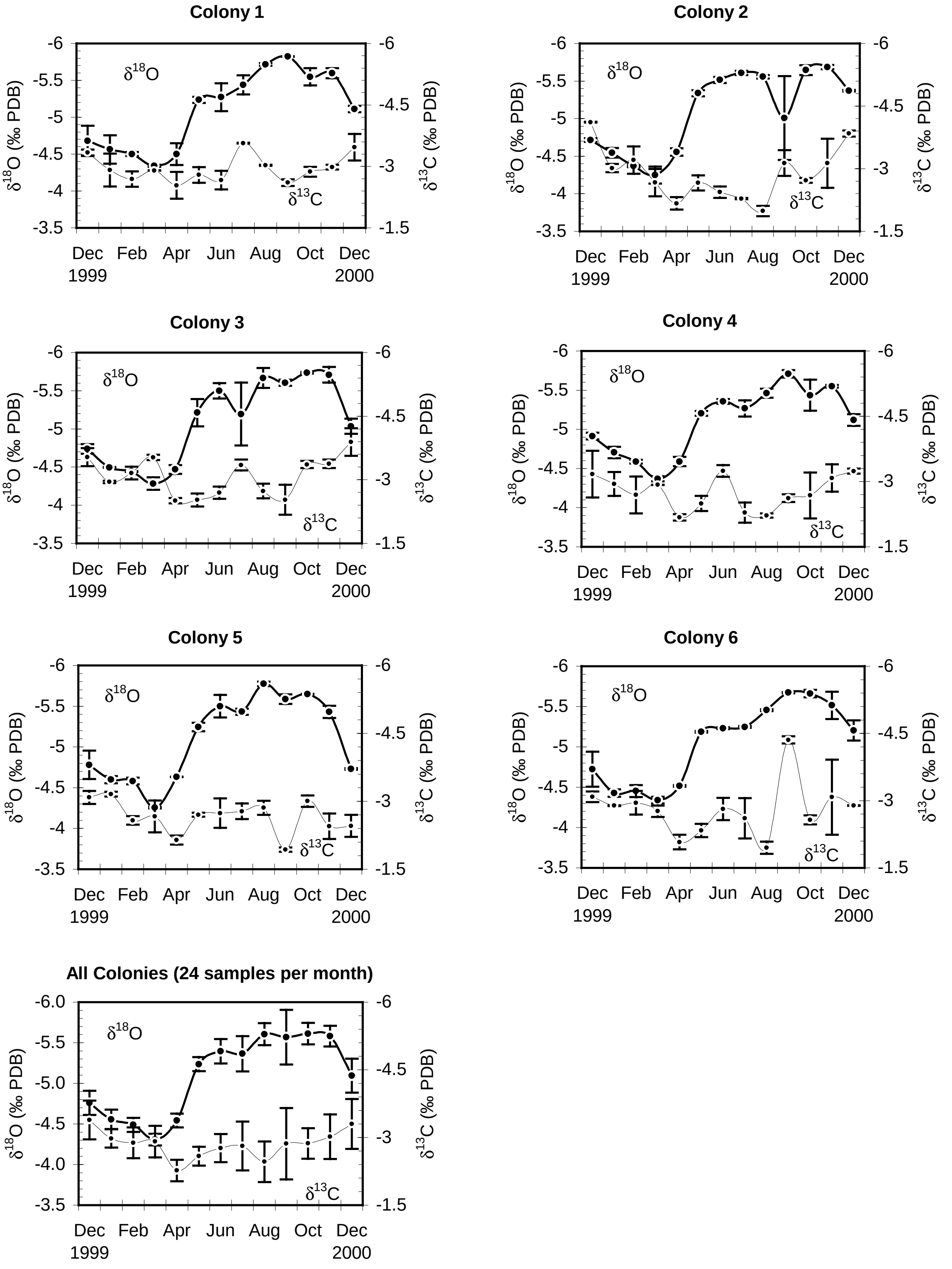

Figure 10 Average (four samples per colony per month) δ^{18}O and δ^{13}C of six *Pavona clavus* colonies sampled on a monthly basis at Bahía Culebra (7 m). Bars mark 1 standard deviation.

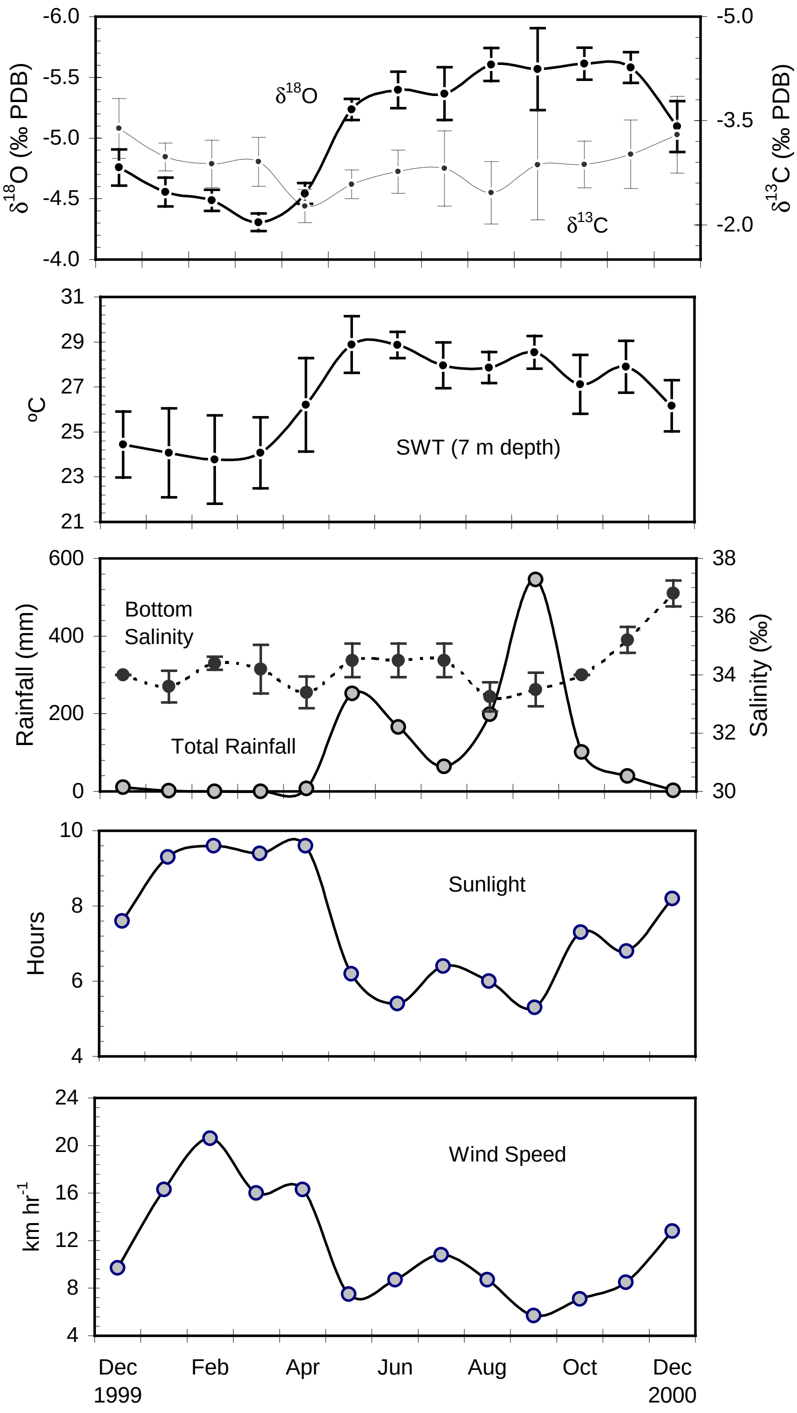

Figure 11 Averaged monthly values of $\delta^{18}O$ and $\delta^{13}C$ (24 samples per month), seawater temperature (SWT) and salinity (7 m depth), and three meteorological variables. Bars mark 1 standard deviation. Only $\delta^{18}O$ values were strongly correlated with SWT, sunlight, and wind, and weakly correlated with rainfall.

results suggest that, for some colonies at least, growth rates are in concert with the upwelling season and $\delta^{18}O$ and $\delta^{13}C$ enrichment. Therefore, it is important to further explore these seasonal trends and to identify whether the highest growth rates occur during the high or low density band deposition, and to identify possible links with the $\delta^{18}O$ and $\delta^{13}C$ variability.

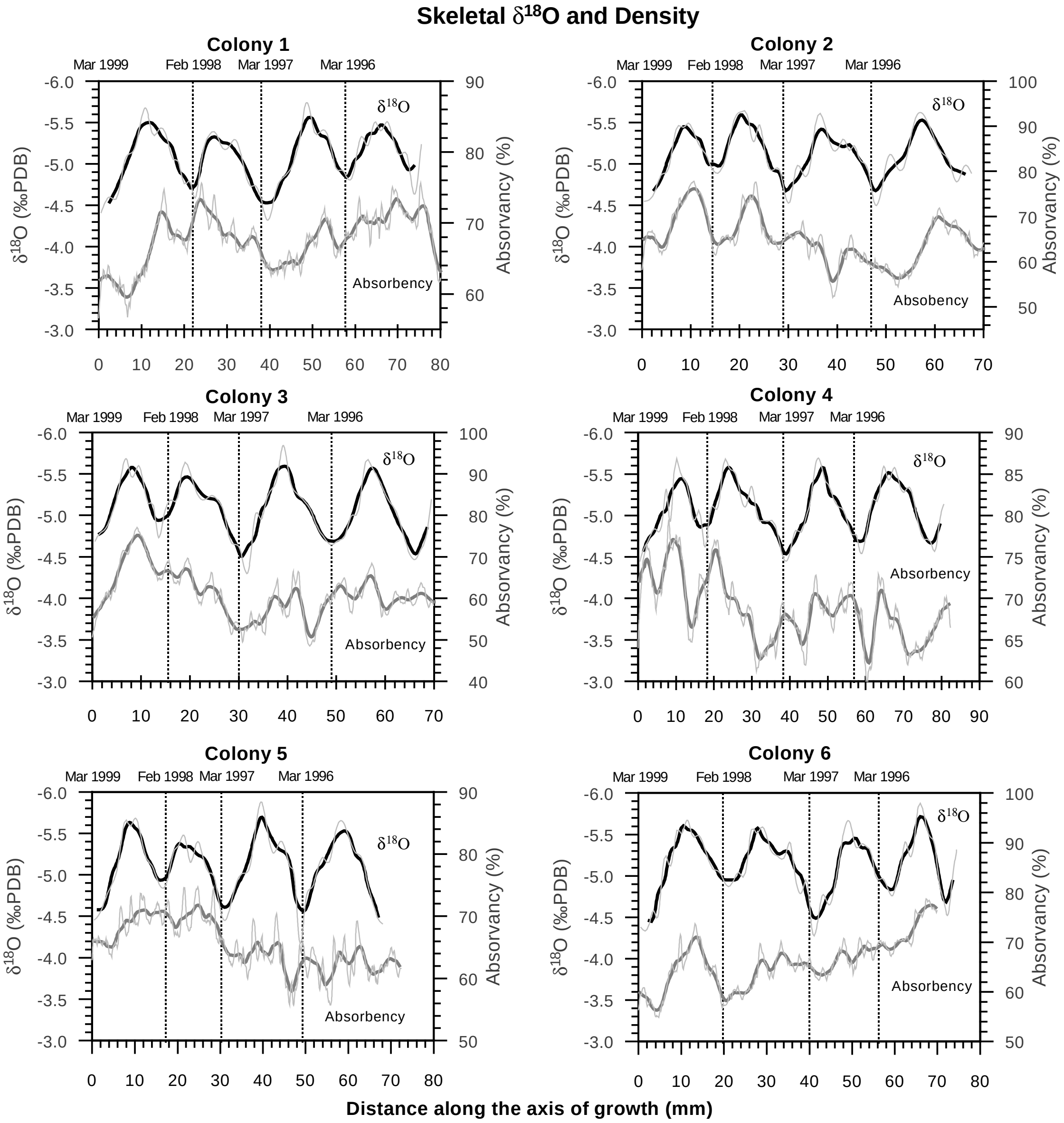

Figure 12 Skeletal $\delta^{18}O$ and density (absorbency %) of *Pavona clavus* colonies from Bahía Culebra (4 m depth). Thick lines are 3-point running averages. $\delta^{18}O$ scale is inverted to follow the temperature pattern. Vertical dashed lines indicate Alizarine red staining dates. Sampling and absorbency measurements were performed along the maximum axis of growth starting from the tissue (0 mm).

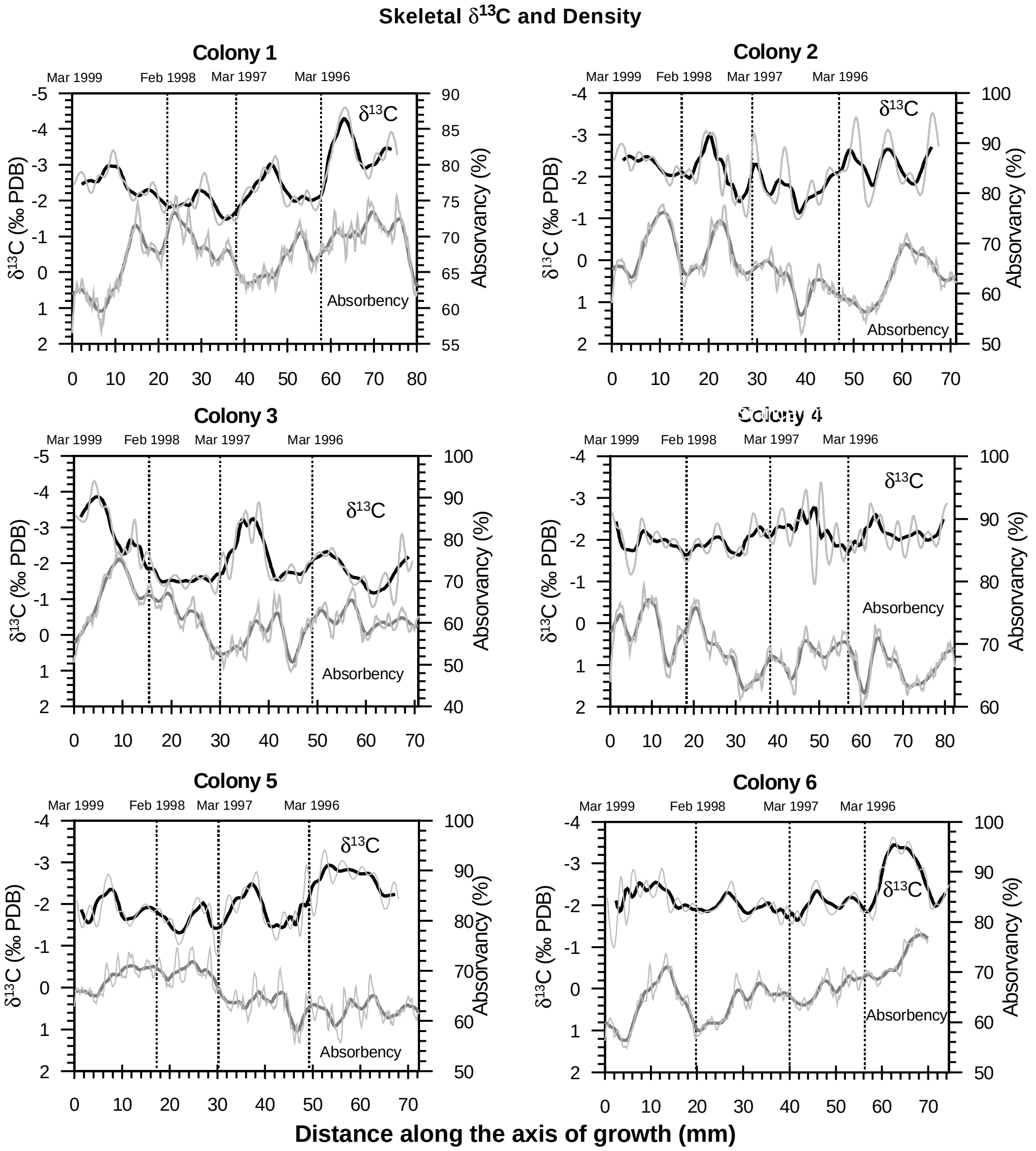

Figure 13 Skeletal δ^{13}C and density (absorbency %) of *Pavona clavus* colonies from Bahía Culebra (4 m depth). Thick lines are 3-point running averages. δ^{18}O scale is inverted to follow the temperature pattern. Vertical dashed lines indicate Alizarine red staining dates. Sampling and absorbency measurements were performed along the maximum axis of growth starting from the tissue (0 mm).

ACTIVITIES TO CONTINUE WITH THE ASSESSMENT OF *P. CLAVUS* RELIABILITY AS A TRACER FOR ENVIRONMENTAL VARIABLES AND ITS δ^{18}O AND δ^{13}C ISOTOPIC COMPOSITION

The preliminary results outlined above, are the first step in providing a comprehensive evaluation of the capacity of massive colonies of *P. clavus*, from the Papagayo area, to record environmental parameters. This coral species has been used before as a surrogate for reconstructing sea temperature variability and cloud cover in the upwelling areas of Panamá (Wellington and Dunbar 1995, Grottoli and Wellington 1999) and Islas Galápagos (Shen et al. 1992, Dunbar et al. 1994, Wellington and Dunbar 1995). Upwelling areas are considered sub-optimal areas to detect El Niño events in corals (Wellington and Dunbar 1995), due to a dampening of the high temperature signal by the seasonal upwelling. But similarly attenuated δ^{18}O signals have been found in other coral species in non-upwelling areas (e.g. Linsley et al. 1994). Thus, it is suggested that other factors rather than the upwelling may be interfering, and preventing us from finding a large δ^{18}O signature (high depletion spike) corresponding to the strongest El Niño episodes.

Our corals may have failed to record the full range of temperature variation, but the seasonal amplitude clearly indicates the anomalously warm interval between 1997-98. We believe that the attenuated δ^{18}O signal corresponding to the highest El Niño warming (between March and November1997) indicates that the coral growth has diminished. Corals may have accreted less skeleton for several months, and the signal in the sample might be obscured in the rest of the carbonate material analyzed for isotope composition. However, overall annual coral growth for the 1997-98 was not statistically different from the previous and following year, but considerably lower than in 1995-96.

Consequently, we will follow up the evidence provided by these preliminary results, to expand our analysis to other coral colonies from different depths and localities. An optical densitometry from these corals still needs to be analyzed in detail and compared to skeletal features such as the mesoarchitecture of the corallites. This approach may help to explain the high variability found in the density and isotope seasonal trends. Another aspect to be considered is the correlation between δ^{18}O and δ^{13}C of corals from different depths. A preliminary regression analysis gave different results between corals collected at 4 m depth and corals from deeper waters. This indicates that we have to consider the role of δ^{13}C and δ^{18}O dissolved in seawater, which may influence the skeletal isotope signal. Therefore, we are currently monitoring the δ^{13}C and δ^{18}O of seawater from samples collected directly above the corals at the Pavona reef, in Bahía Culebra. The sampling stations (4, 7 and 12 m depth) are the same utilized to collect the corals for the skeletal isotope analysis, and compared to water samples at the surface. The objective is to track seawater $\delta^{13}C$ and $\delta^{18}O$ during a complete seasonal cycle (rainy and dry season, upwelling and non-upwelling), and to correct the skeletal isotope concentration for seawater effects. Finally, with the corrected values and the seawater temperature, we intend to produce an equation that describes the relation between those parameters (i.e. paleotemperature equation).

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