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RESEARCH ARTICLE

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Population status of the world's largest limpet, *Scutellastra mexicana* (Mollusca: Patellidae), on María Madre Island, Mexico: Possible last bastion of a species facing global extinction

José Luis Carballo[1,2] | Eric Bautista-Guerrero[3] | Yáñez Benjamín[2] | Luis Rodrigo Carballo[1] | José Carlos García-Gómez[1]

[1]Laboratorio de Biología Marina, Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Seville, Spain

[2]Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (Unidad Académica Mazatlán), Mazatlán, Sinaloa, Mexico

[3]Laboratorio de Ecología Marina, Centro Universitario de la Costa, Universidad de Guadalajara, Puerto Vallarta, Jalisco, Mexico

Correspondence
José Luis Carballo, Laboratorio de Biología Marina, Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Seville, Spain and Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (Unidad Académica Mazatlán), Mazatlán, Sinaloa, Mexico.
Email: jlcarballo.us@gmail.com

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Abstract

1. *Scutellastra mexicana* is the largest patellid in the world, with records of up to 35.5 cm in length, and is one of the most endangered marine invertebrates from tropical Pacific rocky shores.
2. The decline of this species occurred during the 20th century, when fishing cooperatives reported the capture of millions of specimens in less than 2 decades (1970–1980). Since then, the species has continued to be captured illegally to the point that it has practically disappeared.
3. This paper reports the population status of *S. mexicana* in María Madre Island (Mexican Pacific Ocean), which was used as a Federal Prison from 1905 until 2019.
4. A total of 2,381 limpets were recorded in four main populations: Guayacama, Borbollones, Punta Halcones and Papelillos. The density was very low: from 0.05 to 0.3 individuals m^{-2}, with an ageing population structure, and no recent recruitment. The size-frequency distribution of the populations showed that most of the individuals were between 9 and 15 cm. Mean and maximum shell length varied between 10.5 and 19 cm at Papelillos, 13.6 and 20.3 cm at Punta Halcones, 13.7 and 17.6 cm at Borbollones, and 12 and 20 cm at Guayacama.
5. Evidence of illegal extraction was evident in Papelillos since the size of the limpets was significantly the smallest of the four populations studied, and also significantly smaller than those in an adjacent midden.
6. Now that the prison has been closed it is imperative to establish legal measures, to provide extreme protection of María Madre, and to change the current status of *S. mexicana* in the Official Mexican Standard (NOM-059-ECOL-2010) from threatened species to in danger of extinction. This may be the last hope for the species.

KEYWORDS
abundance, endangered species, giant limpet, María Madre Island, *Scutellastra mexicana*, size

1 | INTRODUCTION

Limpets are conspicuous molluscs living in temperate and cold rocky intertidal habitats, subjected to the harshest and most changeable environmental conditions (Henriques, Delgado & Sousa, 2017). They are fundamental in structuring and regulating the ecological balance of intertidal communities, directly through the key grazing process that determines the abundance of macroalgae (Hawkins & Hartnoll, 1983), and, indirectly, as they maintain a mosaic of open spaces that allow the coexistence of many other species, thus contributing to increased marine biodiversity (Coleman et al., 2006; Vafidis et al., 2020). Experimental evidence has also shown that limpets, and particularly patellid limpets in the NE Atlantic, have a strong top–down influence on the community structure of the rocky intertidal (Hawkins et al., 1992; Hawkins et al., 2019).

Due to their accessibility and low mobility, limpets are highly vulnerable to overexploitation, and some species have also been intensively fished by humans around the world, including *Cymbula oculus* (Born, 1778) in South Africa (Branch & Odendaal, 2003), *Cellana* sp. in Hawaii (Bird et al., 2007), and different *Patella* species along the coast of the north-east Atlantic, especially Macaronesia, such as *Patella aspera* Lamarck, 1819, *Patella piperata* Gould, 1846, *Patella candei* d'Orbigny, 1840 (Hawkins et al., 2000; Núñez et al., 2003; Riera et al., 2016; Martins et al., 2017) and *Patella ferruginea* Gmelin, 1791 (Rivera-Ingraham, Espinosa & García-Gómez, 2011).

A particular group of limpets, the so-called 'giant limpets', have been even more intensively fished due to their importance as food and ornaments; some of them even since the Paleolithic, such as *P. ferruginea*, which is the most endangered marine invertebrate at risk of extinction in the Mediterranean Sea (Espinosa & Rivera-Ingraham, 2017). These giant limpets are usually distributed outside of the tropics (Powell, 1973; Ridgway et al., 1998), except the giant Mexican limpet *Scutellastra mexicana* (Broderip & Sowerby, 1829), which is found in tropical waters of the Pacific Ocean (Carballo et al., 2019). This species is the largest known limpet in the world, and probably is also one of the largest intertidal invertebrates, reaching up to 35.5 cm in length (Dall, 1871). It inhabits lower intertidal and subtidal rocky areas in places with intense swells (Esqueda et al., 2000; Espinosa et al., 2020). *S. mexicana* is a gardening limpet, whose activity clears areas upon which a thick algal film develops and upon which it feeds (Branch et al., 1992; Shanks, 2002). These gardens and their home scars where the limpets settle are actively defended (Beebe, 1942; Carballo et al., 2019).

The Chupícuaro culture developed in Mexican central Pacific during the Late Preclassical (500 BC–200 AD), in an area that includes the current states of Nayarit, Jalisco, Colima, Michoacán and part of Guanajuato and Guerrero, although the oldest traces of this culture have been found dating back to 1800 BC (Flores-Villatoro, 2004; López-Austin & López-Luján, 2009). Evidence from middens and archaeological sites shows that this pre-Hispanic culture used this limpet as food and ornaments for centuries, as well as trading with it, since they carried them inland far away from the coast (Laylander, Fujita & Guía, 2013). Different artifacts made from the shells of this species were found in the great temple of the Aztecs of Tenochtitlan (Prehispanic Mexico City), and in the Pyramid of the Plumed Serpents at Xochicalco (750–800 BC) (Morelos).

More recently, in the 1970s and 1980s, an important fishery developed in the state of Michoacán in part of the area occupied by the Chupícuaro culture where, a single cooperative reported in 1982 an annual catch of 180 t of fresh meat (without viscera and shell) (Gorrostieta-Hurtado & Trujillo-Toledo, 2012). Between 1984 and 1986 the captures of this cooperative were reduced to 5 t, and by 1987 only 1 t was reported (Avalos-Vizcarra & Méndez-Reyes, 1992). These collections probably represent millions of specimens. After 1988 there is no 'official' commercial record of landings of *S. mexicana* along the Mexican coast. Something similar was documented in the Azores (Portugal), where *P. candei* and *P. aspera* were subject to uncontrolled harvesting until 1984, when the catch reached a peak of 97 t (Santos, Martins & Hawkins, 1990). Such intense harvesting resulted in a marked decline in the limpet populations, before the fishery collapsed in 1985 (Santos, Martins & Hawkins, 1990; Hawkins et al., 2000; Martins et al., 2008; Sousa et al., 2019).

Due to the decline of the populations of *S. mexicana*, it was included in the Official Mexican Standard NOM-059-ECOL-1994, under 'Special Protection' status updated in 2010 (NOM-059-ECOL-2010). Threatened and endangered species such as *S. mexicana* are also regulated under the general terms of the Ecology Law, the General Wildlife Law and also under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to which Mexico is a Party. Nevertheless, despite the inclusion of the species in the NOM, all the evidence, published studies, personal observations, verbal testimonies, interviews with local fishermen etc., showed that the species continued to be exploited within the Mexican littoral. The species is captured not only to sell the meat, but also for their shells which are sold at international malacological fairs and through social networks (personal observations in social networks) with total impunity and a complete lack of any authority remedying this situation. It is evident that the legal status of *S. mexicana* is not a good indicator of its level of protection. Something similar has happened with other species. For example, the measures adopted by the Portuguese government in 1993 to protect *P. aspera* in the Azores archipelago, had little impact on the recovery of their population and limpet density remained low (Martins et al., 2008). The stocks of *P. aspera* and *P. candei* did slightly recover

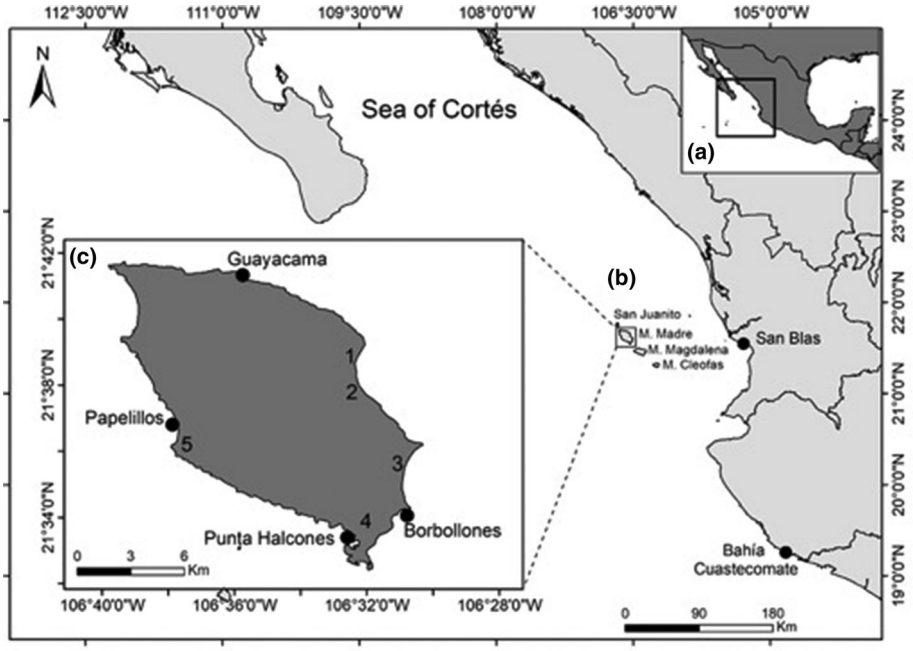

FIGURE 1 (a) Partial map of Mexico showing location of Islas Marías (box). (b) The four Marías Islands. (c) María Madre island. Numbers show the main people settlements named as camps 1 = Nayarit camp, 2 = Puerto Balleto harbour, 3 = Morelos camp, 4 = Laguna del Toro camp, 5 = San Juan Papelillo camp. Also shown in (c) are the four sampling areas to study the populations of *Scutellastra mexicana* (Guayacama, Borbollones, Punta Halcones and Papelillos).

after regulatory measures were enforced, with an increase of mean shell length and dominance of reproductive individuals (Sousa et al., 2019).

Despite the importance as food and ornament that *S. mexicana* has had since pre-Hispanic times, and how conspicuous and abundant it was until the mid-20th century, biological data of this species are absent, and population data mostly consist of scattered and brief records throughout the Mexican Pacific Coast that show that the situation of the species is perilous (Esqueda et al., 2000; Ríos-Jara et al., 2001; Fuentes-Farías, Villarroel-Melo & Solís-Marín, 2005; Holguín-Quiñones, 2006; Ríos-Jara et al., 2006; Bastida-Zavala et al., 2013; Landa-Jaime et al., 2013). For example, in the Bahía de Cuastecomates (central Pacific, Jalisco state; Figure 1), the density of limpets in 2000 was estimated to be up to 6 limpets m^{-2} (Esqueda et al., 2000), but only 0.001 limpets m^{-2} were recorded 2 decades later (Valdez-Cibrián et al., 2021). The species is also collected in the archipelago Islas Marías (Carballo et al., 2019), probably the only place in the entire Pacific Ocean where there are still small self-sustaining populations. On a small islet near María Cleofas Island (Figure 1), Carballo et al. (2019) found a population of 808 individuals of up to 26 cm in length (0.7 individuals m^{-2}), including a number of juveniles (between 4 and 5 cm long). A year later the population was reduced to 304 limpets (0.3 individuals m^{-2}), and a large accumulation of empty shells was found on the sea bottom near the study area, where the fishermen had removed the soft tissue (Carballo et al., 2019).

The archipelago Islas Marías was declared a Biosphere Reserve in 2000 (Diario Oficial de la Federación, 27 November 2000), and later, in 2005, was included in the list of Natural World Heritage Sites as part of the 'Islands and Protected Areas of the Gulf of California' (CONANP, 2022) by UNESCO. The archipelago comprises three main islands; María Madre, María Magdalena and María Cleofas, and a small islet named San Juanito (Figure 1). These islands are uninhabited except María Madre (the largest), which has a lighthouse and also housed for more than 100 years the Federal penitentiary (Revueltas, 1988), which was closed in 2019. María Madre is the one that has received the greatest protection against illegal fishing and therefore there is the possibility that there are still some populations of *S. mexicana* that are large enough to allow the recovery of the species.

The aim of the present study was to evaluate the current status of the *S. mexicana* population in María Madre Island, look for evidence of illegal extraction of the species by the island's own population during the time that it functioned as a prison, and to propose measures to prevent further decline of the remaining populations.

2 | MATERIAL AND METHODS

2.1 | Area of study

Islas Marías archipelago lies off the coast of Nayarit, is located 110 km NW of San Blas, in the mouth of the Gulf of California (Figure 1a,b). The archipelago forms part of the 'Protected Areas of the Gulf of California' designed to protect important ecosystems, including some endemic fauna and flora species.

María Madre, formed as the result of Mesozoic to Tertiary tectonic processes, is the largest island of the archipelago with an area of 145,282 km^2, a coastline of almost 60 km, and a maximum height of 616 m above mean sea level (Figure 1c). The climate is dry with moderate rainfall from June to October.

The island was used as a penal colony (Islas Marías Federal Prison) from 1905 until 8 March 2019 when the last 624 prisoners left the island (Rojas, 2019). After that, the prison was closed with plans to replace it with a cultural centre and an 'eco-friendly tourist hub'. During the time it operated as a prison, it housed some 45,000 prisoners, many of whom lived in semi-freedom but were confined to

different settlements distributed throughout the island (see Figure 1c) and worked outdoors in different activities such as fishing, shrimp farm, agriculture, cattle rearing or in a sawmill in the latter period. Some also lived with their families, so there were times when there were up to about 600 children on the island.

2.2 | Sampling sites

This study was undertaken between March and April 2021 at four sites (Figure 1c). Most of the intertidal rocky habitat is on the western coast, since the east coast is mainly composed of sandy beaches, and limestone cliffs that are continuously eroded by the waves, which causes great turbidity (Figure 2a).

2.2.1 | Guayacama (Figures 1c and 2a)

Located in the north east of María Madre, Guayacama is an area formed by small tertiary sedimentary rocky outcrops (Ojo de Buey Formation). Due to the turbidity of the water, most of the intertidal zone is covered by a thin layer of sediment, and the limpets only find areas for settlement in the uppermost parts of the rocks, which are also the most wave-exposed (Figure 2a; area outlined with white line). The shells at this site are much more eroded and worn than in other places (Figure 2b). In some cases, the horseshoe-shaped footprint is visible dorsally (Figure 2c). The total sample area was approximately of 226 m^2.

2.2.2 | Borbollones (Figures 1c and 2d,e)

Borbollones is a rocky coastal platform in the south east of the island, formed from Tertiary sedimentary rocks, and subject to heavy wave action (Figure 1c). Limpets were sampled on a relatively flat terraced area about 980 m long and a mean width of 4.2 m encompassing a total area of 4,116 m^2. Due to the extreme wave conditions, only the intertidal zone could be studied (Figure 2d,e). A large shell midden found adjacent to the intertidal rocky coast was also sampled.

2.2.3 | Punta Halcones (Figures 1c and 3a)

A rocky bay located in the south-western part of the island, Punta Halcones was formed by Tertiary sedimentary rocks and Cretaceous-Tertiary and volcanic rocks. The rocky intertidal extends along approximately 1,788 m of coastline and on average is about 4.5 m wide, covering a total sample area of 8,046 m^2 (Figure 3a). It has rocky outcrops a few metres out from the coastline as well as a rocky subtidal that reaches approximately 5 m deep (Figure 3c).

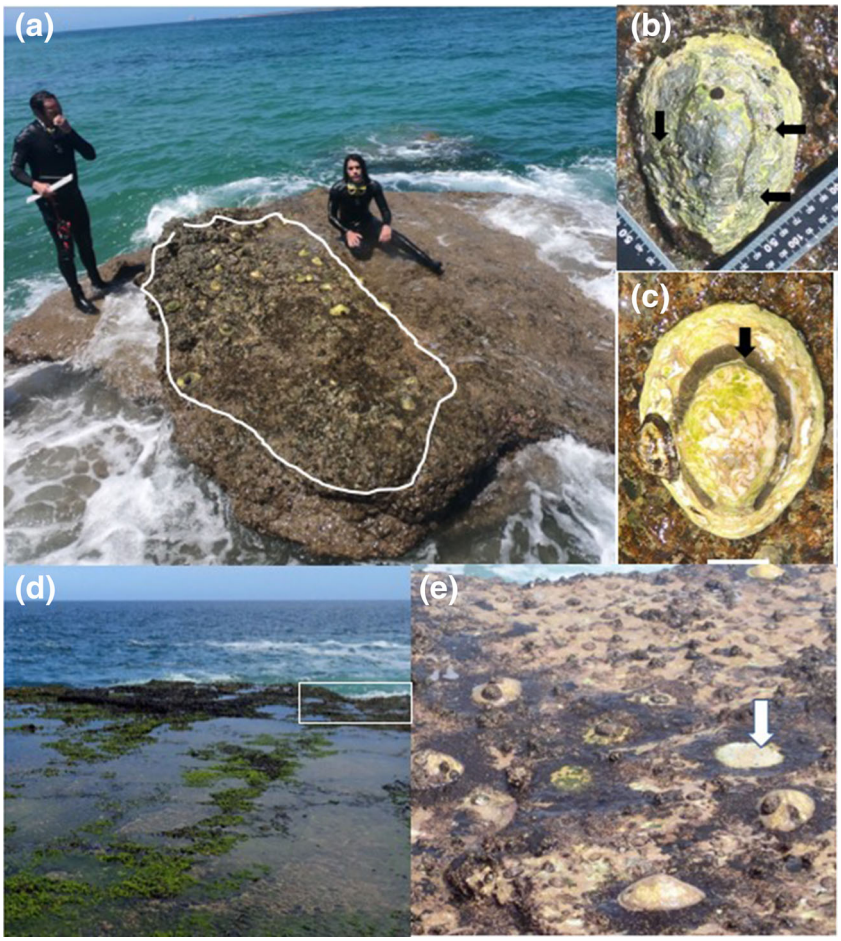

FIGURE 2 (a) Detail of one of the rocky outcrops sampled in Guayacama, where it can be seen that only the highest and most exposed parts are suitable for the settlement of the *Scutellastra mexicana* (continuous line), since most of it is usually covered by sediment. (b) A high degree of erosion and epibiosis by other organisms can be seen on shells in this area. Arrows show some specimens of *Siphonaria* sp. Also shown is the measurement process with a GoPro camera that has two scales installed. (c) The degree of erosion is such that the imprint of the insertion of the palear muscle can be seen through the shell by transparency (arrow). Scale bar 4 cm. (d) Intertidal of Borbollones. (e) Detail of the limpets in the white box marked in (d). Some of them grazing away from their home scars (arrow).

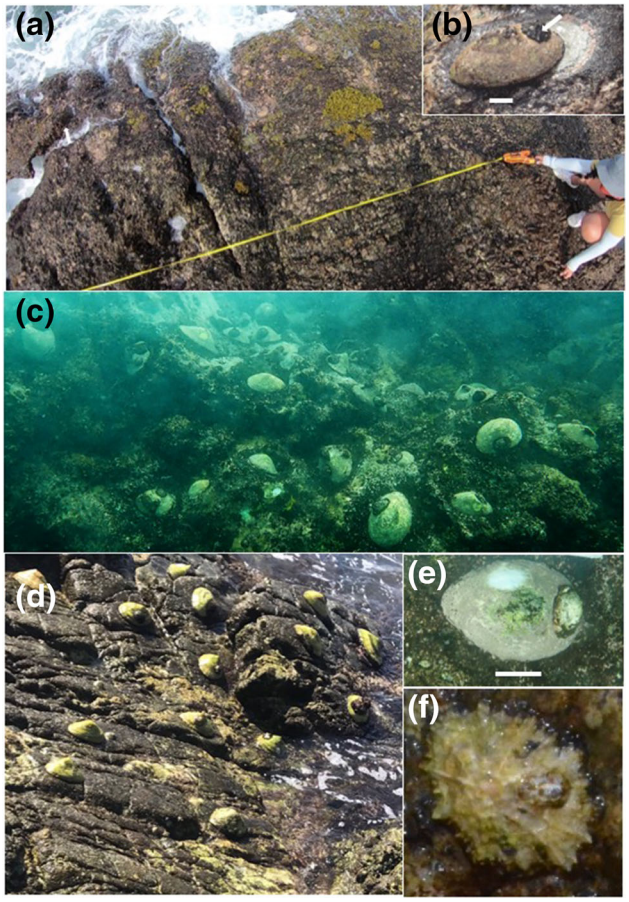

FIGURE 3 (a) Intertidal zone of Punta Halcones Bay. (b) *S. mexicana* with a juvenile (arrow). Scale bar 4 cm. (c) Area of high density of *Scutellastra mexicana* in the subtidal of Punta Halcones Bay. (d) Area of high density of *Scutellastra mexicana* in the subtidal zone of Papelillos. (e) Subtidal image of *S. mexicana* with *Lottia discors* grazing out of its home scar (arrow). Scale bar 3 cm. (f) Juvenile of *S. mexicana* 4 cm long.

2.2.4 | Papelillos (Figures 1c and 3d)

Papelillos is an intertidal rocky area formed by Cretaceous plutonic rocks and Jurassic banded and folded gneiss which run parallel to the coastline. This area comprises an irregular almost continuous platform of rocks and boulders that extends for 1,580 m along the north-western coast of the island, with an average width of 3.4 m covering a total sample area of 5,372 m^2 (Figure 3d).

2.3 | Sampling for abundance and size distribution

2.3.1 | Intertidal zone

S. mexicana is a very conspicuous species, and their populations are very scarce (Carballo et al., 2019; Valdez-Cibrián et al., 2021). For these reasons it was decided to count the total number of specimens per locality. The sampling area at each location was divided into several sections, and the area of each one was estimated by multiplying the length (parallel to the coastline) by the width (perpendicular to the coastline; Figure 3a). A similar methodology has previously been used to quantify low density populations of *Patella* spp. (Núñez et al., 2003), and other giant limpets such as *Scutellastra laticosta* (Scheibling & Black, 2020). Each of these sections were sampled at low tide during spring tides. To optimize sampling time, instead of measuring the specimens *in situ*, they were photographed with a GoPro camera provided with two scales (Figure 2b). Subsequently, approximately one of every four photos (566 pictures from a total of 2,418) was randomly selected to measure the size of the individuals to the nearest mm using the software CPCe (Coral Point Count with Excel extension) (Kohler & Gill, 2006), and to obtain information such as the presence of the smaller limpet *Lottia discors* (up to 5 cm long; Figures 2c and 3e), the presence and dimensions of the 'garden', the state of the shell (Figure 2b) and the associated communities.

2.3.2 | Permanent plots

The distribution of *S. mexicana* in each sampling area was not uniform since there were large areas where no limpets were found, and others where they formed dense aggregations. Four permanent quadrats of 1 m^2 (1 × 1 m) were set up in each study area, where dense aggregations of *S. mexicana* were observed. These permanent plots will allow for the monitoring of illegal fishing over time, as it is such dense aggregations that are targeted by illegal fishermen.

2.3.3 | Subtidal zone

The subtidal zone was also sampled at low tide through transects carried out by four divers simultaneously. Two divers surveyed the population in the top 2 m depth, and the other two surveyed between 2 and 4 m depth. Each group of divers carried a camera that had two scales installed, in such a way that all the specimens found along the transects were photographed. Later, a digital analysis was performed with CPCe software to obtain shell dimensions.

2.3.4 | Supralittoral fringe (shell middens)

The sizes of the shells deposited in the supralittoral fringe, or in middens associated with past human fishery activity were also studied. This could provide information about the average and maximum sizes reached by the species in the past. The use of this approach helps to determine the effects of exploitation in areas where suitable control areas (e.g. no-take marine reserves) are lacking, since harvested populations are subjected to size-selection; so that if the extractive effect was significant, larger sizes would be expected to be found in the shells deposited in the midden than in the live populations. For this, a transect 25 m long and 1 m wide was run through the midden, and all the shells found were counted and measured.

2.4 | Analysis of data

Frequency histograms were made using shells measurements (length) at each locality (both from the live populations and from the middens), and the differences between them were tested with Kolgoromorov–Smirnov two-sample tests (Bonferroni corrected for multiple comparisons) (Stephens, 1974). Data were grouped into 10-mm size class intervals as used by Carballo et al. (2019).

Analysis of variance (ANOVA) was used to test whether shell size differed between the study sites. To check for homogeneity of variances a Levene test was applied. A *post hoc* analysis by Multiple Range test was performed to look for specific differences between pairs of groups. Statistics were performed using Statgraphics Centurion software.

3 | RESULTS

In total, 2,381 limpets were recorded on María Madre island (Figure 4).

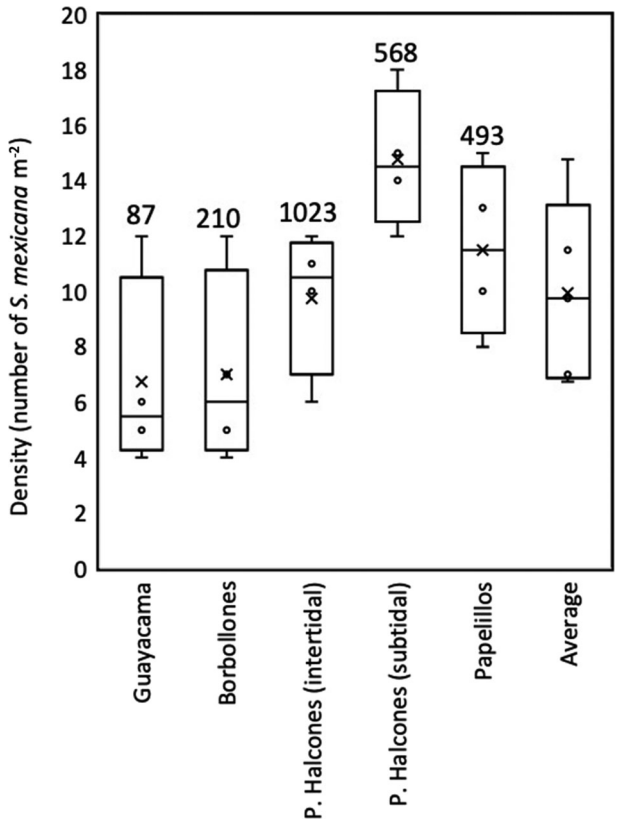

FIGURE 4 Box and whisker plot of number of specimens of *Scutellastra mexicana* per m^2 measured in areas of high density. Average is represented by X, median by the horizontal line inside the box. The maximum and minimum values are displayed with vertical lines ('whiskers') connecting the points to the box. Points are outliers' values. The numbers above the bars show the number of specimens in each locality.

The largest population was found at Punta Halcones, where 1,023 specimens were recorded in the intertidal zone, and 568 in the subtidal zone (Figure 4). In areas with dense aggregations, 6–12 individuals m^{-2} were found (Figure 4), although the mean density in the whole area sampled was 0.07 individuals m^{-2}. The shell length average was 11.9 cm, and the maximum was 17 cm (Figure 5). In this area, many specimens were grazing away from their home scars at the time of sampling (Figure 3b). The density increased in the subtidal zone, with 11–19 individuals m^{-2} (Figure 3c). Average shell length was similar to that in the intertidal zone (12.1 cm), but maximum length was greater in the subtidal (20.3 cm; Figure 5). It is also important to note the presence of some individuals of about 4 cm long, one of them attached to an adult of *S. mexicana* (Figure 3b).

There was a shell midden in the upper littoral running in a strip parallel to the tide line where the average shell length was 12 cm with a range between 5 and 16 cm. The Kolmogorov–Smirnov test did not show significant differences between both distributions (shell middens vs. natural populations; $p = 0.616$).

In the area of Papelillos, 493 specimens were recorded (Figure 4), with densities ranging from 8 to 15 individuals m^{-2} where limpets formed dense aggregations, although the mean density in the whole area sampled was 0.09 individuals m^{-2}. Average and maximum shell lengths were 10.5 and 19 cm respectively (Figure 5), some juveniles of approximately 4 cm long were also found (Figure 3f). It is also

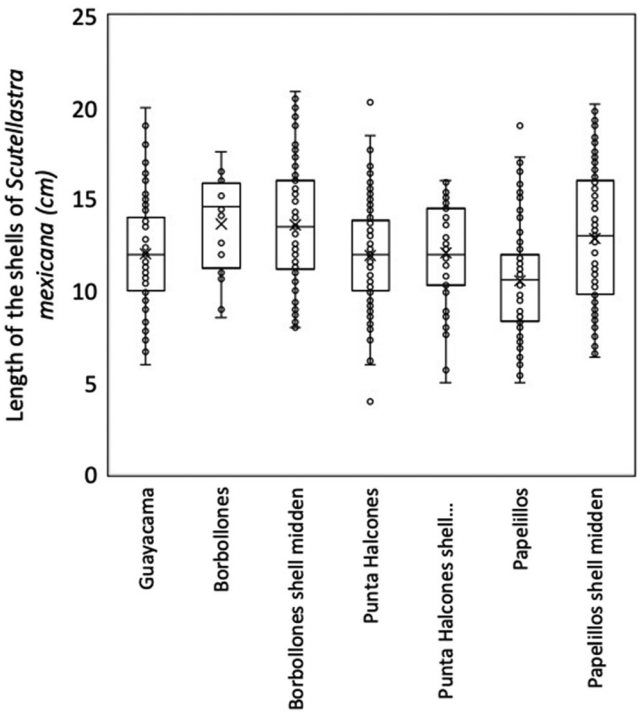

FIGURE 5 Box and whisker plot of the length of the shells of *Scutellastra mexicana* in the different localities, both in natural population and shell middens. Mean is represented by X, median by the horizontal line inside the box. The maximum and minimum values are displayed with vertical lines ('whiskers') connecting the points to the box. Points are outliers' values.

important to point out that the average size of the individuals was significantly smaller than all of the other three locations (Figure 5; $F = 8.14$, $p = 0.001$).

The average and maximum sizes of the shells in the midden were 12.9 and 20.2 cm respectively (Figure 5). Many of these shells, due to their state of preservation, appear to be more recent than those found at the other sample areas. The Kolmogorov–Smirnov test showed significant differences between the two distributions (shell middens vs. natural populations; DN = 0.374384, K-S = 2.58239, $p < 0.0001$).

In Borbollones, 210 specimens were recorded with a mean density in the whole area sampled of 0.05 individuals m^{-2}, with 4 to 12 individuals m^{-2} in the areas where limpets were observed at high densities (Figure 4). The average and maximum lengths of the shells were 13.6 and 17.6 cm, respectively (Figure 5).

There was an enormous shell midden in the supralittoral zone perfectly aligned with the maximum tide line, so probably most of the shells have been deposited naturally. This is also supported by the presence of shells of other species of molluscs that are not consumed by humans. In the midden, the average shell length was 10.1 cm. The largest specimen measured 16.9 cm and the smallest 5 cm in length (Figure 5).

The size-frequencies of shell middens versus natural populations were similar, and a Kolmogorov–Smirnov test (DN = 0.173529; K-S statistic = 0.698237; $p = 0.714168$) showed that there was not a significant difference between the two distributions (Figure 6).

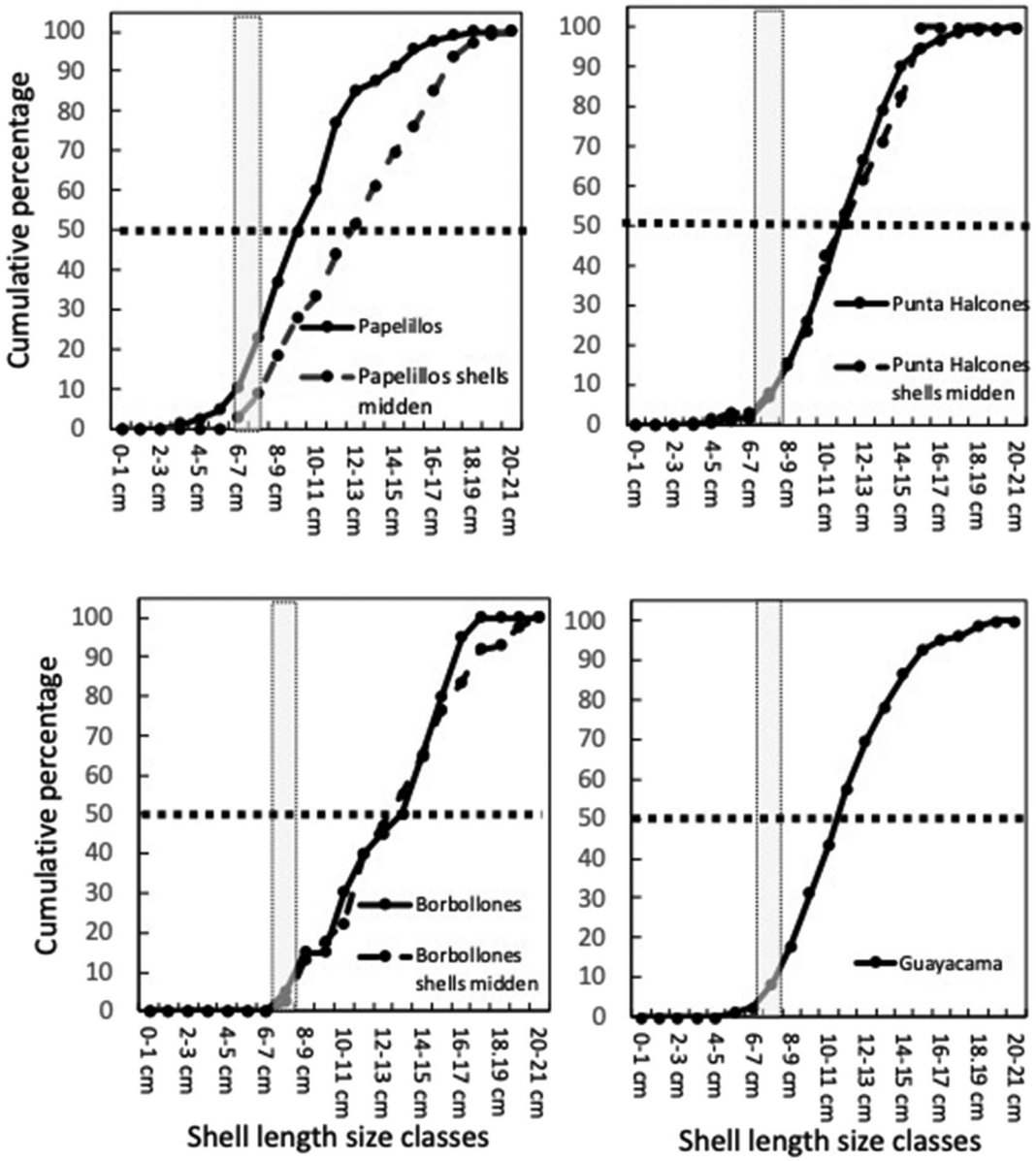

FIGURE 6 Cumulative frequency distribution of the shell size for the four natural populations (Guayacama, Borbollones, Punta Halcones and Papelillos), and shell midden. Horizontal dashed line shows median size for 50% of the population. Gray vertical box shows size at first sexual maturity (male) (sensu Villalpando-Canchola & Acosta-Maya, 1987).

In Guayacama, only 87 specimens were recorded, with a mean density in the sample area of 0.3 limpets m^{-2}. Where there were aggregations of limpets the density varied from 4 to 14 individuals m^{-2} with a mean size of 13.7 cm (Figures 4 and 5). The largest and smallest specimens were 17.5 and 6 cm long respectively.

We compared the cumulative frequency distributions for the four populations simultaneously (Figure 6). The graphs show that the distributions were generally parallel and S-shaped indicating that the most abundant classes were those of intermediate size. For example, at Punta Halcones the size-frequency distribution showed that most of the individuals were between 11.0 and 15.0 cm whilst at Papelillos most of the individuals were between 9.0 and 11.0 cm; these differences were significant when compared to those reported in the other populations. It is also notable that the smallest individuals were typically between 5 and 6 cm and were only found in very low numbers. At Borbollones, the smallest animals were 8.5 cm. This is indicative of ageing populations with very low recruitment rates.

4 | DISCUSSION

Scutellastra mexicana belongs to the Patellogastropoda, the most primitive group of present-day gastropods. It is the only known true patellid living on tropical coasts, and the only New World Patellidae (Nakano & Ozawa, 2007). It is also the largest known patellid limpet reaching up to 35 cm in length (Keen, 1958, specimen from Caleta, Acapulco, México). Their conspicuously large size has made this species the preferred target of human collection as evidenced by its presence in the middens and other archaeological sites along the Mexican Pacific Ocean coast, showing that people used this limpet as food, tools and jewellery long before the Spanish colonization arrived. For centuries, the people who inhabited this coast collected the species in a sustainable manner, but in recent times, hundreds of tons were fished in about a decade, which has practically brought the species to the brink of extinction. Ridgway et al. (1998) indicated that the species has become extinct in certain areas of the Mexican continental coast, while Simison (2000) reported that the species has not been seen in the Baja California area since 1972, and that in six consecutive sampling campaigns no living specimen was recorded, suggesting that the species is now extinct. More recently, Holguín-Quiñones (2006) confirmed that there is no evidence of its presence on the coast of Colima after its populations were overexploited in the 1970s.

Overexploitation, the dearth of knowledge on the biology of *S. mexicana*, but above all, the lack of any strategies for its management and conservation have caused its dramatic decline. This work reports, for the first time, the presence and the population status of *S. mexicana* on María Madre island, probably the only site in the world where there is hope for the survival of the species.

The mean densities obtained in this study (0.07 individuals m^{-2} in Punta Halcones, 0.09 in Papelillos, 0.05 in Borbollones and 0.3 in Guayacama) are slightly higher than those recently recorded in areas of the central Pacific mainland of Mexico (0.001 limpets m^{-2}) (Valdez-Cibrián et al., 2021), and similar to that in María Cleofas (0.3 individual m^{-2}) (Carballo et al., 2019), both areas subject to illegal harvesting. These densities are much lower than those recorded in populations of other species of giant limpets in protected areas not subject to fishing, such as *Scutellastra laticostata* (4–9 individuals m^{-2}) (Scheibling & Black, 2020), and *P. ferruginea* (6–35 individuals m^{-2}) (Espinosa & Rivera-Ingraham, 2017).

Several parameters have been used to determine the level of exploitation of limpets, e.g. size distribution, abundance and disruptions in the population sex ratio, often skewing towards the sex that matures at smaller size/age (Martins et al., 2008; Martins et al., 2017). The results of the current study suggest that the species has been heavily depredated by the inhabitants of the María Madre (prisoners, security personnel, etc.) probably for self-consumption. This is most evident at Papelillos, because of its proximity to the prison camp, where the average size of the individuals was more than 2 cm less compared to the shells in the middens where the harvested limpets were probably cleaned and eviscerated (10.5 vs. 12.8 cm). Similarly, the fishing pressure to which the species has been subjected is evident in the maximum size of the shells: 20.2 cm in the midden versus 19 cm in the habitat. Fishers usually target the largest limpets (Branch & Odendaal, 2003), but as the larger limpets become scarcer, they then tend to collect smaller animals (Guerra-García et al., 2004; Martins et al., 2008; Riera et al., 2016; Sousa et al., 2019) whereas strictly protected sites not only have significantly larger average sized limpet but also a greater size range than unprotected sites (Sagarin et al., 2007; Sousa et al., 2020). This is also observed in the size structure at Papelillos which was significantly smaller than those of the other populations of María Madre (Figure 6). This indicates that this site has been subjected to intensive harvesting that has reduced both the size of the population and the average size of the individuals.

The other large population on the island is in Punta Halcones where the limpets were found grazing away from their home scar in low tide making them very easy to collect by humans and other predators such as raccoons and badgers, which can easily access the area at low tide.

Size-selective harvesting has been shown to have a negative effect on the demography, life history and ecology of marine species, and particularly in recruitment events (Rochet, 1998; Olsen et al., 2004). In Papelillos and Punta Halcones, very few juveniles were found, including one on the shell of an adult *S. mexicana*, a phenomenon previously observed in other species such as *P. ferruginea* (Laborel-Deguen & Laborel, 1991; Casu et al., 2010). In Guayacana and Borbollones, the smallest individual measured more than 6 cm (1 individual), but most were above 8 cm length. This situation also occurs on the continental coasts of the central Pacific, where exhaustive surveys conducted in 2019 found no individuals smaller than 7 cm (Valdez-Cibrián et al., 2021).

The presence of so few juveniles suggests that the density of the populations found in María Madre are probably too low to allow for effective reproductive events leading to the production of sufficient recruits to sustain the species. It is possible that the strong wave shear may limit larval settlement or affect the post-settlement survival

of juveniles in the intertidal zone (Martins et al., 2010), but no juveniles were found in the subtidal zone either. Recruitment depending on the density of adults was studied in *Patella vulgata* where reproductive output was significantly correlated to recruitment events occurring 2–15 years earlier (Sundelöf et al., 2010). *S. mexicana* employs external fertilization, and as such adults of both sexes must be present at a minimum density to ensure sufficient concentration of gametes in the water column to enable fertilization (Espinosa & Rivera-Ingraham, 2017). With strict protection in place that prevents the removal of more individuals, those areas where dense aggregations of the species are found (Figures 2 and 3) could potentially result in effective fertilization to produce sufficient recruits for the population to be self-sustaining and potentially grow.

In addition to overall low population density, another issue that may contribute to the low recruitment rate is the preferential harvesting of the largest specimens that could lead to an imbalance in the sex ratio of the population. It is known that size at maturation can be affected in populations that are heavily exploited, with the larger individuals, mostly females, being preferentially harvested. *S. mexicana* is a sequential protandrous hermaphrodite species that shows alternating sexuality. All reach adulthood as the same sex (males), and then at least some of them change into females (Villalpando-Canchola & Acosta-Maya, 1987) but heavy size-biased exploitation of sequential protandrous hermaphrodite species such as *S. mexicana* can result in disruption to the population sex ratio, often skewing it towards males. This biased sex-ratio, can lead to a marked Allee effect compromising the viability of the species and even leading to local extinctions (Alonzo & Mangel, 2004; Hamilton et al., 2007; Espinosa, Rivera-Ingraham & García-Gómez, 2009). In such a situation, the mean shell sizes of the sexes can decrease in response to the exploitation (Borges et al., 2016), and limpets appear to adapt with males undergoing sex change into females earlier at a smaller size and younger age (Martins et al., 2017). However, given the very critical situation of *S. mexicana*, of which possibly only a few thousand specimens remain, a study to estimate sex ratio that would involve the sacrificing of individuals is not an option.

4.1 | Future measures to preserve this endangered species

While the limited access to María Madre may have acted as a de facto marine reserve, there is evidence that *S. mexicana* has been fished illegally by the inhabitants of the island. A similar situation has occurred on the other islands of the archipelago, such as María Cleofas (Carballo et al., 2019), and San Juanito (unpublished data); in these cases, by fishermen coming from the mainland. Of the four islands that make up the Islas Marías archipelago, the only one for which there is no information to date is María Magdalena. However, given the impunity with which fishermen have acted in the past, it is very likely that the situation on this island is very similar to the others in the archipelago.

Now that the prison population has left, it is imperative to establish legal measures, and extreme protection of these areas to help the viability of *S. mexicana* in the María Islands. This species was included in the Official Mexican Standard NOM-059-ECOL-1994, under the status of 'Special Protection', which was updated in 2010 but without changing its status. Consequently, effective protection measures were never established, and the authorities only limited themselves to seizing or confiscating the meat of the limpet in the few cases where a complaint was made. Based on the information generated in this research, together with that of Carballo et al. (2019) and Valdez-Cibrián et al. (2021), a proposal has been presented to the Mexican government to update the regulations to change the current status of 'threatened species', to 'species in serious danger of extinction'. This will mean stricter protection for the remaining populations, and anyone caught extracting or trading in any part of this species could even go to jail. The process to update the regulation will be completed by the end of 2023.

Several studies have shown that limpet populations respond positively to management measures, as long as there is enforcement of those measures by the responsible authorities and more particularly when there is the active participation of the local communities (Henriques, Delgado & Sousa, 2017; Sousa et al., 2019). Therefore, infographics will be produced to be exhibited in fishing cooperatives, fish markets and diving centres, explaining the change of status and the penalties that would result in its fishing and/or commercialization.

Once this new status is achieved, information and awareness campaigns will be carried out in the fishing communities that have traditionally harvested this species, so that they understand its cultural and ecological value, which is so emblematic of Mexico.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

José Luis Carballo https://orcid.org/0000-0002-5146-7597

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