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**Diferencias Estacionales y Latitudinales de Comunidades
Intermareales Rocosas en Ecuador**



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**Abstract**

Intertidal systems are ideal for the study of the variation produced by natural oscillations and environmental and human perturbations. These systems are also important for humans as barriers against erosion and as a source of food and recreation. However, in Ecuador we lack a basic understanding of the patters of community structure and the variation associated with seasonal cycles and the influence of oceanographic processes at different spatial and temporal scales. In many parts of the world large-scale oceanic atmospheric oscillations (ENSO, PDO) and marine currents largely determine the abiotic conditions experienced by intertidal communities, and modulate the biological interactions that establish community structure. As seasonal and inter-annual variation causes temperature patterns and nutrient and larval supply to change, these communities can be stressed into altered states. Understanding the impacts of these changes in community structure and biodiversity is critical for enabling scientists and policy makers to detect dramatic changes in community structure and to envision management actions. We assessed intertidal communities along a latitudinal productivity and temperature gradient covering 360 km of the Ecuadorian coast. We performed 20 quadrats in the low zone at each of 10 sites during both warm and cold phases of the seasonal cycle, and took algal biomass samples from each quadrat. Community structure was significantly different between sites, and while the biogeographic zone (North vs. South sites) did not explain this variation, quadrats taken at each site were significantly different between phases. Biomass was higher in southern sites than in northern sites, as was diversity, evenness, and species richness and abundance of mesoconsumers. This study provides baseline data for intertidal communities along the continental coast of Ecuador, and illustrates the complex nature of the combination of nutrients, temperature, and biological interactions in determining intertidal community structure.

## Resumen

Ecosistemas intermareales presentan un sistema ideal para estudiar la variación producida por cambios naturales y perturbaciones ambientales y antropogénicos. Estos sistemas son también importantes para los humanos por su función como barreras contra la erosión costera y como fuente de comida y recreación. Sin embargo, en el Ecuador carecemos de un conocimiento de los patrones de estructura de comunidades y la variación en éstas que se asocia a los ciclos estacionales y la influencia de procesos oceanográficos a diferentes escalas temporales y espaciales. En muchas regiones del mundo, ciclos atmosféricos de gran escala (ENSO, PDO) y corrientes marinas grandes determinan en gran parte las condiciones abióticas que se experimentan en las comunidades intermareales, y modulan las interacciones biológicas que determinan la estructura de la comunidad. Con el cambio de patrones de temperatura y fuentes larvarias causado por variación estacional e inter-anual, estas comunidades pueden ser forzadas a estados alternativos por el estrés ambiental. Un conocimiento de los impactos de estos cambios en estructura de comunidades y biodiversidad es necesario para poder detectar cambios dramáticos y crear soluciones y estrategias de manejo. Nosotros evaluamos comunidades intermareales a lo largo de una gradiente de productividad y temperatura que cubre 360 km de costa ecuatoriana. Realizamos 20 cuadrantes en la zona baja de cada uno de 10 sitios durante ambos fases del ciclo estacional (uno caliente y otro frio), y tomamos muestras de biomasa de algas de cada cuadrante. La estructura de las comunidades se difería significativamente entre sitios, y mientras zona biogeográfica (Norte vs. Sur) no explicaba esta diferencia, los diferentes fases de muestreo (caliente y frio) si lo hacían. Biomasa era más alta en sitios del sur que en el norte, como también la diversidad, equidad, y riqueza y abundancia de especies de mesoconsumidores. Este estudio proporciona un base de datos para las comunidades intermareales a lo largo de la costa continental del Ecuador, e ilustra la naturaleza compleja de la combinación de nutrientes, temperatura, e interacciones biológicas para la determinación de patrones de estructura de comunidades intermareales.

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**Introducción**

Ecuador lacks basic information about biodiversity patterns and community structure of many marine systems and how these patterns relate to biological, human and environmental factors. Such understanding is key to enable managers and scientists to detect natural variation from that caused by human or environmental perturbations. Rocky shores have been widely used worldwide to study biodiversity patterns and ecological processes because shores are tractable systems that constitute ideal indicators of impacts such as climate change and fishing. Furthermore, coastal systems are important to humans as a barrier against storms, tsunamis and hurricanes, for recreational purposes or as a source of food. Our study aims to understand patterns of vertical, horizontal, and temporal zonation in the rocky intertidal ecosystems of Ecuador, their importance to both ecological and human coastal areas, and how these systems are being affected by anthropogenic forces of change.

Patterns of community composition in intertidal ecosystems are strongly determined by abiotic conditions, such as nutrient supply (mainly nitrogen and phosphorous), wave exposure, water and air temperatures, and by biological interactions, such as competition for space, predation, herbivory, facilitation and larval recruitment (Posey et al. 1995). Both species interactions (Kraufvelin et al. 2010) and abiotic factors (Broitman et al. 2001, Scrosati and Heaven 2007) are very important in determining the biological communities found in rocky intertidal habitats. These complex interactions are not always predictable, for example, when changes initially appear favorable to a certain species or guild of species, additional impacts such as increased recruitment of predators, which reduces the population of prey, can cause unexpected effects (Cloern et al. 2007).

As conditions change, previously inferior competitors or invading species newly entering the system can become dominant as conditions become more favorable, especially if they are superior dispersers (Gilman et al. 2010).

Abiotic conditions, and in turn biological interactions, are affected by large-scale phenomena, such as ocean oscillation cycles, seasonality, and current patterns (Wang and Fiedler 2006), which manifest on the local scale in the form of upwelling regimes, degree of wave action, nutrient and oxygen supply, and water temperatures. The ecological structure of marine communities is largely governed by variation in these processes and how they modulate species interactions, such as competition and predation. For example, on Galápagos rocky shores, warmer waters associated with low nutrient levels caused a dramatic shift in community structure that was facilitated by grazers (Vinueza et al. 2006). Predation rates can also be modulated by temperature and nutrients. For example, whelks and sea stars increase their metabolic and predation rates with higher water temperature (Yamane and Gilman 2009). This has important implications if such organisms are key species, and can have the effect of reducing diversity. Where strong upwelling produces high levels of plankton food for barnacles, local populations and percent cover is much higher, and predator populations and rates of predation track these increases (Witman et al. 2010). Increased marine nutrient levels can also increase primary productivity and nutritional content of algal species, which in turn increases herbivory rates (Cebrian et al. 2009). The occupation of primary space by algae and sessile invertebrates can effectively create the demersal habitat and thus determine the composition of intertidal communities (Jones et al. 1994, de Juan and Hewitt 2011). Any changes in the control of primary space, whether by the direct effects of variation in

temperature and nutrient/food supply, or by altered levels of competition or consumption by predators and grazers, would therefore have far-reaching effects on diversity and community structure.

The equatorial West coast of South America is heavily influenced by ENSO phenomena. Yearly variation in marine conditions occurs as the strengths of the Panama-Bight (also known as "El Niño") and Humboldt (locally termed "Peru") currents affect the position of the Intertropical Convergence Zone, creating annual warm and cold phases along the coast, with particularly strong El Niño or La Niña years occurring on a semi-decadal basis (Wang and Fiedler 2006). This marine seasonality can cause strong local variation in water temperatures and nutrient supply, with corresponding impacts on marine communities (Vinueza 2006). Under most global climate change models, climatic phenomena such as ENSO events are predicted to become more frequent and more extreme (IPCC 2001), causing more extreme temperature changes for longer durations. Warmer water temperatures increase metabolic rates and lead to higher levels of biomass (Lamberti and Resh 1985) and stronger species interactions (Yamane and Gilman 2009). However, higher sea surface temperatures also correspond to greater stratification and reduced nutrient supply to the photic zone (Hoegh-Guldberg and Bruno 2010). Additionally, the increased storm frequency and strength predicted by climate change models are expected to create stronger wave disturbances (Przeslawski et al. 2008), which have been shown to have mixed effects in rocky intertidal communities (Kraufvelin et al. 2010, Scrosati et al. 2010).

Our study describes patterns of community structure along a latitudinal gradient of the Ecuadorian coast. Ecuador is placed at the mixing zone of two major tropical

eastern Pacific current regimes (Panama-Bight and Humboldt currents), and is strongly affected by ENSO phenomena. Understanding the similarities and differences between the northern and southern coasts is very important, since any disparities in abiotic factors between phases of the ENSO and between biogeographical regions (this may occur as a continuous gradient from North to South) could be expected to create differences in diversity patterns and interaction strengths between sites. In areas where inter-annual variation can be much greater than seasonal variation within a given year, overall diversity has been shown to be much higher than in nearby regions with more stable conditions (Blanchette et al. 2009). Such is the case here, lending even more importance to understanding how these phenomena manifest along the coast of Ecuador.

Rocky shores present an ideal study system for marine ecological processes, as they are accessible, easy to manipulate, and contain several model organisms for tracking changes in abiotic factors, species interactions, and community structure. The continental coast of Ecuador has long been overlooked as a potential research site for intertidal community ecology, with most studies focusing on diversity censuses (Cruz et al. 2003). This has left the area virtually unstudied, creating a large knowledge gap regarding intertidal community composition and the ecological processes and oceanographic phenomena that affect local marine habitats. We sought to investigate how ENSO-driven seasonality affects intertidal communities along the coast of Ecuador, whether distinct biogeographical regions exist based on closer proximity to warm or cold water currents, and how regions of differing productivity and temperatures react to warm and cold phases.

**Métodos**

*Study Sites*

We sampled rocky intertidal communities at 10 different sites stretching North to South along the Ecuadorian coastline. We took visual quadrats and physical samples from intertidal communities at each site during a peak cold La Niña event (August-October) and warm normal phase (February-April) of the seasonal cycle. Our choice of sites was determined by the presence of relatively flat rocky benches with similar abiotic conditions at the landscape level and with semi-regular spacing throughout the entire study area. Based on the environmental variables presented at each site, we grouped our sites into two different categories: "exposed" sites with high wave exposure, low sand burial, and deep nearshore waters, and "protected" sites with low wave exposure, medium-high sand burial, and extended shallow nearshore platforms.

We took a series of qualitative and quantitative measurements of the local environmental conditions at each site, We measured the physical characteristics of each study site, including sand burial by averaging the percent cover of sand in the low zone at each site, and measured wave height visually, by making observations at each site at the same time of day during the same tide series.

*Intertidal Community Surveys*

At each site, we defined intertidal zones based on natural zonation patterns of major primary space occupiers and the relative positioning of each area with regard to tidal height. We defined the low zone as the area dominated by erect algae, followed by

the mid zone dominated by encrusting algae and the high shore dominated by sessile invertebrates and encrusting algae. We then laid out a 100 meter transect tape parallel to shore that followed the contour of the intertidal zone being assessed. Within each low zone, we performed 20 quadrats of 50 x 50 cm placed horizontally on the substrate at 10 m intervals along the length of the transect tape. Within each quadrat, we evaluated the intertidal community, categorizing organisms down to the family, genus, or species level, and quantifying the presence of each taxonomic group. Mobile species were counted individually, and percentages were determined for the amount of the quadrat area taken up by primary space-occupying organisms (e.g., barnacles, algae, etc.) and exposed substrate such as rock or sand. We took photographs of each quadrat for later confirmation of our field assessments. Additionally, we removed all algae from a 10 x 10 cm square at the center of each quadrat and froze it in a plastic bag for later weighing. We took samples and quadrats during both cold (La Niña) and warm (El Niño) phases at each site.

*Sample Processing*

We separated out each algal biomass sample taken from low-zone quadrats in water in a plastic container to remove the sediment. We then removed all fauna from within the blades of algae and identified and recorded their abundance. We placed the algae in individual tin foil cups and placed them in a drying oven at 70° C for 48 hours. We then measured dry mass for each sample.

*Statistical Analyses*

We assessed differences in community structure in low zone quadrats between sites, between phases (warm/cold), and between biogeographical zones (North/South). Percent cover was averaged across all 10 quadrats from each of two transects taken at each site during each seasonal phase. Algal species were classified into functional groups after Steneck and Dethier (1994). We performed a Bray-Curtis similarity analysis using a square-root transformation of the mean percent cover data for each functional group of algae and the group of sessile invertebrates. We performed a nonmetric multi-dimensional scaling (MDS) for visual interpretation of the data, and found that sites were grouped well both by zone and by phase (Figure 2). Based on this analysis, we performed a crossed analysis of similarity (ANOSIM) with replicates to test for significant differences between community composition during each phase at each site, and a nested ANOSIM to test for significant grouping of sites into different zones.

We analyzed the differences in mean dry algal biomass between sites graphically. We also assessed the differences in the invertebrate community living in the algal biomass samples by quantifying evenness ($J'$), species richness and abundance, and diversity ($H'$) at each site during each phase.

**Resultados**

The distribution of our study sites along the coast of Ecuador can be seen in Figure 1, a GIS-created map indicating the relative location of each site along the Ecuadorian coastline. Five of these sites fell within the category of "exposed," and five were "protected" sites. Additional characteristics of each site are summarized in Table 2. Mean distance between sites was 41.63 km, with a range of 0.50 – 132.32 km. Our study design thus encompassed several spatial scales (from 50 x 50 cm quadrats to 361.44 km). For ease of interpretation of the results, we labeled the sites 1-10 from North to South. Our results also led us to classify these sites into five northern and five southern sites, denoted from here forward as N1-5 and S6-10.

The multivariate analysis of intertidal community structure in low zone quadrats indicated that sites were significantly different from each other ($P < .001$). These differences were primarily due to disparities between Northern and Southern sites and between warm and cold phases in the functional groups of corticated foliose, corticated macrophytic, articulated calcareous, and filamentous algae (Figure 3). Southern sites had higher percent covers of articulated calcareous and corticated foliose algae during the cold phase, and increased cover of corticated macrophytes during the warm phase. Conversely, northern sites had higher percent covers of filamentous algae and sessile invertebrates during the cold phase, and increased cover of corticated foliose and crustose algae during the warm phase.

The MDS plots and cluster analysis of community structure data show that sites were grouped by phase, zone, and exposure (Figure 2). The analysis of these relationships using the ANOSIM routine indicated that samples were grouped by phase (that is to say,

community structure in low intertidal zone quadrats was significantly different between phases at each site; $P <.001$), although the grouping was not affected by zone.

Mean dry algal biomass was not significantly different between sites. However, when ordered according to geographic position, we observed that biomass in southern sites was much higher than in northern sites (Figure 4). The community of mobile invertebrates living within each algal sample also varied between sites, with patterns similar to those seen in the biomass results. Mean values for Shannon-Weaver diversity index, evenness index, species richness, and invertebrate abundance were all higher in southern sites than in northern sites during both warm and cold phases (Figure 5). No clearly significant patterns existed between warm and cold phases assessed across all sites.

**Discusión**

Our study offers the first quantitative assessment of intertidal community structure along the coastline of continental Ecuador, and of how that structure varies between local cold and warm phases of the seasonal cycle, including a cold period or La Niña and a normal warm event. The Ecuadorian coastline is relatively small, approximately 650 km in length (compared for instance to the nearby Galápagos archipelago with more than 1800 km of coastline). However, the convergence of two major coastal marine currents, the Humboldt and Panama-Bight currents, creates a unique mix of water temperatures, nutrient levels, and larval supply. Our assessment of the intertidal community along the coast of Ecuador showed that differences do exist in the community composition in low zones between sites.

We expected sites to differ in the percent cover of different primary space occupiers, because even sites that are in close proximity to each other can experience wide variation in community composition due to small-scale oceanographic conditions, type of substrate available, wave exposure, and other confounding factors (Benedetti-Cecchi 2001). This was confirmed by the one-way ANOSIM test, but our interest was in seeing if these differences were grouped based on the geographic location of each site and/or the phase changes in dominating currents (and consequently, water temperatures, nutrient levels, and larval supply). Other studies have observed such variation along latitudinal gradients (Schoch et al. 2006, Konar et al. 2010), but the general belief among marine ecologists has held that such differing results in nutrient supply could not be produced within such a small geographic area based on large-scale dominating currents alone (Menge 1992).

Our visual analyses using MDS plots and cluster analysis pointed out phase, zone, and exposure as possible grouping factors for the differences observed. Wave action is a key factor in determining community structure (Schoch et al. 2006, Kraufvelin et al. 2010) due to the disturbance caused by physical forces such as crashing waves, sand burial, rates of erosion, moving rocks, etc., which reduces the efficiency of consumers (Sousa 1979, Menge and Sutherland 1987). Thus, we selected our study sites in order to provide a mix of exposure levels. While biogeographic zone initially appeared to be a viable factor for site groupings (clusters of N and S sites in Figure 2a), this did not turn out to be a significant factor for defining patterns in community structure. The small scale across which our study sites were spaced, the inclusion of intermediate sites (e.g., La Tiñosa, Cabo Pasado; see Figure 1), and the loss of resolution derived from grouping primary space occupying species into functional groups all may have masked the trend we expected to observe. In spite of these limitations, our results could indicate that, at this spatial scale, the differences in community composition caused by local conditions and marine processes appear to be stronger than large-scale processes, such as dominating ocean currents, which may affect sites at either end of the study range differently. Much of the variation observed across several spatial scales can also be due to differences between quadrats in very close proximity to each other (Benedetti-Cecchi 2001), and the local conditions at each study site can often mask large-scale trends between sites (de Juan and Hewitt 2011). Our division of sites into 5 North and 5 South was not *a priori*, but rather based on biomass data (Figure 4) and satellite imaging (Saba et al. 2008), along with anecdotal evidence from local fishermen. Perhaps a reassessment of our site groupings may yield a more coherent result. Alternatively, oceanographic conditions

along this latitudinal gradient might not be as extreme as those observed in the

Galápagos, or in Peru were the Humboldt current might have a stronger impact on

community, or in Colombia and Panama, where the Panama-Bight current is more

dominant. An extension of this study farther north and south would provide greater

comprehension of the disparate communities created by these two major current systems.

Although biogeographical zone was not a significant factor for differentiating

between site groups, the ENSO phase (warm/cold) was. Based on the ANOSIM test,

transects carried out at all sites during the months of the strong La Niña event from

August-October 2010 were significantly different in community composition from

transects carried out during the weak El Niño event during February-April 2011. These

correlations coincide with the results of previous studies that showed how major

differences in water temperature (Yamane and Gilman 2009, Meager et al. 2011) and

nutrient supply (Vinueza et al 2006, Witman et al. 2010) could change both the amount

of biomass present and the dominance patterns of primary space occupiers. The effects of

nutrient levels on algal diversity and biomass are not constant, but rather are dependent

on the biological interactions inherent to the intertidal community (Kraufvelin et al.

2010).

In addition to direct measurement of nutrient levels, algal biomass is frequently

used as a proxy for productivity in marine ecosystems in the photic zone (e.g., Vinueza et

al. 2006). Our results show that a gradient does exist in marine productivity along the

coast of Ecuador, with greater levels of biomass in southern sites than in northern sites.

Our results also indicate a dividing point in marine productivity between Puerto Cayo and

La Tiñosa, which could signify that a mixing zone exists between the Humboldt and

Panama-Bight currents situated near the Manta Peninsula (closest site: La Tiñosa). This evidence for the location of the mixing zone coincides with satellite imaging techniques for marine productivity (Saba et al. 2008). In addition to the differences observed in biomass between southern and northern sites, the biomass at each individual site was, on average, higher during the cold phase than during the warm phase. We conclude that biomass differences between sites are due to shifts in large-scale dominating currents, rather than to local processes such as upwelling. Measured differences in biomass coincide with results from studies such as Vinueza (in press), which showed that higher marine productivity produces higher levels of biomass in sites across all baseline productivity values. Diversity, evenness, species richness, and abundance of mesoconsumers in algal samples followed similar trends to that of dry algal biomass, with greater values in southern sites, evidence that the impacts of higher productivity levels on the southern Ecuador coast are also felt in consumer groups. Such shifts in long-term oceanographic phases have been shown to propagate up through higher trophic levels before (Vinueza et al 2006, Cloern et al. 2007). Our results using the Shannon-Weaver diversity index also coincide with those from Worm et al. (2002), showing that nutrient supply and diversity in marine ecosystems are closely correlated.

The fact that biomass results segregated well by geographic zone but not phase, and that community structure was significantly grouped by phase but not zone, presents an interesting situation for interpretation. This might indicate that nutrient levels are consistently higher in southern than northern sites, regardless of which phase of the seasonal cycle is dominating. At the same time, the consistent variation observed in the community structure at each site between warm and cold phases could indicate that, as

the confluence zone of the Humboldt and Panama-Bight currents is pushed farther North or South, larval supply changes, as well as the temperature optimums for different algal species and sessile invertebrates. The results support our hypothesis that southern sites, with their closer proximity to the cold water Humboldt current, are more productive than northern sites, and that sites along the Ecuadorian coast change in the composition of the intertidal community with variation caused by the ENSO cycle.

Variation in ocean temperatures and productivity levels cannot be discussed without mentioning the implications of global climate change. Globally, sea surface temperatures have risen by 0.6°C over the past 100 years (Pachauri 2007). As the effects of climate change continue to be revealed to marine scientists, the importance of the role of species interactions is becoming more apparent (Gilman et al. 2010). Although biological interactions can impact between-site patterns of species richness and abundance (Kraufvelin et al. 2010), oceanographic conditions are very strong drivers of community structure (Broitman et al. 2001), and are susceptible to large-scale variation driven by forces such as ENSO and climate change. Studies such as ours that investigate changing patterns in dominance of marine organisms and the scales over which these changes occur are essential for predicting and adapting to modifications to marine ecosystems caused by climate change (Harley et al. 2006). Long-term monitoring of the marine ecosystems along the coast of Ecuador will be needed to gauge the response of these biological interactions to future climate change induced phenomena, such as stronger and more frequent ENSO events (IPCC 2001).

Our study has produced many new questions that need answering in order to better understand the ecological processes at work along the continental coast of Ecuador.

For instance, given the complex and often site-specific interactions between herbivores and nutrients in determining algal community structure (Burkepile and Hay 2006), what role are herbivores playing in the patterns we have described here? Are these rocky shores following similar patterns than for example Galápagos, Panamá, Colombia or Peru? Additionally, we frequently observed local fishermen gathering large numbers of predatory whelks and cone snails from the intertidal areas at our study sites during low tides. Although the complexity of marine food webs reduces the probability of major alterations caused by selective fishing (Bascompte et al. 2005), these predatory whelks may be strong top-down regulators of community structure by limiting the populations of sessile invertebrates and herbivores, as has been shown in other systems (Menge 2000, Przeslawski et al. 2008), and their large-scale removal may cause strong changes to the intertidal community. Future studies that further explore the relationships between varying levels of productivity, intertidal mollusk removal, and the local implications of climate change are certainly warranted. Finally, our grouping of algae into functional classes reduced our ability to assess changes in algal diversity and species presence/absence between sites and phases. A fine-scale evaluation of algal diversity along the Ecuadorian coast would provide this information.
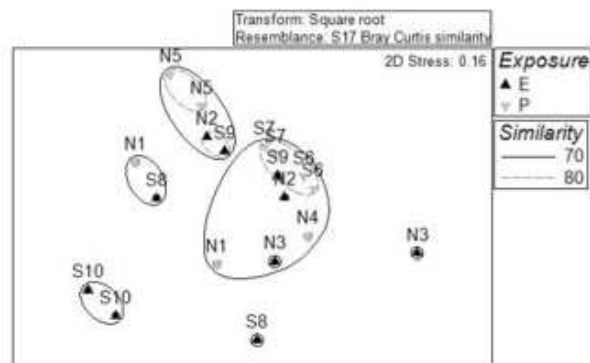
**Figuras y Tablas**
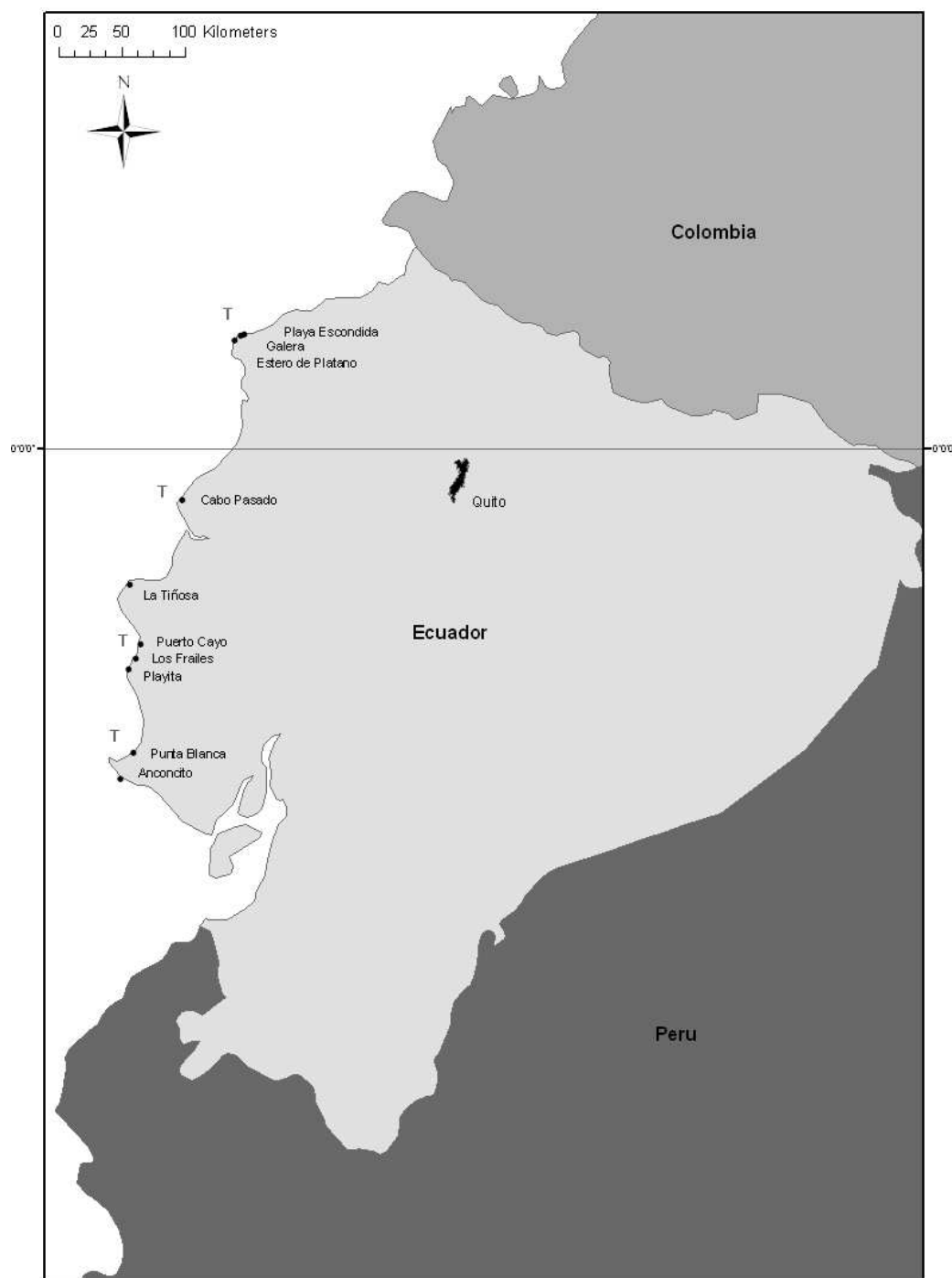
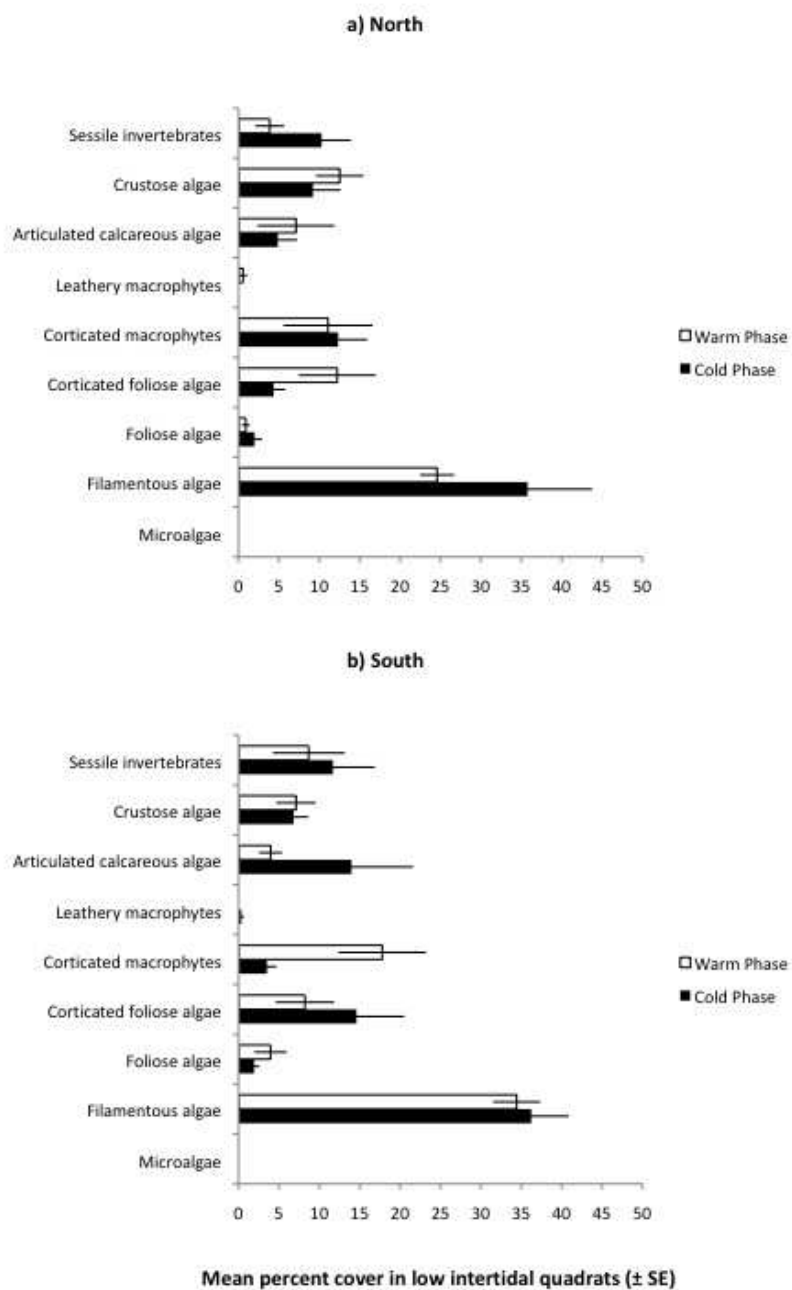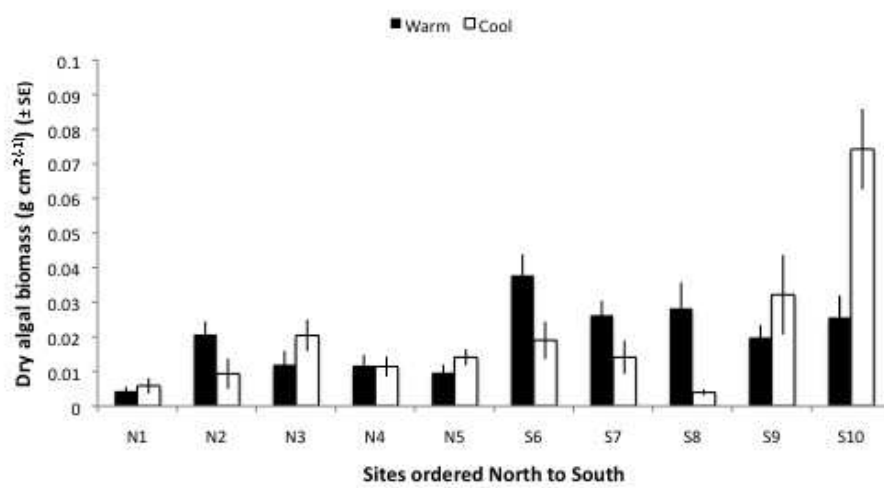a) Dendrogram for all sites in all phases
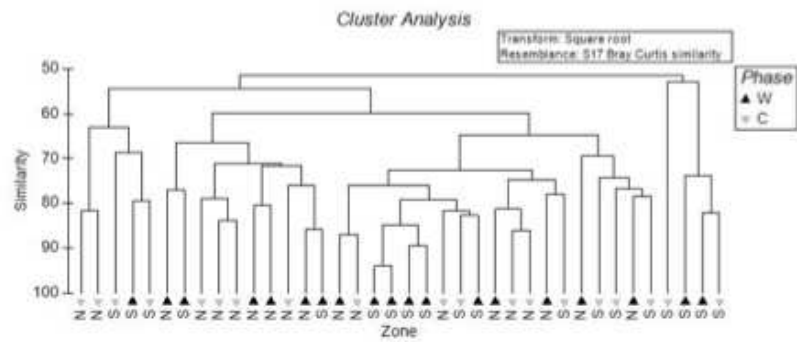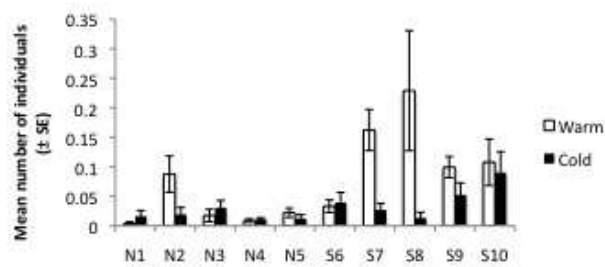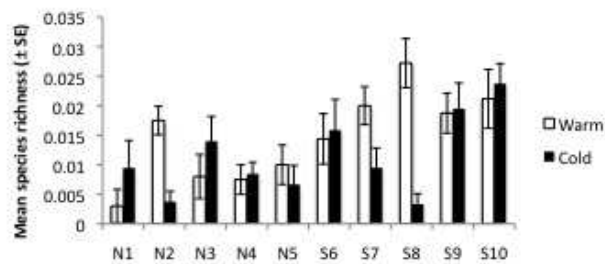
b) Cold Phase MDS plot

c) Warm Phase MDS plot

## a) North



## b) South



Mean percent cover in low intertidal quadrats (± SE)

20
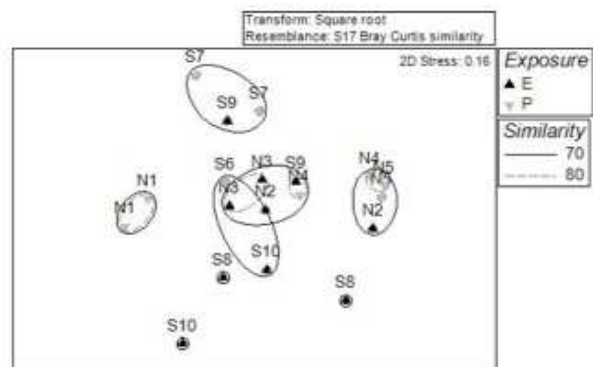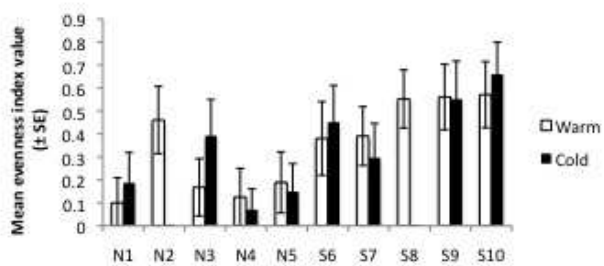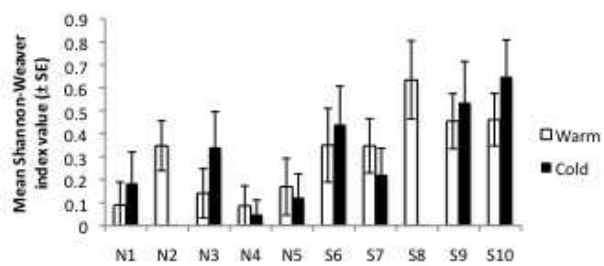


Sites ordered North to South; all values are expressed x cm$^{2(-1)}$

| Site | Sand cover (%) | Wave height (m) | Exposure (E/P) | Site code |
|---|---|---|---|---|
| Playa Escondida | 50.9 | 0.5 | P | N1 |
| Galera | 0.6 | 1.8 | E | N2 |
| Estero de Plátano | 20.7 | 1.0 | E | N3 |
| Cabo Pasado | 16.4 | 1.3 | P | N4 |
| La Tiñosa | 25.2 | 0.9 | P | N5 |
| Puerto Cayo | 11.7 | 0.4 | P | S |
| Los Frailes | 22.6 | 1.0 | P | S |
| Playita | 3.8 | 2.1 | E | S |
| Punta Blanca | 2.8 | 1.8 | E | S |
| Anconcito | 7.0 | 1.5 | E | S |

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