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SUPPLEMENT

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Soft-bottom benthic assemblage changes due to tropical seasonal upwelling (Bahía Salinas, Costa Rican Pacific)

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ABSTRACT

Introduction: Seasonal upwelling is a displacement offshore of surface seawater and replacement by cool deeper water with higher nutrient levels by the influence of the wind. On the north Pacific coast of Costa Rica the upwelling is present from December to April.

Objective: Within this seasonal upwelling area, Salinas Bay was sampled to determine whether the upwelling has an effect on the diversity, composition, and trophic guilds of the soft-bottom benthic community.

Methods: The bay was visited during the upwelling and non-upwelling seasons of 2007-2009. A number of six to nine grab samples were taken in each sampling event.

Results: Richness and abundance were lower in the non-upwelling season and the highest values were observed at the end of the upwelling. The taxa composition of assemblages varied partially across the seasons, depending on the upwelling intensity.

Conclusions: The species composition was more diverse and abundant at the end of the upwelling season than at the start or in the non-upwelling season. Differences in infaunal assemblages during the seasonal upwelling could be explained by the change in characteristics of the sediment-water interface, nutrients, and sediment movements that promote the increase of planktonic productivity, and thus food availability.

Key words: diversity; benthos; sediment processes; recruitment; nutrient dynamics; mollusks; population dynamics.

RESUMEN

Cambios en el ensamblaje bentónico de fondos blandos debido al afloramiento estacional tropical (Bahía Salinas, Pacífico, Costa Rica)

Introducción: El afloramiento estacional es un desplazamiento de agua de mar superficial hacia la costa y su reemplazo por agua más profunda y fría con mayores niveles de nutrientes por la influencia del viento. En la costa norte del Pacífico de Costa Rica, el afloramiento está presente de diciembre a abril.

Objetivo: Dentro de esta área de afloramiento estacional, se muestreó la Bahía de Salinas para determinar si el afloramiento tiene un efecto sobre la diversidad, composición y gremios tróficos de la comunidad bentónica de fondos blandos.

Métodos: La bahía fue visitada durante las temporadas de afloramiento y no afloramiento de 2007-2009. Se tomaron de seis a nueve muestras al azar en cada evento de muestreo.

Resultados: La riqueza y abundancia fueron menores en la temporada sin afloramiento y los valores más altos se observaron al final del afloramiento. La composición de taxones de los ensamblajes varió parcialmente a lo largo de las estaciones, dependiendo de la intensidad del afloramiento.

Conclusiones: La composición de especies fue más diversa y abundante al final de la temporada de afloramiento que al inicio o en la temporada sin afloramiento. Las diferencias en los conjuntos infaunales durante el afloramiento estacional podrían explicarse por el cambio en las características de la interfaz sedimento-agua, los nutrientes y los movimientos de sedimentos que promueven el aumento de la productividad planctónica y, por lo tanto, la disponibilidad de alimentos.

Palabras clave: diversidad; bentos; procesos sedimentarios; reclutamiento; dinámica de nutrientes, moluscos; dinámica poblacional.

INTRODUCTION

In upwelling areas, the warm surface water is pushed offshore by winds and replaced by cool deeper water with higher nutrient levels (Witman, 2007). Marine benthic communities respond to these water column fluctuations (Alongi, 1989a). This coupling between water column processes and the benthos has been documented by Alongi (1990), Graf (1992), Posey et al. (1995), and Witman (2007). In this context, input of organic matter from plankton can result in an increase of benthic biomass, or it could sustain the macrobenthos in posterior oligotrophic environments (Cosentino & Giacobbe, 2008; Escobar-Briones & Soto, 1997).

The upwelling process results in positive and negative effects on the marine fauna. For example, in Peru and Africa the upwelling has a positive influence on the biomass of benthic fauna (Alongi, 1990). Conversely, Alongi (1989b) points out that intense or constant upwelling on these shelves, and on the California coast, can have deleterious effects by exposing the benthos to anoxia. Additionally, the larval recruitment of benthic taxa can be reduced with an increase in the intensity (temporal permanence) of the upwelling (Menge et al., 1997, Menge et al., 2003), by exporting larval stages offshore.

The intensity or temporal permanence of the upwelling causes variations in taxa composition, as observed in rocky shore communities of both temperate and tropical localities (Cortés et al., 2014; Menge et al., 1997; Menge et al., 2003; Sibaja-Cordero & Cortés, 2008). Connolly & Roughgarden, (1999); Menge et al., (1997) and Phillips, (2005) have documented that areas with less intense upwelling, such as Oregon and the north of California, exhibit increased density, biomass, and growth of filter feeders compared to areas with stronger upwelling, like the south of California. These increases are attributed to the more stable and favorable conditions for filter feeders and their recruits in these less intense upwelling zones. Another example is the Galapagos Islands where both the number and the cover of rocky subtidal species (mainly suspension feeders) increased twofold when the upwelling events (causing the water temperature to drop by 3 to 9 ºC in less than a day) became more frequent and predictable from June to February (Witman & Smith, 2003). Sibaja-Cordero & Cortés (2008) report a change in the composition of rocky shore assemblages with more macroalgae cover during the season of upwelling in contrast with a less diverse assemblage dominated by barnacles in the non-upwelling season in Bahía Salinas, Costa Rica. In the case of soft-bottom systems, Quintana et al. (2015) noted that lower abundance values during non-upwelling periods compared to upwelling seasons in southeast Brazil can be the result of the decreased organic matter quality (detritus from phytoflagellate or diatom blooms) on the bottom.

A seasonal upwelling system has a temporal displacement offshore of the coastal surface seawater by the strong influence of wind. As the wind relaxes, the coastal system changes toward its initial condition. Seasonal upwellings in the neotropics occur in the Gulf of Tehuantepec (Mexico), Bay of Panama (Panama), and the Pacific coast of south of Nicaragua to Gulf of Papagayo, Costa Rica. During the dry season (December to April) the Trade Winds blow across Mesoamerica, from the Caribbean to the Pacific, producing strong Northeasterly winds, and resulting in a coastal upwelling of cooler nutrient-rich waters with lowest dissolved oxygen content (Alfaro & Cortés, 2012; Chelton, 2000a, Chelton, 2000b; Legeckis, 1988; McCreary et al., 1989).

During the upwelling season, the water temperature in the Gulf of Papagayo dropped by 7 °C to 9° C, while the nutrient concentrations rose by 3 to 15-fold. This stimulated phytoplankton growth, resulted in a 3 to 6-fold increase in chlorophyll concentration (Stuhldreier et al., 2015). This primary production and nutrient availability in the water column during upwelling possibly promote the development of diverse and abundant macrobenthic populations in the sediments of these areas (Alongi, 1990; Lee 1978; Menge et al., 2003). The small bay of Bahía Salinas (North Pacific of Costa Rica) is located in an area where the Trade Winds blow can blow with more intensity, because this zone has a low altitude of mainland, and a marked east-west axis which allows the winds to pass through without much obstruction (Alfaro & Cortés, 2021).

This study examines how the benthic taxa and feeding guilds vary in number, abundance, and composition between upwelling and non-upwelling seasons in Bahía Salinas. It also describes the oceanological and environmental conditions during the study period and the spatial variability of the benthic macrofauna within the bay.

MATERIALS AND METHODS

The oceanological and environmental conditions were measured to describe the periods of upwelling vs no upwelling in the specific locality of Bahía Salinas, North Pacific of Costa Rica during December 2007 to April 2009 (Fig. 1). Data on chlorophyll (µg/L) concentration, sea surface temperature (ºC), and wind velocity (m/s) to characterize the bay were obtained from the satellite data MODIS, AVHRR P5.1, QuickCAT, respectively available in NOAA Ocean Watch Voyager (http://www.pacioos.hawaii.edu/voyager/oceanwatch.html). The data are monthly averages derived from a box between 85° 38’ 32.64” W to 86° 15’ 0.36” W and 10° 56’ 56.76” N to 11° 9’ 2.16” N (Fig. 1). Additionally, seawater temperature at the bottom was recorded in situ with Hobo® Temp sensors, every 30 min at 3–6 m and 6.5–9 m depth, within the bay and outside the bay, stations H1-H2 and H3-H4, respectively, during the study period (Fig. 1). The mean ± standard deviation, minimum, and maximum values of these variables recorded were presented as indicators of upwelling.

Four sampling visits (December 2007, August 2008, December 2008 and April 2009) were carried out to study the subtidal benthic community of Bahía Salinas. The bottom of the bay (Fig. 1) was divided into three zones: the inner bay (3 to 18 m depth at chart datum), middle bay (18 to 35 m depth) and outside bay (35 to 40 m depth).

A Petite Ponar grab (sampling area: 15.2 x 15.2 cm) was used to sample the sediment and biotic assemblages from an 11 km transect from the inner to outside bay (Fig. 1). In December 2007 (start of the upwelling season), nine grabs were collected, three in each zone of the bay (Fig. 1). In August 2008 (non–upwelling season), five grabs were taken, two in the inner bay, two in the middle bay, and one in the outside bay. In both December 2008 (start of the upwelling season) and April 2009 (end of the upwelling season), six grabs were collected, two in each zone of the bay (Fig. 1). The number of sampled stations vary between

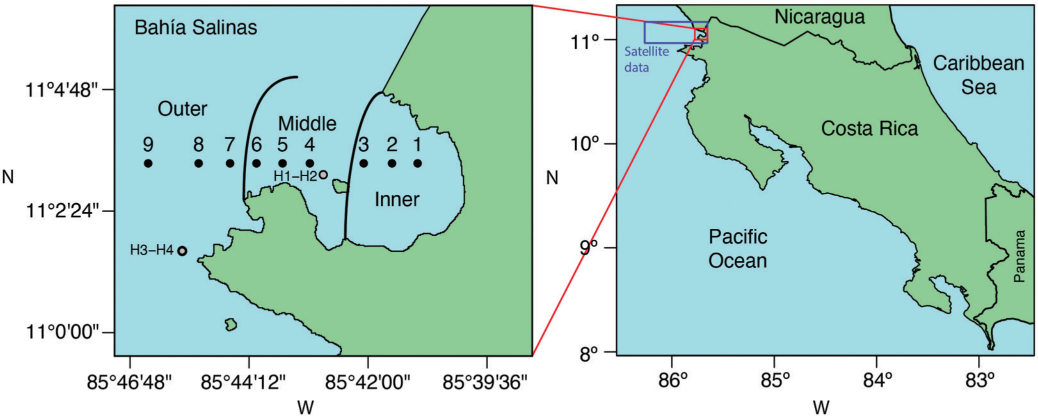

Fig. 1. Stations for benthic grab samples during December 2007 (stations 1–9), August 2008 (stations 1, 3, 4, 6 and 8), December 2008 and April 2009 (stations 1, 3, 4, 6, 8 and 9). Sites for Hobo®Temp sensors, labeled H1-H2 in the bay and H3-H4 outside the bay. The satellite data of wind, seawater temperature and chlorophyll concentration comes from the box on the figure on the right.

dates by the presence of adverse weather or severe oceanographic conditions. All sediment samples were preserved with formalin diluted to 5 % in seawater and stained with Rose Bengal. The samples were sieved through a 500 µm mesh, gently cleaned with fresh water as per Vargas (1987). The organisms were separated and identified to the lowest possible taxonomic category. Polychaetes were identified following Dean (1998), Dean (2001a), Dean (2001b) and de León-González et al. (2009), the mollusks following Keen (1971), and the crustaceans following Fischer et al. (1995), Hendrickx (1997), Hendrickx (1999), Rathbun (1918), Wicksten (1983), and Williams (1986). The identification for other groups was done with Carlton (2007).

Total taxa and total abundance per sampling date and zone of the bay were analyzed using a chi-squared test with expected values corrected by sampling effort (number of grab samples) following Krebs (1999). Additionally, mean diversity (H) using the Shannon-Wiener function with Ln, and mean equitability (J) were compared between dates of the bay with a Friedman test (F). With a Kendall's coefficient (Wt) was determined the degree of concordance in the values of biodiversity measures across zones of the bay (0 = no concordance to 1 = total concordance) (Krebs, 1999; Siegel, 1956). This statics were carried out in R. A non-metric Multidimensional Scaling (nMDS) based in the Euclidean distance of the abundances (transformed by Ln x+1) was used to visualize the dissimilarity between samples according with the zones of the bay and sampling dates (Hammer et al., 2001). Euclidean distance of transformed data represented a gradient in a better way than a Bray-Curtis of the abundance data (Legendre & Gallagher, 2001). This analysis was conducted using the vegan package in R (Oksanen et al., 2019). In the PAST software, a two-way ANOSIM test was carried out to determine the degree of discrimination (R value as in Clarke, l993) between sampling date and zone of the bay, and a SIMPER analysis was applied to the data (Ln x+1) that provides the percentage contribution of each taxa to the between-group dissimilarity by sampling dates and zones (Clarke & Warwick, 1994; Hammer et al., 2001).

Additional, each taxon was catalogued by feeding guild using the information of (Fauchald & Jumars, 1979), Jumars et al. (2015), and MacDonald et al. (2010), assuming that the taxa found feed in a similar manner to species within the same major group: suspension feeder (active, passive, and mixed), deposit feeder (surface and subsurface), mobile predators, scavengers, omnivores, and herbivores to describe the functional composition of the faunal assemblages. Finally, ANOSIM and SIMPER tests were conducted using the feeding guilds data (Ln x+1) with Euclidean distance. The density of individuals per m^2 was calculated from the means through a back transformation from the estimates of the SIMPER output.

RESULTS

Oceanological and environmental conditions: Wind speeds reached above 4 m/s from November to the end of March, and presented the minimum speeds from April to July (Fig. 2A). Sea surface temperature (SST) from satellite data was lowest during the upwelling season (with minimum values of 24–25 °C), than during the non-upwelling season (with minimum values above 28 °C) (Fig. 2B). Mean and minimum seawater temperature from the *in-situ* sensor had lower values during upwelling season (April: 19–21 °C and 15–17 °C), and reached a higher mean during non-upwelling season (August: 28–28.5 °C and 25–26.2 °C) at the two depths and the two sites recorded (Table 1). Water temperature was 3 to 4 °C cooler at 6.5–9 m than 3–6 m in both seasons (Table 1). Increased chlorophyll concentration was concordant with the increase in wind velocity and decrease of SST (Fig. 2C).

Fauna diversity and assemblages composition: A total of 1 969 individuals from 157 taxa were collected (Table 2). The nine grabs from December 2007 contained 683 individuals from 75 taxa; 136 individuals from 40 taxa were found in August 2008 (five grabs); 252 individuals from 76 taxa in December 2008 (six grabs); and 898 individuals from 101 taxa in April 2009 (six grabs). Polychaetes showed the highest percentage of total abundance and taxa, followed by crustaceans and mollusks (Table 3). Other relatively abundant taxa were sipunculids, nemerteans, nematodes, and echinoderms; remaining taxa corresponded to a flatworm (Platyhelminthes), a brachiopod, a cephalochordate, and a demersal fish (Table 2, Table 3).

Differences in the number of taxa between zones of the bay varied across sampling dates ($\chi^2 = 17.09$, d.f. = 6, P = 0.009) (Table 4). Post-hoc comparisons revealed that a similarly low number of taxa were found between the zones in August 2008 (non-upwelling season) ($\chi^2 = 0.52$, d.f. = 2, P = 0.771). In December 2007 (the start of the upwelling season), a lower taxa number were found at mid bay ($\chi^2 = 9.72$, d.f. = 2, P = 0.008). However, in December 2008, there was a peak in the number of taxa in the

Table 1
Sea water temperature in the bottom by depth and date, measured at two sites in the region of Bahía Salinas, Costa Rica.

Depth (m)	Mouth of the bay					Out of the bay				
	H1	Dec 2007	Aug 2008	Dec 2008	Apr 2009	H3	Dec 2007	Aug 2008	Dec 2008	Apr 2009
3-6	Mean	23.4	**28.4**	26.6	19.7	Mean	23.8	**28.3**	24.4	21.2
	Desv	**1.3**	0.9	0.4	0.8	Desv	1.2	0.8	1.0	**3.2**
	Max	26.6	**29.8**	27.3	22.3	Max	26.8	**29.4**	27.4	29.0
	Min	20.0	**25.4**	25.4	17.0	Min	21.3	**25.0**	22.4	16.2
Depth (m)	H2	Dec 2007	Aug 2008	Dec 2008	Apr 2009	H4	Dec 2007	Aug 2008	Dec 2008	Apr 2009
6.5-9	Mean	22.98	**28.28**	24.07	20.41	Mean	23.6	**28.5**	24.0	20.8
	Desv	0.38	0.96	1.01	**3.05**	Desv	1.2	0.7	0.7	**3.1**
	Max	23.64	**29.71**	27.13	28.82	Max	26.7	**30.0**	26.3	28.7
	Min	21.74	**25.16**	21.82	15.77	Min	20.9	**26.2**	22.1	15.4

The highest temperatures are in bold font. The minimum temperatures are underlined. H1 to H4 are the Hobo*Temp sensors.

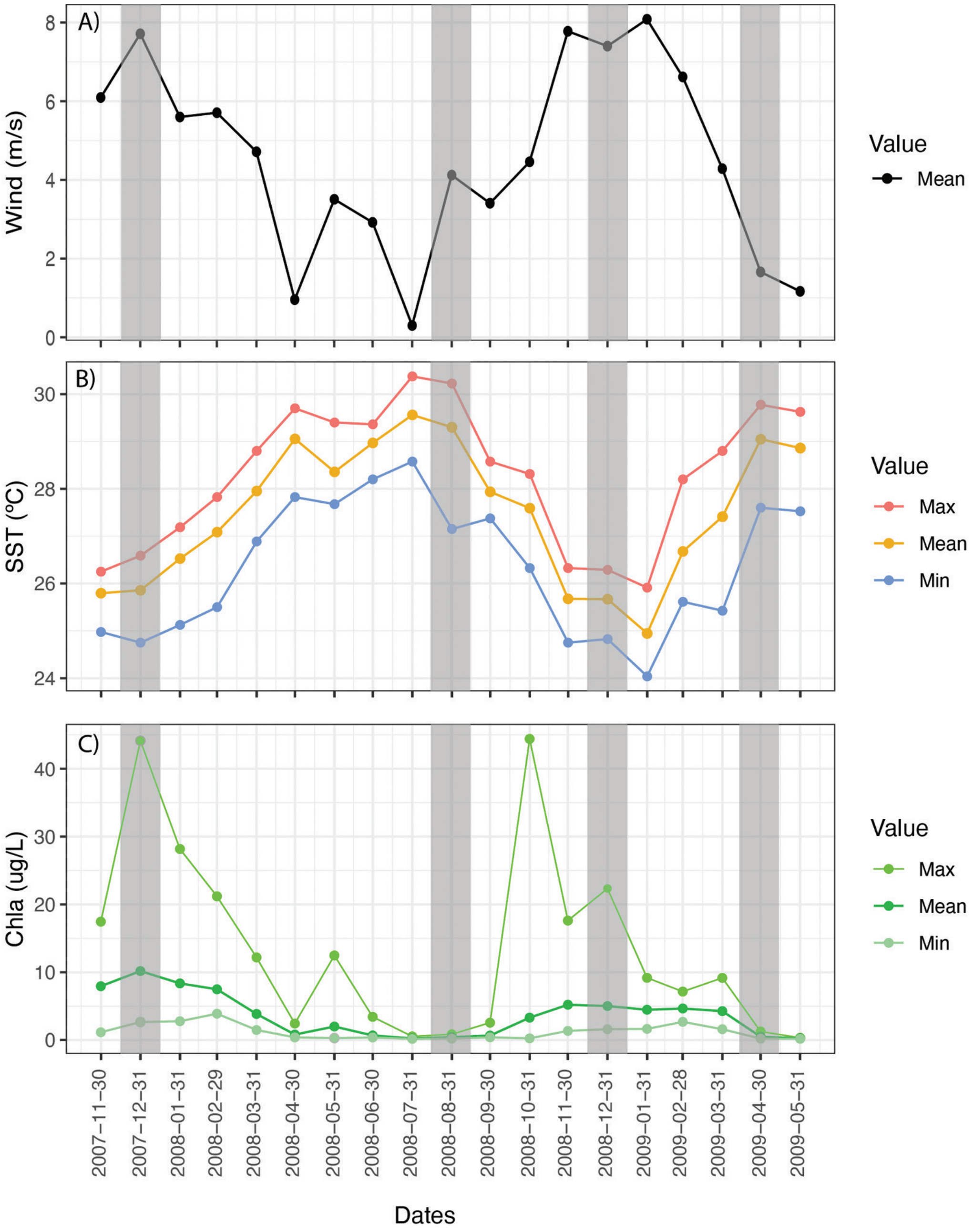

Fig. 2. A. Wind velocity, **B.** superficial seawater temperature, and **C.** Chlorophyll concentration from satellite data offshore of Bahía Salinas, Costa Rica. Data from NOAA Ocean Watch Voyager. The gray areas represent the benthic sampling events.

mid bay (χ^2=9.14, d.f.=2, P = 0.010). The number of taxa was higher and similar across the bay in April 2009 (upwelling season) (χ^2 = 2.87, d.f. = 2, P = 0.238) (Table 4).

Similar to the number of taxa, the values of the total abundance (Table 4) varied in their distribution within the bay (factor zone) across the sampling dates (χ^2 = 145.00, d.f. = 6,

Table 2
Taxa found during the benthic grab samples by dates in Bahía Salinas, Costa Rica.

Taxonomic group		Taxa	Feeding guilds	SU	NU	SU	U	Total
				Dec. 2007	Aug. 2008	Dec. 2008	Apr. 2009	
Polychaeta	Acrocirridae	Acrocirridae indet.	Ds	1		1		2
	Ampharetidae	*Amphicteis* sp.	Ds	7	2	1	9	19
		Melinna sp.	Ds	3			15	18
	Capitellidae	*Capitella* sp.	Dss				2	2
		Capitellidae indet.	Dss				1	1
		Dasybranchus lumbricoides	Dss			1		1
		Decamastus nudus	Dss	1			5	6
		Heteromastus filiformis	Dss				1	1
		Mediomastus ambiseta	Dss	2	1		3	6
		Mediomastus californiensis	Dss				4	4
		Nootmastus tenuis	Dss				2	2
		Notomastus lineatus	Dss			1	1	2
		Peresiella sp.	Dss				1	1
	Chaetopteridae	*Mesochaetopterus* sp.	Sfa				1	1
	Cirratulidae	Cirratulidae indet.	Ds	28	2	16	198	244
	Cossuridae	*Cossura brunnea*	Dss	1	1		3	5
	Dorvilleidae	*Dorvillea* sp.	Pm-Sca	1		1	5	7
	Eulepethidae	*Grubeulepis ecuadorensis*	Pm	1				1
	Glyceridae	*Glycera* sp.	Pm	3		5	4	12
	Goniadidae	*Glycinde armigera*	Pm	2		1	1	4
		Goniada sp. A	Pm	3			18	21
		Goniada sp. B	Pm	4				4
		Goniadidae indet.	Pm	3			1	4
	Hesionidae	*Gyptis* sp.	Pm	1		3	8	12
		Hesione panamena	Pm			2		2
		Hesionides arenarius	Pm	1				1
	Lumbrineridae	Lumbrineridae indet. A	Pm	2			2	4
		Lumbrineridae indet. B	Pm	13	4	3	24	44
	Magelonidae	*Magelona californica*	D-Pm	4		1	2	7
		Magelona pacifica	D-Pm	9		10	11	30
	Maldanidae	*Heteroclyne* cf. *glabra*	Dm			1		1
		Maldanidae indet.	Dm		1			1
		Maldanidae Indet. A	Dm			1		1
	Nepthyidae	*Aglaophamus* sp.	Pm	2				2
		Aglaophamus verrilli	Pm	4	12	10	4	30
		Nepthys panamanensis	Pm	26	4	7	12	49
	Nereididae	*Ceratonereis singularis* (Juvenile)	Om	1				1
		Gymnonereis crosslandi	Om	3	1		1	5
		Neanthes micromа	Om				1	1
		Nereis sp. (Juvenile)	Om				2	2
		Nereididae (Juvenile)	Om	2				2
		Nereid larvae	Om			1	1	2

Taxonomic group		Taxa	Feeding guilds	SU	NU	SU	U	Total
				Dec. 2007	Aug. 2008	Dec. 2008	Apr. 2009	
	Onuphidae	*Diopatra tridentata*	Om	3	1	1	13	18
		Kinbergonuphis microcephala	Om	7	3	4	17	31
	Ophelidae	*Armandia brevis*	Dss	8	1	1	25	35
	Orbiniidae	*Scoloplos armiger*	Dss	1	1		1	3
		Scoloplos sp.	Dss			3	2	5
	Owenidae	*Owenia fusiformis*	SFp-Ds	1				1
	Paraonidae	*Acesta* (*Acmira*) *lopezi*	Dm		1	1	2	4
		Aricidea (*Acmira*) *catherinae*	Dm	25	4	15	42	86
		Aricidea (*Aedicira*) sp. A	Dm	3		2	5	10
		Aricidea (*Aedicira*) sp. B	Dm			2	2	4
		Levensenia gracilis	Dm		1			1
	Phyllodocidae	*Eumida longicornuta*	Pm-Sca				1	1
		Phyllodoce madeirensis	Pm-Sca	2			7	9
		Phyllodoce sp.	Pm-Sca	1	1		11	13
		Phyllodocidae indet. A	Pm-Sca				1	1
		Phyllodocidae indet. B	Pm-Sca				1	1
	Pilargidae	*Loandalia riojai*	Pm	1		2	4	7
		Parandalia tricuspis	Pm	3		4		7
		Sigambra sp.	Pm				1	1
		Sigambra tentaculata	Pm				22	22
	Polynoidae	Polynoidae indet.	Pm	3			1	4
	Sabellariidae	*Idanthyrsus* sp.	SFp-Ds				1	1
	Sabellidae	Sabellidae indet.	SFp	28	4	6	103	141
	Sigalionidae	*Sthenelais fusca*	Pm		2	2	2	6
	Spionidae	*Apoprionospio pygmaea*	SFp-Ds	10		1	2	13
		Dipolydora socialis	SFp-Ds	1				1
		Paraprionospio pinnata	SFp-Ds	167	1	17	25	210
		Prionospio (*Minuspio*) *multibranchiata*	Ds	28		15	18	61
		Prionospio (*Prionospio*) *ehlersi*	Ds				1	1
		Prionospio delta	Ds				5	5
		Prionospio sp. A	Ds				3	3
		Scolelepis (*Scolelepis*) *squamata*	SFp	1			26	27
		Spiophanes duplex	SFp-Ds	19	1	4	3	27
		Spiophanes sp. A	SFp-Ds	1	1			2
	Syllidae	*Brania* sp.	Om	1				1
		Exogone breviantenata	Om	2			1	3
		Exogone dispar	Om	2	1		3	6
	Terebellidae	Terebellidae indet.	Ds	2		1		3
	Trichobranchidae	*Terebellides reishi*	Dss	2	1	2	3	8
Oligochaeta		Oligochaeta indet.	Dss			5		5
Sipuncula	Aspidosiphonidae	*Aspidosiphon* sp.	Dm		1	1	2	4
		Aspidosiphon sp. A	Dm			1	1	2
	Phascolosomatidae	*Apionsoma* sp.	Dm	5	28	14	20	67

Taxonomic group		Taxa	Feeding guilds	SU	NU	SU	U	Total
				Dec. 2007	Aug. 2008	Dec. 2008	Apr. 2009	
Mollusca / Class Gastropoda	Bullidae	Bullidae indet.	H				3	3
	Caecidae	Caecidae indet.	Pm	1				1
	Naticidae	*Natica* sp.	Pm	1		1		2
		Sinum noyesii	Pm		2			2
		Naticidae (Juvenile)	Om			1		1
		Bivalvia indet.	SFa	1			2	3
Mollusca / Class Bivalvia	Corbulidae	Corbullidae indet.	SFa				2	2
	Donacidae	Donacidae indet.	SFa		1		2	3
	Mytilidae	Mytilidae indet. (Juvenile)	SFa				1	1
	Nuculidae	*Nucula* (*Saccella*) *elenensis*	SFa				1	1
	Veneridae	*Pitar helenae*	SFa	1				1
		Veneridae indet. (Juvenile)	SFa			1	12	13
	Tellinidae	*Tellina* (*Eurytellina*) *eburnea eburnea*	SFa	3	1			4
		Tellinidae indet. (Juvenile)	SFa	4	1		30	35
Crustacea / Class Malacostraca / O. Decapoda /I.O. Brachyura	Raninidae	*Raninoides benedicti*	*Om*	4		2	1	7
	Pseudorhombilidae	*Malacoplax californiensis*	Pm	1	6	3		10
	Parthenopidae	*Mesorhoea bellii*	*Om*	1				1
	Pinnotheridae	Pinnotheridae indet.	*Om*				1	1
	Parthenopidae	*Upogebia jonesi*	*Om*		1			1
	Thalassinidea	Thalassinidea indet.	*Om*			3		3
Crustacea / Class Malacostraca / O. Decapoda / I.O. Caridea		Caridea indet. A	*Om*			1		1
		Caridea indet. B	*Om*			1		1
		Caridea indet. C	*Om*			1		1
		Caridea indet. D	*Om*			1		1
	Processidae	*Processa peruviana*	Om	2				2
	Pasiphaeidae	*Leptochela gracilis*	Om		1			1
	Penaeidae	Penaeidae indet.	Om			3		3
	Alpheidae	*Alpheus* sp.	*Pm*	2		1	1	4
		Automate dolichognatha	Pm			1		1
		Zoea larvae	Om		1			1
Crustacea / Class Malacostraca / O. Amphipoda		Amphipoda indet. A	Om	174	36	15	23	248
		Amphipoda indet. B	Om	1		2		3
		Amphipoda indet. C	Om	1		2	7	10
		Amphipoda indet. D	Om			1	1	2
		Amphipoda indet. E	Om			1	6	7
		Amphipoda indet. F	Om			1	10	11
		Amphipoda indet. G	Om			1	2	3

Taxonomic group		Taxa	Feeding guilds	SU	NU	SU	U	Total
				Dec. 2007	Aug. 2008	Dec. 2008	Apr. 2009	
		Amphipoda indet. H	Om			1	2	3
		Amphipoda indet. I	Om		1			1
		Amphipoda indet. J	Om				10	10
		Amphipoda indet. K	Om				1	1
		Amphipoda indet. L	Om				1	1
		Amphipoda indet. M	Om				11	11
		Caprellidae indet.	H			1	7	8
Crustacea / Class Malacostraca / O. Cumacea		Cumacea indet. A	Om	1		1	2	4
		Cumacea indet. B	Om	1				1
		Cumacea indet. C	Om			1		1
		Cumacea indet. D	Om			2	2	4
Crustacea / Class Malacostraca / O. Isopoda	Gnathiidae	*Gnathia* sp.	*Pm*	1				1
		Isopoda indet. A	Om			1		1
		Isopoda indet. B	Om				1	1
		Isopoda indet. C	Om				3	3
		Isopoda indet. D	Om	2				2
Crustacea / Class Malacostraca / O. Leptostraca	Nebaliidae	*Nebalia* sp.	*Pm*	1			1	2
Crustacea / Class Copepoda / O. Harpacticoida		Harpacticoida indet. A	Om			8	1	9
		Harpacticoida indet. B	Om	5		2		7
		Harpacticoida indet. C	Om				1	1
Crustacea / Class Ostracoda		Ostracoda indet. A	Om			2		2
		Ostracoda indet. B	Om			1		1
		Ostracoda indet. C	Om			1		1
		Ostracoda indet. D	Om			6		6
		Ostracoda indet. E	Om			1		1
		Ostracoda indet. F	Om				1	1
Nemertea		Nemertea indet.	Pm	6	1	6	19	32
Platyhelminthes / Class Rabditophora / O. Tricladida		Tricladida indet.	Pm				1	1
Brachiopoda / Class Inarticulata	Lingulidae	*Glottidia albida*	*Sfa*		1		2	3
Nematoda		Nematoda indet.	Om	13				13
Echinodermata / Class Asteroidea		Asteroidea indet.	Pm			3	1	4
Echinodermata / Class Holothuroidea		Holuthuroidea indet.	Dss		1			1
Echinodermata / Class Ophiuroidea	Ophiuroidea	Ophiuroidea indet.	Sfa	1			6	7

Taxonomic group		Taxa	Feeding guilds	SU Dec. 2007	NU Aug. 2008	SU Dec. 2008	U Apr. 2009	Total
Chordata / Subphyllum Cephalochordata / Class Leptocardii	Branchiostomatidae	*Branchiostoma californiense*	*SFa*			2		2
Chordata / Subphylum Vertebrata / Class Teleostei	Ophichthidae	Ophichthidae indet.	Pm		1			1

SU: Start upwelling season, NU: non–upwelling season, and U: upwelling season. Feeding guilds, D: Deposit feeder, s: surface, ss: subsurface, m: mixed; SF: Suspension feeder, a: active, p: passive; Pm: Predator mobile; Sca: Scavenger; Om: Omnivore, H: Herbivore.

Table 3

Percentage of taxa and total abundance of each faunal group by dates. Bahía Salinas, Costa Rica.

Taxa	%			
	Dec–07	Aug–08	Dec–08	Apr–09
Annelida	69	65	53	64
Crustacea	19	15	39	23
Mollusca	8	10	4	8
Others	4	10	4	5
Abundance	Dec–07	Aug–08	Dec–08	Apr–09
Annelida	67	60	67	80
Crustacea	29	34	27	11
Mollusca	2	4	1	6
Others	3	3	4	3

The total number of taxa and individuals was lower during the non-upwelling season, at the start of the upwelling season, these values increased. By the end of the upwelling season, both values were even higher (taxa: $\chi^2 = 29.24$, d.f. = 3, $P < 0.001$; individuals: $\chi^2 = 678.75$, d.f. = 3, $P < 0.001$, Table 4).

$P < 0.001$). Post-hoc comparisons revealed that the middle of the bay showed the lowest abundance in December 2007 ($\chi^2 = 254.46$, d.f. = 2, $P < 0.001$), while higher abundance was observed in the mid bay during August and December 2008 ($P < 0.001$, d.f. = 2, with $\chi^2 = 17.71$ and $\chi^2 = 33.17$, respectively). Finally, the abundance values were high at mid and outer bay areas during April 2009 ($\chi^2 = 91.25$, d.f. = 2, $P < 0.001$) (Table 4).

A temporal effect was found for the Shannon-Wiener diversity index (Friedman test, $\chi^2 = 8.20$, d.f. = 3, $P = 0.042$), with the highest value during upwelling season (April 2009) and the lowest value during non-upwelling season (Table 4). This pattern was concordant in high degree across the zones of the bay (Kendall's concordance: Wt = 0.91). However, a non-temporal trend was found for the equitability (Friedman, $\chi^2 = 1.8$, d.f. = 3, $P = 0.615$) by the low concordance of values between the zones of the bay (Kendall's concordance: Wt = 0.20) (Table 4). The trend consisted in a decrease of equitability from inner to outside bay (Table 4).

The NMDS (Fig. 3) showed that the biological assemblage composition of samples collected in August was more similar to each other than to samples collected during other periods at the same location. In contrast, high variation was found in the samples collected in April 2009. Dimension 1 of the NMDS revealed the pattern of change in the community from non-upwelling to upwelling season, where the assemblages presented a mid-degree of discrimination between sampling dates (ANOSIM, R = 0.46, P = 0.0004). No difference in the assemblages was found between the start of upwelling season (December) and non-upwelling season

Table 4
Biodiversity parameters by date and zone of the bay of the benthic macrofauna of Bahía Salinas, Costa Rica.

Species					
Zone	December 2007	August 2008	December 2008	April 2009	Total number of species
Inner bay	36	16	29	**49**	88
Middle bay	26	19	52	**67**	**103**
Outer bay	53	15	30	**56**	96
Total number of species	75	40	76	**101**	157
Abundance					
Zone	December 2007	August 2008	December 2008	April 2009	Total abundance
Inner bay	137	26	52	**166**	381
Middle bay	122	66	125	**348**	661
Outer bay	**424**	44	75	384	**927**
Total abundance	683	136	252	**898**	1969
Shannon-Wiener					
Zone	December 2007	August 2008	December 2008	April 2009	Mean Diversity
Inner bay	2.04	1.75	2.19	**2.92**	2.20
Middle bay	2.03	1.88	3.16	**3.01**	**2.46**
Outer bay	2.08	1.77	2.53	**2.77**	2.33
Mean Diversity	2.05	1.81	2.63	**2.90**	2.33
Equitability					
Zone	December 2007	August 2008	December 2008	April 2009	Mean equitability
Inner bay	**0.87**	0.84	0.83	**0.87**	**0.86**
Middle bay	0.84	0.73	**0.91**	0.80	0.82
Outer bay	0.62	0.66	**0.91**	0.76	0.73
Mean equitability	0.78	0.76	**0.89**	0.81	0.81

The highest values are in bold font and the lowest values are underlined.

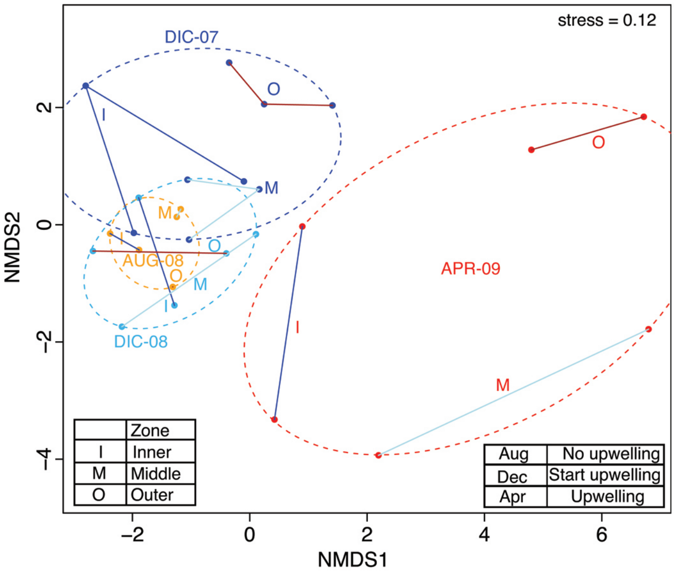

Fig. 3. MDS to show the similarity between sampling dates and zones of the bay based on their benthic macrofauna. Bahía Salinas, Costa Rica. The ellipses are the convex hull that contains all the samples in the group.

(August) (ANOSIM, P > 0.05), but there was degree of discrimination of 0.50–0.59 between the assemblage in the start of upwelling season (December) with the assemblage at the end of the upwelling season (April). Similar situation occurs between assemblages in the non-upwelling and upwelling seasons with a degree of discrimination 0.48 (ANOSIM, P ≤ 0.01).

The taxa that changed the most between sampling dates corresponded to two polychaetes: Cirratulidae indet. that had a peak at the upwelling season (April 2009) and the spionid, *Paraprionospio pinnata* with a peak in December 2007 (Table 5). Both taxa presented their lowest density in August 2008 (non-upwelling season) (Table 5). Additionally, the amphipod indet. A presented low-density values in December 2008, and the polychaete, *Aglaophamus verrilli,* was more abundant during the non-upwelling season (Table 5).

The taxa that mainly contributed to the spatial change in composition of the assemblages between the zones of the bay are presented in Table 6. In December 2007, the amphipod indet. A and three polychaete taxa had high-density values outside of the bay. Additionally, the spionid *Prionospio* (*Minuspio*) *multibranchiata* had a peak of abundance at mid bay, and *P. pinnata* also had high abundance at the inner section (Table 6). In August 2008, a sipunculan worm and the onuphid polychaete *Kinbergonuphis microcephala* presented highest densities at the outside bay. An amphipod and a sabellid polychaete had their highest abundance at mid bay, and the decapod crustacean *Malacoplax californiensis* showed high densities at the inner bay (Table 6). Samples from December 2007 and December 2008 recovered the same taxa but presented higher densities in different zones of the bay (Table 6). For example, the polychete *Aricidea* (*A.*) *catherinae* and the aforementioned amphipod changed the dominance from outside to mid bay (Table 6).

Finally, in April 2009 the five taxa that contributed the most to the change in the bay were completely different from previous sampling dates, and the polychaetes presented higher densities outside of the bay (Table 6).

Table 5

Results of the SIMPER analysis, and individuals per m^2 per sampling date in Bahía Salinas, Costa Rica.

Taxa	Feeding guild	Overall average dissimilarity	Contribution %	Cumulative Contribution %	Dec. 2007	Aug. 2008	Dec. 2008	Apr. 2009
		51.37						
Cirratulidae indet.	Ds	4.188	8.153	8.153	83	14	73	1062
Paraprinospio pinnata	SFp-Ds	3.445	6.707	14.86	402	6	62	147
Amphipoda indet. A	Om	2.851	5.55	20.41	290	134	72	117
Sabellidae indet.	SFp	2.815	5.48	25.89	73	22	30	280
Aricidea (*Acmira*) *catherinae*	Dm	1.885	3.67	29.56	71	28	44	235
Apionsoma sp.	Dm	1.596	3.106	32.67	20	76	71	87
Prionospio (*Minuspio*) *multibranchiata*	SFp-Ds	1.572	3.06	35.73	71	0	58	100
Tellinidae indet. (Juvenile)	SFa	1.502	2.925	38.65	8	6	0	194
Scolelepis (*Scolelepis*) *squamata*	SFp	1.117	2.175	40.83	3	0	0	91
Nepthys panamanensis	Pm	1.068	2.078	42.9	93	22	24	74
Lumbrineridae indet. B	Pm	1.061	2.065	44.97	38	32	18	106
Sigambra tentaculata	Pm	1.06	2.064	47.03	0	0	0	95
Armandia brevis	Dss	1.045	2.034	49.07	29	6	5	61
Kinbergonuphis microcephala	Om	1.037	2.018	51.09	20	14	18	83

The composition of the benthic fauna showed a marked change from inner to outside of the bay (ANOSIM, R= 0.60, P = 0.0001). In the NMDS (Fig. 3) this trend was observed within each sampling date, most notably in April 2009 (average dissimilarity: ad = 69.75, Table 5), followed by December 2007 (ad = 38.85, Table 5) and 2008 (ad = 35.04, Table 6), with the lowest differentiation observed in August 2008 (ad = 21.34, Table 6; Fig. 3).

Table 6

Results of the SIMPER analysis, and individuals per m^2 by zone of the bay. Bahía Salinas, Costa Rica.

Dec 2007	Average dissimilarity 38.85	%	Cumulative %	Inner	Middle	Outer
Amphipoda indet. A	5.26	13.54	13.54	40	290	1307
Paraprinospio pinnata	3.90	10.03	23.56	229	184	1362
Aricidea (*Acmira*) *catherinae*	2.12	5.46	29.02	11	35	300
Sabellidae indet.	1.84	4.73	33.75	35	53	165
Prionospio (*Minuspio*) *multibranchiata*	1.82	4.67	38.42	70	151	25
Aug 2008	Average dissimilarity 21.34	%	Cumulative %	Inner	Middle	Outer
Apiosoma sp.	4.48	21.00	21	0	63	1084
Amphipoda indet. A	4.44	20.81	41.81	18	690	43
Malacoplax californiensis	1.42	6.65	48.46	71	0	0
Kinbergonuphis microcephala	0.96	4.50	52.97	0	0	130
Sabellidae indet.	0.90	4.22	57.19	0	79	0
Dec 2008	Average dissimilarity 35.04	%	Cumulative %	Inner	Middle	Outer
Aricidea (*Acmira*) *catherinae*	2.99	8.52	8.523	0	307	0
Prionospio (*Minuspio*) *multibranchiata*	2.20	6.27	14.79	0	43	229
Paraprinospio pinnata	1.91	5.44	20.23	93	71	32
Amphipoda indet. A	1.47	4.21	24.44	18	246	43
Cirratulidae indet.	1.35	3.85	28.29	63	79	79
Apr 2009	Average dissimilarity 69.75	%	Cumulative %	Inner	Middle	Outer
Sabellidae indet.	5.88	8.43	8.429	63	141	1690
Goniada sp. A	3.31	4.74	13.17	0	0	332
Armandia brevis	3.22	4.62	17.79	0	32	307
Scolelepis (*Scolelepis*) *squamata*	2.42	3.48	21.27	18	141	169
Sigambra tentaculata	2.29	3.29	24.55	32	43	363

Additionally, sabellid worms were the dominant group outside of the bay in that month (Table 6).

The ANOSIM test indicated the change of the feeding guilds composition by sampling dates (R = 0.47, P = 0.001) and zones of the bay (R = 0.34, P = 0.007). The SIMPER test by sampling date indicated that surface deposit feeders, passive suspension feeders, omnivores, and active suspension feeders were the main feeding guilds to explain the changes in the assemblages between sampling dates (Table 7). These groups presented low densities and taxa values during the non-upwelling season, the number of taxa increased at the start of the upwelling season, and the groups reached higher densities during the upwelling season. Among the groups that reached higher densities during the upwelling season, the highest corresponded mainly to the surface deposit feeders and the active suspension feeders. This pattern was present in the rest of the feeding guilds (Table 7). Finally, the assemblage was dominated by omnivores, mobile predators, and deposit feeders with mixed strategies during the non-upwelling season, but their densities were lower than during the upwelling season.

The variation of the assemblages between zones of the bay was marked by the surface deposit feeders, passive suspension feeders, omnivores, and mobile predators (Table 7). The general trend was that the density increased from inner to outside bay in the feeding guilds with contribution higher than 8 %. In

Table 7

Number of taxa (S) and density (D): ind/m^2, and % of the community by feeding guilds of the Bahía Salinas.

Feeding guild	SIMPER			Species				Density (ind/m^2)			
	Av. Dissim. 19.98	Contrib. %	Cumulative %	Dec 2007	Aug 2008	Dec 2008	Apr 2009	Dec 2007	Aug 2008	Dec 2008	Apr 2009
Ds	4.1	20.5	20.5	8	2	5	6	213	22	169	1404
SFp	3.1	15.6	36.1	7	2	3	5	82	22	30	355
Om	2.0	10.2	46.3	8	5	6	6	539	277	332	800
SFa	1.8	9.2	55.6	6	4	6	6	42	32	68	468
Dm	1.8	9.0	64.6	8	4	5	6	122	196	196	463
Pm	1.7	8.6	73.2	9	5	6	6	705	175	495	967
Dss	1.6	8.0	81.2	6	4	5	5	55	53	54	267
SFp-Ds	1.2	6.1	87.3	6	2	4	3	71	14	61	28
D-Pm	1.1	5.4	92.6	6	4	3	5	59	32	22	112
Pm-Sca	1.0	4.8	97.5	2	1	1	5	7	6	5	108
H	0.5	2.6	100.0	0	0	1	4	0	0	5	53

Feeding guild	SIMPER			Species				Density (ind/m^2)			
	Av. Dissim. 40.16	Contrib. %	Cumulative %	Inner	Middle	Outer	Total of species	Inner	Middle	Outer	Mean density
Ds	3.6	18.8	18.8	6	7	8	9	112	252	474	279
SFp	3.1	16.1	34.9	4	7	6	2	24	100	187	104
Om	2.2	11.7	46.6	8	9	8	56	238	690	620	516
Pm	1.8	9.2	55.8	9	9	8	32	367	474	967	603
Dm	1.7	9.1	64.9	7	8	8	11	129	206	340	225
Dss	1.6	8.2	73.2	5	7	8	17	41	80	167	96
SFa	1.5	7.8	81.0	8	7	7	13	99	65	114	93
SFp-Ds	1.2	6.5	87.5	2	7	6	7	23	62	55	47
D-Pm	1.1	5.8	93.3	4	8	6	2	20	78	74	57
Pm-Sca	0.8	4.3	97.7	2	4	3	6	10	24	32	22
H	0.4	2.3	100.0	1	3	1	2	3	22	6	10

Av. Dissim. = Avarage dissimilarity. Feeding guilds, D: Deposit feeder, s: surface, ss: subsurface, m: mixed; SF: Suspension feeder, a: active, p: passive; Pm: Predator mobile; Sca: Scavenger; Om: Omnivore, H: Herbivore.

the rest, the trend was a peak of density at mid bay (Table 7). The number of taxa by feeding guild was less variable between zones of the bay (Table 7).

DISCUSSION

In the present study, the macrofauna had a low diversity and abundance in the non-upwelling season, which increased to a peak with the development of the upwelling season. Lee (1978) also found a change in the subtidal benthos of Panama Bay, concordant with the upwelling seasonality. The opportunist taxa such as spionids and cirratulids polychaetes of the benthos of Bahía Salinas can better utilize the input of food from the high plankton production during the upwelling months, as pointed out by Alongi (1989b) and Alongi (1990) in other localities. In the present study, there was a degree of discrimination (R) of 0.36 in the composition of taxa between December 2007 and December 2008, but the degree of discrimination had lower magnitude (R = 0.17) in the feeding guilds composition between these years.

During the start of the upwelling season (December 2007 and 2008), taxa such as

Cirratulidae, *Paraprinospio pinnata*, Sabellidae, and Amphipoda presented considerable populations in the benthos. At the end of the upwelling season (April 2009), the high abundance of Cirratulidae, Sabellidae, *Aricidea,* and Tellinidae. This trend highlights the impact of seasonal nutrient influx in both the water and the sediment surface, similar to what occurs during the seasonal upwelling in Las Perlas, Panama Bay, which features comparable assemblage components (Mair et al., 2009). In the case of *Kinbergonuphis* possiby utilizing the abundance of phyto and zooplankton preys during this period (Checon et al., 2017; Jumars et al., 2015). In contrast, the non-upwelling season (August 2008) showed a decline in these groups, with a shift towards certain taxa such as Amphipoda, *Apionsoma*, *Prionospio*, *Aricidea* and Lumbrineridae that persisted, forming a resilient core that adapts to food availability in the sediment, ensuring the continuity of the assemblage even in less favorable conditions as in other tropical soft bottom assemblages (Tavakoly-Sany et al., 2018). Pacheco et al. (2010) suggested that diverse pathways in the succession process can produce different end points of the communities in subtidal benthos within the same locality. In the present study, year to year, the decline of certain populations during the non-upwelling season results in variable group of survival taxa. This condition allows other taxa to dominate or to be recruited to fill the empty niches resulted in a major taxonomic dissimilarity than the feeding guild dissimilarity.

During the upwelling season, the community was composed mainly of surface deposit feeders (Cirratulidae and Paraonidae worms) and active suspension feeders (tellinid and venerid clams), both in high densities, but both groups decreased during the non-upwelling season. Guzmán-Alvis et al. (2006) indicated that in Bahía Portete in the Colombian Caribbean deposit feeders dominated the fauna during the upwelling season because of the increase in available food on the seabed. This is the case of a Cirratulidae indet. and *Aricidea* (*Acmira*) *catherinae* (surface or mixed deposit feeders), which were within the main contributors to the total abundance during upwelling season, but had low abundance during the non-upwelling season. Similarly, surface deposit feeders accounted for less than a third of the number of polychaete taxa during the non-upwelling season in the Gulf of Panama (Mair et al., 2009). Another opportunist group that decreased drastically during the non-upwelling season were the passive suspension feeders, for example the tube worms (Sabellidae). Lee (1978) also indicated a rapid decrease in benthic biomass of opportunist taxa when primary production dropped during the reduction of the winds, following the upwelling season in Panama Bay. Similar to the present study, Quintana et al., (2015) found that high abundance of macrofauna is the result of the increase in wind velocity and phytoflagellate blooms in a coastal upwelling system in SE Brazil. It is possible that the macrofauna responds positively to the organic matter from the phytoplankton blooms that occur during the upwelling events in this region of Costa Rica (Morales-Ramírez et al., 2016).

Deposit feeders with a mixed strategy (surface and subsurface) such as sipunculans, mobile omnivores (mainly amphipods), and predators (the polychaete *Aglaophamus verrilli* and the crustancean *Malacoplax californiensis*) were the remaining fauna during the non-upwelling season. Within the deposit feeders, a few taxa of Ampharetidae, Cirratulidae, Cossuridae, Maldanidae, Spionidae, Paraonidae and Capitellidae persisted in low numbers during the non-upwelling season, because these taxa were able to compete during the period of low food supply. One example was the opportunist capitellid *Mediomastus ambiseta*, which was found in the non-upwelling season, whilst other capitellids were not recorded. In contrast, other capitellids have not been recorded during this season because these are opportunist taxa (Fauchald & Jumars, 1979), but this pattern could be due to numerous factors, such as nutrient availability, water temperature changes, and variations in granulometry, or biological interactions whether these factors are directly related to upwelling phenomena or not (Alongi, 1990). Graf (1982) pointed out that some infaunal organisms bury for food into the sediment, thus avoiding competition with surface deposit feeders. That food could be used later during a period of scarcity. Additionally, populations that persist through the year (i.e. spionid worms and tellinid bivalves) would have the capacity to use different food sources by switching between surface detritus or suspension feeding when necessary (Cosentino, & Giacobbe, 2008). This could explain in part the coexistence of some subsurface deposit and filter feeders after the upwelling events in the present study.

Finally, the number of taxa varied among zones of the bay in December, but the number of taxa was similar across the bay during August (non-upwelling season) and April (upwelling season). The abundance was low in August and higher during April. The harsh benthic conditions in Bahía Salinas at the beginning of the upwelling season (December), including lower bottom water temperature and lower concentration of dissolved oxygen are similar to those in the Culebra Bay, Gulf of Papagayo (Rixen et al., 2012). These conditions could explain the pattern of spatial variation, as found in other benthic systems (Alongi, 1990; Gray & Elliot, 2009; Mair et al., 2009). Additionally, dry and rainy seasons can influence tropical benthic systems abundance and distribution as in Golfo de Nicoya, Costa Rica (Maurer & Vargas, 1984; Maurer et al., 1988). The abundance and diversity index values were more spatially variable, but results show low equitability in the outside bay. This is the result of several taxa that changed their distribution within the bay through the study period due to differences in the environmental conditions. For example, changes in the dynamic distribution of sediments (data not available), food availability (low during the non-upwelling season, based on chlorophyll concentration), and depth promote the settling, growth, or prevalence of the different benthic populations (Little, 2000). In this way the spatial variability of the assemblages was higher during the upwelling season, and the populations from the outside bay reached maximum density values. Moreover, the spatial pattern of the feeding guilds within the bay was more stable that the taxonomic composition of the assemblage, with an increase of the main feeding guilds from inner to outside bay.

During the upwelling season, the abundance and diversity of benthic communities increased in comparison with the non-upwelling season. The variation in the composition of assemblages and diversity occurs in all the zones of this bay, although the outside bay presents lower values of equitability. During the upwelling season, the community was composed mainly of surface deposit feeders and active suspension feeders. These groups possibly utilize the organic matter that sinks to the bottom, produced by planktonic organisms. At the non-upwelling season, the community was dominated by deposit feeders with a mixed strategy (surface and subsurface), mobile omnivores, and predators.

During the upwelling season in Bahía Salinas, species richness and abundance of benthic fauna peak, likely due to high plankton productivity. In contrast, the non-upwelling season shows a decline in these parameters, shifting from surface deposit and suspension feeders to mixed strategies and omnivore feeders. These findings highlight the dynamic nature of benthic communities, adapting their traits to environmental variations in tropical seasonal upwelling areas.

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