



Density, size, and biomass of *Diadema mexicanum* (Echinoidea) in Eastern Tropical Pacific coral reefs

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ABSTRACT: *Diadema* is among the most abundant, widely dispersed, and ecologically important genera of sea urchin in tropical shallow waters. *D. mexicanum* is distributed from the Gulf of California to northern Peru, including the oceanic islands of Revillagigedo, Clipperton, Coco, Malpelo, and Galápagos, and it is one of the most important sea urchin species in Eastern Tropical Pacific (ETP) coral reefs. In the 1980s, El Niño caused high coral mortality, resulting in an increase in macroalgal cover. This resulted in higher sea urchin bioerosion activity, which weakened the reef frameworks. Considering the high vulnerability of the ETP coral reefs, the aim of this study was to determine regional differences in the density, size (test diameter), and biomass of *D. mexicanum* at 12 localities in 4 countries between 2009 and 2010, and to determine possible causes of these differences. The average density, size, and biomass of *D. mexicanum* were 0.47 ± 0.15 ind. m^{-2} , 4.38 ± 1.50 cm, and 0.26 ± 0.33 g m^{-2} . The test size frequency that predominated was 2 to 3 cm. Predation by macrophagous fishes seems to be one of the most important factors that explains the presence of low densities and small size of sea urchins throughout the region. The increase in *D. mexicanum* predators is probably a result of overfishing of top predators.

KEY WORDS: Marine protected area · Biomass · Organic matter · Overfishing · Shelter

INTRODUCTION

Diadematidae constitutes one of the most important sea urchin families. The ability of species in this family to occupy different niches, associated with their generalist diet, is an important factor that explains their success in coral reefs (Birkeland 1989). They have an important role in reef areas due to their effect on algal biomass, structure, and distribution, as well as in the composition of coral reef and reef geomorphology (Sammarco et al. 1974, Sammarco 1980, 1982a,b, Scoffin et al. 1980, Birkeland 1989). *Diadema* is among the most abundant, widely dispersed, and ecologically important genera of sea urchin in tropical shallow waters (Lessios et al. 2001).

D. antillarum is one of the most studied tropical sea urchins because of its role in Caribbean coral reefs

before and after its mass mortality in 1983 (Ogden 1977, Scoffin et al. 1980, Sammarco 1980, 1982a,b, Bak et al. 1984, Hughes et al. 1987). Its high densities were probably a result of overfishing of its predators (Hay 1984), and its feeding on algae resulted in a greater availability of substrates for coral settlement and recruitment (Sammarco 1980, 1982a, Carleton & Sammarco 1987). After the mass mortality event, along with other disturbances (Mumby et al. 2006), a phase shift began to be noticed in the Caribbean reefs (Hughes 1994, Bellwood et al. 2004, Bruno et al. 2009).

D. mexicanum plays a prominent role in Eastern Tropical Pacific (ETP) reefs, as has been shown off the western coast of Panama by Glynn (1988) and Eakin (1992, 1996, 2001). After the El Niño event of 1982–1983, its population densities changed from 3

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to 50–150 ind. m⁻². The result of this increase was a significant erosion of the reef framework (Glynn 1988, Eakin 1996, 2001). At Isla del Coco, Costa Rica, an increase in density was seen in *D. mexicanum* (Guzman & Cortés 1992), causing similar effects to those in Panama. However, for most of the ETP, the impact of bioerosion by *D. mexicanum* was not documented. Over time, interest in understanding the status of *D. mexicanum* populations has increased in the ETP, resulting in more data on population density for a variety of sites (e.g. Glynn et al. 1996, Eakin 2001, Edgar et al. 2004, Herrera-Escalante et al. 2005, Guzman & Cortés 2007, Alvarado & Chiriboga 2008, Benítez-Villalobos et al. 2008). However, many of these studies were conducted using different methodologies and focused on the density of sea urchins without providing further information on size, biomass or other factors that affect their populations.

Here we describe for the first time, with a regional focus, the population density, test size, and biomass distribution of *D. mexicanum* in the ETP. These variables are key to understanding ecological processes in coral reefs such as herbivory and bioerosion (Bak 1994, Carreiro-Silva & McClanahan 2001). We applied a standard methodology at 12 localities off the west coasts of Mexico, El Salvador, Costa Rica, and Panama to address the following questions: (1) Are there differences in the population density, test size, and biomass of *D. mexicanum* between localities, biogeographic provinces, or conservation strategies? (2) If there are differences, what are the most probable causes?

MATERIALS AND METHODS

This study was carried out at 12 localities with coral reefs in the ETP (Fig. 1). These included continental, peninsular, and insular environments, both protected (national parks or biological reserves) and non-protected areas (Table S1 in the Supplement at www.int-res.com/articles/suppl/b024p151_supp.pdf). For 2 additional sites, information from the Archipiélago de Revillagigedo (Mexico) was provided by the Reef Systems Laboratory <http://lavisauabcs.blogspot.com/> of the Universidad Autónoma de Baja California Sur (45 transects surveyed in April 2012 in the Socorro Islands, Roca Partida, and San Benedicto), and for the Galápagos Islands (Ecuador) by the Charles Darwin Foundation <http://www.darwinfoundation.org/es/investigacion/investigacion-marina/> (40 transects surveyed in March 2000 and May 2001, at the Darwin and Wolf Islands).

At each locality (A–L, Fig. 1), 3 sites were sampled (i.e. A1, A2, A3, etc.), with the exception of the Coiba and Perlas archipelagos, where 5 sites were sampled, and Carrizales and Marietas, where 2 sites were sampled due to the size of the study area. At each site, the density of *Diadema mexicanum* was quantified along 3 transects (10 × 2 m; total sampled area of 60 m²) parallel to the coast in the forereef area, between 4 and 8 m depth. This was done without removing any live coral colony or destroying any reef structure.

In each transect, test diameters of a minimum of 50 sea urchins were measured using Vernier calipers (0.01 cm). The biomass of *D. mexicanum* was calculated using the regression reported by Hernández et al. (2008) for *D. africanum*:

$$DW = 0.00913 \times (TD^{2.57867}) \quad (1)$$

where DW is the sea urchin dry weight (g ind.⁻¹) and TD is the test diameter (mm).

The average DW of urchins per site was multiplied by density at the site to calculate the biomass (g m⁻²). The biomass represents a standard measurement for all sea organisms and allows a simultaneous analysis across major taxonomic groups of coral reefs. This approximation is not possible with traditional abundance or coverage measures (Newman et al. 2006).

One-way ANOVA was performed to determine differences between the localities in terms of urchin density, size, and biomass (Bakus 2007). To evaluate differences between biogeographic provinces, the sites were grouped *a priori* according to the classification by Briggs (1974) (Fig. 2). The 2 sites of the Cortezian province (Isla Espíritu Santo and Cabo Pulmo) were included in the Mexican province (Islas Marietas, Carrizales, Ixtapa-Zihuatanejo, and Huatulco). The other provinces were Panamic (Los Cóbano, Bahía Culebra, Isla del Caño, Isla Coiba, and Archipiélago Las Perlas) and Oceanic Islands (Archipiélago de Revillagigedo, Isla del Coco, and Darwin and Wolf). A similar analysis was done by levels of protection: (1) marine protected areas (MPAs) without fisheries (no-take MPAs: Isla del Coco, Isla del Caño, Darwin and Wolf, and Revillagigedo); (2) MPAs with fisheries (take MPAs: Isla Espíritu Santo, Cabo Pulmo, Islas Marietas, Huatulco, Los Cóbano, Coiba, and Las Perlas); and (3) non-protected areas (non-MPAs: Carrizales, Ixtapa-Zihuatanejo, Bahía Culebra). One-way ANOVA tests were performed using the biogeographic province and the level of protection as factors, and density, size, and biomass as variables. In the case of any significant differences, *a posteriori* Tukey tests were

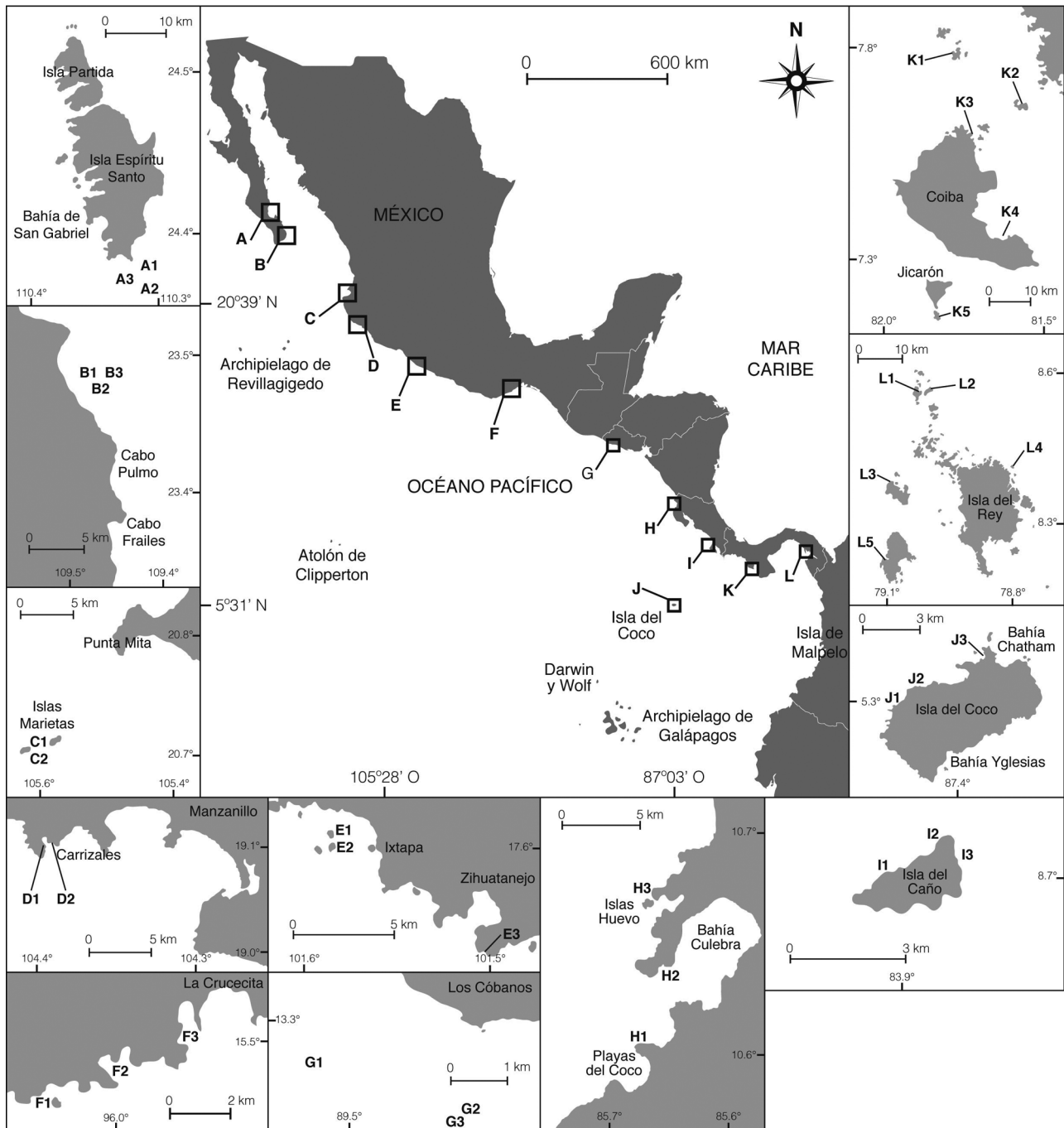


Fig. 1. Localities sampled in the Eastern Tropical Pacific (ETP). A: Isla Espíritu Santo; B: Cabo Pulmo; C: Marietas; D: Carrizales; E: Ixtapa-Zihuatanejo; F: Huatulco; G: Los Cóbano; H: Bahía Culebra; I: Isla del Caño; J: Isla del Coco; K: Isla Coiba; L: Archipiélago Las Perlas

performed to determine which provinces explain the differences. For the analysis of density and biomass, Bahía Culebra was excluded because the extreme values of this locality are the result of a recent recruitment due to the deteriorating environmental conditions of the area (Alvarado et al. 2012).

The frequency distribution of test diameters was compared using a chi-squared test. A Bray-Curtis similarity index was calculated with the standardized data to construct an average clustering dendrogram and a non-metric multidimensional scaling (nMDS) (Clarke & Gorley 2006). In this case, the factors were

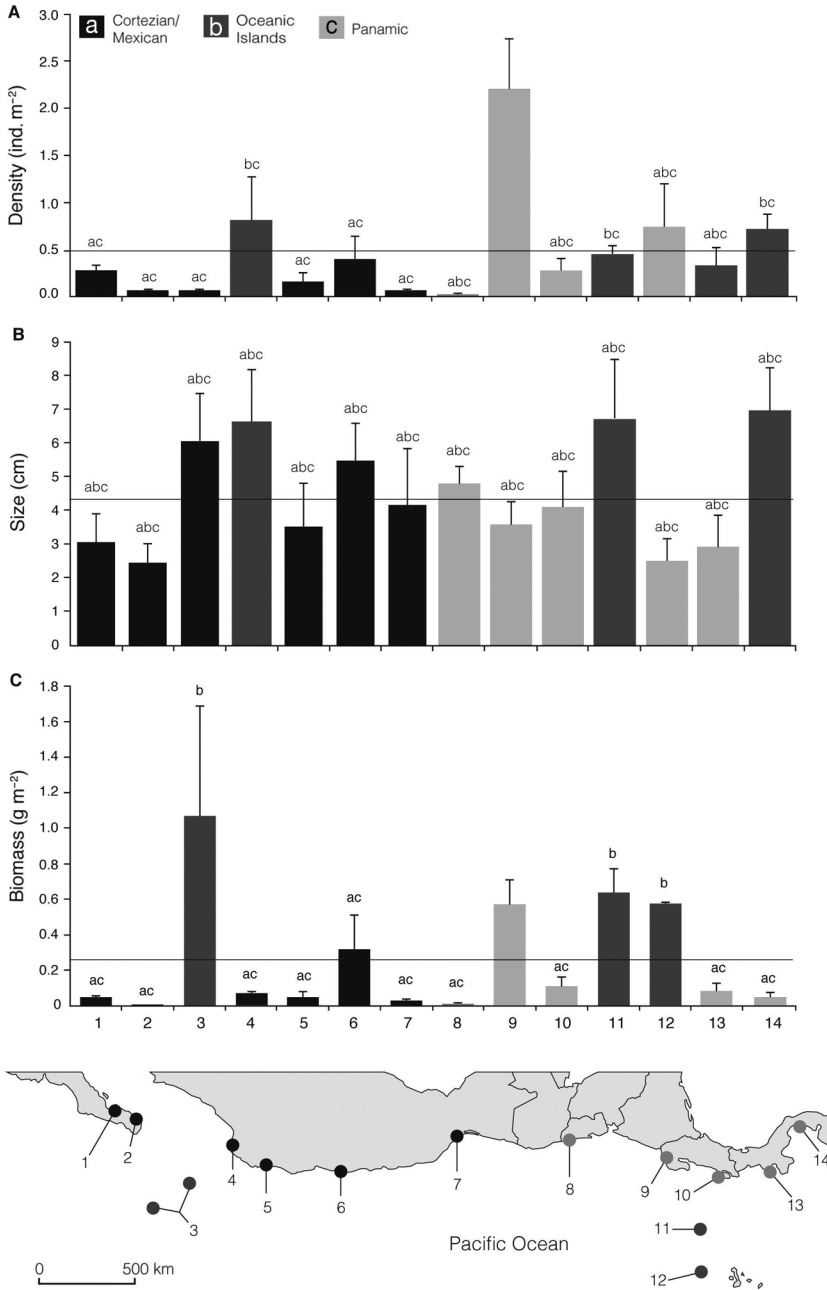


Fig. 2. (A) Density, (B) test size, and (C) biomass of *Diadema mexicanum* along the Eastern Tropical Pacific. (D) Study areas: (1) Isla Espíritu Santo, (2) Cabo Pulmo, (3) Archipiélago de Revillagigedo, (4) Islas Marietas, (5) Carrizales, (6) Ixtapa-Zihuatanejo, (7) Huatulco, (8) Los Cóbanos, (9) Bahía Culebra, (10) Isla del Caño, (11) Isla del Coco, (12) Darwin and Wolf, (13) Coiba, and (14) Archipiélago Las Perlas. Sites allocated to 3 biogeographic provinces (a: Cortezian-Mexican, b: oceanic islands, and c: Panamic) according to Briggs (1974). The horizontal line represents the average. Error bars: SE. Means with different letters are significantly different at $p < 0.05$ (Tukey's post-hoc test)

biogeographic province (Cortezian-Mexican, Panamic, and Oceanic Islands) and the level or protection (0: non-protected areas; I: no-take MPAs; and II: take MPAs). An ANOSIM was done to determine

differences between the provinces. These analyses were performed using PRIMER 6.0 software (Clarke & Gorley 2006).

RESULTS

In total, 114 transects were surveyed (2280 m²), along which 9307 sea urchins were counted and test diameters of 1600 individuals were measured. The average density (\pm SE) of *Diadema mexicanum* in the ETP was 0.47 ± 0.15 ind. m⁻², being highest in Bahía Culebra (2.19 ± 0.57 ind. m⁻²) and lowest in Los Cóbanos (0.02 ± 0.01 ind. m⁻²; $F_{13,185} = 4.557$, $p < 0.001$; Fig. 2A). The Cortezian-Mexican Province had the lowest densities (0.19 ± 0.15 ind. m⁻²), followed by the Panamic Province (0.35 ± 0.30 ind. m⁻²), while the Oceanic Islands had the highest density (0.66 ± 0.19 ind. m⁻²; $F_{2,10} = 5.465$, $p < 0.025$). Sea urchin density was higher in non-MPAs (0.91 ± 1.11 ind. m⁻²), followed by no-take MPAs (0.57 ± 0.24 ind. m⁻²) and take MPAs (0.23 ± 0.36 ind. m⁻²; $F_{2,11} = 1.883$, $p = 0.198$; Fig. 3).

Sea urchin average size (\pm SE) was 4.38 ± 1.50 cm, with the maximum at Isla del Coco (6.71 ± 0.16 cm) and the minimum in Cabo Pulmo (2.39 ± 0.08 cm; $F_{13,185} = 22.381$, $p < 0.001$; Fig. 2B). The largest individual was found at Isla del Coco (12.30 cm), while the smallest was found at Carrizales (0.37 cm). The average size of the sea urchins in no-take MPA localities was 5.77 ± 1.22 cm, 4.11 ± 1.11 cm in non-MPAs, and 3.67 ± 1.36 cm in take MPAs ($F_{2,11} = 3.459$, $p = 0.068$; Fig. 3).

Test diameters ranged from 0.37 to 12.30 cm (Fig. 4). In general, most sizes were 2–3 cm ($n = 406$), 3–4 cm ($n = 300$), and 4–5 cm ($n = 229$). Sizes classes 1–2, 5–6, 6–7, and 7–8 cm included between 200 and 100 individuals each, while the rest of the sizes were represented by fewer than 10 individuals. In the majority of localities, except for Isla del Coco, Revillagigedo, Darwin and Wolf, and Marietas, sea urchins were small ($\chi^2 = 1795.46$, $df = 156$, $p < 0.001$). Isla del Coco was the

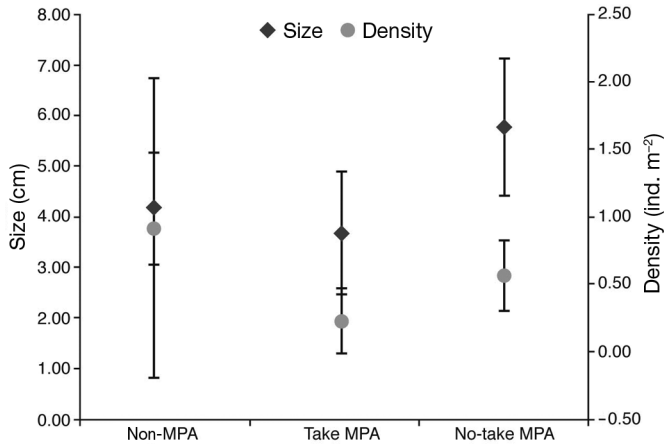


Fig. 3. Mean (\pm SD) test size and density of *Diadema mexicanum* by management category in the sampling localities in the Eastern Tropical Pacific. Non-MPA: non-marine protected area; take MPA: MPA with fishery; no-take MPA: MPA without fishery

only locality that had a high range of size intervals (10). Cabo Pulmo had only 3, Los C6banos 4, Esp3ritu Santo, Isla del Ca6no, and Las Perlas 5, Ixtapa-Zihuatanejo and Bah3a Culebra 6, Carrizales 7, and Marietas had 8 (Fig. 4).

The size frequencies grouped the localities in 4 sets with 60% similarity (Fig. 5A,B): (1) Isla del Coco, Darwin and Wolf, Archipi3lago de Revillagigedo, and Marietas; (2) Los C6banos and Ixtapa-Zihuatanejo; (3) Bah3a Culebra, Isla del Ca6no, Carrizales, and Huatulco; and (4) Las Perlas, Coiba, Isla Esp3ritu Santo, and Cabo Pulmo. Group 1, the larger sizes (6–12 cm), includes all the localities that belong to the Oceanic Islands Province, that are no-take MPAs and 1 locality from the Cortezian-Mexican Province that is a take MPA. The other groups included a mixture of biogeographic provinces. Group 2 included a take MPA and a non-protected area, while group 3

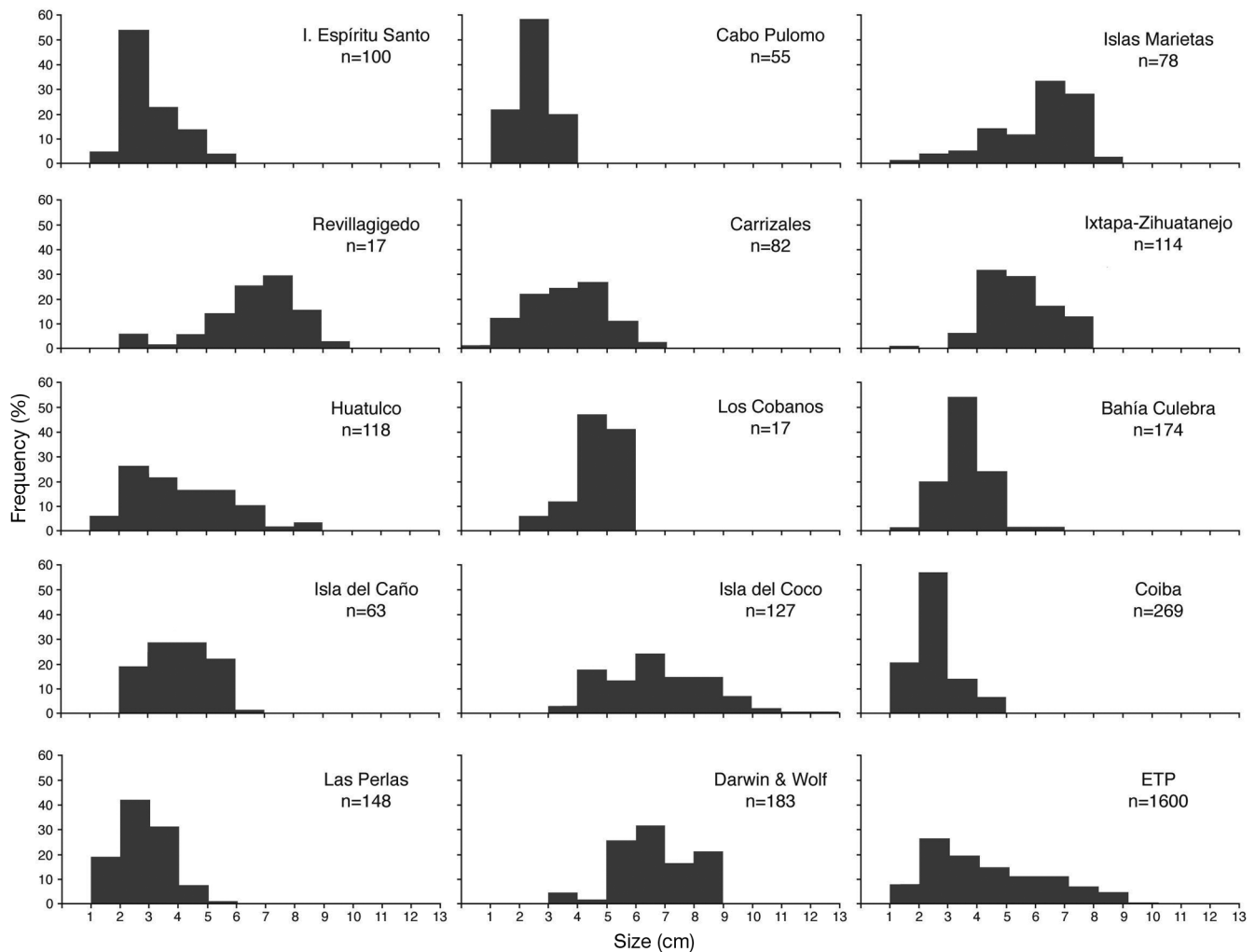


Fig. 4. Test size frequency of *Diadema mexicanum* in the study areas along the Eastern Tropical Pacific. n: number of sea urchins measured

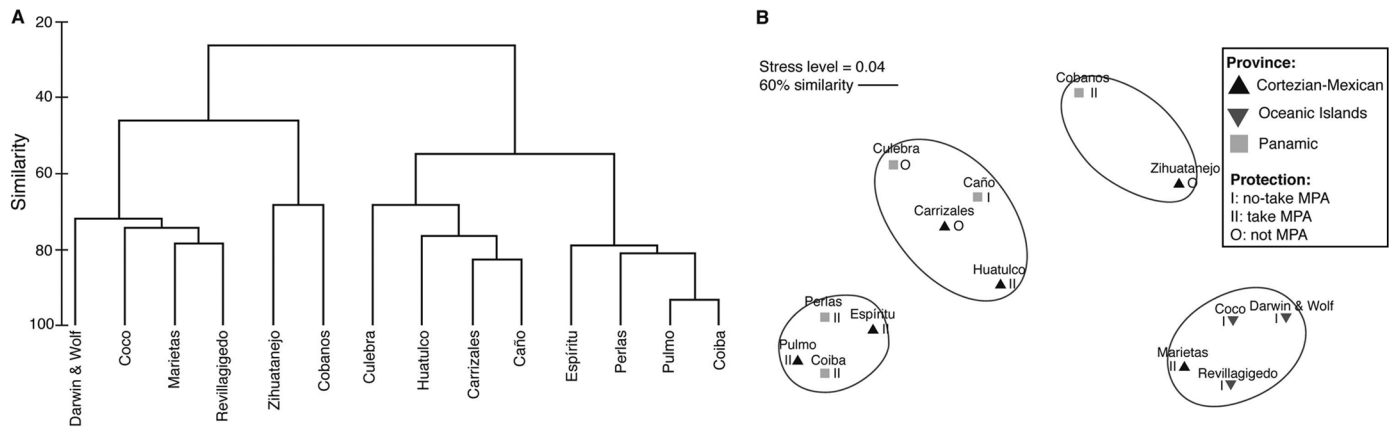


Fig. 5. (A) Single linkage dendrogram and (B) non-metric multidimensional scaling (nMDS) established from a Bray-Curtis similarity index of the frequency distribution of test diameter of *Diadema mexicanum* in the study localities. MPA: marine protected area

included all levels of protection. Group 4, however, included only localities that are take-MPAs. This last group had the smallest sizes (2–4 cm), while groups 2 and 3 had sizes between 3 and 5 cm (ANOSIM, $R = 0.298$, $p < 0.05$).

Sea urchin average biomass (\pm SE) was 0.26 ± 0.33 g m^{-2} , with the maximum at Revillagigedo (1.07 ± 1.52 g m^{-2}) and the minimum at Cabo Pulmo and Los C6banos (0.01 ± 0.01 g m^{-2} , for both localities; $F_{13,185} = 4.433$, $p < 0.001$; Fig. 2C). Significant differences were also found between the biogeographic provinces ($F_{2,10} = 24.750$, $p < 0.001$; Bahía Culebra excluded), the 2 continental provinces being different from the Oceanic Province ($p < 0.001$).

DISCUSSION

Global patterns

The average *Diadema mexicanum* density in the ETP was 0.47 ± 0.15 ind. m^{-2} (min.: 0.02, max.: 2.19 ind. m^{-2}), which is intermediate compared to other reef regions harboring the genus *Diadema* (Table S2 in the Supplement at www.int-res.com/articles/suppl/b024p151_supp.pdf). Low densities (<0.10 ind. m^{-2}) have been found in Fiji, Australia, and Hawaii (Coppard & Campbell 2007, Vermeij et al. 2010, Young & Bellwood 2011). Intermediate densities (0.1–1.0 ind. m^{-2}) have been found in Fiji, Cuba, and the ETP (Coppard & Campbell 2007, Martín Blanco et al. 2010, this study), and high densities (>1.0 ind. m^{-2}) have been found in the Caribbean, Brazil, the Canary Islands, and Kenya (Table S2). The highest densities in the Caribbean (71–100 ind. m^{-2} ; Table S2)

occurred prior to the 1983 mass mortality of *D. antillarum* (Sammarco 1980). As stated by Hay (1984), these high densities were likely the result of the lack of sea urchin predators caused by overfishing. Moreover, the reefs during the 1970s and the early 1980s were structurally more complex, providing shelter to sea urchins (Haley & Solandt 2001, Lee 2006, Álvarez-Filip et al. 2009). Other localities with high densities of Diadematidae such as Kenya (5.7 ind. m^{-2} ; McClanahan & Shafir 1990) and the Canary Islands (2.82 ind. m^{-2} ; Hernández et al. 2008), lack sea urchin predators due to overfishing.

Sammarco (1985) indicated that in the Great Barrier Reef in Australia, the densities of sea urchins are insignificant (i.e. *D. setosum*: 0.06–0.76 ind. m^{-2}). Clark (1938) stated that the sea urchins are conspicuously absent from the Great Barrier Reef. Unlike the Caribbean where overfishing produced high densities of *D. antillarum* (Hay 1984), fishing in the Great Barrier Reef has been more specific and directed toward Serranidae, Lutjanidae, and Lethrinidae (Sammarco 1985). This specific type of fishing probably allowed more predatory fish species to survive, resulting in low sea urchin abundances. This may suggest a similar situation in the ETP with *D. mexicanum*.

Biomasses of *D. mexicanum* in the ETP were lower than those of other *Diadema* species in Tanzania (*D. savignyi*: 54.2 g m^{-2} ; *D. setosum*: 4.3 g m^{-2}), but similar to those found in protected areas in Kenya (*D. savignyi*: 0.03 g m^{-2} ; *D. setosum*: 0.09 g m^{-2} ; Muthiga & McClanahan 2007). In the Canary Islands, *D. africanum* had high biomass in fishing areas (81.6 g m^{-2}) compared to protected areas (2.41 g m^{-2} ; Hernández et al. 2008).

Survivorship and predation

The abundance of macrophagous fish associated with the unavailability of shelter are the factors that seem to explain the density, size, and biomass distribution of *D. mexicanum* in the ETP. It is likely that overfishing of top predatory fish has allowed populations of macrophagous predators to increase. Predation can alter the structure of the communities and ecosystem functions (Hairston et al. 1960, Duffy & Hay 2000), reflecting its influence on the distribution and abundance of prey organisms (Paine 1966, Levitan & Genovese 1989) and on community structure (Clemente & Hernández 2007). Fish predation is one of the most likely causes of differences in size distribution, abundance, and foraging behavior in sea urchins (Birkeland 1989, Sala & Zabala 1996, Guidetti 2007, Coma et al. 2011). However, other factors such as recruitment, competition, diseases, and physical factors may be equally important (Sala 1997, Coma et al. 2011).

Pocillopora reefs (of low complexity) provide very little shelter for sea urchins, compared to reefs that have a greater presence of massive species like *Porites lobata* (of higher complexity) (Palacios & Zapata 2014) (Fig. S1 in the Supplement). In most continental localities, *Pocillopora* reefs dominate, whereas in oceanic islands there is a greater presence of *P. lobata* reefs. As sea urchins grow, they cannot use small shelters such as those provided by *Pocillopora* reefs and become more exposed to predation (Sala & Zabala 1996). More structurally complex reefs provide shelter from predation, and *Diadema* can have higher densities and attain larger sizes (Haley & Solandt 2001), finally reaching a size large enough to escape from predators (Sala & Zabala 1996, Sala 1997). Also, sea urchin populations are small under high predator abundance (McClanahan & Sala 1997), and small increases in fish biomass dramatically reduce sea urchin biomass (Harborne et al. 2009).

The decrease in top predators combined with eutrophication can have drastic impacts on lower trophic levels by generating cascading changes in the composition of herbivores (Sieben et al. 2011). Overfishing of top carnivorous fish (snappers, groupers, sharks) has resulted in an increase in lower trophic level carnivores that prey on sea urchins. This would explain the predominance of small-sized sea urchins in several reefs where they can hide from predators.

The preferential predation on small sea urchins can result in urchins not reaching adult sizes. The most important predators of *D. africanum* in the

Canary Islands prefer sizes between 3 and 5 cm (Clemente et al. 2010). With *D. mexicanum*, we infer that the presence of small or juvenile sea urchins (Fig. 4) is the result of high predation pressure. In environments with moderate- or large-sized urchins, shelters are important as they allow urchins to reach 'escape sizes' (Sala 1997), after which they experience reduced predation (Clemente et al. 2010).

The size frequencies of *D. mexicanum* reported in this study (Fig. 4) represent very specific moments in time. There are 2 possible explanations: (1) they reflect specific settlement events of new recruits, explaining why predominantly small sizes are observed, or (2) they may reflect a pattern typical of the region. Thus, the sizes are the result of other effects such as over-fishing, predators, MPA enforcement, or a non-quantified combination of all of these factors. Whereas several factors influence the presence of sea urchins, such as recruitment, shelter availability, and physical conditions, predation is among the key factors controlling sea urchin populations (Guidetti 2007). It is important to focus on the maximum sizes observed, because they are an excellent indicator not influenced by recruitment events (Ebert 2010). The oceanic localities of the ETP, including Islas Marietas (Fig. 5B), had a higher number of large individuals (6–12 cm; Fig. 4). Size distribution can provide indirect evidence of intensity of predation on sea urchins (Behrens & Lafferty 2004). A bimodal distribution of frequencies occurs when there are spatial shelters against predation for the small sizes and a shelter in size for the larger ones. When sea urchin predators are less abundant, sea urchins have a normal distribution. This type of distribution is found in fished areas, while bimodal frequencies are found in protected areas (Behrens & Lafferty 2004).

In the ETP, 7 species of predators of *D. mexicanum* have been reported (*Arothron meleagris*, *A. hispidus*, *Diodon holocanthus*, *Bodianus diplotaenia*, *Pseudobalistes naufragium*, *Balistes polylepis*, and *Sufflamen verres*; Glynn et al. 1972, Guzman 1988, Eakin 2001). The abundance of these fishes can be a limiting factor for the presence of sea urchins at Isla del Caño, resulting in their cryptic behavior (Guzman 1988). In Cabo Pulmo, sea urchins are the second most important item in the diet of the puffer *A. meleagris* (26.3%), but higher in smaller fishes (9–15 cm, 38.0%) (Moreno et al. 2009). At Isla Espíritu Santo, coral coverage, sea surface temperature, and the interaction between substrate heterogeneity and the abundance of Labridae, specifically the Mexican hogfish *B. diplotaenia*, explained 50.3% of sea urchin

density (Rojero-León 2009). The author stated that environmental variables have a greater effect on sea urchin density than predation, but when the environmental effects decrease, predation by the triggerfish *B. polylepis* seems to be stronger. In the majority of the localities studied in this research, for which information about fish abundance is available, sea urchin predatory species are abundant and common (Dominici-Arosemena et al. 2005, Rodríguez-Romero et al. 2005, Álvarez-Filip et al. 2006, Chávez-Comparán & Macías-Zamora 2006, Dominici-Arosemena & Wolff 2006, Ramírez-Gutiérrez et al. 2007, Benfield et al. 2008).

Trends across management levels

Marine reserves restore populations of predators that reduce sea urchin populations (Harborne et al. 2009), as trophic interactions between sea urchins and their predators are reestablished (McClanahan et al. 1999). Predation in marine reserves with a high abundance of fish predators cannot completely reduce the densities of sea urchins because most of them may be protected in crevices or under large blocks of stone or coral (Hereu et al. 2005). In Fiji, Coppard & Campbell (2007) found a relationship between the quantity and the size of crevices and diadematid distribution. Large sea urchins were found where size and availability of crevices were higher. Small sea urchins were found in areas with small crevices. This may explain why there are larger sea urchins and a larger range of sizes in no-take MPAs located in oceanic islands, compared to take MPAs and localities that are not protected. This same pattern has been observed in other sea urchin species, where large sea urchins are found in protected areas (Shears & Babcock 2002, Tuya et al. 2004). In take MPAs or in areas that are not MPAs, sea urchins cannot reach sizes larger than 4 cm, probably due to predation pressure and lack of shelter for individuals larger than 4 cm.

Low to medium densities of sea urchins have been found in MPAs with high fish densities, while urchin densities were higher in fished areas (Sala & Zabala 1996, Brown-Saracino et al. 2007, Hernández et al. 2008). A similar pattern was found between take and no-take MPAs and localities that are not MPAs (Fig. 3). Nonetheless, in take MPAs, the average density of sea urchins was lower. Tuya et al. (2004) found that the density of *D. antillarum* diminishes as the richness of fish species increases. A low abundance and biomass of predatory fish is associated with high

densities of *D. antillarum*. These fish control the structure of sea urchin populations.

Localities in the ETP with varying levels of protection and management, no-take MPAs, and with a high level of protection (e.g. Isla del Coco) possess a greater biomass of carnivorous fish, low sea urchin densities, and high coral coverage compared to MPAs with limited protection or non-MPAs (Edgar et al. 2011). They found that *D. mexicanum* densities were always higher in no-take MPAs than in take MPAs or fished zones. The highest densities of these sea urchins were found inside no-take MPAs in the oceanic islands, while in the continental localities, densities were lower, being more similar to fishing areas than to take-MPAs. The lowest density values were found in this second category. The authors suggested that the impact of over-fishing on trophic chains has been more intense on the mainland than in the oceanic islands. Similarly, the authors found that certain fish types such as planktivores, herbivores, and some macrophagous predators did not show a significant decrease in their populations in fished areas in relation to no-take MPAs, which differs from what has been reported in other regions such as the Indo-Pacific or the Caribbean. This discrepancy suggests that these species have not been the focus of fisheries in the ETP as they have been in other regions. The consequence of this type of fishing is reflected in the reduction of macroinvertebrate populations in areas with a low protection level. Edgar et al. (2011) stated that the pufferfish *A. meleagris* is more abundant in MPAs with low protection levels than in fishing areas, affecting the sea urchin populations in these localities.

Some take MPAs allow fishing in some parts of the protected areas. Fishing is prohibited in core zones that are small or recently created, where the effect of fishing closure is not yet perceptible. This is an essential aspect in understanding the role of protection of fish populations, and the time that they have had to recover and reach an almost 'pristine' state with unaltered trophic chains. Marine reserves that have been established for over 15 yr have more and larger fish compared to non-protected areas (Molloy et al. 2009). These populations of large fish species take longer to recover because they have larger home ranges that overlap with non-protected areas, but which in turn makes it easier to find and colonize marine reserves. Hence, the older reserves will allow a greater number of recruitment events for this group of fishes (Molloy et al. 2009). In addition, Claudet et al. (2008) stated that by increasing the area of non-fishing zones, the density of commercial fish inside

and outside the marine reserves increases. In marine reserves where populations of sea urchin predators are re-established (Harborne et al. 2009), trophic interactions between sea urchins and their predators are restored (McClanahan et al. 1999). It is likely that in take-MPAs or in the surrounding areas, an increase in the abundance of macroinvertebrate predators is being favored due to more time needed by large predators to reach established populations, as well as by the effect of fishing in the surrounding area. In unprotected areas, fishing may be affecting both top predator populations and macroinvertebrate predators, resulting in higher sea urchin sizes and densities than the ones observed in take MPAs.

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