

Temporal variation of the sea urchin *Diadema mexicanum* population density at Bahías de Huatulco, Western Mexico

F. Benítez-Villalobos¹, M.T. Domínguez y Gómez² & R.A. López Pérez¹

1. Instituto de Recursos, Universidad del Mar, Carretera a Zipolite Km 1.5, Puerto Ángel, Oaxaca, México; fbv@angel.umar.mx, alopez@angel.umar.mx
2. Licenciatura en Biología Marina, Universidad del Mar, Carretera a Zipolite Km 1.5, Puerto Ángel, Oaxaca, México; mtdyg@hotmail.com

Received 04-IX-2007. Corrected 01-IV-2008. Accepted 17-IX-2008.

Abstract: Sea urchins of the genus *Diadema* play an important role as controllers of algal growth in coral reef and rocky reef communities, but high densities cause bioerosion of the reef framework. Between January 2006 and February 2007 (except April, July and August), population densities and mean test diameter of *Diadema mexicanum* were determined at Isla Montosa, La Entrega, Isla Cacaluta and San Agustín, Bahías de Huatulco, Mexico. Mean density of the sea urchins was relatively constant through time at all localities: lowest at San Agustín (0.26 ± 0.13 ind.m⁻²) and highest at La Entrega (4.17 ± 1.4 ind.m⁻²). There were significant differences between La Entrega and other localities. Mean test diameter ranged between 4.41 ± 0.88 cm (Isla Cacaluta) and 4.72 ± 0.27 (San Agustín), and did not vary significantly between localities, but there were monthly variations. Test diameter agrees with other studies. The calculated amount of CaCO₃ removed by *D. mexicanum* showed variations between localities. The lowest rate of bioerosion occurred at San Agustín (0.25 kg.m⁻².yr⁻¹), and the highest at La Entrega (4 kg.m⁻².yr⁻¹). The recent urchin population decrease means a reduction in their removal of coral CaCO₃: 5.55% to 2.36% at Isla Cacaluta, 5.08% to 1.40% at San Agustín and 16.59% to 3.08% at Isla Montosa. The only locality where bioerosion increased was La Entrega, from 27.04% to 33.05%. This reduction of urchin activities could be beneficial for coral reef growing and recovery from stress, nevertheless it could also signify an increase in algal biomass and competition with corals for light and space. We recommend a permanent monitoring and evaluation of population densities of *D. mexicanum* and fishes, as well as coral and algal cover at the area, to discern if changes in sea urchin densities in Bahías de Huatulco are a continuous phenomenon, or part of a natural cycle of increments and reductions. Rev. Biol. Trop. 56 (Suppl. 3): 255-263. Epub 2009 January 05.

Key words: *Diadema mexicanum*, sea urchin, population densities, echinoderms, Huatulco, Eastern Pacific.

Sea urchins in general and echinoids of the genus *Diadema* in particular, are conspicuous and often extremely abundant organisms in shallow-water ecosystems, including seagrass beds, rocky and sandy bottoms and coral reefs. Sea urchins of the genus *Diadema* are among the most widespread, abundant and ecologically important echinoderms in shallow tropical seas (Birkeland 1989, Lessios *et al.* 2001, Tuya *et al.* 2005), and they are found primarily on shallow reef habitats (Bauer 1980). High population densities of the urchins and their

feeding habits have played a very important role in the dynamics and structure of the algal and coral ecosystems (Sammarco 1982a,b, Birkeland 1989, Carpenter 1990, Knowlton 2001, Lessios *et al.* 2001).

The presence of *Diadema antillarum* in the Caribbean reef communities set the limits for the growing areas of algae, maintaining the “halos” around the patches of lagoon reefs (Ogden *et al.* 1973, Ogden 1976, De Ruyter van Stevenick & Bak 1986, Carpenter 1990) and it affected the distribution and biomass of

macroalgae and corals (Ogden and Lobel 1978, Sammarco 1980, Solandt & Campbell, 2001), until early 80's, when a mass mortality event occurred throughout the geographical range of this species in the western Atlantic, produced by an unidentified pathogen (Lessios *et al.* 1984, 1988); which eliminated up to 99 % of the population in some localities (Eakin 1992).

The biological and physical structure of many communities was affected in large proportions by the event of mass mortality of *D. antillarum*, including a rapid and significant increase in the algal biomass up to 439% and changes in the specific composition from small encrusting algae to high cover of macroalgae (Vicente and Goenaga 1984, Liddell and Ohlhorst 1986, Carpenter 1990), a reduction in the recruitment of hard corals, and a subsequent reduction in the coral cover as a result of macroalgal competence (Liddell and Ohlhorst 1986, Hughes 1989, Levitan 1995). In comparison, in Panama, after El Niño 1982-83, populations of *Diadema mexicanum* increased from 3 to nearly 80 ind/m², increasing in consequence the bioerosion rates up to 20 kgCaCO₃/m²/year (Glynn 1988). Posteriorly it was determined a production of 14.86 kgCaCO₃/m²/year for Panama and a total erosion of 33.17 kgCaCO₃/m²/year, being *D. mexicanum* responsible for about 5.51 kgCaCO₃/m²/year (Eakin 1996).

Regarding the Pacific coast of Mexico, the species *Diadema mexicanum* plays an important role on structuring coral reefs communities. However, only one study has focused in evaluating the importance of these sea urchins in the reef community (Reyes-Bonilla and Calderon-Aguilera 1999). A significant development of reef communities exists in Bahias de Huatulco area, considered among the most important of the Pacific coast of Mexico (Reyes-Bonilla 2003), and these communities show an active growing stage (Herrera-Escalante *et al.* 2005). Nevertheless only one study have been carried out in this zone, investigating the importance of *D. mexicanum* as a bioerosive agent, and evaluating the relative magnitude of the coral accretion and the bioerosion caused by these sea urchins (Herrera-Escalante *et al.* 2005).

Therefore it is very important to investigate and monitor permanently the effects of the interaction between the corals, sea urchins populations, and disturbances either natural or induced by human activities. As mentioned by Muthiga and McClanahan (2007) it is of interest to record the historical level of the *Diadema* populations, as it may indicate the degree to which the sea urchins are required for the maintenance of the coral reef ecology or a negative factor that has been released from predation by overfishing.

The aim of the present study is to compare the data on population densities of *D. mexicanum* obtained in 2000-2001 by Herrera-Escalante *et al.* (2005) at Bahias de Huatulco area, with new data obtained in 2006-2007, in order to determine at what degree those densities have changed through time.

MATERIALS AND METHODS

Between January 2006 and February 2007 (except April, July and August), three monthly 25 x 1 m² belt transects parallel to the coastline were conducted at Isla montosa (15° 45' 48" N, 96° 04' 56" W), La Entrega (15° 44' 34" N, 96° 07' 35" W) Cacaluta (15° 43' 08" N, 96° 09' 43" W) and San Agustín (15° 41' 09" N, 96° 14' 05" W) in the coast of Oaxaca, Mexico. The sampling sites were randomly chosen but within the bathymetric interval where reefs occur at all sites (2-13 m; Glynn and Leyte-Morales 1997). Three transects per month per locality were used at all sampling transects were considered permanent, as marks (metal stakes) were conserved in the place and every month the transects were set on the same site. Within each 1 m² interval of the belt transect, densities of *D. mexicanum* were recorded, additionally, 20 sea urchins per locality were captured and measured (test diameter) monthly. All surveys were conducted during the day (10:00-16:00 h.), as proposed by Herrera-Escalante *et al.* (2005), in order to consider sea urchins densities as conservative, since the organisms are active at night (Carpenter 1984, Tuya *et al.* 2001).

We calculated bioerosion exerted by three size class intervals (< 3 cm, 3-5 cm, and > 5 cm test diameter) using the method proposed by Herrera-Escalante *et al.* (2005), who followed modifications to the methods of Glynn *et al.* (1979) and Reyes-Bonilla and Calderón-Aguilera (1999). Based on this data, and on the basis of population densities of *D. mexicanum*, proportion of size classes, and coral carbonate production rate ($\text{kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), taken from Herrera-Escalante *et al.* (2005), the total bioerosive effect of *D. mexicanum* was calculated for one year at each locality.

Deviations of normality and homogeneity of variances for densities of sea urchins were checked using Kolmogorov-Smirnov tests. Densities and test diameter were analyzed by a two way ANOVA (month and locality as factors) in order to distinguish the main effect and possible interactions. All statistical analyses were tested using a p value of 0.05 with the statistical software SigmaStat 9.

RESULTS

At all four localities, *D. mexicanum* occurred where coral reefs were present. Mean density of the sea urchins was maintained relatively constant through time at all localities, being the lowest at San Agustín ($0.26\pm 0.13 \text{ ind}\cdot\text{m}^{-2}$), low at Isla Montosa ($0.36\pm 0.17 \text{ ind}\cdot\text{m}^{-2}$), and Cacaluta ($0.48\pm 0.16 \text{ ind}\cdot\text{m}^{-2}$), and the highest at La Entrega ($4.17\pm 1.4 \text{ ind}\cdot\text{m}^{-2}$) (Fig. 1). Density did not vary significantly through time (ANOVA $F=0.0799$, $df=8$, $p>0.05$), but there were significant differences between localities (ANOVA $F=59.98$, $df=3$, $p<0.001$). Product of the variations, there were differences between La Entrega and the other localities. La Entrega vs. San Agustín (Holm-Sidak=11.24, $p<0.05$), La Entrega vs. Montosa (Holm-Sidak=10.94, $p<0.05$), La Entrega vs. Cacaluta (Holm-Sidak=10.62, $p<0.05$). The internal analysis of density for each locality showed that there were differences among months within La Entrega, being September, December, January and February, the months when mean density was significantly lower than in the other months (Table 1).

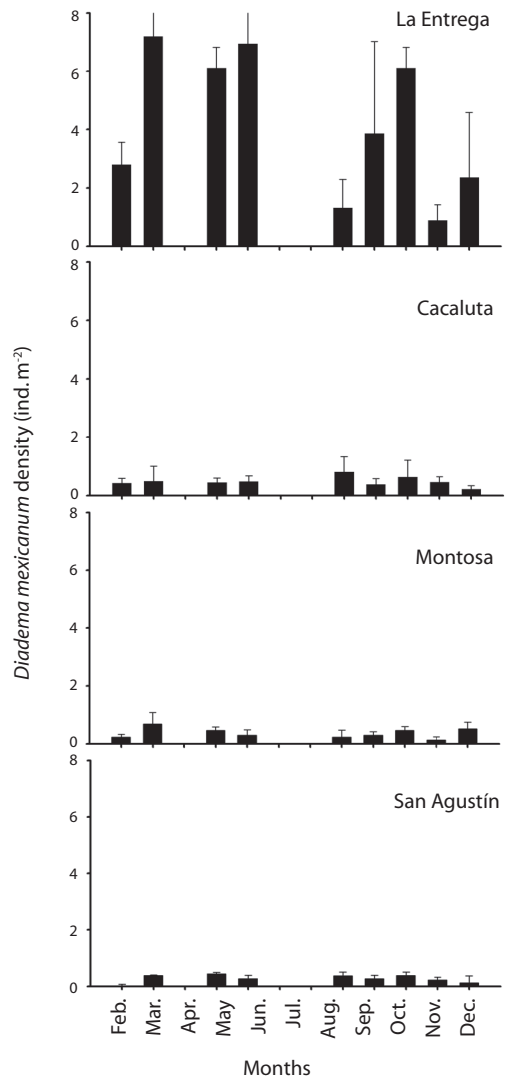


Fig. 1. Mean density (\pm SD) of the sea urchin *Diadema mexicanum* ($\text{ind}\cdot\text{m}^{-2}$) at Bahías de Huatulco, Mexico, from February 2006 through January 2007.

Fig. 1. Densidad media (\pm SD) del erizo *Diadema mexicanum* ($\text{ind}\cdot\text{m}^{-2}$) en las Bahías de Huatulco, México, de febrero 2006 a enero 2007.

D. mexicanum mean test diameter (Fig. 2) was $4.71\pm 0.99 \text{ cm}$ at La Entrega, $4.83\pm 0.19 \text{ cm}$ at Isla Montosa, $4.41\pm 0.88 \text{ cm}$ at Isla Cacaluta, and $4.72\pm 0.27 \text{ cm}$ at San Agustín. The statistical analysis showed that there were not significant differences between localities (ANOVA,

TABLE 1

Months when mean density of *Diadema mexicanum* was significantly different at La Entrega, Bahías de Huatulco, Mexico

CUADRO 1

Meses en los que la densidad media de *Diadema mexicanum* fue significativamente diferente en La Entrega, Bahías de Huatulco, México

Months	March	May	June	November
September	4.62	3.61	4.40	3.61
December	5.86	4.86	5.64	4.86
January	4.50	3.49	4.27	3.49
February	4.09	-	3.86	-

Values are according to the Holm-Sidak method ($p < 0.05$).

Los valores son dados de acuerdo al método de Holm-Sidak ($p < 0.05$).

$F=1.503$, $df=3$, $p=0.259$). The observed pattern of mean test diameter throughout the year was similar for three localities: La Entrega, Isla Cacaluta and Isla Montosa. During February and March, mean test diameter of the urchins was small and it started to increase in May and reached a peak in June. There were no data for July and August; therefore it was not possible to describe the behaviour of the diameter values after the June peak. During September and October the test diameter was again smaller. At la Entrega the values remained low in November, reached a second peak in December and decreased again in January. At Isla Cacaluta, the values descended in November, increased in December and reached a second peak in January. At Isla Montosa, the values reached a second peak in November and decreased during December and January. At San Agustín, the mean test diameter was small in February, the mean diameter increased and reached its largest size in March, showed smaller size in May and reached the smallest mean size in September, in October reached a second peak, decreased in November, increased again in December and it was relatively maintained in January.

The calculated amount of CaCO_3 removed by *D. mexicanum* showed variations between localities. The lowest rate of bioerosion occurred at San Agustín ($0.25 \text{ kg.m}^{-2}.\text{yr}^{-1}$), fol-

lowed by Montosa ($0.37 \text{ kg.m}^{-2}.\text{yr}^{-1}$), Cacaluta ($0.40 \text{ kg.m}^{-2}.\text{yr}^{-1}$), and the highest at La Entrega ($4 \text{ kg.m}^{-2}.\text{yr}^{-1}$).

DISCUSSION

Sea urchins of the genus *Diadema* are typical components of reef communities and frequently exert a decisive influence as grazers (McClanahan *et al.* 1996, Muthiga and McClanahan 2007). Sea urchins are capable of preserving coral cover by constantly grazing algae that potentially compete with the corals for light and space (Sammarco 1982, McClanahan *et al.* 1996); however, when populations are too large, the aggregations of sea urchins might be responsible for most of the erosion of the reef by their feeding activities and the mechanical abrasion produced by the spines (Glynn 1988, Bak 1994, Eakin 1996). In the Bahías de Huatulco area, population densities of *D. mexicanum* are low, compared to those in Panama and Costa Rica (Guzman and Cortes 1992, 2007). Panamá after 1982-83 El Niño, had recorded densities of 60-100 ind.m^{-2} reaching up to 156 ind.m^{-2} (Glynn 1988, Guzmán 1988).

Our results show that densities currently recorded, represent a third of that registered during 2000-2001 by Herrera-Escalante *et al.*

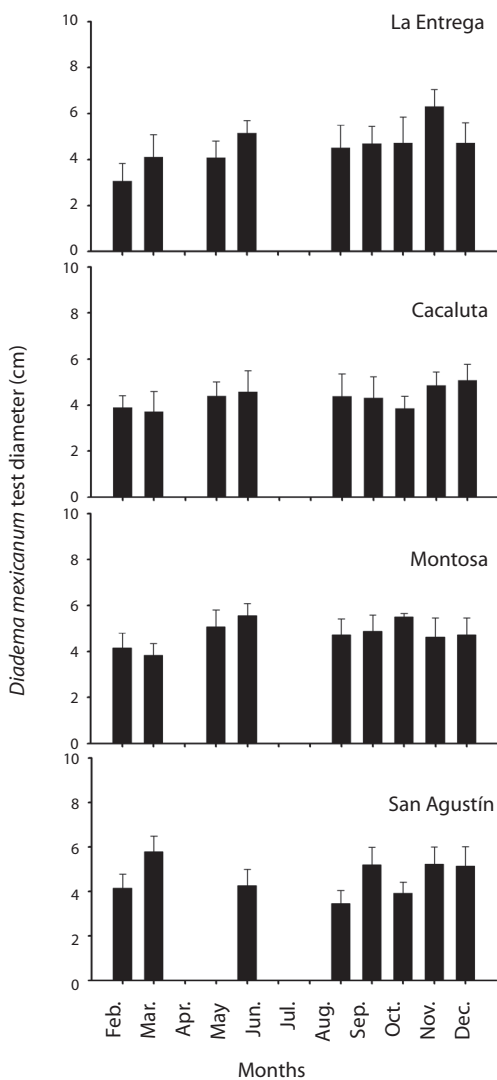


Fig. 2. Mean test diameter (\pm SD) of *Diadema mexicanum* at Bahías de Huatulco, Mexico, from February 2006 through January 2007.

Fig. 2. Diámetro medio de testa (\pm SD) de *Diadema mexicanum* en Bahías de Huatulco, México, de febrero 2006 a enero 2007.

(2005) for Isla Cacaluta and San Agustín, a half for La Entrega, and the more drastic change was observed at Isla Montosa where current density of sea urchins represents only an eighth of that previously reported (Table 2).

In terms of size, test diameter of sea urchins recorded during this study roughly coincides with that reported previously by Herrera-Escalante *et al.* (2005) (Table 2), although the slight increase in size observed, could be the result of a strategy of taking advantage of decreasing population densities by increasing in size, because of more food availability, and considered as density dependant size regulation. This phenomenon has been reported for populations of *D. antillarum* by Levitan (1988, 1989, 1991).

As we could observe during the sampling period, the coral community did not change in cover, then production of CaCO_3 must be the same as that estimated by Herrera-Escalante *et al.* (2005). However, the reduction in population sizes of *Diadema mexicanum* can be translated into a decrease in the bioerosion caused by this species in the coral communities at all localities studied, and therefore into a reduction of the removal of CaCO_3 produced by corals, from 5.55 % to 2.36 % at Isla Cacaluta, 5.08 % to 1.40 % at San Agustín and 16.59 % to 3.08 % at Isla Montosa. The only locality where bioerosion increased was La Entrega, from 27.04 % to 33.05 %. (Table 3).

This reduction of the erosive force represented by sea urchins could be beneficial for coral reef growing and recovery from stress, specially in Bahías de Huatulco, where species richness and composition, and coral coverage is frequently altered by environmental perturbations (Glynn and Leyte-Morales 1997, Lirman *et al.* 2001, Lopez-Perez *et al.* 2002, Reyes-Bonilla *et al.* 2002, Lopez-Perez and Hernandez-Ballesteros 2004). However, because of the already low densities, *D. mexicanum* exerted low to moderated bioerosion at all sites examined in Bahías de Huatulco (Herrera-Escalante *et al.* 2005). On the other hand, it is important to take into account that a decrease in the number of sea urchins that graze heavily on algae, could also signify an increase in algal biomass, and consequently more competition with corals for light and space, consequently, coral reef cover could start to be threatened by a possible uncontrolled overgrowth of the algal

TABLE 2

Comparison of *Diadema mexicanum* densities and test diameters recorded during two periods at Bahías de Huatulco, Mexico

CUADRO 2

Comparación de las densidades y diámetros de testa de *Diadema mexicanum*, registradas durante dos periodos en Bahías de Huatulco, México

Locality	Density 2000-2001 ^A (ind.m ⁻²)	Density 2006-2007 ^B (ind.m ⁻²)	Test diameter 2000-2001 ^A (cm)	Test diameter 2006-2007 ^B (cm)
Isla Montosa	2.98 ± 0.86	0.36 ± 0.17	3.5 ± 0.03	4.83 ± 0.19
La Entrega	6.80 ± 2.09	4.17 ± 1.4	2.9 ± 0.03	4.71 ± 0.99
Isla Cacaluta	1.3 ± 0.25	0.48 ± 0.16	3.4 ± 0.04	4.41 ± 0.88
San Agustín	1.02 ± 0.22	0.26 ± 0.13	4.2 ± 0.04	4.72 ± 0.27

(^A Taken from Herrera-Escalante *et al.* (2005), ^B Data obtained in this study). Values are mean and SD.

(^A Tomado de Herrera-Escalante *et al.* (2005), ^B Datos obtenidos en este estudio). Los valores son media y SD.

TABLE 3

Production of coral carbonate and portion of annual production bioeroded by *Diadema mexicanum* at Bahías de Huatulco, Mexico. Bioerosion and coral carbonate production are in kg CaCO₃m⁻²yr⁻¹.

CUADRO 3

Producción de carbonato de coral y porción de la producción anual bioerosionada por *Diadema mexicanum* en las Bahías de Huatulco, México. Bioerosión y producción de carbonato de coral están dados en kg CaCO₃m⁻²yr⁻¹

Locality	Production ± SD ^A	Bioerosion ± SD 2000-2001 ^A	Bioerosion ± SD 2006-2007 ^B	% Bioeroded 2000-2001 ^A	% Bioeroded 2006-2007 ^B
Isla Montosa	12.11 ± 4.9	2.01 ± 0.38	0.37 ± 0.18	16.59	3.08
La Entrega	12.13 ± 3.3	3.28 ± 0.50	4.00 ± 0.53	27.04	33.05
Isla Cacaluta	17.28 ± 3.8	0.96 ± 0.15	0.40 ± 0.12	5.55	2.36
San Agustín	17.88 ± 3.8	0.91 ± 0.15	0.25 ± 0.11	5.08	1.40

(^A Taken from Herrera-Escalante *et al.* (2005), ^B Data obtained in this study).

(^A Tomado de Herrera-Escalante *et al.* (2005), ^B Datos obtenidos en este estudio).

community. Exclusion experiments and removal of individuals of *D. antillarum* from feeding areas have shown that in the absence of the urchins, the growth of algae is very rapid and detrimental to health of reef corals (Sammarco 1982, Hay 1984, Hay and Taylor 1985) and the best illustrated example of such effect of almost total disappearance of the urchin population is that shown by Lessios (1988) in the Caribbean. Additionally, when urchins are removed from an area, larval settlement of corals is drastically

reduced, because in the process of controlling algal growth, *D. antillarum* also clears space for settlement of larvae of corals (Sammarco 1980, 1982, Levitan 1995).

We strongly recommend a permanent monitoring and evaluation of population densities of *D. Mexicanum* and fishes, as well as algal and coral cover at the Bahías de Huatulco area, similar to the Colombian Coral Reef Monitoring System (SIMAC), which has evaluated the density of echinoid species every year

since 1999 at shallow, mid depth and deep reef sites of important Caribbean and Pacific coral reef of Colombia. It is important also to carry out research on the variation in time and space of larval settling and juvenile recruitment for *D. mexicanum* at the study area, in order to understand the population dynamics of this species, as well as the importance of diverse biological and physical factors controlling the population of the sea urchins and the reef community in general.

ACKNOWLEDGMENTS

We thank the coordinators of the Parque Nacional Huatulco for facilities and permissions to work in the area. This study was supported by the project "Diagnóstico de los recursos naturales de la Bahía y microcuenca del Río Cacaluta" funded by Fondo Secretaría del Ambiente y Recursos Naturales (SEMARNAT)-Consejo Nacional de Ciencia y Tecnología (CONACYT) from México (registro 0605)

RESUMEN

Los erizos del género *Diadema* desempeñan un papel importante como controladores del crecimiento algal en comunidades de arrecifes coralinos y rocosos. Si las densidades poblacionales se incrementan pueden causar bioerosión sobre la estructura del arrecife. Durante febrero 2006 y enero 2007 (excepto abril, julio y agosto), se determinaron las densidades poblacionales y diámetro promedio de testa de *Diadema mexicanum* en Isla Montosa, La Entrega, Isla Cacaluta y San Agustín en Bahías de Huatulco, México. La densidad media se mantuvo relativamente constante en el tiempo en todas las localidades. La más baja fue en San Agustín (0.26 ind.m⁻²) y la más alta en La Entrega (4.17 ind.m⁻²). Existieron diferencias significativas entre La Entrega y las demás localidades. El diámetro de la testa osciló entre 3.9 cm (La Entrega) y 4.72 cm (San Agustín) y no varió significativamente entre localidades, pero si hubo variaciones en el tiempo. La cantidad calculada de CaCO₃ removido por *D. mexicanum* mostró variaciones entre localidades. La tasa mas baja de bioerosión ocurrió en San Agustín (0.25 kg.m⁻².yr⁻¹), y la mas alta en La Entrega (4 kg.m⁻².yr⁻¹). En comparación con reportes previos, la reducción en el tamaño de las poblaciones de *D. mexicanum* significa una reducción en la remoción del CaCO₃ producido, de 5.55 % a 2.36 % en Isla Cacaluta, 5.08 % a 1.40 % en San Agustín y 16.59 % a 3.08 % en

Isla Montosa. La única localidad donde hubo incremento en la bioerosión fue La Entrega, de 27.04 % a 33.05 %. La reducción podría ser beneficiosa para el crecimiento y recuperación del arrecife, aunque podría ocurrir un incremento en la biomasa algal y competencia con los corales por luz y espacio. Se recomienda un monitoreo permanente de las densidades poblacionales de *D. mexicanum* y peces, así como la cobertura de corales y algas en Bahías de Huatulco, para discernir si los cambios en las poblaciones son un fenómeno continuo o parte de un ciclo de incrementos y reducciones.

Palabras clave: *Diadema mexicanum*, erizo de mar, densidad poblacional, equinodermos, Huatulco, Pacifico Oriental.

REFERENCES

- Bak, R.P.M. 1994. Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. *Coral Reefs* 13: 99-104.
- Bauer, J.C. 1980. Observations on geographical variations in population density of the echinoid *Diadema antillarum* within the western north Atlantic. *Bull. Mar. Sci.* 30: 509-515.
- Birkeland, C. 1989. The influence of echinoderms on coral-reef communities, p. 1-79. *In*. M. Jangoux and J.M. Lawrence (eds.). *Echinoderm Studies*. A.A. Balkema, Rotterdam.
- Carpenter, R.C. 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. *Mar. Biol.* 82: 101-108.
- Carpenter, R.C. 1990. Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population dynamics and coral reef algal communities. *Mar. Biol.* 104: 67-77.
- De Ruyter van Stevenick, E.D. & R.P.M. Bak. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Mar. Ecol. Prog. Ser.* 34:87-94.
- Eakin, C.M. 1992. Post-El Niño panamanian reefs: less accretion, more erosion and Damselish protection. *Proc. 7th Int. Coral Reefs Symp.* 1: 387-396.
- Eakin, C.M. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-83 El Niño at Uva Island in the eastern Pacific. *Coral Reefs* 15: 109-119.
- Glynn, P.W. 1988. El Niño-Southern Oscillation 1982-1983: Near shore population, community, and ecosystem responses. *Annu. Rev. Ecol. Syst.* 19: 309-345.

- Glynn, P.W. & G.E. Leyte-Morales. 1997. Coral reefs of Huatulco, west Mexico: reef development in upwelling Gulf of Tehuantepec. *Rev. Biol. Trop.* 45: 1033-1047.
- Glynn, P.W., G.M. Wellington & C. Birkeland. 1979. Coral reef growth in the Galápagos: Limitation by sea urchins. *Science* 203: 47-49.
- Guzmán, H.M. 1988. Distribución y abundancia de organismos coralívoros en los arrecifes coralinos de la Isla del Caño, Costa Rica. *Rev. Biol. Trop.* 36: 191-207.
- Guzmán, H.M. & J. Cortés. 1992. Cocos Island coral reefs after the 1982-83 El Niño disturbance. *Rev. Biol. Trop.* 40: 309-324.
- Guzmán, H. M. & J. Cortés. 2007. Reef recovery 20 years after the 1982-1983 El Niño massive mortality. *Mar. Biol.* 151: 401-411
- Hay, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65: 446-454.
- Hay, M.E. & P.R. Taylor. 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia* 65: 591-598.
- Herrera-Escalante, T., R.A. López-Pérez & G.E. Leyte-Morales. 2005. Bioerosion caused by the sea urchin *Diadema mexicanum* (Echinodermata: Echinoidea) at Bahías de Huatulco, Western Mexico. *Rev. Biol. Trop.* 53 (Supl. 3): 263-273.
- Hughes, T.P. 1989. Community structure and diversity of coral reefs: The role of history. *Ecology* 70: 275-279.
- Knowlton, N. 2001. Sea urchin recovery from mass mortality: new hope for Caribbean Coral reefs? *Proc. Nat. Acad. Sci.* 98: 4822-4824.
- Lessios, H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Ann. Rev. Ecol. Syst.* 19: 371-393.
- Lessios, H.A., J.D. Cubit, R.D. Robertson, M.J. Shulman, M.R. Parker, S.D. Garrity & S.C. Levings. 1984. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* 3: 173-182.
- Lessios, H.A., B.D. Kessing & J.S. Pearse. 2001. Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, 55: 955-975.
- Levitan, D.R. 1988. Density-dependant size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. *Oecologia* 76: 627-629.
- Levitan, D.R. 1989. Density-dependant size regulation *Diadema antillarum*: Effects on fecundity and survivorship. *Ecology* 70: 1414-1424.
- Levitan, D.R. 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. *Mar. Biol.* 111: 431-435.
- Levitan, D.R. 1995. The ecology of fertilization in free-spawning invertebrates. p. 123-156. *In* L. McEdward (ed.). *Ecology of Marine Invertebrate Larvae*. CRC, Florida.
- Liddell, W.D. & S.L. Ohlhorst. 1986. Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *J. Exp. Mar. Biol. Ecol.* 95: 271-278.
- Lirman, D., P.W. Glynn, A.C. Baker & G.E. Leyte-Morales. 2001. Combined effects of three sequential storms on the Huatulco coral reef tract, Mexico. *Bull. Mar. Sci.* 69: 267-278.
- López-Pérez, R.A., L.M. Hernández-Ballesteros & T. Herrera-Escalante. 2002. Cambio en la dominancia de la comunidad arrecifal en Chachacual, Bahías de Huatulco, Oaxaca. *Ciencia y Mar* 16: 33-38.
- López-Pérez, R.A & L.M. Hernández-Ballesteros. 2004. Coral community structure and dynamics in the Huatulco area, western Mexico. *Bull. Mar. Sci.* 75: 453-472.
- McClanahan, T. R. 2007. Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. *Oecologia* DOI 10.1007/s00442-007-0890-0.
- McClanahan, T.R., A.T. Kamukuru, N.A. Muthiga, M. Gilgaber & D. Obura. 1996. Effect of sea urchin reductions on algae, coral, and fish populations. *Conserv. Biol.* 10: 136-154.
- Muthiga, N.A., T.R. McClanahan. 2007. Ecology of *Diadema*, p. 205-219. *In* J.M. Lawrence (ed.). *Edible Sea Urchins: Biology and Ecology*. Elsevier, Amsterdam, The Netherlands.
- Ogden, J.C. 1976. Some aspects of herbivore-plant relationship on Caribbean reefs and seagrass beds. *Aquatic Botany* 2: 103-116.

- Ogden, J.C. & P.S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reefs communities. *Env. Bio. Fish.* 3: 49-63.
- Ogden, J.C., R.A. Brown & N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum philippi*: formation of halos around West Indian patch reefs. *Science* 182: 715-716.
- Reyes-Bonilla H. 2003. Coral reefs of the Pacific coast of Mexico, p. 387-418. *In* J. Cortés (ed). *Latin American Coral Reefs*. Elsevier, Amsterdam.
- Reyes-Bonilla, H. & L.E. Calderón-Aguilera. 1999. Population density, distribution and consumption rates of three corallivores at Cabo Pulmo reef., Gulf of California, Mexico. *Mar. Ecol.* 20: 347-357.
- Reyes-Bonilla, H., J.D. Carriquiry, G.E. Leyte-Morales & A.L. Cupul-Magaña. 2002. Effects of El Niño Southern Oscillation and the anti-El Niño event (1997-1999) on coral reefs of the western coast of Mexico. *Coral Reefs* 21: 368-372.
- Sammarco, P.W. 1980. *Diadema* and its relationship to coral spat mortality: grazing competition and biological disturbance. *J. Mar. Res.* 32: 254-272.
- Sammarco, P.W. 1982a. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *J. Exp. Mar. Biol. Ecol.* 61: 31-35.
- Sammarco, P.W. 1982b. Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J. Exp. Mar. Biol. Ecol.*, 65: 83-105.
- Solandt, J.L. & A.C. Campbell. 2001. Macroalgal feeding characteristics of the sea urchin *Diadema antillarum* Philippi at Discovery Bay, Jamaica. *Carib. J. Sci.* 37: 227-238.
- Tuya, F., J.A. Martín, G.M. Reuss & A. Luque. 2001. Food preferences of the sea urchin *Diadema antillarum* in Gran Canaria (Canary Islands, central-east Atlantic Ocean). *J. Mar. Biol. Ass. UK.*, 81: 845-849.
- Tuya, F., R. Haroun, A. Boyra & P. Sánchez-Jerez. 2005. Sea urchin *Diadema antillarum*: different functions in the structure and dynamics of reefs on both sides of the Atlantic. *Mar. Ecol. Prog. Ser.* 302: 307-310.
- Vicente, V.P. & C. Goenaga. 1984. Mortandades masivas del erizo de mar *Diadema antillarum* (Philippi) en Puerto Rico. Centro para Estudios Energéticos y Ambientales, Div. Ecología Marina, Reporte CEER-M-195, Univ. Puerto Rico, Puerto Rico.

