SUPPLEMENT

**REVISTA DE**
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# Predators of the sea urchin *Diadema mexicanum* (Diadematoida: Diadematidae) at the Eastern Tropical Pacific coral reefs

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ABSTRACT

**Introduction:** The coral reefs of Isla del Coco National Park are some of the most pristine ecosystems on Earth. The sea urchin *Diadema mexicanum* (Diadematoida: Diadematidae) is a common inhabitant with a pivotal role in the ecology of this unique ecosystem.
**Objective:** In this study, we identified the predominant predators of *D. mexicanum* and estimated the predatory consumption rates. We also determined predation rates at different sea urchin sizes and at sites with contrasting refuge availability.
**Methods:** We use field video recording observations and tethering experiments.
**Results:** The balistid *Sufflamen verres* and the labrid *Bodianus diplotaenia* were identified as predators of small and medium size *D. mexicanum*; the labrids *Thalassoma grammaticum* and *B. diplotaenia* (juvenile) and the tetraodontid *Arothron meleagris* were attempted predators; and *Canthigaster punctatissima* and *Holacanthus passer* were scavengers. Larger sea urchins (> 30 mm) were also preyed upon during the tethering experiments. Furthermore, a clear effect of the site on survival of the different sea urchins' sizes was noted. No difference in the sea urchin predator biomass was found among sites, which highlights the importance of site complexity on survival. At high and medium complexity sites, large individuals had better survival, while at the low complexity site, there was almost no differences in survival rates among the three size classes. Our results also show that a high abundance of these predatory fishes, above 0.04 ind m$^{-2}$, guarantees a low sea urchin density. Below this threshold, a higher variability in sea urchin density is observed Despite not being registered with the video recordings, lobsters were observed once preying upon a large sea urchin individual.
**Conclusions:** This study identifies a keystone fish guild with high predation rate for *Diadema* in the National Park, which suggests that protective actions have positively benefited predatory fish and lobster populations.

**Key words:** Balistidae; Labridae; lobsters; Isla del Coco; video; tethering experiment.

RESUMEN

**Depredadores del erizo de mar *Diadema mexicanum* (Diadematoida: Diadematidae)
en los arrecifes de coral del Pacífico Tropical Oriental**

**Introducción:** Los arrecifes de coral del Parque Nacional Isla del Coco son uno de los ecosistemas más prístinos de la Tierra. El erizo de mar *Diadema mexicanum* (Diadematoida: Diadematidae) es un habitante común con un papel ecológico esencial en este ecosistema único.
**Objetivo:** En este estudio, identificamos los depredadores predominantes de *D. mexicanum* y estimamos las tasas de consumos predatorias. También determinamos las tasas predatorias de diferentes tamaños de erizo de mar en sitios con disponibilidad de refugio contrastante.
**Métodos**: Utilizamos grabaciones de video de campo y experimentos de marcaje.
**Resultados:** El pez ballesta *Sufflamen verres* y el lábrido *Bodianus diplotaenia* fueron identificados como depredadores de tamaños pequeños y medianos de *D. Mexicanum*; los lábridos *Thalassoma grammaticum* y *B. diplotaenia* (juvenil) y el tetraodóntido *Arothron meleagris* fueron intento de depredadores; y *Canthigaster punctatissima* y *Holacanthus passer* fueron carroñeros. Los erizos de mar de gran tamaño (> 30 mm) también fueron depredados durante el experimento de marcaje. Además, se encontró un efecto claro del sitio en la supervivencia de los diferentes tamaños de erizo de mar. No se encontraron diferencias en la biomasa de los depredadores del erizo de mar entre sitios, lo que señala la importancia de la complejidad del sitio en la supervivencia. En sitios con complejidad estructural alta y media, los individuos grandes tuvieron mejor supervivencia, mientras que en sitios de complejidad baja apenas hubo diferencias en las tasas de supervivencia entre los tres tamaños. Nuestros resultados también muestran que una alta abundancia de peces depredadores, por encima de 0.04 ind m$^{-2}$, asegura bajas densidades de erizos de mar. A pesar de no ser registrado durante las grabaciones de video, se observó en una ocasión a una langosta depredando sobre un erizo de gran tamaño.
**Conclusiones:** Este estudio identifica el grupo de peces clave con grandes tasas de depredación sobre *Diadema* en el Parque Nacional, lo que sugiere que las medidas de protección han beneficiado positivamente las poblaciones de peces depredadores y langostas.

**Palabras clave:** Balistidae; Labridae; langostas; Isla del Coco; vídeo; experimentos de marcaje.

## INTRODUCTION

Several species of sea urchins play an important role in the ecology of coral reefs, and its grazing activity is crucial to prevent macroalgae overgrowth on corals and to facilitate coral recruitment (Sammarco, 1982; Edmunds & Carpenter, 2001). However, when the sea urchin population increases, its voracious activity can destroy the coral framework, limiting coral reef biodiversity (Bak, 1994; Alvarado et al., 2016a). Therefore, factors that can cause boom–bust changes in the sea urchin density are important for maintaining the health of the coral reefs (Knowlton, 2001; Muthiga & McClanahan, 2020). Deteriorating health of the world's coral reefs threatens global biodiversity and ecosystem function as well as the livelihood of millions of people living in the tropics (Hoegh-Guldberg et al., 2007).

Among the factors that control variations in the sea urchin population density,

anthropogenic influences contribute most frequently, and these included increased primary productivity through eutrophication, ocean warming, disease, overfishing, and species introduction (Uthicke et al., 2009; Hernández, 2017). A remarkable sea urchin abundance fluctuation occurred in 1983 and 1984 due to the Caribbean-wide mass mortality of the sea urchin *Diadema antillarum* (Lessios, 1988). This event provides an excellent study case to evaluate the key role of sea urchins in changes in macroalgal cover and subsequent coral reef deterioration. However, long before the mass mortality, the Caribbean coral reefs were subjected to intense fishing, and this reduced predatory control over *D. antillarum*, which were extremely abundant (Jackson, 1997; Jackson et al., 2001). At that time, the density of *D. antillarum* was sufficiently high to influence characteristics such as community composition and reef grow (Ogden, 1977; Bak et al., 1984). Therefore, although catastrophic

events can quickly alter coral reefs, predatory control upon sea urchins was found to be a key ecological process in the functioning of coral reefs (McClanahan, 1988; McClanahan, 1995).

A recent global metanalysis study showed that predators' impact on the sea urchin populations was higher in tropical coral reefs compared to temperate regions (Sheppard-Brennand et al., 2017). However, the same authors also highlighted that there is an important role of the predator and prey identity, which can modulate or alter this relationship. Therefore, identifying the key sea urchin predators and quantifying predation rates seems to be essential to determine the conservation status of the coral reefs and to propose specific fishing restrictions that will ensure a correct predator–sea urchin balance for a healthy reef. The predator–prey interaction can also be limited by the environmental context (e.g., climatic events or habitat complexity) (Steneck et al., 2002; Shears et al., 2008; Clemente et al., 2010; Tebbett & Bellwood, 2018). Thus, field ecology studies should also consider these regional and habitat characteristics to better explain the observed spatial and temporal predatory patterns.

The sea urchin *Diadema mexicanum* A. Agassiz, 1863 is one of the best-studied echinoid species in the Eastern Tropical Pacific (ETP) area (Alvarado et al., 2015). It is distributed from the Gulf of California (Paz-García et al., 2016) to the Islas Galapagos (Glynn et al., 2015). Different investigations have helped to determine its key role as an herbivore and bioeroder in the dynamics of ETP coral reefs (Alvarado et al., 2016a; Cabanillas-Terán et al., 2016; López-Pérez & López-López, 2016; Obonaga et al., 2017). Although its role as a herbivore has partially been studied (Benítez-Villalobos & Valencia-Méndez, 2015), *D. mexicanum* is well known due to its bioerosive activity, a loss of coral cover and reef framework were observed after the El Niño 1982/1983 and 1997/1998 events (Eakin, 1996; Eakin, 2001; Glynn, 1988). The 1982/1983 El Niño event caused intense coral bleaching, which produced up to 80 % to 100 % mortality in some areas of the ETP (Glynn, 1984). This left space

for colonization of turf-forming seaweeds that served as food for a variety of herbivorous organisms, thus favoring an increase in their populations. Additionally, bioerosion of the coral reefs in some areas of the ETP increased the sea urchin populations of *Eucidaris thouarsii* (L. Agassiz & Desor, 1846), *Eucidaris galapagensis* Döderlein, 1887, and *D. mexicanum* by up to 60 % to 80 % (Eakin, 1996; Eakin, 2001; Glynn, 1988; Guzman, 1988; Guzman & Cortés, 1992). The coral reefs of Isla del Coco, Costa Rica were negatively affected by both El Niño and the intense bioerosive activity of *Diadema* after El Niño (Alvarado et al., 2012; Guzman & Cortés, 1992; Guzman & Cortés, 2001). The effect was such that it was estimated that the coral reef recovery would take one century (Guzman & Cortés, 1992). However, in less than 30 years, the live coral coverage returned to values that were close to those before the 1982–1983 El Niño. Concurrent with the coral reef recovery, the sea urchin density decreased to values where their bioerosive activity was at a minimum (Alvarado et al., 2012; Alvarado et al., 2016a; Alvarado et al., 2016b; Alvarado, Beita et al., 2016).

Isla del Coco has the most diverse coral reefs in the ETP (Alvarado et al., 2016b). However, one of the greatest threats to the ecological integrity of this World Heritage Site was illegal fishing until 2001 when the management efforts increased. In 2001, the marine protected area (MPA) limits of Isla del Coco increased from 15 km to 22 km around the island where extraction of any marine resource, any damage to the fauna or flora, as well as commercial, industrial, and agricultural activities were completely prohibited in the National Park waters. A buffer zone of 7 km within this 22-km MPA, was also implemented, were regulated extraction of fish resources may be permitted. Another remarkable event was the use of coastguard boats since 2003 for surveillance purposes (Alvarado et al., 2016b; Cajiao 2005; Decreto N° 43368). This strengthening of the protective measures resulted in an increase in the control and surveillance of illegal activities such as fish and lobster poaching (López-Garro et al.,

2016), during subsequent years, which led to an increase in fish apex predators (e.g. sharks, jacks, and groupers) (Friedlander et al., 2012). Currently, the National Park is considered to be one of the five best MPAs in the world (Edgar et al., 2014; Strain et al., 2018), and it has one of the highest top predator biomasses among coral reefs (Alvarado et al., 2016a; Alvarado et al., 2016b; Fourriére et al., 2016; Friedlander et al., 2012; White et al., 2014).

Although the increase in fish assemblages coincides with a reduction in *D. mexicanum* densities, no previous studies have identified the key predators or predatory consumption rates of this diadematid in the ETP. However, fishing restrictions that were implemented in the National Park may have benefited this fish (predator) abundance, and thus, controlled the sea urchin population. Other authors have previously found that the fishing restrictions inside the marine reserves in the neighboring archipelago of the Islas Galapagos limits sea urchin populations through top-down control (Dee et al., 2012; Sonnenholzner et al., 2009; Witman et al., 2017).

The Isla del Coco National Park is an interesting place because it biogeographical features together with fishing restrictions in this park seem to favor predatory guild abundances. However, prey and predator identity have an important role in determining variations in strength of the interaction. Therefore, to identify predators and quantify their influence on key sea urchin populations, it is crucial to be able to determine subsequent effects on coral reef ecosystem structures and functions. Additionally, knowledge of predators and how predation rates vary among ETP coral reef locations is of primary interest for management and conservation strategies in the context of anthropogenic changes to predator communities through overfishing. Currently, the fishes *Arothron meleagris* (Anonymous, 1798), *Arothron hispidus* (Linnaeus, 1758) (Tetradontidae), *Diodon holocanthus* Linnaeus, 1758 (Diodontidae), *Bodianus diplotaenia* (Gill, 1862) (Labridae), *Pseudobalistes naufragium* (Jordan & Starks, 1895), and *Balistes polylepis* Steindachner, 1876

(Balistidae) have been proposed as predators of *D. mexicanum* and other sea urchins in the ETP, but there is no data to support this theory (Eakin 2001; Glynn et al., 1972; Guzman, 1988; Sonnenholzner et al., 2009).

As stated previously, the Isla del Coco seems to meet the requirements for a suitable place for predators, at least in a biogeographical and historical context. However, other smaller scale factors must be taken into consideration such as habitat architecture or individual sea urchin size, which are among the most important factors that limit predation (Clemente et al., 2007; McClanahan & Shafir, 1990; Sala et al., 1998). The presence of shelter or larger-sized individuals can increase sea urchin survival (Clemente et al., 2007; McClanahan, 1995). Therefore, the presence of a predator alone does not always ensure low sea urchin densities and other factors must be taken into consideration (Steneck, 2020; Tebbett & Bellwood, 2018).

This work aimed to evaluate the following three parameters: (1) identify *D. mexicanum* predators and their predation rates using video recordings; (2) determine the effects of site and sea urchin sizes on sea urchin predation using tethering experiments; and (3) discuss the potential key role of these predators on the recent decrease in the sea urchin population.

## MATERIALS AND METHODS

**Study area:** Isla del Coco is located in the ETP, and it is 503 km off the southwest shore of Costa Rica. In 1978, Isla del Coco National Park was created, and it was established as an official MPA 10 years later. The protected area consists of 209 506 hectares, of which 98 % is a marine environment (Alvarado, Beita et al., 2016). In this study, two field experiments were performed with the aim of identifying the key predators of the sea urchin *D. mexicanum* and to evaluate the effects of site/location and sea urchin size on urchin survival. The experiments were conducted in December 2016 at three sites on the northern shore of the island because it had the most favorable conditions for scientific diving. The sites chosen were the

Bays of Ulloa (5°33'5.20" N, 87°1'56.80" W), Chatham (5°33'9.20" N, 87°2'27.50" W), and Weston (5°33'8.20" N, 87°3'3.20" W). Each of these bays have a contrasting coral habitat complexity that allowed evaluation of the protective effects of different types of sites on *D. mexicanum* individuals.

**Predators type identification:** To identify key *D. mexicanum* predators and estimate their consumption rates, daylight video observations were performed using three cameras per site that recorded for 30 minutes. Three sizes of sea urchin were offered as bait at each camera: (1) small size, < 20 mm; (2) medium size, 20–30 mm; and (3) large size, > 30 mm. Sea urchins were tethered to nylon and offered as bait to possible predators. A thin metal wire was used to maintain the fixed position of the sea urchins in front of the camera. Videos were recorded using a GoPro Hero 4 (San Mateo, California, USA) with a weighted tripod. The predation experiments were performed at a depth of 6 to 12 m at each site.

After the experiments, all video recordings were examined in our lab, and the fish species and their behavior were recorded. We identified the fish species that interacted with the sea urchins and counted the type of interaction with the sea urchin to calculate the average behavior that was displayed by the different species of fish. Then, we expressed these values as percentages. We defined three types of predators depending on their behavior towards the sea urchins, as follows: (1) predators, which were species that broke open the sea urchin test; (2) attempted predators, which were species that bit but failed to open the test; and (3) scavengers, which were those that were fed on sea urchin remains that were left by other predators. We also use the term "keystone guild" (McClanahan, 1995) to refer to the group of identify predators.

***Diadema mexicanum* survival:** The effects of site and sea urchin test diameter (TD) sizes on survival were determined using the tethering experiments. For each site, we quantified

the habitat complexity as the ratio $l/L$, where $L$ was the actual distance between two points and $l$ was the linear distance between such points (Nichols et al., 2015). A chain was placed directly along the substrate ($L$), and that measurement was compared to the total linear distance ($l$). Three sites with contrasting habitat complexity (HC) were used: (1) Ulloa, which had a low HC (< 0.5 m); (2) Chatham, which had a medium HC (0.5–1 m); and (3) Weston, which had a high HC (> 1 m).

The experimental design consisted of three 10 m transects per site with ten sea urchins per transect. Transects were placed between 6 and 12 m at each site. The three sea urchin TD sizes were distributed randomly along the transect (small TD size, < 20 mm; medium TD size, 20–30 mm; and large TD size, > 30 mm, with ten sea urchins in each size class). Using a tagging gun and following the protocol of Hereu (2005), each sea urchin was marked by inserting a nylon anchor in a 2–3 mm hole that was drilled near the top of the urchin in the interambulacrum. The nylon was 1 m long, and it was tied transverse to the main transect, which facilitated sea urchin movement. Survival of the sea urchins was checked daily for 5 days at each transect and site.

**Fish and *D. mexicanum* surveys:** Fish surveys were performed at three depths (shallow, 4–8; intermediate, 9–12; and deep, 13–16 m) with three 10-m long transects that were parallel to the coast, and there were 10 m separating each transect. To determine the fish composition at the reef, the sizes of all the fish that were observed from the transect line were counted and estimated within 2.5 m on each side of the transect (width) and 5 m above (10 m × 5 m × 5 m), forming an imaginary tunnel. The size of each fish was estimated and classified into the following categories (in cm): (1) < 5; (2) 5–10; (3) 10–15; (4) 15–20; (5) 20–25; (6) 25–50; (7) 50–100; (8) 100–150; (9) 150–200; (10) 200–250; and (11) 250–300. The length frequency of each species was transformed into biomass according to Alvarado, Beita et al. (2016). *D. mexicanum* surveys were also performed

at the three depths, which were mentioned above, for the fish surveys. The abundance was recorded at the three depths levels using three 10 × 2 m transects with 10 m of separation between transects.

**Historical sea urchin and fish predator abundance trends:** For a complete temporal trend of sea urchin abundance and predators at Isla del Coco, we used all of our observed data and our survey data (2016). *D. mexicanum* data from 1987 and 1990 were taken from Guzman & Cortés (1992) and Lessios et al. (1996), respectively. For the fish predators (*Sufflamen verres* (Gilbert & Starks, 1904) and *B. diplotaenia*) and *D. mexicanum* abundances, the 2006, 2008, and 2011 data were taken from the Reef Life Survey (RLS) repository (Edgar & Stuart-Smith, 2014). Using these data, we tried to reconstruct the historical abundance trends. The RLS *D. mexicanum* and predator data were also used for the historical trend. Sites that were sampled during these previous visits to

the Islands have been specified within each figure legend.

**Data analysis:** We recorded the action that was displayed by each fish species and expressed it as a percentage of the behavior that was shown per species during the experiment for all sites. The consumption rate based on video observations was calculated using the number of urchins that were eaten during the experiment and expressed as a percentage of daily consumption ratio. The effects of the site and sea urchin size were analyzed using a multivariate analysis of variance (PERMANOVA) using the PRIMER v7 and PERMANOVA + (Anderson et al., 2008) statistical package. The analysis consisted of a two-factor design, as follows: (1) *site* (fixed, three levels); and (2) *size* (fixed, three levels) using the Euclidean distances in a raw data matrix and 5 000 permutations. When appropriate, *a posteriori* pairwise comparisons were performed using permutations (Anderson, 2005). The effects of site and
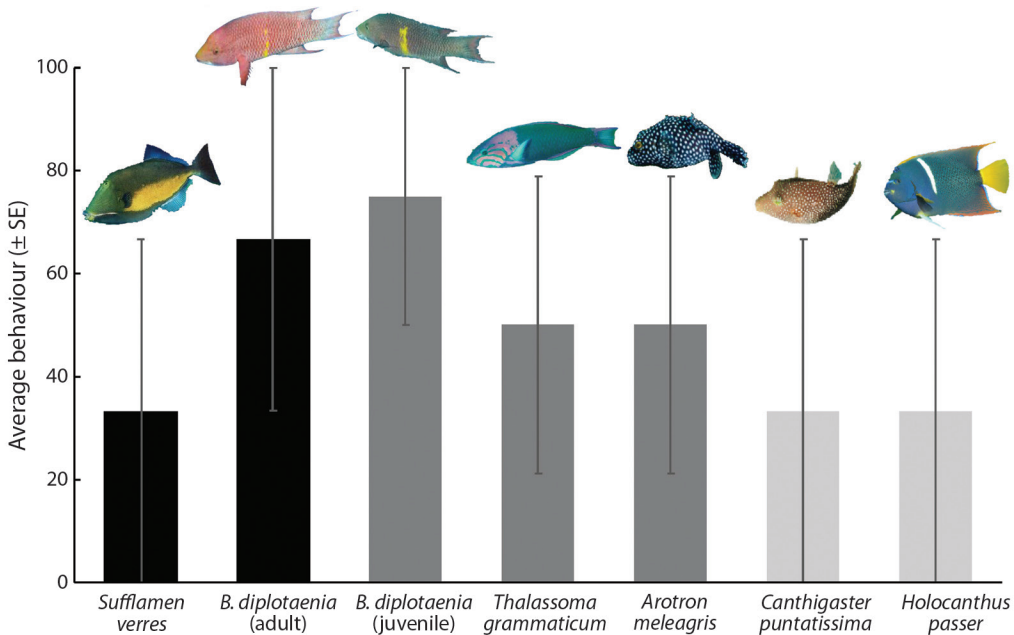


**Fig. 1** Percentage of fish behaviour exhibited per species during the experiments ± standard error. Predator, species that break open the sea urchin test, *S. verres* and *B. diplotaenia* (adult). Attempted predators, species that bite but fail to open the test, *B. diplotaenia* (juvenile), *grammaticum* and *A. meleagris*. Scavengers, those that were feeding on sea urchin remains left by predators, *C. puntatissima* and *H. passer*. Black: predators; Dark grey: attempted predators; Light grey: scavengers.

predator type on the fish biomass data were also analyzed using a PERMANOVA. The analysis consisted of a two-factor design, as follows: (1) site (fixed, three levels); and (2) fish behavior (fixed, three levels) using the same data procedure as described above.

A correlation between sea urchin survival in the tethering experiments and the consumption rates that were obtained during video observations was performed. Finally, a regression analysis between the total density of fish predators and *D. mexicanum* density was performed using curvilinear regression analyses of the abundance data in SPSS 25 (IBM Corp. Released 2017. IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp.).

## RESULTS

Two species of fish, the Balistidae *S. verres* and the Labridae *B. diplotaenia*, were identified as predators of sea urchins that were up to 30 mm in size with 30 % and 66 % of predator behavior, respectively, during the video recording experiment at all sites. The tetraodontid *A. meleagris* and the labrids *Thalassoma grammaticum* Gilbert, 1890 and *B. diplotaenia* (juvenile) were attempted predators. The latter showed the highest percentage of attempting behavior (75 %). Finally, *Canthigaster punctatissima* (Günther, 1870) and *Holacanthus passer* Valenciennes, 1846 were identified as scavengers with an average of 30 % scavenging behavior (Fig. 1).

There was a significant effect of the interaction term "site × sea urchin size" on *D. mexicanum* survival (Table 1). In the pairwise comparison results, small and medium size urchins (20 and 20–30 mm, respectively) were highly preyed upon at all sites. Nearly six of the small *D. mexicanum* (< 20 mm) individual urchins per day were consumed compared to medium-sized sea urchins, of which two urchins were consumed per day. Sea urchins >30 mm were not eaten by predatory fish. At Ulloa, with a low habitat complexity (<0.5 m), many small- and medium-sized sea urchins were preyed upon, whereas at Chatham, small sea urchin consumption was significantly lower than that of medium and larger sea urchins. At Weston, in which the habitat complexity was > 0.5 m, survival rates of large sea urchins were significantly different from small and medium size sea urchins (Fig. 2, Table 1).

There was a significant correlation between survival in the tethering experiments and consumption rates that were obtained based on
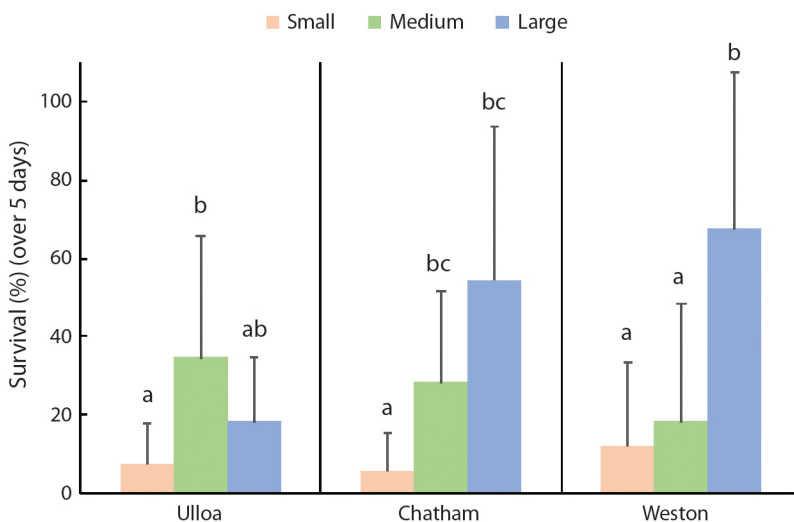


**Fig. 2.** Effect of the interaction of factors "Site" and "Test Diameter Size" on the survival of sea urchin *D. mexicanum*. Results of pairwise analysis is displayed for each site.

**Table 1**

PERMANOVA analysis of site and sea urchin size effect on survival of *D. mexicanum* based on raw data matrix with two fixed factors "Site" (three levels; Ulloa, Chatham and Weston) and "Test Diameter Size" (small TD size < 20 mm, medium TD size =20–30mm and large TD size > 30mm).

| PERMANOVA | | | | | |
|---|---|---|---|---|---|
| Source of variation | df | SS | MS | Pseudo-F | p(perm) |
| Site | 2 | 2495.1 | 1247.5 | 1.676 | NS |
| TD Size | 2 | 19712 | 9856.2 | 13.245 | < 0.01 |
| Site x TD Size | 4 | 12326 | 3081,4 | 4.141 | < 0.01 |
| Residual | 81 | 60274 | 744.12 | | |
| Total | 89 | 92556 | | | |
| Pairwise comparisons | | | | | |
| **Within level "Ulloa" of factor "Site"** | | | | t | p (perm) |
| Large *vs.* medium | | | | 1.539 | NS |
| Large *vs.* small | | | | 1.599 | NS |
| Small *vs.* medium | | | | 2.350 | < 0.05 |
| **Within level "Chatham" of factor "Site"** | | | | | |
| Large *vs.* medium | | | | 1.974 | NS |
| Large *vs.* small | | | | 3.209 | < 0.01 |
| Small *vs.* medium | | | | 2.425 | NS |
| **Within level "Weston" of factor "Site"** | | | | | |
| Large *vs.* medium | | | | 3.145 | < 0.01 |
| Large *vs.* small | | | | 3.782 | < 0.01 |
| Small *vs.* medium | | | | 0.556 | NS |

Estimates for pairwise comparisons of the interaction "Site x TD Size". NS: not significant; P < 0.05, P < 0.01.

video observation, particularly in high complexity habitats ($R^2$ = 0.9) (Fig. 3). Larger *D. mexicanum* urchins (> 30 mm) were also preyed upon during the tethering experiments, particularly in Ulloa, where the sea urchin survival rate decreased to 10 % on day 2; however, in Chatham and Weston, the survival was > 60 % (Fig. 4). One individual of the lobster species *Panulirus penicillatus* (Olivier, 1791) was observed between 7 and 8 a.m. in Chatham holding a large sea urchin individual, which was more likely removed from the tethering experiments during the night. However, no recordings of this event were noted in the daylight hour videos, and this may indicate that predation upon large sea urchin individuals by these lobsters occurs during the night.

No significant differences were found in the predator fish biomass among sites, either among fish behavior or the interaction term (Table 2). Finally, a negative logarithmic regression described the relationship between predators and *D. mexicanum* abundance, but it was not significant (F = 2.205, p = 0.154, Fig. 5). We used the combined *S. verres* and *B. diplotaenia* abundance data in the regression analysis. Abundance of fish predators instead of the biomass was used in this analysis because no fish size data is stored in the RLS repository.

A decrease in *D. mexicanum* abundance was observed from 1987 to 2016. More recently, from 2006 to 2016, an increase in predatory abundance (*S. verres* and *B. diplotaenia*) was observed (Fig. 6).

## DISCUSSION

Six species of fish were observed to have interacted with the sea urchin *D. mexicanum*, and they can be considered to be members of a keystone guild. The Balistidae *S. verres* and the Labridae *B. diplotaenia* (adult) were
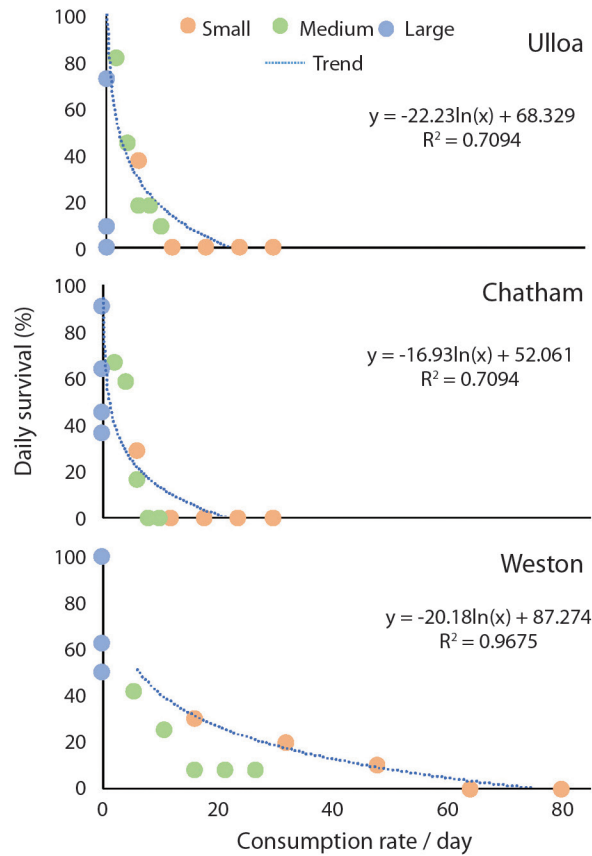
**Fig. 3.** Correlation between percentage daily survival of tethering experiment and consumption rate of video observation experiment. Log-lineal trend equation and $R^2$ value for each site are provided.

**Table 2**

PERMANOVA analysis of site and predator type on predators' biomass based on raw data matrix with two fixed factors "Site" (three levels; Ulloa, Chatham and Weston) and "Predator type" (predators, attempted predator, scavenger).

| PERMANOVA | | | | | |
|---|---|---|---|---|---|
| Source of variation | df | SS | MS | Pseudo-F | p(perm) |
| Site | 2 | 2712.4 | 1356.2 | 1.024 | NS |
| Predator type | 2 | 5260.9 | 2630.4 | 1.986 | NS |
| Site x Predator type | 4 | 3289.5 | 822.38 | 0.621 | NS |
| Residual | 41 | 54289 | 1324.1 | | |
| Total | 49 | 74292 | | | |

Estimates for pairwise comparisons of the interaction "Site x Predator type". NS: not significant. P > 0.05.

predators. The Labridaes *T. grammaticum* and *B. diplotaneia* (juvenile) and the Tetraodontidae *A. meleagris* were attempted predators. Finally, the Tetraodontidae *C. puntatissima* and the Pomacanthidae *H. passer* were identified as scavengers. Recent observations in the Gulf of California (three sites near Cabo San Lucas, October 2018) at the northern-most site for *D. mexicanum* also revealed that both *S. verres* and *B. diplotaenia* preyed upon *D. mexicanum* (size
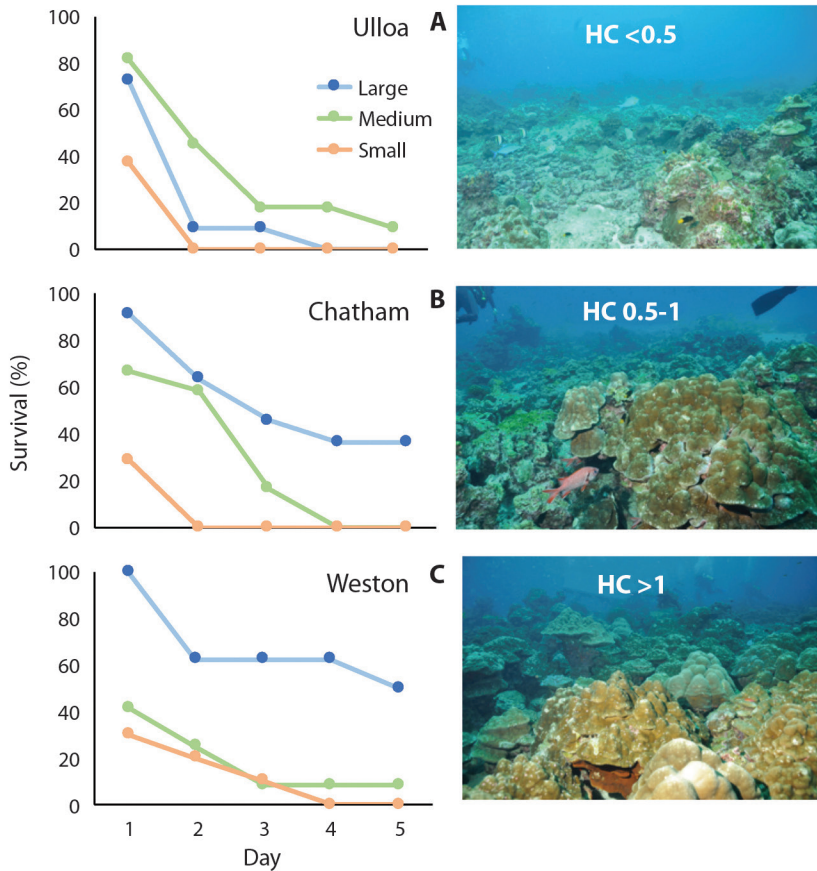
**Fig. 4.** Percentage of *D. mexicanum* size classes survival during five days of tethering experiment in each site. Habitat complexity in (**a**) Ulloa, (**b**) Chatham and (**c**) Weston.

range, 30 to 44 mm test diameter) (S. Ling, personal communication, 2021). These field observations are particularly valuable for our study because they confirm the role of these fishes in most of the *D. mexicanum* geographical range. Therefore, these fishes can be considered to be part of a "keystone guild" for all of the ETP coral reefs.

Our results also show that a high abundance of these predatory fishes, above 0.04 ind m$^{-2}$, guarantees a low sea urchin density. Below this threshold, a higher variability in sea urchin density is observed (Fig. 5). However, this relationship must be viewed with caution because it is not significant. It is likely that other sea urchin predators must be included in the equation to obtain a better fit. Habitat architecture

and the sea urchin size add to the complexity of this relationship. For example, the survival was higher at Weston where some of the medium and largest sea urchins survived during the 5 days of the experiment, while at Ulloa, the survival was very low, and a dramatic decrease in survival was observed starting on the first days of the experiment for all sea urchin sizes. Additionally, no significant difference in fish predator biomass was found among sites. Therefore, it is more likely that the differences that were found in survival are mainly due to the contrasting complexity of the habitat architecture that is found between sites (Fig. 4). Weston is a bay with an impressive *Porites lobata* habitat architecture, which provides refuge to *D. mexicanum*. Conversely, the Ulloa site consists
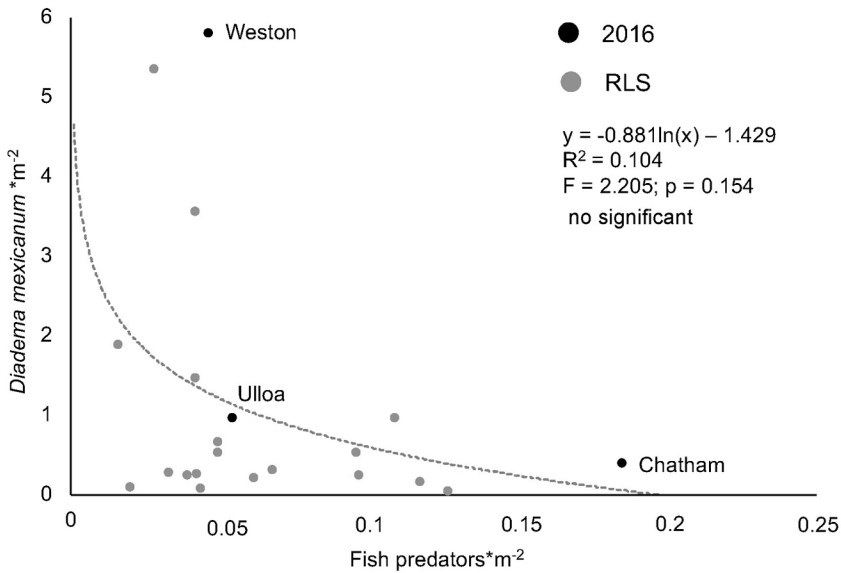
**Fig. 5.** Logarithmic negative regression of fish predators' abundances (*S. verres* and *B. diplotaenia* ) on *D. mexicanum* density at Isla del Coco. Grey dots show the data obtained from the Reef Life Survey (RLS) repository (years 2006, 2008 and 2011; sites: Atrevido, Iglesias Bay, Inutil Bay, Wafer Bay, Dos Amigos, Isla Manuelita, Manuelita Afuera, Isla Pájara, Punta Giessler, Punta Leonel, Punta María, Punta Presidio, Ulloa, Roca Sucia, Roca Sumergida, Rodolitos, Silverado Norte) and black dots show the data obtained in this study (Chatham Bay, Weston Bay, Ulloa Bay).
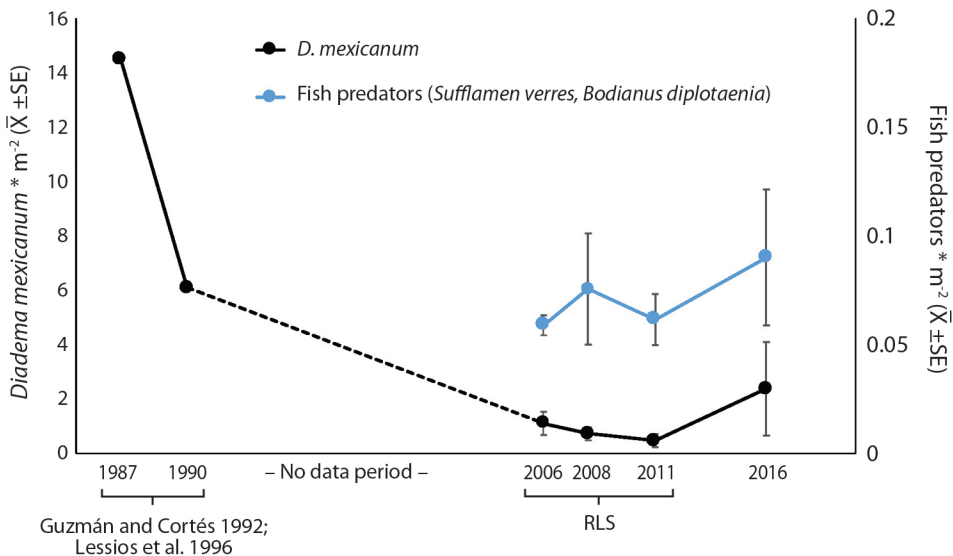


**Fig. 6.** Historical abundance trend of predatory fish and *D. mexicanum* from 1987 to 2016 at several sites at Isla del Coco. Data shown on the graph include the Guzmán & Cortés, 1992 *D. mexicanum* data (year 1987; sites: Punta Presidio, Chatham Bay, Punta Pacheco), Lessios et al., 1996 (year 1990; site: Chatham Bay), the Reef Life Survey (RLS) (years 2006, 2008 and 2011; sites: Atrevido, Iglesias Bay, Inutil Bay, Wafer Bay, Dos Amigos, Isla Manuelita, Manuelita Afuera, Isla Pájara, Punta Giessler, Punta Leonel, Punta María, Punta Presidio, Ulloa, Roca Sucia, Roca Sumergida, Rodolitos, Silverado Norte) predatory and *D. mexicanum* data and the data obtained in 2016 survey.

of a mix of small *P. lobata* corals and sandy patches, which may facilitate predation upon the sea urchins. Habitat architecture influences on predation has been previously studied, and it has been found to be a very important factor that reduces predator success upon Diadematid species (Carpenter, 1984; Clemente et al., 2007; Levitan & Genovese, 1989; Ling & Johnson, 2012; Vance & Schmitt, 1979).

Consistent with other coral reef studies (McClanahan & Muthiga, 2020; Muthiga & McClanahan, 2020; Young & Bellwood, 2012), the most common daylight predators of adult sea urchins were fish. In our case, only two fish, a triggerfish and a hogfish, were observed to prey upon the urchins. This result should be interpreted with caution because only 4.5 hours could be recorded due to the logistics of the field work that was performed at Isla del Coco National Park. It is more likely that other triggerfish species that were observed in the area were also able to prey upon *D. mexicanum*. However, based on the videos, we can state with certainty that the mortality of small and medium-sized sea urchins that was recorded in the tethering experiment was mainly due to the above-mentioned fish predators. This result is also confirmed by the high correlation that is found between the daily survival that was estimated by the tethering experiment and the consumption rate that was estimated using video observations. The low numbers of predatory fish species coincide with observations in the temperate rocky reefs of the Mediterranean Sea (Sala, 1997) and at the subtropical Canary Islands (Clemente et al., 2011). However, many fish predators have been identified in the coral reefs of the Red Sea (Fricke, 1971), East Africa (McClanahan, 1995; McClanahan, 2000), and the Great Barrier Reef (Young & Bellwood, 2012). These numbers seem to show a clear pattern of increasing predator trophic redundancy toward the tropics, as previously suggested in the metanalysis by Sheppard-Brennand et al. (2017).

The most common effective predators of Diadematids are fishes that belong to the families Balistidae, Labridae, Diodontidae, and Tetraodontidae, all of which possess powerful jaw morphologies that are designed for predation upon hard invertebrates (Turingan & Wainwright, 1993; and references therein). However, other families have also been listed as predators, attempted predators, or scavengers of *Diadema* remains, such as Scaridae, Sparidae, Batrachoidinae, Carangids, Ostraciidae, and Haemulidae. Triggerfishes and hogfishes, which have been identified as predominant predators in the Caribbean (Randall et al., 1964), the Red Sea (Fricke, 1971), East Africa (McClanahan, 2000), the Easter Atlantic Archipelagos (Clemente et al., 2010), the Great Barrier Reef (Young & Bellwood, 2012), and now at the ETP, Isla del Coco, are always included among the most voracious types of fish. Both fish species displayed contrasting feeding techniques. While the hogfish, *B. diplotaenia*, engulfs small sea urchin sizes at once or bangs medium size individuals on rocks/corals until the spines are removed, the triggerfish, *S. verres*, can break the sea urchin with a powerful bite. These feeding behaviors of these two fish coincide with previously published reports for fishes that prey upon *D. africanum* (Clemente et al., 2010). The triggerfish also acted as a dominant predator, excluding other fishes, while preying on *D. mexicanum*.

In the Caribbean and the Canary Islands, other fish species, such as some haemullids (*Anisotremus surinamensis*, *Haemulon macrostomum*) or the sparid *Pagrus auriga* are frequently seen with purple dots on their lips and surrounding mouth structures, indicating *Diadema* spine pricks (Randall et al., 1964; and J. C. Hernández author's personal observations, August, 2017). These species have night-time feeding habits and/or live in deeper waters where less experimentation has been done. Therefore, *Diadema* consumption has only been corroborated based on the predators' stomach contents (Clemente & Hernández, 2007; Randall et al., 1964). These previous observations emphasize the possibility that other fish predators could also be predators of *D. mexicanum*; however, due to the inherent

limitation of our experimental design, we did not detect any other predatory behaviors.

The cause of the largest-sized sea urchin mortality remains unknown, but we suspect that predation by lobsters during the night could be responsible for large sea urchin mortality. The lobster *P. penicillatus* was also observed once preying upon a large sea urchin individual during the first hours of the day. However, lobster predation was not observed during the daylight video recordings; therefore, this observation must be viewed with caution. Among the macroinvertebrates, two gastropod species of the genus *Cassis*, the starfish *Coscinasterias tenuispina* (Lamarck, 1816), and the spiny lobster *Panulirus argus* (Latreille, 1804) were observed to prey upon species of the genus *Diadema* (Clemente & Hernández, 2007; Levitan & Genovese, 1989; Randall et al., 1964). The crucial predatory role of lobsters upon large Diadematid sea urchins has been demonstrated (Ling et al., 2009), which supports our hypothesis of lobster predation in Isla del Coco. Ling et al. (2009) also confirmed that predation occurred only at night when sea urchins left their day-time shelters. Thus, our observation of the spiny lobster *P. penicillatus* preying upon *D. mexicanum* is interesting because this lobster is probably the only species that is capable of preying on the largest sea urchins. However, due to this lobster's nocturnal habits, our experimental video approach did not allow observation of its consumption rates and behaviors. Additionally, Diadematid sea urchins show homing behaviors that can also help them to avoid fish predators during the day. For example, in the Caribbean, *D. antillarum* have a nocturnal foraging behavior that allows them to escape trigger fish predation (Carpenter, 1984); this finding is similar to observations for *Centrostephanus coronatus* (Verrill, 1867) in California to avoid hogfish predation (Nelson & Vance, 1979) or for *C. rodgersii* in southern Australia (Andrew & Underwood, 1993). Thus, the lobsters that share nocturnal feeding habits have a higher probability of consuming urchins as prey.

The fishing restrictions, due to implementation of the MPA, may have favored predatory control over *D. mexicanum* populations, which is also supported by the historical trends (Fig. 6). However, we also believe that in highly complex environments such as that found at the Isla del Coco reefs, lobsters may play a crucial functional role by preying on the largest sea urchins due to the natural capacity of the lobsters to creep through the habitat crevices and holes at night. A diverse predatory guild, including fish predators of small- and medium-sized sea urchins in addition to lobsters that prey upon large sea urchins may help to ensure a healthy coral reef in which the bioerosion-related sea urchin activity is controlled.

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