CrossMark

ORIGINAL PAPER

Influence of the coral reef assemblages on the spatial distribution of echinoderms in a gradient of human impacts along the tropical Mexican Pacific

Brenda B. Hermosillo-Nuñez[1,2] · Fabián A. Rodríguez-Zaragoza[3] ·
Marco Ortiz[1] · Luis E. Calderon-Aguilera[4] · Amilcar L. Cupul-Magaña[5]

Abstract Fourteen species of echinoderms and their relationships to the benthic structure of the coral reefs were assessed at 27 sites—with different levels of human disturbances—along the coast of the Mexican Central Pacific. *Diadema mexicanum* and *Phataria unifascialis* were the most abundant species. The spatial variation of the echinoderm assemblages showed that *D. mexicanum, Eucidaris thouarsii, P. unifascialis, Centrostephanus coronatus, Toxopneustes roseus, Holothuria fuscocinerea, Cucumaria flamma*, and *Echinometra vanbrunti* accounted for the dissimilarities among the sites. The spatial variation among the sites was mainly explained by the cover of the hard corals (*Porites, Pocillopora, Pavona, Psammocora*), different macroalgae species (turf, encrusting calcareous algae, articulated calcareous algae, fleshy macroalgae), sponges, bryozoans, rocky, coral rubble, sand, soft corals (hydrocorals and octocorals), *Tubastrea*

✉ Fabián A. Rodríguez-Zaragoza
rzf39259@cucba.udg.mx

[1] Laboratorio de Modelamiento de Sistemas Ecológicos Complejos (LAMSEC), Instituto de Ciencias Naturales AvH, Instituto Antofagasta, Universidad de Antofagasta, P.O. Box 170, Antofagasta, Chile

[2] Programa de Doctorado en Ciencias Aplicadas, Mención Sistemas Marinos Costeros, Facultad de Recursos del Mar, Universidad de Antofagasta, P.O. Box 170, Antofagasta, Chile

[3] Laboratorio de Ecosistemas Marinos y Acuicultura, Departamento de Ecología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Carretera a Nogales Km. 15,5, Las Agujas Nextipac, CP 45110 Zapopan, Jalisco, Mexico

[4] Departamento de Ecología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada, Carretera Ensenada-Tijuana No. 3918, Zona Playitas, CP 22860 Ensenada, BC, Mexico

[5] Departamento de Ciencias Biológicas, Centro Universitario de la Costa, Universidad de Guadalajara, Av. Universidad 203, Del. Ixtapa, CP 48280 Puerto Vallarta, Jalisco, Mexico

🐉 Springer

coccinea coral, *Balanus* spp., and water depth. The coverage of *Porites, Pavona*, and *Pocillopora* corals, soft coral, rock, and Balanos shows a positive relationship with the sampling sites included within the natural protected area with low human disturbances. Contrary, fleshy macroalgae, sponges, and soft coral show a positive relationship with higher disturbance sites. The results presented here show the importance of protecting the structural heterogeneity of coral reef habitats because it is a significant factor for the distribution of echinoderm species and can contribute to the design of conservation programs for the coral reef ecosystem.

Introduction

Coral reefs are considered among the most bio-diverse marine ecosystems in the world (Reaka-Kudla 1997; Glynn and Enochs 2011), which is principally due to the high structural heterogeneity of their habitats. In the eastern tropical Pacific (ETP), the coral reef ecosystems are distributed from the Gulf of California to Ecuador, with *Pocillopora* and *Porites* being the main reef builders, followed by other species, such as *Psammocora stellata, Pavona gigantea, Leptoseris papyracea,* and *Pavona clavus*. These species build small fringing reefs, reef patches, and develop isolated coral colonies (Glynn and Ault 2000; Reyes-Bonilla et al. 2005). In western Mexico, on the coasts of Jalisco, Colima, and Michoacán, there are coral assemblages dominated mainly by the genera *Pocillopora* (Reyes-Bonilla and López-Pérez 1998; Reyes-Bonilla et al. 2013). Unfortunately, different human activities such as fishing, tourism, port industry, and sewage discharge, among others, lead to the fragmentation of these habitats with negative effects on recruitment, protection, and local migration of several benthic and pelagic species (Fahrig 2003; Gosset and Rives 2006; Mora et al. 2007).

Within coral ecosystems, the echinoderms constitute a relevant group because of their important role for maintaining ecosystem function and "stability". Some echinoderms are considered as a keystone species in different marine ecosystems, because they control the abundance and distribution of other benthic species, such as fleshy macroalgae, molluscs, and corals (Reyes-Bonilla and Calderon-Aguilera 1999; Tuya et al. 2004), thus impacting the whole community structure (Paine 1969; Tuya et al. 2004; Gaymer and Himmelman 2008; Ortiz et al. 2013a). Likewise, recent studies based on network analysis show that the echinoderms conform keystone species complexes in different benthic marine ecosystems, controlling the dynamics of several species (Ortiz et al. 2013a, b). In coral reefs, sea urchin and sea star species drive the processes of bioerosion, coral recruitment, and transfer of energy in the ecosystem (Glynn et al. 1979; Carreiro-Silva and McClanahan 2001). Furthermore, several studies indicate that the spatial and seasonal variation of the echinoderms is related mostly to processes such as settlement, recruitment, food availability, depredation, competition, physical factors, and fishing (Hagen and Mann 1992; Tyler et al. 2000; Alves et al. 2001; Hasan 2005; Clemente et al. 2009), as well as to the structural properties of habitats (Entrambasaguas et al. 2008; Alvarado et al. 2012). Such processes operate at different spatial and temporal scales (Legendre and Legendre 1998; Chapman and Underwood 2008).

Although in the tropical Mexican Pacific coast, several studies have been conducted on the ecology and taxonomy of echinoderms that inhabit coral ecosystems (e.g., López-Uriarte et al. 2009; Granja-Fernández and López-Pérez 2012; Alvarado and Solís-Marín 2013; Ríos-Jara et al. 2013; Rodríguez-Troncoso et al. 2013; Hermosillo-Nuñez et al. 2015), few attempts have focused on the assessment of how human interventions change the influence of reef coral on echinoderms. Along the coast of Jalisco, Colima, and Michoacán, there are important coral assemblages with high richness and cover (Reyes-Bonilla et al. 2013), which could be impacted by the proximity to human settlements. Coral reefs have been subjected to a wide spectrum of human disturbances, such as eutrophication, pollution, and land-use changes that have deteriorated the coral ecosystems in terms of coral growth, reproduction and competition (e.g., Wilkinson 1999; Nyström et al. 2000; Koop et al. 2001; Szmant 2002; González-Lozano et al. 2006). In this case, the principal impacts on the marine ecosystems on the coast of Jalisco, Colima and Michoacán correspond to tourism, recreation, industrial activities, harbors, urban development, habitat destruction, and wastewater discharges (Ortiz-Lozano et al. 2005; Nava and Ramírez-Herrera 2012).

It has been widely accepted that habitat heterogeneity and habitat fragmentation promote opposite impacts on the structure, richness, spatial/temporal distribution, density, and coexistence of species (Wilcox and Murphy 1985; Frost et al. 1999; Attrill et al. 2000; Hovel and Lipcius 2001; Kelaher 2003). For example, Rodríguez-Zaragoza et al. (2011) showed that coral communities contribute to the heterogeneity of benthic habitats, promoting the diversity of reef fishes. Likewise, Hermosillo-Nuñez et al. (2015) concluded that the spatial distribution and abundance of echinoderms can be explained by habitat structure. Jiménez (2001) showed that reef areas with recreational activity and commercial diving reflect an equal level of damage to the corals. González-Lozano et al. (2006) determined that water quality in port areas exceeds the permitted limits of anthropogenic pollution, affecting the biota. It is therefore expected that the spatial distribution of echinoderms can be determined by habitat heterogeneity. The aim of this work was to assess how coral assemblages influence the spatial variation of echinoderms in coastal areas under different regimes of human interventions along the coast of Jalisco, Colima, and Michoacán (western Mexico). The information obtained in this study could be used when developing management strategies focused on coastal conservation.

Materials and methods

Study area

The Mexican Pacific coast between the 20° and 17°N includes the states of Jalisco, Colima, and Michoacán (Fig. 1). This area is characterized by an irregular coastline comprised principally of rocky, coral reefs, closed bays, sand beaches, and estuaries. Likewise, the coastal benthic systems are influenced by the California Current (between February and April), the North Equatorial Countercurrent (between August and January) and the convergence of both (between May and June) (Godínez-Domínguez and González-Sansón 1998).

Along this coastal area, it is possible to recognize sites with different levels of disturbances related to the distance to human settlements. The sites of Isla Cocina, Isla Pajarera, Isla Mamut, La Pajarera, Isla Pelicano, and Ensenada Cocinas are located in the state of
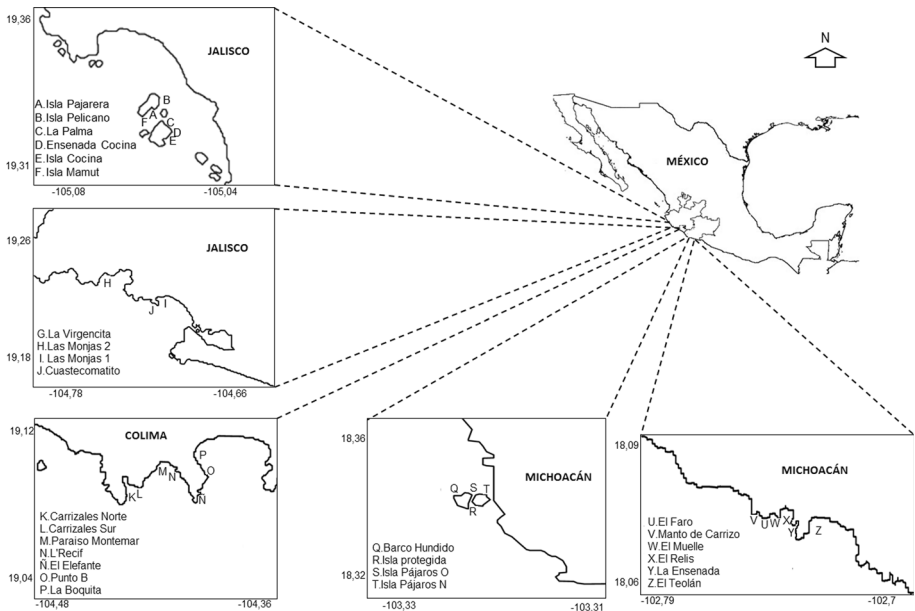
Fig. 1 Study area and sampling sites at Jalisco, Colima, and Michoacán in the western México

Jalisco within the Santuario Islas e Islotes de Bahía Chamela, decreed as a natural protected area (NPA) for protection of biodiversity and richness (DOF 2002). This NPA is relevant because it protects unique environments relatively isolated from human activities. The Santuario Islas e Islotes de Bahía Chamela is exposed to lower levels of human intervention, since only recreational, research and education activities are permitted (CONANP 2008). The sites of La Virgencita and Las Monjas 2, located in Jalisco, Carrizales Norte, Carrizales Sur, Paraiso Montemar, L'Recif, El Elefante in Colima, and Barco Hundido, Isla Protegida, Isla Pajaros O, Isla Pajaros N, El Faro, El Relis, La Ensenada and El Teolán in Michoacán are coastal areas under medium disturbance because they are located at a distance from human settlements. Finally, Cuastecomatito, Las Monjas1, Punto B, La Boquita, El Muelle, and Manto de Carrizo are considered sites under higher disturbance because they are located close to human settlements.

Sampling procedure

The fieldwork was conducted during February and September of 2010. A total of 27 sites with coral assemblages (ten in Jalisco, seven in Colima and ten Michoacán) were chosen for sampling (Fig. 1). Each study site presented different geomorphological features, habitat heterogeneity, depth, and wave exposure. The coral assemblages were dominated mainly by the genera *Pocillopora, Porites*, and *Pavona*, which are distributed between a depth of 2 and 15 m. The abundance of echinoderms, corals, and other benthic groups was assessed by SCUBA diving at three transects per site, and the depth was also recorded. The transects were located parallel to the coast and different sampling strategies were applied per transect: (1) diurnal visual censuses of 20×5 m^2 for sea stars, 20×2 m^2 for sea cucumbers and 20×1 m^2 for sea urchins; (2) video transects of 20×0.6 m^2 were

recorded (0.4 m above the bottom) for other benthic organisms. From each video, 40 frames were subsampled; 50 fixed points from each frame were used to estimate the hard-coral cover (*Pocillopora*, *Porites*, *Pavona* and *Psammocora*), as well as the cover of hydrocorals, bryozoans, octocorals, sponges, fleshy macroalgae, encrusting calcareous algae, articulated calcareous algae, turf, sessile organisms, mobile organisms, rocks, sand, and coral rubble (Rodríguez-Zaragoza et al. 2011; Hermosillo-Nuñez et al. 2015). Organisms were identified in situ to the taxonomic level of species, based on Brusca (1980), Hickman (1998) and using the photographic guides of Gotshall (1998), Kerstitch and Bertsch (2007). All census sampling was carried out by the same person.

Statistical analysis

The sampling effort for the study area was evaluated through the accumulation curves of the exponential function of the Shannon diversity index ($e^{H'}$) and the reciprocal of the Simpson dominance (index) (1/D). All curves were built with 10,000 random combinations without replacement using the software Estimates V9.1 (Colwell 2009). The species richness (S) was defined as the total number of species recorded for each site. The abundance (N) was analyzed based on the density represented as the total number of individuals of each species per square meter (ind/m^2). The heterogeneity of the species was evaluated with the Shannon diversity index (H′, nats) and the Simpson dominance index (D), which were estimated per transect level for comparison among sampling sites using their mean values (Magurran 2004; McCoy and Bell 1991). This was done with Primer V6.1 software (Clarke and Warwick 1994).

The analyses of variances (ANOVA) were performed using permutations to evaluate the changes of the mean values from the species richness, abundance, Shannon diversity and Simpson dominance. These unrestricted analyses were performed because the data did not meet with parametric statistical assumptions. The ANOVAs were constructed using Euclidean distance matrices following the criteria of Anderson et al. (2008). Unrestricted ANOVAs generate a variance partitioning through of the estimation of a statistical *Pseudo-F* following a design similar to a general linear model (Anderson et al. 2008). The experimental design analysis was based on three nested factors (state, area, and site with 3, 6, and 27 levels, respectively), using a type II model with random factors. The spatial variation of the composition and abundance of the species of echinoderms was evaluated through a permutational multidimensional analysis of variance (PERMANOVA), which was based on the same ANOVA design. These data were pretreated with Log (X+1) to reduce the contribution of the most abundant species and increase the contribution of those with very low abundance. Subsequently, a matrix of Bray-Curtis similarity was constructed. All ANOVA and PERMANOVA tests were conducted using the software PRIMER V6.1+PERMANOVA (Clarke and Gorley 2006; Anderson et al. 2008). Several similarity percentage analyses (SIMPER) were performed to compare the contributions of the species within and among sampling sites. SIMPER is based on the Bray-Curtis index for estimating the average dissimilarity between pairs of sample groups and determining the contributions to the average similarity within each group (Clarke and Warwick 2001).

A canonical additive partitioning of the spatial variation of the echinoderms was done between environmental and spatial predictive variables based on canonical redundancy analyses (RDA) (Legendre and Legendre 1998). The spatial variation of the echinoderm assemblage was represented by *Y* vectors (species richness, Shannon diversity index, Simpson dominance index and total species abundance) or the *Y* matrix (echinoderm species composition and abundance). Environmental variables (Env. Var.) were included

in the X matrices using the mean values of the coverage of the benthic organisms and the substrate types estimated from the videotransects. Additionally, the depth was considered in this matrix. The W matrices correspond to spatial variables (Spat. Var.), where x, y, and y^2 were derived from third-order polynomial terms of the geographic coordinates represented as distances in kilometers (Legendre and Legendre 1998). The *Trace* statistic indicated the variation of Y explained by X and Y. Stepwise forward selection was conducted to identify the environmental variables that best explained the variation in Y. The RDA ordinations were developed using the software CANOCO v4.5 (ter Braak and Šmilauer 2002), assuming a linear relationship between the biological and the spatial-environmental components. Multicollinearity was evaluated among the environmental variables because it could modify the RDA model outputs. All RDA analyses were built using the variance inflation factor (VIF) lower than ten to avoid severe multicollinearity (Chatterjee et al. 2000; Graham 2003).

Results

A total of 3754 individuals belonging to 14 echinoderm species (two sea stars, seven sea urchins, and five sea cucumbers) were registered. The accumulation curves of the Shannon diversity index and Simpson dominance index showed an asymptotic behavior (Online Resource 1), indicating that the abundant and very abundant species, which are those that contribute most to the assemblage structure, were well represented. The most abundant species were *Diadema mexicanum* and *Phataria unifascialis*, with 2520 and 477 individuals, respectively.

There was significant spatial variation in the echinoderm assemblage (i.e., community attributes, and composition and abundance) associated with the coral ecosystems (Table 1).

Table 1 ANOVA and PERMANOVA outputs showing the spatial variation analyses of echinoderm assemblage

Source	Pseudo-F	p	Source	Pseudo-F	p
ANOVA					
Echinoderm species richness (S)			Echinoderm abundance (N)		
State	0.16	0.88	State	0.99	0.46
Area (St)	3.56	**0.02**	Area (St)	2.87	**0.04**
Site (Ar(St))	2.25	**0.003**	Site (Ar(St))	3.70	**0.0001**
Shannon diversity (H′)			Simpson dominance (D)		
State	1.31	0.35	State	0.32	0.79
Area (St)	1.18	0.33	Area (St)	3.89	**0.01**
Site (Ar(St))	2.19	**0.004**	Site (Ar(St))	1.75	**0.02**
PERMANOVA					
Echinoderm assemblage structure					
State	1.57	0.19			
Area (St)	1.52	0.11			
Site (Ar(St))	3.33	**0.0001**			

These designs were built: (i) three-way fully nested ANOVA was applied to compare the average echinoderm species richness, abundance, Shannon diversity, and Simpson dominance; (ii) three-way fully nested PERMANOVA was used to compare the echinoderm assemblage structure. Bold numbers correspond to a statistical significance (p ≤ 0.05), Ar corresponds to a source Area and St corresponds to a source Site

The outcomes of the three-way fully nested ANOVA showed that the average values of the species richness, echinoderms abundance, and Simpson dominance index had a significant spatial variation with the area and site levels (Table 1). The sites with the highest average richness were Isla Pájaros Norte, Isla Protegida, La Boquita, and Punto B (Fig. 2). Meanwhile, the sites Isla Cocinas, Ensenada Cocinas, La Boquita, Las Monjas 1, and El Faro showed the highest magnitudes of dominant species (Fig. 2). On the other hand, the Shannon diversity index showed a significant variation at the site scale, where Paraíso Montemar, Las Monjas 2, L'Recif, Isla Pájaros Norte, El Relis, La Ensenada, Carrizales Sur, and Isla Pelicano had the greatest magnitudes of diversity (Fig. 2). Similarly, the three-way fully nested PERMANOVA showed that the echinoderm composition and abundance varied significantly only at the site level (Table 1).

The SIMPER results showed that *D. mexicanum, Eucidaris thouarsii, P. unifascialis, Centrostephanus coronatus, Toxopneustes roseus, Holothuria fuscocinerea, Cucumaria flamma*, and *Echinometra vanbrunti* contributed principally to the dissimilarities among the sites (Online Resource 2). In general terms, these outcomes showed that the site explains the major spatial variation of the echinoderm assemblage in the eastern tropical Pacific.

The canonical additive partitioning showed that the accounted variation [a + b + c] in these models was from 52.8 to 84.1 %, where the Shannon diversity index and Simpson dominance index had the highest values, while the species richness showed the least explanatory power (Table 2). The variations of the abundance, Shannon diversity, Simpson dominance, and the composition and abundance of the echinoderm species were explained mostly by pure environmental component—fraction [a]—with values between 42.1 and 48.7 %. In turn, the spatially structured environmental component—fraction [b]—explained from 17.6 to 33.6 % of the variation of the community attributes and echinoderm assemblage. On the other hand, variation in the species richness was mainly explained (24.6 %) by the spatially structured environmental component [b] and (20.7 %) the pure environmental component [a]. However, spatial variables—fraction [c]—accounted for less than 8 % of the total variation analyzed in all partitions, while the unexplained variation—fraction [d]—was between 15.9 and 47.2 % (Table 2). These results suggest that the spatial variation of the echinoderm assemblage related to the coral ecosystems was mainly explained by the environmental variables, that is, by the reef habitat structure. Nevertheless, the echinoderm species richness depends also on a set of environmental variables, but these covary with the spatial configuration of the sampling sites along the western coast of Mexico.

The environmental variables that contributed to the species richness of the echinoderms were the *Porites* cover, coral rubble, turf, and articulated calcareous algae, while the spatial variables' relationship was x and y^2, representative of the longitudinal and latitudinal variation, respectively (Table 2). Likewise, the environmental variables that explained the greatest variation of the abundance, Shannon diversity, and Simpson dominance were the coral cover of *Porites*, rocky cover, encrusting calcareous algae, fleshy macroalgae, *Balanus, Pavona* coral, and sponges. On the other hand, the environmental variables that explained the greatest variation of the composition and abundance of the echinoderm species were the rocky cover, *Balanus*, soft coral, *Pavona* coral, fleshy macroalgae, coral rubble, *Porites* coral, dead coral, encrusting calcareous algae (ECA), *Pocillopora* coral and sponges, as well as the depth (Table 2). The RDA ordination showed that *E. thouarsii* and *P. unifascialis* had a positive relationship with articulated calcareous algae, and deep and soft coral; however, *P. pyramidatus* and *Euapta godeffroyi* presented a positive relationship with *Porites* cover. The echinoids *D. mexicanum* and *T. roseus* were related with rocky and *Balanus* cover, while *A. pulvinata, T. depresus* and *Isostichopus fuscus*
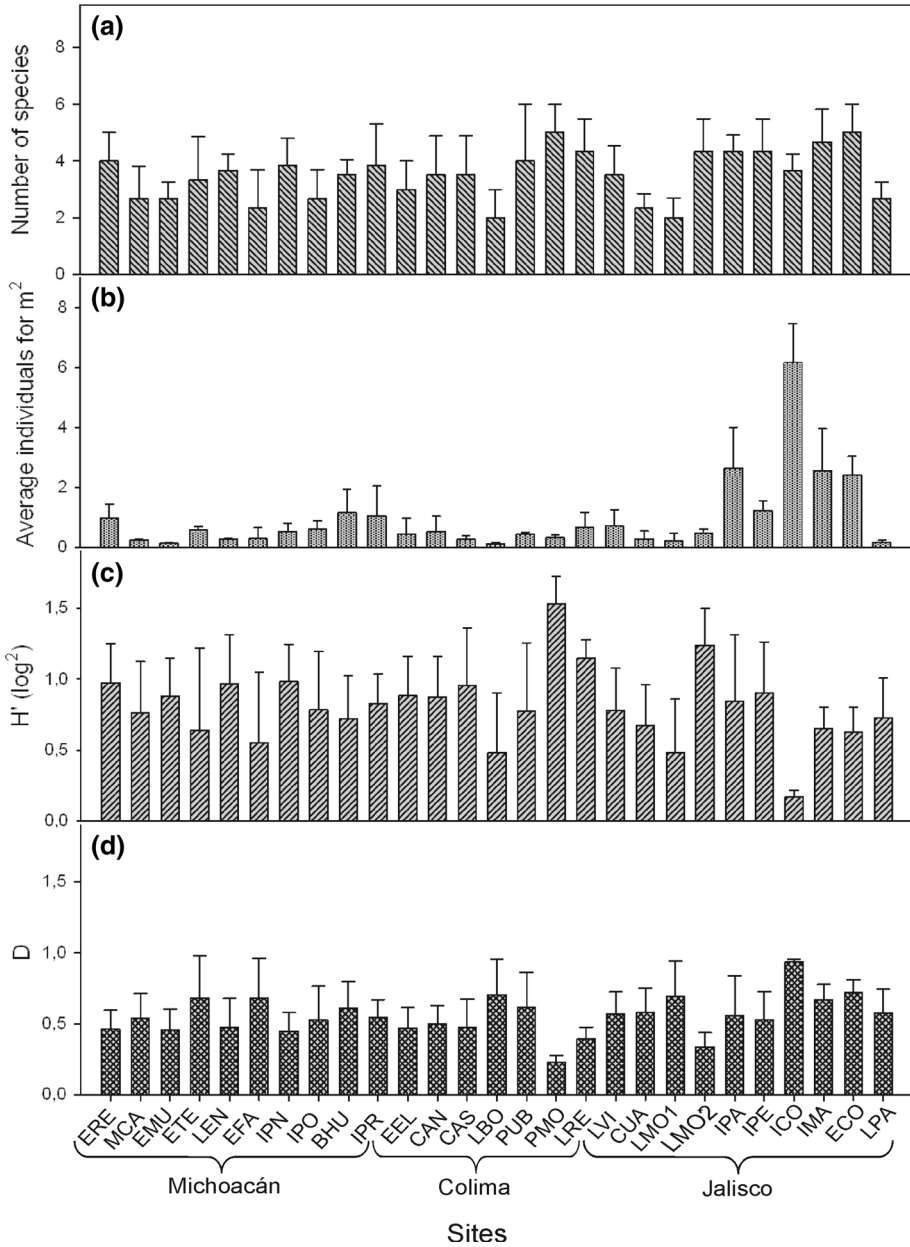
Fig. 2 Species richness (**a**), abundance (**b**), Shannon diversity (**c**), and Simpson dominance (**d**) by sampling sites at Jalisco, Colima, and Michoacán. Sites: Jalisco, La Virgencita (LVI), Cuastecomatito (CUA), Las Monjas 1 (LMO1), Las Monjas 2 (LMO2), Isla Pajarera (IPA), Isla Pelicano (IPE), Isla Cocina (ICO), Isla Mamut (IMA), Ensenada Cocinas (ECO), La Palma (LPA). Colima, Elefante (EEL), Carrizales Norte (CAN), Carrizales Sur (CAS), La Boquita (LBO), Punto B (PUB), Paraíso Montemar (PMO), L' Recif (ĹRE). Michoacán, El Relis (ERE), Manto de Carrizo (MCA), El Muelle (EMU), El Teolan (ETE), La Ensenada (LEN), El Faro (EFA), Isla Pájaros Norte (IPN), Isla Pájaros Oeste (IPO), Barco Hundido (BHU), Isla Protegida (IPR)

Table 2 Canonical additive partition of the echinoderm assemblage's spatial variation at Western Mexican Pacific coral communities

	[a]	[b]	[c]	[d]	Total exp. [a + b + c]	Env. var. [a + b]	Spat. var. [b + c]
Species richness (S)	20.7	24.6	7.5	47.2	**52.8**	**45.3** p = 0.0150 *POR*, RU, TU, ACA	**32.1** p = 0.0122 x, y²
Abundance (no. of Individuals)	42.6	27.4	7.2	22.8	**77.2**	**70.0** p = 0.0252 *RO, UCA*, BA, SA, POR, HC, FMA	**34.6** p = 0.0008 x, y, y²
Shannon diversity index (H')	48.7	33.6	1.8	15.9	**84.1**	**82.3** p = 0.0138 POR, RO, *UCA*, BA, TU, PAV, DC FMA, SPO, ACA, SC, *HC*, BZ	**35.4** p = 0.0036 y, y²
Simpson dominance index (D)	51.2	24.0	8.3	16.5	**83.5**	**75.2** p = 0.0326 BA, RO, POR, UCA, POC, SA, SPO TUB, PAV, DEP, FMA, SC, HC	**32.3** p = 0.0249 x, y, y²
Species composition and abundance (assemblage structure)	42.1	17.6	7.6	32.7	**67.3**	**59.7** p = 0.0036 RO, DEP, BA, SC, PAV, FMA, RU, POR, DC, ECA, POC, SPO	**25.2** p = 0.0006 x, y, y²

The spatial variation of echinoderm assemblage was represented by **Y** vectors (species richness, Shannon diversity index and total species abundance) or **Y** matrix (echinoderm species composition plus abundance). Environmental variables (Env. Var.) were included in **X** matrices (Codes were: POR = *Porites* spp., PAV = *Pavona* spp., POC = *Pocillopora* spp., SC = soft corals, TUB = *Tubastrea coccinea*, HC = hydrocorals, BZ = bryozoan, BA = *Balanus* spp., SPO = Sponges, FMA = fleshy macroalgae, ACA = articulated calcareous algae, ECA = encrusting calcareous algae, TU = Turf, RU = rubble, DC = dead coral, RO = rock, SA = rock, DEP = depth). **W** matrices correspond to spatial variables (Spat. Var.), where x, y, and y² were derived from third-order polynomial terms of geographic coordinates represented as distances in kilometers. The [a + b + c] fraction = Y vs. **X** and **W**; [a + b] = Y vs. **X**; [b + c] = Y vs. **W**; [a] = pure environmental variation; [b] = spatially structured environmental variation; [c] = pure spatial variation; and [d] = unexplained variation. Total Exp. = Total explained variation [a + b + c]. Variables in italic letters correspond to significant fractions: p ≤ 0.05 based on 9999 Monte Carlo permutations
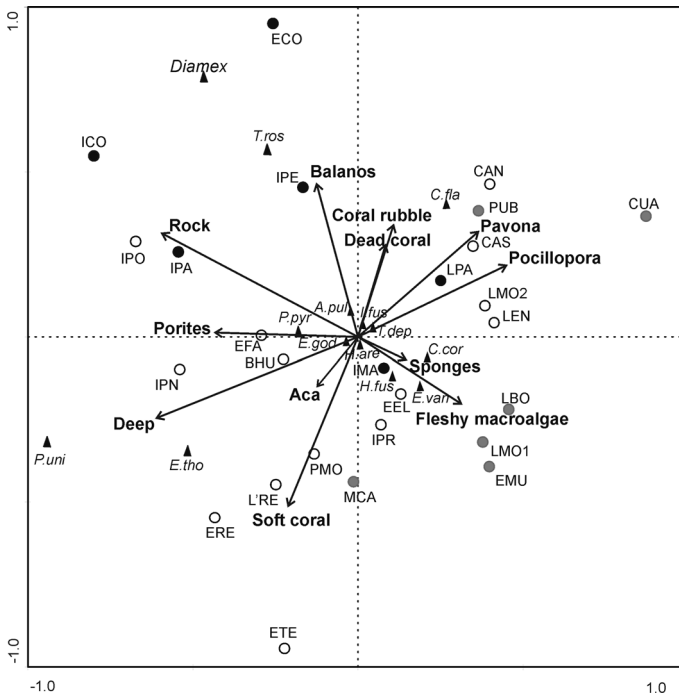
Fig. 3 RDA triplot of spatial variation of echinoderm species at Jalisco, Colima, and Michoacán, México. Ordination of echinoderm species, habitat variables, and sites. *Triangle* represents the echinoderm species, *thick line arrows* show habitat variables, and *circles* represent the sites. *Black circles* represent the sites included within the natural protected area with low human disturbance, *white circles* represent the sites with middle human disturbances and *gray circles* represent the sites with higher human disturbance. Species codes: D. mex is *Diadema mexicanum*, T. ros is *Toxopneustes roseus*, A. pul is *Astropyga pulvinata*, I. fus is *Isostichopus fuscus*, C. fla is *Cucumaria flamma*, T. dep is *Tripneustes depressus*, C. cor is *Centrostephanus coronatus*, E. van *is Echinometra vanbrunti*, H. fus is *Holothuria fuscoscinerea*, H. are is *Holothuria arenicola*, E. tho is *Eucidaris thouarsii*, P. uni is *Phataria unifascialis*, E. god is *Euapta godeffroyi*, P. pyr is Pharia *pyramidatus*, Aca is articulate calcareous algae. Site codes are shown in Fig. 2

presented a positive relationship with coral rubble and dead coral. Meanwhile, *C. flama* was correlated with the coverage of *Pavona*, *Pocillopora*, coral rubble and dead coral. Finally, *H. fuscocinerea, E. vanbrunti, C. coronatus*, and *H. arenicola* showed a positive relationship with the sponges and fleshy macroalgae. Likewise, it is important to mention that the coverage of *Porites, Pavona*, and *Pocillopora* corals, soft coral, rock, and *Balanus* shows a positive relationship with the sampling sites included within the natural protected area (black circles) and with the sites with medium human disturbances (white circles). In contrast, fleshy macroalgae, sponges, and soft coral show a positive relationship with higher disturbance sites (gray circles) (Fig. 3).

Discussion

Fourteen echinoderm species were found associated with the coral, which is fewer than the number of echinoderms recorded in previous studies of comparable areas (Rodríguez-Troncoso et al. 2013; Ríos-Jara et al. 2013). The lower species richness obtained in this

work could be explained as a consequence of different sampling techniques and effort, as well as different aims. Despite the lower species richness, our work shows that *D. mexicanum*, *P. unifascialis, T. roseus, E. thouarsii*, and *C. coronatus* were conspicuous species, which are also representative species of comparable ecosystems in other places of the eastern tropical Pacific (Alvarado and Fernández 2005; Holguín-Quiñones et al. 2008; Alvarado et al. 2012; Hermosillo-Nuñez et al. 2015).

Our results suggest that the structural elements of the habitat play an important role in the spatial variation of the echinoderms inhabiting the coral ecosystems. This latter could correspond to the widely accepted fact that corals are niche constructers (sensu Lewontin 1978) or bio-engineering species that increase the heterogeneity of benthic habitats and in turn provide shelter, foraging, and reproduction zones (sensu Jones et al. 1994). This is corroborated by Hermosillo-Nuñez et al. (2015) who showed that different coral species mainly determine the environmental condition of the habitat for the dominant echinoderm species. The coverage of the different types of algae associations (i.e., turf, encrusting calcareous algae, articulated calcareous algae, fleshy macroalgae), sponges, and bryozoans showed an influence over the spatial variation of the echinoids. This could be explained by the omnivorous diet and grazing behavior of the sea urchins, such as *D. mexicanum*, *T. depresus*, and *E. vanbrunti*, which feed on various species of algae, sponges, and benthic invertebrates (Tuya et al. 2004; Sonnenholzner et al. 2013). Similarly, Vance (1979) described the sea urchin *C. coronatus* as omnivorous, feeding on fleshy macroalgae, tunicates, and sponges. In addition, *E. thouarsii* feeds on coral polyps, coralline algae, and even juvenile molluscs (Glynn and Wellington 1983). It has also been reported that bryozoans are massively depredated by sea urchins and sea stars (Lidgard 2008; Figuerola et al. 2013).

Other environmental variables, such as rocky cover, coral rubble, and dead coral, also contributed to the spatial variation of the echinoderms species. Many of the species studied in this work were sampled in such substrata. For example, most of the species of sea cucumber detected (*I. fuscus, E. godeffroyi*, *H. arenicola*, and *H. fuscocinerea*) were recorded over rocky-sandy bottoms, perhaps because of their detritivore feeding behavior (Roberts et al. 2003; Granja-Fernández et al. 2013). Similarly, in this study*, C. flamma* was observed in the cracks of rocks and coral, which would be explained by this species' feeding behavior of trapping particulate organic matter with its tentacles. Nevertheless, more studies are required for determining the food spectrum of the sea cucumbers because it is not precisely known (Calva 2003). Similarly, the sea urchin *T. roseus* was dominant on the rock and rubble coral, which could be explained by the cover of macroalgae, shells and other rubble, serving as camouflage against predators (Richner and Milinski 2000) and protection against excessive solar radiation (Sigg et al. 2007) and strong bottom currents (Dumont et al. 2007; Amato et al. 2008). Additionally, *A. pulvinata* was observed on the sand and rock coral, which could be related to its ingestion of deposit material from the bottom (as foraminifera and small gastropods) (De Ridder and Lawrence 1982).

The sea stars *P. pyramidatus* and *P. unifascialis* are described as herbivorous species (Luna-Salguero and Reyes-Bonilla 2010), and they are principally recorded on the rocks and the coral. This could be a consequence of the cavities in the coral providing refuge against depredation, and food is available on the rocks due to the algal beds that grow on them. On the other hand, the outcomes show that the soft corals and *Tubastrea coccinea* (hard coral) influence the spatial variation of the echinoderm assemblages, which agrees with other studies that indicate that hydrocorals and soft corals confer suitable habitats for several species of ophiuroids (Castro et al. 2006; Granja-Fernández and López-Pérez 2011). Similarly, it remains unclear how the coral *T. coccinea* contributes to other species.

Despite the insufficient information about the soft-corals, they are a part of the benthic habitat heterogeneity, facilitating the echinoderm spatial distribution.

Water depth and *Balanus* spp. were also determined as important variables in the present study. It has been reported that the differences in depth change the abundance and size of mobile intertidal and subtidal invertebrates, which is attributed to biotic and abiotic components (Larsson 1968; Gaymer et al. 2001; Siddon and Witman 2003). Several authors have concluded that the highest abundance and species richness of echinoderms occurs mainly at the first 18 m due to the availability of food (Hooker et al. 2005; Tuya and Duarte 2012). On the other hand, barnacles may be part of the diet of sea urchins, as echinoids are known for having a wide-range feeding spectrum. Although to date the contribution of *Balanus* spp. to the spatial variation of the echinoderms studied is unclear, *D. mexicanum* presented the highest average density in Chamela coinciding with *Balanus* spp, which was recorded exclusively in this site.

Edgar et al. (2011) showed that protected marine areas with high and low levels of protection present higher coral cover and total densities of mobile macroinvertebrates, respectively, compared to exploited zones. In our study, the sites belonging to the natural protected area and those with medium human perturbations showed a positive relationship with the cover of soft and hard corals. Similarly, thirteen species of echinoderms showed a positive relationship with these sites, and these sites simultaneously presented the highest cover of hard coral and density of echinoderms, which would be explained by the reduced human interventions. The highly perturbed sites were dominated by fleshy macroalgae and sponges while the holothuria *C. flamma* presented a relationship with one these sites. These places are close to human settlements, harbors, and tourist development and are thus frequently impacted by fisheries, tourism, agriculture, and sewage waters, producing a decline in the coral assemblage and associated organisms (Chavez-Comparan and Macias-Zamora 2006; Nava and Ramírez-Herrera 2012). These negative human impacts could be amplified since the sediment in suspension and temperature stresses facilitate the growth of sponges and macroalgae, which constrain the growth of coral reefs (Rützler 2002; Fabricius et al. 2005). However, further studies are required in order to assess the health conditions of the coral assemblages and associated fauna that inhabit the protected and unprotected marine areas along the coast of Mexico.

Conclusions

The outcomes obtained in this work help us to gain a better understanding of the dynamics of the echinoderm assemblage in the coral assemblages located in the coastal ecosystems of Jalisco, Colima, and Michoacán in western Mexico, especially when the echinoderms perform an important functional role in the rocky and coral reefs. This study showed that the habitat structural elements of the coral ecosystems are the most relevant environmental variables for explaining the spatial variation of the echinoderm assemblage. Likewise, the highest cover of hard corals is positively related to highest abundance of echinoderms, especially in locations with low and medium levels of human perturbations. The findings highlight the importance of preserving the structural heterogeneity of the coral ecosystem habitats and the need to protect and create marine-protected area in order to improve biodiversity conservation. In this regard, the information obtained by the current study can contribute to the design of conservation strategies for this kind of marine ecosystem because some study sites show well-developed reefs with high values of richness and

abundance compared to other areas of the Mexican Pacific (Reyes-Bonilla et al. 2013). While our results should be considered as an improvement in the knowledge of coral ecosystems, it remains necessary to conduct studies with an ecosystem ecology perspective, constructing trophic networks, and analyzing the macroscopic or emergent properties.

References

Alvarado JJ, Fernández C (2005) Equinodermos del Parque Nacional Marino Ballena, Pacifico, Costa Rica. Rev Biol Trop 53:275–284

Alvarado JJ, Solís-Marín FA (2013) Echinoderm research and diversity in Latin America. Springer, Berlin

Alvarado JJ, Guzman HM, Breedy O (2012) Distribution and diversity of echinoderms (Asteroidea, Echinoidea, Holothuroidea) in the islands of the Gulf of Chiriqui, Panama. Rev Biol Mar Oceanogr 47:13–22

Alves FMA, Chicharo LM, Serrão E, Abreu AD (2001) Algal cover and sea-urchin spatial distribution at Madeira Island (NE Atlantic). Sci Mar 65:383–392

Amato KR, Emel SL, Lindgren CA, Sullan KM, Wright PR, John JG (2008) Covering behavior of two co-occurring Jamaican sea urchins: differences in the amount of covering and selection of covering material. B Mar Sci 82:255–261

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Attrill MJ, Strong JA, Rowden AA (2000) Are macroinvertebrate communities influenced by structural complexity? Ecography 23:114–121

Brusca RC (1980) Common intertidal invertebrates of the Gulf of California. University of Arizona, Tucson

Calva LG (2003) Hábitos alimenticios de algunos equinodermos. Parte 2 Erizos de mar y pepinos de mar. Contactos 47:54–63

Carreiro-Silva M, McClanahan TR (2001) Echinoid bioerosion and herbivory on Kenyan coral reefs: the role of protection from fishing. J Exp Mar Biol Ecol 262:133–153

Castro SC, Monroy LM, Solano OD (2006) Estructura de la comunidad epifaunal asociada a colonias de vida libre del hidrocoral *Millepora alcicornis* Linnaeus 1758 en Bahía Portete, Caribe Colombiano. Bol Investig Mar Costeras 35:195–206

Chapman MG, Underwood AJ (2008) Scales of variation of gastropod densities over multiple spatial scales: comparison of common and rare species. Mar Ecol Prog Ser 354:147–160

Chatterjee SA, Hadi AS, Price B (2000) Regression analysis by example. Wiley, New York

Chavez-Comparan JC, Macias-Zamora R (2006) Structure of reef fish communities in the Littoral of Colima, Mexico. J Biol Sci 6:65–75

Clarke KR, Gorley RN (2006) Primer v6: user manual/tutorial. Primer-E Ltd, Plymouth

Clarke KR, Warwick RN (1994) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Clemente SJ, Hernández C, Brito A (2009) Evidence of the top–down role of predators in structuring sublittoral rocky-reef communities in a marine protected area and nearby areas of the Canary Islands. ICES J Mar Sci 66:64–71

Colwell RK (2009) EstimateS: statistical estimation of species richness and share species from samples. Version 8.2. [http://viceroy.eeb.uconn.edu/Estimates]

CONANP (2008) Programa de conservación y manejo del Santuario Islas de la Bahía de Chamela. Comisión Nacional de Áreas Naturales Protegidas, México, p 149

De Ridder C, Lawrence JH (1982) Food and feeding mechanisms: Echinoidea. In: Jangoux M, Lawrence JM (eds) Echinoderm nutrition. AA Balkema, Rotterdam, pp 57–115

DOF (2002) Decreto por el que se declara área natural protegida con la categoría de santuario a las islas La Pajarera, Cocinas, Mamut, Colorada, San Pedro, San Agustín, San Andrés y Negrita, y los islotes Los Anegados, Novillas, Mosca y Submarino, situadas en la Bahía de Chamela. SEMARNAT, México, p 5

Dumont CP, Drolet D, Deschenes I, Himmelman JH (2007) Multiple factors explain the covering behavior in the green sea urchin, *Strongylocentrotus droebachiensis*. Anim Behav 73:979–986

Edgar GJ, Banks SA, Bessudo S, Cortés J, Guzmán HM, Henderson S, Martinez C, Rivera F, Soler G, Ruiz D, Zapata F (2011) Variation in reef fish and invertebrate communities with level of protection from fishing across the Eastern Tropical Pacific seascape. Global Ecol Biogeogr 20:730–743

Entrambasaguas L, Pérez-Ruzafa A, García-Charton JA, Stobart B, Bacallado JJ (2008) Abundance, spatial distribution and habitat relationships of echinoderms in the Cabo Verde Archipelago (eastern Atlantic). Mar Freshw Res 59:477–488

Fabricius K, De'ath G, McCook L, Turak E, Williams DMcB (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore great barrier reef. Mar Pollut Bull 51:384–398

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Figuerola B, Núñez-Pons L, Moles J, Ávila C (2013) Feeding repellence in Antarctic bryozoans. Naturwissenschaften 100:1069–1081

Frost MT, Rowden AA, Attrill MJ (1999) Effect of habitat fragmentation on the macroinvertebrate infaunal communities associated with the seagrass *Zostera marina* L. Aquat Conserv 9:255–263

Gaymer CF, Himmelman JH (2008) A keystone predatory sea star in the intertidal zone is controlled by a higher-order predatory sea star in the subtidal zone. Mar Ecol-Prog Ser 370:143–153

Gaymer CF, Himmelman JH, Johnson LE (2001) Distribution and feeding ecology of the seastars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St Lawrence, Canada. J Mar Biol Assoc UK 81:827–843

Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far Eastern Pacific coral reef region. Coral Reefs 19:1–23

Glynn PW, Enochs IC (2011) Invertebrates and their roles in coral reef ecosystems. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Berlin

Glynn PW, Wellington GM (1983) Corals and coral reefs of the Galapagos Islands (with and annotated list of the scleractinian corals of the Galapagos by J.W. Wells). University of California Press, Berkeley

Glynn PW, Wellington GM, Birkeland C (1979) Coral reef growth in the Galápagos: limitation by sea urchin. Science 203:47–49

Godínez-Domínguez E, González-Sansón G (1998) Variación de los patrones de distribución batimétrica de la fauna macrobentónica en la plataforma continental de Jalisco y Colima, México. Cienc Mar 24:337–351

González-Lozano MC, Méndez-Rodríguez LC, López-Veneroni DG, Vázquez-Botello A (2006) Evaluación de la contaminación en sedimentos del área portuaria y zona costera de Salina Cruz, Oaxaca, México. Interciencia 31:647–656

Gosset C, Rives J (2006) Effect of habitat fragmentation on spawning migration of brown trout (*Salmo trutta* L.). Ecol Freshw Fish 15:247–254

Gotshall DW (1998) Sea of cortez marine animals: a guide to the common fishes and invertebrates Baja California to Panama. Sea Challengers, Monterey

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815

Granja-Fernández MR, López-Pérez RA (2011) Nuevos registros de ofiuroideos (Echinodermata: ophiuroidea) para localidades de Zihuatanejo (Guerrero) y Puerto Escondido (Oaxaca), Pacífico mexicano. Rev Mex Biodivers 82:1320–1323

Granja-Fernández MR, López-Pérez RA (2012) Biodiversidad de ofiuroideos (Echinodermata: Ophiuroidea) de Oaxaca y Chiapas, México. In: Sánchez AJ, Chiappa-Carrara X, Brito-Pérez R (eds) Recursos costeros acuáticos del Sureste. UNAM, México

Granja-Fernández MR, Antonio-Pérez V, López-Pérez RA (2013) Euapta godeffroyi (Holothuroidea: synaptidae): filling the distribution gap between Mexico and Costa Rica, eastern tropical Pacific. Hidrobiológica 23:130–132

Hagen N, Mann K (1992) Functional response of the predators American lobster *Homarus americanus* (Milne-Edwards) and Atlantic wolffish *Anarhichas lupus* (L) to increasing numbers of the green sea urchin *Strongylocentrotus droebachinesis* (Müller). J Exp Mar Biol Ecol 159:89–112

Hasan MH (2005) Destruction of a *Holothuria scabra* population by overfishing at Abu Rhamada Island in the Red Sea. Mar Environ Res 60:489–511

Hermosillo-Nuñez BB, Rodríguez-Zaragoza FA, Ortiz M, Galván-Villa C, Cupul-Magaña AL, Ríos-Jara E (2015) Effect of habitat structure on the most frequent echinoderm species inhabiting coral reef communities at Isla Isabel National Park (México). Community Ecol 16:125–134

Hickman CP (1998) A field guide to sea stars and other echinoderms of Galápagos. Sugar Springs, Gladwin

Holguín-Quiñones OE, González-Medina FJ, Solís-Marín F, Félix-Pico EF (2008) Variación espacio-temporal de Scleractinia, Gorgonacea, Gastropoda, Bivalvia, Cephalopoda, Asteroidea, Echinoidea y

Holothuroidea, de fondos someros de la isla San José, Golfo de California. Rev Biol Trop 56:1189–1199

Hooker Y, Solís-Marín FA, Lleellish M (2005) Equinodermos de las Islas Lobos de Afuera (Lambayeque, Perú). Rev Peru Biol 12:77–82

Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. Ecology 82:1814–1829

Jiménez C (2001) Arrecifes y ambientes coralinos de Bahía Culebra, Pacífico de Costa Rica: aspectos biológicos, económico-recreativos y de manejo. Rev Biol Trop 49:215–231

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Kelaher BP (2003) Changes in habitat complexity negatively affect diverse gastropod assemblages in coralline algal turf. Oecologia 135:431–441

Kerstitch A, Bertsch H (2007) Sea of cortez marine invertebrates: a guide for the Pacific coast México to Perú. Sea Challengers, Monterey

Koop K, Booth D, Broadbents A, Brodie J, Bucher D, Capone D, Coll J, Dennison W, Erdmann M, Harrison P, Hoegh-Guldberg O, Hutchings P, Jones GB, Larkum AWD, ÓNell J, Steven A, Tentori E, Ward S, Williamson J, Yellowlees D (2001) ENCORE: the effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. Mar Pollut Bull 42:91–120

Larsson AS (1968) Scuba-studies on vertical distribution of Swedish rocky-bottom echinoderms. A methodological study. Ophelia 5:137–156

Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam

Lewontin RC (1978) Adaptation. Sci Am 293:212–228

Lidgard S (2008) Predation on marine bryozoan colonies: taxa, traits and trophic groups. Mar Ecol Prog Ser 359:117–131

López-Uriarte E, Ríos-Jara E, Galván-Villa C, Juárez-Carrillo E, Enciso-Padilla I, Robles-Jarero EG, Pérez-Peña M (2009) Macroinvertebrados bénticos del litoral somero de Punta La Rosada, Bahía Chamela Jalisco. Sci CUCBA 11:57–68

Luna-Salguero BM, Reyes-Bonilla H (2010) Estructura comunitaria y trófica de las estrellas de mar (Echinodermata: asteroidea) en arrecifes rocosos de Loreto, Golfo de California, México. Hidrobiológica 20:127–134

Magurran EA (2004) Measuring biological diversity. Blackwell Publishing, London

McCoy ED, Bell SS (1991) Habitat structure: the evolution and diversification of a complex topic. In: McCoy ED, Bell SS, Mushinsky HR (eds) Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London

Mora C, Metzger R, Rollo A, Myers RA (2007) Experimental simulations about the effects of overexploitation and hábitat fragmentation on populations facing environmental warming. Proc R Soc B 274:1023–1028

Nava H, Ramírez-Herrera MT (2012) Land use changes and impact on coral communities along the central Pacific coast of Mexico. Environ Earth Sci 65:1095–1104

Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. TREE 15:413–417

Ortiz M, Levins R, Campos L, Berrios F, Campos F, Jordán F, Hermosillo B, González J, Rodríguez F (2013a) Identifying keystone trophic groups in benthic ecosystems: implications for fisheries management. Ecol Indic 25:133–140

Ortiz M, Campos L, Berrios F, Rodríguez F, Hermosillo B, González J (2013b) Network properties and keystoneness assessment in different intertidal communities dominated by two ecosystem engineer species (SE Pacific coast): a comparative analysis. Ecol Model 250:307–318

Ortiz-Lozano L, Granados-Barba A, Solís-Weiss V, García-Salgado MA (2005) Environmental evaluation and development problems of the Mexican Coastal Zone. Ocean Coast Manag 48:161–176

Paine RT (1969) A note of tropic complexity and community stability. Am Nat 103:91–93

Reaka-Kudla ML (1997) The Global Biodiversity of Coral Reefs: A Comparison with Rain Forests. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II. Joseph Henry Press, Washington, DC

Reyes-Bonilla H, Calderon-Aguilera LE (1999) Population density, distribution and consumption rates of three corallivores at Cabo Pulmo Reef, Gulf of California, Mexico. Mar Ecol 20:347–357

Reyes-Bonilla H, López-Pérez A (1998) Biogeografía de los corales pétreos (Scleractinia) del Pacífico de México. Cienc Mar 24:211–224

Reyes-Bonilla H, Calderon-Aguilera LE, Cruz-Piñon G, Medina-Rosas P, López-Pérez RA, Herrero-Pérezrul MD, Leyte-Morales GE, Cupul-Magaña A, Carriquiry-Beltrán JD (2005) Atlas de los corales pétreos (Anthozoa: scleractinia) del Pacífico Mexicano. Centro de Investigación Científica y de Educación Superior de Ensenada, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad,

Consejo Nacional de Ciencia y Tecnología, Universidad de Guadalajara/Centro Universitario de la Costa, Universidad del Mar. p. 128 ISBN: 970-27-0779

Reyes-Bonilla H, Escobosa-González LE, Cupul-Magaña AL, Medina-Rosas P, Calderón-Aguilera LE (2013) Estructura Comunitaria de corales zooxantellados (Anthozoa: scleratinia) en el arrecife coralino de Carrizales, Pacífico Mexicano. Rev Biol Trop 61:583–594

Richner H, Milinski M (2000) On the functional significance of masking behavior in sea urchins: an experiment with *Paracentrotus lividus*. Mar Ecol Prog Ser 205:307–308

Ríos-Jara E, Galván-Villa CM, Rodríguez-Zaragoza FA, López-Uriarte E, Bastida-Izaguirre D, Solís-Marín FA (2013) Los equinodermos de Bahía Chamela, Jalisco, México. Rev Mex Biodiver 84:263–279

Roberts D, Gebruk A, Levin V, Manship BAD (2003) Feeding and digestive strategies in deposit-feeding holothurians. In: Gibson RN, Atkinson RJ, Gordon JD (eds) Oceanography and marine biology: an annual review, vol 38., pp 257–310

Rodríguez-Troncoso AP, Sotelo-Casas RC, Galván-Villa CM, Godínez-Domínguez E, Flores-Ortega JR, del Castillo-Fernández KM, Corgos A, Solís-Marín FA (2013) Equinodermos de la costa sur de Jalisco y Colima. In: Godínez-Domínguez E, Franco-Gordo MC (eds) Inventario de biodiversidad de la costa sur de Jalisco y Colima, vol 2. Universidad de Guadalajara, Mexico, pp 46–60

Rodríguez-Zaragoza FA, Cupul-Magaña AL, Galván-Villa CM, Ríos-Jara E, Ortiz M, Robles-Jarero EG, López-Uriarte E, Arias-González JE (2011) Additive partitioning of reef fish diversity variation: a promising marine biodiversity management tool. Biodivers Conserv 20:1655–1675

Rützler K (2002) Impact of crustose clionid sponges on Caribbean reef corals. Acta Geologica Hisp 37:61–72

Siddon CE, Witman JD (2003) Influence of chronic, low-level hydrodynamic forces on subtidal community structure. Mar Ecol-Prog Ser 261:99–110

Sigg JE, Lloyd-Knight KM, Boal JG (2007) UV radiation influences covering behavior in the urchin *Lytechinus variegatus*. J Mar Biol Assoc UK 87:1257–1261

Sonnenholzner J, Brandt M, Francisco V, Hearn A, Luzuriaga M, Guarderas P, Navarro JC (2013) Echinoderms of ecuador. In: Alvarado JJ, Solís-Marín FA (eds) Echinoderms research and diversity in Latin America. Springer, Berlin. doi:10.1007/978-3-642-20051-9_6

Szmant AM (2002) Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries 25:743–766

ter Braak CJF, Šmilauer P (2002) CANOCO referent manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5) Microcomputer Power, USA

Tuya F, Duarte P (2012) Role of food availability in the bathymetric distribution of the starfish *Marthasterias glacialis* (Lamk.) on reefs of northern Portugal. Sci Mar 76:9–15

Tuya F, Boyra A, Haroun RJ (2004) Blanquizales en Canarias: La explosión demográfica del erizo *Diadema antillarum* en los fondos rocosos de Canarias. Oceanográfica Universidad de Las Palmas de Gran Canaria, Canarias

Tyler PA, Young CM, Clarke A (2000) Temperature and pressure tolerances of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri*: potential for deep-sea invasion from high latitudes. Mar Ecol-Prog Ser 192:173–180

Vance RR (1979) Effects of grazing by the sea urchin, *Centrostephanus coronatus*, on prey community composition. Ecology 60:537–546

Wilcox BA, Murphy DD (1985) Conservation strategy: the effects of fragmentation on extinction. Am Nat 125:879–887

Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. Mar Freshw Res 50:867–878