Vertical zonation in the rocky intertidal at Cocos Island (Isla del Coco), Costa Rica: A comparison with other tropical locations

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Abstract: This study presents a description of the tropical intertidal shores of Cocos Island (Isla del Coco), Pacific, Costa Rica. The intertidal zones were surveyed photographically with 116 digital images of quadrats (25 x 25 cm), and 130 of the cliffs in five days. The percent of cover and abundance of species in the intertidal zones were estimated by digital image analysis. Twenty-three taxa were found, Mollusca was the most specious (12 species). Littorinid and neritid mollusks were dominant in the higher littoral area. The predator snails *Plicopurpura patula pansa*, and *Thais brevidentata*, high densities of the pulmonate limpet *Siphonaria gigas* and some patches with low cover of the barnacle *Tetraclita stalactifera* were present in the mid-littoral zone. The encrusting algae dominate the rock surface at mid and low littoral and erect-frondose forms were only found in sheltered boulder shores. A high similarity in species identity was found between mainland and insular territories of the eastern tropical Pacific. Panamanian islands were most similar in terms of the algae assemblage of Cocos Island. The Galápagos Islands differ from Cocos Island in their higher erect-frondose and crustose algal cover, and lower densities of *S. gigas*. Grazing may be an important factor in structuring the intertidal community of Cocos Island and other regions of the eastern tropical Pacific. The main grazer in the cliffs and boulders was *S. gigas* which was larger in size (5.77 cm ± 1.00) than those of mainland and island sites in Costa Rica and Panama. Boulders and cliffs presented changes in the zonation and densities between sheltered or wave exposed areas. The position of organisms on the intertidal cliffs increased at high tidal level in more exposed sections of the coast. Moreover, topographic characteristics of boulders and cliffs influenced the densities of some gastropods around the island. Shores with ignimbrites, aa lavas or basaltic walls with a slight inclination towards the sea presented high densities of gastropods. The difference in the assemblages at Cocos Island from those of the continental and insular shores indicates high dynamics within intertidal tropical ecosystems. Rev. Biol. Trop. 56 (Suppl. 2): 171-187. Epub 2008 August 29.

Key words: Vertical zonation, Isla del Coco, cliffs, tropical rocky shores, boulders, pulmonate limpets, encrusting algae, digital image analysis, Cocos Island, Costa Rica.

The variation in species richness of terrestrial and marine species between mainlands and islands is due to the degree of isolation and size of the islands. This topic has been well studied and models such as McArthur and Wilson´s (1967) “equilibrium” hypothesis have been used to explain differences in assemblages (Begon *et al*. 1996). The intertidal organisms have larvae or propagules with short life time and settlement in specific height range in the shore; in this way intertidal shores of island present the same problems in colonization that terrestrial habitat. For example, Benedetti-Cecchi *et al*. (2003) found a difference between rocky shores of mainland and islands at the Tuscany Archipelago, Italy (20-150 km apart of mainland), in the composition and high cover of erect-frondose algae (mainland), and the low cover of encrusting algae and barnacles (island). Moreover, the difference may have been the result of human effects on the mainland shores. The islands in the Bay of Panama showed difference in cover and abundance from that of the mainland possibly due to differences in predation and wave exposure (Levings & Garrity 1984, Lubchenco *et al*. 1984).

Rocky shores present high differences in vertical distribution of organisms. The vertical zonation patterns at local and regional scales are caused by structuring factors such as temperature, predation, inter-specific competition, wave action, mean tidal variation, salinity and topography (Doty 1957, Dayton 1971, Connell 1972, Menge & Sutherland 1976). Differences in abundance and frequencies of species between artificial sea walls (lowest values) and horizontal or vertical natural intertidal shores were found by Chapman and Bulleri (2003) in Sydney Harbour, Australia. Mettam (1994) used photographic survey data taken from an aircraft to survey the epibenthos of the rocky cliffs of Bristol Channel and the Servern Estuary and described a change in the communities of estuaries and marine areas. Similar variations between and within sites are found in São Miguel Island with sixteen biotopes (Wallestein & Neto 2006).

In the case of Cocos Island (Isla del Coco), Pacific Costa Rica with 23 km^2, the basaltic cliffs and boulder beaches differing in wave exposure and with a tidal range of up to 4 m. The island lies 495 km from the mainland of Costa Rica, and more than 630 km of Malpelo and the Galápagos Islands (Lizano 2001). It was created by volcanic processes (Garrison 2005) and has a shoreline similar to that of other islands in the eastern Pacific. Cocos Island represented an interesting scenario because its distance or proximity to other locations, for comparisons of the intertidal communities in islands and mainland in the eastern tropical Pacific.

This study presents a description of the vertical zonation of organisms in the intertidal boulders and cliffs at Cocos Island, and comparisons of faunal and algal assemblages and limpet density and size with other locations in mainland and island in the eastern tropical Pacific.

MATERIALS AND METHODS

The rocky intertidal shores of Wafer, Yglesias and Chatham bays (Fig. 1) were sampled at low neap tide on 12, 14 and 17 January 2007, respectively. A total of 116 digital photographs (4 mega-pixels) were taken of a 25 x 25 cm quadrats distributed between the different vertical zonation bands found at each site. Voucher specimens of epifauna were deposited in the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica. Algal species were collected for their identification.

Additionally, the rock walls of the cliffs around Cocos Island and its islets were surveyed photographically during low neap tide from a boat on 15 and 18 January 2007. A total of 130 digital photographs were taking amounting to a survey of approximately 1074 m of coast line (Fig. 1).

From the photographs, the percent cover of sessile species were estimated by digital image analysis using the UTHSCSA Image Tool, developed by the University of Texas Health Science Center, San Antonio, Texas (ftp://maxrad6.uthscsa.edu). Estimates of percent cover were obtained using three methods. The first was a direct measure of the area of the image occupied by each organism. The second procedure was the manual segmentation on gray scale to create a binary image (black and white pixels). The percent of pixels of the category of interest represented in the image was estimate by the “Count Black/White pixels” command. The third percent cover analysis was used for organisms with hard to distinguish coloration on the gray scale. Color saturation was changed (Adobe Photoshop) in each species category and a background subtraction was done between the original and edited image, for each species category prior to cover estimation. The abundance of mobile species in quadrats and cliffs images was determined with the “point” command.

The length and width of *Siphonaria gigas* were measured in the quadrat photographs of

Fig. 1. Study sites of the intertidal rocky shore at Cocos Island. January 2007. Open circles are quadrat sampled sites. Black point and lines are cliffs surveyed photographically.

the three bays. Twenty individuals were measured in situ at Chatham Bay to obtain a size base for calibrating the spatial scale of cliffs images and convert the x-y pixels coordinates to a metric scale. In this way the height above the sea level of each species was estimate.

Data analysis: The statistical analysis were carried out with PRIMER 4 (Clarke & Warwick 1994) and the free software PAST (Hammer *et al*. 2001) (http://folk.uio.no/ohammer/past).

Quadrat images: The data matrix (quadrats/species) was transformed with fourth root for the percent cover data (sessile species), and log (x+1) for abundance data (mobile species). Each species datum was then standardized (mean = 0 and standard deviation = 1) by the difference from the measured scales. A dissimilarity matrix based on the euclidean distance between quadrats was generated and analyzed by two-way crossed ANOSIM (R) (Clarke & Warwick 1994) to find intertidal level and site differences in species composition. The value of R determines the level of difference, if R=1 the groups are completely different from each other. The results of the ANOSIM were showed in a two PCA axes of transformed data that preserve the euclidean distances among attributes (Legendre & Gallagher 2001). Finally, the mean of the transformed data of each species by stratum/site was estimated and expressed back to the original scale by the inverse transformation.

***Siphonaria gigas* size:** The relation between length and width of specimens of *S. gigas* was analyzed using the geometric mean regression to demonstrate uniformity in this relationship between individuals of *S. gigas* from the different bays and those measured in the field (Krebs 1999). The mean length and width of *S. gigas* were estimated with a mixture analysis (PAST) with the goal of determined the mean and standard deviation of size class (juvenile and adults) limpets. Better mean estimation have less negative log likelihood value and a minimal value for Akaike IC indicate the number of size groups that produces the best fit without overfitting.

Cliffs' images: The non-normality of the height above sea level of each species in the cliffs was tested with the Shapiro-Wilk test for both the raw and 4th root transformed data based on the slope in the relation between the log of standard deviation versus the log of the mean by site (Clarke & Warwick 1994). A Kruskal Wallis test (H) for each species was used to find median height difference between site pooled data. For the cliffs the algal cover was estimated in 5 images per transect and the means were used in statistical analyses. The similarity between sites based on algal cover was represented with a Cluster Analysis based in the euclidean distance by the UPGMA method (Quinn & Keough 2003). The abundance of mollusks and crabs was compared between sites using the Chi squared test ($\chi 2$) with expected values based on the photographic survey of the coastline

With the x-y metric coordinates of *S. gigas* for each cliff image, the Thompson Test (Krebs 1999) of spatial pattern for the 1st to the nth nearest-neighbor was carried out. Spatial patterns based on the 1st nearest-neighbor were compared using a Chi squared test in order to recognize dominant patterns. The mean distance to the 1st nearest-neighbor, the number of nearest-neighbors necessary to change a stable clumping pattern, and their mean distances were estimated for each image. For a site comparison the standard error associated with the distance estimation was produced using the Jacknife technique (Krebs 1999).

RESULTS

Quadrat images: A total of 23 taxa were recorded: 12 mollusks, two barnacles, one hermit crab, one anthozoan, two polychaetes, two erect-frondose and two encrusting algae, and an epilithic bacterial bio-film. Seven bands, with different assemblages of species, were found from the low to the high intertidal. At all sites two bands (low intertidal) mainly contained the encrusting algae, the pulmonate limpet *S. gigas*, the barnacles: *Tetraclita stalactifera* and *Chthamalus panamensis*, and the grazer mollusk *Chiton stokesii* (Table 1). These bands differ in abundance or percent cover and in the presence of other species. In the boulders of Yglesias Bay a third band at mid intertidal was found that lacked the pink color, encrusting algae (Rhodophyta) and had low abundances of mobile species. In Chatham Bay the mid low intertidal had a band with red and green erect-frondose algae and the mid high intertidal had an epilithic bacterial bio-film band. All sites in the high intertidal bands contained the typical molluscan species of Littorinidae and Neritidae with high tolerance to desiccation. The abundances of each species differed between bands (Table 1).

The two-way crossed ANOSIM based on the similar bands between sites confirmed the change in composition at different height in the intertidal ($R= 0.541$, $p<0.001$). Moreover, differences in vertical zonation between all sites also occurs ($R=0.472$, $p<0.001$). Results of PCA demonstrated the separation of quadrats by site and intertidal level (Fig. 2) with Yglesias Bay (boulders and cliff) clearly separated from Chatham and Wafer bays by PCA-1. The high intertidal showed less variance between quadrats and sites than the low intertidal (Fig. 2). The low variance explained by PC-1 and 2 was due to species found at different heights within the intertidal at different sites; this is the case for *Lottia mesoleuca*.

The main difference between Yglesias Bay, and both Wafer and Chatham bays was the absence of *S. gigas* in the boulders of Yglesias Bay and its replacement by *Nerita funiculata* and *Planaxis planicostatus*. *Plicopurpura patula pansa* was high in abundances in the intertidal cliff of Yglesias and was absent in Chatham and Wafer, while *S. gigas* was more abundant in Wafer Bay mainly on ignimbrite boulders. Littorinidae and Neritidae were more abundant in Wafer and Yglesias that at Chatham. Finally,

TABLE 1

Mean percent cover of sessile organisms and the abundance per m^2 of the mobile species (italic font) found in the intertidal zones of Cocos Island, Costa Rica, in January 2007

Site	Species	1	2	3	4	5	6	7
Chatham Bay	*Nerita scabricosta*							*10.30*
Boulders	*Nodilittorina aspera*							*8.25*
Sheltered	*Nodilittorina modesta*						*2.38*	*23.86*
Basaltic	*Lottia mesoleuca*						*24.81*	
	Fissurella virescens					*2.38*		
	Bacteria biofilm					12.96		
	Chthamalus panamensis				12.31	<0.01		
	Rhodophyta (erect-frondose)				5.18			
	Rhodophyta encrusting (black)	17.64	38.08		15.77		1.67	
	Chlorophyta (erect-frondose)		<0.01		14.22			
	Siphonaria gigas	*2.38*	*2.38*			*11.86*		
	Tetraclita stalactifera	<0.01	8.46		<0.01			
	Rhodophyta calcareous encrusiting (pink)	0.01	1.98					
	Chiton stokesii	*14.21*	*2.38*					
Wafer Bay	*Nerita scabricosta*							*1.45*
Boulders	*Nodilittorina modesta*						*4.51*	*69.22*
Sheltered	*Tetraclita stalactifera*	0.81					<0.01	
Basaltic	*Chthamalus panamensis*	0.02	0.37				0.14	
	Siphonaria gigas	*1.15*	*7.33*				*8.54*	
	Lottia mesoleuca	*3.70*	*2.72*					
	Anemone	<0.01	0.03					
	Chiton stokesii	*1.86*	*2.72*					
	Bacteria biofilm	0.54						
	Thais brevidentata	*1.15*						
	Serpulidae	<0.01						
	Rhodophyta encrusting (black)	0.37						
	Rhodophyta (erect-frondose)	<0.01						
	Chlorophyta (erect-frondose)	<0.01						
	Rhodophyta calcareous encrusiting (pink)	0.05						

TABLE 1 (Continued)

Mean percent cover of sessile organisms and the abundance per m^2 *of the mobile species (italic font) found in the intertidal zones of Cocos Island, Costa Rica, in January 2007*

Site	Species	1	2	3	4	5	6	7
Wafer Bay	*Nodilittorina aspera*						*25.40*	*23.19*
Boulders	*Nodilittorina modesta*						*16.76*	*53.69*
Sheltered	*Nerita scabricosta*						*10.30*	*5.06*
Ignimbrite	Rhodophyta (erect-frondose)	0.41					0.02	0.02
	Siphonaria gigas	*5.11*	*28.14*				*15.59*	
	Fissurella virescens		*4.16*					
	Tetraclita stalactifera	1.50	0.01					
	Rhodophyta encrusting (black)	10.46	4.05					
Yglesias Bay	*Nodilittorina modesta*							*92.59*
Boulders	*Plicopurpura patula pansa*						*6.63*	
Sheltered	*Nerita scabricosta*						*3.03*	
Basaltic	Anemone			0.06				
	Nerita funiculata	*11.50*	*33.66*	*10.91*				*2.38*
	Planaxis planicostatus	*37.85*	*24.81*	*3.03*			*5.06*	
	Lottia mesoleuca		*6.90*	*5.06*				
	Chiton stokesii	*8.83*	*2.38*	*3.03*				
	Tetraclita stalactifera		<0.01					
	Rhodophyta calcareous encrusiting (pink)	0.01						
	Gastropod	*8.83*						
	Amphinomidae	*2.38*						
Yglesias Bay	*Nodilittorina modesta*						*16.00*	*23.19*
Cliff	*Nerita scabricosta*		*21.62*				*4.16*	
Sheltered	*Siphonaria gigas*		*7.08*					
Basaltic	Anemone	<0.01	0.02					
	Plicopurpura patula pansa	*4.16*	*4.16*					
	Grapsus grapsus	*4.16*						
	Chlorophyta (erect-frondose)	<0.01						
	Rhodophyta calcareous encrusiting (pink)	9.15						
	Fissurella virescens	*4.16*						
	Lottia mesoleuca	*13.07*						

Numbers are the bands of the vertical zonation (1 = lowest tide level and 7 = supralittoral zone).

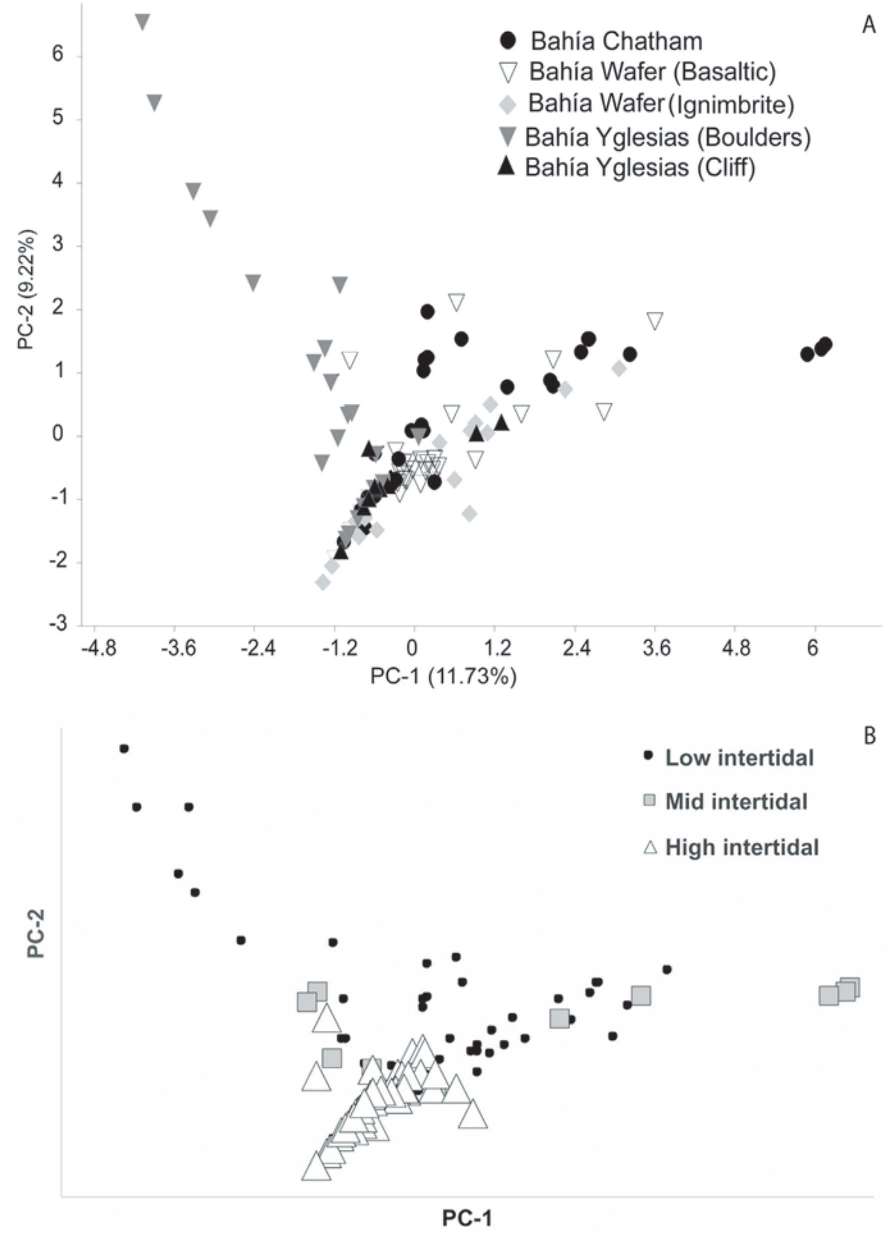

Fig. 2. Principal Component Analysis of the quadrats based on the abundance and cover of organisms by site and intertidal zone of the rocky shores of Cocos Island. January 2007.

algae and barnacles covered more rock surface in Chatham than in the other sites (Table 1).

***Siphonaria gigas* size:** The relationship of the shell morphology of field specimens agreed well with image data estimations. The relationship between length and width showed no significant difference between sites (Fig. 3).

The pooled *S. gigas* data produced two size classes in length (log l.hood = -111.1, Akaike IC = 234.1) and width (log l.hood = -105.9, Akaike IC = 223.7). The juvenile limpets had

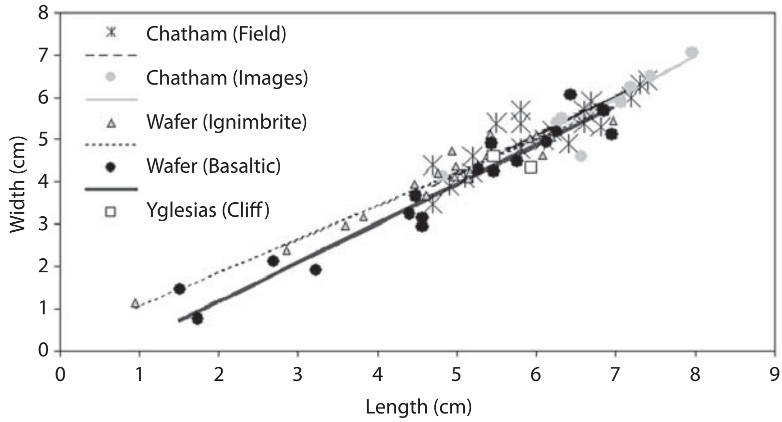

Fig. 3. Geometric mean regression between the length and width of the shell of *Siphonaria gigas* from different sites of Cocos Island. January 2007.

a mean length of 2.19 cm ± 0.90 and a mean width of 1.77 cm ± 0.72. The adult populations had a mean length of 5.77 ± 1.00; and a mean width of 4.83 cm ± 0.93. Several limpet specimens had lengths of over 7 cm (Fig. 4).

Cliff images (zonation): The median height of the main species on the cliffs showed a vertical zonation pattern. The lower intertidal (< 150 cm above sea level) was dominated by a pink color, encrusting algae (Rhodophyta) that formed a continuous band around the walls of the island and their islets. The upper limit of this algal band varied between sites (H = 4229, 16 sites, p<0.001) (Fig. 5). It was greater than 1 m in the southern islets and western walls of the island and lower values in the sheltered zone of Yglesias and Wafer bays, Manuelita and Dos Amigos Pequeño. A band of the barnacles *Megabaluns peninsularis* or *M. coccopoma* was found below the 1.5 m algal band at some sites. The black color, encrusting algae

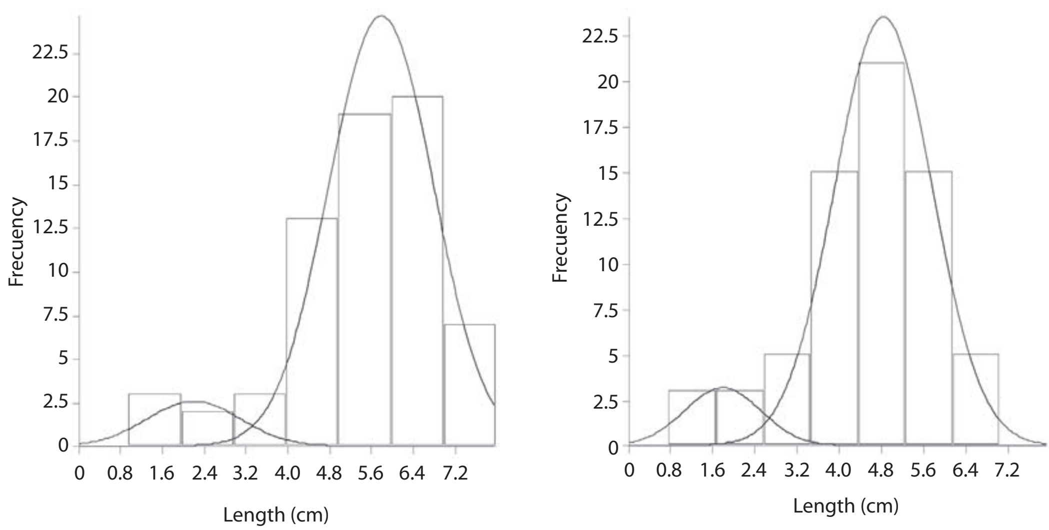

Fig. 4. Size-frequency distribution of *Siphonaria gigas* and normal fit for juvenile and adults. Cocos Island. January 2007.

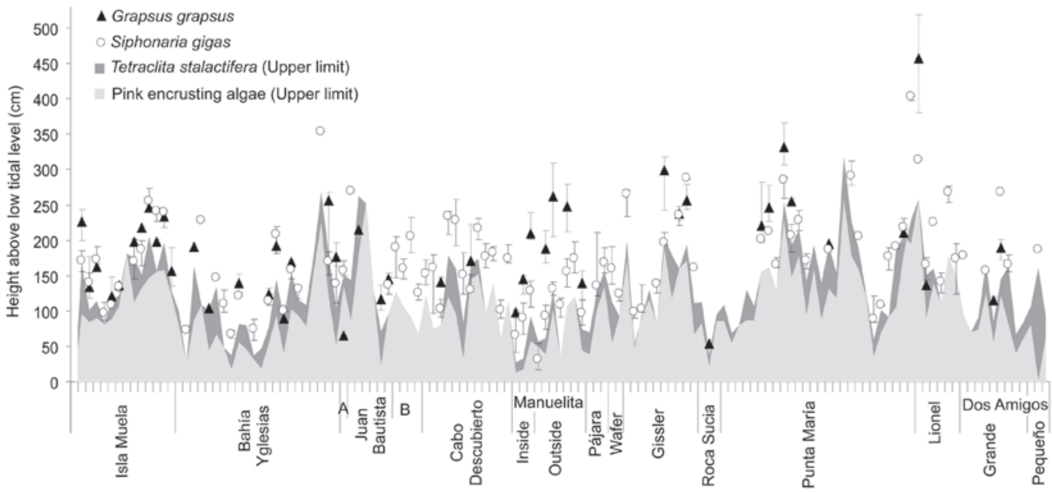

Fig. 5. Median height for some species in the intertidal walls images samples of the cliffs at Cocos Island. January 2007. Locality names are geographic reference for transects in Fig. 1. Lines in *Siphonaria gigas* and *Grapsus grapsus* are the percentiles 25 and 75.

(Rhodpohyta) was found within the pink color band and the barnacle *Tetraclita stalactifera* was in the upper region of this band. *T. stalactifera* was also found above the pink color, encrusting algae band with a median upper limit between 2 to 80 cm above of the pink band upper limit (H = 1190, 15 sites, p<0.001) (Fig 5). Some specimens of this crustacean were found more than 2 m above the pink color algal zone.

The pulmonate limpet *S. gigas* had a median height of between 30 to 400 cm above sea level (H = 1157, 15 sites, p<0.001) and was always found above the pink color algal and barnacle zones. In more exposed sites it occurs above 1.5 m (Fig. 5). The crab *Grapsus grapsus* was found in the upper levels except that in the small islet sites it was present in the lower sections (H = 191.6, 12 sites, p<0.001) (Fig. 5). In general, the bands of the organisms increased in height in the exposed cliffs of Muela, Yglesias, Juan Bautista, Gissler and Punta María (Fig. 5).

Cliff images (algal cover): The cover of black color encrusting algae (Rhodophyta) was low (~20%) in the higher intertidal regions of the cliffs at Juan Bautista and Yglesias Bay (Fig. 6). Manuelita and Punta María had high cover of pink color algae in the low tidal zone and a cover of black color algae of approximately 50% in the higher. Bare rock was very scarce in the lower tidal of Dos Amigos Grande, and in the high intertidal of this site the black color encrusting alga coverage was about 35% (Fig. 6). Pájara and Wafer Bay had only 50% cover in the lower intertidal of the pink color encrusting algae, while in Isla Muela, Cabo Descubierto, Cabo Lionel and Punta Gissler the cover was between 57 and 68% (Fig. 6). These four sites had an approximate 35% coverage of black color encrusting alga in the high intertidal. This similarity pattern was showed in the dendrogram in Fig. 7.

Cliff images (abundance and spatial pattern): A total of 573 crabs and 7088 pulmonate limpets were found in the 1074 m of coastline photographed. The intertidal crab *G. grapsus* had the highest density (Table 2) in Roca Sucia, Manuelita, Muela and Juan Bautista. The only section of the main island with high density was Yglesias (χ^2 = 494.39, d.f. = 15, p<0.001). *S. gigas* had the highest density (Table 2) in

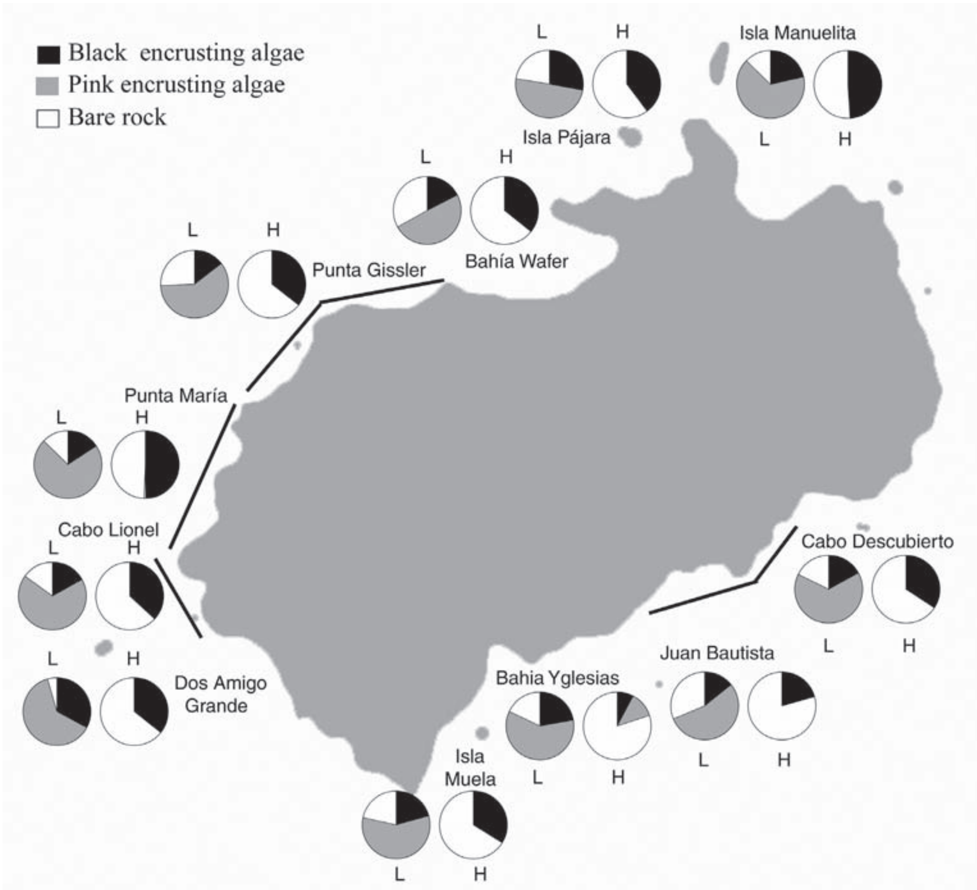

Fig. 6. Spatial distribution and percent cover of encrusting algae in the intertidal walls of cliffs at Cocos Island. January 2007. L = Low intertidal, H = High intertidal.

Islet A, Manuelita and on the walls of Cabo Descubierto and Cabo Lionel (χ^2 = 11946, d.f. = 15, p<0.001).

The spatial pattern of *S. gigas* was clumped. The group size varied between sites, but was generally less than 10 individuals. The nth nearest-neighbor was a measured of the radius of the group and was large in Punta María and Gissler Bay where the groups had radii between 3 and 5.5 m. On the other hand, in the majority of the islets limpet clump size was smaller and there was a uniform distribution of individuals (χ^2 = 53.238, d.f. = 2, p<0.001) (Table 3). The distance to the 1st nearest-neighbor ranged between 8.5-91.4 cm, but in the majority of sites was between 20-35 cm (Table 3).

DISCUSSION

Bakus (1975) visited Cocos Island during the RV Searcher expedition of 1972 and reported the vertical distribution of some organisms in the intertidal at Chatham and Wafer. The 1972 zonation patterns were similar to that found in the present study. The more complete coverage and abundance data reported in this study allowed consideration of the following questions about the structure and reasons for

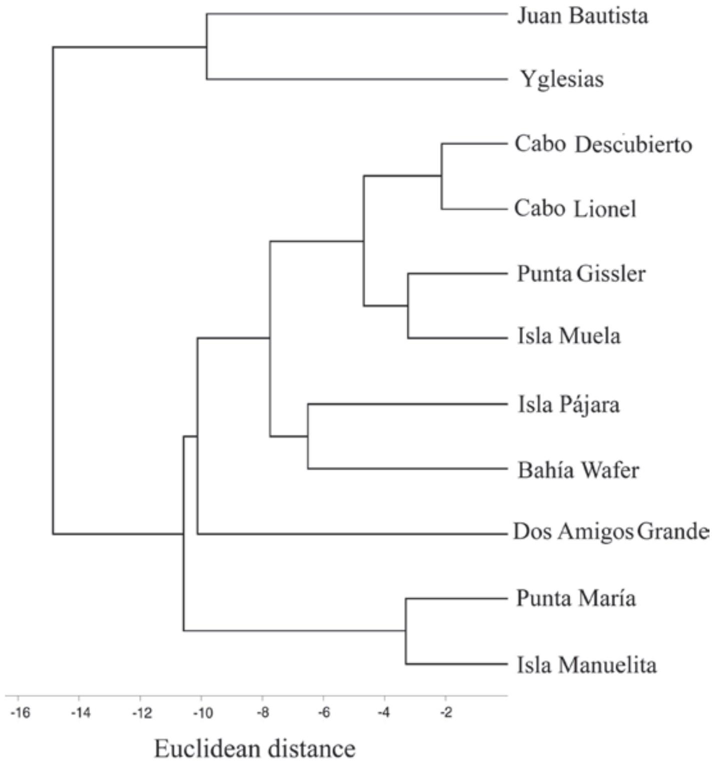

Fig. 7. Cluster Analysis (UPGMA) of transects by the percent cover of encrusting algae in the cliffs of Cocos Island. January 2007.

specific variations in the vertical zonation of Cocos Island:

How does is the vertical zonation of Cocos Island compare to that of the mainland and other islands in the eastern Pacific? The Gulf of Nicoya estuary and the northern Pacific coast of Costa Rica have the highest cover of erect, frondose algae and the barnacle *C. panamensis* (~50%) at low and mid littoral levels, respectively as well as low cover of encrusting algae (Villalobos 1980, Fischer 1981, Sibaja-Cordero & Vargas-Zamora 2006, Sibaja-Cordero & Cortés 2008). This compares to values in the central Pacific of erect, frondose algal cover of about 20% and cover of *C. panamensis* of about 30% (Sutherland & Ortega 1986). The erect, frondose algae have higher cover in the south Pacific (Cortés & Jímenez 1996, pers. obs.). Along the coast the epilithic clams S*accostrea palmula* and *Chama echinata*, and the colonies of the polychaete *Phragmatopoma attenuata* form bands with moderate to high cover in the low and mid littoral (Fischer 1981, pers. obs.). On cliffs and boulders of Cocos Island both these invertebrate species and erect, frondose algae were rare or absent while encrusting algae was dominant.

The rocky intertidal of Panama had the highest values of bare rock in the higher intertidal while encrusting algae dominated the low littoral (Levings & Garrity 1984, Lubchenco *et al.* 1984, Menge *et al.* 1985). The exposed islands of Panama also had an increase in the abundances of pulmonate limpets and a decrease in the cover of sessile species. The cliffs of Cocos Island were most similar to the exposed Panamanian islands in the domination of encrusting algae and the absence of the *C.*

TABLE 2
Density of crabs and pulmonate limpets per 10 meters of coastline in the intertidal cliffs of Cocos Island. January 2007

Site	*Grapsus grapsus* ind/10m	*Siphonaria gigas* ind/10m
Isla Muela	7.38	60.26
Yglesias	11.63	20.09
Islet A	2.09	32.33
Juan Bautista	5.65	8.79
Islet B	0.00	425.61
Cabo Descubierto	2.35	135.83
Manuelita (Inside)	8.63	208.74
Manuelita (Outside)	18.49	137.65
Isla Pájara	0.00	40.99
Wafer	0.00	11.48
Gissler	2.43	6.44
Sucia	8.53	0.00
Punta María	2.73	14.73
Cabo Lionel	1.98	161.06
Dos Amigos Grande	1.05	8.41
Dos Amigos Pequeño	0.00	0.44

panamensis band. In the Galápagos Islands pulmonate limpets are scarce and the barnacle *Tetraclita milleporosa* had only moderate cover (~2 to 14%) while erect, frondose and encrusting algae had high cover (Vinueza *et al.* 2006). The boulders of Cocos Island present had low densities of *S. gigas*, but these values were higher (Table 1) than those reported for the Galápagos (0.12 ind/m^2) (Vinueza *et al.* 2006).

Communities on the basaltic boulders in Yglesias and Wafer bays were more similar to those seen on cliff communities. Although, erect-frondose algae are present at Chatham Bay and on the ignimbrites at Wafer Bay, these two sites were more similar to Galápagos Islands rocky shore communities. The high littoral zone of both islands and mainland was similar in the presence and densities of neritid and littorinid species. The high variability in densities of *G. grapsus* between sites at Cocos Island is similar to Panama and Galápagos (Lubchenco *et al.* 1984, Vinueza *et al.* 2006). The gastropods of Cocos Island are the same species as in the intertidal shores of mainland of Costa Rica, Panamá and Ecuador (Bakus 1968, Lubchenco *et al.* 1984, Willis & Cortés 2001, Arroyo-Osorio *et al.* 2002, Sibaja-Cordero & Vargas 2006, Sibaja-Cordero & Cortés 2008).

Why do encrusting algae dominated the intertidal zone? The low species richness of the littoral zone of Cocos Island may be due to its isolation with few intertidal algae species from nearby areas able to colonize the rock surface. The encrusting coralline algae (pink color), possibly *Porolithon* or *Lithophyllum* (Bakus 1975), has a low cost-low survival propagule strategy but after settlement they can survived some years mainly in the exposed shores. While non-calcareous “tar crust” forms (sporophyte crust) possibly *Hildebrandia* or *Petrocelis* (Bakus 1975), can survive 40 years in the intertidal (Little & Kithching 1996). Additionally encrusting forms can significally inhibit the settlement of some organisms (Lubchenco *et al.* 1984).

Williams (1993) hypothesized that the change in algal assemblages in Hong Kong Bay was related to propagules of ephemeral erect-frondose algae transported by the temperate current (dry-cooler) and long-term maintenance of encrusting forms due to the tropical current (wet-hot). At Cocos Island the North Equatorial Counter Current usually carries warm water from the western Pacific but westerly currents from the mainland reach the island from December to April (Zimmerman & Martin 1999, Lizano 2008). Schiel (2004) mentioned that many intertidal propagules (except fucoids) are transported large distances and the best dispersal mechanism is by adult algae that survived long periods of drift. The difficulty of colonizing the intertidal of an island is not the only reason for the low diversity at Cocos Island, since the Galápagos intertidal has eight species among erect-frondose and encrusting (Vinueza *et al.*

TABLE 3

Thompson`s Test of Siphonaria gigas spatial distribution: Estimate Mean distance (cm) to nearest neighbors and number of neighbors to clumped pattern and their SE (standard error), for sites at Cocos Island. January 2007

		Distance to the 1st nearest-neighbor		Distance to the nth nearest-neighbor		No. of neighbors to clumped pattern	
Site	No. of Images	Mean	SE	Mean	SE	Mean	SE
Isla Muela	10	32.47	6.84	98.71	42.22	6	1
Yglesias	8	34.75	4.45	144.33	39.15	4	1
Islet A	1	37.43	16.33	127.23	21.61	9	-
Juan Bautista	1	28.13	6.97	38.74	6.87	2	-
Islet B	4	8.54	3.25	33.07	12.62	4	1
Cabo Descubierto	11	22.96	10.08	178.80	74.19	12	4
Manuelita (Inside)	3	34.62	2.26	57.99	12.51	5	1
Manuelita (Outside)	6	21.66	8.58	127.70	9.54	9	3
Isla Pájara	1	71.20	10.87	295.16	17.91	17	-
Wafer	2	91.43	59.26	149.01	129.11	3	1
Gissler	2	71.86	16.19	553.01	101.36	7	0
Punta María	9	56.61	12.13	307.80	116.00	8	3
Cabo Lionel	4	12.33	7.68	76.65	19.56	8	1
Dos Amigos Grande	1	54.08	8.80	66.34	9.75	2	-

2006). Other factors may explain the dominance of encrusting "pioneer species".

The dominance of encrusting forms at Cocos Island are probably due to the partly the result of the high density of *S. gigas*. On the Costa Rican mainland densities of the limpet grazer *S. gigas* were low in the north Pacific and Gulf of Nicoya, and erect-frondose algae cover was high (Sibaja-Cordero & Vargas 2006, Sibaja-Cordero & Cortés 2008). Low algal cover in the central Pacific was possibly due to the high density of *S. gigas* (Sutherland & Ortega 1986). The low density of pulmonated limpets in Galápagos could explain the increase of erect-frondose patches, preferred in the diet of marine iguanas and *G. grapsus* (Vinueza *et al.* 2006).

Hawkings and Harnoll (1983) and Little and Kithching (1996) mentioned that grazing in the red encrusting algal zone reduced the epiphytes and development of macroalgal sporelings. The calcareous algae act to protect the thalus from grazers such as limpets thus giving them an advantage. The removal of *Patella cochlear* from the encrusting calcareous band in South Africa produced dense macroalgal growth which took more than 10 years to return to its original state (Hawkings & Hartnoll 1983). Therefore, one could speculate that the crust existence was prolonged in the intertidal cliffs of Cocos Island by the grazing *S. gigas*. The non-calcareous encrusting algae have more organic contents than many erect-frondose algae such as *Ulva* (Maneveldt *et al.* 2006). This important food supply at Cocos Island is reflect in the mean size of 5.8 cm of *S. gigas* in comparison with the reported by Ortega (1987) of 2.5-4-3 cm at Punta Mala and 3.2-3.4 cm at Manuel Antonio National Park both in mainland of Costa Rica and 3.15 cm at Taboguilla Island, Bay of Panama (Lubchenco *et al.* 1984).

Changes in the dominance of algal species coverage were shown to occur in the Galápagos due to the ENSO events (Vinueza *et al.* 2006). The dominant *Ulva* and the encrusting *Gymnogongrus* decreased during the ENSO event, possibly due to reduced nutrients, high temperatures and strong wave action. A similar ENSO event occurred in the waters of Cocos Island during the study but previous comparable community structure data are nonexistent. The only comparisons that can be made are with the data of Bakus (1975) from1972 (a non-ENSO year), but his description of vertical zonation is similar to the report here.

Erect-frondose forms were high in coverage in the more sheltered bays (Chatham and Wafer), while the strong wave action enhance the dominance of encrusting corraline on the cliffs. The articulated coralline and red turf had more cover in less wave action sites in Galápagos (Vinueza *et al.* 2006). The encrusting calcareous *Schizotrix* in Panama presented more coverage in wave exposed shores (with *S. gigas* present) (Levings & Garrity 1984). The wave exposure reduced the ability to remain attached in some algae species (Schiel 2004).

The 4 m tidal range at Cocos Island contributed to the increase in dessication time and the dominance of encrusting forms resistant in the mid intertidal. The Pacific coast of Costa Rica has a tidal range of 3 m while the Caribbean coast is only 0.5 meters; the erect-frondose macroalgal coverage was scarce at mid and high litoral of Pacific coast due to the increase in desiccation (Villalobos 1980). The encrusting *Schizotrix* is resistant to thermal stress at low tide and had an important cover in the mid intertidal of Panama (Levings & Garrity 1984).

What are the environmental factors that change the vertical zonation within the shores at Cocos Island? There was high variability in the zonation patterns on boulders and cliffs around the island and islets. Possible factors that cause these patterns were substrate type, wave exposure, inclination and physical stability of the boulders. Little and Kitching (1996) discussed the importance of this points in the structuring of temperate shores. These factors influence the adherance of snails and propagules to the rock. In this case, ignimbrite boulders of Wafer Bay had irregular surfaces that are preferred by littorinid snails (Jones & Boulding 1999) and neritids (Fischer 1981) to avoid dessication. In the cliffs the densities of limpets might be influence the type of substrate. Shores with ignimbrite or aa lava sections in the walls (Islet B, and Manuelita) or basaltic walls with a slight inclination towards the sea (Cabo Descubierto and Cabo Lionel) had high densities of *S. gigas*, while the hexagonal grid basaltic walls of Juan Bautista and Dos Amigos were low in density. A similar conclusion was presented by Garrity and Levings (1984) for Panama.

In boulder sites differences in the epibenthic community were mainly in the lower littoral zone (Fig. 2) mainly due to changes in sessile species with stability of these boulders the most obvious cause. The boulders of Chatham (basaltic rock) and Wafer bays (ignimbrites), were larger and were partially buried in the sand, while the basaltic boulders of Wafer and Yglesias bays, smaller and were piled on top of one another. Little and Kitching (1996) emphazised that disturbance in the position of boulders produced continuous mortality and recolonization of sessile species. In those sites (Wafer and Yglesias bays), algae and *T. stalactifera* were very scarce. The rolling of the boulders might be the cause of the absence of *S. gigas*, while on adjacent cliffs and blocks *S. gigas* was abundant. Small gastropods replaced *S. gigas* in those shores perhaps because they have a higher chance of returning to the original level after the rock moves. Wave action in Yglesias Bay due to south and southeastern winds (Lizano 2001), caused more instability that in the Wafer Bay community.

The variation in height of organisms on the cliffs was caused by the orientation of the walls to the wave shock or heavy swell. In these areas the intertidal was higher in the surf zone. This pattern was shown by Bakus (1975) on the walls outside of Wafer and Chatham bays (leeward side of the island) in contrast to the windward side where encrusting black algae extended to 4 m. This pattern was reflect in the algal cover in the high intertidal of Yglesias Bay with less cover of black algae that the exposed islets and the cliffs of Cabo Descubieto. In the northwest of the island the low and high intertidal showed a change to greater algal cover at more exposed walls and islets.

The change in cover of non-calcareous patches possibly explains the high variability in distances between neighboors and the uniform patterns found within *S. gigas* groups. This is similar to the negative relationship between territory size and algae cover observed by Stimson (1973) with the intertidal limpet, *Lottia gigantea*. On walls with highest densities of pulmonate limpets (Manuelita, Cabo Descubierto and islet B) a greater number of groups with fewer individuals were found. Moreover, the laying of egg masses by several individuals in groups found in some samples during the study can contribuited to the spatial pattern.

No evident trend was found in densities of *G. grapsus* in relation to algal cover. This crab plays a role in the regulation of algae and invertebrates in the mid to low intertidal zone in Galápagos (Vinueza *et al.* 2006) as does *G. albolineatus* in Hong Kong (Kennish 1997). The presence of 50% of the population of *G. grapsus* at higher levels in the intertidal cliffs of Cocos Island was concordant with their avoidance of submergence as reported by Lubchenco *et al.* (1984). Some individuals move from the high to the low intertidal during low tides to have access to the algal, as observed in the Galapagos Islands (L.R. Vinueza pers. comm.).

In conclusion, the encrusting algae that monopolize the rock surface, the high size of pulmonate limpets and the presence of the crab *G. grapsus* in the high littoral of cliffs makes the zonation pattern obvious. The abundant algal cover of the intertidal of Cocos Island apparently sustains large numbers of grazers and their predators. The similarities and differences between these assemblages and the nearest shores illustrate the high dynamics within intertidal tropical ecosystems.

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RESUMEN

Este estudio presenta una descripción de la zona entre mareas de Isla del Coco, Costa Rica. Se inspeccionó un total de 116 imágenes de cuadriculas (25x25 cm) en cantos rodados y 130 de los acantilados por análisis digital de imágenes. Se encontró 23 táxones y una alta similitud en la identidad de especies con las islas y la costa continental del Pacífico Tropical Oriental. El grupo principal fue Mollusca con 12 especies. El litoral alto presentó litorínidos y neritas, el litoral medio tenía caracoles depredadores, lapas pulmonadas (*Siphonaria gigas*) y parches del cirripedio *Tetraclita stalactifera*. Las algas incrustantes dominan la superficie del litoral medio y bajo; y las formas erectas-frondosas se encontraron solo en cantos rodados protegidos del oleaje fuerte. Este patrón es diferente a la costa Pacifico norte y sur de Costa Rica, donde las algas erectas-frondosas dominan el bajo litoral. En este sentido las islas panameñas resultan más similares en composición a la Isla del Coco. Las islas Galápagos difieren en la presencia de algas erectas-frondosas e incrustantes, ambas con cobertura importante y la baja densidad de *S. gigas*. El ramoneo es uno de los posibles factores en la estructuración la comunidad de entre mareas de Isla del Coco y la región del Pacífico tropical oriental. Los principales herbívoros fueron las lapas pulmonadas, que presentaron una talla más grande (5.77 cm ± 1.00) que en el continente e islas de Costa Rica y Panamá. Cambios en la zonación y densidades se encontraron entre hábitats protegidos o expuestos al oleaje. La altura de los organismos en los acantilados aumentó en las secciones más expuestas de la costa. Además, las características en la topografía de cantos rodados y acantilados cambio las densidades de algunos gasterópodos alrededor de la isla. La composición de la comunidad presentó similitudes y diferencias con las costas cercanas lo que evidencia el alto dinamismo dentro de los ecosistemas tropicales de entre mareas.

Palabras clave: Zonación vertical, Isla del Coco, acantilados, cantos rodados, lapas pulmonadas, algas incrustantes, análisis digital de imágenes.

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