

Effects of 1997-1998 ENSO on coral reef communities in the Gulf of California, Mexico

Roberto Iglesias Prieto¹, Héctor Reyes Bonilla^{2,3} and Rafael Riosmena Rodríguez²

¹ Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, UNAM, Cancún, Quintana Roo, México

² Depto. de Biología Marina, UABCS, La Paz, B.C.S., México

³ Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami FL, USA

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RESUMEN

Las temperaturas superficiales del océano se incrementan significativamente en la zona del Pacífico este durante los eventos El Niño-Oscilación del Sur (ENSO). Este incremento en las temperaturas afecta negativamente a dos comunidades coralinas de la parte sur del Golfo de California. Durante el evento ENSO de 1997-1998, las comunidades bentónicas sésiles estuvieron expuestas a anomalías térmicas de hasta 3.0 °C. El análisis de los cambios en la cobertura de coral vivo en el área durante 1996 (condición pre-ENSO), 1997, 1998 y 1999, indican que aproximadamente el 30% de los corales padeció blanqueamiento. Este evento de blanqueamiento de coral estuvo acompañado de severas mortalidades de hasta 60%. El blanqueamiento de coral fue más intenso en las regiones localizadas más al norte de la zona en estudio, que en las zonas al sur, las cuales comúnmente están expuestas a temperaturas superiores. Los corales localizados en las partes someras experimentaron una mayor incidencia de blanqueamiento que aquéllos localizados en aguas profundas. Los análisis fisiológicos indican que esta distribución vertical responde a diferencias en la temperatura y no a diferencias en la iluminación. Junto con el blanqueamiento y la mortalidad de coral, detectamos variaciones en las densidades poblacionales y en la distribución de tallas de algunos invertebrados asociados al coral. El análisis de las variaciones anuales en riqueza específica de las algas asociadas a los mantos de rodolitos, permiten trazar una línea de base para estudios futuros sobre los impactos del ENSO en estos ecosistemas.

PALABRAS CLAVE: ENSO, estrés térmico, blanqueamiento de coral, mortalidad de coral, Zooxantelas, camas de rodolitos

ABSTRACT

Sea surface temperatures in the eastern tropical Pacific increase dramatically during El Niño Southern Oscillation (ENSO) events. This increase in sea temperature negatively affects two important coralline communities in the southern Gulf of California. During the 1997-1998 ENSO event, benthic sessile communities were exposed to a thermal anomaly of up to 3 °C during the summer. About 30% of live corals in six important communities in the region during 1996 (pre-ENSO conditions), 1997, 1998 and 1999 experienced coral bleaching, accompanied by 60% mortality. Coral bleaching was more intense close to the northern part of the studied area, as the southern area is normally exposed to higher temperatures. Corals located in shallow water experienced a higher incidence of bleaching than in deeper areas. This pattern is a response to temperature stratification and not to differences in light conditions. We detected variations in the densities and size distributions of the coral-associated fauna associated with coral bleaching and mortality. Annual variations in species abundance of the algal community associated with rodolith beds during 1998-2000 should provide us baseline information to assess the effects of future ENSO events on the rodolith community.

KEY WORDS: ENSO, thermal stress, coral bleaching, coral mortality, Zooxanthella, rodolith beds.

INTRODUCTION

In the southern part of the Gulf of California beds of free-living coralline red algae known as rhodoliths, and coral reef communities are common. Both communities are important reservoirs of biological diversity in the region (Foster *et al.* 1997; Reyes Bonilla, 2000). The distribution of these ecosystems is controlled by temperature. Most rodolith beds in the region contain temperate species living below 15 m depth, where they find refuge from summer sea surface temperatures (SST). On the other hand, coral reef communities harbor tropical species close to their northern limit of distribution. The distribution of coral reefs is limited by low winter ocean temperatures. El Niño-Southern Oscillation (ENSO) increases SST in the Eastern Pacific (Glynn 1992), with un-

favorable conditions for both communities. The depression of the thermocline associated with ENSO may expose temperate rodolith species to temperatures above their physiological tolerance. Hermatypic corals, reef-building corals in symbiosis with dinoflagellates, are the dominant component of coral reef communities and may be exposed in summer to acute thermal stress during an ENSO event. The objectives of this work were: (a) to assess the damage caused by the 1997-1998 ENSO event on coral reefs in the Southern Gulf of California, (b) to evaluate their recovery during 1999, and (c) to characterize the rodolith communities for future research.

When corals and other coral reef-dwelling symbiotic invertebrates are exposed to extreme environmental condi-

tions, they lose their symbiotic dinoflagellates in a phenomenon known as coral bleaching, which produces a loss of coloration. Most massive coral bleaching events that have been reported in the last two decades are related to the presence of abnormally high SST. Depending on the intensity and duration of thermal stress, bleaching may result in massive coral mortality, with the consequent impact on the ecosystem, or in a reversible event without major effects on the coral community (Hoegh-Guldberg, 1999).

We recorded daily SST during an extended period including the entire ENSO event in the region of Cabo Pulmo, in the Mexican State of Baja California Sur (23.5 °N). Comparison of this data set with the monthly long-term average (50 years) indicates the presence of positive anomalies from January 1997 to December of 1998. These anomalies showed values above 1°C during 9 consecutive months (Figure 1). We detected two maxima with anomalies > 3°C in the summers of 1997 and 1998. Incidental reports by local divers indicate that coral bleaching started in June 1997 in Cabo Pulmo. Bleaching was formally documented in July 1997 in Cabo Pulmo and La Paz Bay. In the following months coral bleaching was observed in communities located progressively to the North, August in Isla San José (25.5 °N), and September in San Carlos, Sonora and Bahía Concepción, Baja California Sur (27.0 °N).

To assess the conditions of the six most developed reef communities of the Gulf of California, we analyzed data obtained from 10 linear, 50 by 1 m, transects in each of the sampled areas, collected using standard SCUBA techniques. We analyzed the conditions (% of the area cover by corals) during four consecutive years starting in 1996. Comparisons of the coral coverage data obtained during 1996 with those obtained during 1997 and 1998, showed that 30.2 % of the total area covered by living corals experienced bleaching. (Table 1). Coral mortality in the lower Gulf of California after the 97-98 ENSO event was relatively minor compared with that observed during the 82-83 ENSO in Central America (75-95%) and in 1998 in the Indian Ocean (80-90%, Glynn, 1996, Wilkinson *et al.*, 1999). These differences were probably due to the presence of higher thermal anomalies in latter areas.

Eastern Pacific coral communities show characteristic differences in the vertical distribution of the species. Shallow areas (0-6 m) are occupied by branching corals of the genus *Pocillopora*, whereas deeper zones (6-12 m) are dominated by massive corals of the genus *Pavona* (Reyes Bonilla, 2000). The shallow zones experienced higher incidence of coral bleaching (37.4%) relative to the deeper areas (31.3 %). This pattern was also detected for bleaching dependent mortality. Shallow areas experience 21.9% mortality after the ENSO event, whereas deep zones exhibited 13.6% mortality ($p < 0.05$, t). A similar coral bleaching and

Table 1

Summary of the effects caused by the 1997-1998 ENSO event in 6 coral reef communities of the Gulf of California. Relative values of the area covered by living corals, which experienced bleaching, were obtained by comparing the coverage in 1996 with those for 1997. The relative area covered by dead corals was calculated by comparing the 1996 results with those obtained in 1998. The percentage of bleached corals that died after the ENSO event was estimated by the comparison of the 1997 with 1998 data. (SEM Standard Error of the Mean)

	Area of live coral affected by bleaching (%)	Area occupied by death coral (%)	Relative mortality of corals affected by bleaching (%)
Average	30.2	17.7	59.3
SEM	2.4	1.2	3.1

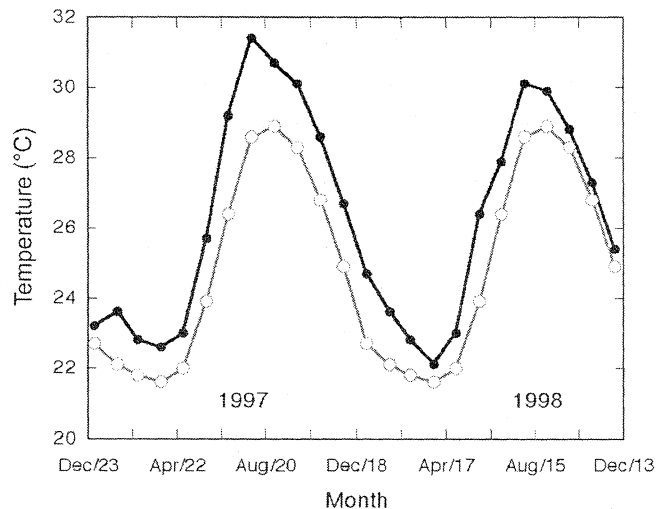


Fig. 1. Variations in the monthly sea surface temperature in Cabo Pulmo B.C.S. (23° N). The heavy line represents the 97-98 ENSO, and the grey line the long-term average for the last 52 years (1947-1999).

mortality pattern was observed in Okinawa in 1998, as branching corals were more affected than massive species (Y. Loya, personal communication). These patterns may be the result from species specific sensitivities to thermal stress (Ayala-Schiaffino and Iglesias-Prieto, unpublished data), or from the existence of depth-related environmental differences.

Algal photosynthesis plays a major role in the biology of reef building corals: translocation of photosynthates to the animal represents in most cases more than 100% of the

basic metabolic needs of the animal, and has been implicated in the high calcium carbonate deposition rates of corals (Muscatine and Weis, 1990). There is still controversy regarding the cellular mechanism responsible for triggering coral bleaching, ever increasing evidence indicates that in the presence of elevated temperatures, symbiotic dinoflagellates experience a dramatic reduction in photosynthetic activity (Iglesias-Prieto *et al.*, 1992; Hoegh-Guldberg, 1999). Under limited photosynthetic capacity, absorbed photons that can no longer be used to reduce carbon, generate enough pressure over the photosystem II (PSII) to produce permanent damage on the photosynthetic apparatus, similar to photoinhibition. When the rate of damage is higher than the rate of recovery, thermal stress may result in algal death and, hence, in coral bleaching (Iglesias-Prieto, 1997). Corals inhabiting the Gulf of California experience a very steep light intensity gradient in comparison with their counterparts in other parts of the Indo-Pacific province (Figure 2). The vertical attenuation coefficient for downwelling irradiance in a typical coral community in the area (24.1 °N) is 0.22 m⁻¹, consequently corals inhabiting shallow environments received in average 80% more irradiance than corals located in deeper habitats (Figure 2).

The use of techniques based on detection of chlorophyll a fluorescence allows us to quantify the physiological status of primary producers activity (Iglesias-Prieto *et al.*, 1992; Hoegh Guldberg, 1999). Comparison of the variable fluorescence in the dark, under complete relaxation, with values obtained *in situ* at noon, under maximum irradiance,

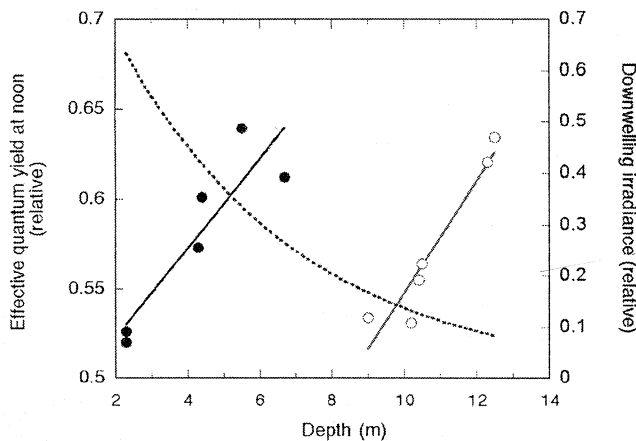


Fig. 2. Variations of the effective quantum yield of photosystem II experienced by the symbionts of *Pocillopora* spp (filled circles) and *Pavona gigantea* (open circles) at noon and relative downwelling irradiance as a function of depth (broken line). Quantum yields were measured *in situ* with a diving Pulse Amplitude Modulated fluorometer, during three cloudless days between October 1998 and July 1999. The vertical attenuation coefficient used for the estimation of the relative irradiance is an average of 3 independent determinations obtained in La Paz Bay during 1999.

allowed us to evaluate the pressure exerted by over-excitation over the photosynthetic apparatus of algae inhabiting corals at different depths. Variations in the effective quantum yields at noon for the two dominant genera, as a function of depth are presented in Figure 2. The data were collected *in situ*, using a submersible Pulse Amplitude Modulated fluorometer during three cloudless days in October 1998 and March and July 1999. The evidence indicate that the algae inhabiting *Pocillopora* spp. colonies experience, at 2.5 m and under 60% of surface irradiance, reductions in the effective quantum yield equivalent to those detected in *Pavona gigantea* colonies growing at 9 m and under 15% surface irradiance. As the reductions in the effective quantum yield are irradiance-dependent, we were expecting a monotonous decrease as a function of depth. Our data suggest that each coral genus possesses different symbionts adapted (*sensu* Darwin) to different light intensities (Iglesias-Prieto & Trench, 1994), but further genetic work is needed. Analysis of the vertical distribution of temperatures indicates a difference of approximately 1.5 °C between the shallow and deep habitats of one of the studied reef communities. Although such difference is significant from the physiological perspective, during the summer of 1997 both habitats experienced at least 2 °C anomalies relative to the warmest month (Figure 1). Taken together, the evidence indicates that the vertical distribution of coral bleaching resulted from differences in temperature. Using information generated from *in situ* determinations of the photosynthesis vs irradiance curves for *P. damicornis* and *P. gigantea* during the winter and summer of 1999, we calculated the Q10 values for the maximum electron transfer rate. We detected Q10 values of 2.28 and 1.98 (n=8 colonies per species) for *P. damicornis* and *P. gigantea* respectively, which indicate that during the summer of 1999 none of the species experienced thermal stress. It is impor-

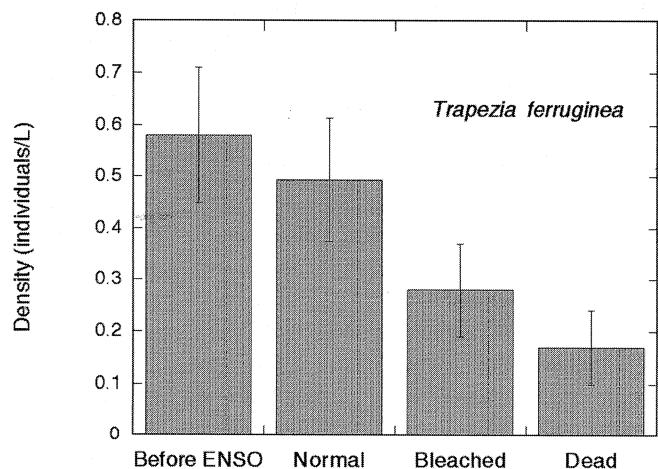


Fig. 3. *Trapezia ferruginea* population density variations relative to the conditions of their habitat (*Pocillopora* spp. colonies) (N= 51). The information for Pre-ENSO conditions comes from 1996 data (N=60).

tant to notice that during the summer of 1999 we detected negative thermal anomalies of 3.5 °C relative to the long-term average.

As a consequence of the dramatic events associated with coral bleaching and mortality, the coral reef can experience a phase shift resulting in irreversible damage (Hoegh-Guldberg, 1999). Changes in the composition of the associated fauna may be a good indicator of degradation of the coral community. Between June of 1997 and November of 1998 we analyzed changes in the composition of the macromollusk and decapoda fauna (with emphasis in the Trapeziidae and Alpheidae families) associated with colonies of *Pocillopora*. In general, the descriptive indexes (species richness, diversity and equitability) for the mollusk fauna showed no significant variations, although this, however, was detected for the analyses of the total mollusk fauna and for the class analyses (Gastropoda and Bivalvia). The results suggest that for these species, corals represent only part of their physical habitat. In contrast, when we separated the species as function of their biogeographic origin (Indo-Pacific and Eastern Pacific taxa), a clear reduction in the abundance of the Indo-Pacific species was detected during and after the ENSO event. The species from the Panamic province did not experience any variation. It is possible that depending on their adaptive history, local species are more resilient to the thermal stress associated with ENSO, than species from the Indo Pacific, which are not normally exposed to dramatic increases in temperature. On the other hand, when we analyzed the data as a function of the trophic habits of the fauna (predators of coral vs predators of other species) we detected significant differences. Gasteropod predators of corals (genus *Quoyula* and *Gastrochaena*) show a dramatic reduction in population density in bleached and dead corals, relative to those inhabiting corals with normal coloration. Similar results were reported for the predator gasteropod *Janeria pustulata*. In Central America during the 82-83 ENSO (Glynn, 1984). These results are predictable as these species show a high nutritional dependency on coral tissue.

Another indicator of the condition of corals is the association between *Pocillopora* and crabs of the genus *Trapezia*. These organisms have an obligated commensalistic symbiosis. A significant part of the crab's diet is provided by the mucus produced by the coral (Glynn and Colgan 1992). As a consequence of the 1997-1998 ENSO, the *Trapezia* population showed significant changes. Comparisons of the population densities (individuals/volume of coral) indicated that for the four species of symbiotic crabs in the area, dead corals showed significant population reductions relative to bleached corals; as well as bleached corals relative to corals with normal coloration (Figure 3). The total populations of the four species demonstrated a strong reduction during September of 1997 relative to those registered in 1996 and in August of 1997 (70-95%). After the ENSO, populations re-

covered gradually until the end of 1998. In contrast to *Trapezia* spp., where individual sizes remained unaltered during the ENSO event, an increment in size in *T. digitalis* was detected in individuals inhabiting bleached colonies. This change in size may be the result of differential mortality of the small individuals, probably as a consequence of the lack of food (mucus) during ENSO. Under those conditions, larger individuals that possess higher metabolic reserves may survive starvation for longer periods.

To characterize the macroalgal community associated with the rodolith beds, we performed monthly analyses of the species richness between January of 1998 and February of 2000 on El Canal de San Lorenzo in La Paz Bay. We detected a clear annual oscillation (Figure 4). Species richness was higher in winter between February and March. There is a strong reduction in diversity during the summer months and early autumn. Analyses of the flora indicate that green algae represent 10% and red algae 70% throughout the entire annual cycle. The dominant species, as determined by the relative substrate area covered by each species, were *Caulerpa sertularioides*, *Codium magnum* y *Gracilaria veleroae*. The highest species richness values were linked to the annual blooming of temperate red macroalgae of the genus *Sciania*, *Halymenia*, *Botryocladia* y *Dasya*, which germinate at the beginning of the winter but disappear after May.

Relative to the effects caused in similar systems in both the Pacific and the Indian oceans (Wilkinson et al. 1999), the 1997-1998 ENSO did not result in irreversible damages to the coralline communities of the Gulf of California. This is probably related to the presence of smaller thermal anomalies in the area. Studies of the benthic communities, such as the one presented here, allow us to evalu-

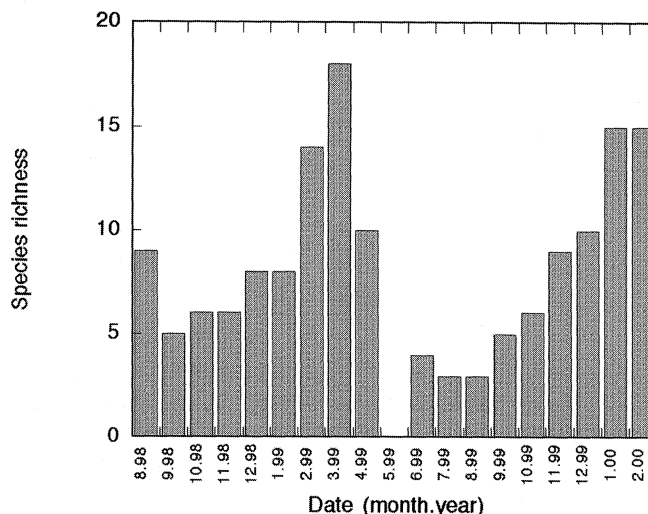


Fig. 4. Changes in species abundance of the macrophyte community associated with the rodolith beds on Canal San Lorenzo in La Paz Bay.

ate from a unique perspective the effects of environmental perturbations. In contrast with other biological communities, benthic sessile organisms can not escape the unfavorable environmental conditions by migrating to favorable locations. In general, the responses of the organisms to environmental variations are non-linear, in particular if such variations exceed the natural range of tolerance. Coral bleaching is a clear example of this type of responses; it can be triggered by increases in SST as small as 1.5 °C above the long-term summer average (Hoegh-Guldberg, 1999). Although there are incidental reports of local coral bleaching events since last century, the intensity, frequency and geographic range of the event has increased significantly during the last two decades. It has been speculated that these increases can be the result of a global warming trend. In 1998 there was an unprecedented coral bleaching and mortality event in the Indian ocean. This massive coral bleaching episode resulted in 90% mortality of coral reefs that were heretofore considered to be in pristine conditions. This event has received special attention by scientific, governmental and civil organizations, as it may represent a warning of future change. If this interpretation is correct, the opportune and accurate assessment of the effects of environmental oscillations requires of baseline studies. In this context, we believe that as a result of the work presented here, we will be able to quantify the effect of future ENSO events in the rodolith communities in the Gulf of California.

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Roberto Iglesias Prieto¹, Héctor Reyes Bonilla^{2,3},
Rafael Riosmena Rodríguez²

¹ Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, A. P. 1152, 77500 Cancún, Quintana Roo, México
Email: iglesias@mar.icmyl.unam.mx

² Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, A. P. 19B, 23080 La Paz, Baja California Sur, México

³ Rosenstiel School of Marine and Atmospheric Science, University of Miami. 4600 Rickenbacker Causeway, Miami FL 33149 USA

