



<https://doi.org/10.15517/rev.biol.trop..v72iS1.58602>

## Variation of the diet of the sea urchin (*Diadema mexicanum* (Diadematoidea: Diadematoidea)) according to its size in the Eastern Tropical Pacific

Andrea Bogantes-Retana<sup>1</sup>; <https://orcid.org/0009-0008-4302-4578>

José Barquero-Jackson<sup>1</sup>; <https://orcid.org/0009-0002-6690-614X>

Mario Vargas-Guerrero<sup>1</sup>; <https://orcid.org/0000-0001-9649-1075>

Juan José Alvarado<sup>1,2,3 \*</sup>; <https://orcid.org/0000-0002-2620-9115>

1. Escuela de Biología, Universidad de Costa Rica; [andrea.bogantesretana@ucr.ac.cr](mailto:andrea.bogantesretana@ucr.ac.cr), [jose.barquerojackson@ucr.ac.cr](mailto:jose.barquerojackson@ucr.ac.cr), [mario.vargasguerrero19@ucr.ac.cr](mailto:mario.vargasguerrero19@ucr.ac.cr), [juan.alvarado@ucr.ac.cr](mailto:juan.alvarado@ucr.ac.cr) (\*Correspondence).
2. Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, 2060-11501 San José, Costa Rica.
3. Centro de Investigación en Biodiversidad y Ecología Tropical (CIBET), Universidad de Costa Rica, 2060-11501 San José, Costa Rica.

Received 23-I-2023. Corrected 14-IX-2023. Accepted 27-IX-2023.

### ABSTRACT

**Introduction:** The sea urchin *Diadema mexicanum*, due to its bioerosion activity, is considered of ecological importance. This phenomenon could negatively or positively affect coral reef ecosystems. The bioerosion process varies according to the abundance and size of the sea urchin.

**Objective:** Juvenile organisms possess different metabolic needs compared to adults, so knowing their stomach content according to size allows us to quantify the selection of substrate bioeroded.

**Methods:** To determine this, *D. mexicanum* individuals were collected in 12 sites from January 2009 to September 2010 along the Eastern Tropical Pacific coast. The stomach content was categorized in Carbonated Fraction (CF), Non-Carbonated Fraction (NCF), and Organic Matter (OM). Stomach content was analyzed according to a) juvenile (< 2.5 cm) or adult (> 2.5 cm) stage and b) locality.

**Results:** Juveniles presented the following stomach content average percentages: 20.7 % OM, 12 % NCF and 67.9 % CF; and adults: 11.4 % OM, 14.8 % NCF and 73.8 % CF. Based on a Wilcoxon test and a Kendall linear regression, the following results were obtained. The carbonated fraction in the stomach increased by 0.47 units on average for every cm of growth ( $p < 0.05$ ). OM consumed by *D. mexicanum* increases only 0.05 units for every cm of growth ( $p < 0.05$ ). We found a difference of stomach content depending on the site ( $p < 0.05$ ) and life stage ( $p < 0.05$ ). Localities like Huatulco and Coco presented significant differences that could be related to local oceanographic conditions.

**Conclusions:** We relate these changes of the stomach fractions to the necessity of the juvenile sea urchins for nutrients to maintain their growth. The amount of OM is crucial for the development of early stages, meaning that there is a difference in substrate selection associated with growth.

**Key words:** organic matter; coral reefs; stomach content; carbonates; growth; bioerosion.



## RESUMEN

Variación de la dieta del erizo de mar (*Diadema mexicanum* (Diadematoidea: Diademataidae)) según su tamaño en el Pacífico Tropical Oriental

**Introducción:** El erizo de mar *Diadema mexicanum*, por su actividad de bioerosión, es considerado de importancia ecológica. Este fenómeno podría afectar negativa o positivamente a los ecosistemas de arrecifes de coral. El proceso de bioerosión varía según la abundancia y el tamaño del erizo de mar.

**Objetivo:** Los organismos juveniles poseen diferentes necesidades metabólicas en comparación con los adultos, por lo que conocer el contenido estomacal según el tamaño, nos permite cuantificar la selección de sustrato bioerosionado.

**Métodos:** Para determinar esto, se recolectaron individuos de *D. mexicanum* en 12 sitios desde enero de 2009 hasta septiembre de 2010 a lo largo de la costa del Pacífico Tropical Oriental. El contenido estomacal se clasificó en Fracción Carbonatada (FC), Fracción No Carbonatada (NCF) y Materia Orgánica (MO). El contenido estomacal se analizó según a) estadio juvenil (< 3 cm) o adulto (> 3 cm) y b) localidad.

**Resultados:** Los juveniles presentaron los siguientes porcentajes promedio del contenido estomacal: 20.7 % OM, 12 % NCF y 67.9 % CF; y adultos: 11.4 % OM, 14.8 % NCF y 73.8 % CF. Con base en una prueba de Wilcoxon y una regresión lineal de Kendall, se obtuvieron los siguientes resultados. La fracción carbonatada en el estómago aumentó en promedio 0.47 unidades por cada cm de crecimiento ( $p < 0.05$ ). La MO consumida por *D. mexicanum* aumenta solo 0.05 unidades por cada cm de crecimiento ( $p < 0.05$ ). Encontramos una diferencia en el contenido estomacal según el sitio ( $p < 0.05$ ) y el estadio de vida ( $P < 0.05$ ). Localidades como Huatulco y Coco presentaron diferencias significativas que podrían estar relacionadas con las condiciones oceanográficas locales.

**Conclusiones:** Relacionamos estos cambios de la composición porcentual del contenido estomacal con la necesidad de los erizos de mar juveniles de nutrientes para mantener su crecimiento. La cantidad de MO es crucial para el desarrollo de las primeras etapas, lo que significa que existe una diferencia en la selección de sustrato asociada con el crecimiento.

**Palabras clave:** materia orgánica; arrecifes de coral; contenido estomacal; carbonatos; crecimiento; bioerosión.

## INTRODUCTION

Sea urchins of the genus *Diadema* can conquer different habitats like coral reefs and rocky grounds, due to their generalist diet (Benítez-Villalobos et al., 2015). Even though, sea urchin *Diadema mexicanum* (A. Agassiz, 1863) are mainly herbivores and feed mostly on algae, it is also common to see them feeding on living and dead corals (Cabanillas-Terán et al., 2016; Glynn & Morales, 1997; Tribollet & Golubic, 2011). Added to this, this species plays an important role in the Eastern Tropical Pacific (ETP) due to its bioeroding action on coral reefs (Alvarado et al., 2016a), which has intensified in El Niño events (Eakin, 2001).

When feeding, *D. mexicanum* scrapes the surface where the food is located, sometimes causing bioerosion to the substrate (Benítez-Villalobos et al., 2008; Hutchings, 2011). Grazing made by sea urchins can be advantageous in some specific cases, as it happens for algae, whose development and abundance

gets restricted, helping corals to easily obtain light and space (Herrera-Escalante et al., 2005; McClanahan et al., 1996). Similarly, they also have an impact on rocky reefs, because they control organisms that grow over them, however high densities of this sea urchins could lead to a negative impact, due to the high abrasion they cause, changing the reef structure (Alves et al., 2003; Eakin, 2001).

Feeding of this sea urchin is related to many dynamic processes of the ecosystem and its composition. Gut content found inside the sea urchin can be divided in three categories: organic matter (OM), non-carbonated fraction (NCF) and carbonated fraction ( $\text{CaCO}_3$ ). This depends on what the sea urchins feed on and the substrate in which they obtained their food. Food availability in the zone and food preference will consequently influence the gut content (Alvarado et al., 2015).

Due to this, knowing the amount of matter that the sea urchins are consuming according to

their stage of development is important, since it makes it possible to quantify their selection of bio-eroded substrate. Taking this into account, determining whether the location of *D. mexicanum* influences stomach content can be a relevant factor to slow down coral reef degradation. Here, we thereby determine if there is a difference in the gut content of *D. mexicanum* according to the study site and development stage and establish if there is a correlation between their gut content and their age. We predict that there is going to be a difference between stomach contents of *D. mexicanum* according to their age and locality. We expect there to be a significant correlation between the sea urchin size and the stomach content type.

## MATERIALS AND METHODS

This study was carried out in 12 localities with coral reefs in the Eastern Tropical Pacific (ETP) (Fig. 1), which included continental, peninsular and insular environments, both protected and non-protected areas (Alvarado et al., 2016a, Alvarado et al., 2016b).

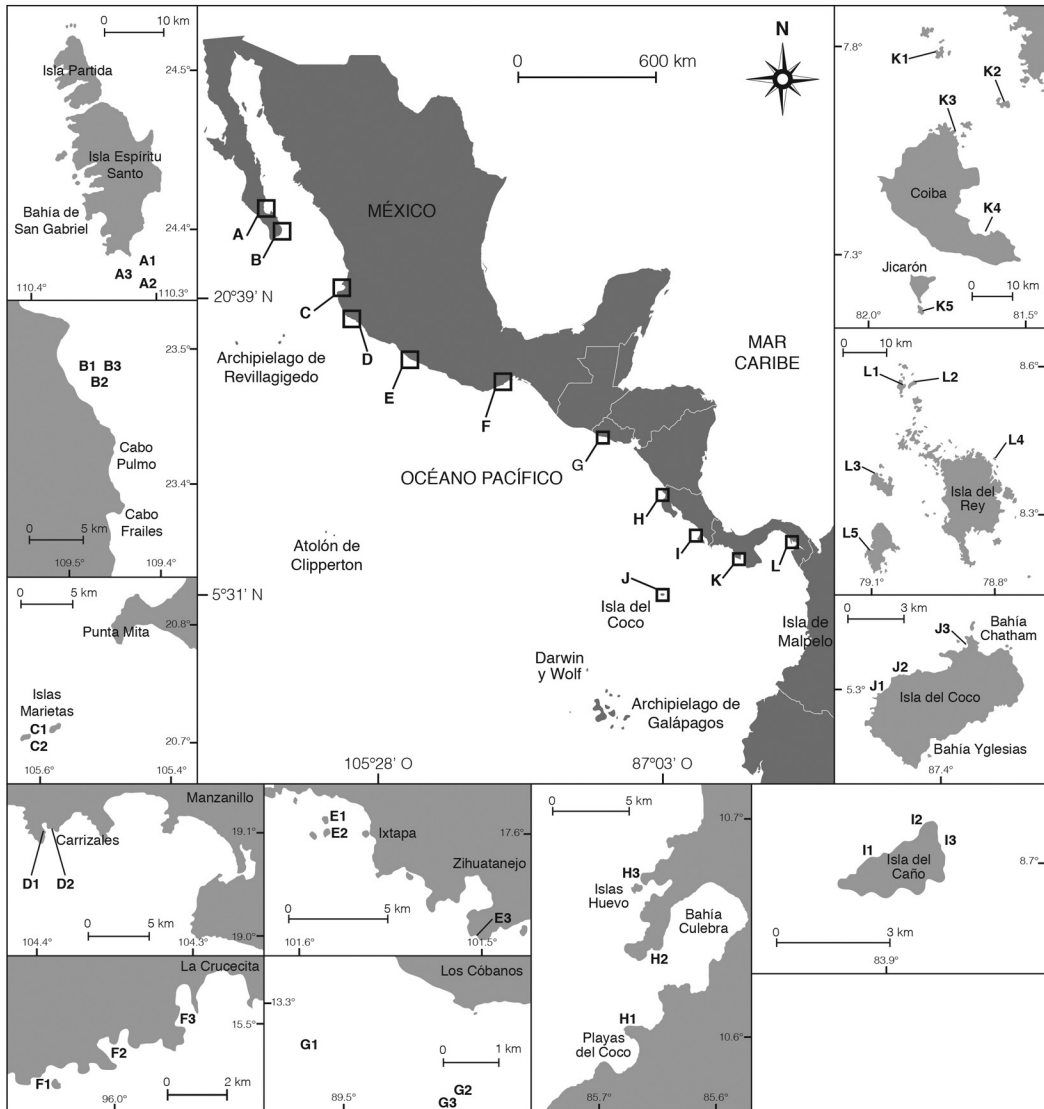
Diet composition was determined by collecting the evacuated gut content (EGC), and organic matter (OM), calcium carbonate fraction ( $\text{CaCO}_3$ ) and non-carbonated fraction (NCF) were analyzed. To obtain the EGC, 30 individuals per locality were collected (50 in Coiba and Las Perlas), from January 2009 to September 2010, and placed in 10 L plastic containers with continuous ventilation, letting them evacuate for 24 hours (*sensu* Glynn, 1988; Reyes-Bonilla & Calderón-Aguilera, 1999). The evacuated material by each individual sea urchin was dried in an oven at 60 °C for 24 hours. The samples were weighed in a top loading balance (0.001 g), and then combusted for 6 hours at 550 °C to burn the OM. The OM starts burning at 200 °C and gets completely burned away at 550 °C, the carbonates are not affected (Griffin et al., 2003). After cooling, the samples were weighed again, and the difference in mass was the organic matter present in the material evacuated (Carreiro-Silva & McClanahan, 2001). The remaining fraction

represents the inorganic fraction that consisted of calcium carbonate ( $\text{CaCO}_3$ ) and insoluble residues (rock fragments, quartz grains, sponge spicules, diatoms, radiolarians and silt). The inorganic fraction was digested in 10 % hydrochloric acid and after the dissolution of  $\text{CaCO}_3$  filtered using pre-weighed fiberglass filters. The weight of the residual material retained on the filter corresponds to the non-carbonated fraction (NCF). The difference between the inorganic fraction weight and the NCF was  $\text{CaCO}_3$  (Carreiro-Silva & McClanahan, 2001). All sea urchins were measured with a caliper, and it was established that a size greater than 2.5 cm corresponds to an adult organism, while those less than or equal to said size were considered juveniles according to Benítez-Villalobos et al. (2015).

A Wilcoxon test (W) was conducted to determine the difference in stomach content between size groups. The difference in stomach content between localities was analyzed using a non-parametric Kruskal-Wallis. Finally, a linear regression model with a Kendall correlation was made to obtain the correlations between their different stomach fractions (g) and their size (cm). All these analyses were performed using R studio (v4.2.2.) (R Core Team, 2023).

## RESULTS

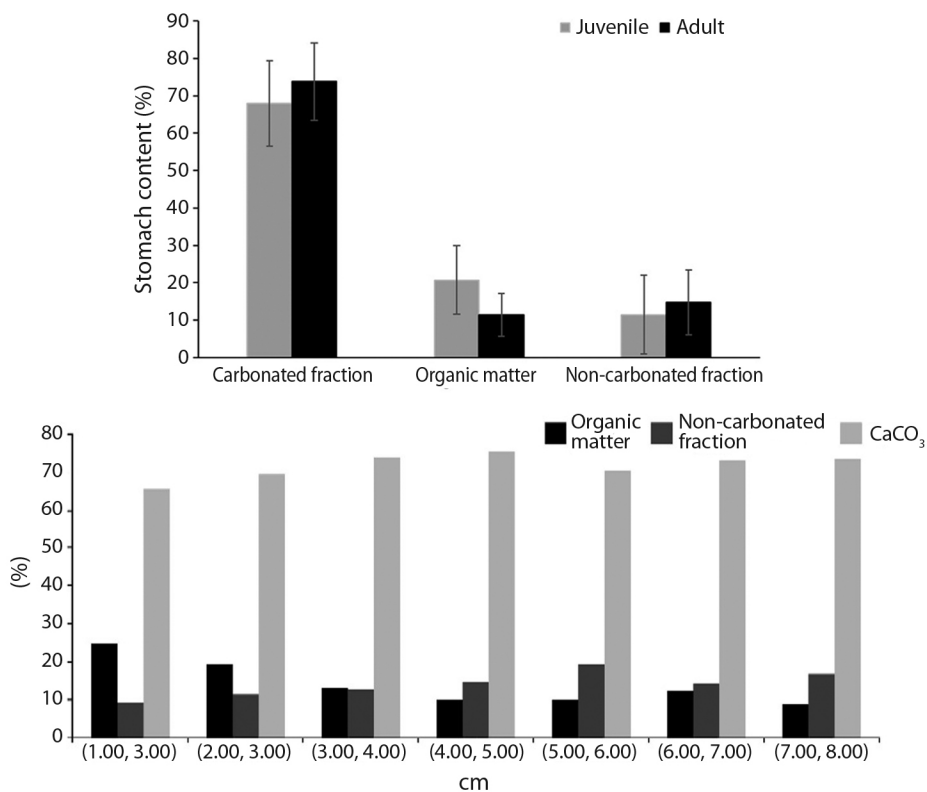
The EGC of 160 juvenile and 210 adults of *D. mexicanum* were analyzed. The organic matter (OM) ( $W = 11\,694$ ,  $p < 0.001$ ), carbonated fraction ( $\text{CaCO}_3$ ) ( $W = 3\,980.5$ ,  $p < 0.001$ ) and non-carbonated fraction (NCF) ( $W = 4224.5$ ,  $p < 0.001$ ) varied between both sizes. Juveniles presented an average of  $0.3708 \pm 0.1745$  g of  $\text{CaCO}_3$ ,  $0.1141 \pm 0.0795$  g of OM and  $0.0606 \pm 0.075$  g of NCF, while adults presented  $1.3527 \pm 1.2244$  g of  $\text{CaCO}_3$ ,  $0.1956 \pm 0.2563$  g of OM and  $0.2553 \pm 0.2579$  g of NCF on average (Fig. 2). Also, the carbonated fraction increased 0.47 g on average for each cm of growth of *D. mexicanum* ( $R\tau = 0.5690$ ,  $p < 0.05$ , Fig. 3), while the organic matter only increased 0.05 g per cm ( $R\tau = 0.2630$ ,  $p < 0.05$ , Fig. 4).



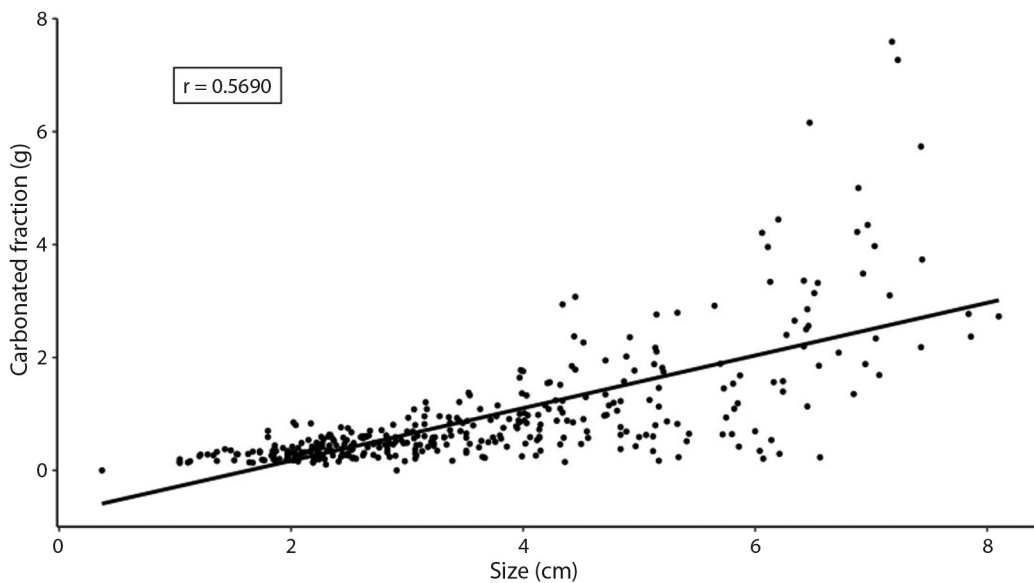
**Fig. 1.** *Diadema mexicanum* study localities along in the ETP. A. Isla Espiritu Santo; B. Cabo Pulmo; C. Islas Marietas; D. Carrizales; E. Ixtapa-Zihuatanejo; F. Bahías de Huatulco; G. Los Cóbanos; H. Bahía Culebra; I. Isla del Caño; J. Isla del Coco; L. Isla Coiba; M. Archipiélago de Las Perlas.

Overall, Coco's Island presented the highest average of the three fractions of the gut content ( $\text{CaCO}_3 = 2.2519 \pm 1.1802$  g,  $\text{OM} = 0.5380 \pm 0.5293$ g,  $\text{NCF} = 0.7525 \pm 0.2909$  g). Coiba had the lowest averages of  $\text{CaCO}_3$  ( $0.4179 \pm 0.2710$ ),

while the lowest value of OM was presented in Pulmo ( $0.0892 \pm 0.0281$  g) and the lowest average of NCF was obtained in Huatulco ( $0.0418 \pm 0.6633$  g). Also, significant differences were obtained between  $\text{CaCO}_3$  ( $\chi^2 = 144.9$ ,  $\text{df} = 11$ ,



**Fig. 2.** A. Percentage of the stomach content of *Diadema mexicanum* according to its development stage. The error bars represent the standard deviation; B. % Gut content per size frequencies of test's (cm).



**Fig. 3.** Correlation of *Diadema mexicanum* between its size and the carbonated fraction, per individual.

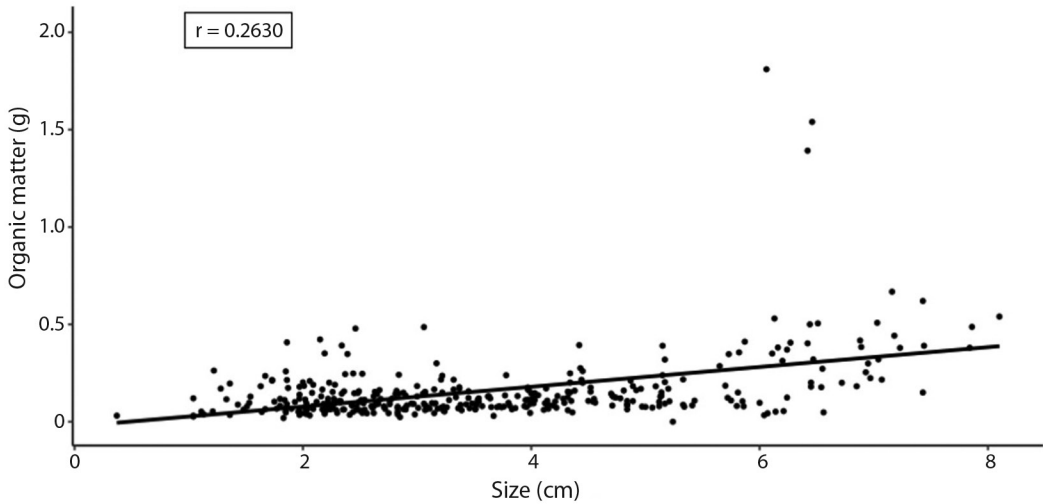


Fig. 4. Correlation of *Diadema mexicanum* between its size and the organic matter, per individual.

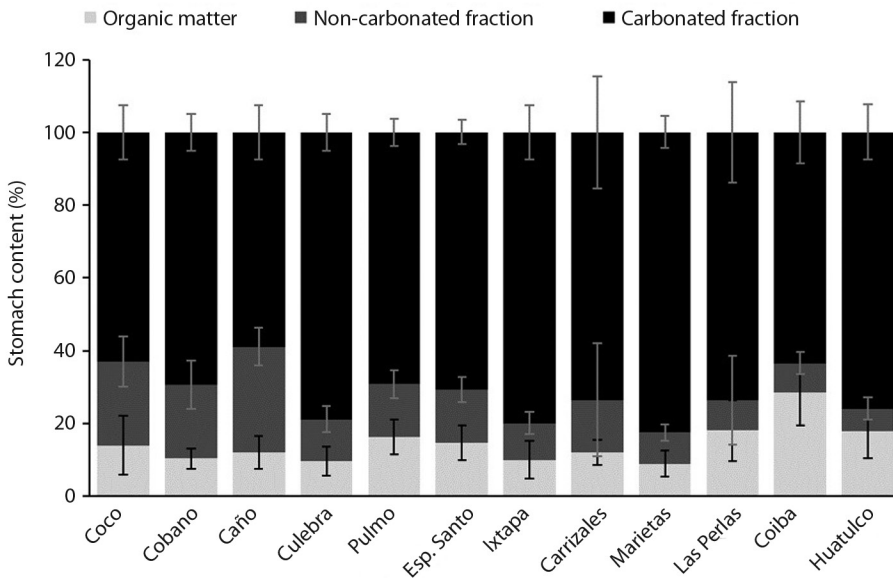


Fig. 5. Percentage of the stomach content of *D. mexicanum* according to the collection sites. The error bars represent the standard deviation.

$p < 0.001$ ), OM ( $\chi^2 = 135.66$ ,  $df = 11$ ,  $p < 0.001$ ) and NCF ( $\chi^2 = 213.67$ ,  $df = 11$ ,  $p < 0.001$ ) by locality (Fig. 5).

## DISCUSSION

The amount of carbonates per individual per size class (Fig. 2) was similar to the

ones observed for *Diadema savigny* (Audouin, 1809), *Echinothrix diadema* (Linnaeus, 1758) and *Echinostrephus molaris* (Blainville, 1825) in French Polynesia (Bak, 1990) or for *D. antillarum* in Barbados (Scoffin et al., 1980) (Table 1). Also, similar to the values found by Herrera-Escalante et al. (2005) for *D. mexicanum* in Huatulco,  $0.47 \text{ g CaCO}_3 \text{ ind}^{-1}$  for sea urchins



**Table 1**

Average carbonate grams per individual ( $\text{g CaCO}_3 \text{ ind}^{-1}$ ) in Barbados (*D. antillarum*; Scoffin et al., 1980), French Polynesia (*D. savigny*, *E. diadema*, *Echinostrephus molaris*; Bak, 1990) and in ETP (*D. mexicanum*; this research).

Class interval	Barbados	French Polynesia	ETP
[1.00, 2.00)	0.273	0.01	0.277
[2.00, 3.00)	0.507	0.04	0.404
[3.00, 4.00)	1.292	0.16-0.36	0.705
[4.00, 5.00)	1.490	0.71-1.06	1.150
[5.00, 6.00)	2.264	1.87-3.03	1.290
[6.00, 7.00)		4.32-6.81	2.478
[7.00, 8.00)			3.886
[8.00, 9.00)			2.728
Average	1.165	1.185-1.885	1.435

smaller than 3 cm,  $1.41 \text{ g CaCO}_3 \text{ ind}^{-1}$  for urchins between 3-5 cm and  $2.96 \text{ g CaCO}_3 \text{ ind}^{-1}$  for urchins between 5 and 7 cm of test diameter.

Hawkins (1981) and Hawkins and Lewis (1982) found a change in the percentage composition of organic matter among sea urchins bigger than 3.5 cm, as we found. The percentage of encrusting coralline algae in the gut content of *D. antillarum* changes between sizes (Hawkins & Lewis, 1982). In sea urchins smaller than 3.5 cm, these algae represent between 70–80 %, while epilithic or endolithic algae represent between 5 % and 20 %. In sizes over 3.5 cm, encrusting coralline algae become a minor element of the gut content (5–20 %), while epilithic algae represent between 50 and 75 %. Sea urchins smaller than 3.5 cm present a higher growth rate ( $3.4 \text{ mm month}^{-1}$ ) than sea urchins above this size ( $1.5 \text{ mm month}^{-1}$ ) (Hawkins & Lewis, 1982). When sea urchins grow, their diet varies from encrusting coralline algae (with high organic matter content) to epilithic algae (with low organic matter content). The highest growth rates in small sea urchins require a higher quality diet with an organic content richer than the diet of sea urchins over 3.5 cm. Additionally, sea urchins that eat encrusting coralline algae possess an absorption efficiency ranging between 26–72 %, while urchins that eat other algae possess an efficiency between 1 % and 24 % (Hawkins, 1981). In the ETP, 51 % of sea urchins are under 4 cm (Fig. 4). Also,

in seven of the studied localities, between 53 % and 100% of the collected individuals were under 4 cm, highlighting the abundance of young urchins. It seems that small individuals prefer calcareous algae, which give them the necessary energy requirements to grow fast and reach adulthood.

Regarding the development of the sea urchins, it has been seen that their growth and gonad development do not occur at the same time (Lawrence, 2000). On the contrary, usually these individuals focus on one process or another, both requiring nutrients, both limited by food availability (Lawrence, 2000). The transition from a larval state to a juvenile has not been studied deeply, and this process involves a drastic change in the urchin's diet (Fadl et al., 2018). There is a period of time, specifically at the beginning of this process, where the urchin is deprived of nutrients, which is related to the development of Aristotle's lantern (Fadl et al., 2018).

What the sea urchins eat during the first juvenile stages is unknown and the change of stage can lead to a different diet (Fadl et al., 2018). Also, it has been proven by experiments that sea urchins with a more calcareous diet do not get to change into an adult stage, meaning they never develop their gonads to a point of sexual maturity (Meidel & Scheiblingl, 1999). This implies that the idea and presence of the organic matter and proper nutrients are necessary during juvenile development stages, which means that a diet based on more organic matter in the early stages is to be expected (Meidel & Scheiblingl, 1999).

In the case of the general increase of the stomach content related to size, *D. mexicanum* gonads grow in proportion to their size (López-Pérez & López-López, 2016). The gonads size not only depends on the increase in number and size of gametes, but also depends on the phagocytes and the nutrient storage needed for the start of gametogenesis. These nutrients need to be recovered with food since individuals who do not eat or do not have a good diet tend to either have smaller gonads or not have them at all (Muthiga & McClanahan, 2007).



Then, the increase in size could be related to a strategy for the urchin to prepare for a reproductive stage. An example of this has been seen in the green sea urchin, *Strongylocentrotus droebachiensis* (O.F. Müller, 1776), which presents a mobilization of nutrients from the nutritive phagocytes, indicating a new gametogenesis, surrounding germ cells with the released nutrients (Benítez-Villalobos et al., 2015). Also, it has been seen that the size is directly proportional to the amount of carbonates consumed (López-Pérez & López-López, 2016), which is supported by the non-parametric test done (Kruskal,  $p < 0.001$ ).

The size of the sea urchins can increase due to external factors not directly related to nutritive requirements, which is the case for the genus *Diadema*, where it has been seen that, in some occasions, when the population density is low, the individual size increases (Benítez-Villalobos et al., 2008). This happens because sea urchins are considered density-dependant, where whenever there are fewer individuals, the resource availability increases, leading to a better general diet (Benítez-Villalobos et al., 2008). Another case where this happens is depending on the substrate of the localities (López-Pérez & López-López, 2016). Generally, the size and density of the organisms changes according to the size of the site, for example, places with bigger rocks tend to have bigger sea urchins (López-Pérez & López-López, 2016).

Lastly, coral reefs are very susceptible to environmental changes, which can create differences between them throughout the Eastern Tropical Pacific (Alvarado et al., 2016a). *D. mexicanum* lives in these ecosystems, which could have been modified by El Niño of 1982-1983, which generated a high mortality rate in the corals, and subsequently an increase in macroalgae growth, that populated the site, considerably increasing their coverage (Alvarado et al., 2016a). This phenomenon is important because the bioerosion of *D. mexicanum* is approximately twice as high in dead coral substrate (Glynn, 1988), which influences considerably, because the sea urchins arrive at these affected places in search of food and this leads

to a localized abrasion of the calcareous deposits (Herrera-Escalante et al., 2005).

Another factor that goes hand in hand with the disturbances in the reefs of the ETP zone is that these are very susceptible to erosive changes due to their little development, meaning any damage would be more drastic. The higher bioerosion rate could also be attributed to *D. mexicanum* generally found in groups (Herrera-Escalante et al., 2005). The feeding of urchins can also have an impact on carbonate levels and algal cover of coral reefs (Alvarado et al., 2016a). Variations in the ecosystems and conditions, like the ones described above, can cause differences in feeding, so, a change can be observed in the type of stomach content in relation to the location.

As a recommendation, for other studies like this one, it is important to note that adult sea urchins have high nutrient stages, where they seem to prepare for their reproductive stage and spawning (Benítez-Villalobos et al., 2015). This is an important consideration since the season for the data collection can influence the results. Another aspect to consider is that some of the areas of study were protected areas and that not all of them have the same level of conservation (Alvarado et al., 2016a). This is important since it has been reported that areas with overfishing, unprotected areas or less protected areas, usually present higher densities of sea urchins and a more noticeable bioerosion effect (Graham et al., 2011).

In conclusion, it seems that the life stage of the sea urchin does influence the stomach content, and the juveniles tend to consume a higher percentage of organic matter related to the necessity of the early-stage sea urchins for nutrients to maintain their growth. The amount of OM is crucial for the development during this stage, meaning that there is a difference in substrate selection associated with growth.

Aside from this, the locality, which relates to the kind of substrate and the availability of nutrients is key to the diet of *D. mexicanum*. At last, there is an important correlation between the size of the urchin and their stomach content, which states that whenever the size increases,



all of the stomach content increases too, being most noticeable in the case of the carbonated fraction. Also, the percentage distribution of the stomach content significantly differs, where it is seen that the carbonated fraction has double the percentage of consumption in the case of juveniles compared to adults. All of this could suggest that in case of a situation of *D. mexicanum* overpopulations, the adults are going to be causing more damage to the ecosystem and mostly to corals, leading to a possible disbalance of carbonate levels and algal covers, so controlling the adult population is advised.

**Ethical statement:** the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

#### ACKNOWLEDGMENTS

We acknowledge the following persons that collaborated during the development of this work: C. Fernández, O. Bredy, C. Sánchez, S. Martínez, E. Gómez, A. Planas, V. Flores, O. Norzagaray, L.E. Calderón-Aguilera, A. Ayala, J. Carrión, L. Hernández, G. Ramírez, V. Vargas, J. Ramírez, and the Bezy, Sánchez-Camacho and García-Zuñiga families. We also thank the following institutions, organizations and companies: Centro de Investigación en Ciencias del Mar y Limnología (CIMAR, Universidad de Costa Rica), Universidad Autónoma de Baja California Sur (UABCS), Laboratorio de Sistemas Arrecifales (LSA), Centro de Investigaciones en Ciencias Marinas (CICIMAR), Universidad de Guadalajara, Centro de Investigación Científica y Educación Superior de Ensenada (CICESE), Universidad del Mar, Ministerios del Ambiente y Recursos Naturales-El Salvador, Universidad de El Salvador, Smithsonian Tropical Research Institute, Liquid Jungle Lab, Charles Darwin Foundation, Hotel

Pacífica, Mero Divers, Vallartec, Fundarrecife, and Reserva Biológica Isla del Caño, Parque Nacional Isla del Coco and Parque Nacional Los Cóbano park rangers, MY Adventure crew, Instituto Costarricense de Turismo, Sistema Nacional de Áreas de Conservación-Costa Rica (SINAC), Autoridad Nacional del Ambiente- Panamá (ANAM), Hotel Punta Marenco Lodge and Águila de Osa Inn. A special acknowledgement for their economic support for this research to Vicerrectoría de Investigación-Universidad de Costa Rica, Ministerio de Ciencia y Tecnología de Costa Rica (MICIT), Consejo Nacional para Investigaciones Científicas y Tecnológicas de Costa Rica (CONICIT), Consejo Nacional de Ciencia y Tecnología de México (CONACYT), Fonds Français pour l'Environnement Mondial (FFEM), Ecodesarrollo Papagayo and Grupo Adelante.

#### REFERENCES

- Alvarado, J., Cortés, J., Guzman, H., & Reyes-Bonilla, H. (2016a). Bioerosion by the sea urchin *Diadema mexicanum* along Eastern Tropical Pacific coral reefs. *Marine Ecology*, 37(5), 1088–1102. <https://doi.org/10.1111/maec.12372>
- Alvarado, J., Cortés, J., Guzman, H., & Reyes-Bonilla, H. (2016b). Distribution, size and diet of *Diadema mexicanum* (Echinoidea) along the Eastern Tropical Pacific coral reefs. *Aquatic Biology*, 24, 151–161. <https://doi.org/10.3354/ab00645>
- Alvarado, J. J., Reyes-Bonilla, H., & Benítez-Villalobos, F. (2015). *Diadema mexicanum*, erizo de mar clave en los arrecifes coralinos del Pacífico Tropical Oriental: lo que sabemos y perspectivas futuras (Diadematoida: Diadematidae). *Revista de Biología Tropical*, 63(S2), 135–157. <http://dx.doi.org/10.15517/rbt.v63i2.23140>
- Alves, F., Chícharo, L., Serrao, E., & Abreu, A. D. (2003). Grazing by *Diadema antillarum* (Philippi) upon algal communities on rocky substrates. *Scientia Marina*, 67(3), 307–311. <https://doi.org/10.3989/scimar.2003.67n3307>
- Bak, R. P. M. (1990). Patterns of echinoid bioerosion in two Pacific coral reef lagoons. *Marine Ecology Progress Series*, 66, 267–272.
- Benítez-Villalobos, F., Gómez, M. D., & Pérez, R. L. (2008). Temporal variation of the sea urchin *Diadema mexicanum* population density at Bahías de Huatulco, Western Mexico. *Revista de Biología Tropical*, 56(S3), 255–263. <https://doi.org/10.15517/rbt.v56i3.27140>



- Benítez-Villalobos, F., Ávila-Poveda, O. H., Díaz-Martínez, J. P., & Bravo-Ruiz, A. R. (2015). Gonad development stages and reproductive traits of *Diadema mexicanum* (Echinodermata: Echinoidea) from Oaxaca, Mexico. *Invertebrate Reproduction & Development*, 59(4), 237–249. <http://dx.doi.org/10.1080/07924259.2015.1108935>
- Cabanillas-Terán, N., Loor-Andrade, P., Rodríguez-Barre-ras, R., & Cortés, J. (2016). Trophic ecology of sea urchins in coral-rocky reef systems, Ecuador. *PeerJ*, 4, e1578. <https://doi.org/10.7717/peerj.1578>
- Carreiro-Silva, M., & McClanahan, T. R. (2001). Echinoid bioerosion and herbivory on Kenyan coral reefs: the role of protection from fishing. *Journal of Experimental Marine Biology and Ecology*, 262, 133–153. [https://doi.org/10.1016/S0022-0981\(01\)00288-X](https://doi.org/10.1016/S0022-0981(01)00288-X)
- 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(1), 171–186.
- Fadl, A. E. A., Mahfouz, M. E., El-Gamal, M. M. T., & Heyland, A. (2018). Onset of feeding in juvenile sea urchins and its relation to nutrient signalling. *Invertebrate Reproduction & Development*, 63(1), 11–22. <https://doi.org/10.1080/07924259.2018.1513873>
- Glynn, P. W. (1988). El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the Eastern Pacific. *Galaxea*, 7(2), 129–160. <https://doi.org/10.1007/s00227-017-3175-0>
- Glynn, P. W., & Morales, G. E. L. (1997). Coral reefs of Huatulco, West Mexico: reef development in upwelling Gulf of Tehuantepec. *Revista de Biología Tropical*, 45(3), 1033–1047.
- Graham, J. E., Banks, S. A., Bessudo, S., Cortés, J., Guzmán, H. M., Henderson, S., Martínez, C., Rivera, F., Soler, G., Ruiz, D., & Zapata, F. A. (2011). Variation in reef fish and invertebrate communities with level of protection from fishing across the Eastern Tropical Pacific seascape. *Global Ecology and Biogeography*, 20(5), 730–743. <https://doi.org/10.1111/j.1466-8238.2010.00642.x>
- Griffin, S. P., García, R. P., & Weil, E. (2003). Bioerosion in coral reef communities in southwest Puerto Rico by the sea urchin *Echinometra viridis*. *Marine Biology*, 143, 79–84. <https://doi.org/10.1007/s00227-003-1056-1>
- Hawkins, C. M. (1981). Efficiency of organic matter absorption by the tropical echinoid *Diadema antillarum* Philippi fed non-macrophytic algae. *Journal of Experimental Marine Biology and Ecology*, 49, 245–253. [https://doi.org/10.1016/0022-0981\(81\)90074-5](https://doi.org/10.1016/0022-0981(81)90074-5)
- Hawkins, C. M., & Lewis, J. B. (1982). Ecological energetics of the tropical sea urchin *Diadema antillarum* Philippi in Barbados, West Indies. *Estuarine, Coastal and Shelf Science*, 15, 645–669. [https://doi.org/10.1016/0272-7714\(82\)90077-4](https://doi.org/10.1016/0272-7714(82)90077-4)
- 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(S3), 263–273. <https://doi.org/10.15517/rbt.v53i3.26784>
- Hutchings, P. (2011). Bioerosion. In: G. Gábrioch, P. Davies, T. J. Done, E. Guschler, I. G. Macintyre, R. Wood, C. D. Woodroffe, & D. Hopley (Eds), *Encyclopedia of Modern Coral Reefs: Structure, form, and Process* (pp. 139–156). Springer.
- Lawrence, J. M. (2000). *Conflict between somatic and gonadal growth in sea urchins: a review* [Technical Inform]. Florida Sea Grant College Program.
- López-Pérez, A., & López-López, D. A. (2016). Impacto bioerosivo de *Diadema mexicanum* en arrecifes de coral del Pacífico sur mexicano. *Ciencias marinas*, 42(1), 67–79. <https://doi.org/10.7773/cm.v42i1.2586>
- McClanahan, T. R., Kamukuru, A. T., Muthiga, N. A., Gilgaber, M., & Obura, D. (1996). Effect of sea urchin reductions on algae, coral, and fish populations. *Biological Conservation*, 10, 136–154. <https://doi.org/10.1046/j.1523-1739.1996.10010136.x>
- Meidel, S. K., & Scheibling, R. E. (1999). Effects of food type and ration on reproductive maturation and growth of the sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology*, 134, 155–166. <https://doi.org/10.1007/s002270050534>
- Muthiga, N. A., & McClanahan, T. R. (2007). Ecology of *Diadema*. In J. M. Lawrence (Ed.), *Edible Sea Urchins: Biology and Ecology* (pp. 205–219). Elsevier.
- R Core Team (2023). R: A language and environment for statistical computing [Computer software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reyes-Bonilla, H., & Calderón-Aguilera, L. E. (1999). Population density, distribution and consumption rates of three corallivores at Cabo Pulmo reef, Gulf of California. *Marine Ecology*, 20, 347–357. <https://doi.org/10.1046/j.1439-0485.1999.2034080.x>
- Scoffin, T. P., Stearn, C. W., Boucher, D., Frydl, P., Hawkins, C. M., Hunter, J. G., & MacGeachy, J. K. (1980). Calcium carbonate budget of fringing reef of the West coast of Barbados. Part II. Erosion, sediments and internal structure. *Bulletin of Marine Sciences*, 30, 475–508
- Tribollet, A., & Golubic, S. (2011). Reef Bioerosion: Agents and Processes. In Z. Dubinsky, & N. Stambler (Eds.), *Coral Reefs: An Ecosystem in Transition* (pp. 435–449). Springer.