



Octocoral populations and connectivity in continental Ecuador and Galápagos, Eastern Pacific

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Contents

1. Introduction	412
2. Materials and methods	414
3. Results	420
4. Discussion	431
4.1 Conclusion	434
Acknowledgements	435
References	435

Abstract

Octocorals are important zoobenthic organisms, contributing to structural heterogeneity and species diversity on hardgrounds. Their persistence amidst global coral reef degradation and ocean acidification, has prompted renewed interest in this taxon. Octocoral assemblages at 52 sites in continental Ecuador and Galápagos (23 species, 3742 colonies) were examined for composition, size distributions within and among populations, and connectivity patterns based on ocean current models. Species richness varied from 1 to 14 species per site, with the richest sites on the continent. Three assemblage clusters were recognised based on species richness and population size, one with a mix of sites from the mainland and Galápagos (defined by *Muricea fruticosa* and *Leptogorgia alba*, *Muricea plantaginea* and *Pacificogorgia darwini*), the second from Santa Elena in southern Ecuador (defined by *M. plantaginea* and *L. alba*) and the third from the northernmost sites on the continent, in Esmeraldas (defined by *Muricea fruticosa*, *Heterogorgia hickmani*, *Leptogorgia manabiensis*). Based on biophysical larval flow models with 30, 60, 90-day Pelagic Larval Duration, good connectivity existed along the South American mainland, and from the continent to Galápagos. Connectivity between Galápagos, Cocos, Malpelo

and the Colombian mainland may explain the wide distribution of *L. alba*. *Muricea planaginea* had the densest populations with the largest colonies and therewith was an important habitat provider both in continental Ecuador and Galápagos. Continental Ecuador harbours the most speciose populations of octocorals so far recorded in the southern Eastern Tropical Pacific (ETP). Most species were uncommon and possibly vulnerable to local extirpation. The present study may serve as a base line to determine local and regional impacts of future disturbances on ETP octocorals.



1. Introduction

Octocorallia is a subclass within Anthozoa (Ehrenberg), phylum Cnidaria (Hatschek), with a wide geographic, bathymetric and solely marine distribution (Bayer, 1981). In shallow water ecosystems such as temperate or tropical hardgrounds and coral reefs, octocorals contribute to carbonate sediments (Cary, 1918; Konishi, 1981) and are an important component of the zoobenthos (Bayer, 1961; Fabricius and Alderslade, 2001; Sammarco and Coll, 1992; Spalding et al., 2001). Similar to stony reef corals (Scleractinia), the presence of octocoral taxa with arborescent growth forms compartmentalize the benthic boundary layer by increasing structural habitat complexity for many epizoid algae and invertebrates (Cantera et al., 1987; Glynn et al., 2019; Lasker and Coffroth, 1988; Mosher and Watling, 2009; Patton, 1972; Ramos, 1995; Vreeland and Lasker, 1989) as well as fishes (Etnoyer and Warehchuck, 2007; Lasker, 1985; Taylor et al., 2013) and other reef biota. Dense octocoral stands also create a mosaic of physio-chemical gradients in light penetration, hydrodynamics and sedimentation rates (Valisano et al., 2016; Wainwright et al., 1976), as well as gas exchange and material cycles (see Fréchette et al., 1989; González-Ortiz et al., 2014), analogous to seagrass meadows (Irlandi, 1996; Vogel, 1994). They thus augment the heterogeneity of conditions in micro-habitats and interstitial spaces driving biodiversity (Graham and Nash, 2013; Plass-Johnson et al., 2016; Richardson et al., 2020), as well as the survival of rare species (Mouillot et al., 2013).

The impacts of the global reef crisis on octocorals have received less attention than in other taxa (but see Lasker et al., 2020a, in this volume). Unlike scleractinian reef corals, at least in Caribbean settings, population densities of octocorals and the ecosystem benefits of increased structural habitat heterogeneity, showed persistence (Lasker et al., 2020b; Lenz et al., 2015; Tsounis and Edmunds, 2017) and even expansion (Ruzicka et al., 2013;

Sánchez et al., 2019) during recent decades, amidst a general structural flattening of reefs caused by the degradation of stony coral communities (Alvarez-Filip et al., 2009, Glynn et al., 2018). Furthermore, Enochs et al. (2016) presented evidence of a degree of octocoral resistance to ocean acidification. These observations were based on zooxanthellate octocoral species sharing habitat with reef-building Scleractinia. In the wake of global bleaching events and mass mortalities (Hughes et al., 2017), winners and losers among mixotrophic zooxanthellate Scleractinia (Loya et al., 2001) were identified, gauged on population performance following disruption. The concept of winners and losers requires an established regional baseline of populations, in which some species have either a disturbance-resistant population or can be effectively replenished through connectivity. It is unclear whether winners and losers can also be identified among octocorals, which despite demonstrated persistence are nonetheless not exempt from population declines and anthropogenic impacts (Cerrano et al., 2000; Gomez et al., 2015; Sánchez and Ballesteros, 2014; Tsounis et al., 2012). Eastern Pacific octocorals are heterotrophic (Van Oppen et al., 2005) and it is unclear how their populations may fare in future disturbances like thermal anomalies.

Octocoral assemblage structure is a building block in defining its constituent populations for comparisons across wider geographic regions. In the Eastern Tropical Pacific (ETP) such studies have so far been limited to select locations in Mexico (Abeytia et al., 2013), Panama (Gomez et al., 2014), Colombia (Sánchez et al., 2011; Sánchez and Ballesteros, 2014) and part of Ecuador (Steiner et al., 2018a, 2018b). The majority of octocoral studies from the region describe species taxonomy and range extensions (summarised in Steiner et al., 2018a, 2018b), but few studies develop data that could be used as baselines to evaluate impacts on populations and assemblages following large-scale, or even local, perturbances.

To identify species and populations that best lend themselves for monitoring and possibly anticipating the susceptibility of octocoral populations towards future disturbances in the ETP, assemblage composition, population and size distributions were examined at 37 sites along the continental coast of Ecuador and 15 sites in Galápagos. In view of the paucity of reproductive data for ETP species (Gomez et al., 2018; Grigg, 1977; Kahng et al., 2011), surface current models were applied to discern possible connectivity patterns among continental and insular regions and to establish the potential role of Ecuador's octocoral populations as larval sources or recipients in a wider geographic context. Similar larval

connectivity models based on hydrodynamics have been successfully applied in shallow and deep communities (Lequeux et al., 2018; Metaxas et al., 2019; Wanatabe et al., 2009; Wood et al., 2016). The emerging picture provides a regional baseline for this habitat-shaping taxon, upon which conservation initiatives and further studies can build.



2. Materials and methods

2.1.1 *Octocoral assemblages*

Octocorallia occur along the entire Ecuadorian coast, exposed to the convergence of the seasonal southward-flowing Panama Flow and the northward flowing Peru Current, as well the southward-flowing sporadic El Niño current in the months between December and April (Fiedler, 1992; Fiedler and Lavine, 2016; Strub et al., 1998), and throughout the Galápagos archipelago (Fig. 1). Local anthropogenic disturbances include colony abrasion and detachment from extensive damage by bottom-trawling up to the year 2009 (Government of Ecuador, 2009; Rivera and Martínez, pers. comm.) and ongoing fishing gear loss (Figueroa-Pico et al., 2020). Octocorals were encountered in 37 of 40 continental sites and in 15 of the

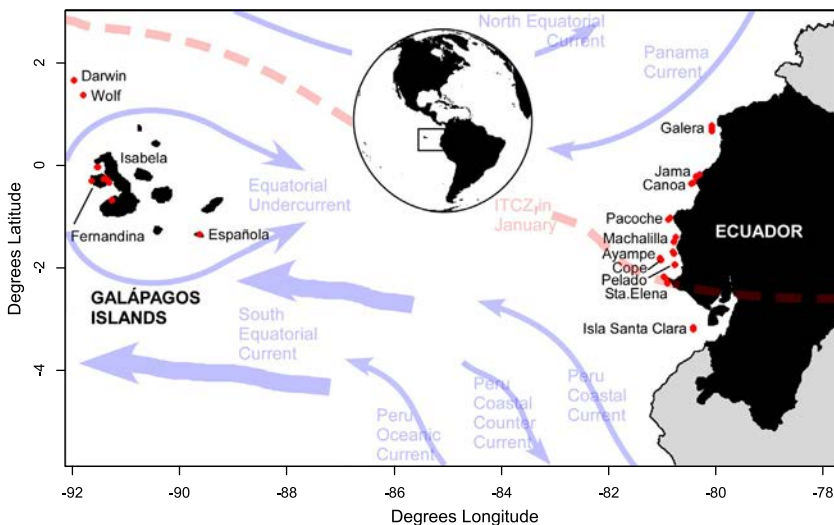


Fig. 1 Sampling sites along the mainland coast and the Galápagos Archipelago in Ecuador, Eastern Tropical Pacific. Cocos and Malpelo Islands, mentioned in the text, are to the north of the mapped area. ITCZ oscillating Intertropical Convergence Zone.

29 Galápagos sites explored in depths between 6 and 20 m (Table 1). Surveys employed belt transects for colony counts and quantification of size classes in evenly distributed subsamples (2015–2018). Sampling effort per site varied among sampling regions and covered 50 m² ($n=29$, mainland sites), 80 m² ($n=8$, mainland), and 100 m² ($n=15$ Galápagos). Colony density per species, per site was determined and assigned to a semi-quantitative, 9-point density scale and ranked along a gradient from rare (lowest density = 1) to common (highest density = 9), to reduce the range of densities and render the data more compatible with the chosen analyses (Borcard et al., 2011; Elzinga et al., 2001; Legendre and Legendre, 2012). Diversity indices (H' = Shannon Entropy, J = Pielou's Evenness; Legendre and Legendre, 2012) were calculated from untransformed colony frequency per species, per site.

The identification of species was based on a previously built photographic repository of in situ colonies, as well as specimen collections (2015–2017), which had been examined macro- and microscopically, in some cases with the extraction of sclerites, and compared to the latest species descriptions as detailed in Steiner et al. (2018a, 2018b).

2.1.2 Evaluation of assemblage patterns

Assemblage patterns were explored by hierarchical, agglomerative cluster analysis in the R-package *vegan* (Oksanen et al., 2017; R Development Core Team, 2012) using procedures outlined in Borcard et al. (2011). A Euclidian distance matrix was calculated for the rank-transformed data and several clustering methods were evaluated (single and complete linkage, UPGMA and Ward; Borcard et al., 2011; Legendre and Legendre, 2012). The optimal number of interpretable clusters was investigated by graphing Silhouette widths, which are a measure of membership of an object to its cluster (Borcard et al., 2011). This was checked against the Mantel-optimal number of clusters, which is a comparison between the distance matrix and binary matrices that represent the partitions (Borcard et al., 2011). Upon coincidence of the number of optimal clusters as checked by these methods, the quality of appropriate group-membership (i.e. the incidence of misclassifications) was examined with another silhouette plot. When misclassifications were minimised, the appropriate clustering method and optimal number of clusters had been determined (Borcard et al., 2011). The chosen dendrogram was then combined with a heatmap to bring forth patterns of similarity, and the species content in the clusters was visualised by sorting them according to weighted averages on site scores.

Table 1 Location of study sites.

	Site code	Site name	Depth	Latitude	Longitude	Area	Province/ Island	Region
1	CEGSF1	Piedra d Quingue	7	0.725000	-80.100000	Reserva Marina Galera San Francisco	Esmeraldas	Continental Ecuador
2	CEGSF2	Tortuga 1	12	0.769000	-80.101000			
3	CEGSF3	Punta Alta	8	0.661000	-80.099000			
4	CEGSF4	Frente al Horno	8	0.665000	-80.098000			
5	CMJAM1	Vaca Brava 1	10	-0.240708	-80.394160	Jama	Manabí	
6	CMJAM2	Vaca Brava 2	12	-0.237985	-80.394880			
7	CMJAM3	Punta Venado	12	-0.223220	-80.387960			
8	CMJAM4	Punta Ballena	10	-0.174546	-80.329940			
9	CMCAN1	Cabo Pasado 1	6	-0.357037	-80.488210	Canoa		
10	CMCAN2	Cabo Pasado 2	7	-0.357589	-80.485070			
11	CMCAN3	La Saibita	12	-0.342415	-80.445000			
12	CMPAC1	Roca Ahogada	7	-1.019466	-80.881630	Refugio Pachoche		
13	CMPAC2	Cabo S. Lorenzo	7	-1.060216	-80.911900			
14	CMMAC1	Bajo Frailes	12	-1.493247	-80.806530	Parque Nacional Machalilla		
15	CMMAC2	Horno de Pan	10	-1.498630	-80.809010			
16	CMMAC3	Isote Sombbrero	12	-1.405504	-80.770590			
17	CMAYA1	Rinconada	10	-1.712225	-80.805660	Ayampe Canta Gallo-Machalilla		
18	CMAYA2	Rinconada 1	12	-1.710244	-80.806620			
19	CMAYA3	Ahorcados E	6	-1.677532	-80.835570			

20	CSCOP1	Bajo Mantas	10	-1.812314	-81.063320	Reserva Marina, Bajo Copé	Santa Elena
21	CSCOP2	Bajo Copé 1	12	-1.845219	-81.052770		
22	CSCOP3	Bajo Copé 2	14	-1.816403	-81.061280		
23	CSCOP4	Bajo Fer 3	14	-1.812929	-81.063670		
24	CSPeL1	EPPNW 2	20	-1.933333	-80.792500	Reserva Marina El Pelado ^a	
25	CSPeL2	EPPNW 3	19	-1.931944	-80.790556		
26	CSPeL 3	Islote Pelado 5	13	-1.933611	-80.788889		
27	CSPeL4	EPPNE 6	14	-1.931389	-80.787222		
28	CSPeL5	I Pelado 8W	15	-1.936111	-80.788889		
29	CSPeL6	I Pelado 8E	15	-1.935833	-80.791111		
30	CSPeL7	EPPSE	15	-1.933889	-80.786667		
31	CSAYA	Ayangue	15	-1.987222	-80.757500	Ayangue	
32	CSSEL1	Guarro	10	-2.2992161	-80.934220	Reserva PFM Santa Elena	
33	CSSEL2	Bajo Ballena	8	-2.1963506	-80.957000		
34	CSSEL3	Casa de Lobos	14	-2.1837304	-81.003650		
35	CSSEL4	Piedras Altas	12	-2.1666222	-81.003300		
36	COSCL1	Sitio Oeste	10	-3.189198	-80.452840	Isla Santa Clara	El Oro
37	COSCL2	Sitio Oeste 1	10	-3.1614192	-80.442280		
38	COSCL3	Sitio NO	10	-3.1623725	-80.448590		

Continued

Table 1 Location of study sites.—cont'd

Site code	Site name	Depth	Latitude	Longitude	Area	Province/ Island	Region	
39	GDDAR1	Arch NE	18	1.673667	-91.989806	Darwin	Darwin I.	Galápagos
40	CDDAR2	Arch E	18	1.673065	-91.989113			
41	GWWOL1	Wolf	15	1.393709	-91.818958	Wolf	Wolf	
42	GEGAR1	Gardener	15	-1.346000	-89.642000	Gardener	Española	
43	GEGAR2	Canones	10	-0.343000	-91.324000	Canones		
44	GICAS	Caseta	10	-0.295000	-91.357000	Caseta	Isabela	
45	GIPNE	Playa Negra	12	-0.244000	-91.395000	Playa Negra		
46	GIPMO1	Pesca	10	-0.686000	-91.270000	Punta Moreno		
47	GIPMO2	Prot	10	-0.686000	-91.270000			
48	GIPMO3	Turismo	10	-0.686000	-91.270000			
49	GIVRO1	Pared	13	-0.051000	-91.560000	Punta Vincente Rocafuerte		
50	GIVRO2	Pesca	11	-0.686000	-91.270000			
51	GFPEs	Punta Espinoza	10	-0.270000	-91.435000	Punta Espinoza	Fernandina	
52	GFDou	Cabo Douglas	12	-0.301672	-91.653835	Gabo Douglas		

^aDetailed site descriptions for El Pelado Marine Reserve available in [Steiner et al. \(2018a\)](#).

2.1.3 Evaluation of population

The structure of individual species populations was examined via the distribution of size-classes, which were expressed as an area based on a planar view of the colony in photographic images and videos containing scale bars with 5 or 10 cm units, from which measurements of colony “width” (x-axis) and “height” (y-axis) were taken. Colony sizes were sorted into four size classes (SC1 < 100 cm², SC2 100–399 cm², SC3 400–899 cm² and SC4 ≥ 900 cm²). The number and dimensions of the size classes were strategically created in order to reflect distinct size classes among the smaller species and the many small colonies of larger species observed during the surveys.

2.1.4 Biophysical model for connectivity

Given the few reproductive strategies available for ETP octocoral species considered, we assumed that the species were gonochoric (Gomez et al., 2018; Kahng et al., 2011; Simpson, 2009) and released actively swimming larvae, with larval durations of up to 90 days (Baird et al., 2009; Coelho and Lasker, 2016; Dahan and Benayahu, 1998), and a spawning period similar to the one reported for stony corals, from January to May (Glynn et al., 2017; Riegl et al., 2019b), which is compatible with Grigg’s (1977) observation of spawning during annual temperature peaks in two EP species, but see Gomez et al. (2018). Whether fertilization was external or internal (brooding), as well as the time from spawning to fertilization and completed embryogenesis (planulae) was unknown. Based on this premise, larval dispersal and connectivity among known occurrences of octocorals were examined with a biophysical model (Johnston and Akins, 2016; Riegl et al., 2019b). The applied model simulated the movement of larvae (planulae) across a 2-D, fixed cell-dimension grid using stochastic, Lagrangian particle tracking. The grid incorporated the Galápagos and northern Eastern Tropical Pacific (ETP) regions with a grid pixel size of 1/12th decimal degree (~9 km), using ocean current data from the global Hybrid Current Ocean Model (HYCOM). Daily data from 2005 to 2015 were employed in a 10-year simulation. This time period included several ENSO events (see Glynn et al., 2017, Riegl et al., 2019a, 2019b). Planulae diffusion in ocean surface currents and recruitment were tracked from points of origin (spawning) to settlement in known octocoral sites in the study region over the 30, 60, 90-day PLD (Pelagic Larval Duration). Known octocoral populations were clustered into precincts (southern and northern Galápagos; Cocos, Costa Rica; Malpelo, Chocó and Gorgona, Colombia, sites on the Ecuadorian coast in Esmeraldas,

Manabí, Santa Elena and El Oro provinces). One geographic location every 9 km within a precinct was selected as a site for a reproductively mature octocoral cluster to seed the simulations (density-independent and one cluster per point, total 350 clusters). Simulations selected reproductive clusters within all precincts at the start of each year. Each mature cluster was allowed to produce larvae every 30 days from January to May. Larval release was simultaneous from all colonies and randomly staggered within each model colony over 5 days.

From HYCOM simulations, a daily vectorized flow-field of ocean currents (measured in m/s) was obtained over which planulae dispersed following a Lagrangian path during the pelagic larval duration (PLD, 30, 60, and 90 days). The u (east-west) and v (north-south) positions of the larvae (P_i = east-west, north-south position at time i) and their hourly transition times were tracked. The vector (\vec{v}_i) traversed by any planula per Δt was calculated by bilinearly interpolating the nearest four ocean current vectors to the planula's x/y position. A timer tracked the hours elapsed over each planula's PLD. After a pre-competency period of two lapsed days, known coordinates of coral areas within 1 km of the planula's position at each Δt were determined. If a planula was within 1 km of a reef, it was allowed to recruit to that position and then remain non-reproductive for the duration of the simulation (10 years), to conservatively account for timing until sexual maturity. Planulae were considered lost if they did not come within 1 km of a suitable recruitment position during their PLD.

Using this protocol, the path from spawning to recruitment was chronicled (as were founder colonies and subsequent recruitment positions) in order to produce a connectivity matrix. To model conservatively, since larval survival rates are unknown, only one larva per colony was incorporated in the simulation per monthly reproductive cycle. To account for possible differences in larval duration, we constructed 30, 60 and 90-day models and connectivity matrices that cross-plotted the founder clusters on the x -axis with the recruitment positions on the y -axis. Each recruitment position was colour coded via a cool (blue—low) to warm (red—high) scale to represent relative densities of recruits.



3. Results

A total of 3742 octocoral colonies were encountered, of which 63 and 8 colonies from continental and Galápagos sites, respectively, could not be

assigned to a species and were predominantly *Muricea* spp. The 23 identified species belonged to the families Clavulariidae (1), Gorgoniidae (13) and Plexauridae (9), (Table 2). From here on, species are referred to as “common” if >500 colonies were encountered in this survey, “uncommon” with 100–500 colonies and “rare” with <100 colonies. Only three species reached locally high densities of >2–3 colonies m⁻², *Muricea plantaginea*, *Muricea fruticosa* and *Leptogorgia alba*, while most species were widely distributed but at low density and rare. Co-occurrence on the mainland and Galápagos was observed in *M. plantaginea*, *Heterogorgia hickmani* and *L. alba*.

3.1 Distribution and structure of octocoral assemblages

Cluster analysis to define assemblage groups expected three major groups of sites. These were based on silhouette width and the correlation between the original distance matrix of rescaled octocoral densities per site and binary matrices from several possible numbers of partitions. Silhouette plotting of partition accuracy in three clusters was satisfactory (Fig. 2). From this point forward, we worked on the assumption that the Ecuadorian octocoral communities differentiated into three broad groups.

The largest cluster (henceforth referred to as cluster C1 and shown in green in Figs. 3, 5, 6, and 7) included a mixture of sites from the mainland and Galápagos (Fig. 3A). The cluster itself partitioned into two further groups, one consisting of sites mainly in Galápagos, the other mainly in continental Ecuador. The species with highest weight in the Galápagos sub-cluster were *M. plantaginea* and *Pacifigorgia darwinii*, which was encountered exclusively in Galápagos. The second sub-cluster, which contained all continental sites plus Darwin (Galápagos), was characterized by the widespread *L. alba* and *M. fruticosa*.

Cluster C2 (shown in red) was made up exclusively by samples from the Santa Elena region (Fig. 3) and was characterized by high species richness and by weight of *M. plantaginea* and the less abundant *L. alba* at Pelado. Almost unique to this cluster were the overall uncommon *Muricea purpurea*, *Leptogorgia taboguillae*, and a colour morph of *M. plantaginea* (Fig. 3B).

A third well-defined cluster (C3, shown in blue) consisted of samples from the northern province of Esmeraldas, with one mis-grouped sample (Fig. 2C) from Santa Elena. This was a species-rich group of samples with high weights of widespread species (*M. fruticosa*, *H. hickmani*, *Leptogorgia manabiensis*) and species largely confined to this region (*Pacifigorgia irene*, *Pacifigorgia firma*, *Pacifigorgia rubicunda*).

Table 2 Species and colonies (out of 3742) recorded in the surveys.

Species	Mainland	Galápagos
Suborder Holaxonia Studer, 1887		
Family Plexauridae Gray, 1859		
1) <i>Heterogorgia hickmani</i> Breedy and Guzman, 2004 ^b	36	17
2) <i>Heterogorgia verrucosa</i> Verrill, 1868	2	–
3) <i>Muricea austera</i> Verrill, 1869	78	–
4) <i>Muricea crassa</i> Verrill, 1868	16	–
5) <i>Muricea fruticosa</i> Verrill, 1869 ^b	528	–
6) <i>Muricea plantaginea</i> (Valenciennes, 1846) ^b	1011	525
7) <i>Muricea purpurea</i> Verrill, 1864	247	–
8) <i>Muricea squarrosa</i> Verrill, 1869	63	–
9) <i>Psammogorgia</i> cf. <i>arbuscula</i> Verrill, 1866	84	–
Family Gorgoniidae Lamouroux, 1812		
10) <i>Leptogorgia alba</i> (Duchassaing and Michelotti, 1860) ^b	104	533
11) <i>Leptogorgia cuspidata</i> Verrill, 1865	4	–
12) <i>Leptogorgia laxa</i> Hickson, 1928	5	–
13) <i>Leptogorgia manabiensis</i> Soler-Hurtado, Megina, Machordom, López-González, 2017	163	–
14) <i>Leptogorgia pumila</i> (Verrill, 1868)	18	–
15) <i>Leptogorgia taboquillae</i> (Hickson, 1928)	38	–
16) <i>Leptogorgia</i> cf. <i>rigida</i> Verrill, 1864	1	–
17) <i>Pacifigorgia adamsii</i> (Verrill, 1868)	30	–
18) <i>Pacifigorgia darwinii</i> (Hickson, 1928) ^a	–	97
19) <i>Pacifigorgia firma</i> Breedy and Guzman, 2003	16	–
20) <i>Pacifigorgia irene</i> Bayer, 1951	12	–
21) <i>Pacifigorgia rubicunda</i> Breedy and Guzman, 2003	16	–
22) <i>Pacifigorgia stenobrochis</i> (Valenciennes, 1846)	5	–
Suborder Stolonifera Thompson and Simpson, 1809		
Family Clavulariidae Hickson, 1894		
23) <i>Carijoa riisei</i> (Duchassaing and Michelotti, 1860)	20	–

^aReported for Galápagos.^bReported for Galápagos and continental Ecuador.

Species are referred to as common with over 500 colonies, uncommon with 100–500 colonies and rare with less than 100 colonies.

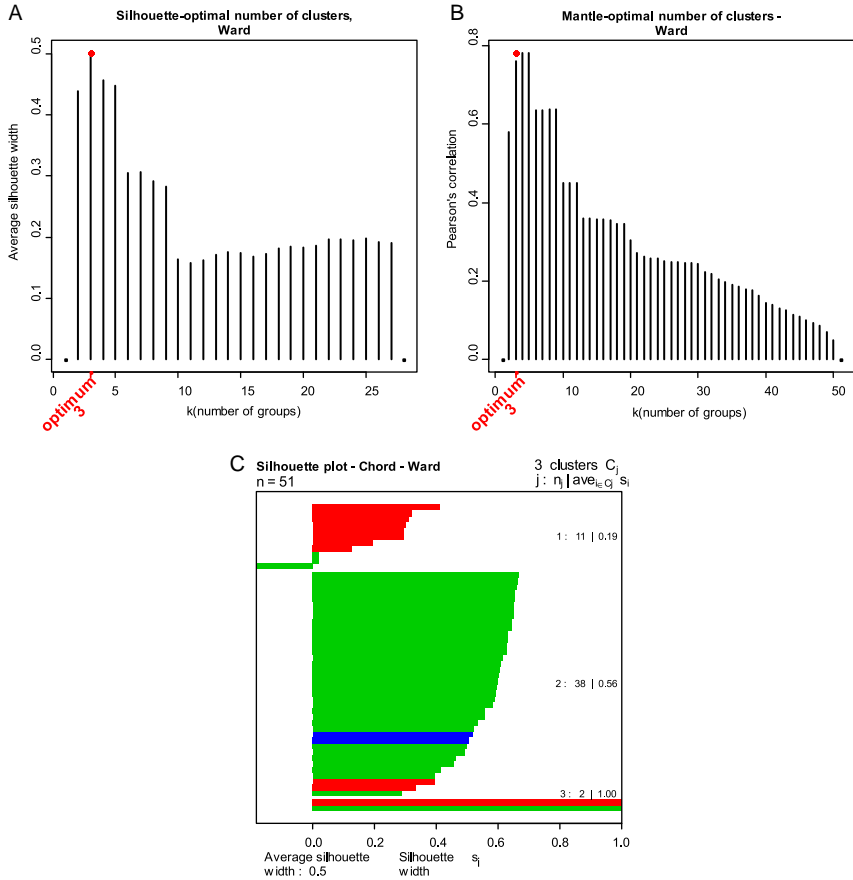


Fig. 2 (A) Bar plot showing the average silhouette widths for 27 groups. The best partition (shown by red text “optimum”) is at the largest silhouette width. (B) Bar plot of correlations between original distance matrix and binary matrices computed from the dendrogram at the level of each vertical bar. Again, the highest correlation is shown at a level of 3 clusters. (C) Silhouette plot of the finally chosen three-group partition from the Ward clustering. Most bars towards the right are properly classified, only one bar to left indicates a misclassification. Relatively poor differentiation between the blue and green (clusters 3 and 1 in Fig. 3) is evident. Overall, the result gives high confidence in the observed clustering pattern (see Fig. 3).

3.2 Distribution and structure of octocoral populations

Species richness was variable across the sampling area, ranging from 1 to 14 species, with the richest sites found on small islands and rocks off the mainland, both in the drier and cooler South (Pelado ($H' = 1.5$, $J = 0.6$ — $H' = 2.0$, $J = 0.8$) and Santa Elena peninsula ($H' = 1.3$, $J = 0.5$ — $H' = 2.3$, $J = 0.6$)) and

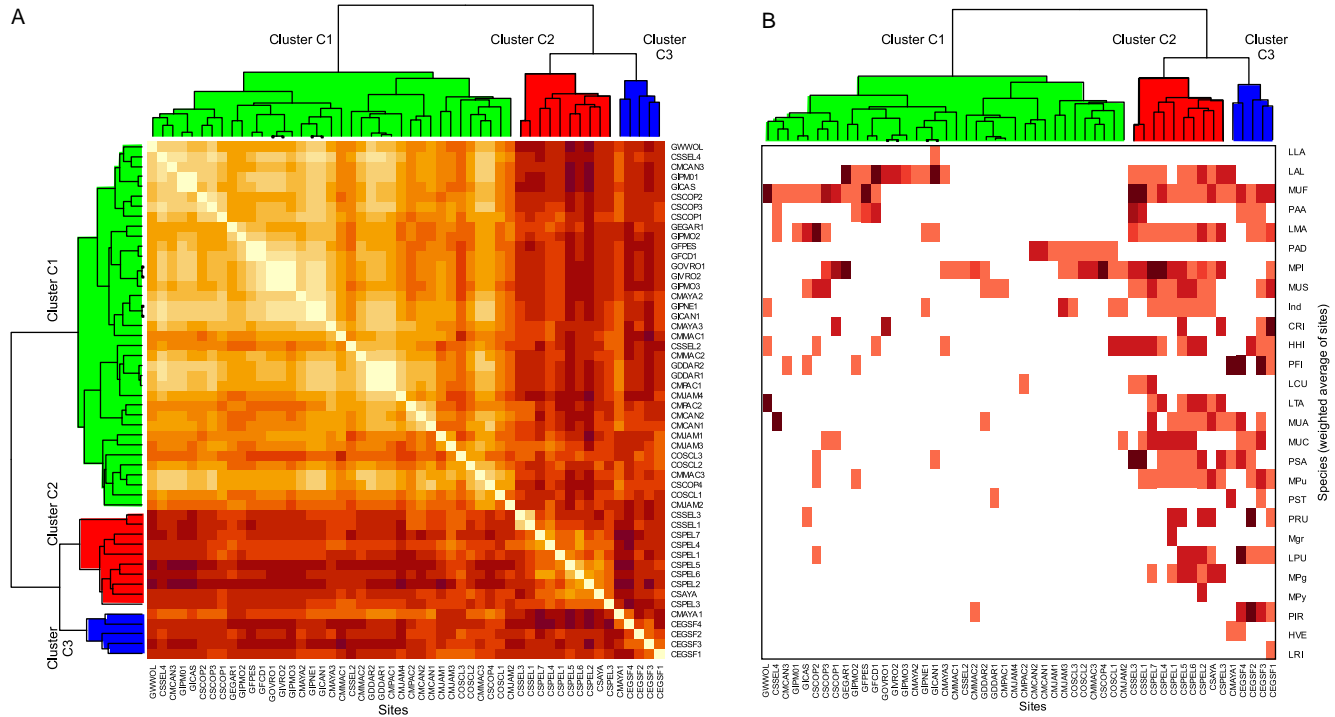


Fig. 3 Heatmap of Euclidian distances among samples and dendrogram. (A) The dendrograms to the left and above the heatmap are identical and the information contained within the heatmap is equivalent to that in the dendrograms. Colour scheme of clusters follows Fig. 2. The combination of these two graphical methods allows easy detection in patterns. (B) The same dendrogram above a heatmap of a community table ordered by cluster grouping and weighted averages on site scores (values between 0 = white, and brown = 9; the redder, the higher the value). This depicts which species can be considered characteristic for specific sites.

the wetter and warmer North (sites in Esmeraldas ($H'=2.2$, $J=0.9$ — $H'=2.4$, $J=0.9$)). Overall, the continent was more speciose than Galápagos (Wilcoxon-test, $W=1$, $p<0.008$; Fig. 4B). Population sizes, however, did not differ significantly between the mainland and Galápagos (Wilcoxon-test, $W=18$, $p=0.839$; Fig. 4A). The largest and densest populations were found at Pelado and Santa Elena Peninsula and Galápagos (Fig. 4A and B), and consisted primarily of *M. plantaginea* and *L. alba*.

Population sizes and size-frequencies of species that were common on both mainland and in the Galápagos, and were found to define clusters in the heatmap (Fig. 3B), namely *M. plantaginea* (cluster C1) *L. alba* (cluster C3) and *H. hickmani* (clusters C1–C3), were further investigated.

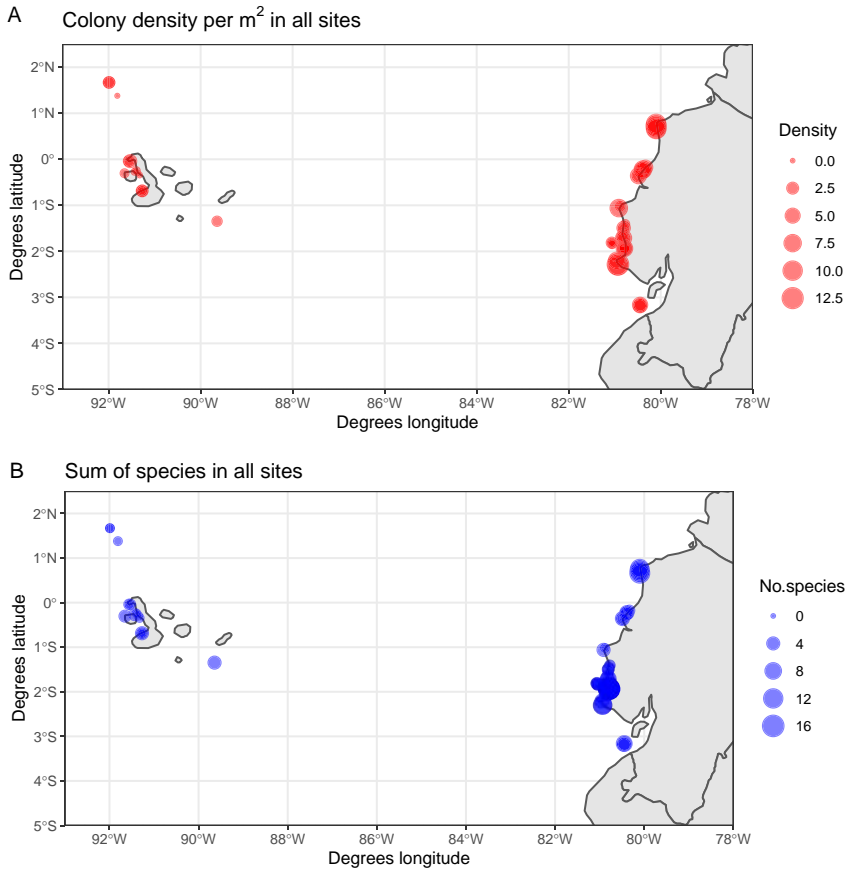


Fig. 4 (A) Sum of colony densities (Sum_dens = number of colonies m^{-2}) in all species and (B) sum of species (Sum_spec) present in each site (including a category “unidentified” and two colour morphs listed separately for *M. plantaginea*), as indicator of population size in the sample sites.

All three species had comparably as dense populations in the Galápagos as on the continent. On the continent and Galápagos (cluster C1), *L. alba* were skewed towards smaller specimens, which was not so clearly the case at Pelado and Santa Elena peninsula (cluster C2) nor at Esmeraldas (cluster C3), which had the sparsest population (Fig. 5A and B). *M. plantaginea*, also had the smallest and least dense populations in Esmeraldas (cluster C3) but

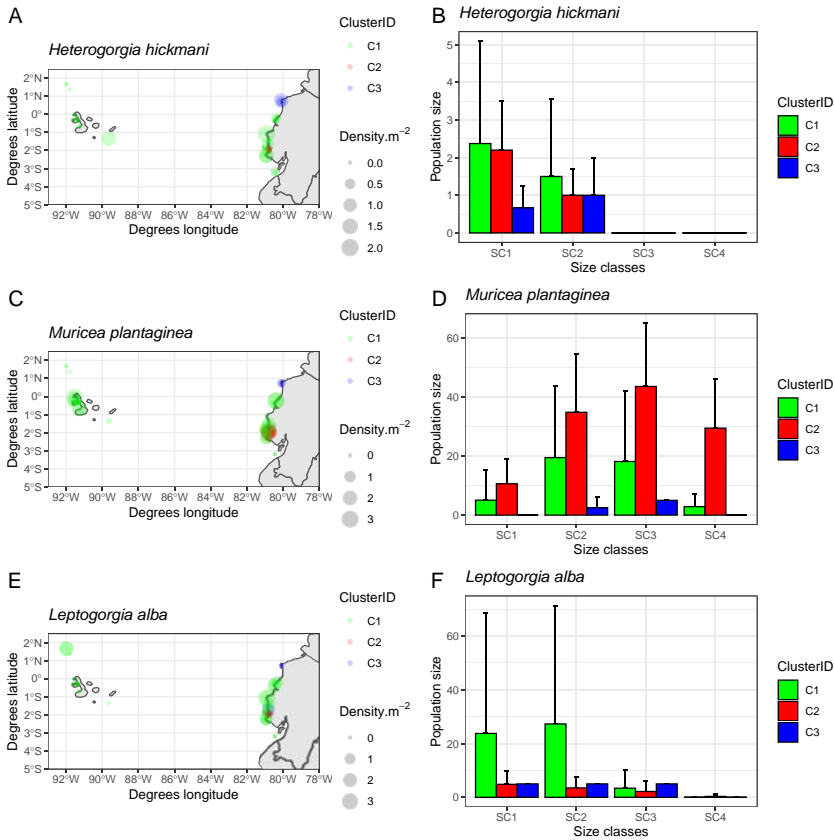


Fig. 5 Characterization of populations of some common octocoral species and defined assemblages on the mainland coast of Ecuador and the Galápagos Islands (A,C, and E) denoting the size of populations, coded by cluster membership (B,D, and F) and the size distribution of the population within each cluster (size classes SC1 <100 cm², SC2 100–399 cm², SC3 400–899 cm² and SC4 ≥900 cm²). Cluster ID refers to the clusters identified in Fig. 2A and B, where the latter also shows the contribution of species to cluster formation. Note that location of all sample sites is indicated, even if empty (smallest circle, see legend). Cluster ID refers to the assemblage clusters (same colour-code) obtained from Fig. 3. HHI in legend is *Heterogorgia hickmani*, MPI is *Muricea plantaginea*, LAL is *Leptogorgia alba*.

was similarly dense on the mainland coast and Galápagos (cluster C1) and at Pelado and the Santa Elena peninsula (cluster C2). The populations in all three clusters were overall clearly skewed towards the larger size-classes (Fig. 5C and D). *H. hickmani* was distributed at similar density in clusters C1 and C2 but had low density in cluster C2 (Pelado). It was densest in western Galápagos (especially at Isabela, cluster C2).

Only one species was widespread in Galápagos and was not found on the mainland coast, *Pacificorgia darwinii*. The species was common in the colder region of Galápagos on the west-coasts of Isabela and Fernandina. It was also encountered, albeit more rarely, on the other islands. Most of the population was encompassed within the smallest two size-classes, and few larger colonies were encountered (Fig. 6A and B).

Among some of the assemblage-defining species that only occurred on the continent, site differences in population sizes and colony size distributions were observed. *Leptogorgia manabiensis* (Fig. 5C and D) was widespread and dense on the continental coast and populations consisted mainly of size class 2 (100–399 cm²). At Pelado (cluster C2), the population consisted of less dense, but larger colonies than at the other sites. No very small individuals were encountered in Esmeraldas (cluster C3). Three *Muricea* species were dense and assemblage-defining on the mainland coast, but population structures differed. *M. fruticosa* had the numerically largest population, which was heavily skewed towards the smallest size class at Pelado and Santa Elena peninsula (cluster C2). This was not the case in the other numerically smaller populations of this species on the mainland (Fig. 7A and B). Also, in *Muricea austera*, the Pelado and Santa Elena peninsula population was skewed towards the smallest size-class, while the middle (SC2) and large (SC3) size-classes characterized the other mainland sites in this species (Fig. 7C and D). *Muricea squarrosa* was relatively dense and had larger colonies in Esmeraldas (cluster C3) compared to other sites.

3.3 Connectivity patterns

Based on biophysical larval flow models under assumption of a variably long (30, 60, 90-day) PLD, octocoral communities along the South American mainland appeared well-connected, and connectivity also existed from the continent to the Galápagos Islands in all three PLD scenaria (Fig. 8). In Galápagos, sites within the southern (all islands except Darwin and Wolf) and northern archipelago (Darwin, Wolf) were modelled as well connected, and connectivity existed between the two parts of the archipelago, but no direct connection back to the mainland existed in the model.

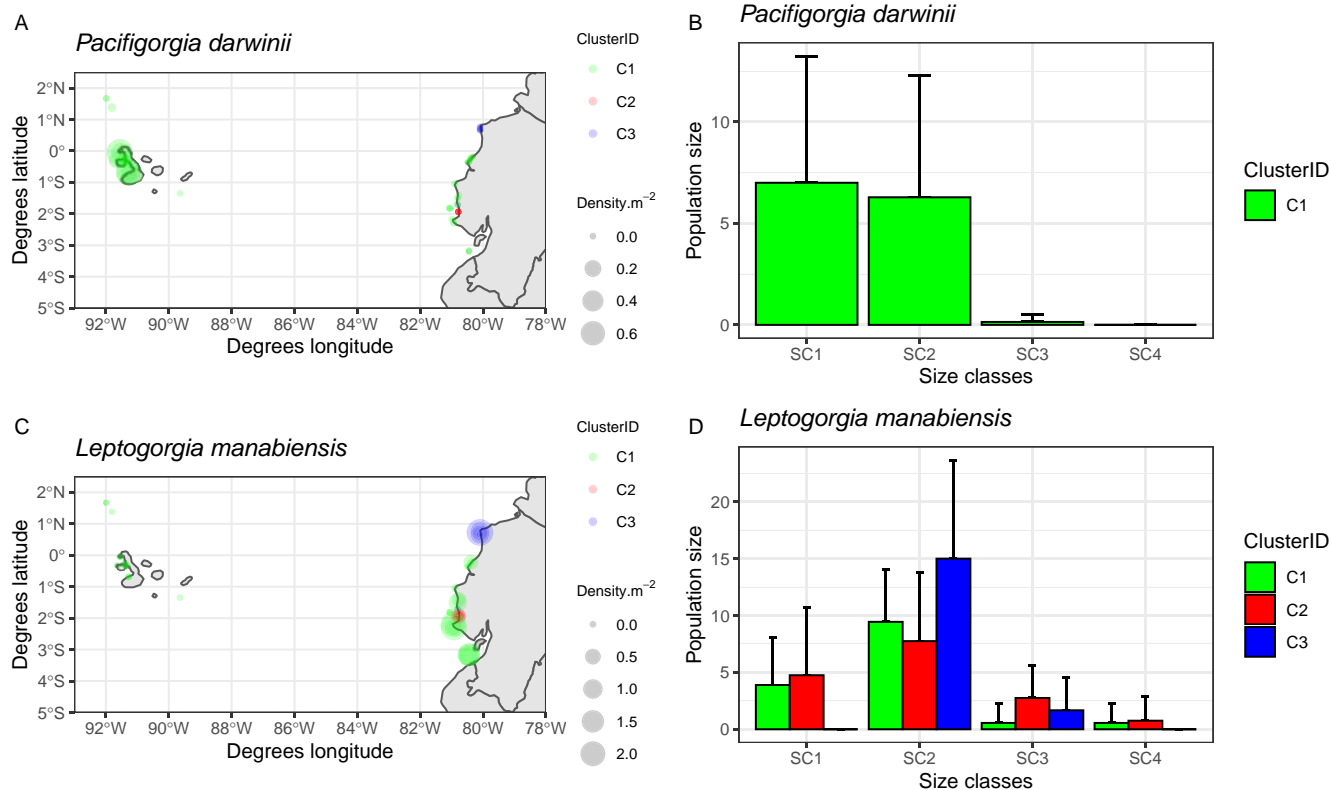


Fig. 6 (A and B) Locally restricted populations of *Pacifigorgia darwinii* were exclusively encountered in Galápagos (A) shows the size of the population (B) shows the size distribution of the population (size classes SC1 <100 cm², SC2 100–399 cm², SC3 400–899 cm² and SC4 ≥900 cm²). Cluster ID refers to the clusters identified in Fig. 2A and B, where the latter also shows the contribution of species to cluster formation. *Pacifigorgia darwinii* occurred only in Isabela (Galápagos), which was contained in cluster C1. (C and D) Colonies of *Leptogorgia manabiensis* were widespread on the continent, but absent in Galápagos (same size classes as B). Note that position of all sample sites is indicated, even if empty (smallest circle, see legend). Cluster ID refers to the assemblage clusters (same colour-code) obtained in Fig. 3. PAD in legend is *Pacifigorgia darwinii*, LMA *Leptogorgia manabiensis*.

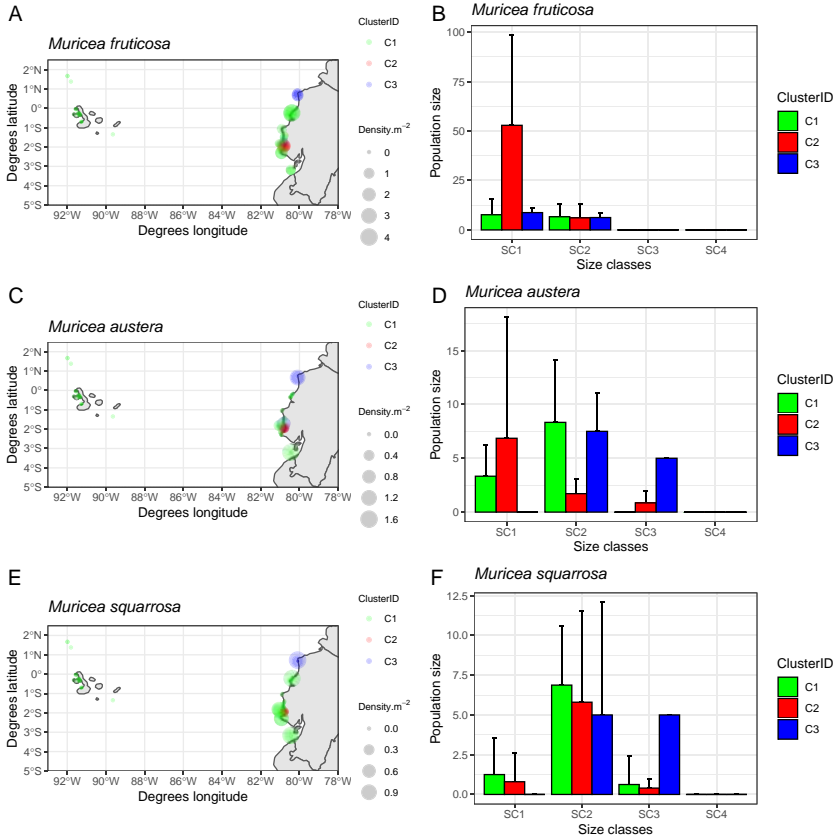


Fig. 7 Characterization of populations of some important octocoral species that defined octocoral assemblages on the Ecuador mainland only (A,C,E, and G) show the size of the population, coded by cluster membership (B,D,F, and H) show the size distribution of the population within each cluster (size classes SC1 < 100 cm², SC2 100–399 cm², SC3 400–899 cm² and SC4 ≥ 900 cm²). Cluster ID refers to the clusters identified in Fig. 2A and B, where the latter also shows the contribution of species to cluster formation. Note that position of all sample sites is indicated, even if empty (smallest circle, see legend). Cluster ID refers to the assemblage clusters (same colour-code) obtained in Fig. 3. MUF in legend is *Muricea fruticosa*, MUA is *Muricea austera*, MUS is *Muricea squarrosa*.

Larvae from Galápagos were dispersed towards Cocos and Malpelo Islands and Mesoamerica. Connectivity from Galápagos back to the Ecuador mainland may exist primarily via Cocos and Malpelo Islands, which can be easily reached by larvae from Galápagos. Larvae released from these islands reached the continent. Some larval trajectories originating from the northern

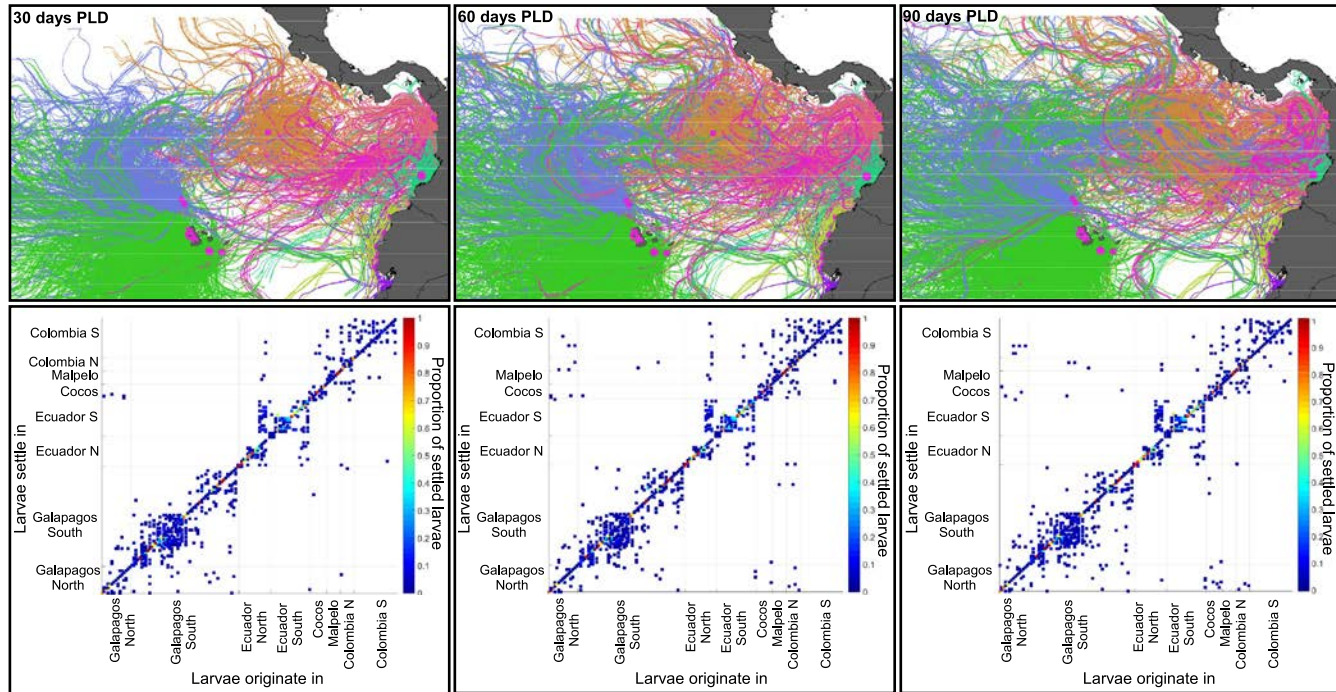


Fig. 8 Potential connectivity pattern of gorgonian corals in the Eastern Pacific under assumption of 30, 60, 90-day PLD. Upper Row: Larval trajectories are colour coded according to site-provenance (originating in southern Galápagos: bright green; northern Galápagos: slate; Cocos: orange; Malpelo: pink; Colombia: turquoise; northern Ecuador [Esmeraldas, Manabí]: gold; southern Ecuador [Santa Elena, El Oro]: purple). Lower row: Connectivity matrices between the four larval precincts shown in above row. The x-axis shows larval provenance (larvae originate in) and the y-axis shows destination (larvae settled in).

Galápagos reached the continent but did not encounter one of the model-defined settlement areas, so were presumed lost. If more suitable settlement areas than assumed in the model exist along the continent (especially in Colombia), then direct two-way connectivity between the continent, Galápagos, and back may indeed exist.



4. Discussion

Of the 26 octocoral species so far reported for continental Ecuador (Breedy et al., 2009; Breedy and Guzman, 2002, 2005, 2007, 2011, 2015, 2016; Figueroa, 2015; Hickman Jr., 2008; Soler-Hurtado et al., 2016; Soler-Hurtado and López-González, 2012), 23 were identified in our surveys, which thus covered a representative species spectrum. In Galápagos only three of the 10–15 species recorded (exact number pending taxonomic classification, see Breedy et al., 2009; Hickman, 2008; Williams and Breedy, 2004) were identified, and many sites without octocorals were encountered. This points to a patchier distribution of octocorals across the archipelago and to possible impacts of the El Niño–Southern Oscillation (ENSO), such as that of 1982/83, after which substantial mortality was observed, following tissue-sloughing in *P. darwinii*, *P. douglasii* (accepted but doubtful species status) and *Muricea* spp., in the Galápagos (Robinson, 1985). *Heterogorgia hickmani*, *M. plantaginea*, and *L. alba* were the only species co-occurring on the mainland and in Galápagos. The only other species so far reported from the mainland and Galápagos were *M. fruticosa* and *Eugorgia daniana* (Breedy et al., 2009; Hickman, 2008), the former was only observed on the mainland, the latter not at all.

Our large-scale structural analysis of assemblages in Ecuador suggested a broad pattern separating the northern and southern mainland provinces of Esmeraldas and Santa Elena, from a larger group of continental and Galápagos sites. The numerical dominance of *M. plantaginea*, *M. fruticosa* and *L. alba*, previously observed at Pelado (Santa Elena, Steiner et al., 2018a, 2018b) was mirrored in the present, geographically much broader, study. This is not to say that local distributional patterns among the uncommon species in this study, which achieved comparatively higher local densities (i.e. *M. purpurea*, *Leptogorgia pumila*), would not be detectible with a finer-scaled survey. For example, the majority of uncommon and rare species were found in the more species-rich areas (Santa Elena, Esmeraldas), while the species-poor sites were more homogeneous in species composition. However, the low species and colony counts encountered at many sites may be a sign of

under-sampling and undocumented previous mortality events, suggesting that more detailed surveys could yet reveal hitherto unseen patterns.

Colony size distributions and, most notably, maximum sizes which relate to the potential for microhabitat creation varied among the 23 species. *Muricea plantaginea* had the tallest colonies, reaching ~130 cm (Breedy and Guzman, 2016), followed by *Psammogorgia arbuscula*, rare in our study. When occurring in high densities, *M. plantaginea* fits the definition of an ecosystem engineer sensu Cuddington (2012) at specific continental locations (Pelado and the Santa Elena Peninsula) and at Isabela (Galápagos). In contrast, *H. hickmani* is a smaller species (Breedy and Guzman, 2005), with a pronounced preference for cryptic settlement spots, limiting extensive multi-colony assemblages. Except for *M. fruticosa*, seldom >15 cm, the other *Muricea* spp. also reached only 20–30 cm height (see Breedy and Guzman, 2016) yet formed the vertically most complex and species-rich assemblages. *Leptogorgia* and *Pacificogorgia* (Gorgoniidae) influenced benthic environments less, either because of their moderate size (*L. alba*,) or due to their scarcity (*P. irene*). However, the depth limits of this study restricted observations to turbulent sites where colony detachment is more frequent. Species-richer, taller and denser octocoral assemblages, visually better associated with animal forests (Rossi et al., 2017), are often found deeper than 20 m (Steiner et al., 2018a, 2018b; Rivera, pers. obs.) and were underrepresented. Such assemblages may serve as octocoral refuges from ENSO surface warming.

A biophysical larval flow model showed a clear N–S connectivity along the Ecuadorian mainland (approx. 600 km between northern and southern-most study site), a notable influx from the Colombian coast to Ecuador, and a pronounced mainly unidirectional E to W connectivity from the continent towards Galápagos (>1000 km). The N–S connectivity may be further enhanced by larvae drifting shorter distances between suitable coastal habitats that connect the wetter and warmer north in Esmeraldas with the drier and cooler south in Santa Elena and El Oro (Gálvez and Regalado, 2007). Mainland assemblages potentially could consist of panmictic populations, but panmixia is not necessarily common (Selkoe et al., 2014).

The E to W connectivity from continental Ecuador towards Galápagos, suggested in the model, also provides further links to Cocos, Malpelo and to continental Colombia (Lequeux et al., 2018; Riegl et al., 2019b; Vanegas and Borrero-Pérez, 2020; Wood et al., 2016). Three mainland species were reported in Galápagos, two of those (*M. plantaginea* and *L. alba*) had the densest and largest populations in our surveys. This may indicate that a certain (yet unquantified) threshold in population size must be attained for greater

geographical dispersion (Edmunds and Lasker, 2019; Privitera-Johnson et al., 2015; Santangelo et al., 2003) and also to replenish the Galápagos populations. Species with smaller populations may simply not produce enough planulae to compensate for pelagic mortality on the drift to Galápagos. Alternatively, co-occurring species might best benefit from the surface currents between January and May, based on their reproductive timing (Carson et al., 2010; Gomez et al., 2018), and/or could be broadcast spawners, which in Scleractinia have longer pelagic distribution potential than brooders (Harrison, 2011; Kahng et al., 2011).

This study provides hints at the overall structure of octocoral populations in the equatorial ETP. Except for *C. riisei*, all are limited to the Eastern Pacific, forming potentially well-mixed and highly inter-connected populations of occasionally dense patches along the Colombian and Ecuadorian continental coasts. The latter is also the more species-rich area in this region (Cortés et al., 2017). Oceanic archipelagoes and islands appeared biogeographically more isolated in our models (Fig. 8) and harboured fewer species. The Galápagos could receive larvae from the continent and serve as a source for dispersal to Cocos, at least for *L. alba* (Cortés et al., 2017), from where Malpelo (Sánchez et al., 2011) can be settled (Lequeux et al., 2018; Riegl et al., 2019b; Wood et al., 2016). Larvae from Malpelo and Cocos seem to reach the continent (Fig. 8). Our models showed a largely unidirectional (clockwise) circular connectivity and thus local “upstream” disturbances or extinctions could interrupt “downstream” replenishment. On islands with low local recruitment and/or small populations, such scenarios could cause a cascading shrinking effect on populations. To date, few species are reported for either Cocos (6 spp.), or Malpelo (4 spp.), with three co-occurring species (*P. curta*, *L. alba* and *C. riisei*; Cortés et al., 2017) or Galápagos (10–15 spp., see Breedy et al., 2009; Cortés et al., 2017). Octocorals in the ETP may thus follow the classical continent-island pattern of species richness (MacArthur and Wilson, 1967). Such a pattern can also be observed when comparing Malpelo to species rich Panama (64 species, in Cortés et al., 2017) and exemplify isolation by distance. The low number of species and co-occurrences among the islands, despite good connectivity, may suggest previous mortality events and/or that the reproductive output of most ETP populations cannot overcome the open ocean distribution barrier (bottleneck).

The broad ETP distribution of *L. alba* may be rooted in connectivity suggested by the biophysical model. This species is reported from every country lining the Pacific from Mexico to Peru, as well as Galápagos,

Cocos, Malpelo, Gorgona (see Cortés et al., 2017; Sánchez et al., 2014) and from northern headlands in Colombia (Vanegas and Borrero-Pérez, 2020). The widespread distribution of *L. alba* may respond to its dispersal ability, due to the high survivorship of its planulae and a high recruitment rate of this broadcast spawner (Gomez et al., 2018). Gomez et al. (2014) also observed recruitment patterns suggestive of an *r*-selected species in Panama. In our surveys, *L. alba* populations primarily comprised small colonies, possibly attributed to ongoing recruitment or an artefact of reduced survival of tall colonies in our shallow turbulent sites. However, this species has also been observed intertidally and occasionally exposed (pers. obs. J. Cortés).

Carijoa riisei is the only species in this study with an Indo-Pacific distribution (Grigg, 2003; Kahng and Grigg, 2005). Kahng et al. (2008) determined that it is a gonochoric broadcast spawner with negatively buoyant eggs in Hawaii, which does not fit a long-distance current-driven distribution well. However, it is a fast-growing invasive Pacific species with vegetative propagation. Interpreting the distribution of *C. riisei* with ocean connectivity is further complicated by its hull fouling capabilities (Concepcion et al., 2010), which provides an alternate mean of dispersal, also suggesting a high risk of introduction to the Galápagos (Keith and Martinez, 2017).

4.1 Conclusion

Ecuador's octocoral fauna was richer on the continent than on its islands. Strong connectivity was suggested for continental sites, with a sharp drop observed towards the islands. Primarily species with large continental populations had dispersed to Galápagos and from there to the other equatorial ETP islands. The Ecuadorian octocoral fauna appears therefore of Eastern Pacific-wide relevance given its species richness and location in ETP connectivity ratchets. The populations currently best fit for monitoring susceptibility of octocorals to disturbance are those of *M. plantaginea*, *H. hickmani* and *L. alba*, due to their co-occurrence on the mainland and Galápagos, regional distribution, and because of the habitat-forming sizes and density of *M. plantaginea*. North - South connectivity along the Colombo-Ecuadorian coasts and the potential structural role of arborescent *Muricea* spp. on the mainland justify closer inspection of their regional population differentiations as baseline for the detection of disturbances. Connectivity between Galápagos, Cocos, Malpelo and Colombian

headlands make *L. alba* a candidate for wider ETP population analysis. Our understanding of regional population dynamics relevant to cross-boundary conservation of this and other taxa shaping tropical marine ecosystems would greatly benefit from additional studies covering broader depth ranges, sampling efforts, and reproductive traits. The greatest challenge herein is the recent speed of habitat alterations rooted in phase shifts (Dudgeon et al., 2010; Vergés et al., 2014), invasive species (Steiner and Willette, 2015a) and the subsequent transformations of benthic organismal landscapes (Lasker et al., 2020a, in this volume; Steiner and Willette, 2015b).

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