Vertical zonation of rocky intertidal organisms in a seasonal upwelling area (Eastern Tropical Pacific), Costa Rica

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Abstract: The intertidal rocky shore of Bahía Salinas (seasonal upwelling area), northern Pacific coast of Costa Rica, was studied to determine the vertical zonation of algae and invertebrates. In two sheltered and two exposed sites the communities were sampled twice, once during the upwelling (April) and again during the non-upwelling season (October). At each site five strata were sampled with 25x25cm quadrats. Each stratum had five quadrats and digital photographs of each quadrat were taken. Digital image analysis was used to estimate the percent cover of sessile species and abundance of mobile fauna. A typical vertical zonation was found using Principal Component Analysis (PCA) biplot and Multiple Discriminant Analysis (MDA). The analysis of similarities (ANOSIM) detected a seasonal change in the biological composition of the inferior strata. This change in the percent cover of the algal assemblage and their herbivores were related to the seasonal upwelling. Sessile invertebrates had a constant percent cover between April and October, but the difference between exposed and sheltered sites was significant. Invertebrates showed a patchy structure in sheltered sites while in exposed sites organisms formed horizontal bands. Interactions between species indicated that predation and space monopolization were possible causes of lower cover of barnacles in sheltered sites and lower abundance of mollusks in the exposed area. Regional difference of intensity in the upwelling event and larval recruitment may explain the high cover of sessile invertebrates of Bahía Salinas in comparison to the Bay of Panama, another seasonal upwelling system. Rev. Biol. Trop. 56 (Suppl. 4): 91-104. Epub 2009 June 30.

Key words: tropical, rocky intertidal, zonation, upwelling, seasonality, digital image analysis, PCA, MDA, eastern Pacific, Costa Rica.

A characteristic of rocky intertidal shores is a pattern of vertical zonation (Stephenson & Stephenson 1949), with bands of differing biodiversity from the upper to the lower intertidal zone (Ellis 2003). This pattern has been observed in tropical zones, although there has been few studies (e.g. in Panama) of tropical rocky shores of Latin America. These studies demonstrated the importance of habitat selection by organisms (Lubchenco *et al.* 1984) and degree of aggregation (Garrity & Levings 1984, Levings & Garrity 1984) in the structuring of assemblages (Menge & Farrel 1989). Some species of mollusks (Bandel & Wedler 1987) and barnacles (Laguna 1985) have been recognized as indicators of specific littoral zones.

The study of intertidal rocky shore ecology in Costa Rica has been a series of isolated efforts with different objectives: food webs analysis (Paine 1966), zonation and taxonomic variation of mollusks between the Caribbean and Pacific coasts (Bakus 1968), comparison of gastropods between temperate and tropical rocky shores (Spight 1977, Miller 1983), habitat and temporal change of snails (Spight 1978), reproduction and recruitment of barnacles (Villalobos 1980a, b, Sutherland 1987), algal community structure (Villalobos 1980c), vertical zonation, bio-erosion and tectonic movements

(Fischer 1981), biological interactions (Ortega 1985, 1986a, Sutherland & Ortega 1986), fish predation on gastropods (Ortega 1986b), habitat segregation (Ortega 1987a), human predation on limpets (Ortega 1987b), local spatial density and distribution of mollusks (Willis & Cortés 2001), zonation and population dynamics of a rocky intertidal crab (Díaz-Ferguson 2000, Díaz-Ferguson & Vargas-Zamora 2001), and variation in the vertical distribution of intertidal organisms in relation to an estuarine gradient (Sibaja-Cordero & Vargas-Zamora 2006).

Rocky shores of upwelling regions were recently analyzed to determine the association between water column characteristics and the structure of the intertidal community (Underwood & Petraitis 1993, Menge *et al*. 1997, 1999, Underwood 2000, Paine 2002). These studies concluded that the amount of invertebrate larval settlement is negatively correlated with the upwelling intensity. Most new hypotheses (Connolly & Roughgarden 1999, Menge *et al.* 2003) derived from the previous conclusion have been critized by Schiel (2004) who stresses the effects of other environmental factors (human impacts, sedimentation, wave exposure, freshwater input) in the structuring of rocky intertidal communities in upwelling areas.

While biological knowledge of the rocky shores of the north Pacific coast of Costa Rica is limited, the oceanographic processes are being studied (unpubl. data), and seasonal upwelling is a potentially important factor for change in the intertidal shores. In this paper we present data on the spatial and temporal variation in vertical zonation of organisms at Bahía Salinas, north Pacific of Costa Rica, from two wave exposed and two sheltered sites, during the upwelling and non-upwelling season.

MATERIALS AND METHODS

Study area: Bahía Salinas (11º00’-11º03’N; 85º42’-85º46’W) located on the north Pacific coast of Costa Rica (Fig. 1) is bordered manly by sandy beaches and by rocky shores, and has a mean tidal range of about 3m. During the dry season months (December to April) the Trade Winds blow across Mesoamerica, from the Caribbean to the Pacific, producing strong Northeasterly winds resulting in a coastal upwelling of cooler nutrient-rich waters known as the Gulf of Papagayo upwelling system (Legeckis 1988, McCreary *et al.* 1989, Chelton 2000a, b).

Methodology: Five strata were established at each site above the spring low tidal level. At each stratum five 25x25cm quadrats were sampled. A digital photograph of each quadrat was taken, and voucher specimens of each species were collected. Epifauna was fixed with 95% ethanol and algal species with 10% formaldehyde in seawater buffered with 1g of sodium bicarbonate.

The percent cover of the sessile species of this study was 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) as well as Adobe Photoshop®.

Percent cover data were obtained by three procedures. The first was a direct measure of the area of the image of the organisms. The software estimated the area with reference to

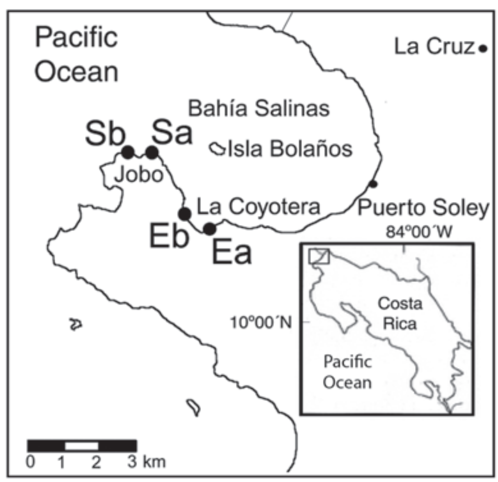

Fig. 1. Sampling sites at Bahía Salinas, Guanacaste, Costa Rica. Sa and Sb:Sheltered sites, Ea and Eb:Exposed sites.

a spatial calibration scale (25cm in this case). The second procedure was based on gray scale photographs by following manual segmentation of the color threshold to create a binary image (black and white pixels). The percent of pixels that the interest category represent 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. In this case, the saturation level of specific pixels changed in each of the categories of interest. A background subtraction was done between the original image and the edited photography for each category, prior to cover estimation. Abundance of the mobile fauna was measured with the "Point and Tag" command that avoids the double counting of individuals.

Data analysis: The data matrix (quadrats on the rows and the species on the columns) was transformed with fourth root for the percent cover data (sessile species) and log (x+1) for abundance data (mobile species). Columns were standardized (mean=0 and standard deviation=1) by the difference on the measure scales. Principal component analysis (PCA) was used to determine the vertical zonation of the species in the intertidal zone. PCA biplots were used to show the ordination of quadrats and the direction and rate of increase, in percent cover and number of individuals, of each species were represented by arrows. Multiple Discriminant Analysis (MDA) of each strata (group variable) were utilized to confirm the results of the PCA.

A dissimilarity matrix based on the euclidean distance between quadrats (rows) was generated and the submatrix of each stratum was isolated and analyzed by ANOSIM (Clarke & Warwick 1994) in order to determine if quadrats were more similar within site ($R>0$, $p<0.05$) or between sites ($R>0$, $p>0.05$). The value of R determines the level of difference, $R=1$ is total difference between groups. One-way ANOSIM (site differences) was applied to stratum one (sampled in two sheltered sites and at one exposed site in April because the tide was not low enough), while two-way crossed ANOSIM was used to identify site (exposed or sheltered) and date (April or October) differences for strata two to five. The relative multivariate dispersion was calculated for strata two to five for each site and date to identify those sites with the highest biological variation within each stratum.

The results of the ANOSIM and dispersion index were showed in graphical subordination of each stratum from the original PCA. The two axes graphical ordination of PCA transformed data preserve the euclidean distances among attributes (Legendre & Gallagher 2001). Finally, the mean of the transformed data of each species by site, stratum and visit was estimated and expressed back to the original scale by the inverse transformation.

RESULTS

Photographs of the study sites recorded 24 taxa: 12 mollusks, four barnacles, one anthozoan, one crab, five macroalgae, and a green epilithic biofilm of microalgae. Two pairs of species cannot be easily discriminated by the image analysis: *Ulva lactuca* vrs. *U. flexuosa* (Chlorophyta) and *Bostrychia radicans* vrs. *Caloglossa* sp. (Rhodophyta). In each pair the species presented similar color and very mixed spatial pattern within quadrats. Thus, the percent cover of both species in each pair was estimated together (Table 1).

The high mean percent cover in the low zone (stratum one and two) was due to a red algae *Hypnea* cf. *spinella* and the green algal pair, *U. lactuca* and *U. flexuosa*. Between stratum two and three, the greatest cover was by the mixture of *B. radicans* and *Caloglossa* sp. In stratum three the invertebrates with high cover were the barnacle, *Tetraclita stalactifera* and the clam *Saccostrea palmula*. In stratum three and especially in stratum four, a high percent cover of the barnacle, *Chthamalus panamensis* was found. The supralittoral zone was dominated by the barnacle, *Euraphia rhizophorae* (Table 1). The high mean abundance of mobile species in stratum two was due to the gastropod, *Siphonaria maura* and in stratum five to

TABLE 1

Mean percent cover of sessile organisms (regular font) and the abundance per m² of the mobile species (italic font) found in the intertidal zones of Bahía Salinas, Costa Rica, in April and October 2005

Site	Species	Stratum-Month								
		1-April	2-April	2-Oct	3-April	3-Oct	4-April	4-Oct	5-April	5-Oct
Sa	*Nerita funiculata*									*11.86*
	Euraphia rhizophorae								2.13	2.45
	Nodilittorina aspera						*25.62*		*118.98*	*16.77*
	Brachidontes sp.						5.20			
	Chthamalus panamensis		0.001	0.84		0.02	28.31	11.23		
	Siphonaria maura		*291.31*	*107.10*	*29.63*	*15.89*	*17.66*			
	Tetraclita stalactifera				11.27	3.12				
	Saccostrea palmula		0.001		3.32	29.68				
	Bostrychia + *Caloglossa*		28.98	8.13	6.94	14.61				
	Fissurella virescens					*4.80*				
	Anthozoa sp.			0.001	0.006					
	Thais brevidentata			*6.90*	*2.38*					
	Chiton stokesii			*32.35*						
	Microalgae			0.30						
	Polyplacophora sp. 1		*19.78*							
	Ulva lactuca + *U. flexuosa*	61.83	26.50			0.010				
	Hypnea cf. *spinella*	10.76								
Sb	*Nerita funiculata*					*2.38*			*5.12*	*13.14*
	Euraphia rhizophorae								1.11	0.12
	Nodilittorina aspera					*5.12*		*22.43*	147.34	91.62
	Brachidontes sp.						1.09			
	Chthamalus panamensis		1.99	0.23	32.10	7.60	37.29	33.36		
	Siphonaria maura		*49.23*	*7.23*		*16.69*				
	Tetraclita stalactifera				1.60	5.23				
	Saccostrea palmula				0.01	0.41				
	Bostrychia + *Caloglossa*		0.38	0.69	0.69	6.37				
	Fissurella virescens					*4.19*				
	Serpulorbis sp. 1					0.001				
	Anthozoa sp.					0.002				
	Thais brevidentata			*5.12*		*9.84*				
	Microalgae			0.21						
	Polyplacophora sp. 1		*20.45*							
	Thais melones			*2.38*						
	Hermit crab			*10.30*						
	Ulva lactuca + *U. flexuosa*	53.37	19.47							
	Hypnea cf. *spinella*	11.33								

TABLE 1 (Continued)

Mean percent cover of sessile organisms (regular font) and the abundance per m² of the mobile species (italic font) found in the intertidal zones of Bahía Salinas, Costa Rica, in April and October 2005

Site	Species	Stratum-Month								
		1-April	2-April	2-Oct	3-April	3-Oct	4-April	4-Oct	5-April	5-Oct
Ea	*Euraphia rhizophorae*								11.25	8.33
	Nodilittorina aspera								10.30	138.88
	Chthamalus panamensis						40.64	44.66		
	Siphonaria maura		*11.09*							
	Saccostrea palmula				56.64	93.33				
	Bostrychia + Caloglossa			58.92	44.55	0.001				
	Anthozoa sp.				0.003					
	Thais brevidentata					*2.38*				
	Balanus inexpectatus			37.30						
	Ulva lactuca + U. flexuosa		17.98	7.23						
	Hypnea cf. *spinella*		30.11							
	Serpulorbis sp. 1		0.13							
Eb	*Euraphia rhizophorae*								9.52	5.51
	Nodilittorina aspera								*149.68*	*155.30*
	Brachidontes sp.				0.02					
	Chthamalus panamensis		0.04		17.58	0.85	79.06	46.95		
	Siphonaria maura		*6.02*							
	Tetraclita stalactifera				0.006					
	Saccostrea palmula		0.006		1.96	39.19				
	Bostrychia + Caloglossa		36.38	0.46	13.67	0.28	0.02			
	Polyplacophora sp. 2		*7.18*							
	Fissurella virescens		0.70							
	Balanus inexpectatus	0.02	6.22	83.76						
	Ulva lactuca + U. flexuosa	58.45	1.73	52.90						
	Anthozoa sp.	0.038	0.004							
	Hypnea cf. *spinella*	0.008								
	Hermit crab	*2.38*								

Sa and Sb= sheltered sites (Playa Jobo), Ea and Eb= exposed sites (Playa La Coyotera). Stratum one was near to the lowest tidal level.

the presence of the snail, *Nodilittorina aspera*. Stratum three and four had some individuals of other species (Table 1).

The zonation pattern in the rocky shores of Bahía Salinas, where stratum one and five represent the ends of the intertidal gradient, was demonstrated by the PCA analysis. The species vector (arrows) indicated the difference in the biological assemblage between zones (Fig. 2). The MDA results (Fig. 3) agree with those obtained by PCA in the separation of the quadrats into five stratum groups (discriminant function 1 and 2 with χ^2, $p<0.001$).

The relative multivariate dispersion indicate than the cover and abundance of species had the following patterns: upper strata (four

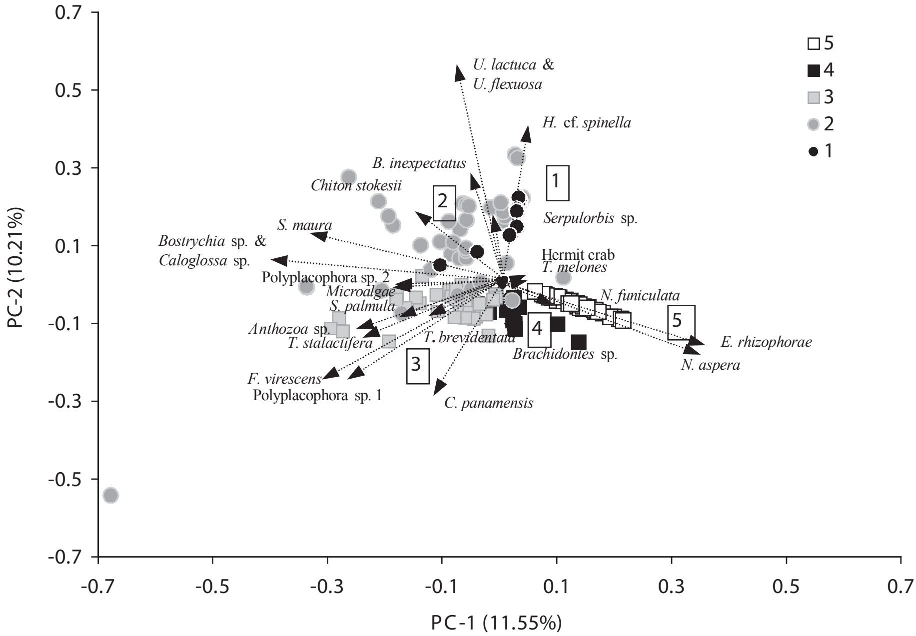

Fig. 2. Principal Component Analysis (PCA) of the vertical zonation of organisms in the intertidal rocky shore of Bahía Salinas, Costa Rica. The arrows are the vectors and show the direction in which the abundance or the percent cover of the species increased. Stratum one was near the lowest tidal level.

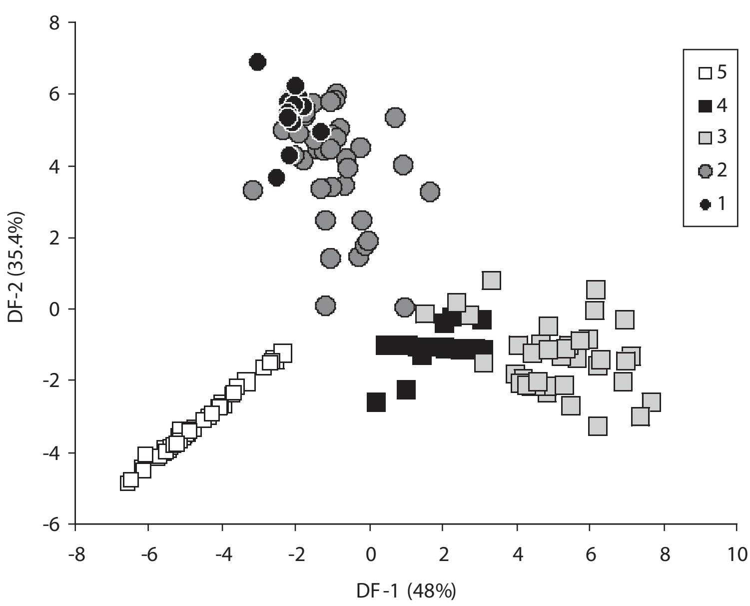

Fig. 3. Quadrats groupings by stratum for stratum at Bahía Salinas, Costa Rica, based on a Multiple Discriminant Analysis (MDA). Stratum one was near the lowest tidal level.

and five) of the sheltered sites in April showed more heterogeneity in the assemblage of intertidal organisms than exposed sites. All strata of sheltered sites in October had more biological variability than exposed sites (Table 2). ANOSIM test confirmed a moderate change in the biological assemblage between sites in stratum one (R=0.192, p=0.009). The quadrats of exposed sites had more variability and different locations in the PCA plot than the sheltered sites (Fig. 4). The main difference was the low cover and the spatial variation of the red algae, *Hypnea* and mobile mollusks in the quadrats of the exposed sites (Table 1).

The PCA plot of stratum two (Fig. 5) show that the principal component 2 (PC-2) produced

TABLE 2

Relative dispersion similarity of five quadrats within the same stratum. Values near zero indicate low variation in the composition between quadrats

Month/ Stratum	Relative Multivariate Dispersion			
April	Sa	Sb	Ea	Eb
2	1.10	0.99	1.04	1.03
3	1.28	0.76	0.98	1.04
4	1.53	1.64	0.31	0.93
5	1.10	1.10	0.29	0.76
October				
2	1.43	1.52	0.63	0.26
3	1.17	1.78	0.48	0.52
4	0.87	1.14	0.66	0.91
5	1.28	1.53	0.94	1.01

Sa and Sb= sheltered sites (Playa Jobo), Ea and Eb= exposed sites (Playa La Coyotera).

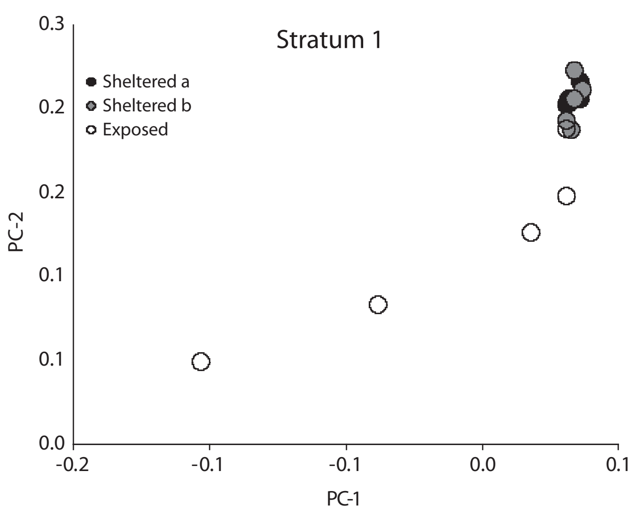

Fig. 4. PCA subordination for stratum one in April 2005, Bahía Salinas, Costa Rica.

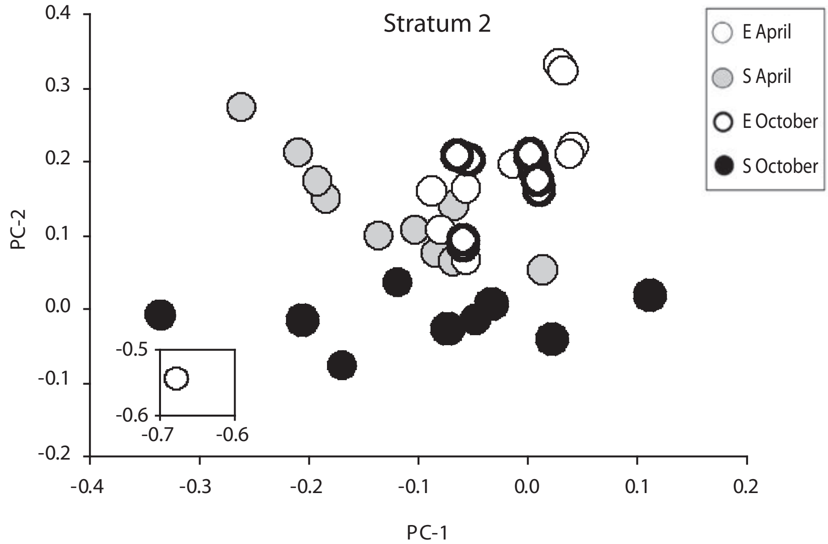

Fig. 5. PCA subordination for stratum two by site and time. E= Exposed site, S= Sheltered site, Bahía Salinas, Costa Rica.

the separation of quadrats as follow: sheltered sites in October with low values of PC-2, sheltered sites in April at mid values and exposed sites on both dates with high values of PC-2. The difference within stratum two (ANOSIM R=0.305, p<0.001) was higher than in stratum one. Moreover, there was a significant biological difference between April and October (ANOSIM R=0.394, p<0.001). Exposed sites had a low number of mobile species in October, and more species were found in the sheltered sites (Table 1). *U. flexuosa* presented a high coverage in October at the exposed sites, while, *U. lactuca* had a reduction of cover in October at both sites. *Balanus inexpectatus* was exposed on the rock surface due to the reduction of the algal canopy in the exposed sites (Table 1). Sheltered sites presented more *S. maura* than exposed sites in both sampling dates. In October the number of this limpet was low in sheltered sites and none were found in the exposed sites.

The quadrats of sheltered sites of stratum three (October followed by April) were spaced out on the left side of the PCA plot (Fig. 6) and the exposed (April and October) were pooled on the right. The differences in similarity between exposed and sheltered sites was moderate (ANOSIM R=0.278, p<0.001). The main sources of variation were the abundant presence of, *T. stalactifera* and the low cover of, *S. palmula* in sheltered sites. A small temporal change in similarity was found (ANOSIM R=0.150, p<0.004). Exposed sites showed a decrease in cover of *B. radicans* and *Caloglossa* sp. and an increase in the cover of, *S. palmula* in October. The cover of *B. radicans* and *Caloglossa* sp. increased in sheltered sites in October.

The quadrats of stratum four were arranged in two groups: the sheltered sites in April (with more variation in the PCA plot: Fig. 7) and the remainder quadrats (ANOSIM R=0.363, p<0.001). The cause of this pattern was the higher cover of *C. panamensis* in exposed sites (on both dates) than in the sheltered sites. The few mobile species in the sheltered sites were absent in October. This reduction in species richness produced a significant temporal change of the assemblage in sheltered sites (ANOSIM R=0.362, p<0.001).

Site and date separation was not produced by the PCA ordination of the quadrats for stratum five (Fig. 8). Although, moderate

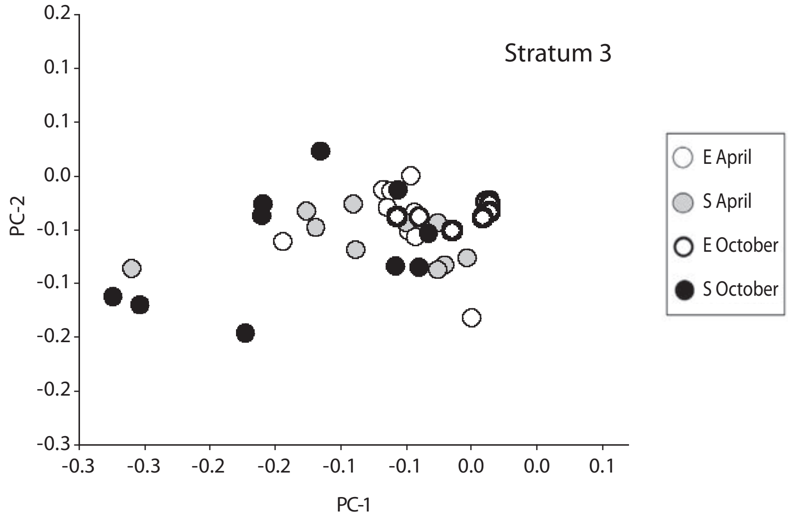

Fig. 6. PCA subordination for stratum three by site and time. E= Exposed site, S= Sheltered site, Bahía Salinas, Costa Rica.

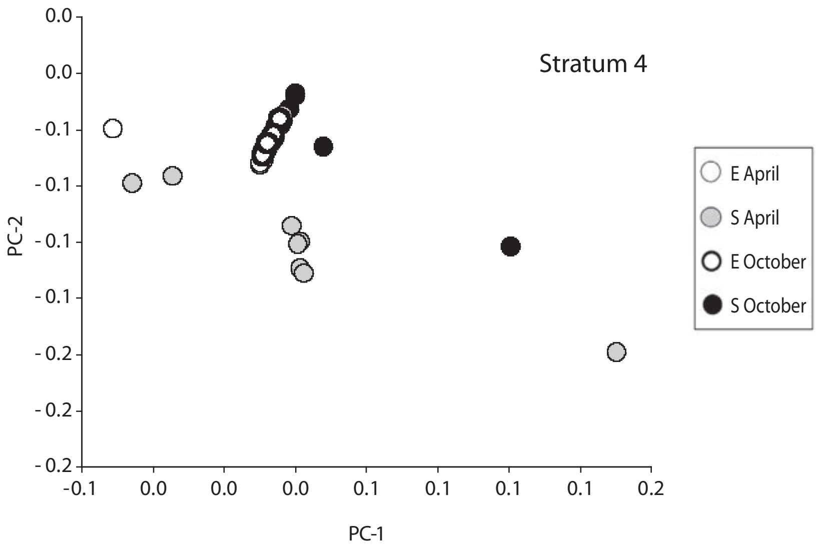

Fig. 7. PCA subordination for stratum four by site and time. E= Exposed site, S= Sheltered site, Bahía Salinas, Costa Rica.

significant differences between sites was detected by ANOSIM (R=0.146, p=0.008). The factor of variation was the barnacle *E. rhizophorae* that had a high mean cover (Table 1) and less variation in exposed sites. A temporal trend was not found with the ANOSIM test (R= -0.050, p=0.777).

DISCUSSION

The intertidal community on rocky shores at Bahía Salinas exhibited a typical vertical zonation pattern, and the relative coverage by sessile invertebrates was stable but differences between exposed and sheltered sites

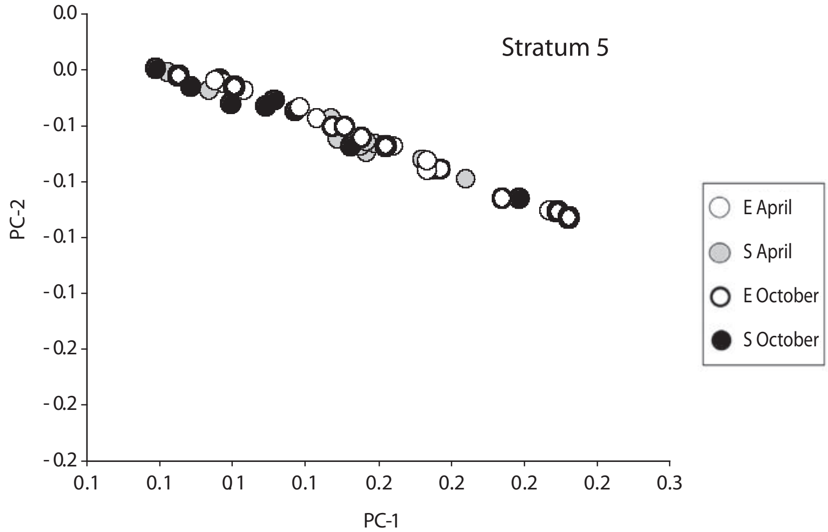

Fig. 8. PCA subordination for stratum five by site and time. E= Exposed site, S= Sheltered site, Bahía Salinas, Costa Rica.

were significant. The main difference between exposed and sheltered sites at Bahía Salinas was the horizontal spatial variation at the same height in the intertidal (Table 2). Exposed sites formed uniform bands of organisms, while the sheltered sites had patches of different species (mosaic structure). These results were concordant with the "Ballantine's scale" of communities in relation to wave exposure; in very exposed sites barnacles are predominant in the upper littoral zone (Little & Kitching 1996). In stratum four at Bahía Salinas, *C. panamensis* was dominant in mean cover (exposed>40%>sheltered) and in stratum five, the barnacle *E. rhizophorae* was dominant (exposed>5%>sheltered) (Table 1).

Underwood (1981) found that barnacles were sparse or absent, while gastropods were very abundant in sheltered areas in New South Wales, Australia, possibly due to the decreased exposure to wave-action resulted in an increase in predation intensity on barnacles. In sheltered sites at Bahía Salinas (with low cover of *C. panamensis* and *E. rhizophorae*) the predatory gastropod, *Thais brevidentata* was more abundant than in exposed sites (Table 1). Spight (1978) found a higher abundance of gastropods in calm-water than in moderate wave-action sites at Playas del Coco, Costa Rica. However, Menge & Lubchenco (1981), working in the Bay of Panama, found the opposite results; the barnacles in the high intertidal showed moderate mean cover (32.1%) on Flamenco Island (sheltered site) and were low in percent cover on Taboguilla Island (exposed site)(1.3%). This pattern was explained by greater importance of larval recruitment intensity relative to exposure characteristic and predation pressure.

The pulmonate limpet, *S. maura*, a grazer, was more abundant in the sheltered sites at Bahía Salinas (Table 1), but Spight (1978) at Playas del Coco, and Levings & Garrity (1984) in the Pacific coast of Panama found higher abundance of this species on exposed sites. Moreover, in the central Pacific coast of Costa Rica the congeneric limpet, *S. gigas*, was affected by dense coverage of *Chthamalus* and benefited indirectly by the predation of *T. brevidentata* on barnacles (Sutherland & Ortega 1986, Sutherland 1987). At Bahía Salinas, strata with *C. panamensis* and *S. maura* present a similar negative relation; more barnacles, fewer gastropods. The high number of *S. maura* in Panama was a result of the low cover of barnacles on offshore islands (Menge & Lubchenco 1981, Menge & Farrel 1989).

Algal cover is low on the upper intertidal of the Pacific coast of Costa Rica, and difference between exposed and sheltered sites are significant at mid height for only a few species. This could possibly be due to the high temperatures and exposure time causing desiccation during low tide (Villalobos 1980c). Changes in the presence of algal assemblages and their herbivores at Bahía Salinas were related to seasonal upwelling events. *Bostrychia* and *Caloglossa* had a higher cover in April, when the nutrient concentrations are higher and temperature lower (unpubl. data) than in October (Table 1). At Bahía Salinas the infralittoral (stratum one) had the highest percent of green alga cover (~58%) mainly of *U. lactuca* in April, while this alga was absent in October. Little & Kitching (1996) mentioned that most species of *Ulva* are rapid growing opportunists. In stratum two *U. lactuca* (large size algae) was replaced by *U. flexuosa* (small size algae) in October (Table 1). Villalobos (1980c) found a green algae (*Ulva* sp.) in Montezuma, Costa Rica, that grew in patches for a few weeks during the rainy season, when there were more nutrients.

The estuarine gradient produced a change in the mean cover percent of sessile organism in the Gulf of Nicoya. The inner zone of the Gulf had low cover (<30%) and the mouth had high cover (~50%) (Sibaja-Cordero & Vargas-Zamora 2006). In Bahía Salinas the low cover was found in the sheltered sites (36%) and high cover in the exposed sites (62%), but the difference in the mean cover percent was determinate by the species interactions that these habitats presented. Moreover, Bahía Salinas had more mean species per site (17.8) than the Gulf of Nicoya (12.8) (Sibaja-Cordero & Vargas-Zamora 2006). The number of intertidal species at Bahía Salinas was similar to temperate rocky shores (15-19) (Little & Kitching 1996).

Species composition and vertical distribution in the intertidal was similar between Bahía Salinas and the Bay of Panama (Luchenco *et al.* 1984), but the mean cover of sessile fauna species and macroalgae were higher at Bahía Salinas. Both bays experience a seasonal upwelling during the dry season (Brenes *et al*. 2003) but, in the Bay of Panama a persistent offshore current is generated year-round by the Panama Current (Sutherland 1987). As a result larval transport offshore from the Bay of Panama is probably higher than Bahía Salinas. Permanent upwelling occurs along the west coast of North America, and is more intense on California than Oregon and barnacle recruitment in California is much lower than Oregon (Menge *et al.* 1997). A similar situation has been observed in New Zealand, where the west coast has an upwelling event similar to Oregon while the east coast has downwelling. These oceanographic conditions resulted in lower sessile invertebrates coverage on the East coast than on the West coast. On the east coast the upwelling current transported larvae seaward and onshore during relaxation (Menge *et al.* 1999). Similarly, the high cover at Bahía Salinas compared with that of the Bay of Panama may be due to the difference in the prevailing oceanographic conditions, i.e. permanent offshore currents in the Bay of Panama. This hypothesis is concordant with the model of Connolly & Roughgarden (1999) that found a relationship between sessile invertebrates and percent cover of bare rock, and how they are associated to upwelling intensity (intensity in the export of larvae). Sites with only temporal upwelling (e.g., Bahía Salinas) have less free space and greater cover of dominant filter-feeders than seasonal upwelling area with an offshore current (e.g., Bay of Panama).

Working in Bahía Ballena in the Gulf of Nicoya, Costa Rica, Villalobos (1980a) found that the larvae of the filter-feeder barnacle *Tetraclita stalactifera* began to settle in mid October and larval release end in early December. If the populations of *Tetraclita* in Bahía Salinas and Bay of Panama are similar in fecundity and larval release to those of Bahía Ballena most larvae would also have settled before upwelling. Sutherland (1987) hypothesized that the larvae of *Tetraclita* in the Bay of Panama may be continuously exported out by the Panama Current, reducing the recruitment. These results in a low mean cover of *Tetraclita* in mid intertidal in Bay of Panama (0.1%) (Lubchenco *et al.* 1984) compared to Bahía Salinas (2.65%). This pattern was also present in the high intertidal where the barnacle *Chthamalus* had mean cover of 17% in Bay of Panama (Menge & Lubchenco 1981) and 40% in Bahía Salinas.

In conclusion interaction between species (predation and space monopolization) was a possible cause of the percent cover and changes in abundance between wave-exposed and calm-water areas. Regional difference in the intensity of upwelling events may also explain the high cover of sessile invertebrates at Bahía Salinas in comparison with the Bay of Panama.

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RESUMEN

La costa rocosa de entre mareas de Bahía Salinas (área de afloramiento estacional), en la costa Pacífico Norte de Costa Rica, se estudió para determinar la zonación vertical de algas e invertebrados. En dos sitios protegidos y dos expuestos se muestreó las comunidades en dos ocasiones, una vez durante el afloramiento (abril) y de nuevo durante la estación lluviosa sin afloramiento (octubre). En cada sitio se muestreó con cuadrículas de 25 por 25cm en cinco estratos. Cada estrato tenía cinco cuadrículas y se tomó fotografías digitales de cada una. Se usó análisis digital de imágenes para estimar el porcentaje de cobertura de las especies sésiles y la abundancia de la fauna móvil. Se encontró una zonación vertical típica con el Análisis de Componentes Principales (PCA) y Análisis Múltiple Discriminante (MDA). El análisis de similitudes (ANOSIM) mostró un cambio estacional en la composición biológica de los estratos inferiores. Este cambio en el porcentaje de cobertura del conjunto de algas y sus herbívoros fue relacionado con la estacionalidad del afloramiento. Los invertebrados sésiles tuvieron un porcentaje de cobertura constante entre abril y octubre, pero la diferencia entre sitios expuestos y protegidos fue significativa. Los invertebrados mostraron una distribución en parches en los sitios protegidos mientras los organismos de los sitios expuestos formaron bandas horizontales. Las interacciones entre especies indican que la depredación y la monopolización espacial son una posible causa de la baja cobertura de cirripedios en sitios protegidos y la baja abundancia de moluscos en el área expuesta. Diferencia regional en la intensidad del evento de afloramiento y reclutamiento larval explicarían la alta cobertura de invertebrados sésiles de Bahía Salinas comparado con la Bahía de Panamá, otro sistema de afloramiento estacional.

Palabras clave: tropical, entre mareas rocosa, zonación, afloramiento, estacionalidad, análisis digital de imágenes, Pacifico Oriental, Costa Rica.

REFERENCES

Bakus, G.J. 1968. Zonation in marine gastropods of Costa Rica and species diversity. Veliger 10: 207-211.

Bandel, K. & E. Wedler. 1987. Hydroid, amphineuran and gastropod zonation in the littoral of the Caribean Sea, Colombia. Senckenb. Marit. 19: 1-129.

Brenes, C.L., J.E. Coen, D.B. Chelton, D.B. Enfield, S. León & D. Ballestero. 2003. Wind driven upwelling in the Gulf of Nicoya, Costa Rica. Int. J. Remote Sensing 24: 1127–1133.

Chelton, D.B., M.H. Freikich & S.K. Esbensen. 2000a. Satellite observations of the wind jets off the Pacific coast of Central America. Part I: case studies and statistical characteristics. Month. Weather Rev. 128: 1993-2018.

Chelton, D.B., M.H. Freikich & S.K. Esbensen. 2000b. Satellite observations of the wind jets off the Pacific coast of Central America. Part II: regional relationships and dynamical considerations. Month. Weather Rev. 128: 2019-2043.

Clarke, K.R. & R.M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Bourne, Bournemouth, UK.

Connolly, S.R. & J. Roughgarden. 1999. Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. Ecol. Monogr. 69: 277-296.

Díaz-Ferguson, E.E. 2000. Descripción de la población de *Petrolisthes armatus* (Crustacea: Porcellanidae) en dos zonas de litoral rocoso intermareal de Playa Blanca, Punta Morales, Golfo de Nicoya, Costa Rica: una aproximación a los factores que regulan las fases bénticas y pelágicas de la población. M.Sc. Thesis, Universidad de Costa Rica, San José, Costa Rica.

Díaz-Ferguson, E.E. & J.A. Vargas-Zamora. 2001. Abundance of *Petrolisthes armatus* (Crustacea:Porcellanidae) on a tropical estuarine intertidal rocky beach, Gulf of Nicoya estuary, Costa Rica. Rev. Biol. Trop. 49 (Suppl. 2): 97-101.

Ellis, D.V. 2003. Rocky shore intertidal zonation as a means of monitoring and assessing shoreline diversity recovery. Mar. Poll. Bull. 46: 305-307.

Fischer, R. 1981. Bioerosion of basalt of the Pacific coast of Costa Rica. Senckenb. Mar. 13: 1-41.

Garrity, S.D. & S.C. Levings. 1984. Aggregation in a tropical neritid. Veliger 27: 1-6.

Laguna, J. 1985. Systematics, Ecology and Distribution of Barnacles (Cirripedia; Thoracica) of Panama, Incluiding an Analysis of Provincialism in the Tropical Eastern Pacific. M.Sc. Thesis, University of California, San Diego, California, USA.

Legeckis, R. 1988. Upwelling off the gulfs of Panamá and Papagayo in the tropical Pacific during March 1985. J. Geophys. Res. 93: 15489-15489.

Legendre, P. & E.D. Gallagher. 2001. Ecologically meaningful transformations for ordinations of species data. Oecologia 129: 271-280.

Levings, S.C. & S.D. Garrity. 1984. Grazing patterns in *Siphonaria gigas* (Mollusca, Pulmonata) on the rocky Pacific coast of Panama. Oecologia 64: 152-159.

Little, C. & J.A. Kitching. 1996. The Biology of Rocky Shores. Oxford University Press, New York, USA.

Lubchenco, J., B.A. Menge, S.D. Garrity, P.J. Lubchenco, L.R. Ashkenas, S.D. Gaines, R. Emlet, J. Lucas & S. Strauss. 1984. Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). J. Exp. Mar. Biol. Ecol. 78: 23-73.

McCreary, J.P., H.S. Lee & D.B. Enfield. 1989. The response of the coastal ocean to strong offshore winds: with application to circulation in the gulfs of Tehuantepec and Papagayo. J. Mar. Res. 47: 81-109.

Menge, B.A. & T.M. Farrell. 1989. Community structure and interaction webs in shallow marine hard-bottom communities: test of a environmental stress model. Adv. Ecol. Res. 19: 189-262.

Menge, B.A. & J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecol. Monogr. 51: 429-450.

Menge, B.A., B.A. Daley, P.A. Wheeler, E. Dahlhoff, E. Sanford & P.T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proc. Natl. Acad. Sci. USA 94: 14530-14535.

Menge, B.A., B.A. Daley, J. Lubchenco, E. Sanford, E. Dahlhoff, P.M. Halpin, G. Hudson & J.L. Burnaford. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecol. Monogr. 69: 297-330.

Menge, B.A., J. Lubchenco, M.E.S. Bracken, F. Chan, M.M. Foley, T.L. Freidenburg, S.D. Gaines, G. Hudson, C. Krenz, H. Leslie, D.N.L. Menge, R. Russell & M.S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proc. Natl. Acad. Sci. USA 100: 12229–12234.

Miller, A.C. 1983. A comparison of the species richness and roles of gastropods and chitons on rocky shores of temperate and tropical West America. Veliger 26: 62-68.

Ortega, S. 1985. Competitive interactions among tropical intertidal limpets. J. Exp. Mar. Biol. Ecol. 90: 11-25.

Ortega, S. 1986a. Spatial and temporal variations and biological interactions among some tropical intertidal populations. Ph.D. Thesis, University of South Carolina, Columbia, South Carolina, USA.

Ortega, S. 1986b. Fish predation on gastropods on the Pacific coast of Costa Rica. J. Exp. Mar. Biol. Ecol. 97: 181-191.

Ortega, S. 1987a. Habitat segregation and temporal variation in some tropical intertidal populations. J. Exp. Mar. Biol. Ecol. 113: 247-265.

Ortega, S. 1987b. The effect of human predation on the size distribution of *Siphonaria gigas* (Mollusca: Pulmonata) on the Pacific coast of Costa Rica. Veliger 29: 251-255.

Paine, R.T. 1966. Food web complexity and species diversity. Amer. Nat. 100: 66-75.

Paine, R.T. 2002 Trophic control of production in a rocky intertidal community. Science 296: 736-739.

Schiel, D.R. 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. J. Exp. Mar. Biol. Ecol. 300: 309-342.

Sibaja-Cordero, J.A. & J.A. Vargas-Zamora. 2006. Zonación vertical de epifauna y algas en litorales rocosos del Golfo de Nicoya, Costa Rica. Rev. Biol. Trop. 54 (Supl. 1): 49-67.

Spight, T.M. 1977. Diversity of shallow-water gastropod communities on temperate and tropical beaches. Amer. Nat. 111: 1077-1097.

Spight, T.M. 1978. Temporal changes in a tropical rocky shore snail community. Veliger 21: 137-143.

Stephenson, T.A. & A. Stephenson. 1949. The universal features of zonation between tide-marks on rocky coast. J. Ecol. 37: 289-305.

Sutherland, J.P. 1987. Recruitment limitation in a tropical intertidal barnacle: *Tetraclita panamensis* (Pilsbry) on the Pacific coast of Costa Rica. J. Exp. Mar. Biol. Ecol. 113: 267-282.

Sutherland, J.P. & S. Ortega. 1986. Competition conditional on recruitment and temporary escape from predators on tropical rocky shore. J. Exp. Mar. Biol. Ecol. 95: 155-166.

Underwood, A.J. 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. J. Exp. Mar. Biol. Ecol. 51: 57-85.

Underwood, A.J. 2000. Experimental ecology of rocky intertidal habitats: what are we learning? J. Exp. Mar. Biol. Ecol. 250: 51-76.

Underwood, A.J. & P.S. Petraitis. 1993. Structure of intertidal assemblages in different locations: how can local processes be compared, p. 38–51. *In* R.E. Ricklefs & D. Schluter (eds.). Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago, Chicago, USA.

Villalobos, C.R. 1980a. Variations in population structure in the genus *Tetraclita* (Crustacea:Cirripedia) between temperate and tropical populations. III. *T. stalactifera* in Costa Rica. Rev. Biol. Trop. 28: 193-201.

Villalobos, C.R. 1980b. Variations in population structure in the genus *Tetraclita* (Crustacea Cirripedia) between temperate and tropical populations: IV. The age structure of *T. stalacnifera* and concluding remarks. Rev. Biol. Trop. 28: 353-359.

Villalobos, C.R. 1980c. Algunas consideraciones sobre el efecto de los factores físicos y biológicos en la estructura de una comunidad de algas en el Pacífico de Costa Rica. Brenesia 18: 289-300.

Willis, S. & J. Cortés. 2001. Mollusks of Manuel Antonio National Park, Pacific Costa Rica. Rev. Biol. Trop. 49 (Suppl. 2): 25-36.