

Density, spatial distribution and mortality rate of the sea urchin *Diadema mexicanum* (Diadematoida: Diadematidae) at two reefs of Bahías de Huatulco, Oaxaca, Mexico

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Abstract: *Diadema mexicanum*, a conspicuous inhabitant along the Mexican Pacific coast, is a key species for the dynamics of coral reefs; nevertheless, studies on population dynamics for this species are scarce. Monthly sampling was carried out between April 2008 and March 2009 at Isla Montosa and La Entrega, Oaxaca, Mexico using belt transects. Population density was estimated as well as abundance using Zippin's model. The relationship of density with sea-bottom temperature, salinity, pH, and pluvial precipitation was analyzed using a step by step multiple regression analysis. Spatial distribution was analyzed using Morisita's, Poisson and negative binomial models. Natural mortality rate was calculated using modified Berry's model. Mean density was $3.4 \pm 0.66 \text{ ind}\cdot\text{m}^{-2}$ in La Entrega and $1.2 \pm 0.4 \text{ ind}\cdot\text{m}^{-2}$ in Isla Montosa. Abundance of *D. mexicanum* in La Entrega was 12166 ± 25 individuals and 2675 ± 33 individuals in Isla Montosa. In Isla Montosa there was a positive relationship of density with salinity and negative with sea-bottom temperature, whereas in La Entrega there was not a significant relationship of density with any recorded environmental variable. Monthly mortality rate was 0.10 in La Entrega and 0.15 in Isla Montosa. Spatial distribution pattern was aggregated for both localities during the sampling period with oscillations in the intensity of aggregation. Higher density and abundance, and a low mortality rate, indicate better conditions for the population of *D. mexicanum* in La Entrega, contrasting with those of Isla Montosa where apparently there are more stressful conditions associated to stronger oceanographic conditions and a higher sedimentation rate resulting from the proximity of the Copalita River. Rev. Biol. Trop. 63 (Suppl. 2): 173-182. Epub 2015 June 01.

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Sea urchins of the genus *Diadema* play perhaps the most important role in comparison to other herbivores inhabiting benthic communities, coral reefs, and tropical rocky shores in the world (Lessios, 1981; Carpenter, 1986; Hernández, 2006). *Diadema mexicanum* is an important algal consumer and similar to the rest of the species of this genus, maintains interaction with the coral community, which can be positive as a controller of algal growth (Edmunds & Carpenter, 2001; Lessios, Lessios & Pearse, 2001; Atrill & Kelmo, 2007), or negative as a bioeroder agent (Eakin,

1996, 2001; Herrera-Escalante, López-Pérez & Leyte-Morales, 2005). *Diadema mexicanum* is widely distributed along the tropical eastern Pacific, from the Gulf of California in Mexico (Caso, 1979; Cintra-Buenrostro & Reyes-Bonilla, 1998; Holguin-Quiñónez, Wright-López, & Solís-Marín, 2000) to the Lobos de Afuera Island in Peru (Hooker, Solís-Marín, & Lleellish, 2005), including Clipperton Islands (Glynn, Vero, & Wellington, 1996), Archipelago of Revillagigedo (Reyes-Bonilla, 1995), del Coco and del Caño Islands in Costa Rica (Guzmán, 1988; Alvarado & Fernández,

2005; Alvarado & Chiriboga, 2008), Galapagos (Hickman, 1998; Edgar, Banks, Fariña & Martínez, 2004) in Ecuador, and Malpelo and Gorgona Islands in Colombia (Neira & Cantera, 2005).

Ecological studies of *D. mexicanum* have focused almost exclusively on population densities and the effect of the species as bioeroders of the Pacific reefs. Despite its wide distribution and ecological relevance, studies regarding population ecology of the species are scarce in Mexican coasts (Espino-Barr, Cibrián & García-Boa, 1996; Zamorano-de Haro, 2004). In our study, we analyzed population features such as density, abundance and, for the first time ever for this species, natural mortality and distribution pattern in two reef communities of the coast of Oaxaca from April 2008 to March 2009. This characterization of the two populations, besides being an important source of new data, becomes essential since a mass mortality event occurred in May 2009 (Benítez-Villalobos, Díaz-Martínez & Martínez-García 2009), which reduced the local population of this sea urchin to almost a complete disappearance in La Entrega, and had a lesser effect in other localities of the area. Therefore, the data we present in this work will be useful as a reference of the state of the populations just before the die-off and will serve to compare and evaluate the population dynamics as well as the possible recovery after the event.

MATERIAL AND METHODS

Field work: The study area comprises the reef communities of La Entrega (15° 44' 34" N - 96° 07' 35" W) and Isla Montosa (15° 45' 48" N - 96° 04' 56" W), which belong to the reef complex of Bahías de Huatulco in the southern Mexican Pacific.

Field work was carried out monthly from April 2008 to March 2009. Ten 2 - m wide and 10 - m long belt transects were haphazardly laid over the reef and all the urchins that were included within every quadrant of 1 X 2 m along the transect were counted (CARICOMP, 2001). In every fieldtrip, environmental variables (pH,

salinity) were recorded using a multiparameter metering device (Hannah HI9828) with a precision of ± 0.01 for both parameters. Bottom temperature was recorded every hour using Hobo Pendant Loggers (Onset Computer Corporation) permanently attached to the sea floor. Pluvial precipitation data were obtained from the meteorological station 0X01 of the National Water Commission, located in Puerto Angel, Oaxaca.

Data analyses: Density was estimated by square meter (ind m^{-2}) every month in both study sites, and a two-way ANOVA was applied to identify statistical differences between localities and months. All results were analyzed with a significant level of 0.05 and values were reported as mean and standard deviation (SD).

Abundance was estimated using the Zippin (1958) model applied to the data resulting from the sum of all urchins counted in the ten transects every month, in order to obtain an estimation of the abundance of the population along the year in each locality. Abundances of seven months were chosen in order to carry out the calculation considering the largest number of trappings proposed by Zippin (1958), which are seven samples.

A step by step multiple linear regression analysis was performed to evaluate the relation between monthly variations of the density (dependent variable) and variations of bottom temperature (BT), salinity (S), pH, and pluvial precipitation (PP) (independent variables).

Rate of natural mortality of *D. mexicanum* in both localities was calculated using Berry's model (1967), which has been used and modified for other marine invertebrates (Ramos-Cruz, Sánchez-Meraz, Carrasco-Ayuso, & Cervantes-Hernández, 2006). This model uses the monthly variation of abundance of an organism recorded in the field (Ramos-Cruz et al., 2006).

The Berry's model assumes that following an event of recruitment occurred during (n) time intervals (considered as independent), abundance of the organisms (in this case monthly) diminishes due to the action of natural mortality

(M) (Ramos-Cruz et al., 2006). In the case of *D. mexicanum* natural mortality was estimated in those intervals in which abundance recorded in the field showed three or more continuously descending values.

The mathematical algorithm used for calculation of mortality is the following:

$$\ln(Nt) = \alpha + \beta(t)$$

Where:

α : origin ordinate of the regression pendant.
 β : is the pendant of the regression or value corresponding to the total mortality (Zprtial).
 t : is the interval in which there exist diminishing of abundance.

Spatial distribution pattern for both sites was estimated with the Morisita's index (1962), which is based in the analysis of the variance-mean relationship. The distribution pattern was corroborated using the Poisson's and Binomial Negative models, obtaining the values of X^2 , calculated and from tables in order to execute the statistical confrontation (Mendenhall & Reinmuth, 1978). The K parameter obtained from the Binomial Negative model indicates the intensity of aggregation of individuals from a population, and two methods were used in order to calculate it. If the first method did not fulfill the assumptions, the second method was used.

First method for calculation of K

$$K = \frac{\mu^2}{(\delta^2 - \mu)}$$

The value is satisfactory if it fulfills one of three assumptions:

1. $\frac{K}{\mu} > 6$
2. $K > 3$
3. $\frac{(k+\mu)(K+2)}{\mu} \geq 15$

If K does not fulfill at least one of them, the second method is used:

Second method for calculation of K

$$\log \frac{N}{N_0} = K_1 * \log \left[1 + \frac{\mu}{k_1} \right]$$

Where:

$N = \sum f(x)$

N_0 = the first date of $f(x)$

K_1 = Comes from the first method

RESULTS

Density and abundance: Mean monthly density in La Entrega was 3.4 ± 0.66 ind m^{-2} , and it fluctuated between 2.5 and 4.4 ind m^{-2} . An increase in density was recorded during June, July, August, and November 2008, reaching a peak in March 2009. Minimum values were observed in May, October, and December 2008, and February 2009 (Fig. 1A). In Isla

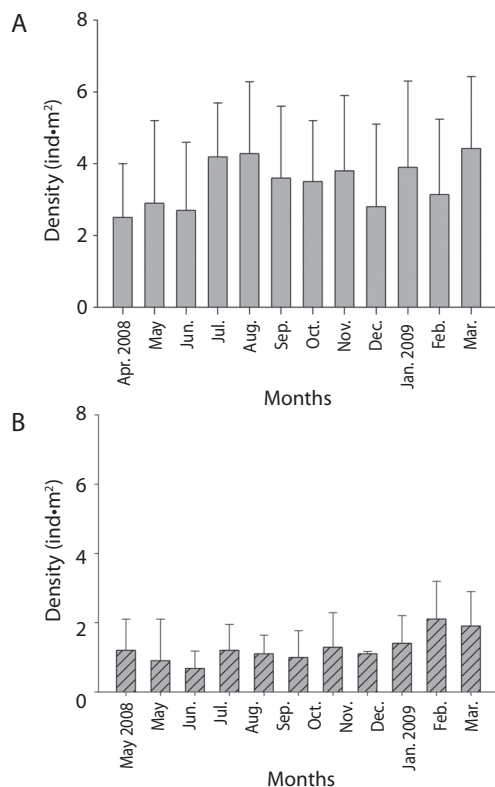


Fig. 1. Temporal comparison of population density (mean \pm SD) of *D. mexicanum* for each study site from April 2008 to March 2009: A) La Entrega; B) Isla Montosa.

Montosa, mean density was $1.2 \pm 0.4 \text{ ind.m}^{-2}$, fluctuating between 0.68 and 2.1 ind.m^{-2} . During August and November 2008 we recorded high values, and a peak was recorded in February 2009, the minimum values corresponded to June and July 2008 (Fig. 1B). There were statistically significant differences between localities ($F_{29,2} = 106.4$, $p < 0.05$). According to Zippin's model, abundance of *D. mexicanum* in La Entrega was $12\ 166 \pm 25$ individuals and $2\ 675 \pm 33$ individuals in Isla Montosa.

Environmental variables: Regarding environmental variables in La Entrega, mean (\pm SD) temperature during the sampling period was 26.58 ± 2.24 °C, the lowest value (23.5 °C) was recorded in March 2009 and the highest (29.8 °C) in August 2008. Mean (\pm SD) salinity was 32.1 ± 1.5 , the lowest value (29.3) was

observed in June 2008 and the highest (34.4) in December 2008. Mean (\pm SD) value for pH was 8.7 ± 0.26 and it oscillated from 8.3 as the lowest during April and May 2008, and 9.1 as the highest in November 2008 (Fig. 2A).

In Isla Montosa mean value for temperature was 29.10 ± 2.26 °C, the lowest value (23.1 °C) was observed in November 2008 and the highest (29.7 °C) in August 2008. Mean (\pm SD) salinity was 32.5 ± 2.6 , the lowest value (28) was observed in July 2008 and the highest (35.3) in December 2008. Mean (\pm SD) value for pH was 8.9 ± 0.3 , the lowest value (8.6) was recorded in October 2008, January and March 2009, and the highest (9.7) in February 2009 (Fig. 2B). The rainy season in the Bahías de Huatulco region during the sampling period occurred from March to September 2008, with a mean pluvial precipitation of 109.69 mm, and the highest precipitation during July (Fig. 2A, B).

Multiple linear regression analysis of Isla Montosa was solved in two steps ($D_n = -2.002 + 0.109 S - 0.0508 \text{ TEMP}$, indicating that the total explained variance over Density, in terms of the selected environmental variables, was 82.67% ($R^2 = 0.894$, $R = 0.9$, p multiple < 0.05). The first variable that went into the model was Salinity, providing 82.5% of the total explained variance. The partial contribution of variable Temperature to explain the variation of the abundance of *D. mexicanum* was 6.32 %. Regarding La Entrega, the analysis did not consider any variable to account for the ability to predict density of *D. mexicanum*.

Mortality rate: The natural mortality rate estimated, using the abundance recorded in the field for La Entrega, and considering one interval of continuous decreasing (August to October 2008) was 0.1. In Isla Montosa considering two intervals (May to July and August to October 2008) the average natural mortality rate was 0.15.

Spatial distribution: According to Morisita's index, the spatial distribution pattern of *D. mexicanum* for both localities was patchy

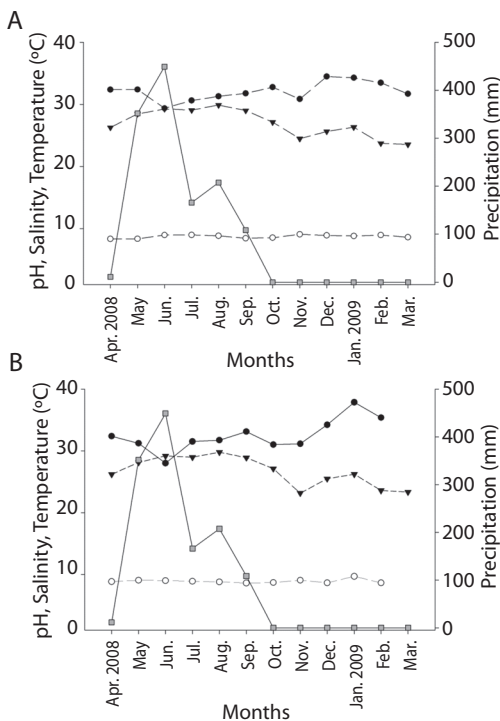


Fig. 2. Monthly variation of pluvial precipitation (solid line with grey squares), temperature (dashed line with black triangles), salinity (solid line with black dots) and pH (dashed line with white dots) in La Entrega (A) and Isla Montosa (B), from April 2008 to March 2009.

TABLE 1
Monthly values of Morisita's (σ^2/μ), Poisson (λ), and negative binomial (k) models for La Entrega and Isla Montosa

Locality Months	Entrega			Isla Montosa		
	σ^2/μ	λ	k	σ^2/μ	λ	k
Apr-08	17.5	2.53	0.063	-	-	-
May-08	24.7	2.97	0.071	7.79	0.96	0.100
Jun-08	24.5	3.26	0.088	15.91	0.91	0.108
Jul-08	20.7	4.19	0.095	6.42	1.36	0.204
Aug-08	21.9	4.29	0.103	8.60	1.29	0.206
Sep-08	16.9	3.65	0.101	7.60	1.10	0.211
Oct-08	17.2	3.51	0.105	5.53	0.99	0.126
Nov-08	17.3	3.88	0.134	7.87	1.29	0.258
Dec-08	16.2	2.71	0.087	4.79	1.11	0.234
Jan-09	18.2	3.90	0.146	7.96	1.44	0.229
Feb-09	16.7	3.14	0.048	8.82	2.11	0.226
Mar-09	27.5	4.42	0.087	6.47	1.93	0.297

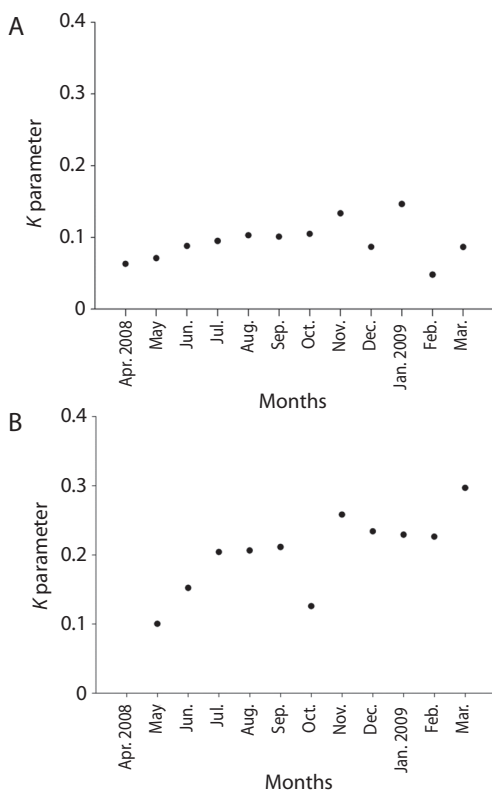


Fig. 3. Aggregation parameter (K) for population of *D. mexicanum* in the two study sites from April 2008 to March 2009: A) La Entrega; B) Isla Montosa.

along the entire sampling period. The negative binomial distribution model confirmed the distribution pattern and Poisson's model showed that the spatial distribution pattern was not

random (Table 1). The aggregation parameter (k) provided by the negative binomial model for La Entrega showed that the months with higher levels of aggregation of *D. mexicanum* were April and December 2008, and February 2009, whereas the months when the urchin exhibited less aggregation were November 2008 and January 2009 (Fig. 3A). In Isla Montosa, the months when the intensity of aggregation was higher were May and October 2008, and December 2009. The lowest value of aggregation was recorded in February 2009 (Fig. 3B). Oscillations of k during the sampling period followed the fluctuation of the variance obtained with Morisita's index in most of the months for both localities, and aggregation intensity was higher in La Entrega than in Isla Montosa.

DISCUSSION

According to Zippin's model, La Entrega is the locality with the highest abundance of *D. mexicanum*. An important difference between both sampled localities is the extension of the reef, which is less than a hectare in Isla Montosa and nearly seven hectares in La Entrega, making this latter one of the most extensive reefs in Bahías de Huatulco (Leyte-Morales, 2001), and is also the community with the largest proportion of death coral (around 25%), as compared to Isla Montosa (around 10

%) (Leyte-Morales, 2001; Herrera-Escalante, López-Pérez, & Leyte-Morales, 2005). An important characteristic of this kind of substrate is that it is appropriate for proliferation of macro algae, which, in turn, constitute the most important source of food for *D. mexicanum* (Glynn & Leyte-Morales, 1997). Zamorano and Leyte-Morales (2009) proposed that in those communities where touristic activities are more intense and, consequently, possess more fragmented and death coral, populations of *D. mexicanum* are more abundant. Results of this study support that observation, since La Entrega is the community with the highest touristic impact in Bahías de Huatulco as well as the community with the most abundant population of *D. mexicanum* in the entire zone.

On the other hand, as a result of the strong influence of discharges from the Copalita River, especially during the summer, Isla Montosa shows the highest sedimentation rate ($653.31 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), of the Bahías de Huatulco zone, whereas La Entrega is a relatively protected bay with minimal contribution of continental water and the sedimentation rate is low ($14.33 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) (Granja-Fernández & López-Pérez, 2008).

Clemente & Hernández, (2008) proposed that the sedimentation rate and the presence of suspended sand are important factors that limit the population density of *Diadema aff. Antillarum* (now *D. africanum*) (Rodríguez, Hernández, Clemente & Coppard, 2013) in several localities of the Canary Islands. The authors observed that high sedimentation rates in rocky and coral communities inhibit algal recruitment and growth, producing adverse environments in terms of food source for the urchins, and suggest that the combined effect of intense waves and sediment covering the substrate may weaken adhesion of the urchins and restrain or, even more, hinder their motility.

Regarding temporal variations of density, monthly values in La Entrega showed the first increase between June and August 2008, which coincided with the rainy season (June-October), which results from the increase in sea temperature, but in both localities the highest

density was observed at the end of 2008 and beginning of 2009. This pattern observed in both localities suggests that the population density of *D. mexicanum* is indirectly influenced by the increase in primary production resulting from the effect of turbulence and mixture produced by the local winds known as “Nortes”. These winds reach their highest intensity from November to April, bringing nutrients from subsurface region and elevating substantially the availability of energy for primary producers and, in consequence, for planktonic and benthic herbivores, and this is reflected in an increase in population density (Fernández-Álamo & Färber-Lorda, 2006; Pennington et al., 2006).

Regarding other populations of *Diadema mexicanum*, the estimated average values calculated for both localities in this study were lower than those obtained previously by other authors (Hernández-Ballesteros, 2002; Herrera-Escalante et al., 2005; Zamorano & Leyte-Morales, 2005; Benítez-Villalobos, Domínguez & López-Pérez, 2008), evidencing a continuous decrease in density since 2002, especially in La Entrega. Considering the Tropical Eastern Pacific, Isla Uva in the Gulf of Chiriquí in Panama is the locality with the highest reported population density ($50 - 150 \text{ ind m}^{-2}$), followed by Isla del Coco, Costa Rica ($0.05 - 11.4 \text{ ind m}^{-2}$), and La Entrega and Isla Montosa in Bahías de Huatulco, Mexico ($0.36 - 7.5 \text{ ind m}^{-2}$), whereas the rest of studied localities show relatively low densities ($0.1 - 2.7 \text{ ind m}^{-2}$). These differences in population densities do not seem to follow a defined latitudinal pattern, but result from particular characteristics inherent to each studied locality.

According to the statistical analysis, in Isla Montosa, the environmental variable that affected the population density of *D. mexicanum* in a negative way was temperature, whereas salinity showed to have a positive effect to a larger extent. The lowest estimations of density occurred during the raining season, coinciding with the highest values of sea temperature and the lowest values of salinity produced by the extensive supply of fresh water from the Copalita River. In general, the poor capacity

of echinoids for ionic regulation makes this group of organisms extremely sensitive to low levels of salinity (Hyman, 1955; Shumway, 1977; Pia, Johnson & George, 2012) and this condition produces deficiency in consumption and utilization of energy, since a larger amount of energy is required to compensate the osmotic regulation at a cellular level, involving an important physiological cost (Forcucci & Lawrence, 1986). Long time exposures to low salinity conditions can be lethal for some echinoid species (Irlandi, Maciá & Serafy, 1997; Campbell & Russell, 2004).

The observed pattern in temperature and salinity reversed during the “Nortes” season (November-April) and coincided with the increase in population density, evidencing that despite the benefits of high temperature for tropical sea urchins, and the presence of this condition during the raining season in Isla Montosa, the combined effects of low levels of salinity, turbidity, and higher sedimentation rates create unfavorable conditions for *D. mexicanum* during that season.

In contrast, according to the statistical analysis, the environmental variables did not affect *D. mexicanum* population in La Entrega in the same way, as none of them showed a significant relationship with density of the urchin.

The apparent incongruent effect of salinity and temperature on the populations of both localities could be reflecting a complex interaction of various factors, such as reef geomorphology, currents, waves, sedimentation rates, and anthropogenic activity (López-Pérez, Hernández-Ballesteros & Herrera-Escalante, 2002), which, in synergy with complex interactions such as competence and predation, induce different scenarios on each community. Thus, probably the almost null influence of rivers in La Entrega did not allow evidencing clearly the effect of the environmental variables as occurred in Isla Montosa. In the latter, temperature had a negative effect, although it is directly related to population growth, it produces precipitation, which, in turn, affects negatively the population of *D. mexicanum*, as well as the low salinity.

The fact that Isla Montosa possesses a more stressful environment for *D. mexicanum* as a consequence of its high sedimentation rates and higher exposure to direct waves, is reflected also in a higher mortality rate as compared to the population of *D. mexicanum* living in La Entrega, and to other species inhabiting the tropical eastern Pacific, such as *D. antillarum* in the Virgin Islands (Randall, Schroeder, & Starck, 1964) and Barbados (Lewis, 1996), as well as *D. paucispinum* in Hawaii (Ebert, 1982).

The aggregated spatial pattern observed for *D. mexicanum* throughout the entire sampling period in both studied localities generally, occurs when the environment is heterogeneous or positive interactions exist between organisms (Ludwig & Reynolds, 1988; Krebs, 1999), this has been documented for a number of echinoderm species (Randall et al., 1964; Pearse & Arch, 1969; Bauer, 1976; Levitan, 1988; Hamel & Mercier, 1995; Campbell, Coppard, D’Abreo, & Tudor-Thomas, 2001; Alvarado, 2008).

Regarding populations of *D. mexicanum*, it has been proposed that the aggregation behavior does not simply correspond to a passive response to environmental limitations, since adjacent areas with similar substrata and feeding conditions show different levels of occupation and aggregation (Pearse & Arch, 1969). In La Entrega, this sea urchin shows a stratified pattern of aggregation, having densities of more than 11 individuals per square meter at higher depths in the reef (Herrera-Escalante et al., 2005), where conditions of large areas of rubble and death coral prevail.

Pearse & Arch (1969) suggest that large exposed aggregations of *D. setosum* and *D. savignyi* in unprotected areas, of the reefs of Papua New Guinea, result from populations with too large sizes, in which the number of individuals exceeds the number of available refuges, and the probability of encounter among organisms to form a patch is larger than the probability of finding an appropriate refuge in the reef. This seems to coincide with findings for the population of *D. mexicanum* in

La Entrega, since this is the locality with the largest aggregations in the deep zone of the reef and also with the largest population density, significantly different from Isla Montosa and other localities of the Bahías de Huatulco area (Herrera-Escalante et al., 2005; Benítez-Villalobos et al., 2008). Additionally, the low level of structural complexity, provided by the prevalence of corals of the genus *Pocillopora* in La Entrega, basically offers fewer crevices that could be used as refuge, propitiating that individuals of *D. mexicanum* compose large aggregations in open areas of the reef, constituted principally by rubble and death coral.

Despite that La Entrega and Isla Montosa are relatively near localities and, theoretically, their oceanic conditions are the same, population dynamics of *D. mexicanum* is different in terms of its population parameters characterized in this study. According to a lower mortality rate and larger densities and abundance, population of La Entrega inhabits an environment with more favorable conditions of food and space and relatively low levels of stress, whereas the population of Isla Montosa undergoes a major environmental stress in terms of high sedimentation rates and a smaller reef surface.

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RESUMEN

Densidad, distribución espacial y tasa de mortalidad de *Diadema mexicanum* (Diadematoidea: Diademátidae) en dos arrecifes de Bahías de Huatulco, Oaxaca, México. *Diadema mexicanum* es un habitante conspicuo de las costas del Pacífico Mexicano y una especie clave en los arrecifes de coral, sin embargo son escasos los estudios acerca de la dinámica poblacional de esta especie. En el presente trabajo se muestreó mensualmente de abril 2008 a

marzo 2009 en Isla Montosa y La Entrega usando transectos de banda. Se estimó la densidad poblacional, así como la abundancia mediante el modelo de Zippin. Se evaluó la relación entre la variación mensual de la densidad y la temperatura, salinidad, pH y precipitación pluvial usando un análisis de regresión lineal múltiple paso a paso. La distribución espacial se analizó con los modelos de Morisita, Poisson y Binomial Negativa. Se calculó la tasa de mortalidad natural usando el modelo de Berry modificado. La densidad media fue 3.4 ± 0.66 ind m^{-2} en La Entrega y 1.2 ± 0.4 ind m^{-2} en Isla Montosa. La abundancia en La Entrega fue $12\ 166 \pm 25$ individuos y $2\ 675 \pm 33$ individuos en Isla Montosa. Se registró una relación positiva de la densidad con la salinidad y negativa con la temperatura en Isla Montosa, mientras que en La Entrega ninguna variable ambiental se relacionó significativamente con la densidad. La distribución espacial fue agregada en ambas localidades con oscilaciones en la intensidad de agregación. La mortalidad mensual fue 0.1 en La Entrega y 0.15 en Isla Montosa. Los resultados indican mejores condiciones para la población de *D. mexicanum* en La Entrega en comparación con Isla Montosa, donde las condiciones oceanográficas son más severas y la tasa de sedimentación es más alta, asociada a la cercanía del Río Copalita.

Palabras clave: Echinodermata, Echinoidea, ecología poblacional, Pacífico Sur mexicano, erizo negro.

REFERENCES

- Alvarado, J. J. (2008). Seasonal occurrence and aggregation behavior of the sea urchin *Astropyga pulvinata* (Echinodermata: Echinoidea) in Bahía Culebra Costa Rica. *Pacific Science*, 62, 579-592.
- Alvarado, J. J. & Fernández, C. (2005). Equinodermos del Parque Nacional Marino Ballena, Pacífico, Costa Rica. *Revista de Biología Tropical*, 53(Supl. 3), 275-284.
- Alvarado, J. J. & Chiriboga, A. (2008). Distribución y abundancia de equinodermos en las aguas someras de la Isla de Coco, Costa Rica (Pacífico Oriental). *Revista de Biología Tropical*, 56(Supl. 2), 99-111.
- Atrill, M. J., & Kelmo, F. (2007). Opportunistic responses of *Diadema antillarum* (Echinodermata: Echinoidea) populations following the 1997-98 El Niño event in Bahía, Brazil. *Estuarine and Coastal Shelf Science*, 73, 243-248.
- Bauer, J. C. (1976). Growth, aggregation and maturation in the echinoid, *Diadema antillarum*. *Bulletin of Marine Science*, 26, 272-277.
- Benítez-Villalobos F., Díaz Martínez, J. P., & Martínez-García, M. (2009). Mass mortality of the sea urchin *Diadema mexicanum* in La Entrega at Bahías de Huatulco, Western Mexico. *Coral Reefs*. 28: 1017.

- Benítez-Villalobos, F., Domínguez, M. T., & López-Pérez, R. A. (2008). Temporal variation of the sea urchin *Diadema mexicanum* population density at Bahías de Huatulco, Western Mexico. *Revista de Biología Tropical*, 56(Suppl. 3), 255-263.
- Berry, R. J. (1967). *Dynamics of the Tortugas (Florida) pink shrimp population* (PhD dissertation). University Microfilms, Ann Arbor, Michigan.
- Campbell, A. C., Coppard, S., D'Abreo, C., & Tudor-Thomas, R. (2001). Escape and aggregation responses of three echinoderms to conspecific stimuli. *The Biological Bulletin*, 201, 175-185.
- Campbell, J., & Russell, M. P. (2004). Acclimation and growth response of the green sea urchin *Strongylocentrotus droebachiensis* to fluctuating salinity. In J. M. Lawrence, & O. Guzmán (Eds.), *Proceedings of the International Conference on Fisheries and Aquaculture* (pp. 110-117). Pennsylvania: DEStech Publication.
- Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs*, 56, 345-363.
- Caso, M. E. (1979). Los equinodermos de la bahía de Mazatlán, Sinaloa. *Anales del Centro de Ciencias del Mar y Limnología Universidad Nacional Autónoma de México*, 6, 197-368.
- Cintra-Buenrostro, C., & Reyes-Bonilla, H. (1998). Los equinodermos (Echinodermata) del arrecife de Cabo Pulmo, Pacífico de México. *Revista de Biología Tropical*, 46, 341-344.
- Clemente, S., & Hernández, J. C. (2008). Influence of wave exposure and habitat complexity in determining spatial variation of the sea urchin *Diadema* aff. *antillarum* (Echinoidea: Diademata) populations and macroalgal cover (Canary Islands - Eastern Atlantic Ocean). *Revista de Biología Tropical*, 56(Suppl. 3), 229-254.
- Eakin, C. M. (2001). A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bulletin of Marine Science*, 69, 171-186.
- Eakin, C. M. (1996). Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs*, 15, 109-119.
- Ebert, T. A. (1982). Life history, and relative body wall size in sea urchins. *Ecological Monographs*, 52, 353-394.
- Edgar, G. J., Banks, S. J., Fariña, M., & Martínez, C. (2004). Regional biogeography of shallow reef fish and macro-invertebrate communities in Galapagos Archipelago. *Journal of Biology*, 31, 1107-1124.
- Edmunds, P. J., & Carpenter, R. C. (2001). Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceeding of the National Academy of Sciences*, 98, 5067-5071.
- Espino-Barr, E., Cibrián, R. R., & García-Boa, A. (1996). Estructura y densidad de la población del erizo tinta *Diadema mexicanum* en el litoral rocoso del estado de Colima. *Ciencia Pesquera*, 2, 60-67.
- Fernández-Álamo, M. A., & Färber-Lorda, J. (2006). Zooplankton and the oceanography of the eastern tropical Pacific: A review. *Progress in Oceanography*, 69, 118-359.
- Forcucci, D., & Lawrence, J. M. (1986). Effect of low salinity on the activity, feeding, growth and absorption efficiency of *Luidia clathrata* (Echinodermata: Asteroidea). *Marine Biology*, 92, 315-321.
- Glynn, P. W., & Leyte-Morales, G. E. (1997). Coral reefs of Huatulco, West Mexico: reef development in upwelling Gulf of Tehuantepec. *Revista de Biología Tropical*, 45, 1033-1047.
- Glynn, P. W., Veron, J. E. N., & Wellington, G. M. (1996). Clipperton Atoll (eastern Pacific): Oceanography, geomorphology, reef-building coral ecology and biogeography. *Coral Reefs*, 15, 71-99.
- Granja-Fernández, M. R., & López-Pérez, R. A. (2008). Sedimentación en comunidades arrecifales de las Bahías de Huatulco, Oaxaca, México. *Revista de Biología Tropical*, 56, 1179-1187.
- Guzmán, H. M. (1988). Distribución y abundancia de organismos coralívoros en los arrecifes coralinos de la isla del Caño, Costa Rica. *Revista de Biología Tropical*, 36, 191-207.
- Hamel, J. F., & Mercier, A. (1995). Prespawning behavior, spawning and development of the brooding starfish *Leptasterias polaris*. *The Biological Bulletin*, 188, 32-45.
- Hernández-Ballesteros, L. M. (2002). *Aspectos biológicos que afectan la estructura de la comunidad de los corales zooxantelados (Anthozoa: Scleractinia) en el arrecife de la Entrega, Bahías de Huatulco, Oaxaca, México* (Tesis de maestría). Universidad del Mar, Puerto Ángel, Oaxaca, México.
- Hernández, J. C. (2006). *Estrategia reproductiva de la población canaria del erizo Diadema aff. antillarum Philippi, 1845: maduración gonadal, asentamiento larvario y reclutamiento* (Tesis de doctorado). Universidad de la Laguna, Tenerife, Islas Canarias.
- Herrera-Escalante, T., López-Pérez, R. A., & Leyte-Morales, G. E. (2005). Bioerosion caused by the sea urchin *Diadema mexicanum* (Echinodermata: Echinoidea) at Bahías de Huatulco, Western Mexico. *Revista de Biología Tropical*, 53(Suppl. 3), 263-273.
- Hickman, C. P. (1998). *A field guide to sea stars and other echinoderms of Galapagos*. Lexington, Virginia, USA: Sugar Spring Press.

- Holguin-Quiñónez, O., Wrigth-López, H., & Solís-Marín, F. A. (2000). Asteroidea, Echinoidea y Holothuroidea en fondos someros de la Bahía de Loreto, Baja California Sur, México. *Revista de Biología Tropical*, 48, 749-757.
- Hooker, Y., Solís-Marín, F. A., & Llellish, M. (2005). Equinodermos de las Islas Lobos de Afuera (Lambayeque, Perú). *Revista Peruana de Biología*, 12, 77-82.
- Hyman, L. H. (1955). *The Invertebrate: Echinodermata. The coelomate bilateria* (Vol. IV). New York, USA: McGraw-Hill.
- Irlandi, E., Maciá, S., & Serafy, J. (1997). Salinity reduction from freshwater canal discharge: effects on mortality and feeding of an urchin (*Lytechinus variegatus*) and a gastropod (*Lithopoma tectum*). *Bulletin of Marine Science*, 61, 869-879.
- Krebs, J. C. (1999). *Ecological Methodology*. Vancouver, USA: Addison-Wesley Educational Publishers, Inc.
- Lessios, H. A. (1981). Reproductive periodicity of the echinoid *Diadema* and *Echinometra* on the two coasts of Panama. *Journal of Experimental Marine Biology and Ecology*, 50, 47-61.
- Lessios, H. A., Kessing, B. D., & Pearse, J. S. (2001). Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution*, 55, 955-975.
- Levitán, D. R. (1988). Asynchronous spawning and aggregation behavior in the sea urchin *Diadema antillarum* (Philippi). In R. Burke, P. V. Mladenov, P. Lambert, & P. L. Parsley (Eds.), *Echinoderm Biology. Proc 6th International Echinoderm Conference* (pp. 181-186). Balkema: Rotterdam.
- Lewis, J. B. (1996). Growth and breeding in the tropical echinoid *Diadema antillarum* Philippi. *Bulletin of Marine Science*, 16, 151-158.
- Leyte-Morales, G. E. (2001). *Estructura de la comunidad de corales y características geomorfológicas de los arrecifes coralinos de las Bahías de Huatulco, Oaxaca, México* (Tesis de licenciatura). Universidad del Mar, Puerto Ángel, Oaxaca, México.
- López-Pérez, R. A., Hernández-Ballesteros, L. M., & Herrera-Escalante, T. (2002). Cambio en la dominancia de la comunidad arrecifal en Chachacual, Bahías de Huatulco, Oaxaca, México. *Ciencia y Mar*, 16, 33-38.
- Ludwig, J. A., & Reynolds, J. F. (1988). *A primer on methods and computing*. New York: John Wiley.
- Mendenhall, W. & Reinmuth, J. E. (1978). *Estadística para administración y economía*. Wadsworth International Iberoamericana.
- Morisita, M. (1962). Iδ-Index, A Measure of Dispersion of Individuals. *Researches on Population Ecology*, 4, 1-7.
- Neira, R. & Cantera, J. R. (2005). Composición taxonómica y distribución de las asociaciones de equinodermos en los ecosistemas litorales del Pacífico Colombiano. *Revista de Biología Tropical*, 53(Supl. 3), 195-206.
- Pearse, J., & Arch, S. W. (1969). The aggregation behavior of *Diadema* (Echinodermata, Echinoidea). *Micronesica*, 5, 165-171.
- Pennington, T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., & Chavez, F. P. (2006). Primary production in the eastern tropical Pacific: A review. *Progress in Oceanography*, 69, 285-317.
- Pia, T. S., Johnson, T., & George, S. B. (2012). Salinity-induced morphological changes in *Pisaster ochraceus* (Echinodermata: Asteroidea) Larvae. *Journal of Plankton Research*, 34, 590-601.
- Ramos-Cruz, S., Sánchez-Meraz, B., Carraco-Ayuso, F., & Cervantes-Hernández, P. (2006). Estimación de la tasa de mortalidad natural de *Farfantepenaeus californiensis* (Holmes, 1900) y *Litopenaeus vannamei* (Boone, 1931) en la zona costera del Golfo de Tehuantepec, México. *Revista de Biología Marina y Oceanografía*, 41, 221-229.
- Randall, J. E., Schroeder, R. E., & Starck, W. A. (1964). Notes on the biology of the echinoid *Diadema antillarum*. *Caribbean Journal of Science*, 4, 421-433.
- Reyes-Bonilla, H. (1995). Asteroidea and Echinoidea (Echinodermata) from Isla San Benedicto, Revillagigedo Archipelago, Mexico. *Ciencias Marinas*, 6, 29-38.
- Rodríguez, A., Hernández, J. C., Clemente, S., & Coppard, S. E. (2013). A new species of *Diadema* (Echinodermata: Echinoidea: Diadematidae) from the eastern Atlantic Ocean and a neotype designation of *Diadema antillarum* (Philippi, 1845). *Zootaxa*, 3636, 144-170.
- Shumway, S. E. (1977). The effects of fluctuating salinities on four species of asteroid echinoderms. *Comparative Biochemistry and Physiology*, 58, 177-179.
- Zamorano-de Haro, P. (2004). *Evaluación de la Comunidad Actual de Moluscos y Equinodermos Asociados al Coral *Pocillopora damicornis* y Comparación con la Comunidad de 1994, en el arrecife de La Entrega, Huatulco* (Tesis). Universidad del Mar, Puerto Ángel, Oaxaca, México.
- Zamorano, P. & Leyte-Morales, G. E. (2005). Densidad poblacional de cuatro especies de erizo (Echinodermata: Echinoidea) en el arrecife La Entrega, Oaxaca. *Océanides*, 20, 65-72.
- Zamorano, P. & Leyte-Morales, G. E. (2009). Equinodermos asociados a formaciones arrecifales en Zihuatanejo y Acapulco, Guerrero, México. *Boletín de Investigaciones Marinas y Costeras*, 38, 7-28.
- Zippin, C. (1958). The removal method of population estimation. *The Journal of Wildlife Management*, 22, 82-92.