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## Community structure of shallow water Alcyonacea (Anthozoa: Octocorallia) from the southern Tropical Eastern Pacific

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**Abstract** Alcyonacea are sessile invertebrates, which can significantly shape the boundary layer in coral reefs and rocky habitats. Ecological aspects in this taxon have been well studied in the Caribbean, Mediterranean, and Indo-Pacific. With few recent exceptions, studies in the Eastern Pacific focused on taxonomy. We present a quantitative assessment of Alcyonacea communities from the southern Tropical Eastern Pacific, based on video transects in the Marine Reserve El Pelado. Seventeen species from the Plexauridae (8), Gorgoniidae (8), and Clavularidae (1) were identified, comprising 6963 colonies dominated by *Muricea* (86.7%), particularly *M. plantaginea* (48.6%). The overwhelming dominance of *M. plantaginea* was the most striking and previously unreported community trait, which contributed to a moderate Shannon entropy ( $n = 31$ ,  $H$  mean 1.40, SD 0.22), equitability ( $n = 31$ ,  $H_E$  mean 0.16, SD 0.4), and species diversity expressed as effective number of species ( $n = 31$ , mean 4.16, SD 0.87). Few common species overprinted a more variable and subtle community pattern among rarer species, suggested in agglomerative hierarchical cluster analyses. Four species (*M. plantaginea*, *M. purpurea*, *M. fruticosa* and *Leptogorgia alba*) had the strongest influence on site groupings in the correspondence analysis between a principal component analysis of a Hellinger-transformed Alcyonacea species matrix and substrate categories, with filamentous turf algae and crustose coralline algae being the main determinants of site differentiation. *Muricea plantaginea*'s qualities of a keystone species, and

the eurytopic and stenoeccious distribution traits among some species are discussed. The invasive *Carijoa riisei* was confirmed as biological threat to other Alcyonacea, and possible physiological distribution limitations are indicated.

**Keywords** Alcyonacea · Community structure · Eastern Pacific · Equatorial Front · Keystone species

### Introduction

Tropical shallow water Alcyonacea (soft corals and sea fans) are among the characteristic sessile and colonial faunal components of rocky habitats and coral reefs. Erect growth forms compartmentalize the benthic boundary layer by creating structural heterogeneity in the form of micro habitats and nurseries for other invertebrates (Patton 1972; Cantera et al. 1987; Vreeland and Lasker 1989; Neira et al. 1992; Ramos 1995; Mosher and Watling 2009) fishes (Lasker 1985; Etnoyer and Warernchuck 2007; Taylor et al. 2013). Where Alcyonacea form dense stands, they further create a complex mosaic of gradients in light penetration, which in turn influence the distribution of sessile photoautotrophic organisms, and of hydrodynamic gradients (Wainwright et al. 1976) that affect water exchange and material cycles, analogous to dense stands of macrophytes (Fréchet et al. 1989; Vogel 1994; Irlandi 1996; González-Ortiz et al. 2014). At least in Caribbean reef settings, population densities of Alcyonacea and therefore also the structural habitat heterogeneity which they offer, showed considerable persistence (Lenz et al. 2015; Tsounis and Edmunds 2017) during recent decades amidst a general flattening of reefs caused by the degradation of stony coral communities (Alvarez-Filip et al. 2009). Alcyonacea are also a viable source of bioactive components (Coll 1992; Gutierrez et al. 2006; Rocha et al. 2011; Blunt et al. 2014). The generally longevous Alcyonacea (Fabricius and Alderslade 2001) are, nonetheless, negatively affected by pollution

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(Fabricius and McCorry 2006) and have been considered as bioindicators (García-Parrado and Alcolado 1996). Hence, the biology and ecology of many Alcyonacea has been well studied in the Caribbean, Hawaii, Indo-Pacific, Mediterranean, and the deep ocean, and quantitative assessments have been a foundation of our understanding of communities from this taxon (see summary in Gomez et al. 2014). Yet studies from the Eastern Pacific, with few exceptions from the northern hemisphere (Abeytia et al. 2013; Gomez et al. 2014; Sánchez and Ballesteros 2014), focused on taxonomy and biogeography, resulting in a stark contrast to our understanding of stony coral assemblages and reefs whose community composition has been amply quantified in the Eastern Pacific (Glynn et al. 2016a). This has led to a knowledge gap regarding the in situ community composition of Alcyonacea within the region in general, and particularly from southern regions of the Tropical Eastern Pacific (TEP).

In the TEP, delineated as the region between southern California and Northern Peru, studies on Alcyonacea began in the mid nineteenth century with Valenciennes (1846; review in Breedy and Guzman 2002), and have revolved around taxonomy and species inventories (Hickson 1928; Bielschowsky 1929; Stiasny 1941, 1943; Prahel et al. 1986; Sinsel-Duarte 1991; Reyes-Bonilla et al. 1997; Breedy and Guzman 2002, 2003, 2005a, b, 2007, 2011, 2014, 2015, 2016; Guzman et al. 2004; Williams and Breedy 2004; Breedy and Cortés 2008, 2014; Guzman and Breedy 2008, 2011; Breedy 2009; Vargas et al. 2008, 2010; Breedy et al. 2009a, b; Sánchez et al. 2011, 2014; Soler-Hurtado and López-González 2012; Soler-Hurtado et al. 2016). Van Oppen et al. (2005) presented initial ecological insights after examining 27 Eastern Pacific species for endosymbiotic zooxanthellae, finding none. Mortality due to epizooics and thermal anomalies (Sánchez et al. 2011, 2014), as well as the impact of the invasive *Carijoa riisei* on other Alcyonacea (Sánchez and Ballesteros 2014) were monitored in Colombia. Species composition and bathymetric distribution were first quantified by Abeytia et al. (2013) in southern Mexico, and by Gomez et al. (2014) in Panama.

In continental Ecuador, extensive coral reefs and coral assemblages are rare (Glynn 2003; Glynn et al. 2016a) and erect Alcyonacea and Antipatharia (see Bo et al. 2012) distinctively shape the architectural complexity of sessile invertebrate communities on rocky substrates. Alcyonacean assemblages appear best developed in well flushed off-shore habitats (like Bajo Montañita and numerous small islands and rocks along the shore of the provinces Manabí and Santa Elena; F. Rivera and P. Martínez, pers.com.) where turbulent environments exposed to strong currents and swells exist, but this was not yet quantified. The knowledge base for continental Ecuadorian Alcyonacea has so far included broad species inventories (Rivera and Martínez 2011), a site-specific account of Gorgoniidae (Figueroa 2015), and the description of new Gorgoniidae and

species range extensions (Soler-Hurtado and López-González 2012; Soler-Hurtado et al. 2016). References to continental Alcyonacea were also made in publications on the Galapagos Islands (Breedy and Guzman 2005a, b; Hickman 2008; Breedy et al. 2009a, b) as well as in reviews of Eastern Pacific *Eugorgia* (Breedy et al. 2009a), *Heterogorgia* (Breedy and Guzman 2011) *Lepetogorgia* (Breedy and Guzman 2007) and *Muricea* (Breedy and Guzman 2015, 2016), constituting 26 reported species.

This study presents a quantitative assessment of shallow water Alcyonacea from the southern TEP, in the Marine Reserve El Pelado (MREP), continental Ecuador. Species composition and diversity, as well as distributional patterns across different substrate types are described and elucidated based on video transects. The study serves as a first step towards a characterization of faunistic community traits that facilitate regional comparisons of the condition of this valuable marine taxon, and justifications for its conservation.

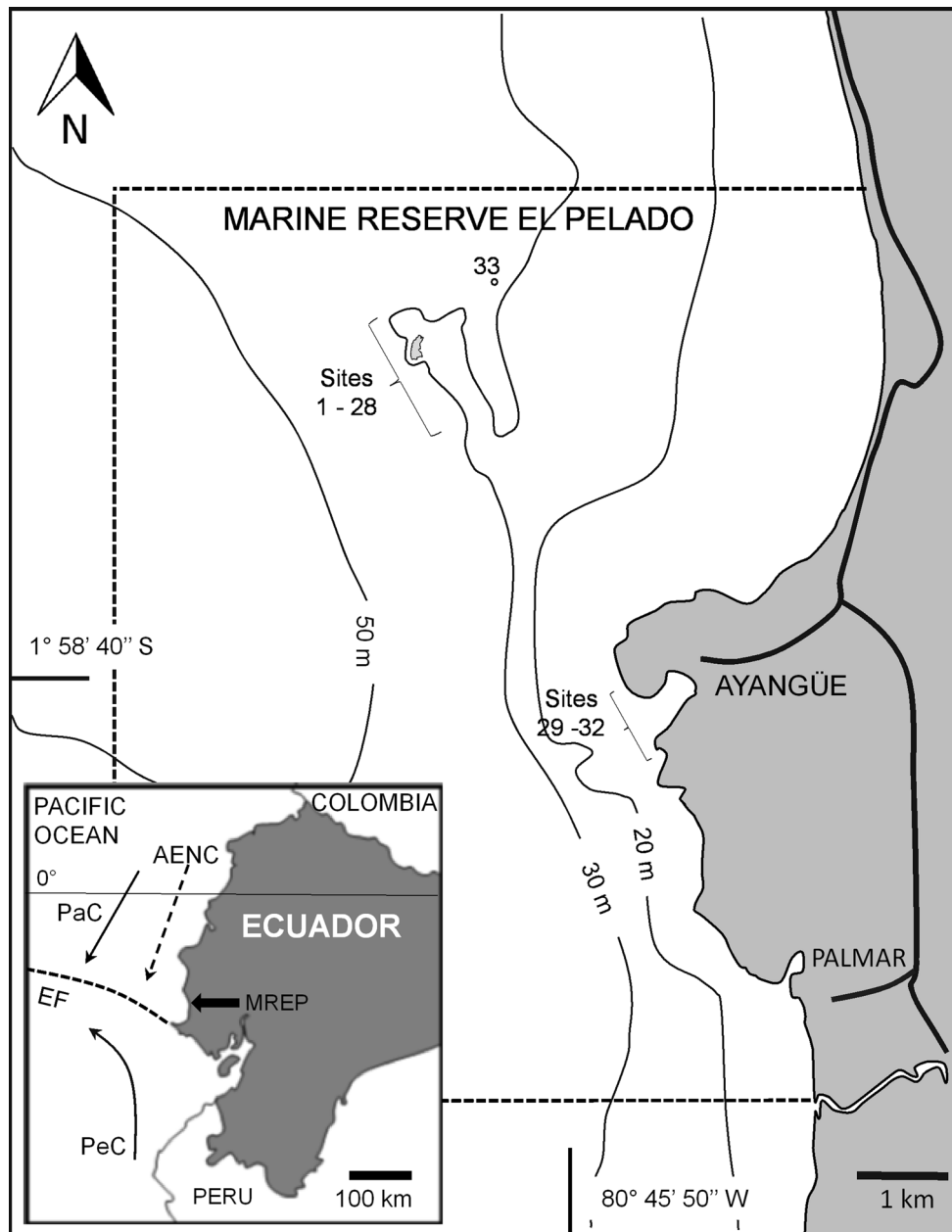
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## Materials and methods

### Study area

The Marine Reserve El Pelado (MREP), province of Santa Elena, Ecuador, lines the coast between the northern limits of Valdivia and the river mouth at Palmar to its south (Fig. 1). It is one of 11 continental protected marine areas, was declared as marine reserve in 2012, and encompassed 13005 and 96 ha of marine and terrestrial environments, respectively (Government of Ecuador 2017). Situated at the convergence of the southward-flowing Panama Flow and the northward flowing Peru Current, as well the southward-flowing annual El Niño current (Fiedler 1992; Strub et al. 1998), the MREP lays within the range of the seasonally and latitudinally migrating Equatorial Front (EF). Consequently it is exposed to fluctuations in salinity and temperature of surface waters (Fiedler and Lavine 2016).

Rocky environments within the MREP extended across the submerged portion of El Pelado Islet, its neighboring northwestern, northeastern and southeastern mounds, all of which are separated by sandy environments, and which are here jointly referred to as the El Pelado Platform (EPP). To a lesser extent, rocky substrates marked the shoreline in the immediate vicinity of Ayangüe (Fig. 2). Additionally, isolated rocky mounds such as Bajo Tello had rich benthic faunal overgrowth. Rocky strata of Islet and its neighboring mounds were characteristically tilted towards ESE, creating plane and gently inclined easterly slopes, while westerly slopes were steeper and included overhangs formed by the erosion of softer sediments. Westerly slopes are in a windward position, as prevailing winds come from the southwest (Gálvez and Regalado 2007). All together, rocky environments covered approximately 15.5 ha and were evident to depths of 27 m, beyond



**Fig. 1** Delineation of the Marine Reserve El Pelado (MREP), Santa Elena. Survey sites 1–28 were located around the El Pelado Islet. Sites 29–32 were located near the northern and southern end of Ayangüe Bay. Insert: Surface currents PaC (Panama Current),

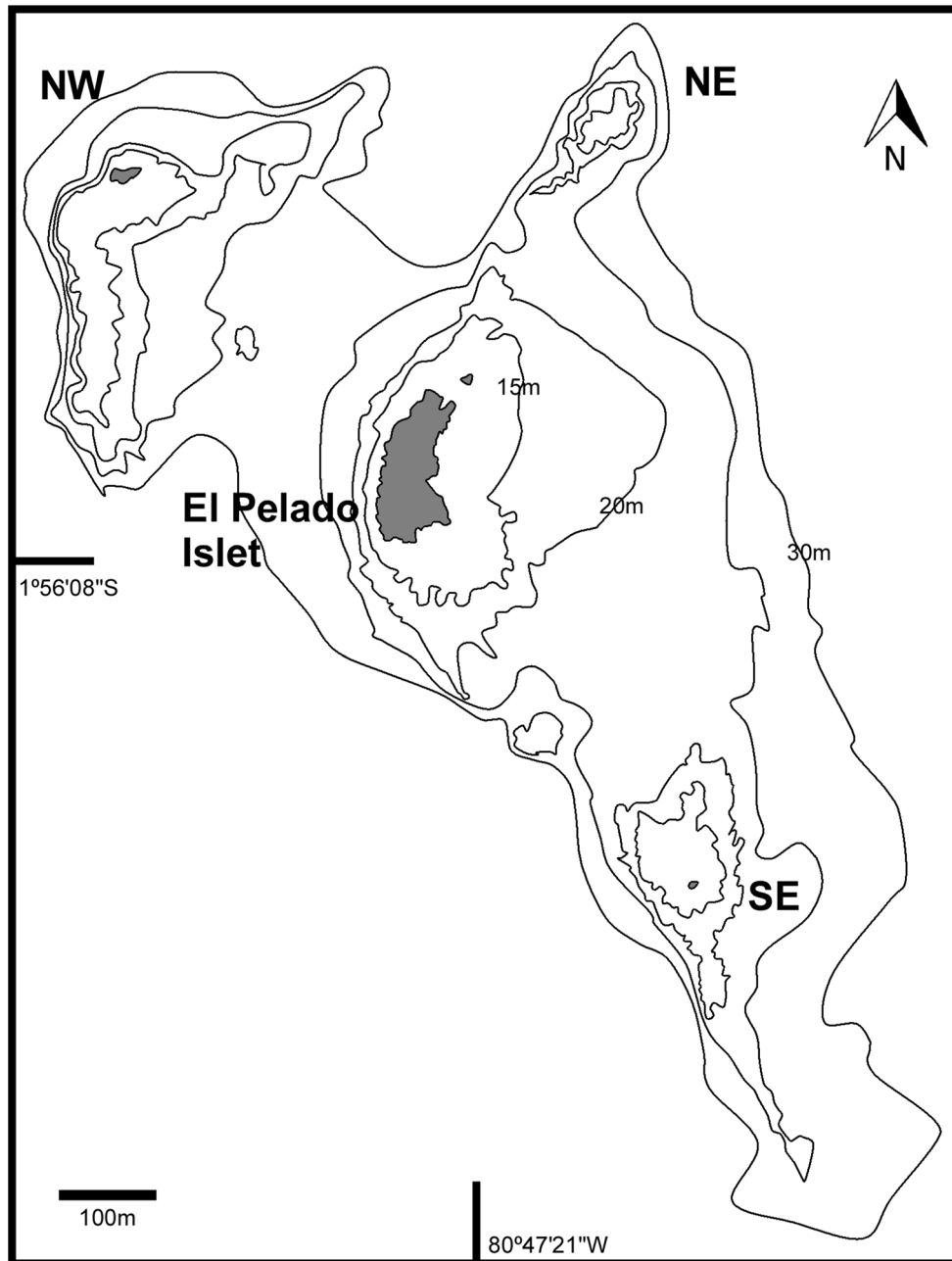
AENC (Annual El Niño Current), and PeC (Peru Current), and the EF (Equatorial Front) during the months January–April. Adapted from Glynn (2003)

with the seafloor was composed of sandy environments. Twenty-eight sites around the Islet were haphazardly selected for quantitative surveys (October 2015–January 2016). Four additional sites near shore were examined in May 2016.

#### Species identification

Alcyonacea were photographed in situ and branch segments collected and dried for identification. With

changing depths and ambient illumination, the white balance settings of the camera (Canon Power Shot D20, with underwater housing WP DC45) was adjusted to match coloration of colonies recorded with the colors seen by the diver. External morphological features detectable in dried specimens from *Heterogorgia* (Breedy and Guzman 2011), *Leptogorgia* (Breedy and Guzman 2007), *Muricea* (Breedy and Guzman 2015, 2016) and *Pacifigorgia* (Breedy and Guzman 2002, 2007, 2011) as well as descriptions of live colonies (Hickman 2008; Rivera and Martínez 2011) were used for identification.



**Fig. 2** El Pelado Platform. Survey sites 1–14 were spread across the NW rocky mound, sites 15, 16 and 19–21 around the Islet, 17 and 18 at NW, and 22–28 at SE. Approximate area of submerged rocky environments: NW 6.2 ha, NE 1 ha, Islet 5.2 ha, and SE 3.1 ha

Additional verification of some species was carried out through the extraction of sclerites from tissue samples with a 2% sodium hypochlorite (Bayer 1961), and their examination with an inverted microscope Olympus LX 52.

#### Video belt transects

At 31 sites, two belt transects (BT), each covering 40 m<sup>2</sup> were surveyed. Transects weighted with 36 g leads every 50 cm, were placed perpendicularly to the depth gradi-

ent, contouring the seafloor to eliminated discrepancies between area considered in the belt transect and the actual area surveyed. Transect length was labeled with small PVC platelets every 2 m to facilitate orientation and to allow repeated video records of certain sections. Starting points (coordinates) and the approximate heading of each transect, maximum depth, as well as rugosity ranks from 1 to 3 (low = 1, mostly planar; moderate = 2, mostly non-planar with amplitudes in terrain roughness < 100 cm; high = 3, non-planar with amplitudes in terrain roughness > 100 cm) were noted (Table 1).

**Table 1** Surveyed sites and transect features

Site no.	Area label	Coordinates of starting points		Approximate headings	Depth (m)	Rugosity rank
1	EPPNW	1°55'58.25"S	80°47'32.85"W	175°	12.8	2.0
2	EPPNW	1°55'59.60"S	80°47'32.90"W	170°	14.6	2.0
3	EPPNW	1°56'01.35"S	80°47'31.94"W	173°, 176°	15.2	1.0
4	EPPNW	1°56'00.80"S	80°47'32.05"W	280°, 180°	13.4	2.0
5	EPPNW	1°56'00.34"S	80°47'32.10"W	200°	12.0	1.0
6	EPPNW	1°56'00.56"S	80°47'32.85"W	170°	19.6	2.0
7	EPPNW	1°56'00.12"S	80°47'33.01"W	165°	20.2	3.0
8	EPPNW	1°56'00.60"S	80°47'33.34"W	165°	23.3	3.0
9	EPPNW	1°55'54.93"S	80°47'26.36"W	215°, 290°	19.3	3.0
10	EPPNW	1°55'54.93"S	80°47'26.36"W	55°, 100°	17.3	2.0
11	EPPNW	1°55'56.85"S	80°47'30.45"W	240°, 260°	10.0	1.0
12	EPPNW	1°55'56.75"S	80°47'30.35"W	15°, 315°	12.2	2.5
13	EPPNW	1°55'56.42"S	80°47'29.28"W	290°	15.4	1.5
14	EPPNW	1°55'55.60"S	80°47'20.10"W	310°, 250°	15.6	1.0
15	EPP Islet	1°56'00.59"S	80°47'19.35"W	230°, 205°	12.4	2.0
16	EPP Islet	1°56'01.65"S	80°47'20.35"W	215°	12.8	2.5
17	EPP Islet	1°55'53.10"S	80°47'14.25"W	150°, 200°	14.3	1.5
18	EPP Islet	1°55'52.85"S	80°47'14.40"W	250°	15.8	1.5
19	EPP Islet	1°56'06.25"S	80°47'19.80"W	170°, 165°	10.0	1.5
20	EPP Islet	1°56'05.90"S	80°47'19.75"W	10°, 15°	09.1	1.5
21	EPP Islet	1°56'10.20"S	80°47'20.12"W	60°	15.2	2.5
22	EPP Islet	1°56'09.60"S	80°47'28.80"W	355°	14.5	1.0
23	EPPSE	1°56'20.25"S	80°47'12.65"W	160°, 150°	14.5	3.0
24	EPPSE	1°56'21.30"S	80°47'11.80"W	325°	17.3	2.5
25	EPPSE	1°56'20.65"S	80°47'13.34"W	135°	19.6	1.0
26	EPPSE	1°56'21.13"S	80°47'12.78"W	135°	19.6	3.0
27	EPPSE	1°56'17.58"S	80°47'12.01"W	164°	12.8	1.5
28	EPPSE	1°56'18.78"S	80°47'11.39"W	155°	15.2	1.0
29	Ayangüe	1°58'57.82"S	80°45'39.16"W	0°, 355°	03.7	1.0
30	Ayangüe	1°59'01.84"S	80°45'37.10"W	180°	07.3	1.5
31	Ayangüe	1°59'14.45"S	80°45'27.10"W	40°	15.0	2.0
32	Ayangüe	1°59'14.45"S	80°45'27.10"W	160°	15.0	2.0
33	Bajo Tello	1°55.41.50"S	80°46'50.00"W	n/a	30	2.5

Site numbers 1–32 are labeled X1–X32, respectively, in Fig. 4

The area within 1 m from either side of the transect line ( $20 \text{ m}^2$ ) was recorded by video ( $23015 \text{ kbit s}^{-1}$ ), at an angle of no more than  $30^\circ$ , from 0 to 20 m on either side of transect. A moderate swimming pace of no more than  $15 \text{ cm s}^{-1}$  was most effective for species identification. Prior to each recording, the white balance settings were adjusted. Thus, a total of  $2480 \text{ m}^2$  were documented.

All Alcyonacea detectable within each BT video were subsequently counted and assigned to a species or classified as unidentifiable. Colonies attached outside of the BT, but with least 50% of the colony within the considered area, were included in the quantification.

#### Benthos composition data

For 20 sites, benthic composition data were collected along each transect via photo-series composed of 20 evenly spaced images, each documenting  $120 \text{ cm}^2$  of benthos. Due to the commonly turbid waters at the MREP, single images of larger areas did not provide the resolution necessary for identifying the benthic make up. Ten points randomly superimposed onto each image (400 points per site) using CPCe (Kohler and Gill 2006)

allowed a proper characterization of the benthic composition. The benthos under each point was visually identified and assigned to one of the categories balanomorph cirripeds (BC), crustose coralline algae overgrowing balanomorph cirripeds (CCA.BC) crustose coralline algae (CCA), filamentous turf algae on rock (FTA.R), filamentous turf algae on sediment (FTA.S), pebbles (P), rock (R), sediments (S), schill (SH) and sessile invertebrates (SI).

#### Species diversity and distribution

Species diversity was expressed and compared in terms of effective number of species (ENS) also referred to as Hill Numbers (see MacArthur 1965; Hill 1973), which were derived from Shannon's entropy equation (H) (Shannon 1948) as described in Jost (2006), ESN being the exponent of Shannon's entropy. This renders an intuitive representation of magnitude of differences between sites as it gives the number of equally abundant species necessary to produce the observed value of diversity.

Data on colonies per species and substrate composition at individual sites were explored for patterns in

**Table 2** Alcyonacea species observed in the Marine Reserve El Pelado

Species	Colonies in transects	Mean number of colonies (m <sup>-2</sup> )	SD
Suborder Holaxonia (Studer, 1887)			
Family Plexauridae (Gray, 1859)			
1. <i>Heterogorgia hickmani</i> (Breedy and Guzman, 2004)	52	0.02	0.04
2. <i>Muricea austera</i> (Verrill, 1869)	181	0.07	0.10
3. <i>Muricea crassa</i> (Verrill, 1868)	13	> 0.01	> 0.01
4. <i>Muricea fruticosa</i> (Verrill, 1869)	1252	0.55	0.75
5. <i>Muricea plantaginea</i> (Verrill, 1864)	3381	1.42	0.84
6. <i>Muricea purpurea</i> (Verrill, 1864)	944	0.39	0.22
7. <i>Muricea squarrosa</i> (Verrill, 1869)	104	4.68	6.86
8. <i>Psammogorgia</i> cf <i>arbuscula</i> (Verrill, 1866)	160	0.05	0.07
Family Gorgoniidae (Lamoroux, 1812)			
9. <i>Leptogorgia alba</i> (Duchassaing and Michelotti, 1860)	487	0.21	0.23
10. <i>Leptogorgia cuspidata</i> (Verrill, 1865)	3	> 0.01	> 0.01
11. <i>Leptogorgia pumila</i> (Verrill, 1868)	28	0.01	0.03
12. <i>Leptogorgia taboguilla</i> (Hickson, 1928)	116	0.05	0.07
13. <i>Pacifigorgia adamsii</i> (Verrill, 1868)	0	0	0
14. <i>Pacifigorgia irene</i> (Bayer, 1951)	2	> 0.01	> 0.01
15. <i>Pacifigorgia rubicunda</i> (Breedy and Guzman, 2003)	28	0.02	0.05
16. <i>Pacifigorgia firma</i> (Breedy and Guzman, 2003)	0	0	0
Suborder Stolonifera (Thompson and Simpson, 1809)			
Family Clavularidae (Hickson, 1894)			
17. <i>Carijoa riisei</i> (Duchassaing and Michelotti, 1860)	12	0.01	0.01

Unidentified specimens were not considered

community structure. Analyses evaluated Alcyonacea and substrate composition of the benthos first individually, then exploring coincidences in pattern. To obtain overview of potential faunal groupings, a hierarchical, agglomerative cluster analysis with Ward's method of linkage (Legendre and Legendre 2012) was performed on raw and log + 1 transformed data. The latter was done to explore whether a greater weighting of rare species might expose otherwise undetected community patterns. Other benthic community patterns were explored with principal components analysis (PCA). With basic groupings known, potential coincidence of Alcyonacean and other benthic community pattern was explored with a Correspondence Analysis (CA) (Borcard et al. 2011; Legendre and Legendre 2012) of the species matrix with an overlay of the ordination of the environmental data. The species data were Hellinger transformed (Borcard et al. 2011; Legendre and Legendre 2012) prior to submission to PCA and CA in order to maintain adequate statistical distances. The number of significant axes required to explain the majority of variation in the dataset was evaluated by following the Kaiser–Guttman and Broken Stick criteria (Borcard et al. 2011). Scaling of the biplot multivariate analyses were performed in R (R Development Core Team 2012) using libraries ape (Paradis et al. 2004) and vegan (Oksanen et al. 2017).

## Results

Alcyonacea were observed at 31 sites, across which a total of 6963 colonies were recorded, including 17 species of Plexauridae (8), Gorgoniidae (8), and Clavulari-

dae (1) (Table 2). Two Gorgoniidae, *Pacifigorgia firma* and *P. adamsii* were observed in 2 m depth on the eastern margins of the islet, but not within the belt transects. No Alcyonacea were observed at site 29, the shallowest (4 m) and closest to shore (110 m). An average of 3.1% ( $n = 31$ , SD 1.9%; in total 200 of 6963) colonies per site could not be identified in the examination of videos.

Overall, 86.7% of the colonies were Plexauridae from the genus *Muricea* and 48.6% were *Muricea plantaginea* alone, causing a leptokurtic distribution in the abundance of individual species (Kurtosis 9.8n3). Most *M. plantaginea* colonies (3215 of 3381) were observed with extended tentacles which displayed four color morphs. The goldenrod-orange, whitish-gray morphs comprised 97.1 and 2.6% of the colonies, respectively, while the medium sea green and bright yellow morphs were rare with only 4 and 3 colonies, respectively. No color variations were noted in the coenenchyme of dried samples. At Bajo Tello, where only qualitative observations were made, the whitish-gray color morph was more common than the goldenrod-orange color morph. Color variations were further observed in *Leptogorgia alba*, the most abundant Gorgoniidae, constituting 7.0% of the recorded colonies. It was the only other species that occurred in distinct color morphs that were also evident in the coenenchyme of dried samples, namely purple (72.7%) and white (27.3%).

Number of colonies per site ranged from 21 to 521 (mean 224.7, SD 148.0), with colony densities ranging from 0.3 to 6.5 m<sup>-2</sup> (mean 2.9 m<sup>-2</sup>, SD 1.9 m<sup>-2</sup>; Table 3). Apart from one site on the EPP and two near Ayangüe, *M. plantaginea* dominated all sites by constituting an average of 49.1% (SD 13.7) of the colonies.

**Table 3** Alcyonacean community composition per site at the Marine Reserve El Pelado

Site	Colonies $N$	Colonies ( $m^{-2}$ )	Species richness	Shannon H	Shannon equitability $H_E$	ENS
1	160	2.00	9	1.50	0.17	4.48
2	283	3.54	8	1.33	0.17	3.77
3	230	2.88	10	1.36	0.14	3.90
4	127	1.59	9	1.29	0.14	3.63
5	133	1.66	6	1.08	0.18	2.95
6	278	3.48	10	1.51	0.15	4.53
7	521	6.51	10	1.49	0.15	4.44
8	479	5.99	12	1.27	0.11	3.55
9	370	4.63	12	1.49	0.12	4.45
10	319	3.99	11	1.63	0.15	5.11
11	140	1.75	9	1.37	0.15	3.95
12	181	2.26	10	1.22	0.12	3.40
13	201	2.51	9	1.23	0.14	3.41
14	191	2.39	9	1.13	0.13	3.09
15	92	1.15	5	1.19	0.24	3.29
16	162	2.03	8	1.28	0.16	3.60
17	327	4.09	11	1.55	0.14	4.72
18	188	2.35	11	1.45	0.13	4.26
19	22	0.28	8	1.55	0.19	4.70
20	30	0.38	2	0.69	0.35	2.00
21	197	2.46	14	1.64	0.12	5.18
22	144	1.80	12	1.78	0.15	5.93
23	205	2.56	11	1.35	0.12	3.85
24	248	3.10	10	1.59	0.16	4.88
25	177	4.43	9	1.34	0.15	3.82
26	735	9.19	13	1.66	0.13	5.26
27	192	2.40	10	1.46	0.15	4.33
28	156	1.95	10	1.42	0.14	4.15
29	0	0	0	n/a	n/a	n/a
30	21	4.40	6	1.23	0.21	3.43
31	179	3.46	10	1.71	0.17	5.55
32	275	2.00	10	1.70	0.17	5.48

ENS effective number of species

Abundant species were generally widely distributed across sites and vice versa, but the rare *L. taboguilla* (116 colonies, 2.6%) was present at 30 sites, whereas *P. arbuscula* (160 colonies, 2.3%) was present at 19 sites (Fig. 3).

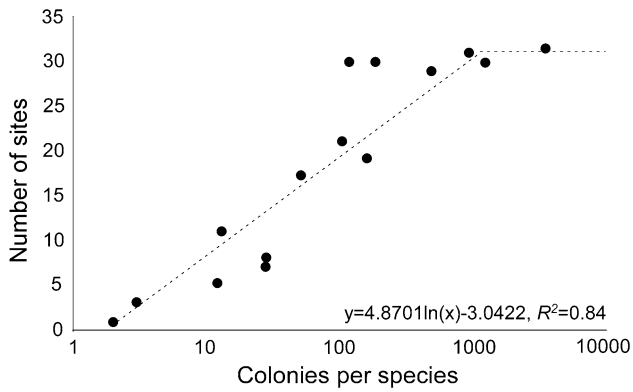
Species richness ranged from 2 to 13 between sites, Shannon's entropy (H) ranged from 0.69 to 1.78 ( $n = 31$ , mean 1.40, SD 0.22) and equitability ( $H_E$ ) ranged from 0.11 to 0.18 ( $n = 31$ , mean 0.16, SD 0.4), reflecting the numerical dominance of few species, especially *M. plantaginea*. Species diversity (effective number of species, ENS) per site ranged from 2 to 5.95 ( $n = 31$ , mean 4.16, SD 0.87). The most species diverse sites (ENS > 5) were from depths between 15 and 17 m, including four very turbulent locations, two on the EPP (sites 22 and 23) and two near the coast (sites 31 and 32).

Community structure, compared by untransformed and log-transformed datasets in agglomerative hierarchical cluster analysis, indicated that weighing rare species more heavily (log-transformed), exposed a more subtly subdivided pattern. This suggested that few very common species overprinted a much more variable and subtle community pattern in rarer species (Fig. 4a, b). Also, ordination of sites explained post hoc by a species biplot in PCA (Fig. 5), indicated that four common

species (*M. plantaginea*, *M. purpurea*, *M. fruticosa* and *Leptogorgia alba*) had the strongest influence on site grouping.

Gradients in substrate composition were observed between sites, their ordination by PCA showing discrete groupings. The biplot (Fig. 6a) suggested that presence or absence of filamentous turf algae (on rock FTA.R or sand FTA.S) and crustose coralline algae (CCA) were the main determinants of site differentiation. This was supported by the scree plot (Fig. 6b), which suggested that the first three principal components (FTA.R, FTA.S, CCA) explained most of the variability. The strongest correlations were found between filamentous algae and the first two PCs with correlations decaying increasingly from PC3 (Fig. 6c), and with rugosity and depth being unimportant.

During the installation of transect lines, epizooic organisms were incidentally detected on Alcyonacea including amphipods, decapods, bivalves, and ophiuroids. Zoanthids and encrusting bryozoa had partially colonized a variety of *Muricea* spp., generally starting at the base of the affected colony. *Carijoa riisei* also overgrew *Muricea* spp. but from any point of contact. It was most prominent between 10 and 17 m depth, diminishing in abundance with increasing depth, and principally



**Fig. 3** Linear regression of species abundance vs. site presence. Species with more than 100 colonies that fall above the trend line (i.e. *L. taboguilla*) show a eurytopic distribution, whereas those below the trend line (*P. arbuscula*, *M. austera*) maybe more stenoeicous. With a limit of 31 sites, *M. plantaginea*'s overwhelming numerical dominance automatically falls under the trend line, giving no indication of possible site preferences in this evaluation

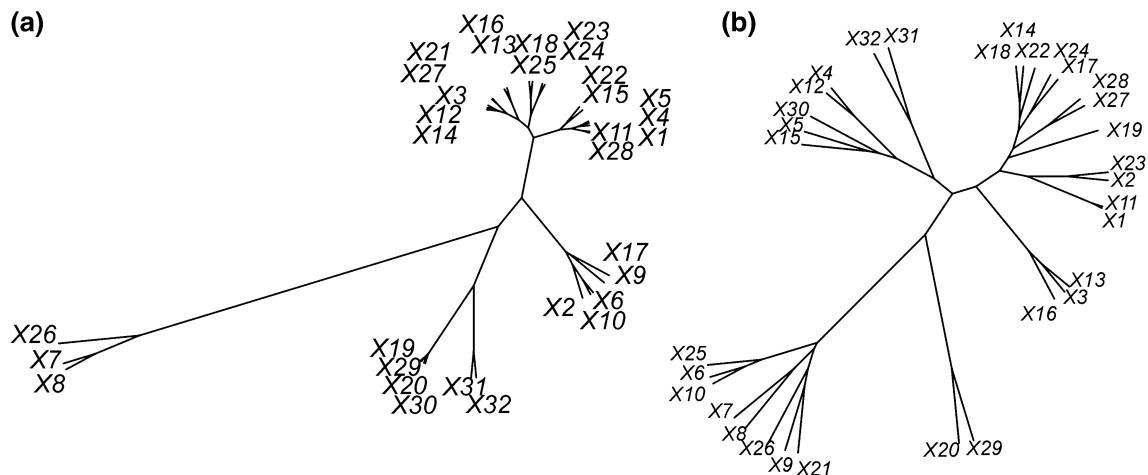
grew on vertical surfaces and overhangs, which were usually within in the alignment of the transects. Epizooic Zoanthids and *C. riisei* were not observed on *Psammogorgia*, *Leptogorgia*, and *Pacifigorgia*. *Carijoa riisei* also overgrew branching hermatypic stony corals, bivalves, and ascidians, but it stayed clear of ahermatypic encrusting stony corals such as Caryophyllidae, even when a coral patch had been surrounded.

## Discussion

A rich Alcyonacean community exists in the Marine Reserve El Pelado, in southern continental Ecuador, encompassing 17 of the 26 species so far reported for the mainland in taxonomic studies by Breedy and Guzman (2005a, b, 2007, 2011, 2015, 2016); Hickman (2008); Breedy et al. (2009a, b); Rivera and Martínez (2011);

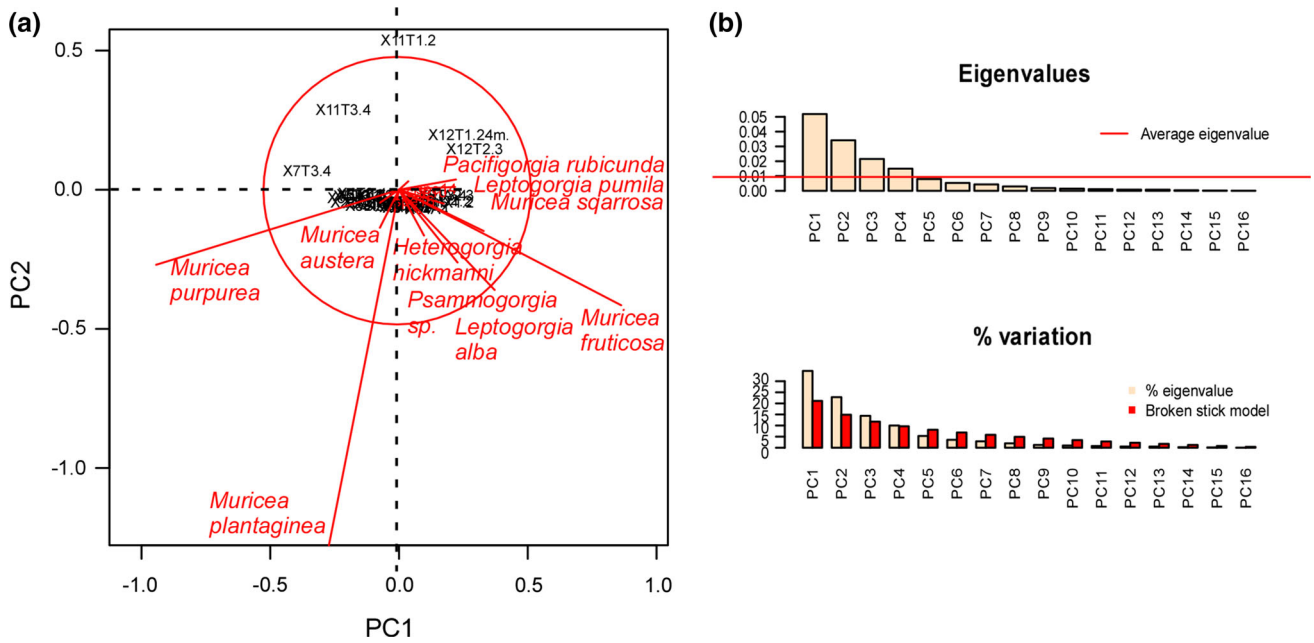
Soler-Hurtado and López-González (2012); Figueroa (2015); and Soler-Hurtado et al. (2016). *Muricea plantaginea*, *M. fruticosa*, *M. purpurea*, and *Leptogorgia alba* had the strongest influence on site groupings of Alcyonacea but *M. plantaginea* was overwhelmingly dominant in all habitats, resulting in the community's moderate species diversity. This stock-forming (Bestandsbildend) quality of *M. plantaginea* at the MREP was the most striking Alcyonacean community trait, has so far not been reported from other locations in the TEP and may represent a faunistic distinction of continental Ecuador. Previous quantitative studies were exclusively from the northern hemisphere. Contrasting the *Muricea* dominated MREP community, Alcyonacea in Mexico were dominated by *Leptogorgia*, particularly *L. alba*, *L. cuspidata* and *L. ena* (Abeytia et al. 2013), whereas *Leptogorgia alba* and *Pacifigorgia rubicunda* dominated in Panama (Gomez et al. 2014).

Given the overwhelming occurrence of *M. plantaginea*, only subtle heterogeneity in the community structure was detected among the rarer species in the hierarchical, agglomerative cluster analysis. Habitat characteristics that significantly shaped Alcyonacea distribution, were the substrate types, filamentous turf algae (FTA) and crustose coralline algae (CCA), which were the main determinants of site differentiation as indicated in the PCA. Both were associated with underlying rocky foundations offering long-term stability for Alcyonacean holdfasts (see Wanatabe et al. 2009) allowing the development and persistence of (large) colonies. Rugosity and depth, on the other hand, played no significant role in shaping the community structure at the examined depths (10–30 m) consistently exposed to strong currents and turbulence. Contrastingly, light penetration related to depth can be excluded as factor directly influencing the Alcyonacean community composition in the region, as Alcyonacea from the TEP are azooxanthellate and thus heterotrophs rather than mixotrophs (Van Oppen et al. 2005). Other depth-re-



**Fig. 4** Cladograms of hierarchical cluster analyses of species abundance-per-site data from the Marine Reserve El Pelado. Site numbers 1–32 are labeled X1–X32, respectively, in the cladograms **a** untransformed dataset and **b** log-transformed dataset





**Fig. 5** Correspondence analysis between site groupings and Alcyonacea. **a** Biplot with circle of equilibrium contribution showing variables that with equal (within circle) or lower (longer than  $r$  circle) contribution than average to dimensions of PCA space. Thus, the species represented by the longest vectors are those with most influence on site grouping. **b** Kaiser-Guttman

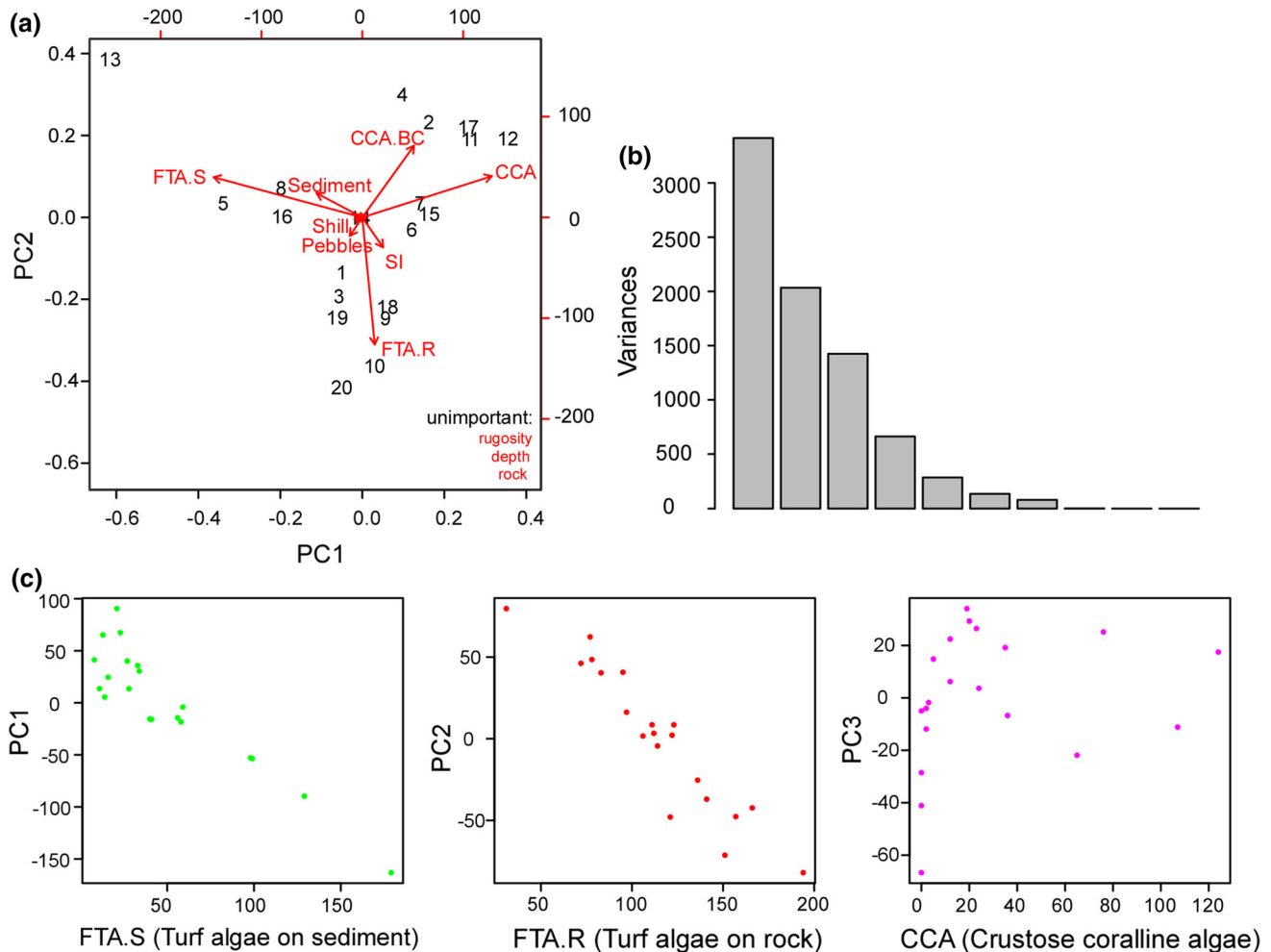
(above, those PCs > red line are most important) and Broken-Stick (below, those PCs that are greater than Broken-Stick simulation in red are most important) criteria that support that only 4 PCs explain the majority of the variation. Color figure online

lated physiological adaptations may account for the bathymetric distribution patterns observed in 10–70 m in Mexico (Abeytia et al. 2013). In this context, *M. plantaginea* may be considered a generalist (eurytopic species) as it was consistently among the most common species at all sites. Also, the broad distribution of *L. taboguilla* across all substrate types, despite the comparatively low number of colonies, suggests a generalist species, whereas *P. arbuscula* and *M. austera* may have narrower ecological tolerances (stenoecious species) based on their limited site distribution. Gomez et al. (2014) also reported an uneven site distribution of *P. arbuscula* around Coiba Island, Panama. Such differing habitat requirements among the rarer species may be at the root of the observed community differentiation.

The ecological implication of *M. plantaginea*'s dominance at the MREP is linked to its trait of being by far the largest (Breedy and Guzman 2002, 2007, 2011, 2015, 2016) of the common species at MREP. *Muricea plantaginea* consequently constituted the most abundant Alcyonacean microhabitat and host for epibiotic fauna (Lasker and Coffroth 1988). As such, it holds qualities of a keystone species or more specifically an autogenic ecosystem engineer sensu Cuddington (2012) in that its presence alters the environment (structuring the boundary layer and providing habitat) through non-trophic interactions with associated organisms (facultative and obligatory). Furthermore, this species is evidently well adapted to the seasonally migrating Equatorial Front and its accompanying fluctuations surface water in salinity and temperature (Fiedler and

Lavine 2016). Temperature records from 1996 to 2016 show mean annual fluctuations of 8.6 and 11.9 °C in depths of 0 and 40 m, respectively (pers.com. S. Sonnenholzner). Sudden decreases in its population, as induced by mass mortality events (Sánchez et al. 2014; Cerrano et al. 2000), could consequently trigger cascading changes in the community structure of Alcyonacea in general and the availability of foundation species sensu Grigg (1975) for commensal organisms (see Mosher and Watling 2009) in particular. Furthermore diseases and predation leading to partial mortality or entire colonies devoid of live tissue also favor opportunistic epizoic and fouling species. From a habitat and underwater landscape conservation standpoint, *M. plantaginea* thus plays an important role within the MREP.

Studies on reproductive patterns and recruitment rates are key elements in explaining community structure in many sessile Anthozoa (Fautin 2002; Santangelo et al. 2003; Harrison 2011). Yet of the 17 species considered here, the reproductive patterns of only two have been studied so far, *M. fruticosa* (Grigg 1970, 1975, 1977) and *C. riisei* (Kahng 2006; Kahng et al. 2008). Both are gonochoric like the majority of Alcyonacea (Kahng et al. 2011). Reproductive success in Alcyonacea may therefore partially dependent on the proximity of male and female colonies, as demonstrated for *C. riisei* (Kahng et al. 2008), but also on colony size (Yoshioka 1994). If gonochorism proves to be common among other Alcyonacea surveyed in this study, the abundant species may have a competitive advantage over rare



**Fig. 6** PCA of substratum data. (a) Groupings were evident along the PCs representing filamentous turf algae with sediment accumulation (FTA.S), on rocks (FTA.R), and crustose coralline algae (CCA). The scree plot **b** shows that the first three PCs

explain the majority of the variability (c) correlation of measurements with PC scores of the most important three substrata. Color figure online

species. However, successful fertilization, whether among gonochoric or hermaphroditic species, does not inherently imply successful larval recruitment. Ecuador's continental waters may also receive Alcyonacean planulae from a broad geographic range due to their position at the convergence of the southward flowing Panama Flow and the northward flowing Peru Current, as well as the southward-flowing annual El Niño current (Fiedler 1992; Strub et al. 1998). The paucity of studies on sexual reproductive patterns and recruitment rates in Eastern Pacific Alcyonacea (Simpson 2009; Kahng et al. 2011; Gomez et al. 2014), thus obscures a clearer interpretation of community structure, and the ability of formulating well-founded conservation measures for this taxon.

Potential biological threats to Alcyonacea along the Eastern Pacific Equatorial Front include the spread of *Carijoa riisei*, a fouling species (Bayer 1961) with fast growth (Kahng and Grigg 2005) and the ability to overgrow other sessile organisms (Grigg 1977). Native to the Pacific (Concepcion et al. 2010) and not alien as

previously interpreted (Grigg 2003), its invasiveness is undisputed. In Colombia, it overgrew and killed numerous colonies from various Alcyonacean species at depths of up to 15 m at Gorgona Island (Sánchez and Ballesteros 2014). In the MREP *C. riisei* occurred at five of the quantified sites, typically on vertical surfaces, in depths between 10 and 17 m, commonly overgrowing different Alcyonacea and other sessile invertebrates, but not in the shallower coastal sites. *Carijoa riisei* also appeared to be unable to invade patches of encrusting ahermatypic stony corals (Caryophyllidae), pointing to chemical defenses in the latter (see Kelman et al. 2009). Physiological limitations of *C. riisei* include irradiance and low temperatures in shallow and deep settings, respectively (Kahng and Grigg 2005), as demonstrated in Hawaii where it occurred from 30 to 120 m depth (temperature range 22–28 °C). This raises the question whether *C. riisei* can colonize depths beyond 17 m along the Equatorial Front, exposed to annual bathymetric fluctuations in thermoclines (Wang et al. 2016). In other words, can *C. riisei*, a gonochoric species exhibiting no

lunar periodicity in gametogenesis (Kahng et al. 2008), benefit from downward shifting thermoclines as temporal bathymetric expansion windows in the TEP? The answer will indicate whether deeper sites may serve as refugia for the dominant species *M. plantaginea* and others.

In conclusion, Alcyonacea from the southern TEP showed a moderately diverse community of 17 species, dominated by *Muricea plantaginea* with qualities of a keystone species structuring the benthic boundary layer and providing microhabitats, thus differing from Mexican and Panamanian communities. Variable distribution patterns correlated to benthic substrate composition, primarily FTA and CCA were noted. Species abundance and site overlap pointed at *L. taboguilla* being a generalist and *P. arbuscula* more specialized in its distribution. The invasive *C. riisei* posed a biological threat to other Alcyonacea, which it overgrew, showed bathymetric distribution limitations, and appeared to be unable to overgrow ahermatypic caryophyllid stony corals. These findings narrowed a long-lasting ecological information gap on Alcyonacea from Eastern Pacific Equatorial Front, a region at the heart of studies addressing effects of phenomena like the El Niño Southern Oscillation on benthic communities in the light of climate change (Glynn et al. 2016b). Alcyonacean community traits from Ecuador provide a baseline for a better understanding their resistance or resilience to future environmental changes.

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