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Pocillopora damicornis-associated echinoderm fauna: richness and community structure across the southern Mexican Pacific

Andrés López-Pérez[1] · Rebeca Granja-Fernández[2] · Francisco Benítez-Villalobos[3] ·
Octavio Jiménez-Antonio[4]

Abstract The reef-associated echinoderm cryptofauna has received scarce attention notwithstanding its large-scale effects on reef community structures and ecosystem functioning world-wide. In the present study, a spatially hierarchical quantitative sampling protocol was designed to address *Pocillopora damicornis*-associated echinoderm diversity within and across southern Mexican Pacific reef localities. It was also aimed to evaluate if species composition and abundance varies across several spatial scales. The number of sampled echinoderm species from 36 *P. damicornis* coral heads was 24, which fell inside the 95 % confidence interval of the Chao1 species richness estimator, while as many as 42 species were expected to occur. The analysis indicated that the echinoderm diversity was not particularly large among the samples (4–6 species) or across localities (5–12 species). Nevertheless, the observed associated echinoderm richness resulted from a small, although significant, species replacement among the coral heads and reef localities across the southern Mexican Pacific. The relative large number of echinoderms associated with *P. damicornis* may serve as a proxy for predicting potential biodiversity loss caused by the coral reef degradation currently observed in the study area.

Introduction

Echinoderms constitute a conspicuous element of the marine invertebrate fauna of coral reefs. Some of them may play pivotal roles and changes in their abundance or biomass can have large effects on reef community structure and ecosystem functioning (Birkeland 1989). Numerous studies have addressed species richness and distribution of echinoderm communities associated with coral communities and reefs via visual censuses of relatively large epibenthic individuals (De Beer 1990; Starmer 2003; Sandin et al. 2008; Fabricius et al. 2014; Hermosillo-Nuñez et al. 2015; Netchy et al. 2015; and a large number of references therein), but few have focused on coral-associated echinoderm cryptofauna (Sloan 1982; Black and Prince 1983; Zamorano and Leyte-Morales 2005; Enochs and Hockensmith 2008; Stella et al. 2011b; Alvarado and Vargas-Castillo 2012; Enochs 2012; Enochs and Manzello 2012; and references therein).

The coral reef cryptofauna consists of a diverse suite of organisms that live within the cavities of the reef framework structures (Reaka-Kudla 1997), which provide them with a variety of physical structures for their movement, conceal-ment, escape, refuge, reproduction, breeding and feeding (Goldberg 2013). Cryptobenthic species are functionally connected and comprise large biomass, even in dead reef

✉ Andrés López-Pérez
alopez@xanum.uam.mx

1 Departamento de Hidrobiología, División CBS, UAM-Iztapalapa, San Rafael Atlixco 186, Col, Vicentina 09340, Ciudad de México, México

2 Doctorado en Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana, San Rafael Atlixco 186, Col, Vicentina CP 09340, Ciudad de México, México

3 Instituto de Recursos, Universidad del Mar, Campus Puerto Ángel, 70902 San Pedro Pochutla, Puerto Ángel, Oaxaca, México

4 Programa de Licenciatura en Biología Marina, Universidad del Mar, Campus Puerto Ángel, 70902 San Pedro Pochutla, Puerto Ángel, Oaxaca, México

frameworks of the most eroded rubble environment of the Pacific Gulf of Panama (Enochs 2012; Enochs and Manzello 2012). Moreover, they are important in supporting complex coral reef food webs, and are known to protect corals from predators and to clean coral tissue surfaces (Enochs and Hockensmith 2008; Glynn and Enochs 2011).

The local distribution and abundance of reef-associated organisms are positively correlated with the total available habitat (Kohn and Leviten 1976). By virtue of their extensive available habitat and coral morphology, species of the genera *Pocillopora* along with those of *Acropora* and *Stylophora* are commonly preferred as host by invertebrates (Stella et al. 2010, 2011a, b). *Pocillopora* is a widely distributed genus (family Pocilloporidae) of scleractinian corals known to harbor a large number of invertebrate species (Stella et al. 2011b). In particular, *P. damicornis* has a widespread distribution in the tropical Indo-Pacific (Veron 2000), although it is also believed that it actually consists of a species complex (Schmidt-Roach et al. 2013, 2014). In the Eastern Pacific, *P. damicornis* ranges from the Gulf of California, Mexico, to Easter Island, Chile, including oceanic islands such as Revillagigedo, Clipperton Atoll, Malpelo, Cocos and the Galapagos Islands (Reyes-Bonilla 2002). Along with *P. verrucosa* and *P. capitata*, this species is considered largely responsible for reef framework construction in the Eastern Pacific (Glynn and Ault 2000; Reyes-Bonilla 2003).

The cryptic invertebrate fauna associated with *P. damicornis* has been very well studied in the Indo-West Pacific (Tsuchiya 1999; Stella 2012; Stella et al. 2014; and references therein) and the Eastern Pacific (Enochs and Hockensmith 2008; Alvarado and Vargas-Castillo 2012; Enochs 2012; Enochs and Manzello 2012; and references therein), but few of them have documented the presence of echinoderms. In the Eastern Pacific, studies addressing cryptic echinoderms associated with *P. damicornis* have been mostly conducted in Central America (see above), including two in Mexico (Benítez-Villalobos 2001; Zamorano and Leyte-Morales 2005), despite the fact that southern Mexican Pacific coral reefs are considered among the most abundant in the entire region, consisting of over 41 patch reefs (López-Pérez and López-García 2008; López-Pérez et al. 2012) with 3- to 4-m-thick reef frame buildups (Glynn and Leyte-Morales 1997; López-Pérez et al. 2012) and a surface area that may reach up to 120 ha (López-Pérez unpublished data).

A previous survey addressing biodiversity associated with coral reefs (Granja-Fernández et al. 2014; López-Pérez et al. 2016) revealed that echinoderms were conspicuous, common and widespread, but surprisingly poorly known in the area. Therefore, the present study aims to assess the echinoderm cryptofauna inhabiting *P. damicornis* corals across reefs in the southern Mexican Pacific, a region of moderate to high marine biodiversity in the tropical eastern Pacific (Bastida-Zavala et al. 2013). For this purpose, a spatially hierarchical quantitative sampling protocol was designed to: (1) address the total species diversity of the *P. damicornis*-associated echinoderm fauna, and (2) to evaluate if species composition and abundance varied across spatial scales.

Materials and methods

Study area

The study area (Fig. 1) comprises coral communities and reefs from the southern Mexican Pacific. The region experiences a dry season that extends from November to April, and a rainy season (800–1500 mm year) from May to October. The Eastern Pacific warm pool (SST >28 °C) has an influence on these coastal waters. This oceanographic feature is centered off Guatemala and the southwestern coast of Mexico, and is characterized by high water temperatures, small annual thermal oscillations (<2 °C), an average surface salinity of 34 psu, and the presence of a shallow (20–40 m) and quite stable thermocline (Fiedler and Talley 2006). Except for a recent study recording echinoderm faunal turnover during the 2009–2010 El Niño event in the area (López-Pérez et al. 2016), it is still unknown if seasonal changes exert any influence on the epifauna or crypto-echinoderm fauna of the region.

In the study area, up to 19 coral communities and reefs occur along the coast of Guerrero state (López-Pérez et al. 2012) and up to 28 along the coast of Oaxaca (López-Pérez and López-García 2008). Thirty-four species of zooxanthellate corals belonging to seven genera (*Pocillopora*, *Pavona*, *Porites*, *Psammocora*, *Leptoseris*, *Gardineroseris*, and *Fungia*) inhabit the Mexican Pacific (Reyes-Bonilla et al. 2005b). Three mushroom coral species reported for the latter genus (Reyes-Bonilla et al. 2005b) are presently classified with the genus *Cycloseris* (Gittenberger et al. 2011). Finally, three *Pocillopora* species (*P. capitata*, *P. damicornis*, and *P. verrucosa*) are largely responsible for the reef framework construction in the eastern Pacific (Glynn and Ault 2000).

Sampling

By virtue of its widespread distribution (Veron 2000), commonness and large contribution to reef framework construction in the area (Glynn and Leyte-Morales 1997; López-Pérez et al. 2012), the coral species *P. damicornis* (sensu lato) was chosen as the host species for conducting the study. Four similar-sized heads of *P. damicornis* (height + width + depth ≈ 75 cm) were collected from nine localities in the southern Mexican Pacific (36 coral heads in total). During February–March 2010, coral heads were retrieved from Estacahuite, Salchi, San Agustín and Montosa island localities in the region of Mazunte-Bahías de Huatulco, Oaxaca; during
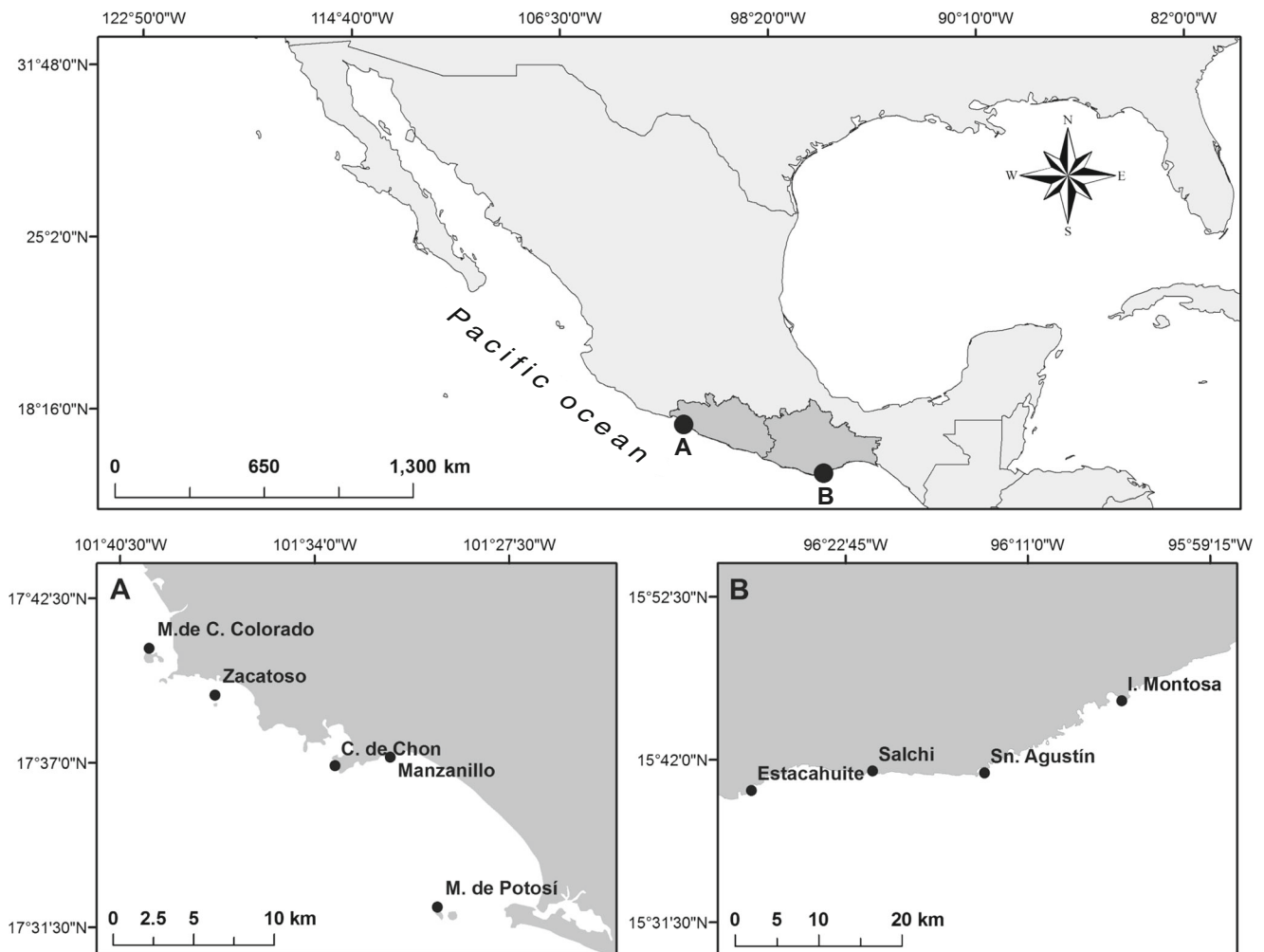
Fig 1 Sampled localities in Ixtapa (*A*), Guerrero (*B*) and Mazunte-Bahías de Huatulco, Oaxaca, southern Mexican Pacific coast

December 2010, coral heads were collected in Morro de Cerro Colorado, Zacatoso, Caleta de Chon, Manzanillo and Morros de Potosí localities in the region of Ixtapa, Guerrero (Fig. 1). Only coral heads without visible signs of damage or stress (i.e., partial mortality, bleaching, algal overgrowth) were randomly selected within each locality.

The coral heads were gently broken from the bottom with a hammer and chisel after which they were quickly placed in a 20-l bucket, underwater. Branches of each coral head were detached separately and all macroinvertebrates (>5 mm in size) and vertebrates encountered were extracted from the coral head. The remaining rubble was placed in a bucket of seawater and examined again for any remaining animals. Finally, the seawater, in which the coral head and later on the coral fragments were kept, was sieved through a 2-mm sieve. All macroinvertebrates and vertebrates were deposited in the Natural History Museum of the Universidad del Mar, Oaxaca, México, where they have been properly curated.

Although all associated animals were extracted, echinoderms were selected as a model group for the current study because identification to the species level could be more

adequately done for these animals (Granja-Fernández et al. 2014, 2015a, b) compared to other invertebrate taxa in the area (Bastida-Zavala et al. 2013). Echinoderms were identified to the species level following the taxonomic criteria of Caso (1979) for Asteroidea, Granja-Fernández et al. (2014) for Ophiuroidea, Caso (1978) and Mortensen (1928) for Echinoidea, and Solís-Marín et al. (2009) for Holothuroidea.

Data analysis

Coral heads were considered as replicates per locality. Echinoderm abundance was used for generating individual-based rarefaction curves of observed species richness for each of the two regions, Guerrero and Oaxaca, and it was used to calculate the species richness estimator Chao 1 for echinoderms of the whole southern Mexican Pacific. The former analysis is for comparing observed species accumulation curves between regions, while the latter is an abundance-based non-parametric estimator for addressing species completeness of the southern Mexican Pacific. The programme EstimateS (Colwell 2015) was used to compute individual-

based rarefaction curves of observed species richness and to calculate the species richness estimator Chao 1. In each case, estimates were done with a randomized order of samples with replacements for 1000 runs.

Echinoderm abundance data were further used to estimate for each coral head: species richness (S), abundance (N), diversity (Shannon H'), evenness (Pielou J'), and dominance (Simpson λ). A principal component analysis of replicate indexes was used to evaluate community patterns in *P. damicornis*-associated echinoderm diversity estimates across the sample localities.

The effect of region and locality on the *P. damicornis*-associated echinoderm fauna in the southern Mexican Pacific was tested by a nested (locality nested into region) permutation-based analysis of variance (PERMANOVA). PERMANOVA was implemented on a Bray–Curtis similarity matrix after square-root transformation of the obtained echinoderm abundance data. Furthermore, an ordination procedure (principal coordinate analysis, PCO) was used to graphically determine whether region or locality could be meaningfully grouped based on their overall *P. damicornis*-associated echinoderm assemblages. A PCO was selected because this technique plots the similarity among coral heads based on their distance from each other in multivariate space. The PCO was conducted on the Bray–Curtis similarity matrix of square-root transformed echinoderm abundance data (Anderson et al. 2008). In addition, as an exploratory tool, vector overlay on the PCO of the echinoderm-abundance fauna was drawn for those cases where Spearman rank correlations between ordination axes (PCO) and abundance data were >0.5.

Finally, abundance and biomass of the *P. damicornis*-associated-echinoderm data were used to explore levels of disturbance across southern Mexican Pacific localities using the abundance/biomass comparison (ABC) method (Warwick 1986). Based on the abundance/biomass relationship, the W statistic was determined for each coral head and used as a dependent variable, which was evaluated via nested (localities nested into region) analysis of variance.

Results

A total of 1834 individuals belonging to 24 echinoderm species were sampled from 36 *Pocillopora damicornis* coral heads. The mean ± standard deviation abundance of echinoderms per locality is presented in Table 1. Twelve recorded species belonged to Holothuroidea, nine to Ophiuroidea and two each to Echinoidea and Asteroidea. *Holothuria* was the most species-rich genus within the Holothuroidea (eight species) followed by *Neothyone* (two species), while *Ophiactis*, *Ophiocoma* and *Ophiothrix*, with two species each, were the

most dominant genera in the Ophiuroidea, whereas the rest of the genera contributed by a single species each.

The ophiuroid *Ophiothrix* (*Ophiothrix*) *spiculata* contributed by far the largest number of individuals (1082, 59 %), followed by *Ophiactis simplex* (278, 15 %) and *Ophiactis savignyi* (222, 12 %). Three ophiuroid species (12.5 % of the total species) contributed ~86 % of the echinoderm abundance associated with *P. damicornis*, while 21 species (87.5 %) were less abundant since they accounted for only ~14 % of the total echinoderm abundance. In total, 14 species (58 %) contributed less than ten individuals each, and of these, seven species (~29 %) were represented by a single individual, and an additional three species (12.5 %) were represented by several specimens found in a single locality.

Rarefaction curves were constructed to estimate the completeness of sampling effort and, therefore, the reliability of species richness estimates for the *P. damicornis*-associated echinoderm fauna of the southern Mexican Pacific (Fig. 2). None of the rarefaction curves (Fig. 2) reached an asymptote, indicating that the number of individuals (1834), and hence the number of examined *P. damicornis* coral heads (36), was insufficient to reliably estimate the total number of echinoderm species within this habitat and the study area based on these curves. Even when rarefaction curves did not reach an asymptote, the number of observed echinoderm species (24) fell inside the 95 % confidence interval expected for the study area calculated via Chao 1 (Fig. 2a). When compared to the lower limit of the confidence interval, the observed richness is 27 % higher than predicted by the model, but when compared to the upper limit, it represents just 57 % of the potential expected species richness (42 species) in *P. damicornis* in southern Mexican Pacific reefs. Finally, the curves also suggest that *P. damicornis* harbors more echinoderm species in coral localities located in the Ixtapa region than in localities at the Mazunte-Bahías de Huatulco region (Fig. 2b).

The PCA of replicate (per coral head) diversity indexes (S, N, H', J', λ) across the southern Mexican Pacific localities (Fig. 3) indicated that the *P. damicornis*-associated echinoderm fauna experienced negligible changes in species richness (S), diversity (H'), evenness (J') and dominance (λ) but large changes in abundance (N) across the study area. In general, coral heads retrieved from localities from Ixtapa region harbored a higher echinoderm abundance than heads collected in localities of the Mazunte-Bahías de Huatulco region, along the coast of Oaxaca.

The PCO ordination (Fig. 4) accounted for 52 % of the total variation in the two first axis (PCO1, 34 %; PCO2, 18 %). The ordination indicated that, in general, strong differences between regions (Ixtapa, Guerrero, and Mazunte-Bahías de Huatulco, Oaxaca) occurred in the *P. damicornis*-associated echinoderm fauna. Plotted Spearman rank correlation vectors (>0.5) suggested that coral heads collected in Ixtapa localities have higher abundances of the holothuroids *Neothyone*

Table 1 Distribution and abundance of echinoderm species associated with *Pocillopora damicornis* coral heads

Regions	Ixtapa, Guerrero					Mazunte-Bahías de Huatulco, Oaxaca			
Localities	MCC	ZA	CC	MA	MP	ES	SAL	SA	IM
Phataria unifascialis							0.25 ± 0.5		
Amphipholis squamata								0.25 ± 0.5	
Ophiactis savignyi	3 ± 6	13.3 ± 11	8.3 ± 10.9	0.25 ± 0.5	19 ± 8	7.5 ± 6.7	0.5 ± 1	3.3 ± 6.5	0.5 ± 1
Ophiactis simplex	11.3 ± 12.3	4 ± 1.4	14 ± 5.9	0.25 ± 0.5	16.3 ± 16	9.3 ± 10.6	1.5 ± 1.9	1.3 ± 2.5	9.5 ± 6.5
Ophiocoma aethiops			1 ± 1.2	0.25 ± 0.5		0.75 ± 1.5			2.3 ± 2.9
Ophiocoma alexandri	0.75 ± 1.5	0.25 ± 0.5			0.25 ± 0.5	0.5 ± 1	4.8 ± 6.2	0.75 ± 0.96	5.5 ± 10.3
Ophionereis annulata									0.75 ± 1.5
Ophiothela mirabilis					0.25 ± 0.5				
Ophiothrix (Ophiothrix) rudis	4.8 ± 6.6	2 ± 2.7	2.8 ± 2.2	0.25 ± 0.5		0.5 ± 1	0.25 ± 0.5		1.8 ± 2.4
Ophiothrix (Ophiothrix) spiculata	61.8 ± 73.2	92.3 ± 85.4	33.3 ± 15.6	2.3 ± 1.9	74.5 ± 33.9	3.8 ± 1.7	0.5 ± 1	0.5 ± 1	0.75 ± 1.5
Diadema mexicanum						0.25 ± 0.5			0.75 ± 1.5
Hesperocidaris asteriscus			0.5 ± 1		0.75 ± 1.5	0.25 ± 0.5			0.5 ± 1
Afrocucumis ovulum	0.25 ± 0.5	0.25 ± 0.5							
Holothuria (Thymiosycia) impatiens	0.5 ± 1	2.3 ± 2.6	4.8 ± 2.2	1.8 ± 1.5	0.25 ± 0.5	0.75 ± 1.5	0.5 ± 1	3.8 ± 2.6	3.8 ± 3.3
Holothuria (Halodeima) kefersteini			0.25 ± 0.5						
Holothuria (Mertensiothuria) hilla			0.25 ± 0.5						
Holothuria (Platyperona) difficilis				1 ± 1.2					
Holothuria (Selenkothuria) theeli		1 ± 0.2			4.5 ± 2.9				
Holothuria (Semperothuria) imitans				0.25 ± 0.5					
Holothuria (Semperothuria) languens			0.5 ± 1						
Holothuria (Thymiosycia) arenicola			0.25 ± 0.5						
Neothyone gibber			0.75 ± 1.5						
Neothyone gibbosa	0.25 ± 0.5	0.75 ± 0.96	0.25 ± 0.5						
Pentamera chierchiae			1.5 ± 1.3						

Values are mean number of individuals per 0.25 m^2 ± standard deviation. In each locality, $n = 4$

MCC Morro de Cerro Colorado, *ZA* Zacatoso, *CC* Caleta de Chon, *MA* Manzanillo, *MP* Morros de Potosí, *ES* Estacahuite, *SAL* Salchi, *SA* San Agustín, *IM* Isla Montosa

gibbosa, *Holothuria* (*Selenkothuria*) *theeli*, *Holothuria* (*Thymiosycia*) *impatiens* and the ophiuroids *Ophiothrix* (*Ophiothrix*) *spiculata*, *Ophiactis savignyi* and *Ophiactis simplex*, when compared to coral heads retrieved from localities from the Mazunte-Bahías de Huatulco region. The observed pattern (Fig. 4) is fully supported by a nested PERMANOVA analysis (Table 2). There are significant differences in the *P. damicornis*-associated echinoderm composition and abundance among localities nested into regions (Ixtapa, Guerrero, and Mazunte-Bahías de Huatulco, Oaxaca) (pseudo-$F_{8,34} = 2.58$, $p < 0.01$) and between regions themselves (pseudo-$F_{1,34} = 3.34$, $p = 0.03$). The analysis also indicated that larger differences in echinoderm fauna occurred mainly among coral heads within localities (36.7 %), followed by differences among localities (24.9 %) and lastly between regions (22.5 %), with the last two being closely similar.

Finally, the nested analysis of the W statistic resulting from the ABC method indicated that the *P. damicornis*-associated echinoderm fauna experienced less stressful conditions in Mazunte-Bahías de Huatulco localities (large W statistic) than in localities along the coast of Ixtapa, Guerrero ($F_{1,25} = 8.49$, $p < 0.01$). In addition, the results also suggested that, among localities within each region (Ixtapa, Guerrero; Mazunte-Bahías de Huatulco, Oaxaca), the *P. damicornis*-associated echinoderm fauna may have undergone similar stressful conditions ($F_{1,25} = 2.36$, $p = 0.053$).

Discussion

The echinoderm fauna of the southern Mexican Pacific has been studied for more than a century by conventional collection methods such as dredging and hand-collecting (Clark 1940; Caso 1951; Granja-Fernández et al. 2014). This allowed the recording of its marine biodiversity (Granja-Fernández et al. 2015a, b), but precluded direct faunal comparisons
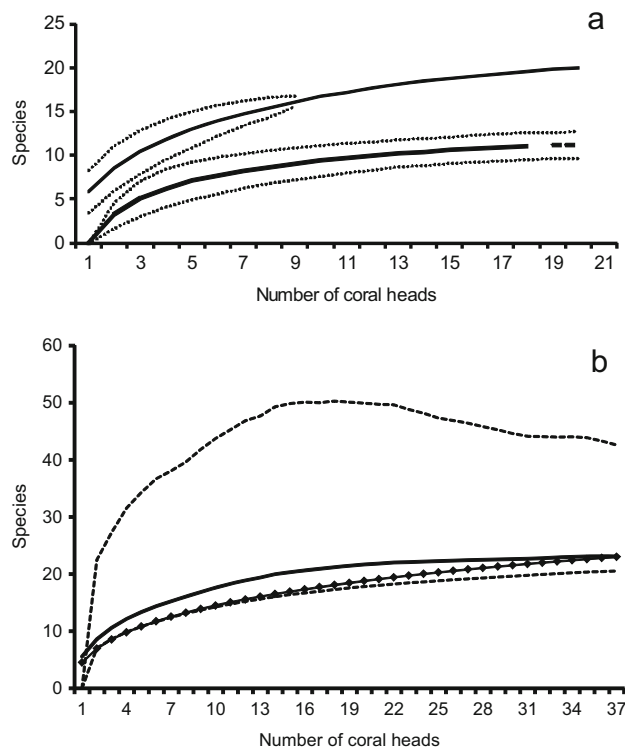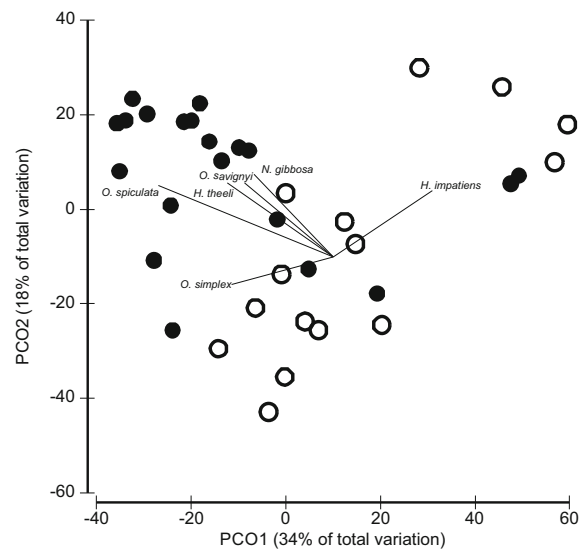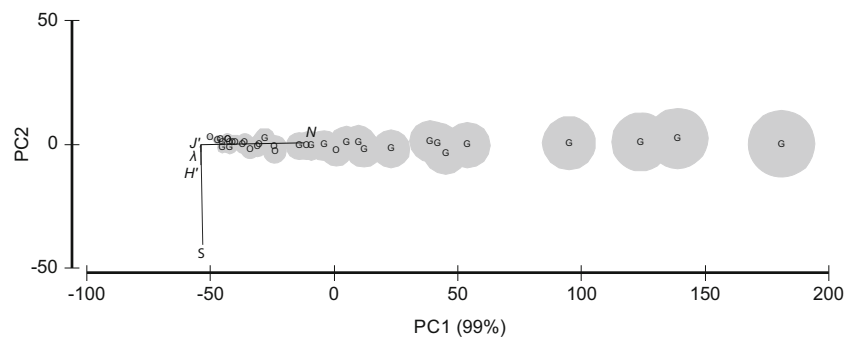
Fig 2 Rarefaction curves for the echinoderms sampled in *Pocillopora damicornis* coral heads in Guerrero and Oaxaca patch reefs, Southern Mexican Pacific. **a** Individual-based rarefaction curves of observed species richness for each region (Ixtapa [*upper curve*] and Mazunte-Bahías de Huatulco [*lower curve*]). **b** Observed and expected (Chao 1 estimator) echinoderm species richness in southern Mexican Pacific patch reefs. *Dashed lines* 95 % confidence interval, *solid line* expected richness, *solid line with diamonds* observed richness

Fig 4 Principal coordinate analysis ordination of *Pocillopora damicornis*-associated echinoderm fauna across southern Mexican Pacific. Each *dot* represents a coral head. *Filled circles* Ixtapa, Guerrero, *open circles* Mazunte-Bahías de Huatulco, Oaxaca. Spearman rank vectors represent those cases were correlation between ordination axes and abundance data were >0.5

among habitats or localities by virtue of their poorly designed sampling protocol. The standardized quantitative sampling protocol practiced in the present study resulted in an estimation of the diversity and showed the spatial variation of the *P. damicornis*-associated echinoderm fauna across southern Mexican Pacific reef localities.

In contrast to micro-crustaceans and polychaetes, which are numerous but too small to be easily detected, the echinoderms accounted for a small fraction (12.5 %) of the macrofauna (Annelida, Arthropoda, Mollusca, Echinodermata) encountered in *P. damicornis* coral heads. Nevertheless, our sampling

protocol allowed for a thorough sampling of the echinoderm cryptofauna, even for small ophiuroids such as *Ophiactis* spp., *Ophiothela* spp. or *Ophiothrix* spp. and juveniles of large ophiuroids, asteroids and echinoids. Therefore, the *P. damicornis*-associated echinoderm diversity reported here is an adequate estimate for the coral heads sampled, but may represent a relatively small fraction (4 coral heads, ~ 0.25 m² per locality) of the echinoderm fauna associated with *P. damicornis* in each locality, which itself is an even smaller fraction of the reef habitat as a whole. One has to bear in mind that *P. damicornis* corals represent just one of an endless number of potential habitats able to host echinoderms in the study area. For example, Granja-Fernández et al. (2014) identified up to eight kinds of habitats for ophiuroids in Mexican Pacific reefs, namely rocks, sponges, free-living rhodoliths, attached algae, sand, soft corals and dead and live corals, the last of which consists of 16 coral species (Reyes-Bonilla et al. 2005b).

The *P. damicornis* coral heads sampled in the southern Mexican Pacific reefs rendered 24 echinoderm species. The

Fig 3 Principal component analysis of echinoderm diversity indexes (richness *S*, diversity *H'*, evenness *J'*, dominance λ, abundance *N*) across southern Mexican Pacific. *G* Ixtapa, Guerrero, *O* Mazunte-Bahías de Huatulco, Oaxaca. Each *dot* represents a coral head. *Bubble sizes* represent relative abundance

Table 2 Nested (locality within region) non-parametric permutation-based analysis of variance of 24 echinoderm species abundance data

Source	df	SS	MS	Pseudo-F	P	Unique perms
Region	1	9127.9	9127.9	2.1479	0.0478	1259
Locality (region)	8	37,393	4674.1	2.3865	0.0002	9885
Residual	27	52,881	1958.6			
Total	36	1.01E + 05				

rarefaction curves did not approach an asymptote value, even for this relatively restricted habitat, which suggests that more coral heads need to be sampled in order to have a more accurate estimate of the number of echinoderm species associated with *P. damicornis*. However, rarefied observed values fell inside the 95 % interval expected by Chao 1 and they are still large when compared to the lower bound level (20 spp.) of the confidence interval. According to the upper limit of the confidence interval, up to 42 echinoderm species are expected to occur in *P. damicornis* corals, which is still far from the 72 species currently recognized to inhabit shallow (0–60 m) hard substrate (rocky and coral reef areas) in the southern Mexican Pacific (Maluf 1988; Granja-Fernández et al. 2015a), and may potentially use *P. damicornis* as a refuge. It is tempting to think that the observed species richness ($n = 24$) is a non-representative small fraction of the expected echinoderm richness in southern Mexican Pacific reef environment (Granja-Fernández et al. 2015a). It is indeed 33.3 % of the total echinoderm fauna but hosted by just a single reef coral species. In the near future, studies should concentrate on how many echinoderm species depend on each coral host species, and especially how many of these are host-specific.

Considering the numbers of collected echinoderms, 45.8 % belonged to Holothuroidea, 37.5 % to Ophiuroidea, and 8.3 % each to Asteroidea and Echinoidea. When compared to the potential echinoderm standing stock of 72 species for the area (Granja-Fernández et al. 2015a), *P. damicornis* corals harbor 39 % of Holothuroidea, 50 % of Ophiuroidea and 16 % each of Asteroidea and Echinoidea. According to these figures, rather than any other echinoderm taxa, Ophiuroidea stands as the taxon with more affinity and/or ability to inhabit *P. damicornis* coral heads in the study area. As suggested by previous studies, the observed pattern is a common place in cryptofauna evaluations since, among echinoderms, ophiuroids are well represented in *Pocillopora* spp., occurring in high densities (Sloan 1982; Black and Prince 1983; Benítez-Villalobos 2001; Matos-Nogueira 2003; Zamorano and Leyte-Morales 2005; Martins-Garcia et al. 2008; Glynn and Enochs 2011; Stella et al. 2010, 2011b; Alvarado and Vargas-Castillo 2012). The observed pattern may be closely tied to the *P. damicornis* branching morphology, as the species offers highly complex three-dimensional microenvironments and complex physical structures for the movement, concealment, escape, refuge, reproduction, breeding and feeding

of numerous marine animals (Glynn and Enochs 2011), such as small (<1.1 cm: *Ophiactis* spp., *Ophiothela* spp., *Ophiothrix* spp.) and large-sized (>1.1 cm – <2.9 cm: *Ophiocoma* spp., *Ophionereis* spp.) ophiuroids (Granja-Fernández et al. 2014).

Compared to previous studies of the cryptofauna inhabiting *Pocillopora* species, the echinoderm richness recorded here is remarkable even when the sample size is equivalent or smaller than observed during past studies. For example, 2 echinoderm species were recorded in Playa Blanca, Costa Rica (Alvarado and Vargas-Castillo 2012); 8 species in Rottnest Island (Black and Prince 1983) and 11 species in Lizard Island (Stella et al. 2010), Australia; and up to 13 species in La Entrega and Casa Mixteca reefs, in the southern Mexican Pacific (Benítez-Villalobos 2001; Zamorano and Leyte-Morales 2005). This is more than the single species recorded from mushroom corals in the Philippines and elsewhere (Hoeksema et al. 2012; Bos and Hoeksema 2015); 6 species from *Millepora alcicornis* colonies (Martins-Garcia et al. 2008) and 4 from *Mussismilia hispida* in Brazil (Matos-Nogueira 2003); and 15 species from *Millepora exaesa*, 23 from *Porites nigrescens*, and 37 from *Porites* spp. in Aldabra Atoll, Seychelles (Sloan 1982). This difference is particularly striking when compared to previous studies conducted in the southern Mexican Pacific (Benítez-Villalobos 2001; Zamorano and Leyte-Morales 2005) and Central America reefs (Alvarado and Vargas-Castillo 2012) since the occurrence of reefs (Glynn and Ault 2000) along with echinoderm species richness and composition among areas is quite similar (Pérez-Ruzafa et al. 2013; Solís-Marín et al. 2014; Granja-Fernández et al. 2015b). These differences in species richness may be explained by differences in methods.

Regarding species richness, the PCA analysis of diversity estimators indicated that echinoderm species richness is not particularly high in *P. damicornis* coral heads (4–6 species) or across localities (5–12 species) in the southern Mexican Pacific. Instead, the observed echinoderm species richness ($n = 24$) resulted from small, although significant, species variation (i.e., beta diversity) among coral heads, localities and lastly between regions (Ixtapa, Guerrero, and Mazunte-Bahías de Huatulco, Oaxaca). The last is not uncommon since it is known that species richness associated with *P. damicornis* can vary among adjacent and extremely separated samples (coral heads) resulting in a high regional diversity without a corresponding high local diversity (Black and Prince 1983).

According to a study conducted on several host species (*P. damicornis*, *Acropora nasuta*, *Acropora millepora* and *Seriatopora hystrix*) in Lizard Island (Stella et al. 2010), differences in species richness and abundance among coral colonies of the same species may result from differences in the amount of live tissue and living space, yet the relationship between abundance and species richness and coral attributes was weak overall and more research on this aspect needs to be conducted.

The present analysis revealed that species composition and abundance of *P. damicornis*-associated echinoderm cryptofauna showed meaningful variations at scales ranging from tens of meters (among coral heads within localities) to hundreds of kilometers (~650 km) across southern Mexican Pacific reefs. Larger variation occurred among *P. damicornis* coral heads within localities (36.7 %), followed by variation among localities (24.9 %), and lastly between regions (22.5 %). The relatively large variation in echinoderm cryptofauna at a small spatial scale may be related to species interactions and its effects on spatial species distribution and abundance, and the probability of recording rare species and randomness (Whittaker 1972), while the minor variation observed at large spatial scales may be related to environmental homogeneity across reef localities and regions in the southern Mexican Pacific (Glynn and Ault 2000).

The abundance/biomass relationship summarized by the W statistic suggested that the *P. damicornis*-associated echinoderm fauna across southern Mexican Pacific reefs may undergo a wide range of stressful conditions. There is no clear pattern among localities within regions, but the results clearly signal that the echinoderm fauna in Ixtapa (Guerrero) is exposed to relatively greater stressful conditions than in the Mazunte-Bahías de Huatulco region. Both these regions are adjacent to major tourist destinations in the southern Mexican Pacific, namely Ixtapa-Zihuatanejo, Guerrero, and Bahías de Huatulco, Oaxaca. While no conservation management plans exist for the former, the latter has been part of a Natural Protected Area (Parque Nacional Huatulco) since 1998 (CONANP 2003). There is no firm ground to suggest that the reefs of the Mazunte-Bahías de Huatulco region are more protected, but the relative high abundance of the suspension-feeding brittle star *Ophiothrix* (*Ophiothrix*) *spiculata* (Hendler 1996) in waters around Ixtapa localities during this study suggest a high sediment load here. Alternatively, the sediment load in waters around Ixtapa may not be related to poorer conservation status when compared to Mazunte-Bahías de Huatulco, Oaxaca. Instead, it may have resulted from upwelling during sampling (ALP, personal observation). Therefore, future sampling should be performed in different seasons (rainy and dry) in order to compare the echinoderm abundance/biomass in the study area.

The relative large number of echinoderm species associated with *P. damicornis* documented in the current work, along with a far larger expected number of other invertebrate taxa based on records from elsewhere in the Indo-Pacific (Glynn and Enochs 2011; Stella et al. 2011b), may serve as a proxy for predicting potential biodiversity loss associated with coral reef degradation in the area. Recent declines in coral cover due to coral bleaching (Reyes-Bonilla et al. 2002; López-Pérez et al. 2016) and human-induced disturbance in southern Mexican Pacific patch reefs (López-Pérez and Hernández-Ballesteros 2004) may have profound but unknown implications for coral reef cryptofauna in the area. Therefore, conservation management strategies should be designed to preserve live coral cover and its ecosystem functioning.

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