

Variable El Niño-Southern Oscillation influence on biofacies dynamics of eastern Pacific shallow-water carbonate systems

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ABSTRACT

The El Niño-Southern Oscillation (ENSO) is a periodic climatic and oceanic event caused by sea-surface temperature and nutrient anomalies over the eastern tropical Pacific Ocean (ETP). Recurring ENSO events have a significant impact on climate and the ecosystems of the circum-Pacific region. In the marine realm, ENSO is known for altering temperature and nutrient patterns, affecting the pelagic food chain, and causing widespread bleaching of corals due to temperature stress. The potential impacts of ENSO on shallow benthic ecosystems as a whole, however, are poorly understood. Here, we compared biogenic sedimentary facies of ETP shallow-water carbonate systems in a strongly ENSO-influenced area (Galápagos Islands, Ecuador [GAL]) with similar systems in an area less strongly influenced by ENSO (Gulf of California, Mexico [GOC]). Carbonate assemblages in both study regions range from coral-algal-dominated (photozoan) to molluscan-dominated (heterozoan) assemblages. Linear statistical models, comparing the distribution of carbonates against prominent local oceanographic parameters, show that minimum chlorophyll-*a* and maximum sea-surface temperature (which are both strongly influenced by ENSO) are dominant drivers shaping carbonate sediment facies in the GAL. In contrast, GOC carbonates have a distinct mean chlorophyll-*a* signature that is the result of an upwelling-induced north-south nutrient gradient not significantly influenced by ENSO.

INTRODUCTION

The structure and composition of carbonate sediments are intimately tied to the oceanographic conditions in which they develop (Hallock and Schlager, 1986; James, 1997; Wilson, 2012). This relationship to oceanographic controls renders marine carbonate production potentially highly responsive to climatic and environmental fluctuations, especially those associated with the El Niño-Southern Oscillation (ENSO). With respect to shallow marine carbonates, ENSO has been

linked to widespread bleaching events of corals and foraminifera (Glynn et al., 2001). ENSO impacts are particularly evident in the eastern tropical Pacific Ocean (ETP), because the region is in proximity to the oscillation epicenter and features areas of contrasting high and low nutrient levels and well-defined thermal gradients (Glynn and Wellington, 1983; Reijmer et al., 2012), and it contains regions with the lowest aragonite saturation states and ocean pH of any modern tropical ocean (Manzello et al., 2014). This unique oceanographic character forces carbonate-secreting organisms within the ETP to live near their physiological limits (Halfar et al., 2006). ENSO effects are well known from the Galápagos Archipelago (GAL), an equatorial volcanic island chain in the southern ETP, which experienced widespread impacts on carbonate biota, most typically coral reefs, caused by the 1982-1983 and 1997-1998 ENSO events (Glynn et al., 2001). Maximum ENSO sea-surface temperatures (SSTs) have been shown to be strongly associated with coral bleaching and die-off events in the GAL when temperatures exceed average summer conditions (average max $\sim 25.7^{\circ}\text{C}$; annual min-max variability $\sim 4.2^{\circ}\text{C}$) by $2\text{-}4^{\circ}\text{C}$ (bleaching threshold: 28°C) for 8-10 weeks (Podestá and Glynn, 1997). Additionally, the southern GAL represents the only known case of total degradation of coral framework following coral mortality (Manzello et al., 2014). These findings run contrary to those for the Gulf of California (GOC), where coral loss subsequent to the 1997-1998 ENSO was minimal (Reyes-Bonilla et al., 2002), despite maximum summer temperatures of 28.5°C (min-max variability: 8°C , Cabo Pulmo; Carriquiry and Villaescusa, 2010) being exceeded by 4°C (Reyes-Bonilla et al., 2002).

While the specific oceanographic-carbonate interactions in the GAL and GOC are complex (Halfar et al., 2006; Reymond et al., 2016), continued climate change has the potential to strengthen El Niño (Latif et al., 2015), which could enhance ENSO-related signatures on shallow-water ETP carbonates. Here, we used exploratory analyses and statistical models to compare

biogenic constituents from GAL and GOC shallow-water carbonate environments in relation to dominant oceanographic controls.

METHODOLOGY

Sand-sized (63 μm to 2 mm) biogenic constituents were point counted (>300 points) from SCUBA and Van Veen grab samples (1-40 m water depth) collected off seven islands throughout the GAL (128 samples) and four sites spanning the latitudinal extent of the western margin of the GOC (115 samples; Fig. 1; Halfar et al., 2006). Oceanographic data, including chlorophyll-*a* (Chl-*a*, a proxy for nutrients), SST, sea-surface salinity (SSS), and pH, were obtained from various sources. Agglomerative hierarchical cluster analyses (Euclidian distance, Ward linkage) were conducted on the untransformed point count data for the GAL and GOC using R. A univariate linear regression tree analysis (Zuur et al., 2010) was performed for the response (binned result of the cluster analyses) and explanatory (oceanographic controls and sample depths) variables. Additional linear models were run to isolate the dominant biogenic drivers of cluster splits. For detailed statistical treatment, see the GSA Data Repository material.

RESULTS

ENSO-Driven Oceanographic Variability

Galápagos Archipelago

Oceanographic results reveal high-oligotrophic to low-mesotrophic conditions at Darwin Island (GAL-North; average: 0.21 mg/m^3), moderate mesotrophic conditions at the islands of Baltra, Santa Fé, San Cristóbal, Española, and Floreana (GAL-SE; average: 0.30-0.49 mg/m^3), and eutrophic conditions at Isabela (GAL-SW; average: 2.02 mg/m^3), caused by Equatorial Undercurrent (EUC) upwelling (Figs. 1 and 2; Table DR1 in the Data Repository). Aside from the

northern and westernmost islands, the GAL settings fall within the coral reef turn-on/turn-off zone (CRTTZ), demarcating the Chl-a maximum ($\sim 0.3 \text{ mg/m}^3$) for true reef development (Hallock, 2001; Fig. 2A). The slowing of upwelling during recurring ENSO events causes Chl-a levels throughout the GAL to decline sharply and give way to lower mesotrophic conditions (Fig. 1B), while temperatures in this warm-temperate (GAL-South) to tropical (GAL-North) setting can increase by up to 8°C (Figs. 1A, 1B, and 2).

The average SSS of 34 practical salinity units (PSU) is slightly elevated during ENSO events (mean anomaly ~ 0.4 PSU). Ocean pH fluctuated by ~ 0.09 pH units (total scale) from 2003 (La Niña, average 7.88) to 2009 (El Niño, average 7.97; overall mean ~ 7.91 Table DR1; Manzello, 2010).

Gulf of California

The GOC was characterized by a gradual increase in average Chl-a values, representing low to moderate mesotrophic conditions in the south (0.5 mg/m^3) to eutrophic conditions in the north (2.6 mg/m^3 ; Figs. 1 and 2). Hence, mean Chl-a values were higher than in the GAL. However, while ENSO events were manifested by a reduction in the north-south Chl-a gradient in the GOC, overall Chl-a values exhibited only a moderate decline during ENSO (Fig. 1E). With respect to SST, the warm-temperate GOC experienced greater north-south variability than the GAL (Fig. 2E). Unlike dramatic ENSO-related temperature increases in the GAL (up to 8°C), GOC SSTs increased by no more than 4°C in El Niño years (Figs. 1 and 2). GOC SSS decreased north-south from 35.8 to 35.1 PSU, reflecting high evaporation in the northern GOC basin (Halfar et al., 2006). In El Niño years, GOC pH (total scale) was highest at the southernmost Cabo Pulmo (8.09) and lowest in the upwelled waters of Bahia de Los Angeles (7.97, Table DR1).

Biogenic Carbonate Distribution

Following a spatial pattern of declining temperature and increasing nutrients, GAL carbonates are characterized by increasing coralline algal and diminishing coral contents from GAL-North to GAL-SE, with a near absence of coral in GAL-SW (Fig. DR1A). Similarly, GOC carbonate biota track the prevailing latitudinal temperature and nutrient gradients by exhibiting a north-south increase in coral content, a dominance of coralline algae in its central portion, and heterotrophs (molluscs, bryozoans) in the north. High-nutrient–low-temperature sites are characterized by high numbers of heterotroph barnacles in both carbonate systems. While the overall distribution of carbonate biota, and its relationship to dominant oceanographic controls, is comparable between the GAL and GOC, major sedimentary differences include a near absence of benthic foraminifera tests throughout the GAL (<1% avg.) compared to the GOC (7% avg.). Furthermore, bryozoans play a lesser role throughout the GAL than they do in the GOC (Fig. DR1).

Five GAL and GOC sedimentary facies can be distinguished based on Euclidean-Ward clustering (Fig. 3). GAL group I denotes a coral-dominated (58%) photozoan facies in GAL-North. Similarly, GAL group II in GAL-SE shows a photozoan signature, containing a mixture of molluscs (32%), corals (31%), and coralline algae (~12%). GAL groups III and IV represent transitional heterozoan-photozoan assemblages (defined as a 1%–20% combination of zooxanthellate corals and large benthic foraminifera within a heterozoan-dominated association; Halfar et al., 2006), with significant contributions from molluscs, coralline algae, serpulids, barnacles, and bryozoans, plus 7%-10% corals. GAL group V represents a coralline algal-dominated group (49%). Spatially, groups III-V occupy the mid-mesotrophic peripheral islands in GAL-SE, with GAL group III—exhibiting the highest heterozoan contribution from all GAL groups—represented most strongly in the upwelling region of Isabela (Fig. 3A).

GOC group A, in the low mesotrophic south, is a mollusc-dominated (41%) photozoan group, with significant contributions from corals (26%; Fig. 3B). In contrast, the bryozoan (46%) GOC group B is solely found in the northern upwelling site and represents a heterozoan assemblage. The mixed photozoan-heterozoan GOC group C is represented in the higher-latitudinal collection sites of Punta Chivato and Los Ángeles. GOC groups D and E are distinguished by high percentages of coralline algae (34% and 56%, respectively) and predominate in the moderate to high mesotrophic sites of San José and Punta Chivato (Fig. 3B).

Statistical Model Results

At the GAL, following depth (~14 m), which divides higher coral (shallow) from higher coralline algal content (deep), maximum (max) SST and minimum (min) Chl-*a* are the dominant controls over the distribution of the biogenic cluster groups (Fig. 4A), and coralline algae and corals are the most significant biogenic constituents, affecting the group divisions within the cluster analysis (Fig. 4B). Hence, the most defining aspect of GAL biogenic constituents is varying abundances of coralline algae and coral at different sites. This is similar to the GOC, where varying abundances of coralline algae and coral, as well as molluscs, best group sites based on the clustered biogenic data (Fig. 4D). At the GOC, mean Chl-*a* was the dominant control on carbonate systems throughout the region (Fig. 4C).

DISCUSSION

Temperature and nutrient fluctuations, resulting from seasonal and long-term upwelling processes, have a significant impact on carbonate-producing communities (Hallock and Schlager, 1986). In the GAL and GOC, examinations of long-term averages and cluster analysis clearly show Chl-*a* to control CRTTZ. A photozoan association was observed in the low mesotrophic-upper

oligotrophic (<CRTTZ) sediments of GAL-North (Darwin), a transitional biogenic spectrum was associated with moderate-upwelling (inter-CRTTZ) GAL-SE sites (Figs. 1 and 3A), and a heterozoan association was found in EUC upwelling waters west of Isabela (GAL-SW; >CRTTZ; Fig. 3; Fig. DR1). However, in addition to this EUC/nutrient-driven sediment pattern, there was a strong, but short-term, ENSO-mediated SST and Chl-*a* control (shown in the dominant max SST and min Chl-*a* signatures), which primarily influenced coralline algae and coral fluctuations (Figs. 4A and 4B). The overriding ENSO signatures in the model cannot be separated from the nutrient/CRTTZ trend we see in Figure 2, but they reveal the integral role of these periodic El Niño stressors on GAL sediment evolution.

The importance of short-pulse ENSO events on long-term sediment distribution is clearly discernible. The model results (Fig. 4), based on 2002-2014 data, represent average-strength ENSO events and do not signal the strong 1982-1983 and 1997-1998 ENSO events, which caused much of the recent sedimentological change in the GAL. These findings could indicate a long-term influence of average-strength ENSO/seasonal cycles on time-averaged GAL sediments, which drive the southern sites to teeter on a biogenic fulcrum. The strong 1982-1983 and 1997-1998 events caused widespread heat-related coral degradation throughout the entire GAL (Glynn et al., 2001), and while strong regeneration was documented at the low-nutrient Darwin Island site (Riegl et al., 2015), near-total loss of corals in the southern, mesotrophic archipelago as a result of the 1982-1983 ENSO was followed by minimal recovery (Glynn et al., 2001), and a subsequent shift to a coralline algae dominance of sediments (Halfar and Riegl, 2013). These findings highlight the potential for temporally significant fluctuations in shallow-water carbonate budgets following environmental perturbations such as those experienced during strong ENSO or tropical cyclone events (Perry and Larcombe, 2003). Some southern GAL sediment producers like corals,

which develop within higher-on-average nutrients and lower-on-average SSTs (compared to those at the oligotrophic Darwin site), exist near their upper environmental tolerance threshold and suffer far greater changes during the simultaneous high SST and low Chl-*a* anomalies of El Niño events (Glynn et al., 2001). In addition, higher background nutrient levels during La Niña periods and subsequent to ENSO events could play a role in inhibiting coral reef recovery at these southern sites (Riegl et al., 2015). These changes tip the balance to net erosion (Perry et al., 2012), which affects sediment composition by allowing coralline algae, as well as heterozoan carbonate producers, to fill the ecological void. These SST and Chl-*a* anomalies may ultimately be responsible for the observed lack of foraminifera in the GAL (Reymond et al., 2016); however, additional research is needed.

Higher average nutrient concentrations in the GOC serve as the primary driver of carbonate distribution (Fig. 4C). While the high Chl-*a* levels (>CRTTZ) and low SSTs throughout the GOC limit significant coral development in all but the southern site of Cabo Pulmo, the GOC maintains a facies pattern similar to that of the GAL. Coralline algae exert the strongest influence on the cluster distribution, although corals are present at all sites (Halfar et al., 2006). In contrast to the GAL, significant coral mortality has not been observed despite ENSO events causing an increase of SSTs throughout the GOC up to 4°C (Reyes-Bonilla et al., 2002). These geographic disparities reveal that corals not only respond to prevailing temperatures, but also temperature duration and rate of change (Podestá and Glynn, 1997).

CONCLUSIONS

The overriding importance of average nutrient and temperature regimes on the global carbonate facies distribution (Halfar et al., 2006; Riegl et al., 2015) is supported by our ETP data. However, the surprisingly strong influence of relatively short-term, yet significant, excursions

from the long-term means—due to events like ENSO—on time-averaged carbonate sediments is shown here. In the mesotrophic southeast Galápagos Archipelago (GAL), these carbonates are susceptible to long-term ecological shifts associated with strong, short-term ENSO-related temperature and nutrient anomalies. The higher presence of corals throughout the southern GAL prior to the 1982-1983 ENSO is suggestive of the historically seesaw-like nature of these anomaly-driven phase shifts. However, with the acceleration in frequency of strong ENSO events due to anthropogenic climate change (Cai et al., 2014), it is unlikely that recent biotic changes in the southern GAL will revert in the near future. In contrast, the apparently greater resilience of the GOC coral environments, with respect to ENSO, may indicate the potential for the southern Gulf of California to serve as a refugium for eastern tropical Pacific corals.

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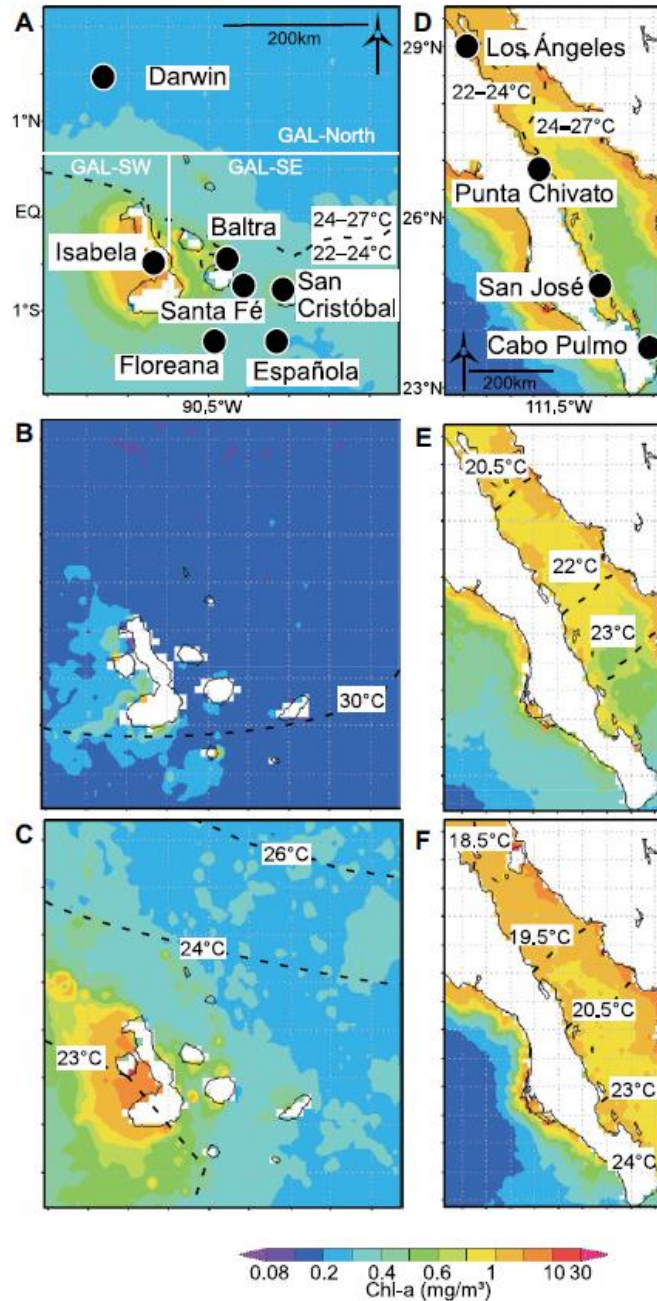


Figure 1. Maps of chlorophyll-*a* (Chl-*a*) and sea-surface temperature (SST) for Galápagos Archipelago (GAL), Ecuador (A-C), and Gulf of California (GOC), Mexico (D-F). Colors represent Chl-*a*, and dotted lines show SST isolines. A, D: Average Moderate Resolution Imaging Spectroradiometer (MODIS)-Aqua Chl-*a* and SST from July 2002 to November 2014. B, C, E, F: SeaWiFS (Sea-Viewing Wide Field-of-View Sensor) Chl-*a* records (NASA Giovanni, <http://giovanni.gsfc.nasa.gov/giovanni/>) and National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation (OI) SST data. B, E: El Niño conditions from December 1997 to March 1998. C, F: La Niña conditions from November 1999 to February 2000. Map A is divided into northern (GAL-North), southeast (GAL-SE), and southwest (GAL-SW) sections. Figure reveals strong SST and Chl-*a* anomalies in GAL during El Niño-Southern Oscillation (ENSO). ENSO date ranges were selected from Oceanic Niño Index (ONI, <https://data.noaa.gov/dataset/climate-prediction-center-cpcoceanic-nino-index>).

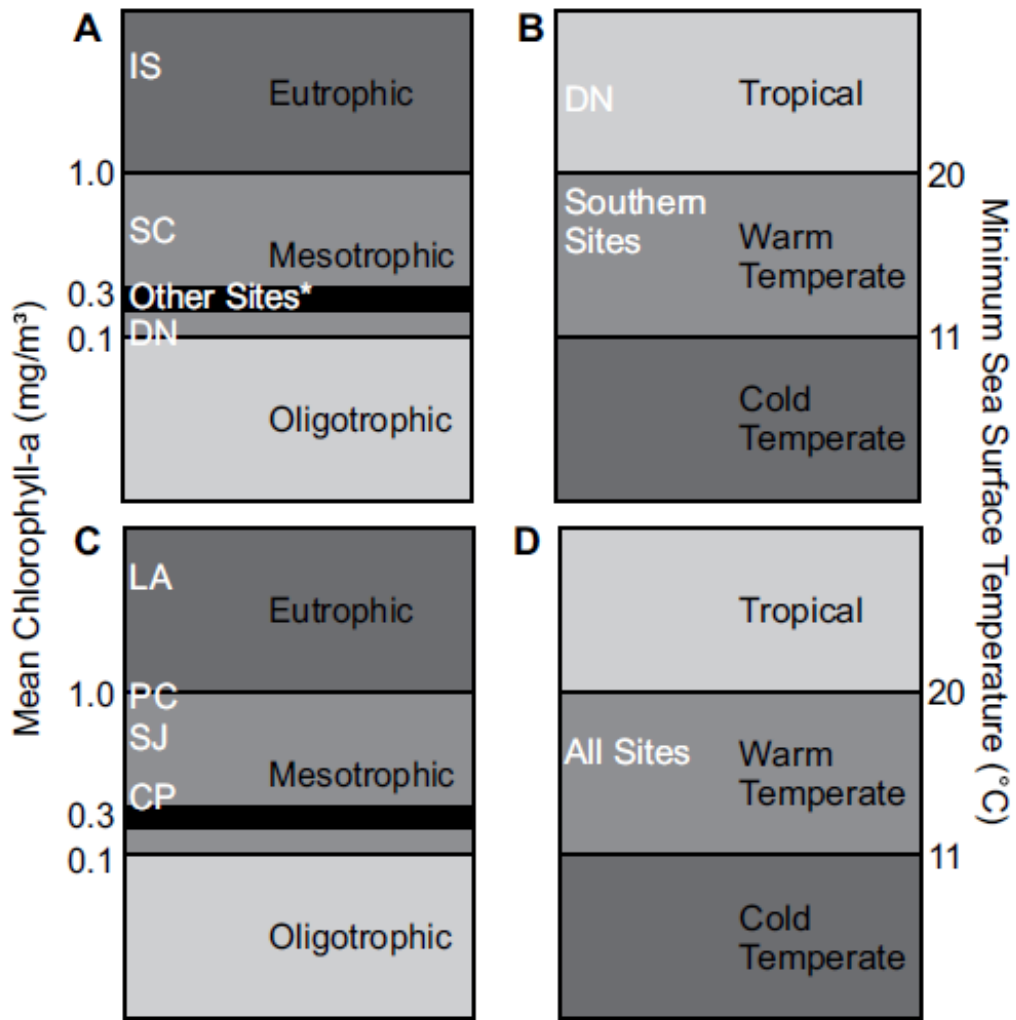


Figure 2. Relative trophic categorizations of each collection site at Galápagos Archipelago, Ecuador (A, B), and Gulf of California, Mexico (C, D). Black bars in A and C represent coral reef turn-on, turn-off zone (CRTTZ; $\sim 0.3 \text{ mg/m}^3$; Hallock, 2001). Abbreviated sites: DN—Darwin, SC—San Cristóbal, IS—Isabela. Other sites are Baltra, Santa Fé, Floreana, and Española, which have average chlorophyll-a levels within CRTTZ. In Gulf of California: LA—Los Ángeles, PC—Punta Chivato, SJ—San José, CP—Cabo Pulmo.

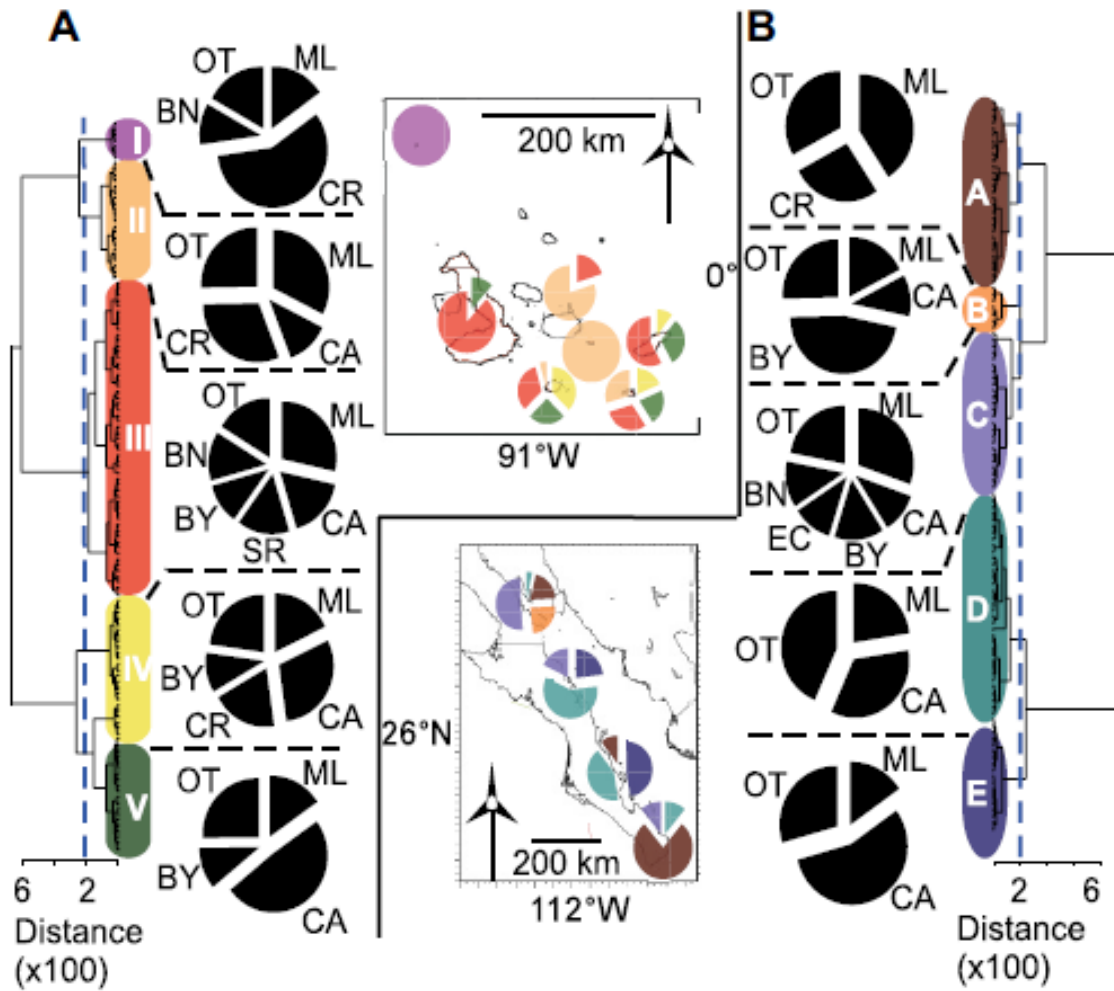


Figure 3. Euclidean-Ward cluster analyses for Galápagos Archipelago (GAL), Ecuador (A), and Gulf of California (GOC), Mexico (B) showing five predominant biogenic groupings (I-V in the GAL, A-E in the GOC). Blue dotted lines show cutoff distance (200). Maps show general percent representation of cluster groups at each collection site. Black pies represent average percent component of prominent (>10%) biogenic categories within cluster groups. ML—mollusc, BN—bar-nacle, CR—coral, CA—coralline algae, SR—serpulid, BY—bryozoan, EC—echinoderm, OT—other. See Figure DR2 and Table DR3 (see text footnote 1) for biogenic detail.

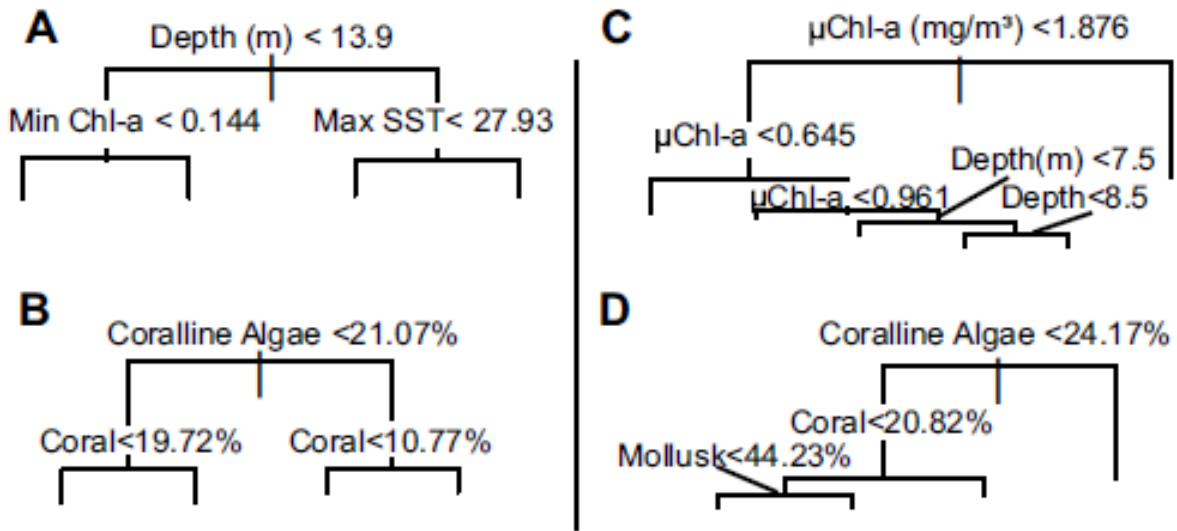


Figure 4. Relationships between oceanographic controls and biogenic distribution of cluster analyses (Fig. 3). A, C: Relationships between oceanic parameters and biogenic arrangements within cluster analyses, showing dominant oceanographic controls on sediment distribution throughout Galápagos Archipelago (GAL), Ecuador, and Gulf of California (GOC), Mexico, respectively. B, D: Dominant biogenic categories defining clusters for GAL and GOC, respectively. GOC sediment distribution is governed primarily by mean chlorophyll-a ($\mu\text{Chl-a}$); GAL sediments show strong El Niño-Southern Oscillation control. SST—sea-surface temperature.