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ANÁLISIS ESPACIO-TEMPORAL DE LA FAUNA BENTÓNICA DEL MANGLAR DE TÉRRABA-SIERPE, COSTA PACÍFICA DE COSTA RICA

Tesis sometida a la consideración de la
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A la memoria de Socorro Sánchez Quesada

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RESUMEN

Los estuarios son ecosistemas altamente dinámicos que ocurren entre los ecosistemas marinos y continentales, con una diversidad distintiva y alta productividad. No obstante de la gran variedad de servicios que los estuarios proveen al ser humano, son uno de los ecosistemas más amenazados a nivel mundial. Los sedimentos marinos son uno de los ambientes más extensos, y en ellos se encuentra una de las comunidades biológicas más diversas y antiguas, la cual se ha utilizado ampliamente para identificar los factores que modulan los patrones de la biota marina. A pesar de los avances en el área de la ecología estuarina, todavía existen vacíos de conocimiento en cuanto a la diversidad, interacciones con las variables ambientales y ecología funcional de estuarios tropicales, principalmente en el Pacífico Tropical Oriental, donde pocos estuarios han sido estudiados. Los objetivos de esta tesis fueron analizar la variación espacio-temporal de los sedimentos (Capítulo 1), la diversidad (Capítulo 2), composición del ensamble (Capítulo 3) y la diversidad funcional (Capítulo 4) de la macrofuna en dos estuarios de Térraba-Sierpe, Pacífico Sur de Costa Rica. Los sedimentos estuvieron dominados por arenas medias (133.22 µm), con un contenido medio de materia orgánica (5.2%) y carbonatos (5.7%). Desde la parte interna hacia la parte externa del estuario, la hetereogenidad de los sedimentos aumentó mientras que la materia orgánica disminuyó. Se recolectaron 3391 individuos, pertenecientes a 146 taxones, con una densidad promedio de 934 $\mathrm{ind \cdot m^{-2}}$ (mínimo 0, máximo 9436 $\mathrm{ind \cdot m^{-2}}$). Esta tesis reporta 20 nuevas especies para las costas continentales del Pacífico de Costa Rica. La riqueza de especies fue mayor hacia la zona externa del estuario y durante la época seca, mientras que la densidad fue influenciada solo por la zonación estuarina, pero únicamente en uno de los estuarios estudiados. La composición de macrofauna fue distinta entre la estación interna y la estación externa de ambos estuarios, sin embargo solamente en uno se observó una separación entre las épocas. La salinidad, la materia orgánica y la contribución de gravas fue la combinación de variables ambientales que mejor explica la composición de especies observada en la macrofauna de Térraba-Sierpe. Las 146 especies encontradas se clasificaron en 48 entidades funcionales, siendo los depositívoros superficiales/sub-superficiales reptadores de vida libre epi/infaunales los que contribuyeron con mayor biomasa. Las entidades funcionales con mayor contribución presentaron características generalistas. La riqueza funcional de la macrofauna fue mayor durante la época seca que durante la época lluviosa. La originalidad funcional de la macrofauna fue baja, lo que significa que las especies principales comparten características funcionales con otras, pero un 60% de las entidades funcionales estaban representadas por una o dos especies, aumentando la vulnerabilidad de perder funciones en el sistema. Los resultados de este estudio demuestran que los estuarios tropicales pueden comportarse de manera muy distinta en cuanto a sus sedimentos y su macrofauna, aún dentro de una misma región.

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INTRODUCCIÓN

Los manglares son bosques tropicales estuarinos caracterizados por la presencia de plantas leñosas que proliferan en la interface entre la tierra y el mar (Hogarth 1999). Estos ecosistemas se distribuyen de forma circumtropical, sin embargo, también se pueden situar en zonas subtropicales que mantengan una isoterma de 20°C durante el invierno, debido a la influencia de las grandes corrientes marinas (Spalding *et al.* 1997, Alongi 2002). Los manglares ocurren únicamente bajo condiciones físicas, químicas y geomorfológicas restringidas (Woodroffe 1992, Hogarth 1999). Estos bosques soportan inundaciones periódicas de las mareas, cambios de salinidad, altas temperaturas y fuertes vientos (Duke 1992, Kathiresan & Bingham 2001, Giri *et al.* 2011). Se desarrollan en fondos sedimentarios, generalmente en substratos lodosos y anóxicos, pero también se pueden encontrar en fondos arenosos (Woodroffe 1992).

Los manglares son ambientes dinámicos que están en constante cambio, incluso a escalas de tiempo cortas (Woodroffe 1992). Factores como las corrientes marinas, el oleaje, los ciclos de mareas, precipitación pluvial, sedimentación y la interacción de estos factores, convierten a los manglares en ecosistemas complejos de estudio, con múltiples clinas ambientales que pueden cambiar constantemente (Hogarth 1999). Además, el ciclo de nutrientes y el flujo de energía involucran gran cantidad de organismos por lo que las redes tróficas de los manglares son muy complejas (Hsieh *et al.* 2002).

Los manglares son ecosistemas que proveen varios servicios ambientales a las poblaciones humanas aledañas: fuente de alimento para la extracción de recursos pesqueros, fabricación de bebidas, endulzantes y saborizantes, elaboración de tintes, textiles, aceites, medicamentos y papel, extracción de madera como materia prima o producción de carbón, también facilitan el transporte entre asentamientos cercanos, y brindan protección contra oleajes y mareas (Ewel *et al.* 1998, Hogarth 1999, Nielsen & Quesada 2006, Zhang *et al.* 2012). Además, se ha demostrado que los manglares son sumideros importantes de carbono, donde el *carbono* es fijado principalmente bajo el agua, en las raíces y en la materia orgánica sepultada por el sedimento (Twilley *et al.* 1992, Cifuentes 2012).

Debido a sus características ambientales, los manglares presentan una gran biodiversidad y biomasa (Alongi 2002, Ellison 2008), con productividades primaria y secundaria altas (Ellison 2008). Además, sirven como sitios de crianza y reproducción para elasmobranquios, peces óseos, moluscos, crustáceos, poliquetos y otros invertebrados (Rönnbäck 1999, Nagelkerken *et al.* 2001, 2008), muchos de los cuales son de importancia comercial (Campos *et al.* 1990, Rönnbäck 1999, Nagelkerken *et al.* 2000; Quesada-Alpízar & Cortés 2006). Esta fauna habita principalmente en las raíces del mangle, así como en sus sedimentos intermareales y canales submareales (Alongi & Sasekumar 1992). Los hábitats submareales estuarinos tropicales pueden presentar una abundancia y diversidad de organismos bentónicos relativamente altas (Alongi & Sasekumar 1992). En ese sentido, se ha observado que las abundancias de epifauna y fauna que habita sobre o dentro de las raíces del mangle exceden a la de la infauna (Alongi 2002).

La comunidad bentónica está compuesta por organismos de filos distintos (Little 2010), con una gran variedad de formas de alimentación (e.g. carnívoros, herbívoros, detritívoros y suspensívoros). Además, son alimento para muchos organismos (Alongi & Sasekumar 1992). Por lo tanto, los organismos bentónicos cumplen un papel importante en el reciclaje de nutrientes y mantenimiento de la calidad del agua (Harris 1999, Peterson & Heck 1999). Una mejor comprensión de la fauna bentónica podría ayudar a entender los procesos ecológicos de las comunidades bentónicas de estuarios tropicales (Alongi 1990, Chainho *et al.* 2006). Los organismos bentónicos han sido utilizados para determinar la riqueza de especies y calidad del agua en ambientes estuarinos y de manglar (Chainho *et al.* 2006, Shokri *et al.* 2009). Sin embargo, existen vacíos importantes de información acerca de los patrones de diversidad, distribución e interacciones ecológicas de las especies bentónicas que utilizan estos sistemas estuarinos (Maurer & Vargas 1984, Alongi 1989, Alongi & Sasekumar 1992, Ramírez & Pringle 1998, Shokri *et al.* 2009).

La estrecha relación entre la fauna bentónica y la composición del sedimento que habita es bien conocida (Gray 1974, Butman & Grassle 1992, Sundberg & Kennedy 1993, Seiderer & Newell 1999). Las características del sedimento (como granulometría, materia orgánica y carbonatos) pueden determinar la composición de la fauna (Sanders 1968, Maurer *et al.* 1984, Alongi 1990, Currie & Small 2006, Sibaja-Cordero 2012). Sin embargo, los organismos que habitan los fondos sedimentarios pueden también alterar las características de este (Rowe 1974). Se han reportado múltiples factores abióticos que afectan la distribución de la fauna bentónica, incluyendo profundidad, salinidad e hidrología (Gray 1981, Pearson & Rosenberg 1987, Gaston & Nasci 1988). Los sistemas estuarinos tienden a contar con sedimentos lodosos más en los bosques de manglar, y sedimentos arenosos en el fondo de los canales, por la suspensión y depositación que produce el cambio de marea. Estos patrones de distribución de sedimento, pueden crear cambios en la composición de fauna encontrada (Gray & Elliott 2009). Por otro lado, factores bióticos como la depredación (Peterson 1979), la competencia (Peterson & Andre 1980) y el reclutamiento (Butman 1987), también pueden afectar la distribución de la fauna bentónica.

El bentos en estuarios tropicales ha sido poco estudiado (Alongi 1990, Dittmann & Vargas 2001). Se han reportado riquezas de especies bajas a moderadamente altas en comparación con otros fondos sedimentarios (e.g. zonas intermareales y plataforma continental), mostrando dominancia de especies pequeñas y oportunistas (Alongi 1989). Además, las densidades de organismos se encuentran en los rangos más bajos en comparación con estuarios de zonas templadas (Alongi 1990). Estas bajas estimaciones se han relacionado con altas tasas de depredación, estrés por la baja salinidad debido a la influencia del agua dulce, erosión, alta sedimentación, turbidez, bajos niveles de oxígeno disuelto, poca producción de plancton, altas temperaturas y altas concentraciones de ácidos sulfúricos y polifenólicos (Alongi 1989, 1990). La fauna submareal que habita sistemas estuarinos, responde negativamente a la influencia de agua dulce durante eventos lluviosos, sin embargo, estas zonas son recolonizadas rápidamente por organismos pequeños, principalmente depositívoros superficiales y suspensívoros, como poliquetos y bivalvos (Alongi 1989, Currie & Small 2006).

En Centroamérica se han realizado pocos estudios sobre la fauna bentónica en sistemas estuarinos. En la zona intermareal del estero de Jaltepeque en El Salvador (Molina-Lara & Vargas-Zamora 1994, 1995) los poliquetos fueron los organismos más abundantes y diversos. Para la zona intermareal del Golfo de Nicoya (con manglar en su zona interna) en Costa Rica (Vargas 1987), la diversidad y densidad de fauna bentónica, resultó baja en comparación con la reportada en zonas templadas.

La composición de la macrofauna bentónica submareal en fondos sedimentarios de sistemas estuarinos ha sido aún menos estudiada en el Pacífico Oriental Tropical y Centro América. Maurer & Vargas (1984) encontraron un descenso de la diversidad relacionado a la influencia de agua dulce en el Golfo de Nicoya, Costa Rica. Por otro lado, Nicholds-Driscoll (1976) y León-Morales & Vargas (1998) estudiaron la fauna bentónica de Golfo Dulce (Pacífico de Costa Rica) y concluyeron que la diversidad decrece en función de la profundidad, debido a que este sistema, presenta condiciones anóxicas hacia la parte profunda (Hebbeln *et al.* 1996), al ser un fiordo tropical de origen tectónico (Quesada-Alpízar & Cortés 2006).

Otro sistema estuarino, importante por ser el manglar más extenso en Costa Rica, pero que no ha sido estudiado en cuanto a su fauna bentónica, es el Humedal Nacional Térraba-Sierpe (HNTS) declarado sitio RAMSAR de interés mundial en 1995 (RAMSAR 2011). Este sistema estuarino presenta una estructura y riqueza de taxones relativamente alta en relación a ecosistemas similares en Latinoamérica y África (Echeverría-Sáenz *et al.* 2003, Nielsen & Quesada 2006). Se encontró una alta riqueza de taxones de crustáceos decápodos (52 species), alcanzando valores comparables con arrecifes de coral (Echeverría-Sáenz *et al.* 2003). Presenta poblaciones abundantes de bivalvos del género *Anadara*, donde su extracción ha sido una de las principales actividades económicas de la zona

(Nielsen & Quesada 2006). Además, estudios recientes han demostrado que este manglar es el sumidero de carbono más importante en la región Centroamericana (Cifuentes 2012). Sin embargo, no existe información para otros grupos de invertebrados como crustáceos no decápodos, poliquetos y moluscos (Quesada-Alpízar & Cortés 2006).

Actualmente, la cuenca del río Grande de Térraba, uno de los principales afluentes del HNTS, se está considerando para construir un proyecto hidroeléctrico (Una mirada al Proyecto Hidroeléctrico El Diquís ICE 2013, accedido desde http://www.pheldiquis.cr/). Los proyectos hidroeléctricos pueden alterar las variaciones naturales en el cauce de los ríos al disminuir las diferencias entre los caudales de la época de alta precipitación y poca precipitacion (Poff *et al.* 1997), cambiando de esta forma la influencia de agua dulce que llega al estuario. Uno de los casos más estudiados es el delta del río Colorado (Golfo de California), donde los múltiples proyectos hidroeléctricos han provocado una disminución del flujo de agua, nutrientes y sedimentos hacia el delta, lo que ha provocado el deterioro del ecosistema deltaico (Kowalewski *et al.* 2000).

La poca información sobre la fauna bentónica asociada al estuario del manglar Térraba-Sierpe señala la necesidad de estudiar la macrofauna bentónica submareal de los fondos sedimentarios del manglar del HNTS. La información generada puede ayudar a comprender patrones estacionales de la fauna estuarina, ya que la infauna bentónica es alimento de otros organismos (e.g. peces, aves y otros invertebrados de mayor tamaño) (Alongi & Sasekumar 1992). Varios estudios en otras localidades han reportado que la diversidad y distribución de la macrofauna bentónica puede estar sujeta a cambios temporales en la salinidad, granulometría de los sedimentos y otras variables ambientales (Sanders 1968, Maurer *et al.* 1984, Alongi 1990, Diehl 1992, Death & Winterbourn 1995, Dittmann 2000, Currie & Small 2006, Sibaja-Cordero 2012). Por lo tanto, es necesario estudiar las interacciones entre la macrofauna bentónica y las variables abióticas del HNTS, y así esclarecer el funcionamiento de sus procesos ecológicos. Varios estudios realizados previamente en el HNTS sugieren la importancia de incrementar la comprensión del ecosistema con el fin de que ese conocimiento sea tomado en cuenta para desarrollar un manejo adecuado (Echeverría-Sáenz *et al.* 2003, Quesada-Aplízar & Cortés 2006, Arroyo-Mora 2008, McLarney *et al.* 2010). Asimismo, la zona está sujeta a la construcción de un proyecto hidroeléctrico, que impone la necesidad de obtener información previa sobre la diversidad, distribución y abundancia de la comunidad bentónica que sirva como punto de comparación ante ésta y otras alteraciones del hábitat natural del HNTS. Con base a los argumentos anteriores, este estudio pretende analizar durante un año la composición de la macrofauna bentónica en dos estuarios del HNTS, donde se espera una variación espacial y temporal en la composición de especies, así como una asociación con las variables ambientales del sistema estuarino.

OBJETIVOS

Objetivo general

- *Determinar en escala espacio-temporal el efecto de variables ambientales del sedimento y la columna de agua sobre la diversidad y composición de macrofauna bentónica en el manglar Térraba-Sierpe.*

Objetivos específicos

- *Analizar la variación espacio-temporal de las características ambientales del bentos del manglar Térraba-Sierpe.*
- *Elaborar un listado taxonómico de las especies que conforman la macrofauna bentónica del manglar Térraba-Sierpe.*
- *Analizar la variación espacio-temporal de la riqueza, abundancia, composición de especies y biomasa de la macrofauna bentónica del manglar Térraba-Sierpe.*
- *Determinar la asociación de las variables ambientales (granulometría, materia orgánica y carbonatos del sedimento, temperatura, salinidad y oxígeno disuelto en la columna de agua) con la composición de la macrofauna bentónica del manglar Térraba-Sierpe.*

CAPÍTULO 1

Spatial and temporal dynamics of subtidal sediments in two tropical mesotidal estuaries: influence of estuarine zonation and river basin land-use.

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ABSTRACT

Mangroves are one of the most threatened coastal environments and are considered to be highly vulnerable to the effects of climate change. Sediments at mangrove forests form the substrate for trees, provide habitats for benthic fauna, and contribute to blue carbon stocks. It is thus important to understand how the sediment dynamics are affected by the input of particles, precipitation, runoff, and currents. This study aims to explain how the sediment dynamics operate in tropical mesotidal estuaries at the Térraba-Sierpe mangroves in the Pacific of Costa Rica (8 N, 83 W) identifying the drivers of spatial (estuary and estuarine gradient) and temporal (month) variation in sediment traits (i.e, grain size, sorting, skewness, kurtosis, carbonates, and organic matter). Most sediments were sand-dominated and moderately well sorted. The mean grain size (±SD) was 133.2 ± 71.36 µm, with a carbonate content of 5.7 ± 7.4% and 5.2 ± 4.6% organic matter. Sediment in the upper and lower stations had larger proportions of coarse particles and was poorly sorted compared to the sediment in the outer station. The heterogeneity of the sediments in the upper and lower estuary was probably related to the existence of both coarse (associated with high water velocities in mangrove channels) and fine particles (associated with low water velocities in nearby swamps). The fine sediment composition in the outer station suggests that part of the exported mangrove sediments are probably being deposited in the offshore bar outside the estuary. Particle size, skewness, kurtosis, and carbonates did not show spatial nor temporal differentiation. Total organic matter was higher in the upper station than in both lower and outer stations due to autochthonous (mangrove litter) and allochthonous (terrestrial runoff) production. The total organic matter was the only variable differing between estuaries; this difference was probably related to the higher erosion along the Coronado estuary, characterized by a higher percentage of non-forest surface, large population centers and highways along the river shore. The spatial estuarine gradient was the main driver of the observed sediment patterns in these tropical mesotidal estuaries.

HIGHLIGHTS

- Subtidal sediments in subtidal channels are sand-dominated
- Sediments in the upper estuary are more heterogeneous than outside the estuary
- Spatial estuarine gradient was the main driver of the observed sediment patterns
- River basin's land use and deforestation influences estuarine sediment composition
- Seasonality had a small effect on sediments or tropical mesotidal estuaries

KEYWORDS

mangroves; estuaries; estuarine dynamics; estuarine sedimentation; organic matter; Costa Rica

1 INTRODUCTION

Mangroves are coastal forests occurring in intertidal regions along tropical and subtropical shorelines –delimited by the 20°C seawater winter isotherm and major ocean currents– generally associated with lagoons, river deltas, and estuarine systems (Alongi, 2009; Giri et al., 2011; Thom, 1984). Mangroves are among the most productive and biologically important ecosystems, providing unique goods and services to coastal human populations, such as food, medicine, fuel and building materials (Ewel et al., 1998; Giri et al., 2011). Although they only cover ~0.1% of world's continental surface, mangroves account for 11% of total terrestrial carbon input into oceans, 10% of terrestrial dissolved organic carbon exports, and serve as sink for ~22.8 million metric tons of carbon each year (Dittmar et al., 2006; Giri et al., 2011; Jennerjahn and Ittekkot, 2002). Mangroves' below-ground biomass can equal the standing crop rising above-ground (Alongi, 2002; Clough, 1992). The root system of the mangrove trees stabilizes coastal sediments and helps to protect shorelines against both erosion and extreme weather events (e.g. hurricanes, cyclones, tsunamis) (Das and Crépin, 2013; Hayden and Granek, 2015; Zhang et al., 2012). In these mangrove forests, a significant amount of carbon is buried as organic matter in the sediments (Alongi and Mukhopadhyay, 2015; Twilley et al., 1992).

Mangrove sediment dynamics are influenced by turbulence and mixing generated by ocean currents, waves, tides, tidal channels, river runoff, and precipitation (Duke et al., 1998; Tolhurst and Chapman, 2005). Mangrove sediments are characterized by specific and complex physical, chemical and microbiological properties, all interacting with each other (Pearl, 2016; Tolhurst et al., 2005). Sediment properties (i.e., grain size composition, nutrients, dissolved oxygen, carbonates and organic matter) directly affect the distribution, development and survival of mangrove trees and benthic fauna (Alongi, 1990; Castañeda-Moya et al., 2006; Feller et al., 2003; Gray, 1974, 1981). Although mangroves are considered highly dynamic ecosystems (Woodroffe, 1992), they do not necessarily show a high seasonal variation in sediment composition (i.e, Laguna de Términos, Mexico: Hernández-Alcántara and Solis-Weiss, 1995). Moreover, research efforts have focused on intertidal sediments, while the subtidal sediments are less known (Alongi, 1990).

Although mangroves provide valuable ecological, social and economic services to both ecosystems and humans, they are declining at a faster rate than inland tropical forests and coral reefs (Duke et al., 2007; Halpern et al., 2008; Hamilton and Casey, 2016). Currently, the main threat to mangrove forests is deforestation caused by the expansion of agriculture, aquaculture, tourism, and urban development (Alongi, 2002; Giri et al., 2008). However, sea-level rise could become the greatest threat to mangroves in the nearby future (Gilman et al., 2008a).

Térraba-Sierpe is one of the largest and most complex mangrove estuarine system in Central America (Proyecto Humedales, 2015). This ecosystem is highly diverse, sustains commercially important ark-clam stocks, and is probably a nursery ground for some species of rays and sharks (Clarke et al., 2014; Echeverría-Sáenz et al., 2003; Nielsen and Quesada, 2006; Proyecto Humedales, 2015; Sibaja-Cordero and Echeverría-Sáenz, 2015). The Térraba-Sierpe mangroves contain important carbon stocks, sinking between 391 and 438 $Mg \cdot ha^{-1}$ (BIOMARCC-SINAC-GIZ, 2012). However, ecosystem services provided by Térraba-Sierpe are diminished by agrochemical and pesticide pollution, wetland drainage, deforestation, agricultural expansion, and over-exploitation of forest and fisheries resources (Proyecto Humedales, 2015). Moreover, there is a plan to build one of the largest hydroelectric dams in Central America on the Térraba-Sierpe's main tributary (PHED, 2010). Dams can modify the river flow and sediment dynamics, which in turn influence coastal morphology (Kowalewski et al., 2000; Poff et al., 1997). It is thus necessary to broaden our understanding on how this estuarine system operates. We provide baseline information on the sedimentary processes in the Térraba-Sierpe mangrove before the construction of the dam. Specifically, our study aims to explain the spatio-temporal variation of the sediment dynamics in this tropical estuarine system and to identify its driving factors. The results provide a basis for further understand the distribution and species richness of the benthic fauna.

2 MATERIALS AND METHODS

2.1 Study site

The Térraba-Sierpe wetland (Humedal Nacional Térraba-Sierpe) has been a RAMSAR protected site since 1995 and is located in the southern Pacific coast of Costa Rica (Fig. 1), with a mangrove area of ~14337 ha (Proyecto Humedales, 2015). The wetland's two main tributaries, Grande de Térraba and Sierpe, have basin catchment areas of 5077 km^2 and 790 km^2, respectively (Umaña et al., 2015). The rainy season spans from May to November, while the dry season extends from December to April, with a mean monthly precipitation of 860 mm and 520 mm, respectively (Rojas, 2011). The concentration of suspended sediments and nutrients in the water column of these estuaries increases during the rainy season, while salinity decreases (Lizano et al., 2001; Umaña-Villalobos and Springer, 2006).

2.2 Sampling

To record the spatial variation, the sampling was conducted at the Coronado and Sierpe estuaries. There, three stations were sampled at each estuary: 1) upper station: ~5 km landward from the river mouth, 2) lower station: <1 km landward from the river mouth, and 3) outer station: ~1 km seaward from the river mouth (Fig. 1, Table 1S2). The temporal variation was recorded by monthly surveys (from January to December 2013, except in February), alternating between estuaries. At each station, one sediment sample from the center of the main channel was collected using a Petit-Ponar grab (152 mm × 152 mm). Samples were stored in plastic bags and kept frozen until analysis.

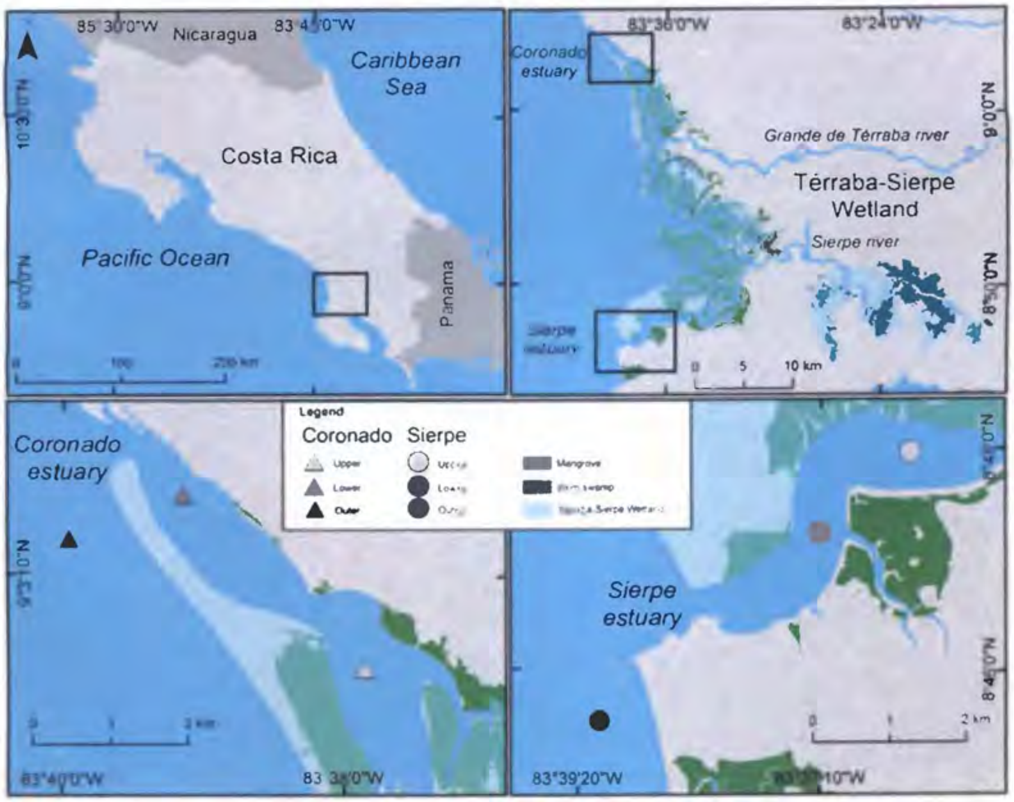


Figure 1. *Location of the Térraba-Sierpe mangrove, and sampling stations at the Coronado and Sierpe estuaries, Pacific coast of Costa Rica.*

2.3 Laboratory analysis

The sediments were oven-dried at 60°C during five days, and stored in a desiccant jar to keep the sediment sample dry until reaching room temperature. The following sediment properties were analyzed to determine the possible influence of spatial and temporal factors on sediment dynamics.

2.3.1 Grain size

A ~100 g sub-sample was sieved through a set of mesh sieves (Fisherbrand U.S.) in descending sequence of opening-pore size (4000, 2000, 1000, 850, 710, 500, 355, 250, 125 and 63 µm), which was closed at the bottom with a pan and covered with a lid at the top. Dry sieving was performe with an electronic sieve-shaker (Retsch AS-200) for 15 minutes with 95 amplitude. The remaining sediment fraction from each sieve was weighed (Eleftheriou and McIntyre, 2005; Sibaja-Cordero et al., 2014) using an electronic balance (Denver Instrument SI-603; ±0.01 g). The grain size (median value), sorting (grain size standard deviation), skewness (asymmetry towards a given particle size), and kurtosis (shape of the size distribution curve) were estimated considering the weight of the fractions, using GRADISTAT 8.0 and following the classification therein (Blott and Pye, 2001).

2.3.2 Carbonates

The carbonate content was calculated through the back titration method (Sibaja-Cordero et al., 2014). Three ~0.5 g sub-samples were prepared using an electronic analytical balance (AND HR-200; ±0.0001 g). Sub-samples were placed in 150 ml Erlenmeyer flasks. Then 25.00 ml of hydrochloric acid (HCl) 0.5 M, 20 ml of distilled water and three drops of phenolphthalein were added. The flasks were heated to 50°C using an ultrasonic cleaner (Fisher Scientific FS-14) during 15 minutes. Once cooled to room temperature, the solution was titrated with sodium hydroxide (NaOH) 0.5 M standard dissolution using a burette. The carbonate content percentage ($CaCO_3\%$) was calculated following the equation from Sibaja-Cordero et al. (2014):

$$CaCO_3\% = [(V_{HCl} \times M_{HCl}) - (V_{NaOH} \times M_{NaOH})] \times \left(\frac{1\ mol\ HCl}{1000\ ml}\right) \times \left(\frac{1\ mol\ CO_3}{2\ mol\ H^+}\right) \times \left(\frac{100\ g\ CaCO_3}{1\ mol\ CaCO_3}\right) \times \left(\frac{100}{W_t}\right)$$

where V_{HCl} is the HCl volume, M_{HCl} is the HCl dissolution molarity, V_{NaOH} is the NaOH volume, M_{NaOH} is NaOH dissolution molarity, and Wt is the total weight of dry sediment. The carbonate content percentage of each sample was estimated as the average from the three sub-samples.

2.3.3 Total organic matter

Total organic matter (TOM) was determined using the loss-on-ignition method, following Sibaja-Cordero et al. (2014). Three subsamples of ~5.000 ± 0.0001 g were obtained from each sediment sample. Sub-samples were placed in oven-dried ceramic crucibles (previously weighed) and then weighed (crucible + sub-

sample). The crucibles with sub-samples were ignited in a muffle furnace at 450°C during four hours, and subsequently placed in a desiccant jar until reaching room temperature and then weighed again. The sediment sub-sample weight difference between before and after ignition represents the TOM. The TOM percentage was calculated for each sub-sample, and the average TOM was calculated from the three sub-samples (Eleftheriou and McIntyre, 2005; Lourido et al., 2008; Sibaja-Cordero et al., 2014).

2.4 Statistical analysis

A ternary plot (fine particles: ≤125 µm; medium particles: >125 - <1000 µm; coarse particles: ≥1000 µm) was used to observe general trends of sediment composition. A Principal Component Analysis (PCA) of the sediment size fraction percentage, arcsine transformed (Krebs, 1999), was applied to observe spatial and temporal variation. The results of both analyses were both plotted in PAST (Hammer et al., 2001). A Two-way Non-Parametric Multivariate Analysis of Variance (Two-way PERMANOVA; 9999 permutations) was performed using PAST to analyze spatial (upper, lower, outer stations) and temporal (rainy and dry season) variations using the sediment size fraction percentage as input data. A Spearman correlation was applied to observe relations among all the sediment properties. Moreover, a post-hoc Spearman correlation was used to analyze relations between the mean monthly precipitation and the sediment properties. The mean monthly precipitation data from three meteorological stations within the basins of Coronado and Sierpe estuary was obtained from the Instituto Meteorológico Nacional (https://www.imn.ac.cr).

Generalized Additive Models (GAM) were used to analyze spatial and temporal factors that influenced the following response variables: grain size, sorting, skewness, kurtosis, carbonates, and TOM. Explanatory variables were 1) estuary (Coronado, Sierpe), 2) station (upper, lower, outer), both as spatial factors; 3) the interaction between estuary and station (estuary × station), and 4) the sampling month as a temporal factor. We used GAM because it allows to describe the relationship between the response variable and explanatory variables without choosing any particular parametric shape (Crawley, 2007; Wood, 2011). Models were tested using the mgcv library (Wood, 2011) in RStudio v 0.99.484 (RStudio Team, 2015). We first evaluated a saturated model for each response variable considering all the explanatory variables. Then, the models were simplified – excluding factors that did not explain the variation of the response variable; and selecting those models with higher percentage of explained variation– in order to determine the factors that better explained the spatial and temporal trends of the response data (Crawley, 2007; Wood, 2011).

2.5 Geospatial analysis

In order to elucidate a possible relation between the land use –as a driving factor of spatial variation– and the sediment dynamics a post-hoc geospatial analysis was performed to determine the type of cover and its area, in the watersheds of the Sierpe and Térraba rivers. The layer of forest coverage was provided by SIREFOR (2012), and the river basin layers by ITCR (2014).

The land cover classes of the forest types layer, were reclassified in three broad groups: 1) Forest (primary and secondary forest, mangrove, palm-forest, forest plantation, and paramo), 2) Non-Forest (pasturelands, agriculture, infrastructure), and 3) No-Data (cloud and cloud's shadows). For more details of coverage reclassification see Table 1S1. The total area of Forest, Non-Forest, and No Data were measured for all the sub-basins that flow into the mangrove system, for both Coronado and Sierpe estuaries. The data was analyzed using ArcGIS 10.3 (Esri, 2014).

3 RESULTS

3.1 General results

General sediment properties for each sample are shown in Table 1S2. Most samples were composed of medium-size particles and characterized as slightly gravelly sand. The general average grain size (±SD) was 133.22 ± 71.36 µm, with samples ranging from 15.96 µm to 270.61 µm. Most samples were moderately well sorted, but skewness and kurtosis were highly variable (Table 1S2).

Spatial variation of the sediment was observed along the estuarine gradient of both estuaries, showing higher proportion of fine particles (63 and 125 µm) in the outer *stations*, while medium particles (250 and 355 µm) had a higher presence in the upper and lower stations (Fig. 2). However, there were six samples with a higher influence of very fine particles: Coronado's upper station during January and lower station during April, and Sierpe's upper station during March and July and lower station during May (Fig. 2, 3). The PCA revealed a slight temporal variation between rainy and dry seasons at the outer stations (Fig. 3). On the other hand, the PCA did not support differences between the two estuaries (Fig. 3). The results of the Two-way PERMANOVA showed spatial differences between stations regarding the size fraction percentages, but it did not provide evidence of temporal differentiation between seasons (Table 1).

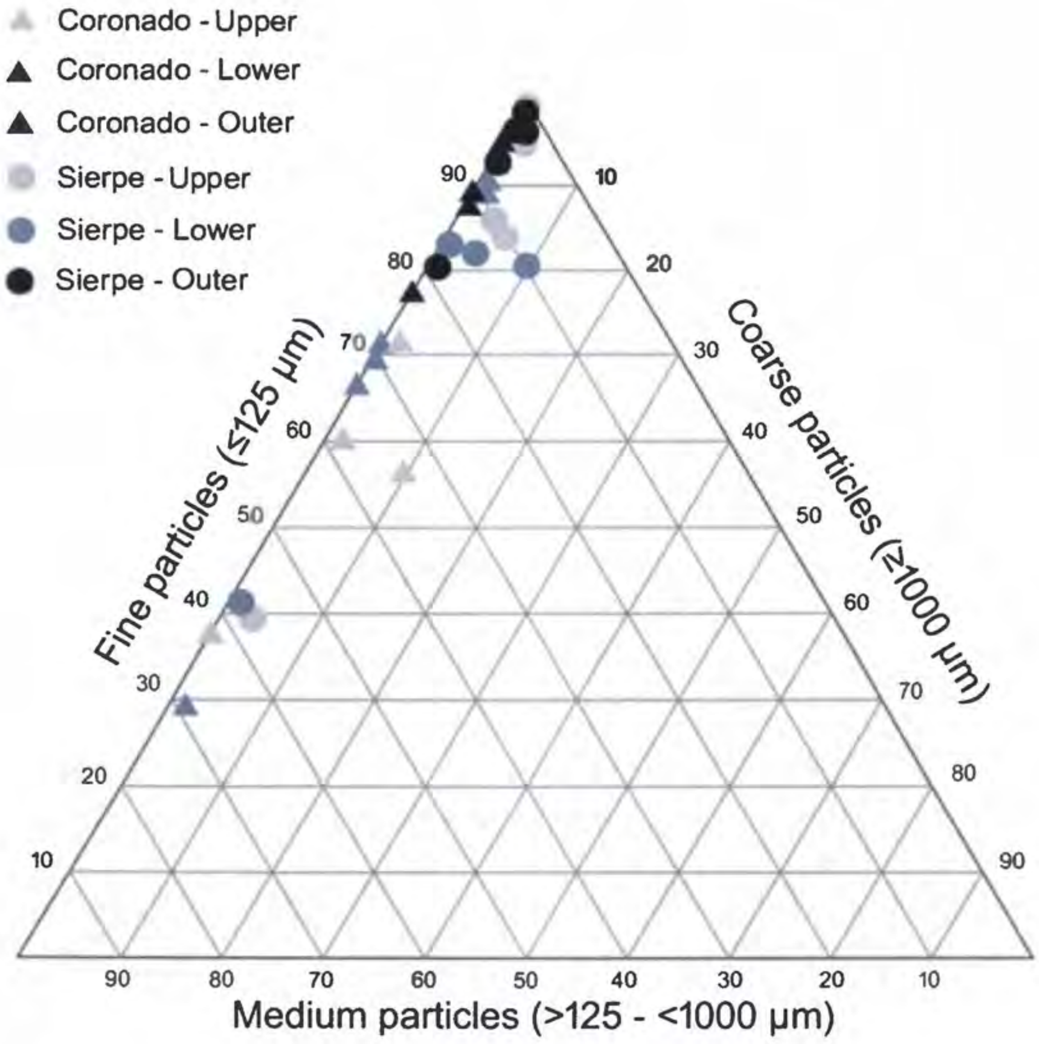


Figure 2. *Ternary plot of spatial variation of sediment's grain size composition at two tropical mesotidal estuaries, Costa Rica.*

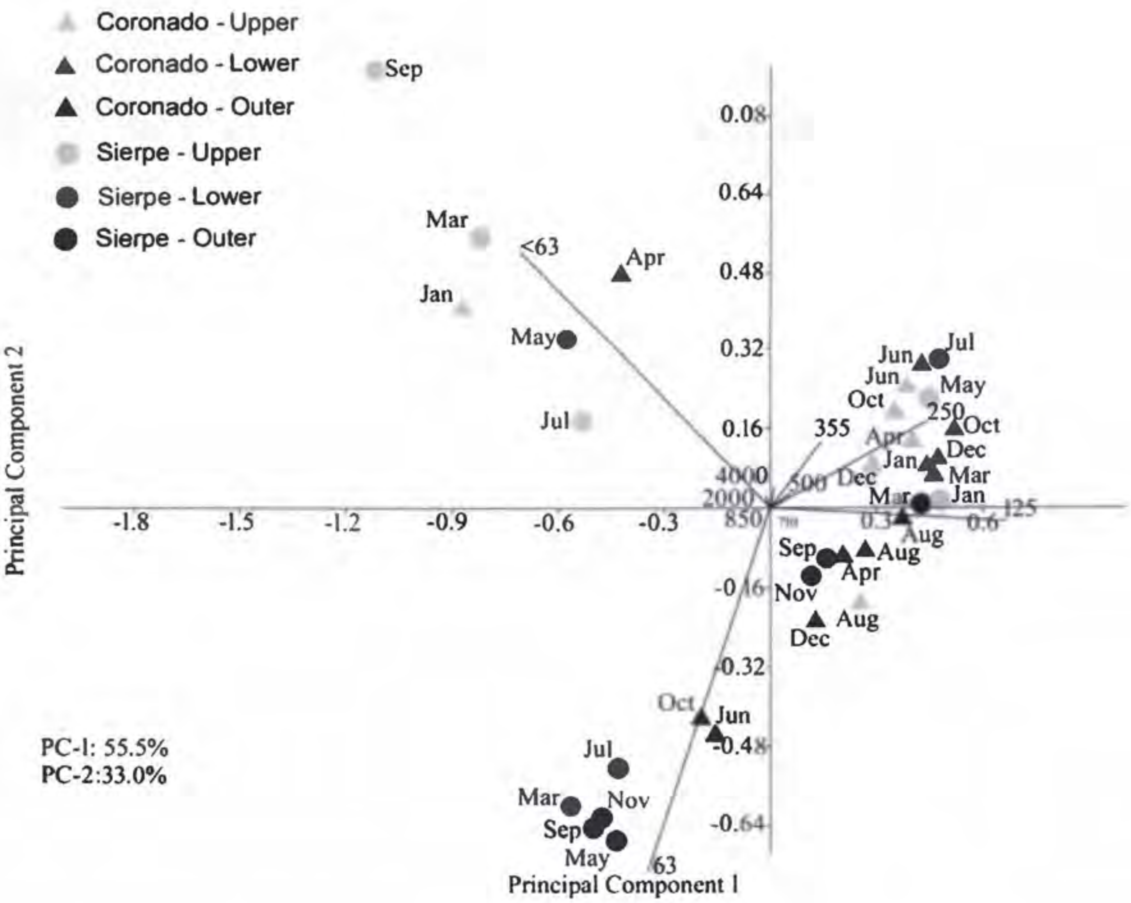


Figure 3. *Principal Component Analysis showing spatial and temporal variation of sediment's particle size fraction at two tropical mesotidal estuaries, Costa Rica. Vectors: grain size fractions (µm).*

Table 1. *Two-way Non-Parametric Multivariate Analysis of Variance of sediments from two tropical mesotidal estuaries in Costa Rica, using size fraction percentage as input data, and station (upper, lower, outer) and season (dry: from December to April; and rainy: from May to November) as groups. Permutations: 9999.*

Source	Sum of squares	Degrees of freedom	Mean square	F	p
Station	2.22	2	1.11	2.65	0.014*
Season	0.23	1	0.23	0.54	0.560
Station × Season	-0.25	2	-0.13	-0.30	0.091
Residual	11.32	27	0.42		
Total	13.52	32			

The TOM was negatively correlated to sand percentage, and positively related to mud percentage and grain size (Table 1S3). The sorting was positively correlated to gravel percentage, mud percentage and grain size, and negatively correlated to sand percentage (Table 1S3). The sand percentage was also negatively correlated to grain size and mud (Table 1S3). The average monthly precipitation of all the pluviometric stations within the Coronado and Sierpe basins are shown in Table 1S4. Precipitation was not correlated with sediment properties at the Coronado estuary (Table S5). In the case of the Sierpe estuary, most of the sediment properties were not correlated with precipitation; with the exception of skewness and kurtosis (Table 1S5).

3.2 Grain size

The final Generalized Additive Model (GAM) for the grain size explained a low variance (Table 2). There were no spatial effects of estuary, station or estuary × station on the grain size (Table 2, Fig. 1S1A-D). The model did not provide evidence of a temporal effect (sampling month) in median grain size (Fig. 1S1E,F).

Table 2. *General Additive Models for spatial and temporal variation of sediment properties at two tropical mesotidal estuaries in Costa Rica, F-statistical value, probability, and model's explained variance. Models considered estuary (Coronado, Sierpe) and station (upper, lower, outer) as fixed factors and time as continuous explanatory variable.*

Response variable	Estuary		Station		Time		Estuary × Station		Model's R^2
	F	p	F	p	F	p	F	p	
Grain size	2.60	0.119	0.58	0.569	ns	ns	0.27	0.767	0.01
Sorting	ns	ns	6.50	0.005*	4.26	0.048*	ns	ns	0.19
Skewness	0.48	0.491	0.12	0.891	ns	ns	0.93	0.407	0.01
Kurtosis	0.04	0.840	0.33	0.719	ns	ns	0.46	0.636	0.11
Carbonate content	2.43	0.131	0.30	0.746	ns	ns	2.24	0.126	0.04
Total organic content (both estuaries)	9.46	0.004*	8.72	0.001*	ns	ns	4.90	0.015*	0.66
Total organic content Coronado estuary	–	–	7.32	0.006*	ns	ns	–	–	0.33
Total organic content Sierpe estuary	–	–	29.21	<0.001*	ns	ns	–	–	0.71

*: presence of influence on the response variable. ns: not selected ($p > 0.05$). –: not valid.

3.3 Sorting

The GAM for sorting explained 19% of the variance (Table 2). There was no spatial effect of the estuary on the sorting, but sorting was affected by the estuarine zonation (Fig. 4A,B). Our results revealed that upper and lower stations (through time in both estuaries) had the highest sorting values (Fig. 4C,D), suggesting the presence of poorly sorted and more heterogeneous sediments. The outer stations were generally well sorted (lower sorting values) and dominated by finer particles (63 and 125 µm) (Fig. 4C,D). The GAM detected a temporal effect of the season, with poor sorting occurring during the dry season, but gradually changing to well sorted (decrease in the sorting values) at the end of the rainy season (Fig. 4E,F).

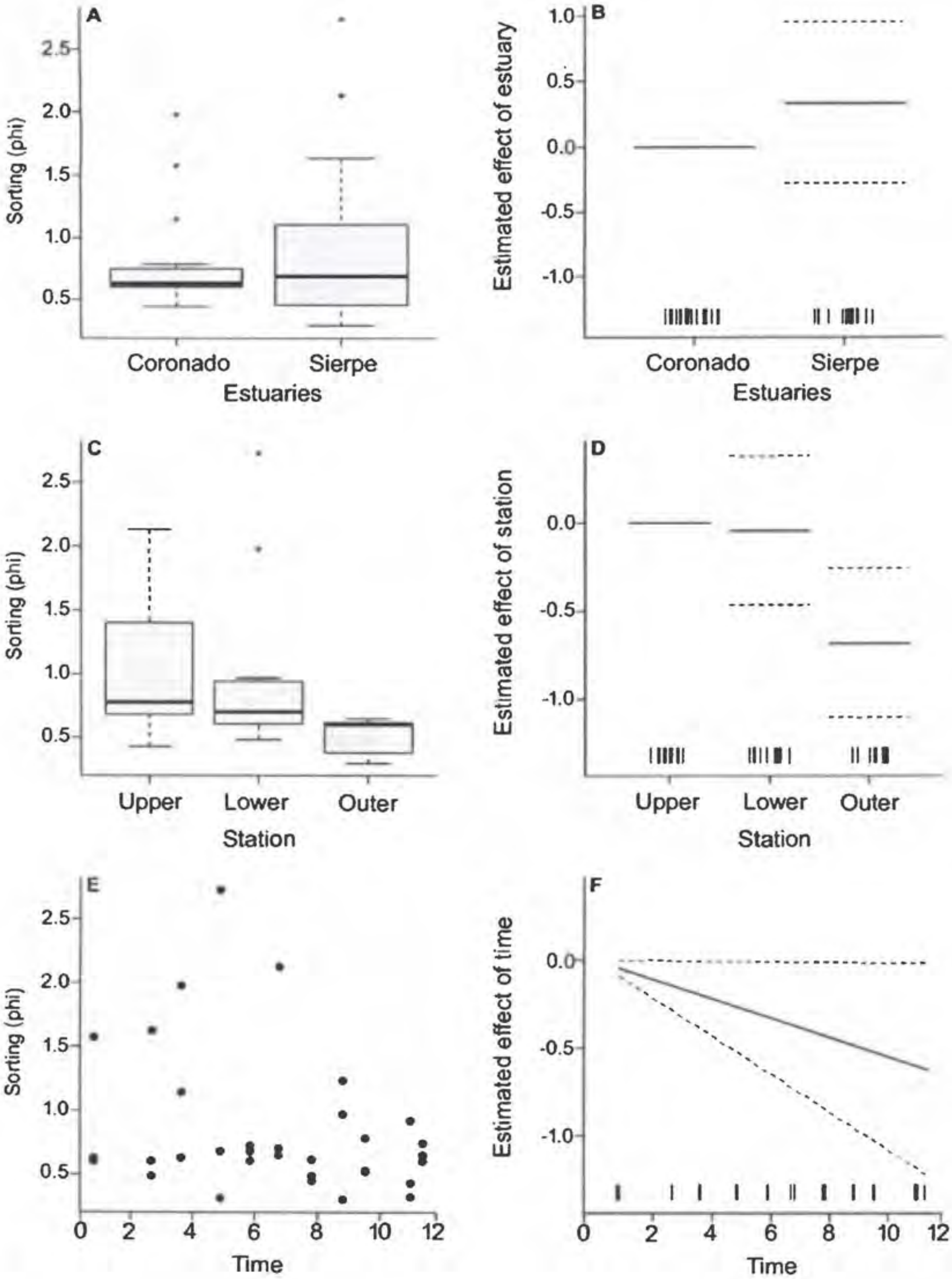

A
Sorting (phi)
2.5
2.0
1.5
1.0
0.5
Coronado
Sierpe
Estuaries
B
Estimated effect of estuary
1.0
0.5
0.0
-0.5
-1.0
Coronado
Sierpe
Estuaries
C
Sorting (phi)
2.5
2.0
1.5
1.0
0.5
Upper
Lower
Outer
Station
D
Estimated effect of station
0.0
-0.5
-1.0
Upper
Lower
Outer
Station
E
Sorting (phi)
2.5
2.0
1.5
1.0
0.5
0
2
4
6
8
10
12
Time
F
Estimated effect of time
0.0
-0.5
-1.0
0
2
4
6
8
10
12
Time

Figure 4. *Sediment sorting by estuary (A. boxplot, B. estimated effect), station (C. boxplot, D. estimated effect) and time (E. scatter plot, F. estimated effect) at two tropical mesotidal estuaries, Costa Rica.*

3.4 Skewness

The GAM for skewness had low explained variance (Table 2). The model did not provide evidence for estuary, station nor sampling month have effects on the sediment skewness (Fig. 1S2A,F).

3.5 Kurtosis

The GAM for kurtosis explained 11% of variance (Table 2). However, the results of the model did not provide evidence estuary, station, its interaction, or sampling month influencing the sediment kurtosis (Fig. 1S3A-F).

3.6 Carbonate content

The general average carbonate content was 5.7 ± 7.4%, and varied from 0.9% to 42.2% (Table 1S2). In Coronado, the highest carbonate content was found at the outer station during April (5.3%) and all the remaining samples varied from 2.9% to 4.9% (Table 1S2). In Sierpe, the highest carbonate content was obtained during May at the lower station (42.2%) and in March at the upper station (22.74%). Both samples contained several fragments of shells. The remaining samples varied from 0.9% to 5.8% (Table 1S2).

The GAM for carbonate content explained low percentage of variance (Table 2). The results of the model did not detect spatial (estuary and station) nor temporal (sampling month) effects on the carbonate content (Fig. 1S4A-F).

3.7 Total organic matter content

The general average TOM was 5.2 ± 4.6%, ranging from 1.3 % to 18.0% (Table 1S2). In Coronado, the highest TOM (12.3%) was registered in January at the upper station (Table 1S2), with an average of 4.0 ± 2.7 %. In Sierpe, high TOM values (>12%) were recorded at the upper station during several months (March, May, July, September; Table 1S2); the average was 6.7 ± 6.0%.

The TOM's GAM explained about 66% of the variance (Table 2). The results of the model detected spatial effects of estuary and station on the TOM (Table 2). The TOM was higher in Sierpe than in Coronado (Fig. 5A,B), and higher in the upper station compared to lower and outer stations (Fig. 5C,D). Temporal effects were not detected by the model (Fig. 5E,F).

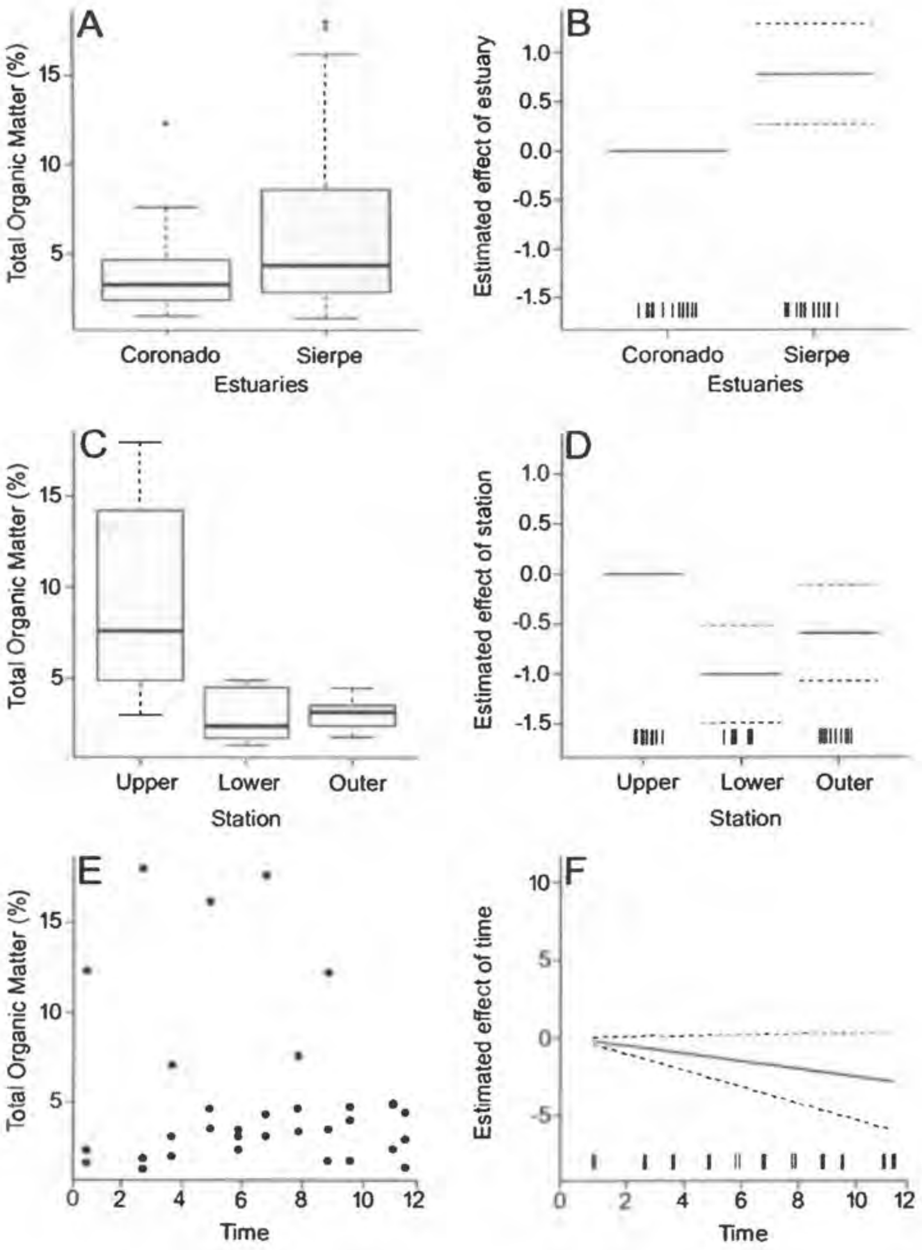


Figure 5. *Total Organic Matter percentage in sediments by estuary (A. boxplot, B. estimated effect), station (C. boxplot, D. estimated effect) and time (E. scatter plot, F. estimated effect) at two tropical mesotidal estuaries, Costa Rica.*

Since the detected an effect of the interaction of the spatial factors –estuary × station– on TOM (Table 2), two models for TOM were performed separately for each estuary. For Coronado, only the factor station was selected as an explanatory variable, and the highest TOM occurred at the upper station (Table 2; Fig. 6A,B). In Sierpe, the factor station was selected as the only explanatory variable, and the highest TOM values occurred at the upper station (Table 2, Fig. 6C,D).

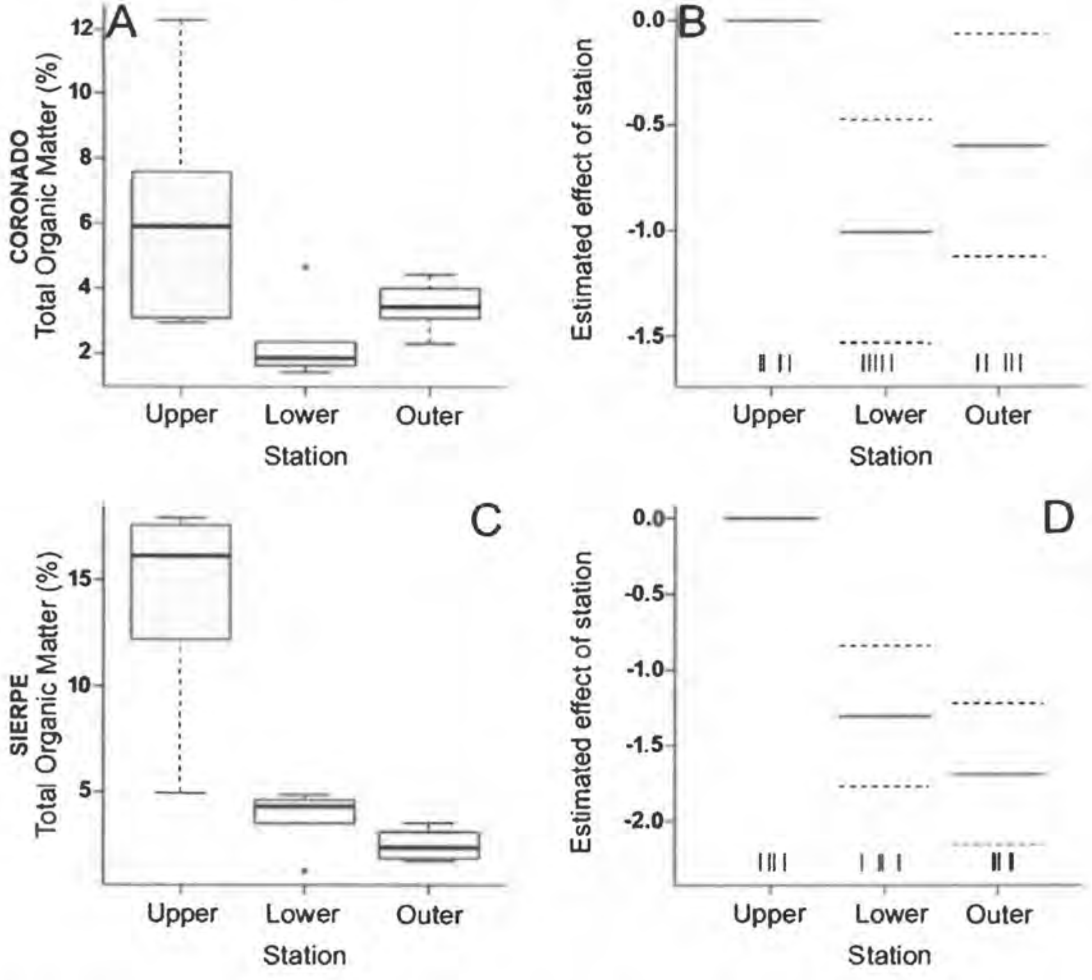


Figure 6. *Total Organic Matter percentage in sediments at each station in the Coronado (A. boxplot, B. estimated effect) and Sierpe (C. boxplot, D. estimated effect) estuaries, Costa Rica.*

3.7 Land use cover

The land use cover between Grande de Térraba and Sierpe river basins were very different (Fig. 7). During 2012, the Grande de Térraba basin (Coronado estuary) had 45% non-forest coverage and 55% forest coverage. There are eight large (>5000 people) population centers (San Isidro, Daniel Flores, Buenos Aires, San Vito, Palmar, Pejibaye, Potrero Grande, and Ciudad Cortés) and ~42 km of the Pan-American Highway running through rocky cliffs along the Grande de Térraba river (Fig. 7). During 2012, the Sierpe basin (Sierpe estuary) had 40% non-forest coverage and 60% forest coverage (Fig. 7). There are no large population centers in this basin nor highways along the Sierpe river (Fig. 7).

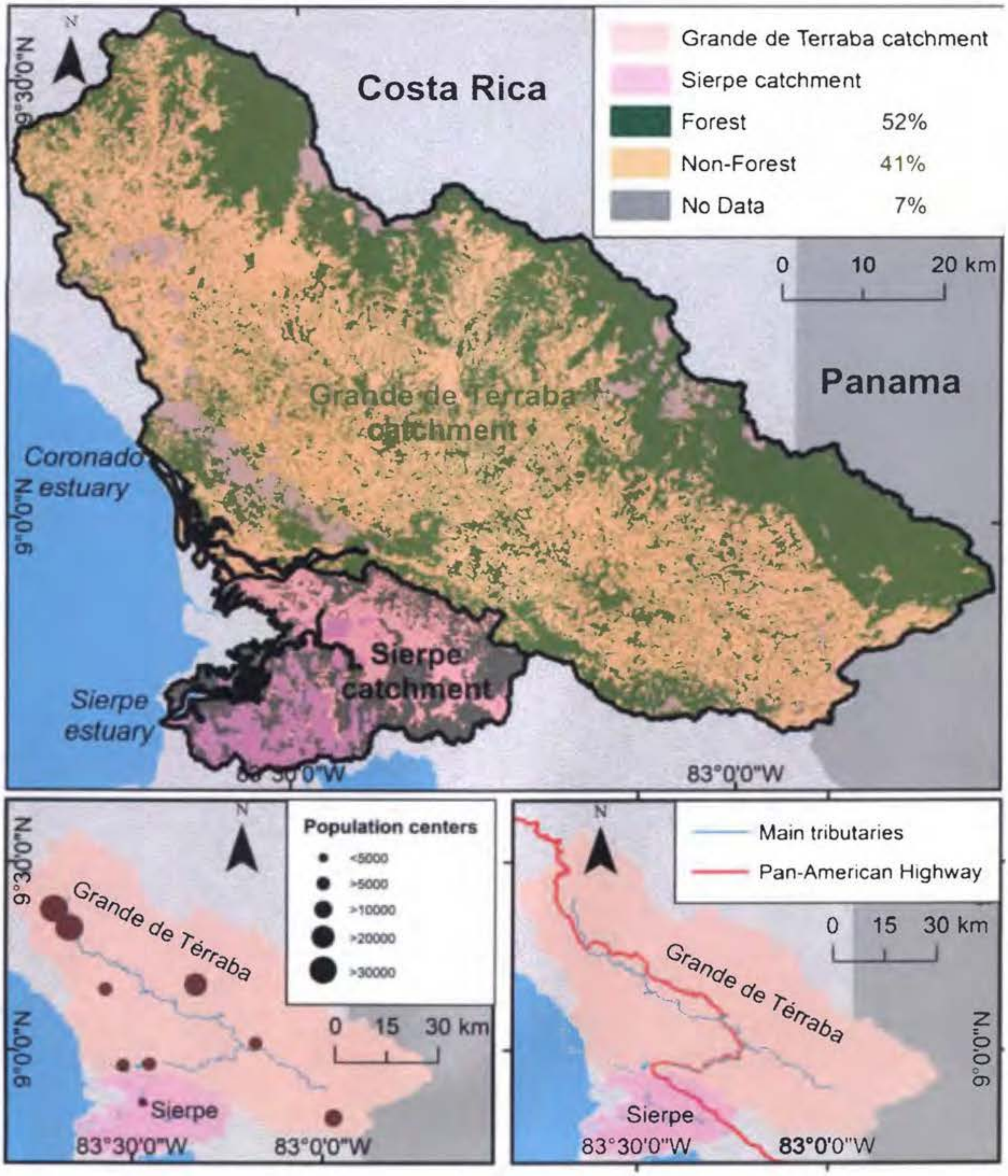


Figure 7. *Map of land use cover, population centers and highways of the sub-basins that flow into two tropical mesotidal estuaries, Costa Rica.*

4 DISCUSSION

4.1 General sediment composition dynamics

Our results on the sediment composition at Térraba-Sierpe estuaries differ from patterns described for tropical (Gulf of Nicoya, Costa Rica: Maurer and Vargas, 1983) and a temperate (Ría de Aldán, Spain: Lourido et al., 2008) estuaries: where coarser particles were found at outer (exposed) areas, and finer particles at inner (sheltered) areas. Since mangroves diminish the water-motion energy (Zhang et al., 2012), which results in the accumulation of fine sediment particles (Komar, 1976), we expected to find finer particles in the upper and lower stations. However, our results are similar to those from a sub-tropical estuary (Port Curtis, Australia), where coarser particles were observed at the channels and entrances (Currie and Small, 2006). We assume that the coarser and heterogeneous sediments found at the upper and lower stations (inside the estuary) may be related to the removal of fine particles by currents. Strong currents ($>1\ \mathrm{m \cdot s^{-1}}$) are common in mangrove channels during tidal cycles, which can remove fine particles from the bottom (Wolanski et al., 1992). On the other side, the presence of finer sediments in the outer stations (out of the estuary and behind the incoming waves) was probably related to weak currents at deeper waters behind the offshore bar. This is supported by the results of Komar (1976) who suggested that grain size generally starts decreasing at this point towards deeper waters.

We found a pattern of higher TOM at stations with fine sediments (muds) than those with coarse sediments (sands) (Table 1S3). Higher aerobic conditions are known to occur in sandy- compared to muddy-bottoms (Brotas et al., 1990). In accordance with our results, the anaerobic conditions commonly found in muddy sediments can result in lower mineralization rates and higher TOM (Yang et al., 2013). Precipitation influenced the soft-bottom sediments at Sierpe estuary, which was positively correlated with skewness and negatively correlated with kurtosis (Table 1S5). Heavy rains cause terrestrial runoffs thus skewing the sediments to an excess of finer particles (Evans, 1990; Kulm and Byrne, 1966; Storlazzi and

Jaffe, 2008). , The terrestrial input may also promote a more dispersed particle size distribution, tending towards a platykurtic distribution (low kurtosis values) (Blott and Pye, 2001).

4.2 Spatial and temporal variation of sediment sorting

Our results revealed a sorting gradient from the upper and lower stations – with poorly sorted sediments – to the outside stations with well sorted sediments (Fig. 4C,D). Sediment's sorting is understood as the standard deviation of the sediment grain size (Blott and Pye, 2001), therefore, in well sorted sediments most particles are similar in size, while poorly sorted sediments have particles with very diverse sizes. Sediment is well sorted in areas with weak currents (i.e, behind the offshore bar), while poorly sorted in locations with strong currents (i.e, plunge points, offshore bars, and channels) (Komar, 1976). This pattern was also shown by ours results with the best sorting at the outside stations behind the offshore bar.

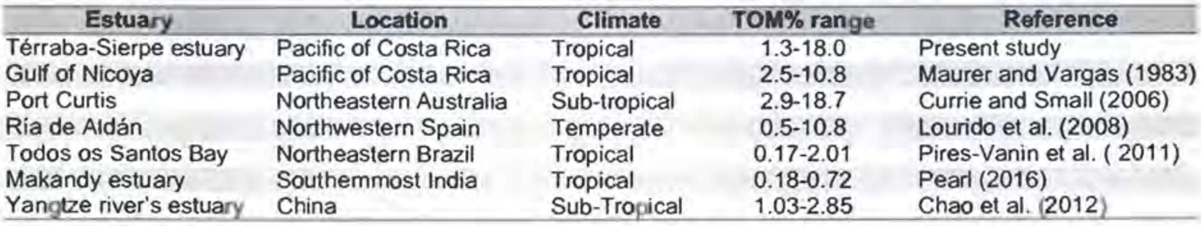
Sorting improved during the rainy season compared to the dry season (Fig. 4C,D). Large proportions of very fine particles (63 µm and <63 µm) were found at the beginning of the rainy season, while medium particles (fine sands: 125, 250, and 355 µm) were present in larger proportions at the end of the rainy season (Fig. 3). Suspended sediments increase remarkably during the rainy season in the rivers along the studied area (Rojas and Rodríguez, 2008; Umaña-Villalobos and Springer, 2006). This particle input probably influences the estuaries' sediment composition during the rainy season, homogenizing it through deposition of fine sands (improving the sediment sorting). Further analyses of suspended sediments associated with bottom-surface sediment studies will be necessary to better understand the sedimentary process in this estuary.

4.3 Spatial variation of organic matter

The average TOM of 5.2% in the Térraba-Sierpe estuaries was higher than the expected 2-4% for sandy bottoms (Alongi, 1990). However, high organic matter content is expected near river discharges (Alongi, 1989a; De Haas et al., 2002;

Radke et al., 2004). In contrast, Currie and Small (2006) considered <10% TOM as low values for sub-tropical estuaries. TOM in Térraba-Sierpe was highly variable, coinciding with similar reports from other tropical, sub-tropical and temperate estuaries (Table 3). However, tropical and sub-tropical estuaries with TOM lower than Térraba-Sierpe are also common (Table 3). Several factors such as soil composition, land use, precipitation rates, and river flow can influence the organic matter of littoral sediments (Alongi, 1990; Noronha-D'Mello and Nayak, 2015; Wildsmith et al., 2011), resulting in the wide variation reported in the literature (Table 3).

Table 3. *Tropical Organic Matter (TOM) percentage range of the sediments from tropical, sub-tropical and temperate estuaries.*



Estuary	Location	Climate	TOM% range	Reference
Térraba-Sierpe estuary	Pacific of Costa Rica	Tropical	1.3-18.0	Present study
Gulf of Nicoya	Pacific of Costa Rica	Tropical	2.5-10.8	Maurer and Vargas (1983)
Port Curtis	Northeastern Australia	Sub-tropical	2.9-18.7	Currie and Small (2006)
Ría de Aldán	Northwestern Spain	Temperate	0.5-10.8	Lourido et al. (2008)
Todos os Santos Bay	Northeastern Brazil	Tropical	0.17-2.01	Pires-Vanin et al. (2011)
Makandy estuary	Southernmost India	Tropical	0.18-0.72	Pearl (2016)
Yangtze river's estuary	China	Sub-Tropical	1.03-2.85	Chao et al. (2012)

We found a spatial gradient in organic matter, decreasing from landward to seaward stations, which is in accordance with patterns reported from other estuaries: Gulf of Nicoya in the Pacific of Costa Rica (Maurer and Vargas, 1983), Tamandaré in Brazil (Sanders et al., 2010), Babeldoab and Yap islands in Micronesia (Kauffman et al., 2011), Waitemata harbor in New Zealand (Yang et al., 2013), and Port Curtis, Peel-Harvey and Swan-Canning in Australia (Currie and Small, 2006a; Wildsmith et al., 2011, 2009).

Mangrove forests produce and transport large amounts of leaf litter, decayed wood, and rhizomes; although part of these carbon sources are exported out of the system, most of it remains in the upper estuary (Hogarth, 2015). Yang et al. (2013) suggested that mangrove's upper zones have higher organic matter content in the sediments due to higher amounts of root-derived carbon and prevailing anaerobic conditions, resulting in low mineralization. Some particles containing nutrients and organic matter are transported from the swamps to the channels and creeks (Akamatsu et *al.*, 2009). The high precipitation rates in the Térraba-Sierpe area (Rojas, 2011; Umaña et al., 2015) are probably contributing with the transport of terrigenous organic matter from the basins to the upper estuary. Mangroves also have high sediment trapping and binding capacities (Scoffin, 1970). We assume that high TOM values at the upper stations are related to the organic biomass production of the mangrove forests and organic matter imports from the terrestrial runoff. Low organic matter content in sediments from the lower and outside stations probably reflects regular flushing of oxygenated marine waters and recent deposition of marine sediments (Wildsmith et al., 2009).

4.4 Effect of land use cover on sediment's spatial variation

Wildsmith et al. (2011) observed in the Swan-Canning estuary (western Australia) a lower organic matter contribution in 2003 compared to 1986, and suggested that this difference was related to an increasing non-organic material deposition. These authors argued that increasing erosion from catchments was related to a clearing of native vegetation in the basin and unlimited access by livestock along the river during recent years. The land use cover of the basins flowing into each estuary of Térraba-Sierpe was very different. The non-forest cover percentage was higher for Coronado than Sierpe (Fig. 7). Other differences between both estuaries were the presence of large population centers and several highway kilometers running along the rocky cliffs of the Grande de Térraba river – Coronado's main tributary – while there were no large population centers or highways along the Sierpe's tributaries (Fig. 7). We suggest that upper station's TOM difference between Coronado and Sierpe may be associated with the different land use of their basins. The more intense use in the Grande de Térraba basin probably results in higher erosion and transport of high amounts of non-organic sediments to Coronado estuary. However, further satellite imagery studies on suspended and surface sediments in both catchments are required to evaluate this hypothesis.

4.5 Other sediment parameters

The main grain size tended to be slightly higher in Coronado than in Sierpe, and higher through rainy season (both probably related with runoff), but in both cases the data were highly variable. The spatial variability on some fractions of the sediment may conceal any temporal patterns, such as in some southwestern Australian estuaries (Tweedley et al., 2012), and our study. Also, we did not find a spatial or temporal pattern in the skewness, kurtosis or carbonates. High variability of skewness and kurtosis were probably related to precipitation as previously mentioned. Other factors, such as productivity and shell fragmentation by waves are responsible of driving carbonates content (Komar, 1976). Some samples had many shell fragments, corresponding to the highest carbonate contents.

4.6 Future perspectives

El Diquís is a massive hydroelectric project that involves the construction of a 173 m high dam upstream in the Grande de Térraba catchment (PHED, 2010). Despite the implementation of impact mitigation measures, El Diquís's dam construction will modify the current sediment dynamics and freshwater input into the Coronado estuary, including changes in the natural fluctuations of sediment inputs, and retention of organic and non-organic particles (see Xu and Dong, 2017). It seems feasible that TOM% at Coronado will rise after the dam construction due to lower non-organic particle input. Substantial modifications of river flow patterns may cause a collapse of adjacent littoral ecosystems as observed in the Colorado delta ecosystem, Gulf of California (Kowalewski et al., 2000). Therefore, managers are urged to develop solutions to reduce possible negative effects on the estuarine and coastal downstream environments. Furthermore, the installation of a close monitoring program is strongly recommended to detect any changes in the ecosystems.

Térraba-Sierpe supports a high biological diversity, artisanal fisheries and stores up to 8 TgC in the entire mangrove – with 76% buried in sediments (Proyecto Humedales, 2015; BIOMARCC-SINAC-GIZ, 2012; Nielsen and Quesada, 2006). Due to its undeniable ecological and socio-economic value, further studies are required to understand 1) the spatial and temporal sediment patterns and their interaction with the distribution of mangrove forests and its associated fauna, 2) the role of sediments in sinking the carbon, and 3) to assess possible impacts associated with the intended construction of PHED.

Mangroves are threatened by climate change, rising sea level, and other climate-driven perturbations (i.e, floods and biodiversity loss) (Duke et al., 2007; Gilman et al., 2008a; Halpern et al., 2008; Hamilton and Casey, 2016). Therefore, it is important to understand the interactions between mangroves and their adjacent environments to enhance their protection and conservation (Munji et al., 2014). Nascimento et al. (2013) suggested that tropical countries should focus on mapping and monitoring mangroves, especially where human disturbances occur. The Térraba-Sierpe mangrove is threatened by agricultural expansion, deforestation, pollution, and possible modification of its natural flow and sedimentation regimes (Proyecto Humedales, 2015). Therefore, further studies considering satellite imagery, suspended sediments and sedimentation rates, river basin erosion, land use, and circulation are required to enhance our understanding of its ecosystem dynamics.

5 CONCLUSIONS

Subtidal sediments of both tropical mesotidal estuaries studied herein were sand dominated and moderately well-sorted. Sediments at the upper and lower stations had higher proportions of coarse particles and were more heterogeneous in composition, probably due to strong currents flowing through the channels, river runoff and the contribution of fine particles from adjacent swamps. Sediments in the outer stations contained more fine sediments and were well sorted than upper and lower stations, due to fine sediment import from mangroves and weak currents behind the offshore bar. The TOM was higher in the upper part of the estuaries due to autochthonous (mangrove litter) and allochthonous (runoff) organic matter production, organic matter trapping in the mangrove forest and low mineralization. Differences in TOM between estuaries were probably related to higher soil erosion and non-organic particles input in Coronado associated with land use cover. Our results show that sediments at these tropical mesotidal estuaries are mainly influenced by spatial factors (such as different estuaries and estuarine zonation) and to a lesser extent by temporal factors (sampling month).

6 ACKNOWLEDGEMENTS

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CAPÍTULO 2

Overlooked estuarine biodiversity: Benthic macrofauna from subtidal channels and nearshore turbid zones at two tropical mesotidal estuaries, Eastern Tropical Pacific

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ABSTRACT

Estuaries are highly dynamic and productive coastal environments harboring a unique biodiversity. Despite its important ecological features and ecosystem services provided to human coastal populations, estuaries are one of the most threatened environments worldwide due to urban, port, and industrial developments, in addition to climate change impacts. Estuaries have been extensively studied; however, the benthic macrofauna of flooded habitats such as subtidal channels and nearshore turbid zones has been largely neglected. Therefore, this study reports on the benthic macrofauna biodiversity of subtidal channels and nearshore turbid zones of the largest estuarine mangrove system of Costa Rica, Térraba-Sierpe. Between January and December of 2013 we collected a total of 3391 organisms with a mean density of 934 ± 1030.2 ind·m^{-2}, ranging from 0 to 9436 ind·m^{-2}. Overall 146 taxa were identified – 81 to species level – distributed in 12 phyla, 21 classes, 28 orders, 72 families and 94 genera. This inventory contains 20 new additions to the Costa Rican marine biodiversity, including one genus of benthic sea arrow worms (*Spadella*), new for the western mainland of the Americas. Annelids contributed with most of the taxa (41.1%), followed by mollusks (28.1%) and arthropods (17.1%). The taxa accumulation curve suggested that further efforts would increase the number of taxa, up to an estimated 203 ± 25.3 benthic macrofauna taxa. The species richness pattern was different between the two estuaries studied in Térraba-Sierpe: In Coronado, seasonality influenced the richness, being higher during the dry season than during the wet season. Otherwise, in Sierpe, the estuarine zonation had an influence, being higher at the nearshore turbid zone (outer station) and the lower estuary – more oceanic influence– with a total of 89 taxa each, compared to the upper estuary –subtidal channels and less oceanic influence– which harbored 75 taxa. The macrofauna density was only influenced by the estuarine zonation in Sierpe. The estuarine zonation had an effect only in Sierpe estuary, being higher at the outer station than in the upper station. The high density at Coronado's upper station was associated with large abundances of the polychaete *Scolelepis*

(*Scolelepis*) *acuta*. The benthic macrofauna responded to salinity variation, organic matter inputs, and sediment composition heterogeneity. Our results support that Térraba-Sierpe subtidal benthic macrofauna is influenced by complex and dynamic spatial and temporal interactions of environmental conditions, which complicates both the identification of general patterns and the development of adequate management approaches. Due to the importance of estuaries for conservation and human welfare, its associated biodiversity needs to be assessed, and further studies should focus on overlooked habitat zones and their impacts on the adjacent ecosystems.

HIGHLIGTHS

- The Térraba-Sierpe benthic macrofauna was comprised by a total of 146 taxa
- A total of 21 new records are reported for Costa Rican Pacific
- Taxa richness was higher at the stations out of the estuary and during dry season
- Density was higher at the outer station in Sierpe but not in Coronado
- Biodiversity was differently affected by zonation and seasonality between estuaries

KEYWORDS: biodiversity, coastal habitats, Costa Rica, estuary, GAM, macrofauna, mangrove.

1 INTRODUCTION

Estuaries are semi-enclosed coastal water bodies connected permanently or periodically to the sea, with a different salinity than the open ocean due to freshwater influence (Elliott and Whitfield, 2011; Snedden et al., 2012). These ecosystems show distinct ecological features such as a transition zone between freshwater to oceanic waters, strong environmental gradients (e.g. salinity, temperature, oxygen, etc.), high biological productivity, and a very characteristic biota (Basset et al., 2013). The highly changing conditions (e.g. salinity) of estuaries represent a stress factor for many freshwater and oceanic species, but not for estuarine-adapted species, which are more tolerant and resilient to these changes and can develop large populations and biomass (Elliott and Whitfield, 2011). Estuaries also function as nursery grounds for many freshwater, coastal and oceanic species of mollusks, crustaceans and fishes, including commercially important species (Clarke et al., 2014; Peterson et al., 2000; Sheaves et al., 2012).

Estuaries are likely to be one of the most threatened ecosystems in the world, because many of these areas have geomorphologic characteristics favoring urban, port, and industrial development (Kennish, 2002; McLusky and Elliott, 2004). Moreover, impacts occurring at the upper river catchment and adjacent coastal marine areas may also affect the estuaries (Elliott and Whitfield, 2011). Climate change poses another risk to the estuarine ecosystems due to rising sea levels, rising temperature, which facilitates water stratification (modifying nutrient availability, sometimes favoring eutrophication), and increasing storm activity (increasing sediment, nutrient, and freshwater inputs from the catchments) (Gilman et al., 2008b; Scavia et al., 2002; Statham, 2012). Climate change effects are a threat to the estuarine biodiversity and associated human activities, such as fisheries (Roessig et al., 2004). During the past decades, the alarming extinction rate of species has shown the necessity to increase biodiversity assessment efforts, and to focus conservation efforts on biodiversity hotspots (Jenkins and Van Houtan, 2016; Pereira et al., 2010). Taconomic biodiversity studies should be carried out with precise taxonomic identifications to allow a better understanding of marine coastal ecosystem functioning and to develop adequate management tools (Costello et al., 2013; Worm et al., 2006).

Biodiversity of subtidal benthic macrofauna inhabiting soft bottoms in tropical estuaries has been poorly studied, while these ecosystems have been relatively well studied in the northern and southern hemispheres (Alongi, 1990; Dittmann and Vargas, 2001; Elliott and Whitfield, 2011; Maurer et al., 1984). Estuaries are usually less biodiverse than adjacent freshwater and oceanic environments due to the wide range of environmental variation (Remane and Schlieper, 1972). Recent studies, however, demonstratde that is not always the case and biodiversity is highly influenced by local features (Elliott and Whitfield, 2011). The estuarine macrofauna comprises mainly short-lived, small-bodied, and fast colonizing species, which are often more generalists than specialists, regarding physiological tolerances and feeding guilds (Gray and Elliott, 2009; McLusky et al., 1993). These species play an important role as food source for larger organisms (e.g. fishes and birds), nutrient recycling (e.g. detritivores consuming decayed organic matter), and water cleaning (e.g. filter feeding) (Alongi, 1990; Harris, 1999; Nguyen et al., 2017; Peterson and Heck Jr, 1999). There is, however, a lack of information regarding species distribution, biodiversity patterns, ecological interactions and functional ecology of subtidal benthic macrofauna from estuaries (Alongi, 1989b; Maurer et al., 1984; Shokri et al., 2009; Thompson et al., 2012). A better understanding of these benthic assemblages will enhance our capacity for effective coastal management (Alongi, 1990; Gorman et al., 2017).

Térraba-Sierpe is the largest Costa Rican estuarine mangrove system and the second in the Central American isthmus (Loría-Naranjo et al., 2018; Nielsen and Quesada, 2006). This estuarine system harbors a high biodiversity of certain aquatic groups, such as fishes (Chicas, 2001; Rojas and Rodríguez, 2008), polychaetes associated to decaying wood (Sibaja-Cordero and Echeverría-Sáenz, 2015), as well as large epibenthic and tree-associated decapods (Echeverría-Sáenz et al., 2003). Térraba-Sierpe also supports ark-clam and estuarine fishes populations harvested in artisanal fisheries (Chicas, 2001; Nielsen and Quesada, 2006; Proyecto Humedales, 2015). Moreover, it has been suggested as an important nursery ground for rays and sharks (Clarke et al., 2014). Despite its important natural goods and services, Térraba-Sierpe is threatened by agrochemical and pesticide pollution, wetland drainage, deforestation, agricultural expansion, and over-exploitation of forest and fisheries resources (Proyecto Humedales, 2015). Therefore, it is necessary to increase the knowledge on the biodiversity from this tropical estuary. This study provides the first comprehensive biodiversity assessment of benthic macrofauna and its variation along subtidal channels and nearshore turbid zones of the Térraba-Sierpe estuarine system. Our results will provide necessary information for future assessments of human-induced impacts and will help to understand the interconnection of this coastal system with adjacent terrestrial, freshwater and marine environments.

2 MATERIALS AND METHODS

2.1 Study site

Térraba-Sierpe, located at the Costa Rican southern Pacific coast in the Coronado Bay (Fig. 1), is an important wetland area for conservation and reponsible use under the RAMSAR Convention on Wetlands since 1995 (Nielsen and Quesada, 2006). Térraba-Sierpe comprises a total area of 30654 ha, including two main rivers (Grande de Térraba and Sierp), lagoons, sandy beaches, cliffs, palm swamp forests (*Raffia taedigera* palms, known as "yolillo"), and 14337 ha of periodically inundated mangrove forests with several subtidal channels (Barrantes and Cerdas, 2015; Proyecto Humedales, 2015). The mangrove area is influenced by the Intertropical Convergence Zone (ITCZ), with an annual precipitation over 5000 mm, and a dry season (520 mm monthly precipitation) from December to April and a wet season (860 mm monthly precipitation) from May to November (Rojas, 2011). During the rainy season, the amount of suspended sediments and nutrients increase while salinity decreases to brackish conditions even at the nearshore turbid zones outside the estuaries (Lizano et al., 2001; Picado, 2015; Umaña-Villalobos and Springer, 2006).

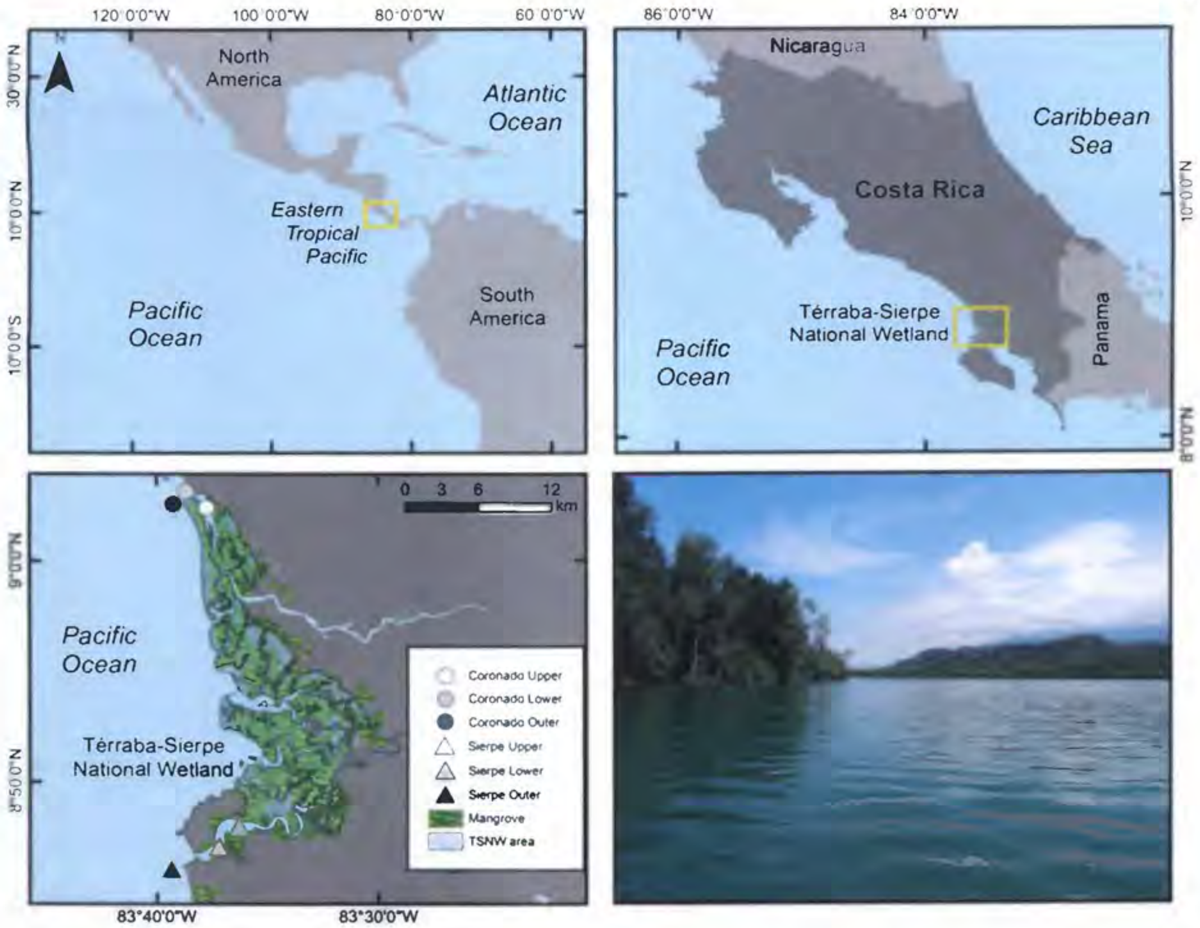

Figure 1. *Map of the Térraba-Sierpe estuarine system, mangrove forest coverage, and sampling stations of the subtidal benthic macrofauna at the Coronado and Sierpe estuaries, Pacific coast of Costa Rica. Low-right corner shows the typical landscape at estuarine subtidal channels at Térraba-Sierpe.*

2.2 Sampling

The estuarine subtidal diversity was assessed by monthly surveys from January to December 2013 (except in February), alternating between Coronado and Sierpe estuaries. At each location, we sampled three stations along the estuarine zonation: 1) upper station: ~5 km landward from the river mouth, 2) lower station: <1 km landward from the river mouth, and 3) outer station: ~1 km seaward from the river mouth (Fig. 1). We collected sediment samples from the middle of the main channel using a Petit-Ponar grab (152 mm × 152 mm, ~0.023 m^2). In order to record the benthic macrofauna biodiversity at soft-bottoms, a minimum 0.1 m^2 area is required (Eleftheriou and McIntyre, 2005); therefore we collected five sediment samples (~0.11 m^2) per sampling station (herein referred as the sum of the five sediment samples at each station – upper, lower, outer – at a given estuary during each month). The samples were stored in plastic bags and fixed using a solution of sea water –filtered with a 63 µm sieve–, 5% formalin, and Bengal Rose (Vargas, 1987). The samples were transported to the laboratory, and gently water-washed through a 500 µm sieve to separate the macrofauna from the finer particles. The obtained material was stored in 95% ethanol, examined under a light dissecting microscope (10X, MOTIC SMZ-168), and all the fauna was separated from remaining particles using dissecting forceps (Vargas, 1987). Additionally, we recorded medium grain size (µm), sorting (ϕ), and organic matter content (%) (see methodological details in Chapter 1) as well as the bottom salinity (psu) using a CTD Sea Bird Electronics 19plus (Table 1S2, Table 3S1).

2.3 Biodiversity

Specimens were identified to the finest taxonomic category possible using the taxonomic keys available for the Eastern Tropical Pacific (ETP) and in some cases with the aid from experts on some groups: Hydrozoa (Carolina Sheridan personal communication), Scaphopoda and Gastropoda (Keen, 1971), Bivalvia (Coan and Valentich-Scott, 2012), Sipuncula (Cutler, 1994a), Polychaeta (Blake et al., 1996; de León-González et al., 2009; Dean, 2001, 1998; Dean and Blake, 2015; Glasby, 1999), Cumacea (Jarquín-González and García-Madrigal, 2013), Isopoda (Brusca and Iverson, 1985), Amphipoda (Rita Vargas personal communication), Stomatopoda (Salgado-Barragán and Hendrickx, 2010), Penaeoidea (Farfante, 1988), Caridea and Brachyura (Fischer et al., 1995), Insecta (Lidia Avilés personal communication), Brachiopoda (Emig and Vargas, 1990), Ophiuroidea (Granja-Fernández et al., 2017, 2016, 2014, Rebeca Granja-Fernández personal communication), Chaetognatha (Tovar and Suárez-Morales, 2007, Rosa Hernández-Flores personal communication), Cephalochordata (Poss and Boschung, 1996; Vargas and Dean, 2010), and Pisci (González-Acosta et al., 2017, Omar Valencia-Méndez personal communication). We identified the absolute relative taxa richness as well as their contribution to the total abundance for the main taxonomical groups. The presence of new records of species in our study area was assessed by comparing our species list with that of Costa Rican marine biodiversity, Central America and the ETP (Coan and Valentich-Scott, 2012; Dean and Blake, 2015; Sibaja-Cordero et al., 2016; Skoglund, 2002; Wehrtmann and Cortés, 2009; Wicksten and Mendez, 1988). For all the species, the updated taxonomic status was corroborated according to the World Register of Marine Species (Board WoRMS Editorial, 2018).

2.4 Spatial and temporal variation of taxa richness

We prepared taxa accumulation curves by sampling effort (both number of sampling stations and sediment samples) for all the macrofauna data from Térraba-Sierpe. .Additionally, we also prepared taxa accumulaitoncurves for season (dry and wet), estuary (Coronado and Sierpe), and station (upper, lower, and outer). The accumulation curves were calculated using the "random" method (Colwell et al., 2004; Gotelli and Colwell, 2010). We calculated the numerical value of the accumulation curves' slopes as a method to test if an asymptote was reached (slope = 0), and the taxa richness for the TS was extrapolated to predict the possible maximum number of benthic macrofauna taxa (Oksanen et al., 2013). These statistics were estimated using the "vegan" package in RStudio (Oksanen et al., 2013; RStudio Team, 2015). The taxa richness (number of taxa) was compared using a Chi-squared test, using the sampling effort (number of sediment grabs) to estimate the expected taxa richness (Krebs, 1999).

Generalized Additive Models (GAM) were performed to analyze the effect of spatial (station and estuary) and temporal (season) variation on taxa richness (number of taxa) of benthic macrofauna using the "mgcv" package in RStudio (Crawley, 2007; RStudio Team, 2015; Wood, 2011). The saturated model considered as factors: 1) station (upper, lower, and outer), 2) estuary (Coronado and Sierpe), 3) season (dry and wet), and 4) all the interactions between these three factors (station × estuary, station × season, estuary × season, station × estuary × season). The model was simplified (excluding factors which did not explain the variation of the benthic macrofauna taxa richness) to determine the factors that best explained the spatial and temporal trends of the response data (Crawley, 2007; Wood, 2011). The results were presented with a boxplot of the median of the values and a plot of the estimated effect over the mean with credible intervals (Wood, 2011).

2.5 Diversity indexes and rarefaction curves

We estimated the Shannon-Wiener index (H'), Equitability index (J), and the Simpon's index of dominance (1-D) per sampling station. The rarefaction curves for each sampling station were calculated to compare the diversity between them. These statistics were estimated using the "vegan" package in RStudio (Oksanen et al., 2013; RStudio Team, 2015).

2.6 Spatial and temporal variation of density

Generalized Additive Models (GAM) were applied to analyze the effect of spatial (station and estuary) and temporal (season) variation on the density of individuals of benthic macrofauna per m^2. The same methodology explained in section 2.4 for the taxa richness was applied to the density (Crawley, 2007; RStudio Team, 2015; Wood, 2011).

3 RESULTS

3.1 Biodiversity

We collected a total of 3391 specimens from 165 sediment grabs and 33 sampling stations. A total of 146 taxa were identified, distributed in 12 phyla, 21 classes, 28 orders, 72 families, and 94 genera (Table 2S1). We identified 81 (54.3%) taxa to the species level (Table 2S1). Annelida was dominant with 60 taxa (41.1%), followed by Mollusca with 41 (28.1%) and Arthropoda with 25 (17.1%), while the other nine was comprised by 20 taxa (13.7 %) (Fig. 2). Pyllodocida had the highest richness of annelids (28), followed by Eunicida (20). Within the mollusks, Bivalvia had more species (24) than Gastropoda (15) and Scaphopoda (2). Decapoda was the crustacean group with the highest richness (11). We found 20 new records for the Costa Rican Pacific: eight mollusks (*Acanthotrophon sorenseni*, *Olivella aureocincta*, *Microglyphis estuarina*, *Donax culter*, *Macoploma hesperus*, *Tellinella zacae*, *Nucula schencki*, *Crassinella coxa*), ten annelids (*Cirriformia violacea*, *Protocirrineris socialis*, *Aricidea* (*Aricidea*) *sanmartini*, *Hemipodia armata*, *Aglaophamus paucilamellata*, *Eteone pacifica*, *Chaetacanthus pilosus*, *Owenia johnsoni*, *Fabrisabella similis*, *Scolelepis* (*Scolelepis*) *acuta*), one estuarine longeye shrimp (*Ogyrides alphaerostris*), and one arrow worm genus (*Spadella*) new for the mainland west coast of the Americas (Table 2S1). A total of 27 taxa were first recorded from subtidal channels of estuarine mangroves and nearshore turbid zones in the Pacific of Central America (Table 2S1).

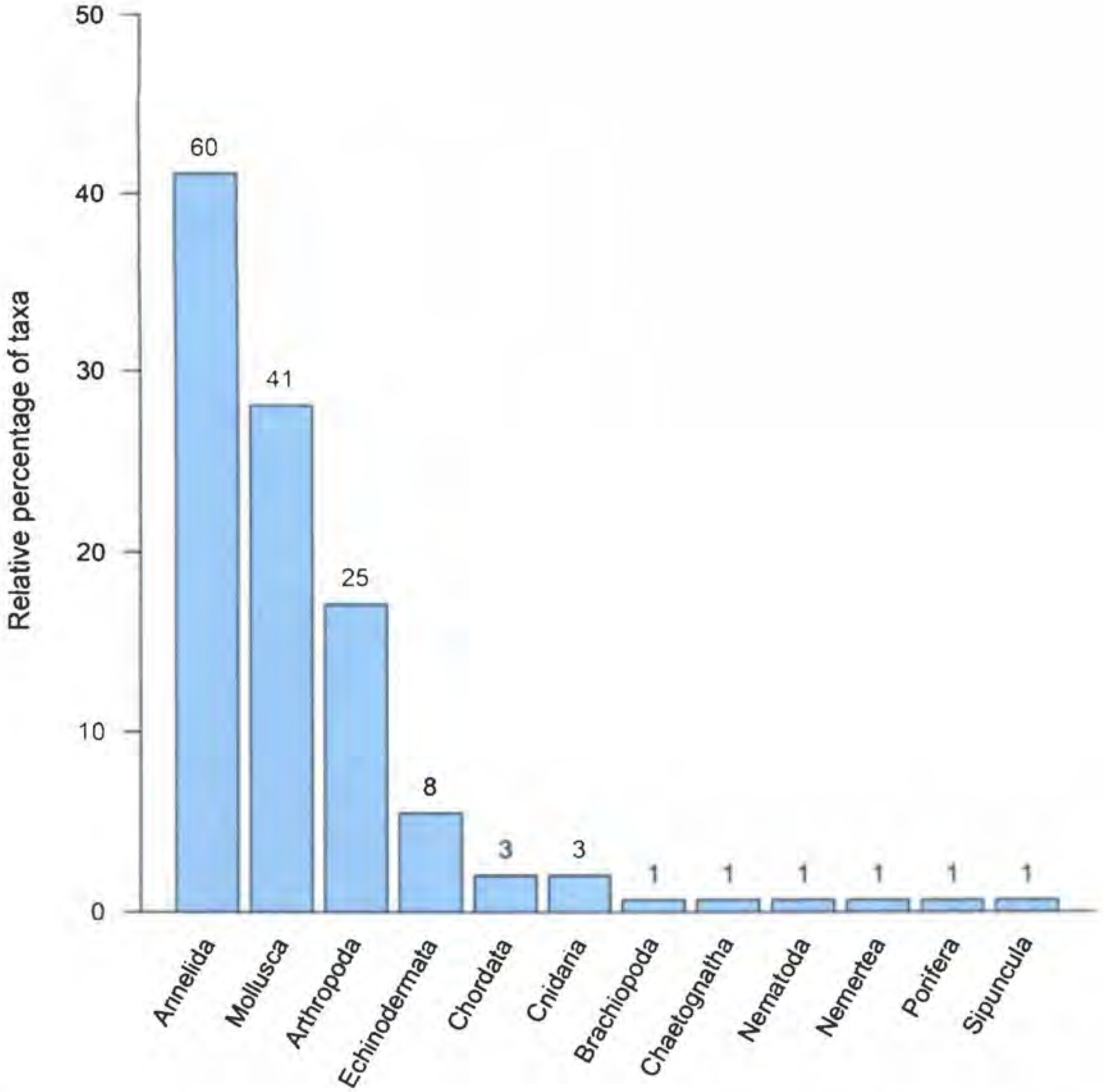

Figure 2. *Biodiversity account: Relative taxa richness (bars) and absolute richness (numbers above the bars) by phyla of subtidal benthic macrofauna from two tropical mesotidal estuaries, Pacific coast of Costa Rica.*

3.2 Spatial and temporal variation of taxa richness

The accumulation curves, both by sampling stations and sediment grabs, reached no asymptote, and their slopes were 0.19 and 0.28, respectively (Fig. 3A-B). We estimated that nearly 203 ± 25.3 taxa could be collected until reaching an asymptote if we increase the sampling effort. The accumulation curves regarding the estuarine zonation showed that the outer and lower stations had steeper curves (0.65 and 0.60, respectively) than the upper (0.40) station (Fig. 4A). But this general pattern was not supported when data were corrected by the sampling effort ($X^2_{2, 165}$ = 1.55.14, p = 0.460). Considering the two estuaries studied herein, Sierpe showed a steeper (0.49) slope than Coronado (0.25) (Fig. 4B), but results corrected by sampling efforts revealed a similar taxa richness between the two estuaries ($X^2_{1, 165}$ = 2.29, p = 0.131). The accumulation curves regarding the season showed that the dry season had a steeper (0.53) slope than the wet season (0.37) (Fig. 4C), the taxa richness was different between the dry and wet season as expected by the sampling effort ($X^2_{1, 165}$ = 11.56, $p < 0.001$). The mean taxa richness per sampling station was 19 ± 10.5 taxa$\cdot$m^{-2}.

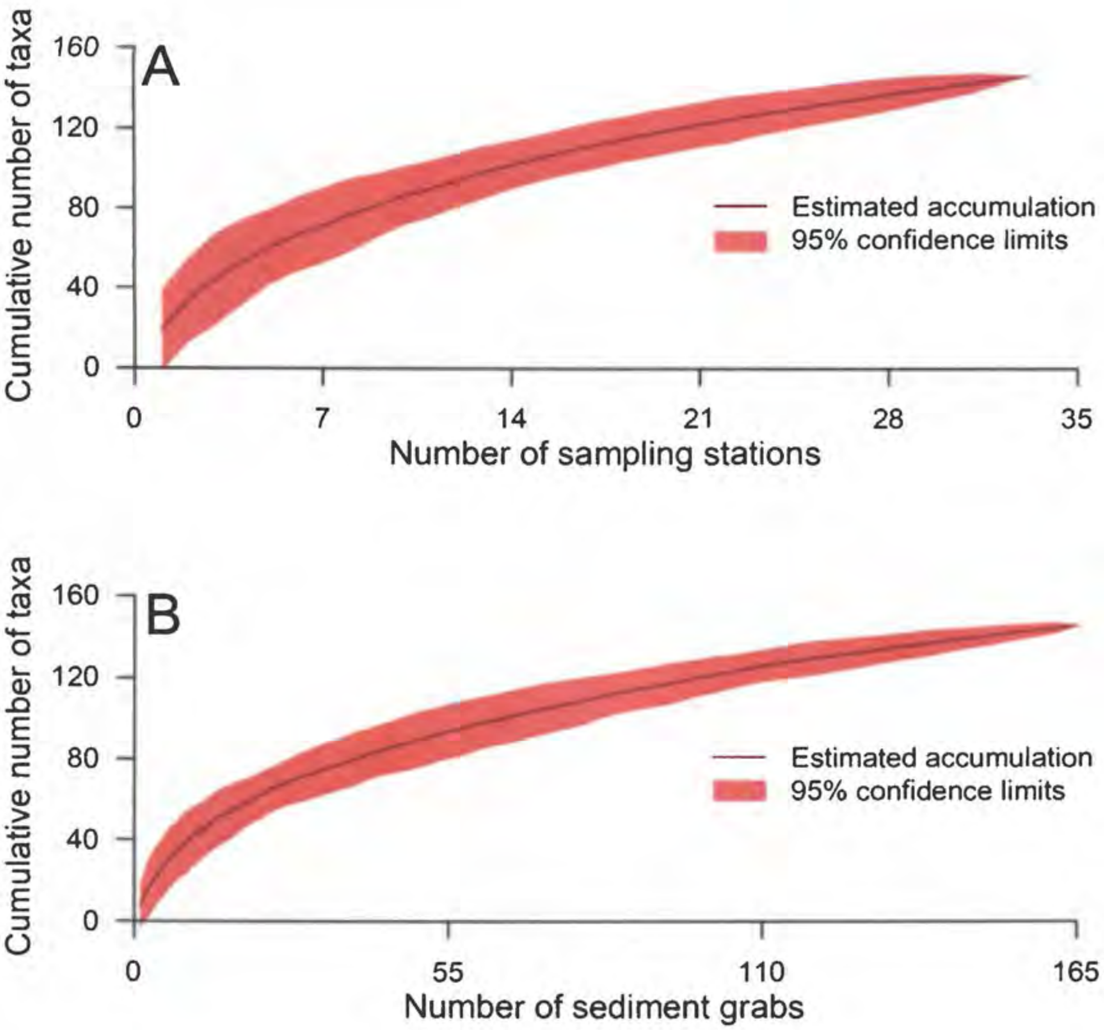

Figure 3. *Taxa accumulation curves estimated using the "random" method and showing 95% confidence limits by A) sampling stations and B) sediment grabs of subtidal benthic macrofauna from two tropical mesotidal estuaries, Pacific coast of Costa Rica.*

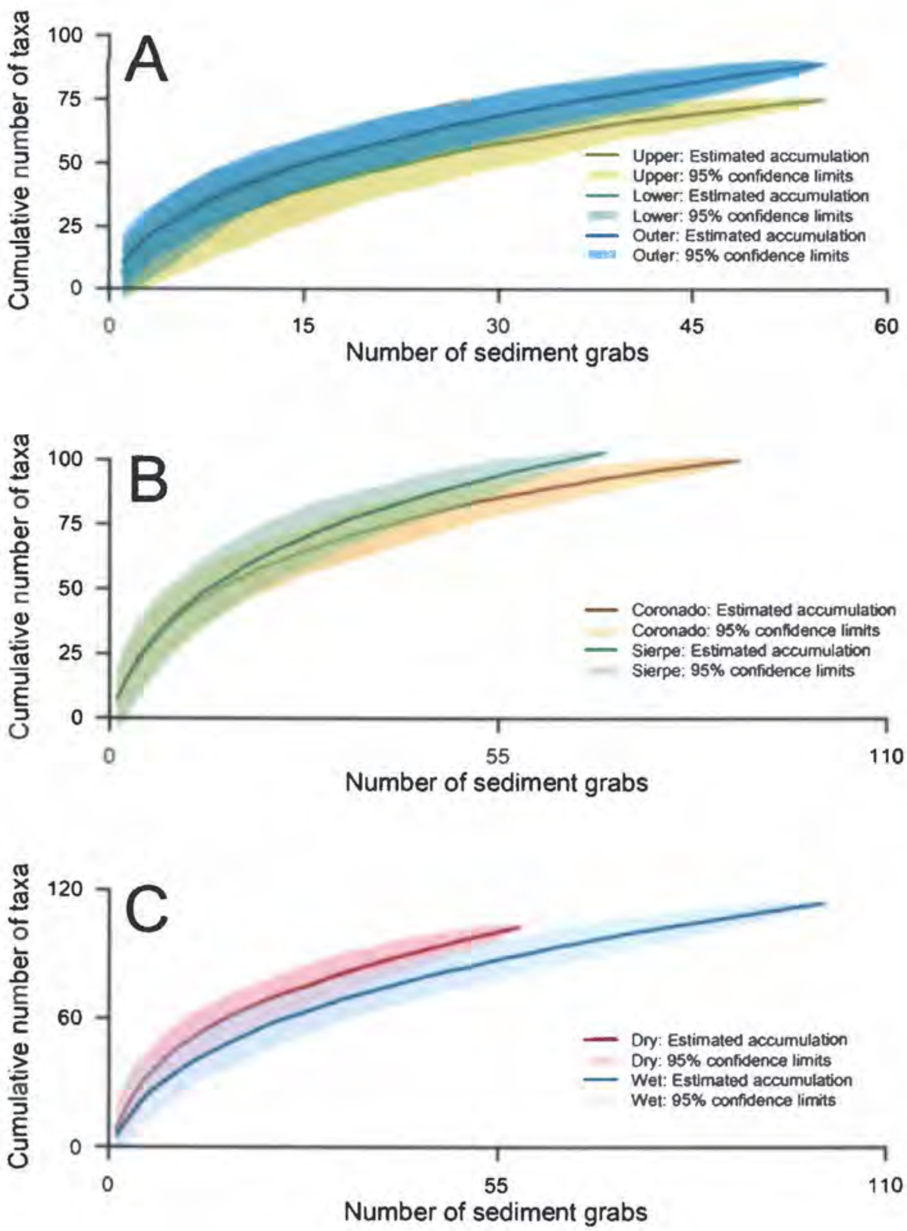

Figure 4. *Taxa accumulation curves estimated using the "random" method and showing 95% confidence limits by A) estuarine zonation (upper, lower, and outer stations), B) estuary (Coronado and Sierpe), and C) season (dry and wet) of the subtidal benthic macrofauna from two tropical mesotidal estuaries, Pacific coast of Costa Rica.*

The GAM for taxa richness explained about 50% of the variance, and detected effects of both season and the interaction station × estuary, but effects of station and estuary alone were not detected (Table 1A, Fig. 5A-F). The taxa richness was higher during the dry season than during the wet season (Fig. 5E,F). Since the GAM detected effects of the interaction station × estuary, we performed two additional GAMs for each estuary, considering the effects of station and season. The GAM for Coronado revealed no effect of station, but it did find an effect of season on the taxa richness (Table 1B, Fig. 6A,B), with higher richness during the dry season than wet season (Fig. 6C,D). The GAM for Sierpe indicated an effect of station on the taxa richness, showing higher richness in the outer station than in the upper station (Table 1C, Fig. 6E,F). In Sierpe, taxa richness was similar between the dry and wet season (Table 1C, Fig. 6G-H).

Since we observed that the taxa richness was differently influenced by season in each estuary, we estimated the taxa accumulation curves for each estuary separately, including both dry and wet season samples. In Coronado, the dry season has a steeper and higher curve than the wet season, indicating that the dry season in Coronado had major diversity than the wet season (Fig. 2S1A). In Sierpe, the dry season did also appear to have a steeper curve than the wet season, but further comparison was truncated by the lesser number of samples from the dry season at Sierpe estuary (Fig. 2S1B).

Table 1. *General Additive Model for spatial and temporal variation of subtidal benthic macrofauna taxa richness (number of taxa) at two tropical mesotidal estuaries at the Pacific coast of Costa Rica, F-statistical value, probability, and model's explained variance. Models considered station (upper, lower, outer), estuary (Coronado, Sierpe) and season (Dry, Wet) as fixed factors.*

A) Macrofauna taxa richness

Saturated model: taxa richness ~ station × estuary × season

Simplified model: taxa richness ~ station × estuary + season

Factor	DF	F	*P* value
Station	2	0.597	0.558
Estuary	1	1.484	0.234
Season	1	7.225	0.012*
Station × Estuary	2	4.381	0.023*

B) Macrofauna taxa richness of Coronado estuary

Saturated model: taxa richness ~ station × season

Simplified model: taxa richness ~ station + season

Factor	DF	F	*P* value
Station	2	0.543	0.593
Season	1	8.390	0.012*

C) Macrofauna taxa richness of Sierpe estuary

Saturated model: taxa richness ~ station × season

Simplified model: taxa richness ~ station + season

Factor	DF	F	*P* value
Station	2	5.107	0.027*
Season	1	0.079	0.784

*: presence of influence on the response variable.

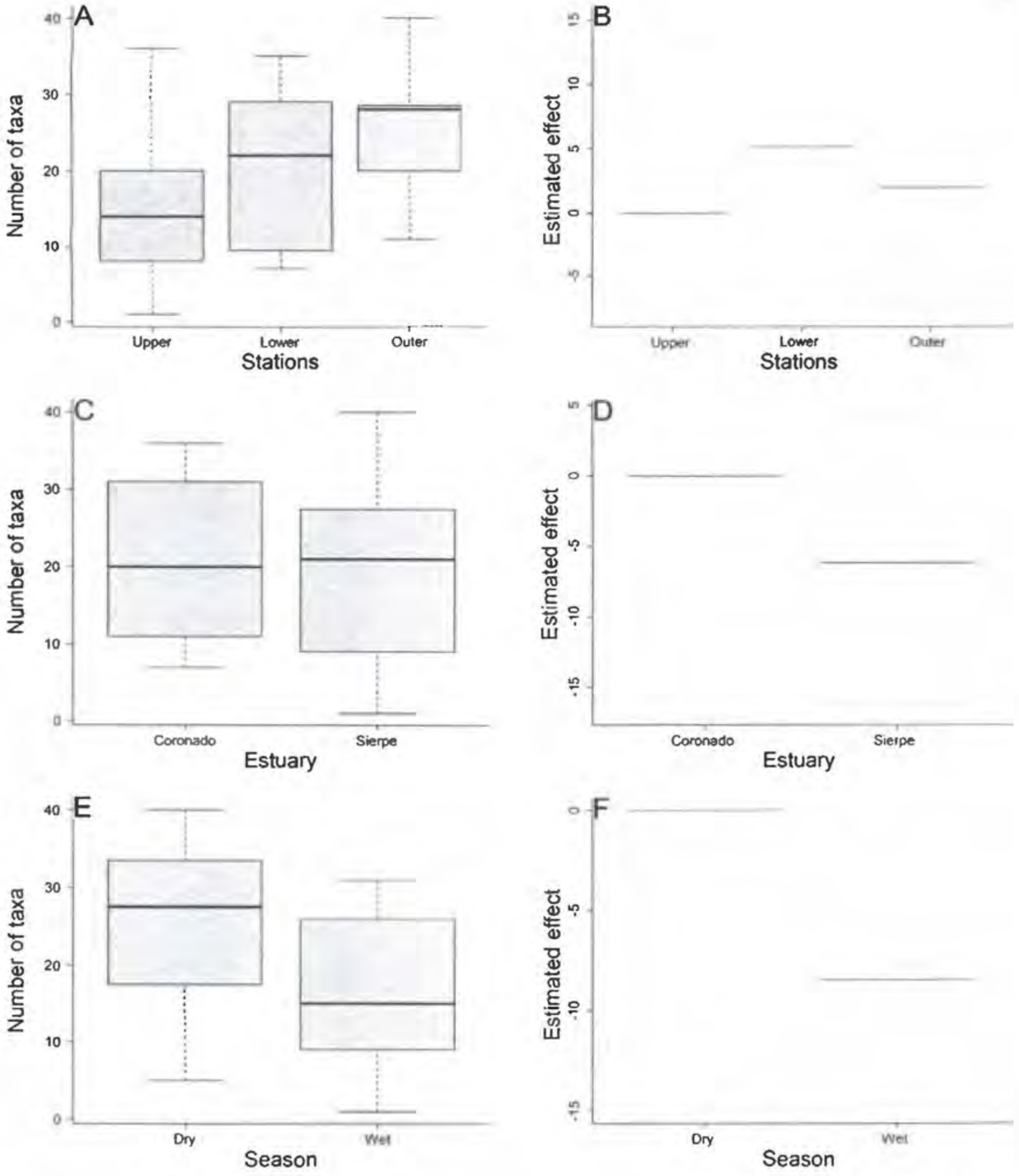

Figure 5. *Taxa richness (number of taxa) of the subtidal benthic macrofauna by station (A. boxplot, B. GAM estimated effect), estuary (C. boxplot, D. GAM estimated effect), and season (E. boxplot, F. GAM estimated effect) for all the samples from two tropical mesotidal estuaries, Pacific coast of Costa Rica.*

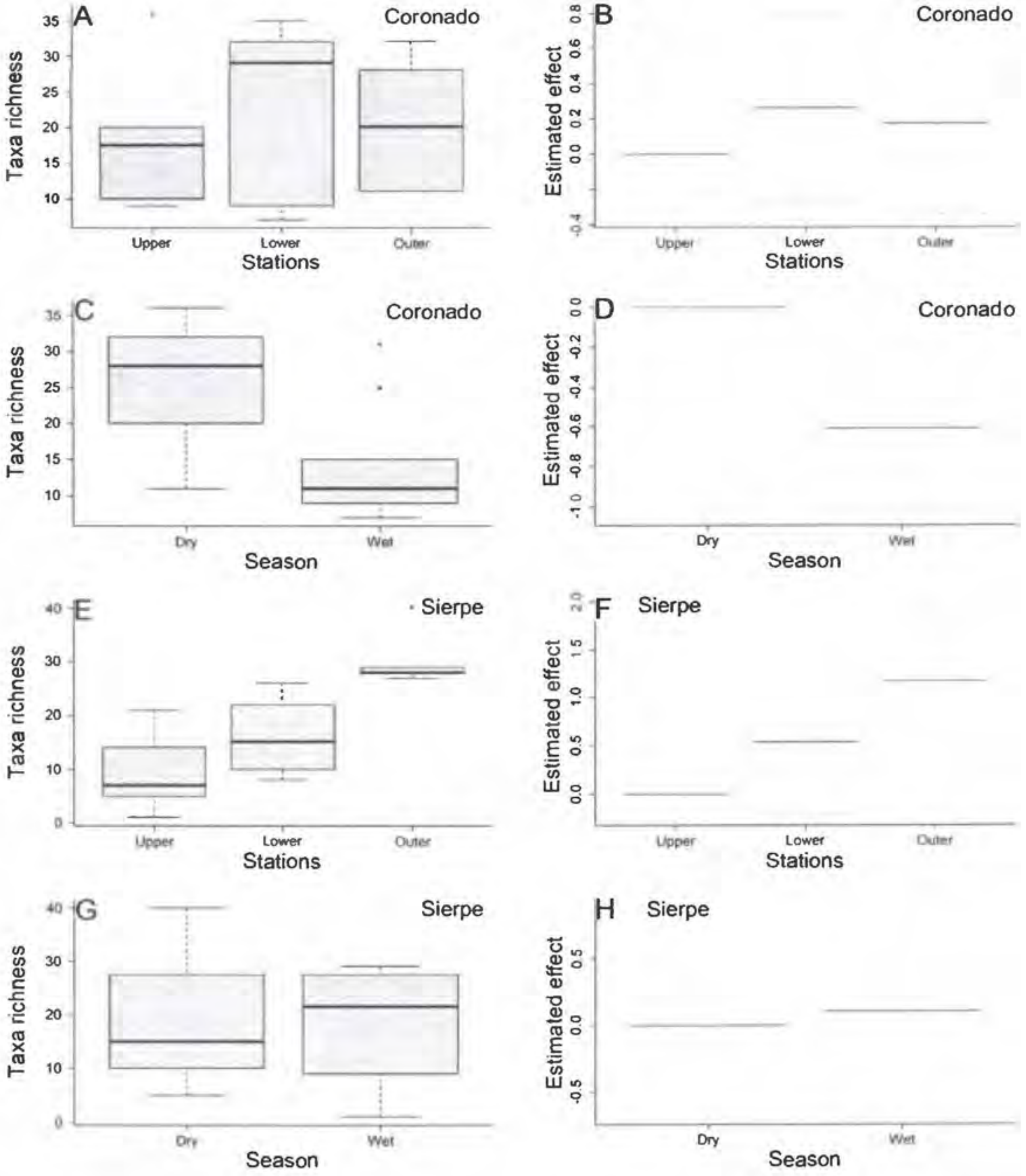

Figure 6. *Taxa richness (number of taxa) of the subtidal benthic macrofauna by station (A. boxplot, B. GAM estimated effect) and season (C. boxplot, D. GAM estimated effect) at Coronado estuary, and by station (E. boxplot, F. GAM estimated effect) and season (G. boxplot, H. GAM estimated effect) at Sierpe estuary, Pacific coast of Costa Rica.*

3.3 Spatial and temporal variation of density

The *mean abundance* per station was 102 ± 113.4 organisms, with a minimum of 0 organisms in the upper station at Sierpe during July, and a maximum of 479 organisms in the upper station at Coronado during October (wet season's peak). The most abundant phylum was Annelida with 58.7% of the organisms, followed by Arthropoda (18.5%) and Mollusca (14.3%), while the other nine phyla contributed with nearly 8.5% (Fig. 7). The most abundant taxa were the polychaetes *Scolelepis* (*Scolelepis*) *acuta*, *Paraprionospio pinnata*, *Malacoceros indicus*, *Leptonereis laevis*, *Magelona riojai*, *Armandia* cf. *salvadoriana* and *Nephtys oculata*, the peracarids of the family Corophiidae and Cumaceans, bivalves of the family Tellinidae, and Nematods. These 11 taxa constituted 59.9% of all the collected organisms, each with more than 100 individuals (Fig. 2S2). A total of 28 species contributed with more than 10 but less than 100 individuals, and 107 species contributed with less than 10 individuals (Table 1). The average macrofauna density was 934 ± 1030.2 ind$\cdot$m^{-2}, (from 0 to 9436 ind$\cdot$m^{-2}).

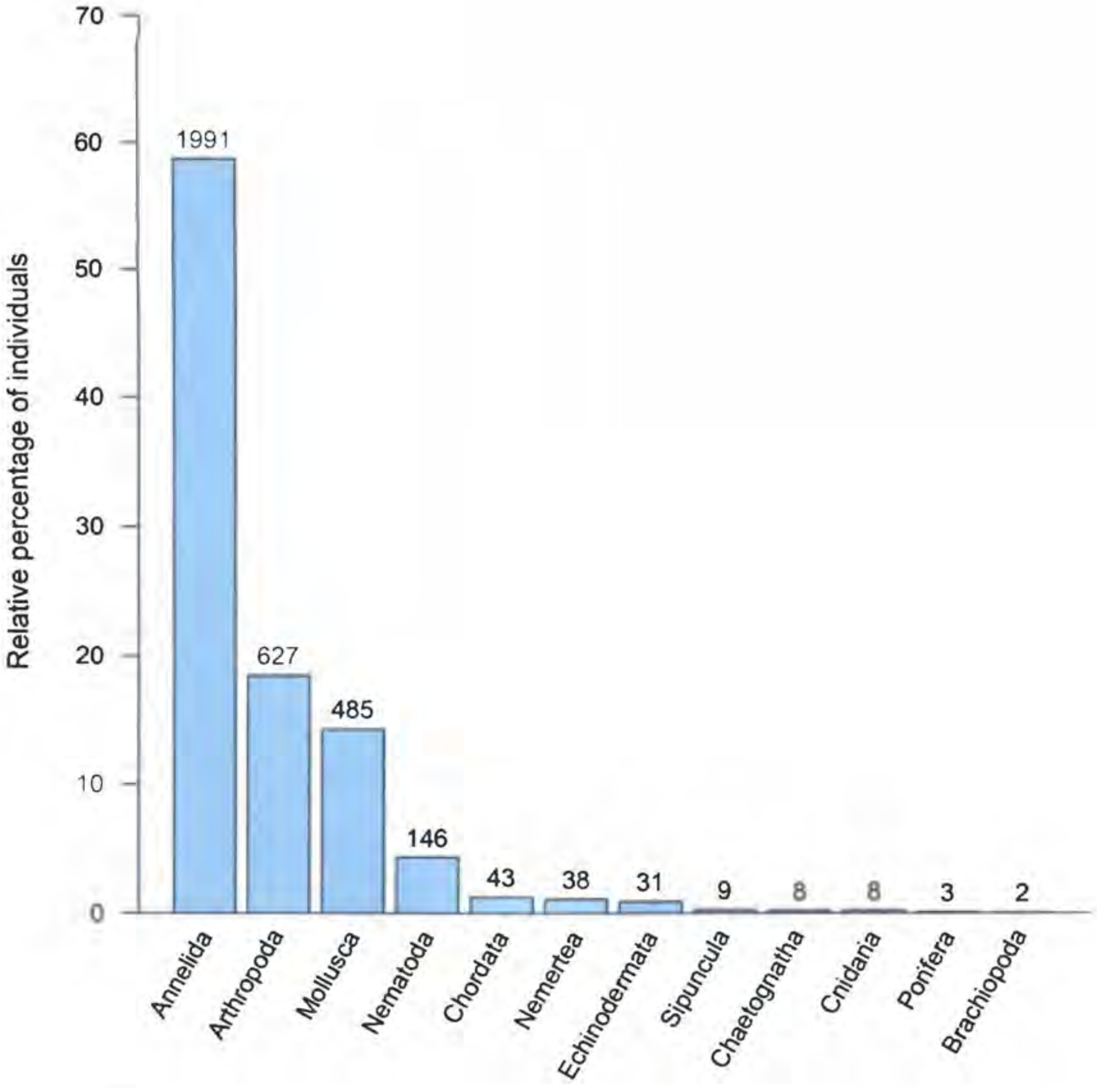

Figure 7. *Relative abundance (bars) and absolute abundance (numbers above the bars) by phyla of the subtidal benthic macrofauna from two tropical mesotidal estuaries, Pacific coast of Costa Rica.*

The GAM for density explained about 30% of the variance, and detected effects of estuary; effects of station alone, however, were not found (Table 2A, Fig. 8A,B). The season was not maintained as a factor in the model for macrofauna density (Table 2A). The benthic macrofauna density was higher in Coronado than in Sierpe (Fig. 8C,D). Since the GAM revealed effects of the interaction station × estuary, we performed two additional GAMs for each estuary. Both models did not keep season as a factor (Table 2B,C). In Coronado, GAM showed that station had no effect on the density (Table 2B, Fig. 8E,F), the GAM for Sierpe, however, detected an effect of station on the density, which was higher in the outer than in the upper station (Table 2C, Fig. 8G,H).

Table 2. *General Additive Model for spatial and temporal variation of subtidal benthic macrofauna density (organisms·m^{-2}) at two tropical mesotidal estuaries at the Pacific coast of Costa Rica, F-statistical value, probability, and model's explained variance. Models considered station (Upper, Lower, Outer), estuary (Coronado, Sierpe), and season (Dry, Wet) as fixed factors.*

A) Macrofauna density (organisms·m^{-2})

Saturated model: density ~ station × estuary × season

Simplified model: density ~ station × estuary

Factor	DF	F	*P* value
Station	2	0.402	0.673
Estuary	1	10.300	0.004*
Station × Estuary	2	4.178	0.030*

B) Macrofauna density (organisms·m^{-2}) of Coronado estuary

Saturated model: density ~ station × season

Simplified model: density ~ station

Factor	DF	F	*P* value
Station	2	0.497	0.618

C) Macrofauna density (organisms·m^{-2}) of Sierpe estuary

Saturated model: density ~ station × season

Simplified model: density ~ station

Factor	DF	F	*P* value
Station	2	5.537	0.020*

*: presence of influence on the response variable.

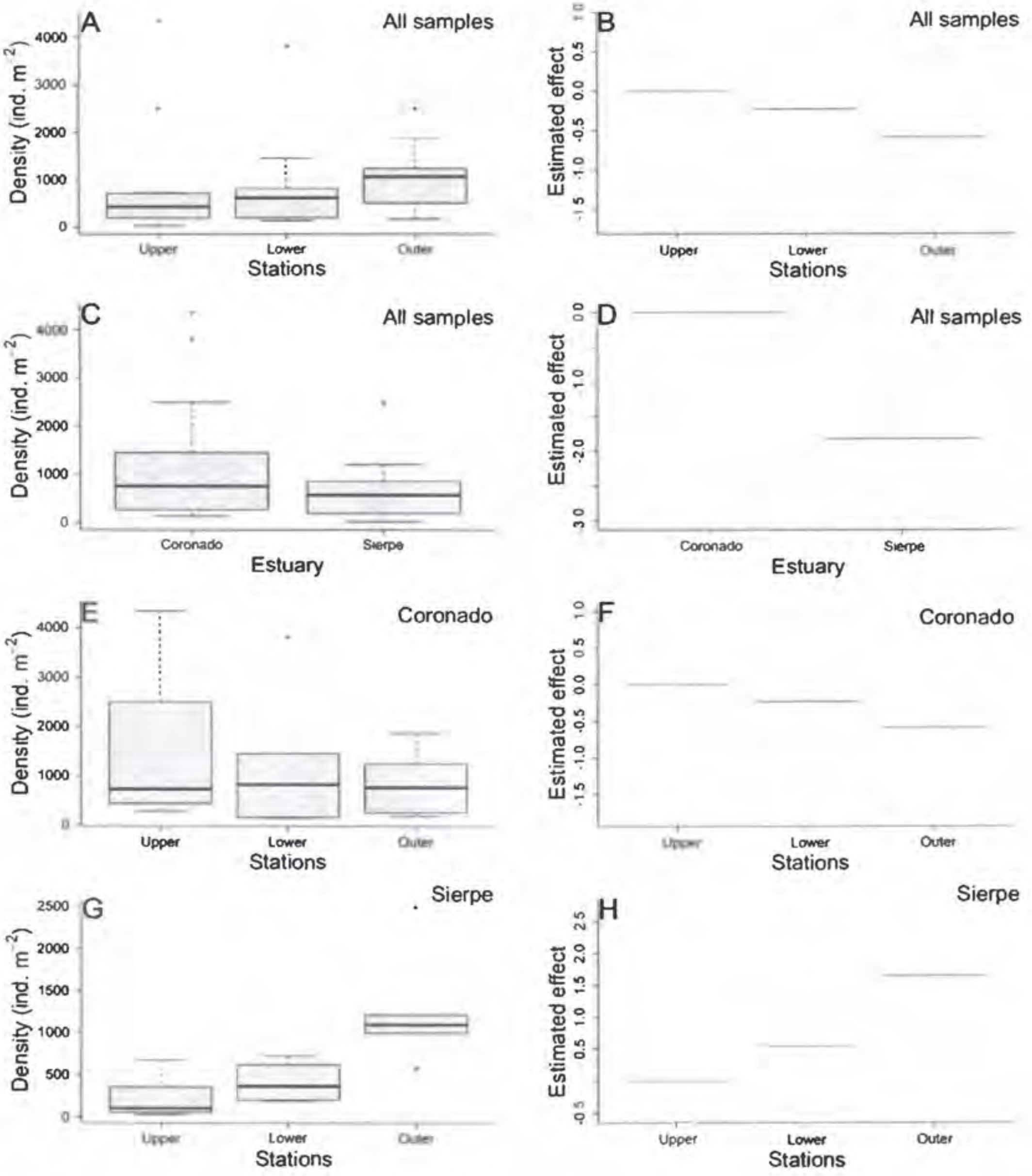

Figure 8. *Density (ind·m^{-2}) of subtidal benthic macrofauna by station (A. boxplot, B. GAM estimated effect), estuary (C. boxplot, D. GAM estimated effect) for all the samples from two tropical mesotidal estuaries, Costa Rica. Density (ind·m^{-2}) of subtidal benthic macrofauna by station at Coronado estuary (E. boxplot, F. GAM estimated effect) and Sierpe estuary (G. boxplot, H. GAM estimated effect), Pacific coast of Costa Rica.*

3.4 Diversity indexes and rarefaction curves

The overall Shannon-Wiener index (H') for subtidal benthic macrofauna of TS was 2.23, with a mean H' of 2.71 per sampling station. The highest mean H' (3.41) was found in Sierpe's lower station during the wet season, while the lowest mean H' (1.06) occurred in Coronado's upper station during the wet season (Table 3). We observed a pattern of H' increasing from the upper station to the outer station, but were very similar between seasons and estuaries (Fig. 2S3). The total mean Equitability index (J) was 0.81, with a mean J of 0.78 per sampling station. The highest J (0.97) occurred in Sierpe's upper station during the dry season, when only five taxa (peracarids of the family Corophiidae, the polychaete *Mediomastus californiensis*, the bivalve *Crassinella* cf. *ecuadoriana*, and the gastropods *Natica scethra* and *Strioturbonilla* sp.) were collected, the abundance was evenly divided between them (Table 3). The lowest J (0.32) was estimated for Coronado's upper station during the wet season, when up to 11 species were found. One polychaete, *Scolelepis* (*Scolelepis*) *acuta*, however, was remarkably abundant with 432 individuals and dominated the abundance (Table 3). No spatial or temporal pattern was detected regarding the J (Fig. 2S3). The Simpson index of dominance (1-D) had a total mean of 0.80, with a mean 1-D of 0.86 per sampling station. The highest 1-D (0.95) was found at both lower and outer station of Sierpe during the wet season (Table 3). The lowest 1-D (0.39) was recorded at Coronado's upper station during the wet season, when *S.* (*S.*) *acuta* was dominant (Table 3). We observed no spatial or temporal pattern regarding the 1-D (Fig. 2S3).

Table 3. *Mean (± SD) and range of depth (m), number of individuals, taxa richness, mean (± 95% confidence limits) and range of Shannon-Wiener index (H'), and range Equitability index (J) and Simpson index (1-D) per sampling stations (by season, estuary, and station) regarding the subtidal benthic macrofauna of two tropical mesotidal estuaries, Pacific coast of Costa Rica.*

Season	Estuary	Station	Number of sampling stations (grabs)	Mean depth ± SD (range, m)	Mean number of individuals ± SD (range)	Mean number of taxa ± SD (range)	Mean Shannon-Wiener (range, H')	Mean Equitability (range, J)	Mean Simpson (range, 1-D)
Dry	Coronado	Upper	3 (15)	3.7 ± 0.59 (3-5)	144 ± 113.46 (77-275)	20.4 ± 7.06 (20-36)	2.79 (2.74-2.99)	0.70 (0.69-0.75)	0.86 (0.85-0.90)
		Lower	3 (15)	5.1 ± 0.69 (4-6)	221.7 ± 175.6 (86-420)	31.3 ± 3.35 (27-35)	3.01 (2.96-3.13)	0.75 (0.74-0.78)	0.91 (0.90-0.93)
		Outer	3 (15)	8.0 ± 0.89 (7-9)	120.3 ± 94.11 (19-205)	23.6 ± 3.03 (11-32)	2.92 (2.84-3.07)	0.75 (0.73-0.79)	0.91 (0.89-0.92)
	Sierpe	Upper	1 (5)	10.4	6	5	1.56	0.97	0.78
		Lower	1 (5)	9.0	40	15	2.33	0.86	0.86
		Outer	1 (5)	8.0	274	40	2.84	0.77	0.90
Wet	Coronado	Upper	3 (15)	6.1 ± 2.68 (4-10)	185.3 ± 254.46 (30-479)	11.3 ± 1.79 (9-15)	1.06 (0.99-1.24)	0.32 (0.30-0.38)	0.39 (0.35-0.45)
		Lower	3 (15)	3.6 ± 0.07 (3-4)	41.3 ± 44.75 (15-93)	15.7 ± 2.35 (7-31)	3.16 (2.99-3.27)	0.88 (0.85-0.92)	0.94 (0.92-0.95)
		Outer	3 (15)	13.2 ± 2.63 (7-15)	63.7 ± 46.52 (27-116)	17.0 ± 3.21 (11-25)	2.67 (2.52-2.84)	0.76 (0.72-0.81)	0.87 (0.84-0.90)
	Sierpe	Upper	4 (20)	7.2 ± 2.33 (5-12)	31.8 ± 32.12 (3-74)	10.8 ± 5.36 (1-21)	3.09 (2.97-3.21)	0.88 (0.85-0.92)	0.94 (0.93-0.95)
		Lower	4 (20)	9.0 ± 1.58 (8-13)	47.5 ± 30.36 (21-79)	16.5 ± 5.36 (8-26)	3.41 (3.29-3.53)	0.87 (0.85-0.9)	0.95 (0.94-0.96)
		Outer	4 (20)	8.3 ± 0.16 (8-9)	106.3 ± 30.46 (63-133)	28.0 ± 5.85 (27-29)	3.35 (3.32-3.49)	0.81 (0.8-0.84)	0.95 (0.94-0.96)
Total			**165**	**7.6 ± 2.77 (3-15)**	**102 ± 113.4 (3-479)**	**19 ± 10.5 (1-40)**	**2.23 (0.00-3.06)**	**0.81 (0.19-0.97)**	**0.80 (0.00-0.93)**

There was no obvious pattern of the rarefaction curves; however, most of the outer and lower stations had steeper and higher curves than upper stations, meaning that the upper estuary had the lowest diversity (Fig. 9). Regarding the estuary, Sierpe's samples had steeper and higher curves than samples from Coronado, indicating that Sierpe was generally more diverse than Coronado (Fig. 9). Some samples from the wet season had steeper curves than samples from the dry season (Fig. 9), suggesting that the macrofauna was more diverse at these stations during the wet season than during the dry season. Two samples from Coronado's upper station, however, had the lowest curves (lower diversity) during the wet season due to the dominant abundance of *S.* (*S.*) *acuta* (Fig. 9).

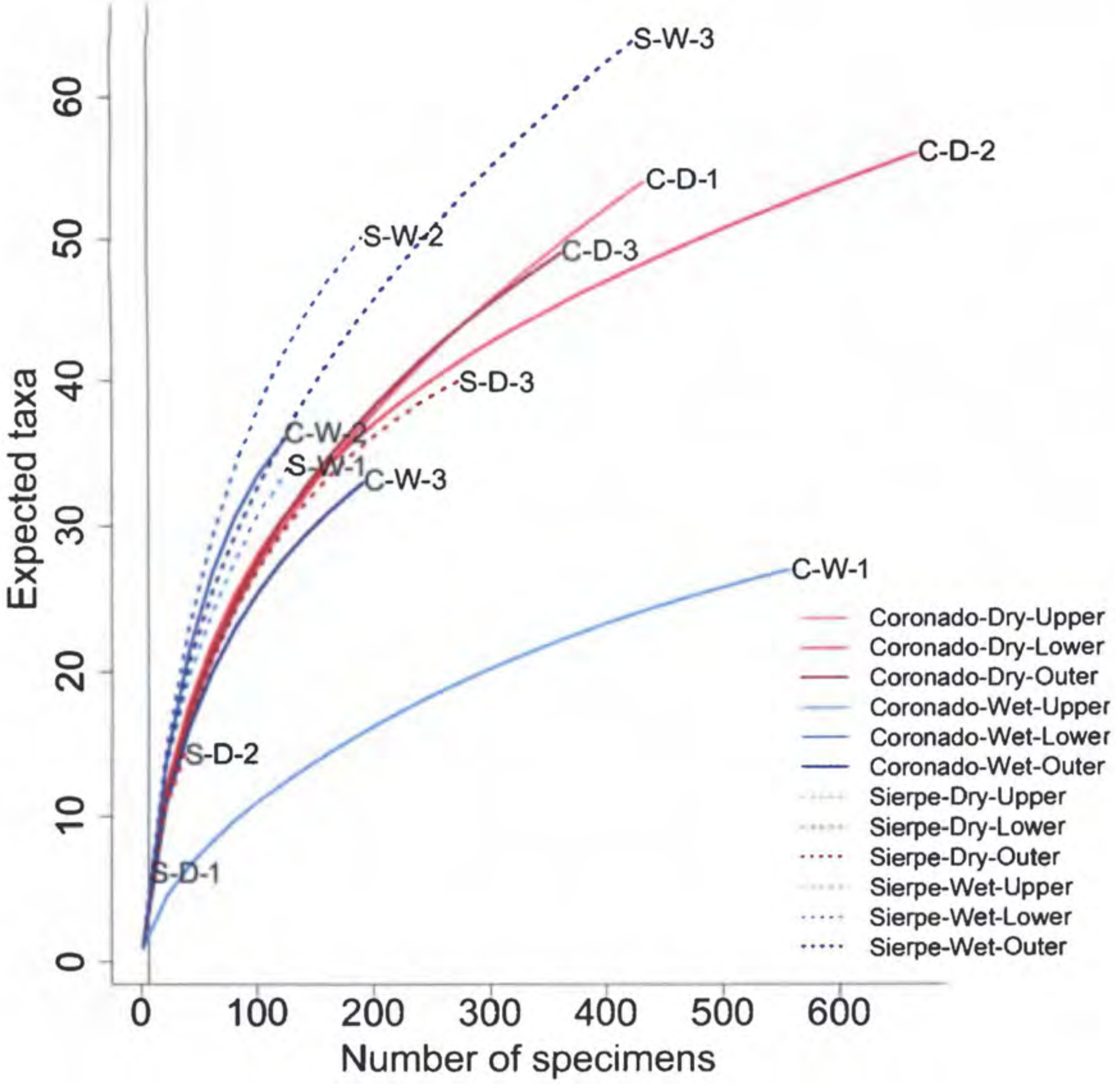

Figure 9. *Rarefaction curves for the sampling stations (regarding estuary: Coronado and Sierpe; season: dry and wet; and estuarine zonation: Upper, Lower, and Outer) by the number of specimens of the taxa from two tropical mesotidal estuaries, Pacific coast of Costa Rica. Estuary: Coronado = c, Sierpe = s; Season: dry = d, wet = w; Stations: 1 = upper, 2 = lower, 3 = outer.*

4 DISCUSSION

4.1 Biodiversity and new records

Here we report a total of 146 taxa inhabiting the subtidal channels and nearshore turbid zone of the Térraba-Sierpe estuary. This value is higher than that from some sub-tropical and temperate estuaries, such as Shuangtaizi estuary (29 spp.), China (Zhang et al., 2016), Broke inlet (32 spp.), Australia (Tweedley et al., 2012), Peel-Harvey (63 spp.), Australia (Wildsmith et al., 2009), but lower compared to others such as Port Curtis estuary (466 spp.), Australia (Currie and Small, 2006b) and Gulf of Nicoya (206 spp.), Costa Rica (Maurer et al., 1984). It is important to notice that the estimated number of taxa is 203, which is very similar to the value indicated for the Gulf of Nicoya (Maurer et al., 1984). Comparisons between estuaries based on total number of species, however, should be revised with caution, due to the different sampling techniques, sampling effort (e.g. area, number of specimens analyzed, etc.), and capacities for detailed identification (e.g. complete checklists, taxonomic specialists, and taxonomic guides). Moreover, identifying the marine and coastal subtidal benthic macrofauna is highly time-consuming and often costly, and as a consequence detailed taxonomic studies on the biodiversity of these environments are scarce (Corte et al., 2017). Therefore, comparisons of general spatial and temporal patterns of biodiversity and productivity in estuaries are more useful (Elliott and Whitfield, 2011). Dominance (both taxa richness and abundance) of annelids, mollusks and arthropods in Térraba-Sierpe estuary is similar to results from other tropical and subtropical estuaries such as Shuangtaizi (Zhang et al., 2016), Peel-Harvey (Wildsmith et al., 2009), Todos Os Santos bay (Pires-Vanin et al., 2011), Port Curtis (Currie and Small, 2006b), and Gulf of Nicoya (Maurer and Vargas, 1984).

The Costa Rican Pacific harbors a marine biodiversity of more than 4745 species (Wehrtmann and Cortés, 2009), and the 20 new records found in this study increase this biodiversity by approximately 0.42%. Most of these new records (16) are species which could be expected in Costa Rica considering the distribution range of these species; however, no previous sampling had recorded them in Costa Rica (Coan and Valentich-Scott, 2012; Dean and Blake, 2015; Sibaja-Cordero et al., 2016; Skoglund, 2002; Wehrtmann and Cortés, 2009; Wicksten and Mendez, 1988). On the other hand, four of these new records represent range extensions: (1) The paraonid worm *Aricidea* (*Aricidea*) *sanmartini* was described from Coiba Island, Panama (Aguado and López, 2003), and now its distribution is extended northward to Térraba-Sierpe in Costa Rica (~257 km). (2) The distribution range of the nucule shell, *Nucula schencki*, is extended from Puerto Huatulco, Oaxaca, Mexico, to Térraba-Sierpe, Costa Rica (~1596 km). (3) The estuarine longeye shrimp, *Ogyrides alphaerostris*, was reported from California, USA, and Sinaloa, Mexico, in the ETP (Ayón-Parente and Salgado-Barragán, 2013; Wicksten and Hendrickx, 2003; Wicksten and Mendez, 1988), and our collected specimens extent its range distribution southward to Térraba-Sierpe, Costa Rica (~3187 km). (4) Our report of the arrow worm genus *Spadella* represents the first one for the western mainland of the Americas (Pacific coast). This genus has been reported in the eastern mainland of the Americas (Atlantic) (Tovar and Suárez-Morales, 2007) and in Isla del Coco in the oceanic region of the ETP (~532 km from Térraba-Sierpe) (Sibaja-Cordero et al., 2016). Moreover, we identified several organisms to a *confer* status, and some even to genus or higher levels, because the information available at the time does not allow a more specific identification. Future taxonomic work, including molecular tools, should be carried out to enhance the identification and clarify if some of these organisms correspond to new species or represent a species complex. Our results suggest that more taxa will be recorded in this estuarine system if sampling effort increases. Therefore, a continuous effort to assess and publish biodiversity records is necessary to improve future efforts on research, conservation and management of this coastal habitat.

A total of 27 species have not been recorded previously from subtidal channels and nearshore turbid zones in the Pacific of Central America. Estuarine mangroves represent environments rich in microhabitats (e.g. decaying wood, sediments, log, leaf litter, etc.) promoting high biodiversity (Loría-Naranjo et al., 2018; Sibaja-Cordero and Echeverría-Sáenz, 2015). Despite this potential for biodiversity and ecological studies, tropical estuaries have been less studied than its temperate counterparts (Alongi, 1990; Dittmann and Vargas, 2001; Elliott and Whitfield, 2011; Maurer et al., 1984). Future studies should address a comprehensive revision of biodiversity at tropical estuaries, including records from subtidal and intertidal sediments, the water column, and the vegetation.

4.2 Spatial and temporal variation of taxa richness

Taxa richness was similar between the two studied tropical estuaries, Coronado (n = 97) and Sierpe (n = 104). A total of 57 taxa were shared between the two estuaries. Tropical estuaries are considered as highly variable regarding its diversity patterns, and local features of each estuary are considered to be highly influential on its diversity (Elliott and Whitfield, 2011). Moreover, two estuaries may show the same taxa richness, but different assemblages structures (Sanders, 1968). Therefore, further analyzes including numerical values for each taxa will be necessary to properly assess the spatial biodiversity patterns of the Térraba-Sierpe macrofauna.

The positive correlation between the richness and the estuarine gradient (from inner estuary to seaward) has been mentioned for temperate estuaries: Loch Linhe and Eil, Scotland (Feder and Pearson, 1988) and Tees estuary, England (Tapp et al., 1993); as well as for tropical estuaries: Gulf of Nicoya, Costa Rica (Maurer et al., 1984; Maurer and Vargas, 1983), Laguna de Términos, Mexico (Hernández-Alcántara and Solis-Weiss, 1995) and Todos Os Santos Bay, Brazil (Pires-Vanin et al., 2011). Our results do not reflect this pattern of increasing biodiversity from the upper stations (upper estuary, more freshwater influence) towards lower and outer stations (lower estuary, mixing zone, nearby turbid zone, more marine influence) at the overall system; however, the appearent slight increase trend in one fo the estuaries is discussed further below. Estuarine biodiversity is expected to decrease with wide salinity fluctuations and freshwater inputs (Remane and Schlieper, 1972), however, some estuarine assemblages have shown a strong relation with other variables such as organic matter input, water-motion energy, and sediment features (Currie and Small, 2006b; Gray, 1981; Maurer and Vargas, 1983; McLusky et al., 1993; Sanders, 1968). Therefore, Térraba-Sierpe estuarine macrofauna should be analyzed in relation to these other environmental variables, and how they influence the species level and the assemblage structure.

Térraba-Sierpe macrofauna's taxa was more diverse during the dry season than during the wet season. We assume that this result was related to the freshwater input during the wet season (Table 3S1). Wide variability of environmental factors (e.g. salinity) may affect the survival of some species inhabiting estuaries and affect the assemblage structure (Remane and Schlieper, 1972). Temporal variation in tropical estuaries can be driven by the high precipitation rates and associated freshwater inputs from the catchment area into the estuarine system during the wet season. A negative relation between diversity (number of taxa) and the freshwater influence has been observed in benthic diatoms (Patil and Anil, 2008), zooplankton (da Costa et al., 2008), fish assemblages (Barletta et al., 2005; Ortiz-Araya et al., 2018), intertidal (Dittmann and Vargas, 2001; Vargas-Zamora et al., 2015, 2012; Vargas-Zamora and Sibaja-Cordero, 2011; Vargas, 1987) and subtidal (Hernández-Alcántara and Solis-Weiss, 1995; Maurer et al., 1984; Maurer and Vargas, 1983) benthic macrofauna of tropical estuaries. Similarly, we found less diversity during the season with higher freshwater input.

Although taxa richness was similar between estuaries and between stations at a general system level, our results indicate an influence of the interaction estuary × station on the richness. Analyses performed separately for each estuary showed that station had effect only on Sierpe's taxa richness, while in Coronado taxa richness was influenced primarily by the season. Therefore, our results suggest that these close-by estuaries are differently affected by spatial and temporal factors, supporting Elliott and Whitfield (2011) statement that estuarine biodiversity patterns are highly influenced by local features at each estuary.

Heterogeneous sediments generally favor macrofauna diversity by the increase of interstitial habitats available for invertebrates (Gray, 1981, 1974; Gray and Elliott, 2009; Sanders, 1968). We previously observed that sediments in Térraba-Sierpe changed from poorly sorted (more heterogenous) during the dry season to well sorted sediments (more homogeneous) towards the end of the wet season (see Chapter 1). Moreover, the sorting improved from upper and lower stations (more heterogeneous) toward the outer stations (more homogeneous) (see Chapter 1). The general pattern of high macrofauna diversity linked to heterogeneous sediments would suppose a higher macrofauna richness during dry season than during wet season, and at outer stations compared to upper and lower stations in the case of Térraba-Sierpe. Such a seasonality pattern, however, was only observed at Coronado, with higher richness during the dry season than during the wet season. The estuarine zonation pattern was only observed at Sierpe, where richness was higher at the outer station compared to the upper station. According to Umaña et al. (2015) sedimentation rates at Coronado estuary are very high, and probably have an effect on the sediment composition (see Chapter 1). The land use between the catchment area of Coronado and Sierpe is significantly different, with several large population centers (>5000 people), 45% of non-forest coverage, and ~42 km of highways running through rocky cliffs along the Grande de Térraba river (Coronado's main tributary), while in Sierpe the non-forest coverage is 40%, and there are not large population centers neither highways running along the river shores. Therefore the effects of erosion processes at Coronado are probably more tangible (see Chapter 1). This may cause a mayor homogenization of sediments at Coronado, precluding differences between upper, lower and outer stations. High erosion rates at the catchment area may have shown to affect the benthic macrofauna at the estuaries (Wildsmith et al., 2011) and even areas off the coast (Bone et al., 2011).

The organic matter composition and abundance are important factors driving benthic marine biodiversity (Lee, 2008). In a previous study we observed that the organic matter was lower at the lower and outer stations compared to the upper station (higher value in Sierpe than Coronado) (see Chapter 1). High amounts of organic matter may decrease the dissolved oxygen in the sediment down to anoxic condition, negatively affecting the macrofauna (McArthur et al., 2010). This may explains in part the low richness value encountered at the upper station of Sierpe.

4.3 Spatial and temporal variation of density

The overall mean density of macrofauna in Térraba-Sierpe (934 ind·m^{-2}) was relatively low compared with another tropical estuary: Gulf of Nicoya (1269 ind·m^{-2}), Costa Rica (Maurer and Vargas, 1984). The bottom salinities at Térraba-Sierpe reached lower values (down to 13.20 ppt, Table 3S1) than Gulf of Nicoya (down to 26.6 ppt) (Maurer and Vargas, 1984). Wide variations of salinity may affect the survival of organisms at estuaries (Elliott and Whitfield, 2011; Gray, 1981; Remane and Schlieper, 1972) and may be responsible for the lower macrofauna density in our study area.

The density of macrofauna at Térraba-Sierpe was influenced by the estuary, with Coronado presenting higher densities than Sierpe. We also found that there was an effect of the interaction estuary × station on the macrofauna density. These results suggest that density was similar between stations in Coronado, while in Sierpe there was a gradient of increasing density from the upper estuary to the seaward. The most common species in our study, *Scolelepis* (*Scolelepis*) *acuta* (12.8% of total abundance), was only found at the upper station of Coronado, precluding differences between stations. This spionid worm is considered to be a deposit and suspension feeder (Fauchald and Jumars, 1979; Jumars et al., 2015), taking advantage of both the few competitors and the organic matter inputs at the upper estuary (Elliott and Whitfield, 2011; Gray, 1981). A similar pattern was observed off the Orinoco river delta at Venezuela, where the densities of another spionid worm *Dipolydora socialis* (Spionidae) were higher at areas closer to the estuary (higher sedimentation and lower diversity) (Bone et al., 2011). On the other hand, Sierpe estuary showed a clear gradient of increasing density from inner to seaward stations. We assume that the combination of high organic matter and low salinities (Table 3S1, see Chapter 1) is responsible for the low densities observed at the upper estuary (dicussed below). The pattern in Sierpe agrees with the findings from other estuaries such as the temperate estuaries: Tees estuary (Tapp et al., 1993) and Shuangtaizi estuary(Zhang et al., 2016), and the tropical estuaries: Todos Os Santos Bay (Pires-Vanin et al., 2011) and Gulf of Nicoya (Maurer and Vargas, 1984). Contrarily, the subtropical estuary, Port Curtis, showed an increase of macrofauna's density in sites with freshwater influence (Currie and Small, 2006b).

4.4 Diversity indexes and rarefaction curves

The diversity pattern found at Térraba-Sierpe showed an increasing diversity from the upper station to the outer station. This pattern is associated with the physiological stress for non-tolerant species at estuarine conditions, where generally few tolerant species can occur (Elliott and Whitfield, 2011; Remane and Schlieper, 1972). Moreover, the diversity index of the sampling stations was related with the equitability (J), because stations where one or few species dominated the assemblage composition also had the lowest diversity index value. The rarefaction curves followed the same pattern as described above for the equitability. Outer and lower stations tended to have steeper curves (highest equitability) than upper station curves. Samples from dry Season in Sierpe had the steeper, compared to Sierpe in wet season, followed by Cornado during the dry and wet season. We hypothesize that diversity patterns in Térraba-Sierpe are affected by interactions of environmental factors at different spatial and temporal scales.

4.5 Implications for management and conservation

Estuaries are often regarded as dynamic habitats which ecosystem variability complicates implementing management and conservation approaches (Basset et al., 2013). The biodiversity patterns observed at Térraba-Sierpe unveiled these complex ecosystem interactions. Although Coronado and Sierpe, only separted by ~32.6 km, form part of the same estuarine system, the taxa richness and density of macrofauna showed distinct patterns, differently influenced by estuarine zonation and seasonality. This may be related to the size and precipitation rates of the catchment area, land use, soil composition, pollution, and other human disturbances.

Térraba-Sierpe supports a high biological diversity, artisanal fisheries, tourism attractive, and stores up to 8 TgC in the entire mangrove – with 76% buried in sediments (Proyecto Humedales, 2015; BIOMARCC-SINAC-GIZ, 2012; Nielsen and Quesada, 2006). On the other hand, this estuary is threatened by agricultural expansion, deforestation, pollution, and possible modification of its natural flow and sedimentation regimes (Proyecto Humedales, 2015). There is currently a plan to construct a hydroelectric power plant with a 173 meter high dam in one of the tributaries of Térraba-Sierpe, wich will include a freshwater outfall pipe a few kilometers upstream the mangrove (PHED, 2010). This construction will probably modify the sediment dynamics and freshwater input, including changes in the natural fluctuations of sediment inputs, and retention of organic and non-organic particles (Xu and Dong, 2017). Changes in temperature from outfall waters can change assemblage structure and productivity (Basset et al., 2013), and modifications of river flow can induce negative effects in downstream littoral ecosystems (Kowalewski et al., 2000). Therefore, further studies will be necessary to understand how the modification of the ecosystem caused by the construction of the hydroelectric power plant will affect the biodiversity of Térraba-Sierpe.

Tropical estuaries and mangroves are critically endangered (Munji et al., 2014), and tropical countries should enhance efforts on mapping and monitoring these systems (Nascimento et al., 2013), which provide undeniable ecological and socio-economic goods and services (Basset et al., 2013; Ewel et al., 1998). Knowledge of the biodiversity of a particular locality improves future management initiatives and is required to assess natural and human impacts on marine ecosystems and its biodiversity (Costello et al., 2013; Worm et al., 2006). Research and conservation efforts should focus on identifying and understanding the factors driving the spatial and temporal variation of the biodiversity in tropical estuaries.

5 CONCLUSIONS

This study identified 146 subtidal benthic macrofauna taxa inhabiting the soft sediments at the channels and nearshore turbid zones of the Térraba-Sierpe mangrove ecosystem, which is comparable to other tropical and sub-tropical estuaries. We recorded 20 new records for Costa Rica, and more taxa are expected to be found if the sampling effort increases, and 27 new records for mangrove channels and nearshore mixed zones in the Pacific of Central America. The complex variability of the biodiversity patterns makes it difficult to come up with general prediction and management approaches, because the environmental dynamics are different in each of the studied estuaries. Lower density during the wet season was probably due to negative effects of higher sediment and freshwater inputs. Taxa richness was also influenced by the estuarine zonation, and was higher at the outer station (marine influence) than in the upper stations (freshwater influence), probably related to the physiological stress (due to salinity changes) in the upper estuary. The density of macrofauna at this estuarine system was also distinctly influenced by spatial factors (estuarine zonation) between estuaries, but no effect of seasonality was detected. The estuaries had higher macrofauna density at the outer station than in the upper station, but this pattern can be hidden by abundant opportunistic species in the upper estuary. The biodiversity patterns at these two nearby tropical estuaries seem to be driven differently by estuarine zonation and seasonality, and these differences are probably related to features of each catchment-estuary-coast system dynamics.

6 ACKNOWLEDGEMENTS

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CAPÍTULO 3

Assessment of spatial and temporal drivers of the subtidal benthic macrofauna assemblage in a tropical mesotidal estuarine system

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ABSTRACT

Estuaries are ecologically complex environments that support important ecological goods and services for human populations. However, estuaries are probably one of the most threatened environments due to human pressures, including current and future impacts of the climate change. Estuaries have been less studied than adjacent freshwater and oceanic environments, and this situation is even more noticeable for tropical estuaries. The present study aims to identify the spatial and temporal drivers of the variation of benthic macrofauna inhabiting the subtidal channels and nearshore turbid zones of two estuaries within the second largest estuarine mangrove system of Central America, Eastern Tropical Pacific. Between January and February 2013 we collected a total of 3391 organisms distributed in 146 taxa with a mean density of 934 ± 1030.2 ind$\cdot$m^{-2}, while the environmental variability was estimated from the sediment (mean grain size, sorting, kurtosis, skewness, gravel, sand, mud, organic matter, and carbonates) and the water column (temperature, salinity, dissolved oxygen). The results demonstrated that the two studied estuaries are affected in different ways by spatial and temporal factors despite being closely located. The macrofauna assemblage was different between the inner areas (upper and lower station) and the outer areas (outer station) in both estuaries. A separation by season was observed at Coronado estuary only. The marine worms' families Spionidae, Magelonidae, Nephtyidae and Nereididae, and the amphipods Corophiidae contributed the most to the observed variation. Salinity, organic matter, and gravel were selected as the best combination of variables explaining the variation observed in the macrofauna. The macrofauna assemblage was different between dry and wet season, supporting the idea that tropical coastal environments are not as temporally stable as previously thought. We conclude upstream catchment features driving the variation observed at these tropical estuaries.

HIGHLIGHTS

- Spatio-temporal factors influenced macrofauna differently at two nearby tropical estuaries
- Macrofauna assemblage showed differentiation along estuarine zonation
- Stability of macrofauna along time is not a general rule in tropical estuaries
- In these tropical estuaries few generalist taxa contributed the most to the temporal variation
- Main environmental drivers of macrofauna were salinity, organic matter, and gravel

KEYWORDS: ADONIS, BIOENV, Partial Mantel, organic matter, salinity gradient, tropical sediments, tropical instability

1 INTRODUCTION

Estuaries are highly dynamic coastal ecosystems characterized by the transition between freshwater and ocean waters, with unique ecological features, strong environmental gradients, high biological productivity, and distinct associated communities (Basset et al., 2013; Elliott and Whitfield, 2011; Snedden et al., 2012). These ecosystems can provide important ecological goods and services to human populations, such as coastal protection, food source, and raw material for buildings, fuel, medicine, sweeteners, oils, textiles, dyes, and paper (Basset et al., 2013; Ewel et al., 1998; Giri et al., 2011; Hogarth, 2015; Zhang et al., 2012). Although estuaries are considered less biologically diverse than freshwater and oceanic habitats (Elliott and Whitfield, 2011; Remane and Schlieper, 1972), their communities help to support these ecological services through its biological activity (e.g. nutrient and organic matter recycling, water cleaning by filter feeding); moreover, some species can develop large populations and biomass, supporting important fisheries (e.g. mussels and shrimps) (Alongi, 1990; Harris, 1999; Houde and Rutherford, 1993; Lenanton and Potter, 1987; Nguyen et al., 2017; Peterson and Heck Jr, 1999; Roessig et al., 2004). Estuarine systems are often nursery grounds for freshwater, coastal, and oceanic species of mollusks, crustaceans, and fishes, including important species for fisheries (Clarke et al., 2014; Peterson et al., 2000; Sheaves et al., 2012).

Estuaries are probably one of the most threatened ecosystems in the world, due to the many uses and pressures induced by human activities (Elliott and Whitfield, 2011; Kennish, 2002; McLusky and Elliott, 2004). Additionally, present and future effects of climate change are threatening estuaries, such as rising sea levels (constraining of the narrow estuarine zones), water stratification (facilitating eutrophication), increasing storm activity (promoting catchment and coastal erosion processes), and rising water temperatures (affecting metabolism and survival of estuarine species) (Gilman et al., 2008b; Scavia et al., 2002; Statham, 2012). The current biodiversity loss crisis has made clear an urgent necessity for biodiversity and ecosystem function assessment in order to develop adequate management and conservation approaches (Chapin et al., 2000; Costello et al., 2013, 2010; Jenkins and Van Houtan, 2016; Pereira et al., 2010; Thompson et al., 2012; Underwood et al., 2000).

Estuaries have been less studied than adjacent freshwater and oceanic environments (Elliott and Whitfield, 2011). This pattern is even more pronounced considering the poorly studied tropical estuaries in contrast to the relatively well studied estuaries temperate regions (Alongi, 1990, 1989b; Barros et al., 2012; Dittmann and Vargas, 2001; Maurer and Vargas, 1984). The marine benthic fauna (epifauna and infauna) is considered one of the richest species groups on the planet, and a very important component of soft sediments (Alongi, 1990; Gray, 2002; Snelgrove, 1997). Some general patterns have been widely discussed regarding the relation of the benthic fauna with spatial factors (e.g. increasing diversity from poles to tropics, and from shallow to deep waters) and environmental variables (e.g. increasing diversity with increasing microhabitats in sediments) (Anderson, 2008; Gray, 2002, 1974; Gray and Elliott, 2009; Sanders, 1968). Recent studies revealed that estuarine biological communities are highly variable and influenced by local features (Elliott and Whitfield, 2011). There is, however, a lack of information regarding the ecology of subtidal benthic macrofauna from tropical estuaries (Alongi, 1989b; Maurer et al., 1984; Shokri et al., 2009; Thompson et al., 2012).

Previous studies have assessed the influence of spatial and temporal variation of environmental variables on subtidal benthic macrofauna assemblages in tropical estuaries, mainly in India, South America and Australia (Alongi, 1990; Barros et al., 2012; Bone et al., 2011; Checon et al., 2018; Corte et al., 2017; Pires-Vanin et al., 2011; Tweedley et al., 2012; Wildsmith et al., 2011, 2009). Studies in Eastern Tropical Pacific (ETP) estuaries, however, are less common, with some exceptions such as the Jaltepeque estuary in El Salvador (Molina and Vargas, 1994), the Gulf of Nicoya (Maurer et al., 1984) and Golfo Dulce in Costa Rica (Nichols-Driscoll, 1976). The ETP is an ocean region frequently impacted by the El Niño Southern Oscillation (ENSO) (Fiedler, 2002) and is predicted to be critically affected by the climate change (Karmalkar et al., 2011). Therefore, further studies on how the macrofauna assemblages are influenced by spatial and temporal variation of environmental factors in the ETP are required to identify general patterns and to develop effective management measures for estuarine habitats (Gorman et al., 2017). This study provides the first comprehensive assessment of spatial (between and within estuaries) and temporal (between dry and rainy seasons) variability of the subtidal benthic macrofauna assemblage structure in Térraba-Sierpe, the second largest estuarine mangrove in the Pacific coast of Central America.

2 MATERIALS AND METHODS

2.1 Sampling sites

Térraba-Sierpe is regarded as the largest mangrove in Costa Rica and the second largest in Pacific Central America (Fig. 1), with 146 km^2 of periodically inundated mangrove forest (Barrantes and Cerdas, 2015; Loría-Naranjo et al., 2018). These estuarine system's two main river basins, Grande de Térraba (5077 km^2) and Sierpe (790 km^2), present annual precipitations over 5000 mm, a dry season (December-April) with 520 mm monthly precipitation and a wet season (May-November) with 860 mm monthly precipitation (Rojas, 2011). The high precipitation during the wet season increases suspended sediments (up to 1234 ± 59 $mg{\cdot}L^{-1}$) and nutrients (Fosfates: 9.4 $\mu mol{\cdot}L^{-1}$, Nitrite: 2.2 $\mu mol{\cdot}L^{-1}$, Amonium: 5.0 $\mu mol{\cdot}L^{-1}$, Silicates: 1388.3 $\mu mol{\cdot}L^{-1}$), and decreases primary productivity rates affecting the development of marine phytoplankton (0.79 $gC{\cdot}m^{2}{\cdot}day^{-1}$) (Lizano et al., 2001; Umaña-Villalobos and Springer, 2006; Umaña et al., 2015). Salinity decreases to brackish and even freshwater conditions during the wet season inside the estuaries and the nearshore turbid zones outside the estuaries (minimums down to 1 psu at the bottom) (Picado, 2015).

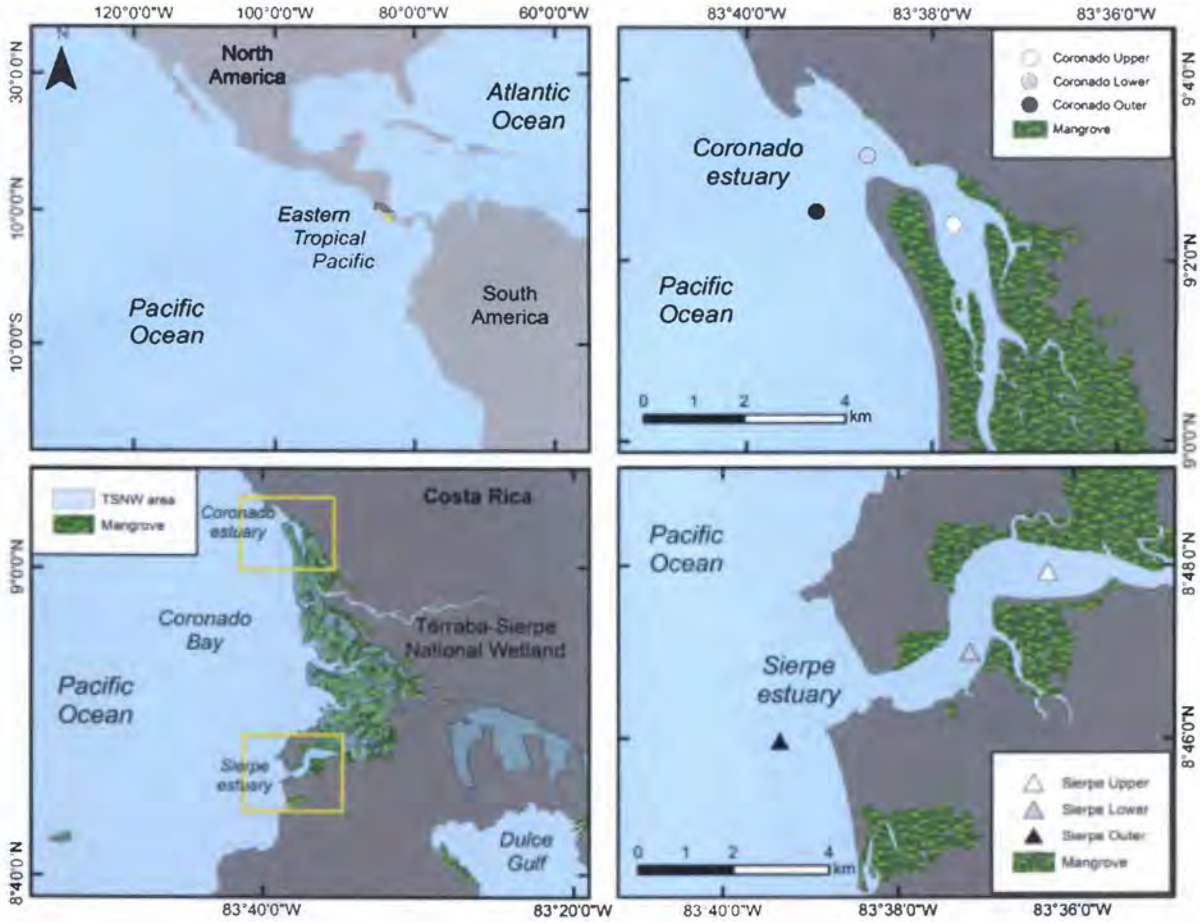


Figure 1. *Sampling sites of the subtidal benthic macrofauna along the estuarine zonation (Upper estuary, Lower estuary, Outer estuary) in A) Coronado and B) Sierpe estuaries, at Térraba-Sierpe (TS), Pacific coast of Costa Rica. C) Location of the TS in relation to the Costa Rican coast and D) to the Eastern Tropical Pacific, West coast of the Americas.*

2.2 Sample collection

Sampling was monthly performed from January to December 2013 (except February) aboard a small vessel (5 m length) as part of a project of the Unidad de Investigación Pesquera y Acuicultura (UNIP) of the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica. We visited two nearby estuaries, Coronado and Sierpe, alternating between the months. At both estuaries, we established three sampling stations along the estuarine zonation: 1) upper station, ~5 km landward from the river mouth; 2) lower station, <1 km landward from the river mouth; and 3) outer station, ~1 km seaward from the river mouth (Fig. 1). At each sampling station, five sediment samples were taken from the bottom using a Petit-Ponar grab (152 mm × 152 mm, 0.023 m^2) to collect 0.11 m^2 of sediment, which exceeds the minimum 0.1 m^2 sampling area suggested for studies of soft-bottom macrofauna (Eleftheriou and McIntyre, 2005). The sediment samples were deposited on plastic bags and fixed using a solution of seawater with 5% buffered formalin and Bengal Rose to facilitate the detection of small animals (Vargas, 1987). In the laboratory, samples were gently water-washed through a 500 µm sieve and stored in 95% ethanol. The macrofauna was separated from the remaining sediment under a dissecting microscope and light microscope (MOTIC SMZ-168 and MOTIC BA-310, respectively). For details on taxonomic identification see Chapter 2. Percentage contribution by number of taxa and abundance was estimated for each group.

At each sampling station, one additional sediment sample was collected to measure granulometric variables (such as contribution of mud, sand, and gravel, grain size, sorting, skewness, and kurtosis), organic matter content and carbonate content (Table S1, see details in Chapter 1). Water variables (temperature, salinity and dissolved oxygen) were measured at the bottom using a CTD Sea Bird Electronics 19plus (Table S2).

Biodiversity collection permission was obtained through the National System of Conservation Areas (SINAC) of the Costa Rican Ministry of Environment and Energy (MINAE): License for biodiversity collection # 181-2013-SINAC. Research permission for working in the Osa Conservation Area (ACOSA) was facilitated by the Costa Rican Institute of Electricity through the SINAC of the Costa Rican MINAE: resolution # INV-ACOSA-006-14. Permission for working on marine areas under Costa Rica jurisdiction was obtained through the Port Maritime Division of the Costa Rican Ministry of Public Works and Transportation (MOPT): License for work aboard in the Costa Rican marine waters # Z024317.

2.3 Estuary and season effects

We pooled the data from the five grabs sampled at each station (upper, lower, and outer) in each estuary (Coronado, Sierpe) during each month for all the analyses (for a total of 33 data set = sampling stations). To analyze the composition of the benthic macrofauna assemblages between sampling stations, we first log-transformed the abundance data of the 146 taxa (e.g. log(x+1)) and estimated the Bray-Curtis dissimilarity index of the 33 sampling stations (Beals, 1984; Krebs, 1999). A Multidimensional Scaling (MDS) was performed to visualize the similarities of the macrofauna assemblages between the sampling stations along spatial (estuarine zonation and estuaries) and temporal (seasonality) variation. The MDS allows the detection of non linear relations (Borcard et al., 2011; James and McCulloch, 1990). These analyses were performed using the "vegan" package in RStudio (Oksanen et al., 2013; RStudio Team, 2015). However, the MDS has a limitation of not providing a statistical probability, and therefore a Permutational Multivariate Analysis Of Variance Using Distance Matrices (ADONIS) was performed to detect the influence of the spatial (station, estuary) and temporal (season) factors on the macrofauna assemblage distance matrix, and to compare the assemblage composition per sampling station between stations (upper, lower, outer), estuaries (Coronado, Sierpe), and seasons (dry, wet). The ADONIS analysis partitions a distance matrix (e.g. macrofauna assemblage composition) among its sources of variation (spatial and temporal factors) and fits linear models to the distance matrix using a permutation test with pseudo-F ratios (McArdle and Anderson, 2001). The ADONIS test was performed using the "adonis" function of "vegan" in RStudio (McArdle and Anderson, 2001; Oksanen et al., 2013; RStudio Team, 2015).

2.4 Species contribution for the spatio-temporal patterns

A Similarities Percentage analysis (SIMPER) was used to estimate the individual contribution of each taxon to the similarities between the sampling stations regarding the factors significantly influencing the matrix of benthic macrofauna abundance according to the ADONIS (Clarke and Warwick, 1994). The SIMPER analysis (based on the Bray-Curtis dissimilarity index) was performed using "vegan" in RStudio (Oksanen et al., 2013; RStudio Team, 2015). If differences were detected between estuaries, further MDS and ADONIS were performed to visualize and analyze the influence of station and season on the benthic macrofauna assemblage composition at each estuary. Similarly, SIMPER analyses were applied to determine the contribution of individual taxon to the similarities between sampling stations considering those factors significantly influencing the assemblages according to the ADONIS.

2.5 Assessment of environmental drivers of macrofauna assemblage composition

A Partial-Mantel test was used to estimate the correlation between the distance matrix of similarity of the macrofauna assemblage composition and the distance matrix of environmental variables (based on Euclidean distance of the values of nine sediment and three water column variables measured at the 33 sampling stations), while controlling the effect by the distance matrix of spatio-temporal variation (based on Euclidean distance of the geographic coordinates and sampling dates transformed into a continuous variable). The significance of the statistic was evaluated by permuting rows and columns of the first dissimilarity matrix (e.g. the macrofauna matrix) (Legendre and Legendre, 2012, 1998). The Partial-Mantel test was performed using the "mantel.partial" function of "vegan" in RStudio (Oksanen et al., 2013; RStudio Team, 2015). A Multiple Matrix Regression (MRM) analysis was used to determine which matrix, either environmental or spatio-temporal, had a higher regression coefficient with the benthic macrofauna abundance matrix, which uses a permutation test to obtain the significance of regression coefficients (Goslee and Urban, 2007; He et al., 2016; Legendre et al., 1994; Lichstein, 2007; Wang, 2013). The MRM analysis was performed using the "MRM" function in the "ecodist" package (Goslee and Urban, 2007; RStudio Team, 2015).

A BIOENV analysis was used to identify relations between the patterns of benthic macrofauna assemblage structure (based on the Bray-Curtis dissimilarity index) and environmental variables (based on the Euclidean similarity index). This statistical tool allows identifying the environmental variables (individual or combined) that "best match" the patterns of community structure (Clarke and Ainsworth, 1993). The BIOENV was performed using the "bioenv" function of the "vegan" package in RStudio (Clarke and Ainsworth, 1993; Oksanen et al., 2013; RStudio Team, 2015). Using only the selected environmental variables according to BIOENV, we performed another Partial-Mantel test and MRM analysis, to estimate the correlation between the distance matrix of similarity of the macrofauna assemblage composition and the distance matrix of environmental variables.

3 RESULTS

3.1 Environmental variation

The sediments at the subtidal channels and nearshore turbid zones of Térraba-Sierpe were moderately well sorted medium sands, with a grain size average of 133.22 µm, organic matter content of 5.2%, and carbonate content of 5.7% (Table S1, see Chapter 1). The sediments were more heterogeneous during the dry season, and became more homogeneous during the wet season (Table S1, see Chapter 1). Moreover, sediments were more heterogeneous at the upper and lower stations, and more homogeneous at the outer station (Table S1, see Chapter 1). The organic matter contribution was higher at the upper station than in lower and outer stations; this pattern was more pronounced at Sierpe than in Coronado (Table S1, see Chapter 1). There was no spatial or temporal variation detected regarding the medium grain size, skewness, kurtosis, nor carbonate content (Table S1, see Chapter 1).

The water column temperature, salinity and dissolved oxygen were more variable at the upper station than in the lower and outer stations (Table S2). The temperature showed a slight decrease at the upper station during the wet season months (Table S2). The salinity was lower at the upper stations than in the lower and outer stations, and did was generally lower during the wet season than during the dry season, and more variable at Coronado estuary (Table S2). The dissolved oxygen showed no apparent pattern of variation (Table S2).

3.2 General estuarine community composition

We identified a total of 146 taxa of subtidal benthic macrofauna at the Térraba-Sierpe estuarine system; 97 taxa at Coronado, 104 taxa at Sierpe, and 57 of these taxa were shared between the two estuaries. Overall, 72 families were recorded and 81 taxa were identified to species level (Table S3). For further details on Térraba-Sierpe overall biodiversity see Chapter 2. The dominant groups in taxa richness and abundance at both estuaries were Annelida, Mollusca, and Arthropoda (Fig. S1). Coronado had higher total abundance contribution of annelids (65.3%) than Sierpe (44.3%), while mollusks and arthropods were more abundant in Sierpe (16.8% and 24.3%, respectively) than in Coronado (13.2% and 15.8%, respectively). A total of 3391 organisms were collected at Térraba-Sierpe, showing a mean density of 934 ± 1030.2 ind$\cdot$m^{-2}, with a minimum of 0 ind$\cdot$m^{-2} to a maximum of 9436 ind$\cdot$m^{-2}. For further details on Térraba-Sierpe overall density variation see Chapter 2. The most abundant taxa were the polychaetes *Scolelepis* (*Scolelepis*) *acuta*, *Paraprionospio pinnata*, *Malacoceros indicus*, *Leptonereis laevis*, *Magelona riojai*, *Armandia* cf. *salvadoriana*, *Nephtys oculata*, the peracarids Corophiidae indet., and Cumacea indet, the bivalves Tellinidae indet. and the Nematoda indet., accounting together 59.9% of the overall abundance (Table. S3).

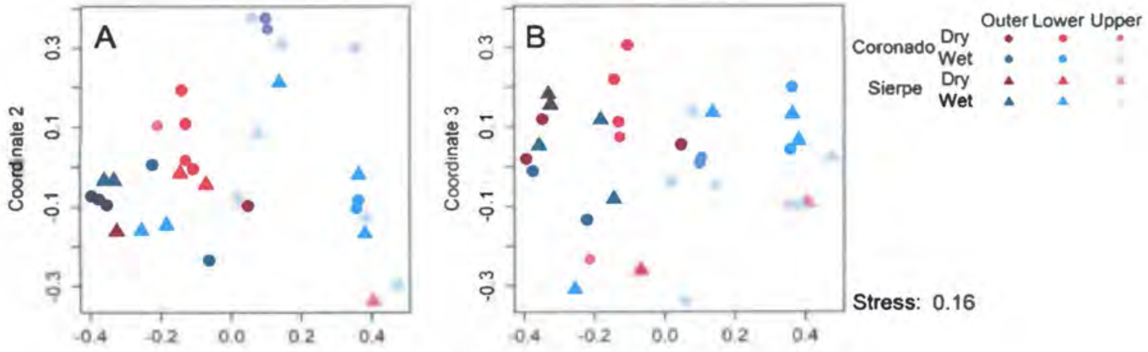
3.3 Spatial and temporal patterns of the macrofauna assemblage composition

3.3.1 Estuary and Season effects

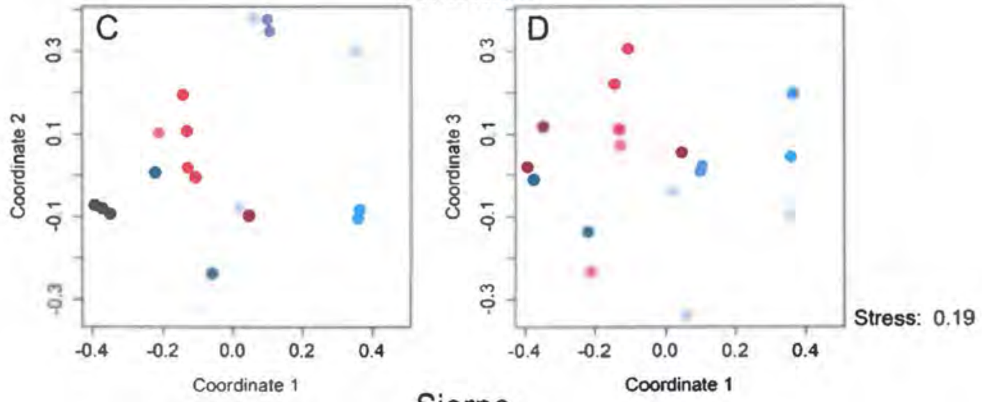
The MDS revealed that benthic macrofauna assemblages differed by estuarine zonation, being the outer stations of both estuaries grouped at the left side of the plot with less variability (closely grouped). The upper and lower stations tend to be located at the center and to the right side of the plot with more variability (more dispersed in the plot) (Fig. 2A). The macrofauna also showed a separation between seasons in Coronado along the Coordinate 3 with dry season mainly at the positive values, and rainy at negative values (Fig. 2B). The ADONIS test supported a differentiation of the macrofauna assemblage zonation between estuaries (Station × Estuary, $p < 0.05$), with seasonal differentiation ($p < 0.05$) only in Coronado (Table 1A).

The ADONIS test for Coronado samples revealed a differentiation of the macrofauna composition between stations and between seasons (Table 1B). The MDS for Coronado showed that macrofauna assemblages were different between stations, with outer stations located towards the lower left side of the plot, and lower and upper stations towards the upper right side of the plot (Fig. 2C). The macrofauna at Coronado also showed separation between seasons along the Coordinate 3 (Fig. 2D).

The ADONIS test supports a differentiation of the macrofauna assemblage composition by stations only at Sierpe (Table 1C). The MDS showed a separation of samples between stations, with the outer stations located at the left side, and the upper and lower stations at the right side of the plot (Fig. 3E). The outer stations were closely grouped, while upper and lower stations were more dispersed (Fig. 3E).



Coronado



Sierpe

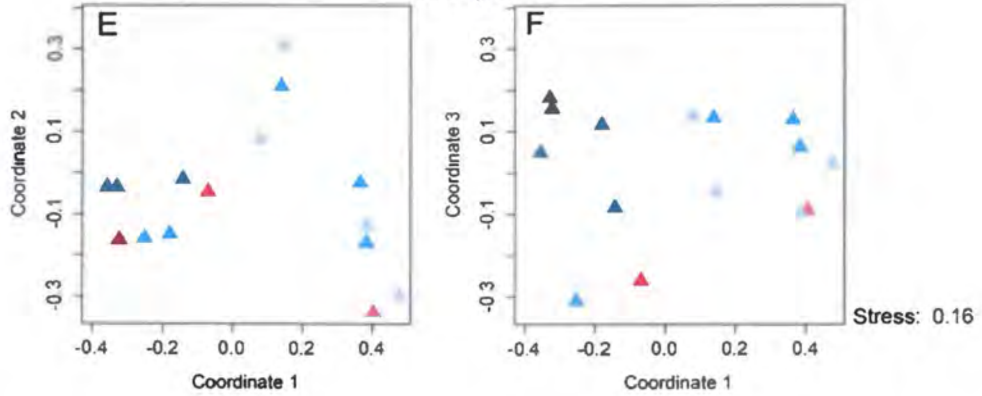


Figure 2. *Multidimensional Scaling (MDS) shows the similarity for the sampling stations (regarding season, estuary, and stations) based in the Bray-Curtis index estimated for the subtidal benthic macrofauna community composition at: A and B) both Coronado and Sierpe estuaries, C and D) Coronado estuary, and E and F) Sierpe estuary, Pacific coast of Costa Rica. A, C, and E show the ordination along the Coordinate 1 (x-axis) and 2 (y-axis), while B, D, and F show the ordination along the Coordinate 1 (x-axis) and 3 (y-axis).*

Table 1. *Results of the Permutational Multivariate Analysis Of Variance Using Distance Matrices (ADONIS) comparing the distance matrix of the subtidal benthic macrofauna per sampling sites (based on Bray-Curtis distance) between stations (Upper, Lower, Outer), estuaries (Coronado, Sierpe), season (Dry, Wet), and the interaction between these factors, showing the degrees of freedom (DF), sum of squares, and F and p values. ADONIS for A) All samples, B) Coronado estuary only, and C) Sierpe estuary only, Pacific coast of Costa Rica.*

A. All samples.

Factors	DF	Sum of squares	F	*p* value
Station	2	1.817	2.95	0.001*
Estuary	1	0.490	1.59	0.063
Season	1	0.461	1.50	0.064
Station × Estuary	2	0.938	1.52	0.033*
Station × Season	2	0.687	1.12	0.253
Estuary × Season	1	0.349	1.13	0.256
Station × Estuary × Season	2	0.432	0.70	0.951
Residual	21	6.469		

B. Coronado estuary.

Factors	DF	Sum of squares	F	*p* value
Station	2	1.261	2.09	0.001*
Season	1	0.526	1.75	0.031*
Station × Season	2	0.527	0.87	0.693
Residuals	12	3.613		

C. Sierpe estuary.

Factors	DF	Sum of squares	F	*p* value
Station	2	1.494	2.35	0.002*
Season	1	0.285	0.90	0.541
Station × Season	2	0.592	0.93	0.610
Residual	9	2.856		

*: factors are significantly different.

3.3.1 Species contribution for the spatio-temporal patterns

The SIMPER analysis for all the samples revealed that the taxa contributing the most to the variation of the assemblages composition between stations (upper, lower, outer) were amphipods of the family Corophiidae (9.7%), followed by eight polychaete species, cumaceans, and nematods, which together accounted for 52.4% of the variation (Table 2). The distribution patterns of these species along the estuarine zonation were different: corophiids were more abundant at the outer station (205) than at the upper or lower stations (78 and 32, respectively) (Table 2). A similar pattern was observed for *Malacoceros indicus*, *Magelona riojai*, Nematoda, Cumacea, and *Scoletoma* sp (Table 2). Some species, however, showed a contrary pattern such as *Scolelepis* (*S.*) *acuta* and *Nephtyis oculata*, with higher abundances at upper station (432) than at the lower and outer stations (2 and 0, respectively) (Table 2). The following species were more abundant at middle estuarine zonation (lower station), than at upper and outer station: *Armandia* cf. *salvadoriana* and *Mediomasuts californiensis* (Table 2). *Paraprionospio pinnata* followed an opposite pattern, with higher abundance at both upper and outer station (Table 2).

Table 2. *Mean abundance, total abundance (n), relative abundance (%) and average dissimilarity (Av. Diss), percentage contribution to dissimilarity (Contrib.) and accumulation of the percentage contribution to dissimilarity based on Similarity of Percentages (SIMPER) analysis for the main species contributing to dissimilarities between the stations along the estuarine zonation (Upper, Lower, Outer) from two tropical mesotidal estuaries (Coronado and Sierpe), Pacific coast of Costa Rica.*

Taxa	**Upper**			**Lower**			**Outer**			**Av. Diss.**	**Contrib.**	**Acc.**
	Mean	**n**	**%**	**Mean**	**n**	**%**	**Mean**	**n**	**%**			
Corophiidae	7.09	78	7.0	2.91	32	3.1	18.60	205	16.4	8.4	9.7	9.7
Nephtys oculata	7.64	84	7.5	2.73	30	2.9	0.82	9	0.7	4.8	5.6	15.3
Scolelepis (*Scolelepis*) *acuta*	39.30	432	38.5	0.18	2	0.2	0.00	0	0.0	4.8	5.5	20.8
Malacoceros indicus	0.27	3	0.3	4.64	51	5.0	10.80	119	9.5	4.7	5.4	26.2
Paraprionospio pinnata	13.00	143	12.8	1.64	18	1.8	5.00	55	4.4	4.2	4.8	31.1
Magelona riojai	0.46	5	0.4	4.64	51	5.0	7.45	82	6.6	3.8	4.4	35.5
Nematoda	0.09	1	0.1	2.09	23	2.3	11.10	122	9.8	3.8	4.4	39.8
Armandia cf. *salvadoriana*	1.27	14	1.2	5.82	64	6.3	4.82	53	4.2	3.0	3.5	43.3
Cumacea	1.27	14	1.2	1.55	17	1.7	7.64	84	6.7	2.8	3.2	46.5
Mediomastus californiensis	1.91	21	1.9	4.18	46	4.5	0.36	4	0.3	2.6	3.0	49.4
Scoletoma sp.	0.64	7	0.6	0.73	8	0.8	7.00	77	6.2	2.5	2.9	52.4

Regarding Coronado estuary only, differentiation of composition between stations was mainly attributed to corophiids and six polychaete species, contributing to 50.1% of the variation (Table 3). Some taxa presented higher abundances at the outer stations (e.g. corophiids and magelonid worms), others at upper stations (e.g. poychaetes *S.* (*S.*) *acuta*, *N. oculata*, and *P. pinnata*), and some presented higher abundances at the lower station (e.g. *M. riojai* and *L. laevis*) (Table 3). The taxa contributing the most to composition differences between seasons were corophiids and seven polychaete species, accounting together to 53.3% of the variation (Table 4). Most of these taxa were more abundant during the dry season (e.g. Corophiidae, *P. pinnata*, *M. indicus*, *A.* cf. *salvadoriana*, *M. riojai*, and *L. laevis*), while the spionid worm *S.* (*S.*) *acuta* was only present – with very high abundances (n = 434) – during the wet season (Table 4). Another species with higher abundances during wet than dry season was *N. oculata* (Table 4).

The SIMPER analysis by stations of Sierpe showed that the taxa contributing the most to variation in composition between stations at Sierpe were amphipods, cumaceans, mysids, nematods, six polychaete species, and two mollusks (*Nucula schencki* and *Natica scethra*), accounting together to 51.8% of the variation (Table 5). Most of these taxa were more abundant in the outer station than in the upper and lower stations (e.g. Corophiidae, Nematoda, *Scoletoma* sp., *N. schencki*, *M. riojai*, *M. indicus*, and *A.* cf. *salvadoriana*) (Table 5), while, *Cossura laeviseta* was more abundant at the upper stations; mysids, *M. californiensis*, and *N. scethra* were more abundant at the lower station (Table 5).

Table 3. *Mean abundance, total abundance (n), relative abundance (%) and average dissimilarity (Av. Diss), percentage contribution to dissimilarity (Contrib.) and accumulation of the percentage contribution to dissimilarity based on Similarity of Percentages (SIMPER) analysis for the main species contributing to dissimilarities between the stations along the estuarine zonation (Upper, Lower, Outer) from Coronado estuary, Pacific coast of Costa Rica.*

Taxa	**Upper**			**Lower**			**Outer**			**Av. Diss.**	**Contrib.**	**Acc.**
	Mean	**n**	**%**	**Mean**	**n**	**%**	**Mean**	**n**	**%**			
Corophiidae	12.80	77	7.8	0.33	2	0.3	22.20	133	24.1	8.8	10.4	10.4
Scolelepis (*Scolelepis*) *acuta*	72.00	432	43.7	0.33	2	0.3	0.00	0	0.0	8.6	10.2	20.6
Nephtys oculata	11.80	71	7.2	4.50	27	3.4	0.67	4	0.7	6.9	8.1	28.7
Paraprionospio pinnata	23.30	140	14.2	2.17	13	1.7	5.83	35	6.3	5.8	6.9	35.6
Malacoceros indicus	0.33	2	0.2	8.50	51	6.5	12.80	77	13.9	5.4	6.3	41.9
Magelona riojai	0.50	3	0.3	8.00	48	6.1	7.17	43	7.8	3.6	4.3	46.2
Leptonereis laevis	0.67	4	0.4	22.70	136	17.3	0.00	0	0.0	3.3	3.9	50.1

Table 4. *Mean abundance, total abundance (n), relative abundance (%) and average dissimilarity (Av. Diss), percentage contribution to dissimilarity (Contrib.) and accumulation of the percentage contribution to dissimilarity based on Similarity of Percentages (SIMPER) analysis for the main species contributing to dissimilarities between the seasons (Dry, Wet) from Coronado estuary, Pacific coast of Costa Rica.*

Taxa	**Dry**			**Wet**			**Av. Diss.**	**Contrib.**	**Acc.**
	Mean	**n**	**%**	**Mean**	**n**	**%**			
Scolelepis (Scolelepis) acuta	0.00	0	0.0	48.20	434	52.9	7.9	9.5	9.5
Corophiidae	14.30	129	8.8	9.22	83	10.1	7.9	9.4	18.9
Paraprionospio pinnata	20.20	182	12.5	0.67	6	0.7	6.6	7.9	26.8
Malacoceros indicus	11.70	105	7.2	2.78	25	3.0	5.5	6.6	33.4
Nephtys oculata	4.89	44	3.0	6.44	58	7.1	5.2	6.2	39.6
Armandia cf. *salvadoriana*	10.20	92	6.3	0.44	4	0.5	4.3	5.1	44.7
Magelona riojai	8.00	72	4.9	2.44	22	2.7	3.6	4.3	49.0
Leptonereis laevis	15.60	140	9.6	0.00	0	0.0	3.6	4.3	53.3

Table 5. *Mean abundance, total abundance (n), relative abundance (%) and average dissimilarity (Av. Diss), percentage contribution to dissimilarity (Contrib.) and accumulation of the percentage contribution to dissimilarity based on Similarity of Percentages (SIMPER) analysis for the main species contributing to dissimilarities between the stations along the estuarine zonation (Upper, Lower, Outer) from Sierpe estuary, Pacific coast of Costa Rica.*

Taxa	**Upper**			**Lower**			**Outer**			**Av. Diss.**	**Contrib.**	**Acc.**
	Mean	**n**	**%**	**Mean**	**n**	**%**	**Mean**	**n**	**%**			
Corophiidae	0.20	1	0.8	6.00	30	13.0	14.40	72	10.8	7.4	8.3	8.3
Nematoda	0.00	0	0.0	2.40	12	5.2	15.80	79	11.8	5.7	6.4	14.7
Scoletoma sp.	1.40	7	5.3	0.80	4	1.7	14.00	70	10.5	5.4	6.1	20.8
Cumacea	0.60	3	2.3	0.00	0	0.0	12.20	61	9.1	3.7	4.2	24.9
Nucula schencki	0.00	0	0.0	0.00	0	0.0	8.80	44	6.6	3.6	4.1	29.0
Magelona riojai	0.40	2	1.5	0.60	3	1.3	7.80	39	5.8	3.6	4.0	33.0
Malacoceros indicus	0.20	1	0.8	0.00	0	0.0	8.40	42	6.3	3.1	3.5	36.5
Armandia cf. *salvadoriana*	0.00	0	0.0	0.20	1	0.4	6.80	34	5.1	3.0	3.3	39.8
Cossura laeviseta	2.80	14	10.5	1.60	8	3.5	0.00	0	0.0	2.9	3.2	43.1
Mysida	0.00	0	0.0	3.40	17	7.4	0.00	0	0.0	2.7	3.0	46.1
Mediomastus californiensis	2.00	10	7.5	3.20	16	7.0	0.40	2	0.3	2.6	2.9	49.0
Natica scethra	0.40	2	1.5	2.00	10	4.3	1.60	8	1.2	2.5	2.8	51.8

3.4 Assessment of environmental drivers of macrofauna assemblage composition

The Mantel test revealed the correlation between the distance matrix of the macrofauna assemblage composition and the distance matrix of environmental variables (r = 0.23, p = 0.009) (Table 6). There was also a correlation between the macrofauna matrix and the spatiotemporal matrix (Mantel test: r = 0.21, p = 0.001) (Table 6). The Partial Mantel test showed an effect of the distance matrix of environmental variables on the distance matrix of macrofauna assemblage composition when controlling the spatiotemporal variables matrix (Partial Mantel test: r = 0.18, p = 0.024) (Table 6). The MRM analysis supported that the matrix of environmental variables had a significant regression coefficient over the matrix of the macrofauna assemblage (β = 0.02, p = 0.009).

Table 6. *Results of the Mantel test (vector and p value) Partial Mantel test, and Multiple Matrix Regression (coefficient and p value) analyzing the correlation between the distance matrices of environmental variables (based on Euclidean distance) and the matrix of geospatial and temporal variables (based on Euclidean distance) to the distance matrix of the subtidal benthic macrofauna assemblage composition (based on Bray-Curtis distance) at Térraba-Sierpe, Pacific coast pf Costa Rica.*

Matrices	**Mantel**		**Partial Mantel**			**MRM**	
	r	***p* value**	**r**	***p* value**	**Controlling by**	***β***	***p* value**
acrofauna assemblage × nvironmental variables	0.23	0.009*	0.18	0.024*	Geospatial and temporal variables	0.02	0.009*
acrofauna assemblage × nvironmental variables IOENV selection)	0.22	0.007*	0.32	0.001*	Geospatial and temporal variables	0.02	0.014*
acrofauna assemblage × eospatial and temporal variables	0.21	0.001*	-	-	-	0.03	0.001*

*: test value (r, β) is significant.

The combination of environmental variables that best explained the macrofauna composition patterns was salinity, organic matter, and gravel (BIOENV analysis: $\rho = 0.340$) (Table 7). Salinity was the most recurrent variable in the selections of the BIONEV analysis (Table 7).

Table 7. *Summary of the 10 best results obtained from BIOENV analysis of combined environmental variables matching subtidal benthic macrofauna community composition (using Spearman correlation), from two tropical mesotidal estuaries, Pacific coast of Costa Rica.*

Number of variables	ρ (rho)	Variables
3	0.340	Salinity, OM, Gravel
3	0.320	Salinity, OM, Carbonates
3	0.316	Salinity, CaCo, Gravel
2	0.307	CaCO, Gravel
3	0.301	OM, Carbonates, Gravel
2	0.299	OM, Gravel
3	0.296	Salinity, Carbonates, Sorting
1	0.280	Gravel
3	0.275	Salinity, OM, Sorting
2	0.269	Salinity, Carbonates

The Mantel test revealed a higher correlation between the distance matrix of the macrofauna assemblage composition and the distance matrix of the selected environmental variables (Mantel test: $r = 0.22$, $p = 0.007$) (Table 6). We detected an effect of the distance matrix of selected environmental variables on the distance matrix of macrofauna assemblage composition when controlling the spatiotemporal variables matrix with a steeper slope (Partial Mantel test: $r = 0.32$, $p = 0.001$) (Table 6). The MRM analysis also supported that the matrix of selected environmental variables had a significant regression coefficient over the matrix of the macrofauna assemblage ($\beta = 0.02$, $p = 0.014$).

4 DISCUSSION

4.1 General estuarine community composition

The total number of taxa (146) found at Térraba-Sierpe is similar compared to other tropical and subtropical estuaries (for further discussion see Chapter 2). At a family level, Térraba-Sierpe harbored 72 families considering 165 sediment samples, which is comparable to other tropical estuaries such as Todos Os Santos bay (Brazil), where 87 families were found in 360 sediment samples (Barros et al., 2012). The subtidal benthic macrofauna assemblage of soft sediments in Térraba-Sierpe was dominated (in terms of species richness and abundances) by annelids, mollusks and arthropods, which is the global patterns found in estuaries: Australia in Tasmania (Hedge and Kriwoken, 2000), southeast (Wildsmith et al., 2011, 2009) and southwest (Currie and Small, 2006a) Australia, central Atlantic coast of Brazil (Pires-Vanin et al., 2011), Baffin Bay area in northern Canada (Mäkelä et al., 2017), Bohai Sea in northern China (Zhang et al., 2016), Gulf of Nicoya in Costa Rica (Maurer et al., 1984; Maurer and Vargas, 1984), northeast USA (Heck et al., 1995), and Orinoco delta in Venezuela (Barros et al., 2012). In our study, the most abundant species belonged to the polychaete families Spionidae, Nereididae, Magelonidae, Opheliidae, and Nephtyidae, to the phylum Nematoda, to the amphipod family Corophiidae, to the Cumacea order, and to the bivalve family Tellinidae (Table S2). These groups often dominate subtidal soft-sediments of tropical and subtropical (Barros et al., 2012; Currie and Small, 2006a; Maurer et al., 1984; Pires-Vanin et al., 2011), temperate (Heck et al., 1995; Hedge and Kriwoken, 2000) and arctic estuarine systems (Mäkelä et al., 2017). These results support the idea of similar ecological surrogates in estuaries (McArthur et al., 2010).

4.2 Spatial effects

The interaction of the station and estuary was most important to explain the variation of the macrofauna assemblages, because the spatial and temporal factors were acting at each estuary in different ways. These results corroborate the conclusion of Elliott and Whitfield (2011), who stated that estuarine biological communities are highly influenced by local features of each estuary. In the case of *Térraba-Sierpe*, both estuaries present very different catchments, which might influence the estuarine communities. Sanders (1968), based on studies from the coasts of India, also acknowledged that despite having higher biodiversity than other environments, tropical sediments show very high variability regarding its biodiversity. In tropical estuaries, biological communities are mostly subjected to local variability (Alongi, 1990).

Different benthic macrofauna assemblages were observed in each studied estuary, resulting in a zonation pattern. During the dry season, the changes reflected an ecocline, with one assemblage mainly occurring in the outer station, a "transitional" assemblage in the lower station, and another assemblage in the upper station, forming an overall gradual change along the estuarine zonation (Fig. 2). During the rainy season the changes reflected an ecotone, with one assemblage in the outer station, and another assemblage occurring in both lower and upper stations (Fig. 2). The changes of benthic assemblages along the estuarine zonation have been widely discussed (Attrill and Rundle, 2002; Remane and Schlieper, 1972; Whitfield et al., 2012). This zonation pattern has been observed in other tropical estuaries such as Gulf of Nicoya in Costa Rica (Maurer et al., 1984; Maurer and Vargas, 1984), Jaltepeque estuary in El Salvador (Molina and Vargas, 1994), Laguna de Términos in Mexico (Hernández-Alcántara and Solis-Weiss, 1995), Todos Os Santos bay in Brazil (Barros et al., 2012; Pires-Vanin et al., 2011), and the continental shelf off the Orinoco delta in Venezuela (Bone et al., 2011). These differentiations have been also observed at temperate and polar estuarine systems: Gamtoos estuary in South Africa (Schlacher and Wooldridge, 1996), Schelde and Ems estuaries in The Netherlands (Ysebaert et al., 1998), Loch Linnhe and Loch Eil in Scotland (Feder and Pearson, 1988), Tees estuary in England (Tapp et al., 1993) and the Kongsfjorden Arctic fjord (Włodarska-Kowalczuk et al., 2016).

4.3 Species contribution for the spatial patterns

Estuarine *macro*faunal assemblages are usually conformed by short-lived, small bodied, and fast colonizing species, which are often more generalists than specialists regarding physiological tolerances and feeding guilds (Gray and Elliott, 2009; McLusky et al., 1993). The variation of salinity is one of the most important drivers of these changing patterns along the estuaries, and is closely related to the species' physiological tolerance to salinity changes (Elliott and Whitfield, 2011; Gray, 1981; Gray and Elliott, 2009; McLusky et al., 1993; Whitfield et al., 2012). Our results from subtidal sediments in Térraba-Sierpe support this pattern and are in accordance with results of polychaete diversity associated to decaying wood (Sibaja-Cordero and Echeverría-Sáenz, 2015). Other variables such as the organic matter and sediment features, however, can also influence the estuarine macrofauna distribution (Currie and Small, 2006a; Gray, 1981; Maurer and Vargas, 1983; McLusky et al., 1993; Sanders, 1968). In our study, the main taxa contributing to the assemblage differentiation along the estuarine zonation have different life-history traits (e.g. feeding guilds, salinity tolerances, etc.), which are influencing their distribution patterns. For example, spionid worms are often abundant towards the upper estuary or towards areas with relatively high loads of sediments and organic matter (Bone et al., 2011; Pires-Vanin et al., 2011). Barros et al. (2012) also found other influencing polychaete families such as Nereididae, which were often more abundant towards the upper estuary, while other families such as Cirratulidae and Orbinidae were more abundant towards the outer estuary. The results from these studies concur with the pattern found at Térraba-Sierpe in the present study. Other important group in both estuaries studied herein was the amphipod family Corophiidae, being more abundant towards outer estuary. This distribution pattern towards more oceanic influence has also been recorded in other estuarine system for species of the family Corophiidae (McLusky et al., 1993; Nichols-Driscoll, 1976; Rodrigues et al., 2011).

4.4 Temporal effects

No general seasonal pattern of the macrofauna assemblage in the estuarine system of Térraba-Sierpe was observed. The influence of seasonality, however, was not acting uniformly between the two studied estuaries. In the case of Sierpe estuary, no seasonal pattern of the macrofauna assemblage was detected, which coincided with similar findings from other studies at tropical and subtropical coastal systems (e.g. Todos Os Santos bay in Brazil, and three Mediterranean estuarine ports) (Barros et al., 2012; Chatzinikolaou et al., 2018). Contrarily, our results revealed a significant effect of season on the macrofauna assemblages in Coronado estuary, and other studies reported also temporal variation of the macrofauna assemblage composition in tropical estuarine sediments, for example in Sungei Buloh, Malaysia (Broom, 1982), Celestun coastal lagoon in Mexico (Hernández-Guevara et al., 2008), and Gulf of Nicoya, Costa Rica (Maurer and Vargas, 1984; Vargas, 1987).

There has been extended discussion among the scientific community on how diversity is affected by environmental stability. This ideas have been generally used to explain that the higher diversity found in tropics, compared to temperate regions, is associated to more stable environmental conditions of the tropical areas (Abrams, 1976; Dunbar, 1960; Fischer, 1960; Klopfer, 1959; Nisbet et al., 1978). On the other hand, several studies have provided evidence for environmental temporal variability significantly influencing tropical intertidal and subtidal marine communities, and in many of these cases the high precipitation rates and freshwater inputs were drivers of the temporal instability in these tropical marine environments (Abesamis et al., 2015; Aller et al., 2017; Broom, 1982; da Costa et al., 2008; Maurer and Vargas, 1984; McClanahan, 1988; Vargas, 1987). The particular and unique set of local conditions at each estuary are important to determine the estuary's biodiversity patterns (Elliott and Whitfield, 2011). Therefore, we hypothesize that there are drivers acting differently at each of the two estuaries studied herein.

The closely located (~32.6 km apart) Coronado and Sierpe estuaries are both affected by the marked precipitation rates differences between the dry and wet seasons (Rojas, 2011), which also influence the nutrients, sediments, and salinity dynamics in these estuaries (Lizano et al., 2001; Picado, 2015; Umaña-Villalobos and Springer, 2006; Umaña et al., 2015). Moreover, the catchment area of the Coronado estuary is considerably larger (5077 km^2) than Sierpe's (790 km^2) (Umaña-Villalobos and Springer, 2006), and the land use is also very different between these two catchments: Coronado has less forest coverage (55%) than Sierpe's (60%), and is characterized by the presence of eight large population centers (>5000 people) as well as by ~42 km of highways running along the river shore through exposed rocky cliffs. In contrast, Sierpe catchment lack large population centers and highways along the river shore (see Chapter 1). Human activities can modify the erosion rates at terrestrial landscapes, which can alter the exportation of sediments to the world's oceans (Syvitski et al., 2005). Many studies have demonstrated the effects of catchment land use and cover on aquatic ecosystems, from freshwater streams (Hartman et al., 1996; Lammert and Allan, 1999; Trombulak and Frissell, 2000) to estuarine (Thrush et al., 2004; Umaña-Villalobos and Springer, 2006; Umaña et al., 2015; Wildsmith et al., 2011) and marine coastal habitats (Gorman et al., 2009; Sklar et al., 1998; Thrush et al., 2004). Moreover, some studies have demonstrated that efforts of land and coastal management (e.g. reforestation) can stabilize temporal effects of high precipitations and erosion rates (Aller et al., 2017; Vanacker et al., 2007). We hypothesize that the observed effect of seasonality on the macrofauna assemblage at Coronado estuary is related to the lower forest coverage, higher agricultural area, and larger human pressures than in Sierpe, which can affect the sediment flux into the estuarine and coastal systems downstream. Moreover, the river flow of the Grande de Térraba river (Coronado estuary's main tributary) and Sierpe river are notably different (PHED, 2010). However, the major influence of river flow affecting the lower estuary at Coronado is evidenced by lower salinities during the wet season (Picado, 2015). Likewise, the larger forest coverage, fewer human pressures, and lower river flow at Sierpe (PHED, 2010, see Chapter 1) probably preclude the effect of seasonality on the estuarine subtidal benthic macrofauna assemblage.

4.5 Species contribution for the temporal effect

The spionid polychaete *Scolelepis* (*Scolelepis*) *acuta* was one of the main taxa contributing to the assemblage differences between dry and wet season at Coronado estuary. This species accounted for 12.8% (n = 434) of the total abundance, and was only found at the upper station of Coronado during the wet season. The species is considered to be a facultative deposit and suspension feeder (Fauchald and Jumars, 1979; Jumars et al., 2015). Therefore, the generalist trait of *S.* (*S.*) *acuta* can represent an advantage compared to other few competitors, which can also cope with the low salinities at the upper estuary (Elliott and Whitfield, 2011; Gray, 1981; Gray and Elliott, 2009; McLusky et al., 1993). Another spionid worm (*Dipolydora socialis*) showed a similar pattern off the Orinoco river delta at Venezuela (Bone et al., 2011). On the other hand, most of the other species contributing to the seasonal differentiation were more abundant during the dry season. Many of these species belong to mostly marine groups, which can cope better with more marine conditions towards the seaward areas of the estuary (Elliott and Whitfield, 2011; Remane and Schlieper, 1972; Whitfield et al., 2012).

In the Sierpe estuary, some species showed different contributions between seasons; however, the overall assemblage was not different between dry and wet season. This is probably related to the similar abundances of several species among the season, such as the bivalve *Nucula schenkci* and the gastropod *Natica scethra*.

4.6 Assessment of environmental drivers of macrofauna assemblage composition

Multiple environmental variables are involved in shaping the patterns of macrofauna differentiation at Térraba-Sierpe. The main environmental factors explaining the variation of the macrofauna assemblage were bottom salinity, organic matter and gravel percentage in the sediments of Térraba-Sierpe. These results are in agreement with previous studies who showed that the distribution of species in estuarine systems was highly influenced by the variation of salinity in the habitat (Elliott and Whitfield, 2011; Gray, 1981; Gray and Elliott, 2009; McLusky et al., 1993). The organic matter has also been recognized as an important variable driving the distribution and survival of marine benthic species; however, the quality and abundance of organic matter affect each species in a different way (Currie and Small, 2006a; Gray, 1981; Lee, 2008; Maurer and Vargas, 1983; McLusky et al., 1993; Sanders, 1968). Moreover, the characteristics of the sediments are also closely related to the structure of benthic macrofauna (Currie and Small, 2006a; Gray, 1981; Maurer and Vargas, 1983; McLusky et al., 1993; Sanders, 1968). Therefore, the inputs of gravel from the tributaries to the upper mangrove (see Chapter 2) are probably also influencing the macrofauna at Térraba-Sierpe, as suggested by our results.

4.4 Ecological considerations for management

There is currently a plan to build one of the largest hydroelectric projects in Cnetral America, involving the construction of a 173 m high dam upstream in the Grande de Térraba catchment, one of the main tributaries of Coronado estuary (PHED, 2010). This project will modify the current sediment dynamics and freshwater input into the Coronado estuary, including changes in the natural fluctuations of sediment inputs, and retention of organic and non-organic particles (see Xu and Dong, 2017). Considering that Coronado estuary exhibited a seasonal dynamic regarding its estuarine benthic macrofauna, the construction of this hydroelectric power plant represent a potential threat for this natural temporal variation. Moreover, the project will include an outfall pipe of freshwater from the hydroelectric plant a few kilometers upstream the mangrove (PHED, 2010). The discharge of large volumes of freshwater with high energy motion could negatively affect the brackish-adapted biodiversity of the Térraba-Sierpe mangrove. As shown in the Colorado river delta in the Gulf of California (Kowalewski et al., 2000), modifications of the river flow can induce negative effects in downstream littoral ecosystems. Therefore, solutions are needed to reduce possible negative effects from the seasonal alteration of flow and sediment dynamics as well as the freshwater input close to the estuarine system on the benthic macrofauna of Térraba-Sierpe.

The Térraba-Sierpe estuarine system supports a high biodiversity (Chicas, 2001; Echeverría-Sáenz et al., 2003; Rojas and Rodríguez, 2008; Sibaja-Cordero and Echeverría-Sáenz, 2015), vital ark-clam and estuarine fishes populations for local artisanal fishers (Chicas, 2001; Nielsen and Quesada, 2006; Proyecto Humedales, 2015), and nursery grounds for rays and sharks (Clarke et al., 2014). This important ecosystem is being threatened, however, by agrochemical and pesticide pollution, wetland drainage, deforestation, agricultural expansion, and over-exploitation of forest and fisheries resources (Proyecto Humedales, 2015). The identification of spatial and temporal patterns of other estuarine benthic assemblages (e.g. fishes, intertidal fauna, subtidal megafauna and meiofauna, etc.) will allow the development of effective management measures for this important area. Furthermore, the implementation of a macrofauna monitoring program is strongly recommended to detect any changes during and after the construction of the hydroelectric project.

5 CONCLUSIONS

The assemblages at tropical estuaries are dominated by relatively few short-lived, small-bodied, and fast colonizing species, which are also responsible for most of the spatial and temporal differentiation. The macrofauna at both studied estuaries followed a zonation pattern typical for estuarine environments. Moreover, the differentiation between the macrofauna assemblages at the two estuaries of Térraba-Sierpe supported the conclusion that estuarine communities are closely related to unique and distinct conditions at each estuary. The seasonal differentiation between dry and wet season macrofauna assemblages at Coronado estuary was probably influenced by the combination of high precipitation rates and erosion processes due to deforestation and land used changes in the Grande de Térraba *catchment*. In contrast, Sierpe estuary showed no seasonality of the macrofauna assemblage, which was probably related to the low river flow, higher marine influence, higher forest coverage, and low human pressures compared to Coronado catchment. The finding of seasonality patterns at Coronado estuary provides further evidence that tropical marine environments are not as temporally stable as previously thought. Additional studies at tropical estuaries and other coastal environments are required to obtain more detailed information on the spatial and temporal patterns of the benthic fauna inhabiting these habitats.

6 ACKNOWLEDGEMENTS

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CAPÍTULO 4

Seasonality of the functional structure of the subtidal benthic macrofauna in a tropical mesotidal estuary

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ABSTRACT

Ecosystem's biodiversity and functioning are critically threatened worldwide, which has raised concerns about our understanding of ecosystem's processes, management and conservation approaches. Estuaries are one of the most threatened ecosystem due to the urban, port and industrial developments at its shores, rising sea levels, over-extraction, and collateral impacts of activities in the adjacent upstream catchments and coasts. Functional ecology studies are increasingly accepted as a more adequate approach to identify key ecological processes driving the ecosystem functioning than classical taxonomical approaches. The present study aims to identify spatial and temporal variation of the functional assemblage structure of the subtidal benthic macrofauna in the second largest estuarine mangrove of Central America, Térraba-Sierpe, located at the Eastern Tropical Pacific. Sediments were sampled in two estuaries along the estuarine zonation during 2013. A total of 146 taxa (3391 organisms) were collected and classified in 48 functional entities considering four life-history traits (habitat, activity, motility, and feeding guild). The average number of functional traits per sampling station was 13 ± 5.9, and average biomass of 13.9 ± 15.20 g·m^{-2}. The functional entity with major biomass contribution, epifaunal/infaunal free-living crawling surface/sub-surface deposit feeders, had facultative generalist habitat and feeding guild traits. The number of functional entities was higher at the outer stations than at upper and lower stations, and was also higher during the dry than the wet season. The biomass showed no differences between estuaries, stations neither seasons. Considering the different multidimensional functional diversity indices, only the functional richness (FRic) showed differentiation between seasons with higher values during the dry than the wet season, suggesting that the functional entities occurring during the dry season created a more fdiverse unctional assemblage. The functional originality was relatively low (close to zero) meaning that the dominant functional entities were shared among more than two species. However, 46% and 21% of the functional entities were represented only by one and two species, respectively, indicating that the loss of these species could potentially extirpate these poorly represented functional entities. In conclusion, the functional ecology approach revealed a significant functional change between the dry and wet seasons of the subtidal benthic macrofauna in a tropical estuary.

HIGHTLIGHTS

- Number of functional entities was higher at the outer station and during the dry season
- The average benthic biomass per sampling station was 13.9 ± 15.20 $g \cdot m^{-2}$
- Functional entities with facultative generalist traits were abundant in these tropical estuaries
- The functional richness was highes during the dry than during wet season
- Functional originality was low and most functional entities were represented by one or two taxa

KEYWORDS: estuarine ecology, functional ecology, functional entities, functional richness, functional space, Costa Rica, Eastern Tropical Pacific.

1 INTRODUCTION

Human-derived pressures are severely threatening world's ecosystems principally through degradation, land-use changes, and over-extraction (Hansen et al., 2013; Limburg et al., 2011; Newbold et al., 2015). Marine and coastal ecosystems have experienced critical extirpation of species or severe changes in their abundances (Dulvy et al., 2003; Jackson et al., 2001; Myers and Worm, 2003; Pandolfi et al., 2003). Disruptions of the diversity and community structure of marine ecosystems can affect the ecological functions they provide (Hughes et al., 2003), and there are raising concerns over expected loss of their ecological goods and services (Cardinale et al., 2012; Thompson et al., 2012). This biodiversity and ecosystem crisis has underlined the need to assess ecosystem's diversity and functioning in order to develop measures to prevent, conserve, and restore the natural ecosystems (Chapin et al., 2000; Costello et al., 2013, 2010; Jenkins and Van Houtan, 2016; Pereira et al., 2010; Thompson et al., 2012; Underwood et al., 2000). Moreover, there are still critical questions which need to be answered, such as how the biodiversity loss impacts at community and ecosystem levels, and how this will affect human populations through loss of ecosystem functioning (Duffy et al., 2007).

One of the most important aims of community ecologist has been trying to understand the influence of abiotic and biotic factors on the temporal and spatial variation of biological communities in order better understand the ecosystem functioning (Jones and Syms, 1998; Lavorel and Garnier, 2002; Ricklefs, 2006). Historically, taxonomic biodiversity approach has been the most widely used method to try to unravel ecosystem processes (Mouillot et al., 2013). However, a purely taxonomic approach has its limitations regarding the identification of general patterns and broad conclusions, but is an essential keystone to identify functional traits in a group of species (Flynn et al., 2009; Mouillot et al., 2013; Villéger et al., 2010). There is increasing evidence showing that a functional ecology approach is more adequate for trying to understand ecological processes and make general conclusions because key ecological processes are more closely related to diversity of functional traits (Hooper et al., 2005; Matias et al., 2017; Mora et al., 2014; Mouillot et al., 2013; Villéger et al., 2017). Ecosystem functioning is the result of multiple filters at a hierarchy of scales (temporal and spatial) that assemble taxa with appropriate responses resulting in varying communities (Keddy, 1992; Woodward and Diament, 1991). These methods consider the functional structure of the biota (assessing the identity and diversity of functional traits) and can potentially unveil rapidly and consistently the effects of disturbances and provide signals of species and functional loss (Flynn et al., 2009; Leitão et al., 2016; Mouillot et al., 2013, 2011; Naeem et al., 2012; Villéger et al., 2010). The functional ecology can also assess the functional redundancy of the ecosystem, which is an important feature correlated to the ecosystem vulnerability of loosing functional traits (Díaz and Cabido, 2001; Loreau et al., 2001).

The functional ecology could close the existing gap between community ecology, based on purely taxonomic diversity, and ecosystem functioning (Mouchet et al., 2010). One way to model the ecosystem functioning is using the distribution of the biological assemblage within a multidimensional functional space with axes defined by the functional traits (also known as the functional diversity), which can be quantified in functional units within this multidimensional functional space (Rosenfeld, 2002; Villéger et al., 2008). The classification of aquatic species in functional traits is a useful method to compare communities over large spatial and temporal scales and detect changes in assemblage's structure that influence the ecosystem functioning (Bellwood et al., 2003; Floeter et al., 2004).

Functional ecology studies of aquatic environments such as lakes, rivers, estuaries, sandy beaches, rocky shores, kelp forests, reefs, etc., have increased recently (Darr et al., 2014; Franco et al., 2008; Gusmao et al., 2016; Henriques et al., 2017; Krumhansl et al., 2016; Lefcheck and Duffy, 2015; Quimbayo et al., 2016; Tribot et al., 2016; van der Linden et al., 2012). In tropical regions, functional ecology studies have been essential to understand coral reef functioning (Hughes et al., 2003; Mora et al., 2014; Parravicini et al., 2013). Marine sediments are good prospects to study their functional ecology, being one of the largest ecosystems in the world occurring along broad environmental and biogeographic gradients (Alongi, 1990; Costanza et al., 1997; Liquete et al., 2013), which is highly desirable for designing studies to explore general rules driving functional diversity patterns (Snelgrove et al., 2014). Benthic macrofauna assemblages are one of the most diverse species pools in the world (Gray, 2002; Snelgrove, 1997), and are often used to identify main drivers of biota patterns and to describe environmental changes (Arasaki et al., 2004; Saiz-Salinas, 1997; Thouzeau et al., 1991). These organisms generally have a wide array of physiological tolerances, trophic guilds, and ecological roles within soft bottom sediments (Alongi, 1990; Dauer, 1993; Harris, 1999; Houde and Rutherford, 1993; Lenanton and Potter, 1987; Nguyen et al., 2017; Peterson and Heck Jr, 1999; Roessig et al., 2004). The relatively extensive information on habitat, biota, biogeochemical, and hydrodynamic processes within multitrophic communities of benthic macrofauna, facilitates studies of its functional ecology (Levin et al., 2001; Snelgrove, 1999; Solan et al., 2004). Many studies, however, focusing on benthic macrofauna functional ecology have only addressed feeding guilds without considering other traits such as habitat, activity or motility (Magalhães and Barros, 2011; Schückel et al., 2013).

Among benthic habitats, there is an urgent need to understand how human impacts could affect the estuariene ecosystem functioning. Estuaries provide many ecological goods and ecosystem services to humans (Basset et al., 2013; Ewel et al., 1998; Giri et al., 2011; Hogarth, 2015; Zhang et al., 2012), however, estuaries are one of the most threatened environments on Earth (Elliott and Whitfield, 2011; Kennish, 2002; McLusky and Elliott, 2004). Most of the functional ecology studies of estuaries have addressed the functional diversity of fishes in temperate regions (Franco et al., 2008; Henriques et al., 2017; Lefcheck and Duffy, 2015; Villéger et al., 2010) and very few were conducted in the tropics (Gusmao et al., 2016). The Eastern Tropical Pacific (ETP) has been recognized as a hotspot for functional diversity (Stuart-Smith et al., 2013), however, attempts to understand the ecosystem functioning in the ETP are restricted to: the oceanic island Malpelo (Quimbayo et al., 2016), and two estuaries (1) the Gulf of Nicoya (Wolff et al.,

1998) and (2) Dulce Gulf (Wolff et al., 1996). Therefore, the present study aimed to explore the variation of the functional diversity structure of the benthic macrofauna along an estuarine gradient and between the dry and wet season in the second largest estuarine mangrove in Central America.

2 MATERIALS AND METHODS

2.1 Study site

The Térraba-Sierpe estuarine system is located at the southern Pacific coast of Costa Rica in the ETP (Fig. 1) and is protected under the RAMSAR convention since 1995. The area contains the largest mangrove forest (~14337 ha) of Costa Rica (Loría-Naranjo et al., 2018; Proyecto Humedales, 2015). Térraba-Sierpe's two main tributaries are Grande de Térraba and Sierpe rivers, having total catchment areas of 5077 km^2 and 790 km^2, respectively (Umaña et al., 2015). The region is subjected to mean annual precipitations of over 5000 mm, with a strong difference of precipitation rates between dry (December-April) and wet (May-November) seasons, with 520 mm and 860 mm monthly precipitation, respectively (Rojas, 2011). In Grande de Térraba river, the mean river flow during the dry and wet season are 115 $m^3 \cdot s^{-1}$, and 615 $m^3 \cdot s^{-1}$, respectively (Picado, 2015), with a record volume up to 8000 $m^3 \cdot s^{-1}$ during a hurricane (PHED, 2010). During the wet season, there is an increase of suspended sediments (up to 1234 ± 59 $mg \cdot L^{-1}$) and nutrients (phosphate: 9.4 $\mu mol \cdot L^{-1}$, nitrite: 2.2 $\mu mol \cdot L^{-1}$, ammonium: 5.0 $\mu mol \cdot L^{-1}$, silicates: 1388.3 $\mu mol \cdot L^{-1}$), while primary productivity rates (0.79 $gC \cdot m^{2} \cdot day^{-1}$) and salinity (down to 1 psu at the bottom) decrease (Lizano et al., 2001; Picado, 2015; Umaña-Villalobos and Springer, 2006; Umaña et al., 2015).

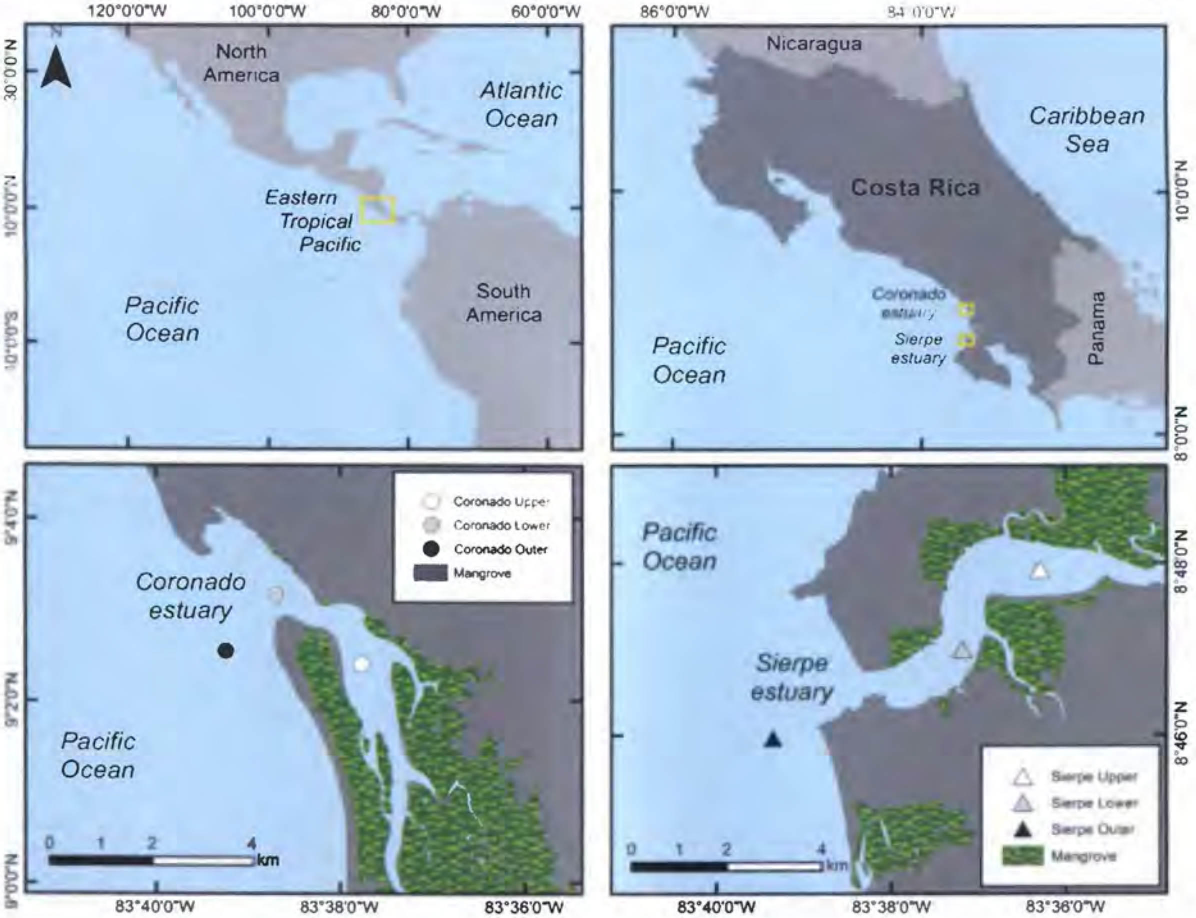


Figure 1. *Sampling sites of the subtidal benthic macrofauna along the estuarine zonation (upper estuary, lower estuary, outer estuary) in Coronado and Sierpe estuaries, at the Térraba-Sierpe National Wetland (TSNW), Pacific coast of Costa Rica.*

The subtidal sediments at the channels and nearshore turbid zones of Térraba-Sierpe are sand-dominated and moderately well sorted, with average grain size of 133.22 µm, organic matter content of 5.2%, and carbonate content of 5.7% (Table S1, see Chapter 1). During the dry season sediments are more heterogeneous than during the wet season (Table S1, see Chapter 1). Sediments are also more heterogeneous towards the upper and lower stations, while they are more homogoneous at outer stations (Table S1, see Chapter 1). The organic matter content of the sediments is higher at the upper station than in lower and outer stations, and this pattern is more conspicuous at Sierpe than in Coronado (Table S1, see *Chapter* 1).

2.2 Sampling of benthic macrofauna

Field sampling was conducted in Coronado and Sierpe estuaries, and in each estuary three stations were visited: 1) upper station, ~5 km landward from the river mouth; 2) lower station, <1 km landward from the river mouth; and 3) outer station, ~1 km seaward from the river mouth (Fig. 1). Sampling was carried out on a monthly basis from January to December 2013 (except in February), alternating between estuaries. In order to assess the benthic macrofauna assemblage, five sediment samples were recollected using a Petit-Ponar grab (152 mm × 152 mm). The minimum area suggested for sampling soft-bottom macrofauna is 0.1 m^2 (Eleftheriou and McIntyre, 2005), and therefore the data of the five sediment grabs was combined (for a total sampled area of 0.11 m^2) for the analyses. Hereinafter, "sampling station" will be referred as the sum of the five sediment grabs at a given station (upper, lower, outer), in a given estuary (Coronado, Sierpe), during a given month. In the field, the sediment grabs were stored in plastic bags and fixed with a solution of sea water (filtered with a 63 µm sieve) with 5% formalin and Rose Bengal dye (Vargas, 1987). At the laboratory, samples were gently washed using a 500 µm sieve to separate the macrofauna from the finer particles (Vargas, 1987). The material was then stored in 95% ethanol and reviewed using a light dissecting microscope. For the full taxonomic identification see Chapter 2. Once identified, the wet weight of each taxa was measured using an electronic analytical balance (AND HR-200; ±0.0001 g). The biomass ($g \cdot m^{-2}$, wet weight per area) was calculated for each taxa per sampling station.

2.3 Assessment of environmental variables

For each sampling station, one additional sediment sample was collected to measure abiotic variables of the sediment. At the laboratory, measurements of mud, sand and gravel contributions, mean grain size, sorting, skewness and kurtosis, and organic matter and carbonates content in the sediment were performed (for details in methodology see Chapter 1, Table S1). To record the water column variables at the bottom a CTD Sea Bird Electronics 19plus was used to measure temperature, salinity and dissolved oxygen (Table S2).

2.3 Macrofauna's functional richness

To evaluate the functional structure of the benthic macrofauna, all the 146 taxa found at Térraba-Sierpe were classified regarding four life-history traits following the definitions and classifications in the literature for each group: (1) Habitat: epifaunal, infaunal, interstitial, and epizooic; (2) Activity: free-living, sedentary, sessile, and parasitic; (3) Motility: tube-dwelling, burrowing, crawling, and swimming; and (4) Feeding guild: carnivore, scavenger, detritivore, omnivore, sub-surface deposit feeder, surface deposit feeder, parasitic, and algaevore (for details see Table 1; Brusca and Iverson, 1985; Coan and Valentich-Scott, 2012; Cutler, 1994; de León-González et al., 2009; Fauchald and Jumars, 1979; Fischer et al., 1995; González-Acosta et al., 2017; Jangoux and Lawrence, 1982; Jarquín-González and García-madrigal, 2013; Jumars et al., 2015; Keen, 1971; Macdonald et al., 2010; Salgado-Barragán and Hendrickx, 2010; Tovar and Suárez-Morales, 2007; Vargas and Dean, 2010). For some taxa more than one category within a given trait were annotated because of the facultative generalist traits of those particular taxa (Table S3). For each taxa, the combination of categories of the four life-history traits was defined as the functional entity (FE) (Quimbayo et al., 2016). The functional entities (FEs) can be shared between more than one species, which share the same combination of life-history traits' categories. Accumulation curves of FEs by sampling stations were estimated for all the data from Térraba-Sierpe, and separately for station (upper, lower, outer), for estuary (Coronado, Sierpe), and for season (dry, wet). The accumulation curves were calculated using the "random" method of the "vegan" package in RStudio (Colwell et al., 2004; Gotelli and Colwell, 2010; Oksanen et al., 2013; RStudio Team, 2015). The variation of the biomass contribution of the categories per life-history trait was explored using a One-Way Analysis of Variance (ANOVA).

Table 1. *Type and definitions of the categories of the four life-history traits used to classify the functional entities of the subtidal benthic macrofauna taxa at the Térraba-Sierpe estuarine system, Pacific coast of Costa Rica.*

Traits	Description
Habitat	
Epifaunal	Living mainly above the surface of the sediments.
Infaunal	Living mainly under the surface of the sediments.
Interstitial	Living among the particles of the sediments.
Epizooic	Living on other animals.
Activity	
Free-living	Free movement, and usually highly motile.
Sedentary	Capable of free movement, but usually stays at one site.
Sessile	Mainly restricted to one site, movement very limited.
Parasitic	Limited to the association to other animals.
Motility	
Tube-dwelling	Inhabiting self-built tubes or tubes built by other organisms.
Burrowing	Usually stay at and move through building of burrows in the sediment.
Crawling	Generally moves by crawling across the sediment.
Swimming	Movement is mainly restricted to the water column through swimming.
Feeding guild	
Carnivore	Feeds mainly on live preys.
Scavenger	Feeds mainly on corpses or rooted flesh from other organisms.
Detritivore	Feeds mainly on decayed organic matter.
Omnivore	Feeds on several sources of food without showing a clear bias.
Sub-surface deposit feeder	Feeds on organisms and / or organic matter deposited under the surface of the sediments.
Surface deposit feeder	Feeds on organisms and / or organic matter deposited on the surface of the sediments.
Suspension feeder	Feeds on the decaying particles and plankton organisms suspended in the water column.
Parasitic	Feeding depends on its parasitic relation with other organisms.
Algaevore	Feeds mainly on algal organisms (such as diatoms and dinoflagellates).
Chemosynthetic symbionts	Nutrition is based on the derived metabolites of endosymbiotic organisms

2.4 Spatial and temporal variation of functional richness and biomass

In order to explore the spatial (station and estuary) and temporal (season) variation of the FEs and biomass of benthic macrofauna at Térraba-Sierpe, two Generalized Linear Models (GLM) were performed using the "glm" function with a Gamma distribution in RStudio (Crawley, 2007; RStudio Team, 2015). The models considered as factors: 1) station (upper, lower, and outer), 2) estuary (Coronado and Sierpe), and 3) season (dry and wet).

2.5 Functional structure of benthic macrofauna

The functional distance between each pair of taxa at each sampling station was calculated using the Gower dissimilarity distance, because the functional variables were categorical (Villéger et al., 2008). A principal coordinate analysis based on the functional distance matrix was performed to build a multidimensional functional space for each station, each estuary, and each season, and to estimate the different functional facets of the macrofauna assemblage structure (Maire et al., 2015). The multidimensional functional spaces were computed using the "quality_funct_space" (coded by Eva Maire and Sébastien Villéger, available at villeger.sebastien.free.fr), which is an updated version of the function in Maire et al. (2015), which uses the mean squared-deviation between the initial functional distance and the standardized distance in the functional space for all the multidimensional functional spaces (2 to N dimensions) (Villéger et al., 2016).

The multidimensional functional diversity indices for the macrofauna assemblage were computed using the "multidimFD" function (villeger.sebastien.free.fr) following the indices' formulas at Mouillot et al. (2013) (Villéger et al., 2016). The coordinates are based on the macrofauna assemblage and the multidimensional functional space matrix, weighted by the matrix of taxa contribution's magnitude to the assemblages (in this case biomass, $g \cdot m^{-2}$). Therefore, considering the position and the biomass of the macrofauna taxa regarding the multidimensional functional spaces built for each station, estuary, and season levels, four functional indices were estimated to complement the description of the benthic macrofauna's functional structure: functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), functional dispersion (FDis), functional specialization (FSpe), and functional originality (FOri) (see Table 2, Laliberté and Legendre, 2010; Mouillot et al., 2013; Villéger et al., 2008). The community-weighed means of traits were used to select the main category of each life-history trait for the sampling stations (Laliberté and Legendre, 2010). The community-weighted mean of a trait (CWM) was used to describe the functional identity of the sampling stations' assemblage regarding the four life-history traits (Lavorel et al., 2008; Ricotta and Moretti, 2011).

The "multidimFbetaD" function was used to compute and illustrate multdimensional functional beta-diversity indices for pairs of species assemblages (villeger.sebastien.free.fr) based on the formulas of Villéger et al. (2013), using the "betapart" package for the computation (Villéger et al., 2016). The function requires a coordinate matrix of taxa (minimum three) along axes of a functional space (from two to four traits), based on a matrix of presence/absence of taxa. GLM were used to explore spatial (station and estuary) and temporal variation (season) of the multidimensional functional diversity indices (FRic, FDiv, FEve, FDis, FSpe, and FOri) in RStudio (Crawley, 2007; RStudio Team, 2015). The models considered as factors: 1) station (upper, lower, and outer), 2) estuary (Coronado and Sierpe), and 3) season (dry and wet).

Table 2. *Functional indices and definitions used to describe the functional structure of the subtidal benthic macrofauna taxa at the Térraba-Sierpe estuarine system, Pacific coast of Costa Rica.*

Functional index	Definition	Reference
Functional richness (FRic)	Convex-hull volume of the functional space created by all the taxa within the given sample pool, which indicates the range of the combination of life-history traits	Villéger et al. (2008)
Functional divergence (FDiv)	Deviation of the species weight from the center of the convex-hull volume of the functional space	Villéger et al. (2008)
Functional evenness (FEve)	Regularity of the abundance distribution within the functional space, ranging from 0 to 1, when a higher value is related to the evenly distribution of species abundance in the functional space	Villéger et al. (2008)
Functional dispersion (FDis)	Mean distance of an individual taxa to the centroid of the taxa assemblage within the functional space, and is not affected by taxa richness	Laliberté and Legendre (2010)
Functional specialization (FSpe)	Weighted mean distance to the taxa pool centroid, such as the average position of all the taxa present in the set of assemblages, divided by the maximum distance to the centroid	Villéger et al. (2008) Mouillot et al. (2013)
Functional originality (FOri)	Weighted mean distance to the nearest taxa from the assemblage, divided by the maximum distance to the nearest neighbor	Villéger et al. (2008) Mouillot et al. (2013)

3 RESULTS

3.1 General results

A total 165 sediment grabs were analyzed from the subtidal soft bottoms, which recollected 3391 macrofauna specimens, accounting for a total of 146 taxa in 72 families (Table S3, see Chapter 2). The dominant phyla (both in number of taxa and abundance) were Annelida, Mollusca and Arthropoda (Table S3, see Chapter 2). The most abundant taxa were *Scolelepis* (*Scolelepis*) *acuta*, Corophiidae indet., *Paraprionospio pinnata*, *Malacoceros indicus*, Nematoda indet, *Leptonereis laevis*, *Magelona riojai*, *Armandia* cf. *salvadoriana*, *Nephtys oculata*, Cumacea indet, and

Tellinidae indet, accounting together 59.9% of the overall abundance (Table S3, see Chapter 2).

3.2 Functional entities and biomass

A total of 48 functional entities (FEs) were identified in the subtidal benthic macrofauna assemblage of Térraba-Sierpe (Table S4). The average (± SD) number of FEs per sampling station was 13 ± 5.9 FEs, varying from 1 to 23 FEs. The accumulation curve by sampling station reached no asymptote but the slope was close to 0 (b = 0.12, Fig. 2A). The number of FEs was higher at the outer station, followed by the upper station, and finally the lower station (Fig. 2B). Sierpe showed more FEs than Coronado (Fig. 2C). The number of FEs was higher in the dry season than the wet season when considering a similar sampling effort (Fig. 2D). The average number of FEs was higher at the outer stations than the upper and lower stations (Table 3A, Fig. 3A), and was also higher during the dry season than the wet season (Table 3A, Fig. 3A).

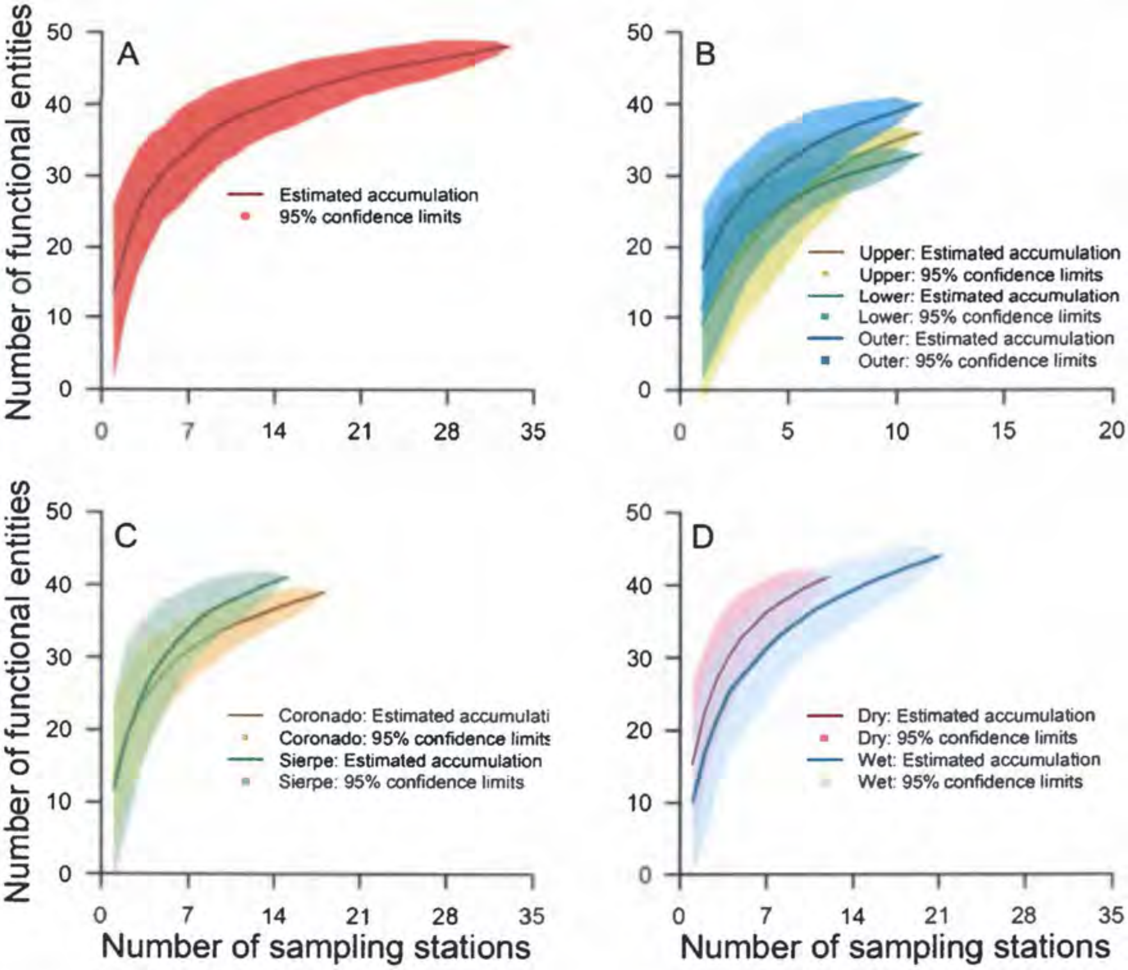
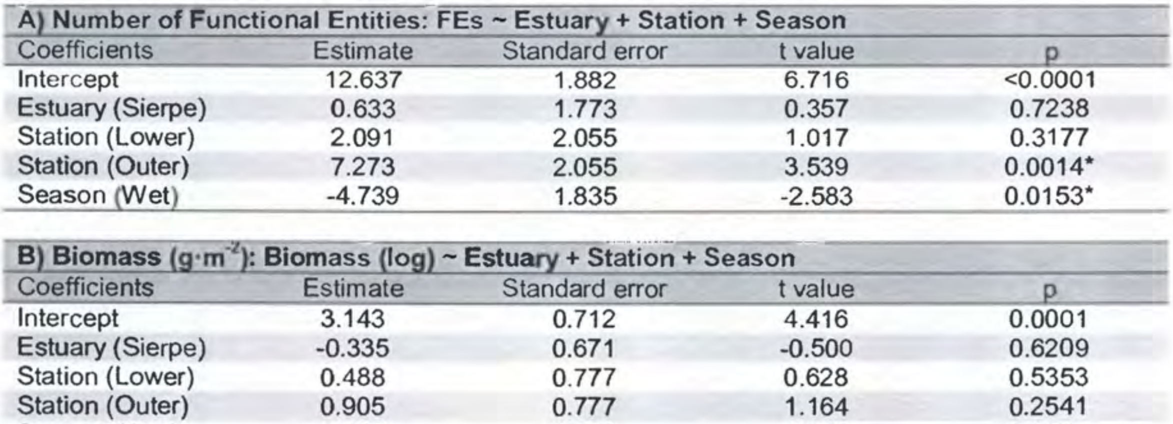


Figure 2. *Accumulation curves estimated using the "random" method and showing 95% confidence limits of the number of functional entities at the Térraba-Sierpe estuarine system by A) considering all samples, B) estuarine zonation (upper, lower, outer), C) estuary (Coronado, Sierpe), and D) season (dry, wet), Pacific coast of Costa Rica.*

Table 3. *General Lineal Models for spatial and temporal variation of subtidal benthic macrofauna A) functional entities and B) biomass (wet weights of macrofauna per sampled area) at Térraba-Sierpe estuarine system, Pacific coast of Costa Rica.*



A) Number of Functional Entities: FEs ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	12.637	1.882	6.716	<0.0001
Estuary (Sierpe)	0.633	1.773	0.357	0.7238
Station (Lower)	2.091	2.055	1.017	0.3177
Station (Outer)	7.273	2.055	3.539	0.0014*
Season (Wet)	-4.739	1.835	-2.583	0.0153*

B) Biomass ($g \cdot m^{-2}$): Biomass (log) ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	3.143	0.712	4.416	0.0001
Estuary (Sierpe)	-0.335	0.671	-0.500	0.6209
Station (Lower)	0.488	0.777	0.628	0.5353
Station (Outer)	0.905	0.777	1.164	0.2541
Season (Wet)	-1.322	0.694	-1.905	0.0671

*: factors are significantly different.

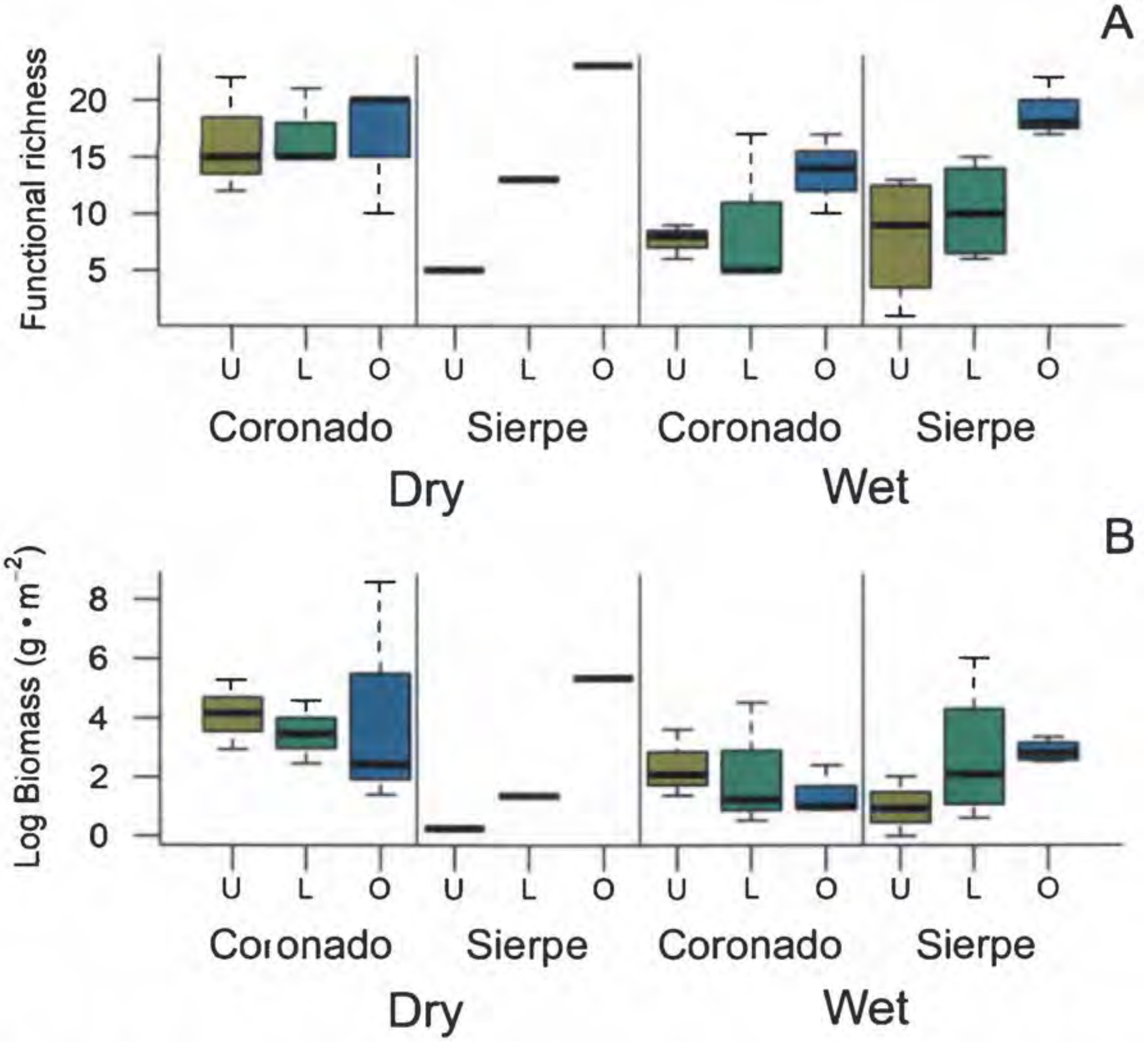


Figure 3. *Box plot representing the number* of *functional entities (FEs) and the biomass (g·m^{-2}), log transformed (log(x+1)), regarding the station (upper = U, lower = L, outer = O), estuary (Coronado, Sierpe) and season (Dry, Wet) at the Térraba-Sierpe estuarine system, Pacific coast of Costa Rica.*

The total weight of the collected specimens was 10.6 g, with an average biomass (± SD) 13.9 ± 15.20 g·m^{-2} per sampling station, ranging from 0.01 to 63.0 g·m^{-2}. The higher biomass was found at the outer station of Coronado estuary during the dry season, where the gastropods *Olivella aureocincta* and *Natica scethra* contributed the most to the biomass, but also 32 other taxa were collected accounting for 205 specimens. Otherwise, the lower biomass was observed at the upper station of Sierpe estuary during the wet season, when only three specimens of the polychaete *Mediomastus californiensis* were collected. The average of biomass similar between the station, estuary, and season levels (Table 3B, Fig. 3B)

The species that contributed the most to biomass was the gastropod *N. scethra* with a total of 68.28 $g \cdot m^{-2}$, while the most abundant species ($n = 434$), the polychaete *S.* (*S.*) *acuta*, had a total biomass of only 4.19 $g \cdot m^{-2}$ (Table S4). Other taxa with high biomass were the amphipod family Corophiidae (44.22 $g \cdot m^{-2}$) which was also very abundant ($n = 315$), and crabs of the family Xanthidae (43.62 $g \cdot m^{-2}$) which was rather rare in this study (Table S4). The functional entity with the largest biomass contribution was the epifaunal/infaunal free-living crawling surface/sub-surface deposit feeders (72.45 $g \cdot m^{-2}$), which includes *N. scethra*. Other following functional entities with large biomass were the epifaunal/infaunal free-living crawling carnivore/scavengers (70.74 $g \cdot m^{-2}$) (including the gastropods *O. aureocincta* and *Olivella semistriata*), and epifaunal free-living crawling carnivore/omnivores (61.52 $g \cdot m^{-2}$), which includes almost all the decapods (such as Xanthidae crabs) (Table S4).

The macrofauna's habitat type with the largest biomass contribution was the infaunal ($F_{5,32} = 8.069$, $p < 0.001$, Fig. 4A). The macrofauna's activity with the most biomass contribution was the free-living macrofauna ($F_{3,32} = 1.254$, $p = 0.289$, Fig. 4B). The crawling fauna accounted for the largest biomass of the motility trait ($F_{8,32} = 9.581$, $p < 0.001$, Fig. 4C). The suspension feeders had the largest biomass contribution among the feeding guilds ($F_{18,32} = 6.635$, $p < 0.001$, Fig. 4D).

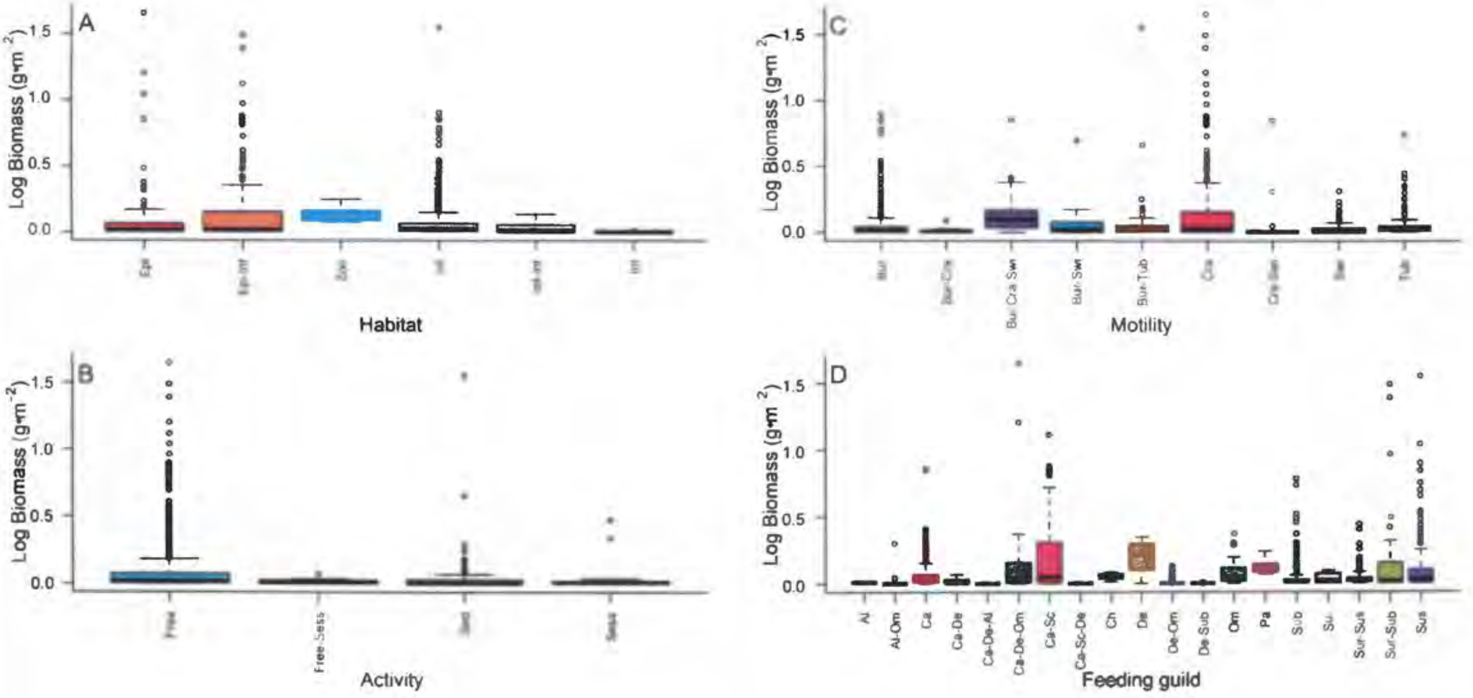


Figure 4. *Box plot representing the biomass (g·m^{-2}), log transformed (log(x+1)), of the subtidal benthic macrofauna regarding the categories of four life-history traits: A) Habitat (Epi = Epifaunal, Epi-Inf: Epifaunal and Infaunal, Zoo = Epizoic, Inf = Infaunal, Inf-Int = Infaunal and Interstitial, Int = Interstitial), B) Activity (Free = Free living, Free-Sess = Free living and Sessile, Sed = Sedentary, Sess = Sessile), C) Motility (Bur = Burrowing, Bur-Cra = Burrowing and Crawling, Bur-Cra-Swi = Burrowing, Crawling and Swimming, Bur-Swi = Burrowing and Swimming, Bur-Tub = Burrowing and Tuve-dwelling, Cra = Crawling, Cra-Swi = Crawling and Swimming, Swi = Swimming, Tub = Tube-dwelling), and D) Feeding guild (Al = Algaevore, Al-Om = Algaevore and Omnivore, Ca = Carnivores, Ca-De = Carnivores and Detritivores, Ca-De-Al = Carnivores, Detritivores, and Algaevores, Ca-De-Om = Carnivores, Detritivores, and Omnivores, Ca-Sc = Carnivores and Scavengers, Ca-Sc-De = Carnivores, Scavengers, and Detritivores, Chi = Chemosynthesis, De = Detritivores, De-Om = Detritivores and Omnivores, De-Sub = Detritivores and Sub-surface deposit feeders, Om = Omnivores, Pa = Parasites, Sub = Sub-surface deposit feeders, Sur = Surface deposit feeders, Sur-Sus =*

Surface deposit and Suspension feeders, Sur-Sub = Surface and Sub-surface deposit feeders, Sus = Suspension feeders).

2.5 Functional structure of benthic macrofauna

The functional richness (FRic) is the volume of the convex-hull created by the functional assemblage in the multidimensional functional space. Therefore, a higher FRic means a broader spectrum of functional traits in the assemblage. Interestingly, the higher FRic (0.546) was associated to the second higher functional entities (FEs) value (20), while the second highest FRic (0.534) was associated to the first largest higher FEs (23) (Table 4). These both highest FRic were found at the outer station of Sierpe and Coronado, respectively (Table 4). A low FRic means a narrow spectrum of functional traits in the assemblage. The lowest FEs found was 1, but the "multidimFD" cannot compute the multidimensional functional diversity indices of assemblages with less taxa than number of traits (four in this case). The second lowest FEs was 5, and was associated to the lowest FRic (0.001) (Table 4). The results supported differences of the FRic between seasons only and not between stations neither estuaries ($p = 0.025$) (Table S4A), indicating that the functional space created by the benthic macrofauna of both dry and wet season were different. During the dry and wet season the average FRic was 0.247 and 0.116, respectively.

The functional divergence (FDiv) measures how the functional traits diverge from the center of the functional trait range (= assemblage centroid) in the multidimensional functional space. High FDiv indicates that the dominant taxa (higher biomass in this case) have extreme functional traits (far from the assemblage centroid) while low FDiv indicates that dominant taxa present functional traits close to the assemblage centroid. In Térraba-Sierpe the highest FDiv (0.997) was found at the outer station of Coronado estuary in October (peak of the wet season) meaning that the assemblage of that station had extreme functional traits compared to the more common traits within the functional space. Otherwise, the lowest FDiv (0.654) occurred at the upper station of Coronado during December (the first month of the dry season) meaning that this station had functional traits considered normal, and close to the centroid, of the assemblage. No differences of FDiv were found between stations, estuaries, neither seasons (Table S4B).

The functional evenness (FEve) indicates the evenness of the distribution of taxa's contribution (in this case biomass) filling the multidimensional functional space, being lower when the taxa's contributions are less evenly distributed, and higher when their contribution is more evenly distributed. The highest FEve (0.610) found in Térraba-Sierpe occurred in the outer station of Coronado estuary during January, dry season, while the lowest (0.143) occurred at the upper station of the Coronado estuary during April, end of dry season (Table 4). The results support no differences of FEve between stations, estuaries neither seasons (Table S4C).

The functional dispersion (FDis) describes the average distance of the taxa weighted by their contribution (in this case biomass) to the assemblage centroid within the multidimensional functional space, accounting then for relative contribution of the taxa and shifting the position of the centroid towards the taxa contributing the most. FDis has a value of 0 when the assemblage has only one taxon, and has no upper limit. The highest FDis (0.711) was found at the outer station in Sierpe during May, first month of wet season, meaning this station's assemblage had more taxa with traits far from the weighed centroid, while the lowest FDis (0.088) was at the outer station in Coronado during October, peak of wet season, meaning this sample had an assemblage composed of species located closely to the assemblage centroid in the multidimensional functional space (Table 4). There was no evidence for FDis separation between stations, estuaries neither seasons (Table S4D).

The functional specialization (FSpe) is the mean distance of a given taxon from the rest of the taxa pool in the assemblage. A high FSpe means that dominant species are specialists (far from the assemblage centroid), while low FSpe means that dominant species are generalists (close to the assemblage centroid). The FSpe showed no variation between the stations, estuaries neither seasons (Table S4E).

The functional originality (FOri) measures the modification of functional redundancy between species regarding the changes in taxa contribution, where high FOri means that dominant taxa are functionally more original in the assemblage (taxa with high contribution, in this case biomass, tend not to share traits with other taxa), while low FOri means that dominant taxa are functionally less original in the assemblage, sharing traits with other close taxa. The highest FOri (1.62) was found at the outer station of Sierpe estuary during November, last month of wet season, meaning that taxa with more contribution in this assemblage tend to be more functionally original in the sense that these species tend not to share their traits with close other taxa (Table 4). Otherwise, the lowest FOri (1.32×10^{-16}) at the lower stations of Coronado estuary during June, wet season, which means that this sample's dominant taxa do share functional traits with close other taxa in the functional space (Table 4). The FOri showed no difference between stations, estuaries, nor seasons (Table S4F).

Table 4. *Functional diversity of subtidal benthic macrofauna at the Térraba-Sierpe estuarine system, Pacific coast of Costa Rica. Number of taxa, number of functional entities (FE), functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), functional dispersion (FDis), functional specialization (FSpe), and functional originality (FOri) and the most important category of habitat, activity, motility, and feeding guild per sampling station is included.*

Season	Month	Estuary	Station	Taxa	FE	FRic	FDiv	FEve	FDis	FSpe	FOri	Habitat	Activity	Motility	Feeding guild
Dry	Jan	Coronado	1	36	22	0.389	0.981	0.263	0.263	0.537	4.84×10^{-3}	Epi	Free	Cra	Car-Det-Omn
			2	32	15	0.242	0.833	0.310	0.677	0.479	5.06×10^{-4}	Inf	Free	Cra	Car-Sca
			3	11	10	0.128	0.958	0.610	0.417	0.564	5.96×10^{-4}	Epi-Inf	Free	Cra	Car-Sca
	Mar	Sierpe	1	5	5	0.005	0.988	0.366	0.283	0.495	5.21×10^{-2}	Epi-Inf	Free	Cra	Sur-Sub
			2	15	13	0.171	0.863	0.314	0.643	0.477	3.87×10^{-2}	Inf	Free	Cra	Car-Det-Omn
			3	40	23	0.534	0.857	0.251	0.696	0.509	2.54×10^{-2}	Epi-Inf	Free	Cra	Sus
	Apr	Coronado	1	20	15	0.300	0.719	0.143	0.625	0.454	5.01×10^{-2}	Inf	Free	Bur	Sus
			2	27	15	0.092	0.695	0.284	0.343	0.401	3.26×10^{-3}	Inf	Free	Bur	Sus
			3	32	20	0.546	0.936	0.369	0.378	0.525	7.08×10^{-3}	Epi-Inf	Free	Cra	Sur-Sub
	Dec	Coronado	1	20	12	0.063	0.654	0.461	0.392	0.429	9.02×10^{-5}	Inf	Free	Bur-Cra-Swi	Car
			2	35	21	0.219	0.797	0.234	0.623	0.458	4.47×10^{-3}	Inf	Free	Bur	Car
			3	28	20	0.276	0.853	0.268	0.631	0.492	7.58×10^{-2}	Inf	Free	Bur	Car
Wet	May	Sierpe	1	7	6	0.002	0.988	0.292	0.173	0.542	2.06×10^{-7}	Epi-Inf	Free	Cra	Sur-Sub
			2	8	7	0.016	0.860	0.539	0.639	0.449	1.63×10^{-2}	Inf	Free	Cra	Sus
			3	28	19	0.291	0.860	0.289	0.711	0.562	7.76×10^{-3}	Epi-Inf	Free	Cra	Sus
	Jun	Coronado	1	10	6	0.004	0.736	0.305	0.365	0.393	4.71×10^{-4}	Inf	Free	Bur	Car
			2	9	5	0.001	0.976	0.155	0.500	0.528	1.32×10^{-16}	Epi-Inf	Free	Cra	Car-Sca
			3	11	10	0.027	0.710	0.380	0.182	0.408	4.24×10^{-2}	Inf	Free	Bur	Sus
	Jul	Sierpe	1	1	1	NA	NA	NA	NA	NA	NA	Inf	Free	Bur	Sub-Sur
			2	22	13	0.122	0.743	0.261	0.521	0.480	1.10×10^{-1}	Inf	Free	Bur-Cra-Swi	Car
			3	27	17	0.319	0.995	0.365	0.456	0.550	4.97×10^{-4}	Epi	Free	Cra	Car-Det-Omn
	Aug	Coronado	1	9	8	0.100	0.696	0.166	0.682	0.548	2.23×10^{-3}	Inf	Free	Bur	Car
			2	7	5	0.003	0.892	0.596	0.583	0.518	3.69×10^{-4}	Epi-Inf	Free	Cra	Car-Sca
			3	15	14	0.041	0.895	0.407	0.475	0.514	2.63×10^{-2}	Inf	Free	Bur	Sur-Sus
	Sep	Sierpe	1	21	13	0.095	0.705	0.339	0.467	0.440	3.16×10^{-4}	Inf	Free	Bur-Cra-Swi	Car
			2	26	15	0.133	0.893	0.369	0.559	0.493	1.12×10^{-2}	Epi	Free	Cra	Sus
			3	28	22	0.215	0.844	0.365	0.653	0.482	3.37×10^{-2}	Inf	Free	Cra	Car-Sca
	Oct	Coronado	1	15	9	0.067	0.746	0.314	0.409	0.416	2.75×10^{-2}	Inf	Free	Bur	Sur-Sus
			2	31	17	0.262	0.944	0.182	0.400	0.516	2.10×10^{-3}	Epi-Inf	Free	Cra	Sur-Sub
			3	25	17	0.196	0.997	0.449	0.088	0.651	3.28×10^{-1}	Inf	Sed	Bur-Tub	Sus
	Nov	Sierpe	1	14	12	0.218	0.718	0.403	0.451	0.423	1.33×10^{-3}	Inf	Free	Bur-Cra-Swi	Car
			2	10	6	0.017	0.943	0.150	0.510	0.510	2.81×10^{-2}	Epi	Free	Cra-Swi	Car
			3	29	18	0.197	0.935	0.398	0.571	0.518	1.62	Epi-Inf	Free	Cra	Car-Sca

NA = not applicable. Assemblages with less taxa than functional traits (four in this case) cannot be computed.

Since the GLM showed that FRic was the only functional index significantly influenced by the factors (Table S4A-F), plots representing the FRic by estuary, stations and season levels were performed (Fig. 5). The first and second plots in each row of the Figure five refer to the volume of the convex-hull occupied by the functional assemblage macrofauna in the multidimensional functional space (FRic) in two different assemblages, while weighing contributions of the taxa (size of the circles). The third plot of each row displays the FRic overlap between the two assemblages. These plots show that the functional space occupied by the macrofauna between estuaries, stations and seasons is relatively similar, with few FEs (squares in the plot) occurring only in one of the assemblages. However, considering the first and second plots of each row, the differences on the distribution of the biomass (allocation and size of the circles in the plot) along the functional space is noticeable. For example, the portion of the functional space not filled towards the positive values of Coordinate 2 in Coronado, is filled in Sierpe, but the FEs driving that had relatively low biomass (Fig. 5A). Because the FRic in Coronado occupies a lesser volume than Sierpe's, that means Coronado has a narrower functional range than Sierpe (Fig. 5A). Comparing the outer station to the lower station, the functional space and the distribution of the biomass is relatively similar, with dominant traits towards the positive values of Coordinate 1 (Fig. 5B). Considering upper and outer station, the functional spaces are relatively similar, however is slightly narrower in the upper station, which did not fill a space towards the negative values of Coordinate 1, which is filled in the outer station (Fig. 5C). Moreover, the distribution of the biomass is noticeably different between these stations, with upper station having more biomass towards the positive values of the Coordinate 1, while the outer stations had two main distributions of the biomass, one towards the negative and one towards the positive values of the Coordinate 1 (Fig. 5C). Comparing the lower and upper stations, the functional spaces were more similar than comparing the upper and outer stations, for example both lower and outer stations filled the space to the negative values of the Coordinate 1 that the upper stations did not fill (Fig. 5C,D). However, the distribution of the biomass was also dissimilar between the lower and outer stations (Fig. 5D). The functional space of the assemblage during dry and wet season were very similar, with only two FEs (with relatively low biomass) occurring at one season alone (Fig. 5E). However, the distribution of the biomass was relatively different, distributed at both positive and negative values of the Coordinate 1, but in the case of dry season, the functional trait allocating the biomass towards the negative values of the Coordiante 1 was closer to the assemblage centroid than in the wet season (Fig. 5E).

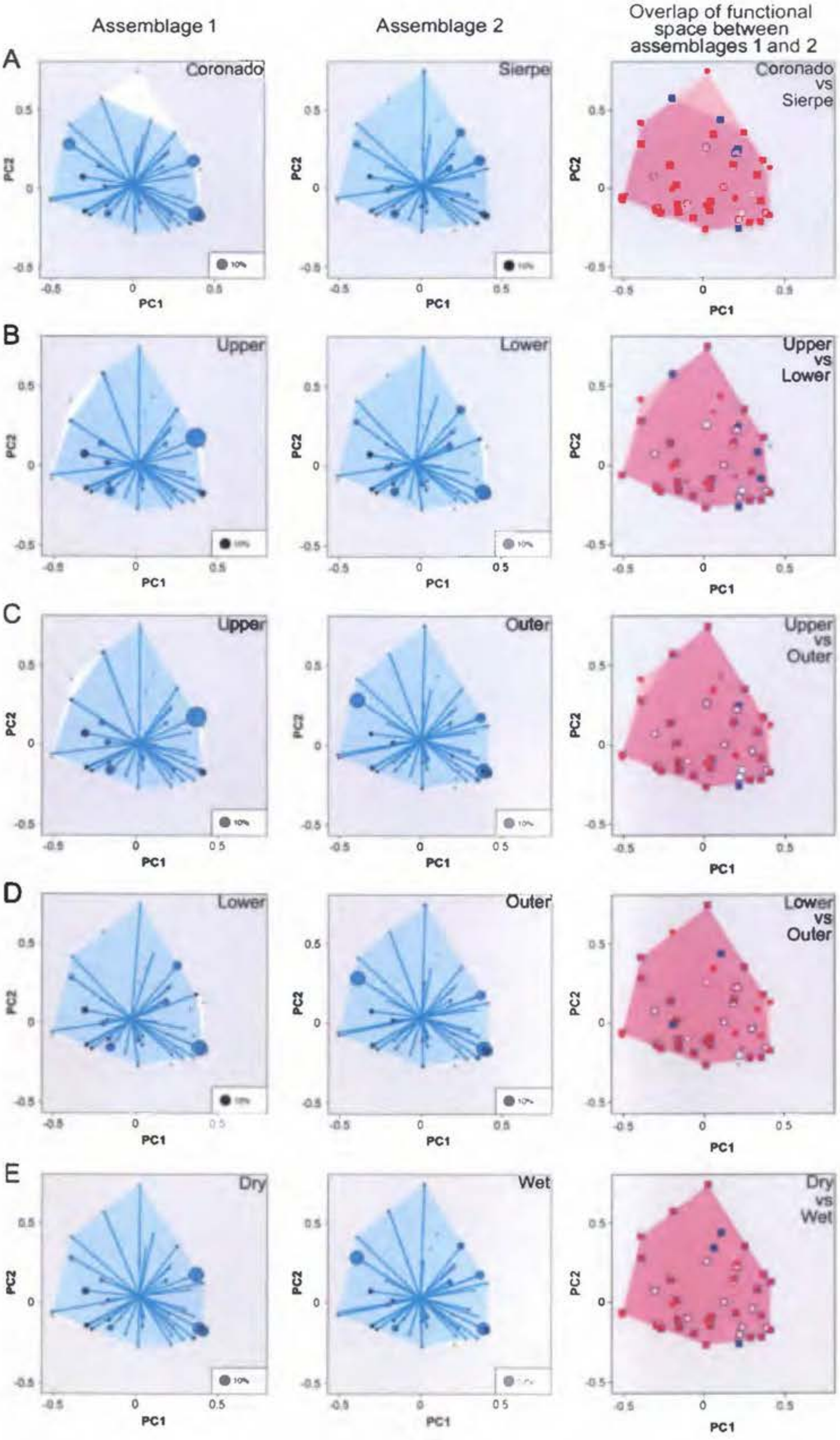

Assemblage 1
Assemblage 2
Overlap of functional space between assemblages 1 and 2
A
Coronado
Sierpe
Coronado vs Sierpe
B
Upper
Lower
Upper vs Lower
C
Upper
Outer
Upper vs Outer
D
Lower
Outer
Lower vs Outer
E
Dry
Wet
Dry vs Wet
PC1
PC2
-0.5
0
0.5
10%

Figure 5. *Representation of the volume occupied in the multidimensional functional space by the subtidal benthic macrofauna assemblage at the Térraba-Sierpe estuarine system, Pacific coast of Costa Rica. All the plots represent the Coordinate 1 (PC1) and the Coordinate 2 (PC2) of the Principal Coordinate Analysis. All the plots illustrate values for the functional richness (FRic). Comparisons from top to bottom (Assemblage 1 and Assemblage 2): A) Coronado and Sierpe estuaries, B) Upper and Lower stations, C) Upper and Outer stations, D) Lower and Outer stations, and E) Dry and Wet seasons. Size of the circles represents the relative contribution (percentage) of each functional entity to the total biomass at the assemblage.*

4 DISCUSSION

4.1 Functional structure of benthic macrofauna

The functional entity with major contribution in Térraba-Sierpe estuarine system (epifaunal/infaunal free-living crawling surface/sub-surface deposit feeding) was composed by taxa with the faculty to inhabit both over and burrowed in the sediments, and the capacity to obtain food from deposited organic particles in the surface and under the surface of the sediments as well. The faculty to switch functional traits, such as the feeding guild, can be advantageous during environmental and stressful changes, such as pulses of sediment loads (Riisgård and Kamermans, 2001; Taghon and Greene, 1992). Regarding physiological tolerances, the estuarine macrofauna is composed mainly by generalist rather than specialists (e.g. tolerance to salinity variation and sediment load impulses) and feeding guilds (Gray and Elliott, 2009; McLusky et al., 1993). Sedimentation in Térraba-Sierpe during the wet season can play an important role modifying the sediment sorting (which is more homogeneous during wet season due to input of particles) (see Chapter 1), productivity (Umaña et al., 2015), and benthic macrofauna assemblages composition (see Chapter 3). The particles imports from the catchment and the upstream river to the estuary also carry organic matter, which can be influencing that the feeding guild with most biomass corresponds to the suspension feeding (mostly bivalves and some polychaetes) (Venturini et al., 2011).

4.2 Functional entities and biomass

The average number of functional entities (FEs) in Térraba-Sierpe was higher at the outer station, followed by the upper station and lastly the lower station, which was similar to a parallel study of the taxonomic diversity, in which we found that the taxa richness in Térraba-Sierpe increases from the upper station to the lower and outer station (see Chapter 2). Changes in the number of FEs (combination of functional traits among the assemblage's taxa) are usually correlated with changes in the number of species (Törnroos et al., 2015) and environmental variables (Bertocci et al., 2017; Leitão et al., 2018). Estuarine conditions are harsh for many freshwater and marine-coastal species, and particularly the outlet region (where this study's lower station was located), which presents with wide salinity variation, has generally fewer species due to physiological stress (Elliott and Whitfield, 2011; Gray, 1981; Gray and Elliott, 2009; McLusky et al., 1993; Remane and Schlieper, 1972). Changes in salinity can drive not only taxonomic richness but also changes in the FEs (Darr et al., 2014). It is possible that physiological limitations are also driving the lower number of FEs at the lower stations in Térraba-Sierpe.

The macrofauna biomass was not different among estuaries, stations or seasons. Although the loss in species richness due to physiological stress in estuaries might suggest a decrease of the biomass, the few generalist species coping with the wide environmental variation (e.g. salinity, sediment pulses) have few competitors and can develop large biomasses (Alongi, 1990; Harris, 1999; Houde and Rutherford, 1993; Lenanton and Potter, 1987; Nguyen et al., 2017; Peterson and Heck Jr, 1999; Roessig et al., 2004). The occurrence of some opportunistic species developing large biomass can be homogenizing the patterns observed at Térraba-Sierpe. For example, many of the Spionid worms were noticeably more abundant towards the upper estuary, and the most abundant species, *Scolelepis*

(*Scolelepis*) *acuta*, occurred only at the upper station of Coronado estuary during the wet season (see Chapter 3).

4.3 Functional diversity patterns

Most of the multidimensional functional diversity indices showed no differences between estuaries neither stations. Similar results were obtained in the Mondego estuary, Portugal, were the functional groups of benthic macrofauna were similar along the estuarine gradient (van der Linden et al., 2012). Two localities with the same habitat can share similar functional groups, however, the contributions of those group could differ between localities (Barnes and Hendy, 2015). The contributions of the FEs were allocated differently within the functional space in the Térraba-Sierpe (size and position of circles in Fig. 5). For example, in the upper estuary the allocation of biomass towards the negative values of Coordinate 1, but is noticeably higher in the outer station, and this was related to contribution of the *Olivella* cowries. The benthic macrofauna at Térraba-Sierpe presented different taxonomic assemblages between estuaries and stations in another study (see Chapter 3). Results at the Térraba-Sierpe estuaries support that taxonomic and functional approaches, could find different patterns from the same system. However, the functional homogeneity among estuaries and stations found at Térraba-Sierpe means that despite changes in the taxonomic assemblage, the ecosystem functioning is fairly similar between estuaries and along the estuarine zonation, probably because different species occupy similar niches in different distributions.

The only multidimensional index showing differences between seasons in Térraba-Sierpe was the functional richness (FRic). A similar pattern was observed for the benthic macrofauna in a sub-tropical estuary in Brazil between summer and winter (Gusmao et al., 2016). The FRic was higher during the dry season, when more stable environmental variables and less freshwater influence is expected. Usually stable environmental conditions favor functional diversity (Gusmao et al., 2016). Taxonomical differences of the macrofauna assemblages' between seasons were also found at Coronado estuary (see Chapter 3). Is very significant than not only assemblage's taxonomic composition, but also the functional richness (volume occupied by the assemblage within the multidimensional functional space) change between seasons in these tropical estuaries. Despite the general idea that tropical marine environments are temporally stable (Abrams, 1976; Dunbar, 1960; Fischer, 1960; Klopfer, 1959; Nisbet et al., 1978) there is increasing evidence of the contrary using a taxonomic approach in community ecology (Abesamis et al., 2015; Aller et al., 2017; Broom, 1982; da Costa et al., 2008; Hernández-Guevara et al., 2008; Maurer and Vargas, 1984; McClanahan, 1988; Vargas, 1987).

Most of the sampling stations had low functional originality (FOri) values (close to zero, Table 3), meaning that dominant taxa share functional traits with other taxa, making the functional assemblage less original (Mouillot et al., 2013; Villéger et al., 2008), which means high functional redundancy of the subtidal benthic macrofauna in Térraba-Sierpe. For example, regarding biomass contribution, the dominant FEs (epifaunal/infaunal free-living crawling surface/sub-surface deposit feeders, epifaunal/infaunal free-living crawling carnivore/scavengers, and epifaunal free-living crawling carnivore/omnivores) were shared by six, ten, and nine taxa. Otherwise, 46% and 21% of the FEs are only occupied by one or two species. Results from coral reefs have shown that the benefits of high species richness are uncertain to maintain ecosystem functioning when the functional redundancy is low (Bellwood et al., 2003; D'Agata et al., 2016; Hughes et al., 2003). This low functional redundancy should raise alarm over the vulnerability of these estuaries (Barros et al., 2012; Micheli and Halpern, 2005).

Limitations of the study

The present study represents an initial effort for understanding the ecological processes of the tropical estuaries in the ETP using multidimensional functional diversity indices. However, there should be pointed out some of the limitations of this study should be addressed in future efforts. This study focused on functional traits related to habitat preferences, locomotion capacities, and food acquisition.

However, the distribution and survival of benthic macrofauna inhabiting estuaries is highly influence by variations in salinity (Elliott and Whitfield, 2011; Gray, 1981; Gray and Elliott, 2009; McLusky et al., 1993), including Térraba-Sierpe (see Chapter 3), but these information is scarce or absent for many benthic invertebrates (Evans, 2008). Moreover, salinity has proven to influence also the functional structure of estuarine assemblages: benthic invertebrates (Mondego estuary, Portugal) and fishes (global study) (Henriques et al., 2017; van der Linden et al., 2012). Therefore, future studies should incorporate salinity tolerances as a functional trait.

Conservation implications

Management and conservation of marine and coastal habitats demand the understanding on how ecological processes impact the ecosystem functioning across local and regional scales and through a range of intensities of human impacts (Micheli and Halpern, 2005; van der Zee et al., 2015). Habitat modification can influence the functional diversity of coastal environments (Leitão et al., 2018; van der Zee et al., 2015). Moreover, modifications of the functional structure of ecosystems may lead to changes of phases, such as the switch from coral to algal dominated reefs in the Caribbean Sea after the drastic loss of herbivorous fishes and sea urchin populations (Hughes, 2010). Loss of the macrofauna functional roles could influence hydrological, particulate matter, nutrients and gases exchange dynamics near the sea bottom (Coco et. 2016). Functional ecology has proven to be useful for ecosystem management (Strong et al., 2015). The effective application of functional ecology studies at the services of human populations needs represents the next grand challenge for ecologists (Snelgrove et. 2014).

The Térraba-Sierpe estuarine system supports a high biodiversity (Chicas, 2001; Echeverría-Sáenz et al., 2003; Rojas and Rodríguez, 2008; Sibaja-Cordero and Echeverría-Sáenz, 2015), vital ark-clam and estuarine fishes populations for local artisanal fishers (Chicas, 2001; Nielsen and Quesada, 2006; Proyecto Humedales, 2015), and nursery grounds for rays and sharks (Clarke et al., 2014). However, this important ecosystem is being threatened by agrochemical and pesticide pollution, wetland drainage, deforestation, agricultural expansion, and over-exploitation of forest and fisheries resources (Proyecto Humedales, 2015). There is also a plan to create a massive hydroelectric project involving the construction of a 173 m high dam upstream in the Grande de Térraba catchment, in one of the main tributaries of Coronado estuary (PHED, 2010). This project could alter the natural dynamics of sediment and freshwater input into the estuarine system, including changes in the natural fluctuations of sediment inputs, and retention of organic and non-organic particles (see Xu and Dong, 2017). Modifications of river flow can induce negative effects in downstream littoral ecosystems, as in the Colorado delta in the Gulf of California (Kowalewski et al., 2000). If the dam interrupts the seasonal natural hydrological and sedimentary dynamics of the estuary, is possible that it causes impacts on the functional structure of the estuary. The functional ecology of Térraba-Sierpe has several functional entities represented only by one or two species of the macrofauna. Therefore, if human disturbances negatively affect the distribution and survival of these species in the estuaries, their functional role can be lost.

5 CONCLUSIONS

The functional structure of Térraba-Sierpe subtidal sediments was dominated by few functional entities with facultative traits (such as the capacity of inhabiting within and over the sediments, or feeding from particles within and over the sediments as well), which agrees with the common idea that estuaries are inhabited by generalist species. Moreover, the macrofauna had different functional structures between the dry season and wet season, which supports the evidence that tropical marine coastal environments are not as temporally stable as previously though. Mitigation efforts should focus on diminishing possible alterations of the seasonal hydrological dynamics in the upstream catchments, particularly in Grande de Térraba river, where a hydroelectric project is being planned. The low functional redundancy of several functional entities in Térraba-Sierpe raises concerns about the vulnerability of the ecosystem to loosing functions if biodiversity of the estuary is lost. More functional ecology studies at tropical estuaries and other coastal environments are needed to identify the spatial and temporal patterns driving the ecosystem functioning.

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CONCLUSIONES

Este trabajo de investigación cumplió con el objetivo principal y especificos propuestos en el anteproyecto de tesis. Los sedimentos submareales de los estuarios Coronado y Sierpe están dominados por arenas medias de selección moderada. Los sedimentos en las estaciones del estuario superior e inferior fueron granos gruesos y más heterogéneos en su composición en comparación con la estación fuera del estuario. Posibles explicaciones a este patrón son las fuertes corrrientes que fluyen por los canales durante los cambios de marea, los aportes de sedimento por los ríos y las planicies de inundación del manglar adyacente. Por otro lado, en la estación externa la presencia de los sedimentos finos y homogéneos se debe al aporte proveniente del manglar y a un menor efecto de corrientes detrás de la barrera externa. Un mayor aporte de materia orgánica en los sedimentos de la estación superior estuvo relacionado a la producción autóctona (hojarasca del manglar) y alóctona (acarreada por los ríos), así como por la capacidad de captura de materia orgánica y otras partículas por parte del bosque de manglar y por la baja mineralización debido a las condiciones anóxicas. La diferencia en el porcentaje de materia orgánica que se observó entre estuarios podría estar causada por el mayor uso de suelo destinado a actividades humanas en Coronado que en Sierpe, lo que posiblemente genere diferente grado de erosión y acarreamiento de partículas no orgánicas. Los resultados de este estudio mostraron que los sedimentos de los estuarios tropicales estudiados están influenciados principalmente por factores espaciales (como por ejemplo el estuario y el gradiente estuarino), y en menor grado por factores temporales.

En lo referente a la diversidad de macrofauna bentónica se encontraron en total 146 taxones habitando los fondos sedimentarios submareales de los canales y la zona turbia externa de los estuarios Coronado y Sierpe en el Pacífico Sur de Costa Rica. De estos taxones, 20 corresponden a nuevos registros para Costa Rica, y los análisis sugieren que todavía se pueden encontrar más taxones si se aumenta el esfuerzo de muestreo. Se encontró una compleja variación de los patrones de biodiversidad, comportándose de forma distinta entre los dos estuarios, lo que dificulta hacer predicciones generales y propuestas de manejo, debido a la dinámica distinta de ambos sistemas. Se puede resaltar que la riqueza de taxones de macrofauna responde al gradiente de salinidad, porcentaje de materia orgánica y a la hetereogenidad de las partículas del sedimento. La mayor riqueza de taxones observada durante la época seca en comparación con la época lluviosa posiblemente esté relacionada con los efectos negativos que tiene un alto aporte de sedimentos y agua dulce sobre la mayoría de los componentes de la macrofauna estuarina. La riqueza de taxones estuvo influenciada por el gradiente estuarino, en donde la mayor riqueza fue observada en la estación externa (más influencia marina), esto también relacionado con el estrés que puede darse en la zona superior del estuario debido al aporte de sedimentos y agua dulce. La densidad de la macrofauna en Sierpe fue mayor en la estación externa, pero este no fue el caso en Coronado, donde la estación superior (interior del estuario) tuvo una alta densidad también, pero principalmente debido a una sola especie oportunista. Los patrones de biodiversidad en estos dos estuarios cercanos son influenciados de manera distinta por el gradiente estuarino y la estacionalidad, lo que posiblemente está relacionado con las características locales de cada estuario (dinámica cuenca-estuario-costa).

La composición de la macrofauna en los esteros Coronado y Sierpe estuvo dominada principalmente por especies de vida corta, cuerpo pequeño y capacidad de colonizar rápidamente, los cuales también fueron los principales en contrbuir a las disimiliridades observadas espacial y temporalmente. Además, se observó una diferenciaciación en la composición de la macrofauna entre ambos estuarios a pesar de su cercanía, lo que apoya la hipótesis de que las comunidades estuarinas son determinadas principalmente por las condiciones particulares de cada estuario (lo que genera un ensamble para cada sitio). También se observó una diferenciación entre la época seca y la época lluviosa en Coronado, debido posiblemente a la influencia combinada de altas tasas de precipitación y erosión, junto con los procesos de deforestación y uso de suelo en la cuenca del estuario de Coronado. Esta variación temporal brinda más soporte a la idea de que los ambientes marinos tropicales no presentan estabilidad temporal como se creía anteriormente. Sin embargo, más estudios en estuarios y ambientes costeros tropicales son necesarios para identificar patrones generales de las comunidades bentónicas.

La estructura funcional de los ambientes submareales de Térraba-Sierpe estuvo dominada por pocas entidades funcionales, las cuales presentan características facultativas para más de una función (como por ejemplo la capacidad de habitar sobre o entre los sedimentos, o bien la capacidad de alimentarse de partículas sobre o dentro del sedimento). Esto es concordante con la idea de que los organismos estuarinos son generalistas. Además, se observaron estructuras funcionales distintas entre la época seca y la época lluviosa, tal y como se observó a nivel taxonómico. Estos resultados suman evidencia que apoya la idea de la inestabilidad temporal en los trópicos. Debido a esto, se debe prestar especial atención a los esfuerzos dirigidos a mitigar las posibles alteraciones estacionales que va a provocar la construcción del proyecto hidroeléctrico El Diquís en la cuenca media del río Térraba. Por otro lado, un 60% de las entidades funcionales estuvieron representadas por uno o dos taxones (baja originalidad funcional), lo que aumenta la preocupación respecto a la vulnerabilidad del ecosistema por perder entidades funcionales si se diera una pérdida de la diversidad debido a las presiones actuales que sufre el estuario (contaminación, expansión agrícola, deforetación), y las futuras (construcción del proyecto hidroeléctrico, cambio climático). Se necesitan más estudios de ecología funcional en la región para poder identificar patrones espaciales y temporales de la ecología funcional de estos ecosistemas.

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MATERIAL SUPLEMENTARIO

ANEXO 1

Table 1S1. *Land cover sub-classes of the Forest Resources Information System of Costa Rica (SIREFOR) from the RapidEye satellital imagery, definition by SIREFOR, and classification used in this study.*

Sub-class SIREFOR	Definition in SIREFOR	Classification used in this study
Primary forest	Forests with uninterrupted ecological succession during 75-100 years or more, formed by native species, without evident effects of human activities.	Forest
Secondary forest	Area with woody vegetation where native vegetation was once deforested by human activities or natural events. Density is larger than 500 trees·ha^{-1} of al species with minimum 5 cm DBH.	
Mangrove forest	Tropical forest located in the intertidal zone. Trees are specially adapted to survive in flooded soils and high salinities. In Costa Rica, mangrove forests are dominated by mangrove trees (*Rhizophora mange*, *R. racemosa*, *R. harrisonii*, *Langucularia racemosa*, *Conocarpus erecta*, *Avicennia germinans*, *A. bicolor*, and *Pelliciera rhizophorae*), but associated species are also included in the mangrove forest (*Mora oleifera*, *Acrostichum aureum*, and *Hibiscus tiliaceus*).	
Palm-swamp forest	Area dominated by the Yolillo palm (*Raphia taedigera*), developed in water-saturated soils. Flooded during some months of the rainy season.	
Paramo (Costa Rican highland environments)	Natural vegetation located at highlands, over 3100 meters. Dominated by the dwarf bamboo (*Chusquea* sp.) mixed with shrubbery of the families Ericaceae, Hypericaceae, Rosaceae and Asteraceae. Usually low-height forests.	
Forest plantation	Forested surface through plantation. Most of the trees belong to the same species and have the same age, with regular or homogeneous spatial distribution.	
Pasturelands with scattered trees	Trees growing in areas dedicated to pasture.	Non-Forest
Pasturelands without trees	Areas dedicated to pasture, without or less than 10% forestall forest cover.	
Agriculture	Plantations of banana, African oil palm, pineapple, orange, plantain, sugar cane, melon, rice, mango, coffee, ornamental plants, etc.	
Wetland of watery or grassy surface	Wetlands with surface covered by water (exposed) or covered by grasses.	
Water	Clean water or water with sediments.	
Sand	Areas covered by sand.	
Infrastructure, urban areas	Areas with urban development and/or human infrastructures	
Clouds	Areas covered by clouds, land cover not visible.	No Data
Shadow of clouds	Areas covered by shadow of clouds, land cover not visible.	

Table 1S2. *Sedimentary and chemical characteristics of subtidal sediments from two tropical mesotidal estuaries, Costa Rica. Grain size parameters were calculated following the method of Folk and Ward (Blott and Pye, 2001).*

Estuary	Month	Station	Depth (m)	% TOM	% Carbonates	% Gravel	% Sand	% Mud	Median grain size (µm)	Median grain size (ϕ)	Sorting (ϕ)	Skewness (ϕ)	Kurtosis (ϕ)	Bottom Type
Coronado	Jan	Upper	3.18	12.30	3.28	0.52	23.66	75.82	23.23	5.43	1.57	0.03	0.74	Slightly Gravelly Sandy Mud
		Lower	5.25	1.62	2.85	0.24	99.54	0.22	186.05	2.43	0.63	-0.30	0.92	Slightly Gravelly Sand
		Outer	6.70	2.83	4.40	0.00	99.84	0.16	180.06	2.47	0.60	-0.32	2.31	Sand
	Apr	Upper	3.61	7.07	3.86	7.69	92.10	0.21	211.11	2.24	1.14	-0.58	1.69	Gravelly Sand
		Lower	8.70	2.00	3.39	0.55	41.18	58.27	38.44	4.70	1.98	0.06	0.71	Slightly Gravelly Sandy Mud
		Outer	8.76	3.08	5.26	0.34	97.28	2.38	124.71	3.00	0.63	0.27	1.02	Slightly Gravelly Sand
	Jun	Upper	4.20	2.87	3.04	0.03	99.36	0.6	253.63	1.98	0.68	0.23	0.68	Slightly Gravelly Sand
		Lower	3.40	2.36	4.95	0.96	99.04	0.00	270.61	1.89	0.72	0.17	0.77	Slightly Gravelly Sand
		Outer	7.00	3.48	4.33	0.18	98.20	1.62	96.46	3.37	0.60	-0.58	0.83	Slightly Gravelly Sand
	Aug	Upper	3.99	7.60	3.05	0.03	99.59	0.38	123.74	3.01	0.49	0.54	1.57	Slightly Gravelly Sand
		Lower	2.99	4.65	3.80	0.75	98.00	1.25	128.05	2.97	0.61	0.26	2.42	Slightly Gravelly Sand
		Outer	7.15	3.40	4.43	0.29	98.95	0.76	149.27	2.74	0.44	0.00	2.50	Slightly Gravelly Sand
	Oct	Upper	6.85	4.75	3.39	1.40	96.36	2.24	198.29	2.33	0.78	-0.35	1.03	Slightly Gravelly Sand
		Lower	13.07	1.75	2.89	0.06	99.91	0.03	189.39	2.40	0.52	-0.50	0.62	Slightly Gravelly Sand
		Outer	8.05	4.01	4.73	0.18	96.24	3.58	95.37	3.39	0.53	-0.51	0.63	Slightly Gravelly Sand
	Dec	Upper	5.51	2.95	3.53	1.52	95.59	2.88	183.02	2.45	0.75	-0.32	1.16	Slightly Gravelly Sand
		Lower	8.00	1.42	3.02	0.02	99.83	0.15	184.77	2.44	0.60	-0.33	0.90	Slightly Gravelly Sand
		Outer	8.46	4.44	4.02	0.02	98.77	1.21	119.99	3.06	0.65	0.21	0.90	Slightly Gravelly Sand
Sierpe	Mar	Upper	10.40	17.96	22.74	1.21	18.25	80.55	21.89	5.51	1.62	-0.07	0.85	Slightly Gravelly Sandy Mud
		Lower	9.05	1.29	5.69	0.00	92.67	7.33	75.36	3.73	0.48	0.11	3.38	Slightly Gravelly Sand
		Outer	8.03	1.88	4.44	0.56	99.31	0.13	174.16	2.52	0.60	-0.29	2.42	Slightly Gravelly Sand
	May	Upper	12.630	16.14	4.11	1.39	98.59	0.02	239.47	2.06	0.68	0.18	0.89	Slightly Gravelly Sand
		Lower	13.41	4.65	42.15	7.30	39.54	53.16	57.00	4.13	2.73	-0.15	1.11	Gravelly Mud
		Outer	8.08	3.55	4.53	0.28	97.81	1.91	77.11	3.70	0.31	-0.30	1.87	Slightly Gravelly Sand
	Jul	Upper	5.41	17.60	0.90	2.68	53.98	43.34	50.83	4.30	2.12	0.16	1.07	Gravelly Muddy Sand
		Lower	8.82	4.32	5.10	0.29	99.63	0.08	252.53	1.99	0.70	0.11	0.74	Slightly Gravelly Sand
		Outer	8.50	3.13	5.02	0.58	94.05	5.37	87.20	3.52	0.65	-0.55	3.30	Slightly Gravelly Sand
	Sep	Upper	4.60	12.21	2.93	0.00	1.40	98.6	15.96	5.97	1.23	0.01	0.72	Mud
		Lower	3.60	3.52	5.81	2.27	95.67	2.06	144.29	2.79	0.97	-0.16	1.43	Slightly Gravelly Sand
		Outer	13.66	1.73	4.50	0.26	95.51	4.23	76.29	3.71	0.30	-0.29	1.75	Slightly Gravelly Sand
	Nov	Upper	5.01	4.95	2.45	1.95	98.05	0.00	151.91	2.72	0.43	-0.06	2.60	Slightly Gravelly Sand
		Lower	3.72	4.87	4.53	0.02	97.65	2.33	139.48	2.84	0.92	-0.12	1.23	Slightly Gravelly Sand
		Outer	7.64	2.40	3.39	0.58	95.56	3.86	76.57	3.71	0.32	-0.30	1.89	Slightly Gravelly Sand

= dry season, = rainy season, = very well sorted, = well sorted, = moderately well sorted, = moderately sorted, = poorly sorted, = very poorly sorted, = very fine skewed, F = fine skewed, S = symmetrical, C = coarse skewed, VC = very coarse skewed, VP = very platykurtic, P = platykurtic, M = mesokurtic, L = leptokurtic, VL = very leptokurtic, EL = extremely leptokurtic. Sorting, skewness, and kurtosis were calculated with the phi parameter (ϕ).

Table 1S3. *Spearman correlation coefficients and probability between sedimentary and chemical features of subtidal sediments from a tropical mesotidal estuarine system, Costa Rica.*

Sedimentary variables	% TOM	% Carbonates	% Gravel	% Sand	% Mud	Median grain size (µm)	Sorting (ϕ)	Skewness (ϕ)	Kurtosis (ϕ)
% TOM		0.749	0.915	0.002*	0.001*	0.006*	0.237	0.365	0.489
% Carbonates	0.058		0.874	0.560	0.548	0.784	0.877	0.429	0.831
% Gravel	-0.019	0.029		0.249	0.428	0.971	0.001*	0.293	0.986
% Sand	-0.527	0.105	-0.206		<0.001*	<0.001*	<0.001*	0.386	0.084
% Mud	0.534	-0.108	0.143	-0.998		<0.001*	<0.001*	0.344	0.080
Median grain size (µm)	0.466	-0.050	-0.006	-0.876	0.887		0.001*	0.669	0.674
Sorting (ϕ)	0.212	-0.028	0.577	-0.769	0.740	0.540		0.455	0.050
Skewness (ϕ)	0.163	0.143	-0.189	-0.156	0.170	0.077	0.135		0.615
Kurtosis (ϕ)	-0.125	0.039	0.003	0.305	-0.309	-0.076	-0.343	-0.091	

Table 1S4. *Average monthly precipitation of the pluviometric stations within the Coronado and Sierpe basins, Costa Rica, during 2013. Data provided by Instituto Meteorológico Nacional, Costa Rica.*

Estuary	Month	Average monthly precipitation (mm)
Coronado	January	53.8
	April	232.5
	June	270.6
	August	408.1
	October	501.2
	December	36.2
Sierpe	March	35.6
	May	467.8
	July	501.6
	September	370.5
	November	305.4

Table 1S5. *Spearman correlation coefficients and probability between sedimentary characteristics and precipitation at basins of two tropical mesotidal estuaries, Costa Rica.*

Sedimentary variables	Coronado		Sierpe	
	r	p	r	p
% TOM	-0.03	0.902	0.08	0.765
% CaCO3	0.10	0.683	-0.05	0.863
% gravel	0.14	0.589	0.17	0.536
% sand	0.18	0.481	-0.24	0.384
% mud	-0.19	0.446	0.24	0.399
Median grain size (µm)	-0.22	0.385	0.20	0.472
Sorting (ϕ)	-0.09	0.728	0.26	0.340
Skewness (ϕ)	0.10	0.699	0.74	0.002*
Kurtosis (ϕ)	-0.28	0.258	-0.59	0.022*

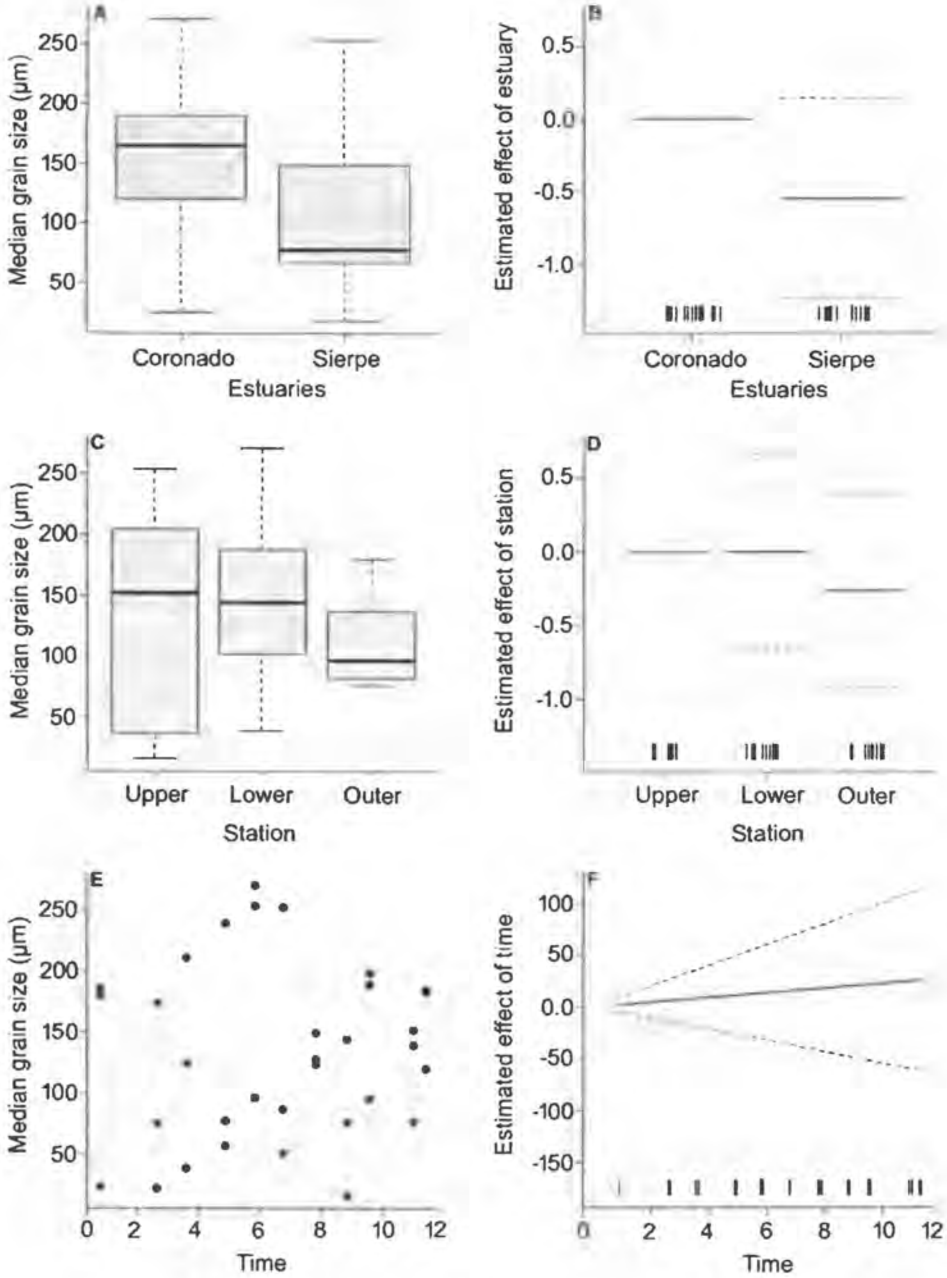

Figure 1S1. *Median grain size (µm) of sediments by estuary (A. boxplot, B. estimated effect), station (C. boxplot, D. estimated effect) and time (E. scatter plot, F. estimated effect) in two tropical mesotidal estuaries, Costa Rica.*

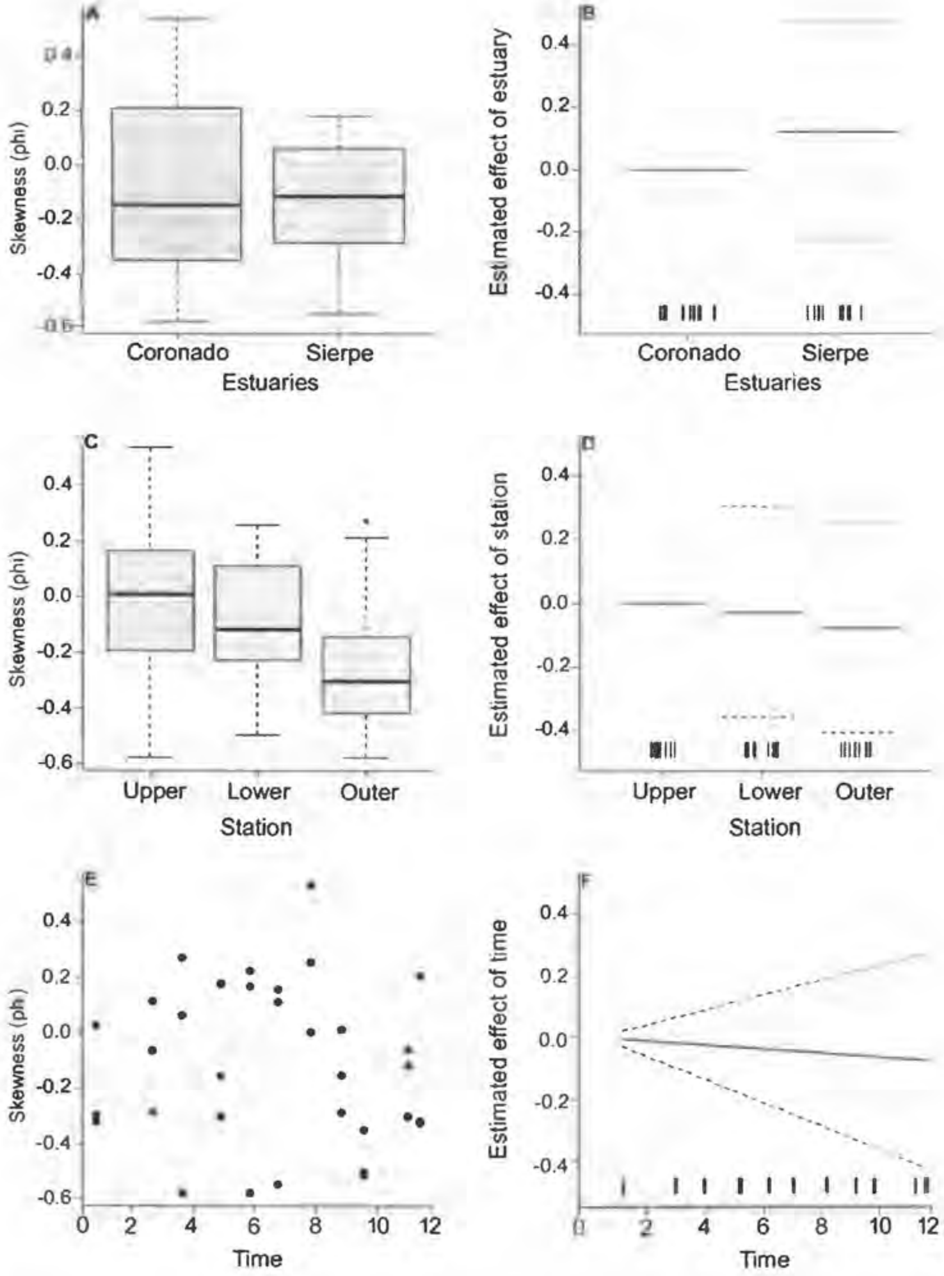

Figure 1S2. *Skewness (phi) of sediments by estuary (A. boxplot, B. estimated effect), station (C. boxplot, D. estimated effect) and time (E. scatter plot, F. estimated effect) in two tropical mesotidal estuaries, Costa Rica.*

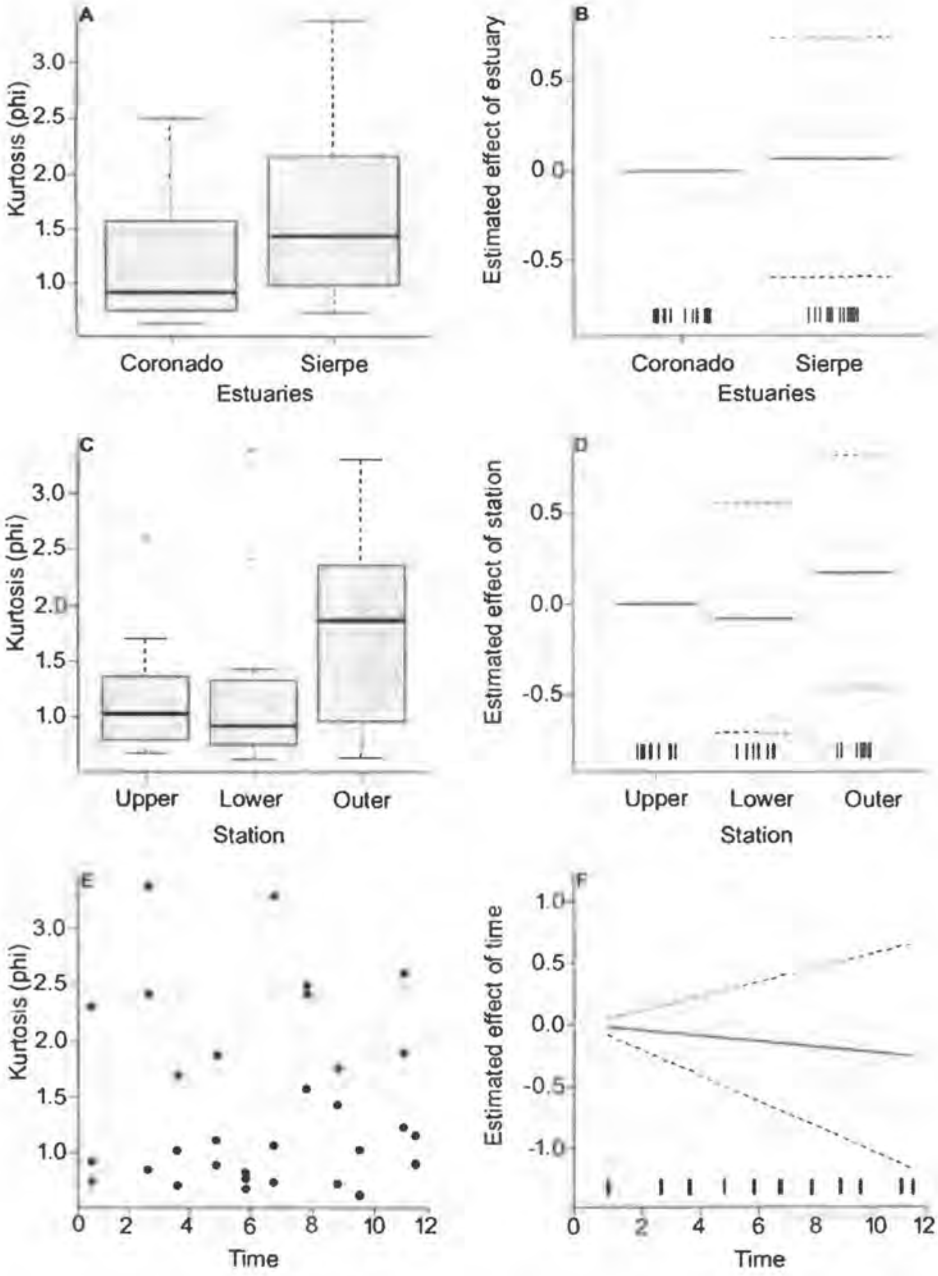

Figure 1S3. *Kurtosis (phi) of sediments by estuary (A. boxplot, B. estimated effect), station (C. boxplot, D. estimated effect) and time (E. scatter plot, F. estimated effect) in two tropical mesotidal estuaries, Costa Rica.*

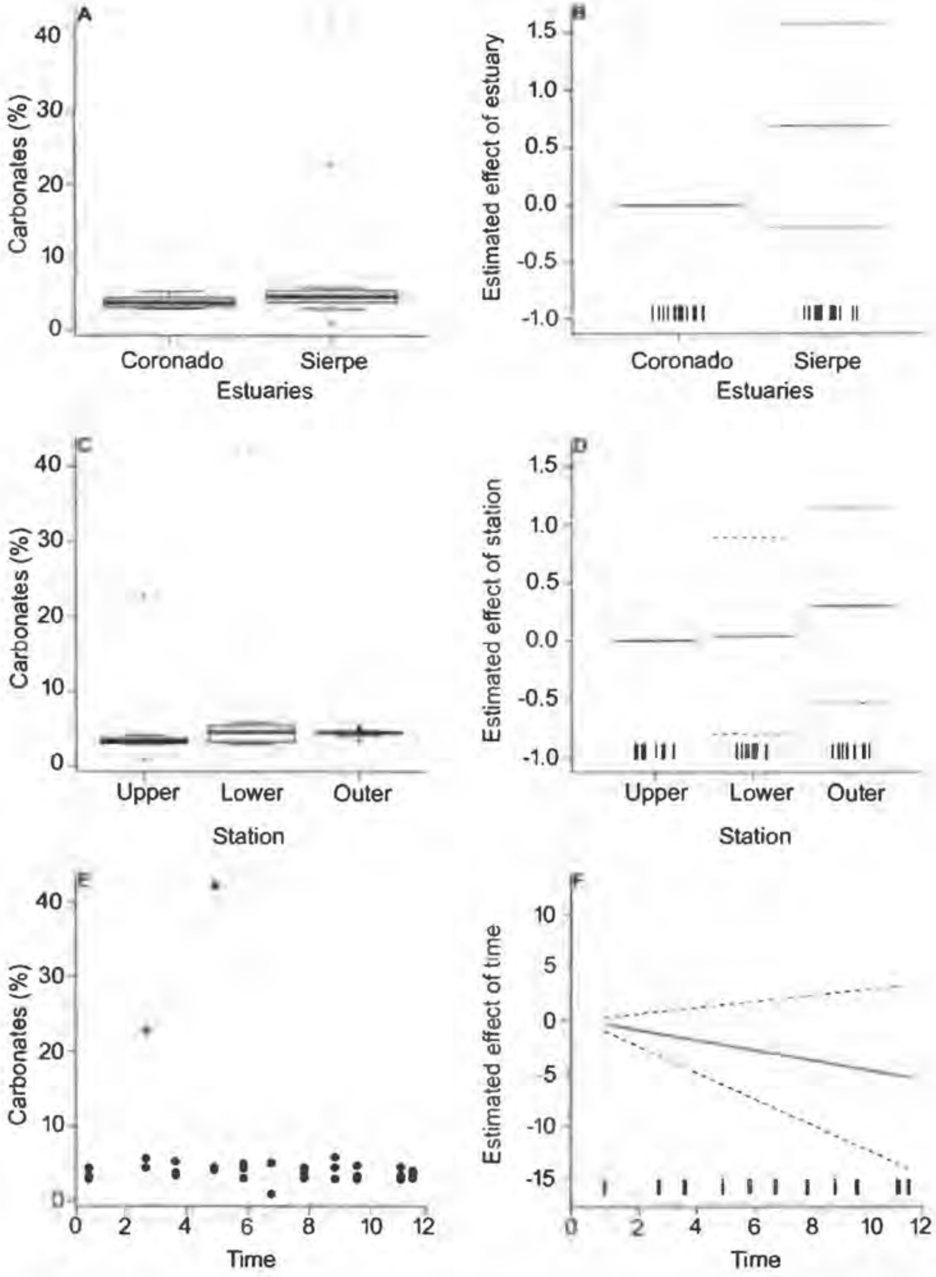

Figure 1S4. *Carbonates (%) of sediments by estuary (A. boxplot, B. estimated effect), station (C. boxplot, D. estimated effect) and time (E. scatter plot, F. estimated effect) in two tropical mesotidal estuaries, Costa Rica.*

ANEXO 2

Table 2S2. *Taxa, absolute abundance and relative abundance (%) of the subtidal benthic macrofauna from two tropical mesotidal estuaries, Costa Rica.*

Phylum	Class	Order	Family	Genus	Taxon	Abundance	Relative abundance	New record (CR, MA, CA)	New record at mangrove estuaries	Record at Coronado	Record at Sierpe
Porifera					Porifera indet.	3	0.09			x	
Cnidaria	Anthozoa				Anthozoa indet.	5	0.15				x
	Hydrozoa	Leptothecata	Sertulariidae	*Diphasia*	*Diphasia* sp.	2	0.06				x
			Campanulariidae	*Clytia*	*Clytia* sp.	1	0.03				x
Nematoda					Nematoda indet.	146	4.31			x	x
Nemertea					Nemertea indet.	38	1.12			x	x
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae		Cerithiidae indet.	3	0.09			x	
		Littorinimorpha	Caecidae	*Caecum (Fartulum)*	*Caecum (Fartulum)* sp.	11	0.323			x	x
			Calyptraeidae	*Crepidula*	*Crepidula* cf. *excavata* (Broderip, 1834)	4	0.12			x	x
			Naticidae	*Natica*	*Natica scethra* Dall, 1908	44	1.3		x		x
		Neogastropoda	Columbellidae	*Anachis*	*Anachis* sp.	1	0.03				x
				Bifurcium	*Bifurcium bicanaliferum* (G. B. Sowerby I, 1832)	1	0.03				x
			Muricidae	*Acanthotrophon*	*Acanthotrophon sorenseni* (Hertlein & A. M. Strong, 1951)	2	0.06	x	x		x
			Olividae	*Olivella*	*Olivella aureocincta* Carpenter, 1857	9	0.27	x	x	x	x
					Olivella semistriata (Gray, 1839)	34	1		x	x	x
					Olivella sp.	27	0.8			x	x
			Terebridae	*Terebra*	*Terebra* cf. *crenifera* Deshayes, 1859	2	0.06				x
			Nassariidae	*Phrontis*	*Phrontis* cf. *complanata* (Powys, 1835)	3	0.09			x	
			Pyramidellidae	*Strioturbonilla*	*Strioturbonilla* sp.	6	0.18				x
			Ringiculidae	*Microglyphis*	*Microglyphis estuarina* (Dall, 1908)	1	0.03			x	
	Scaphopoda	Dentaliida	Dentaliidae	*Antalis*	*Antalis* cf. *pretiosa* (Sowerby, 1860)	1	0.03				x
				Graptacme	*Graptacme* cf. *semistriata* (W. Turton, 1819)	2	0.06				x
	Bivalvia	Cardiida	Donacidae	*Donax*	*Donax culter* Hanley, 1845	2	0.06	x	x	x	

					Donax gracilis Hanley, 1845	9	0.27			x	
					Donax rothi Coan, 1983	1	0.03			x	
			Semelidae	*Semelina*	*Semelina* cf. *subquadrata* (Carpenter, 1857)	21	0.62			x	x
			Tellinidae	*Ameritella*	*Ameritella* cf. *carpenteri* (Dall, 1900)	5	0.15			x	
				Macoploma	*Macoploma hesperus* (Dall, 1908)	1	0.03	x			x
					Tellinidae indet.	100	2.95			x	x
				Strigilla	*Strigilla* cf. *ervilia* (Philippi, 1846)	3	0.09			x	x
				Tellinella	*Tellinella zacae* (Hertlein & A. M. Strong, 1949)	2	0.06	x		x	
		Lucinida	Lucinidae	*Divalinga*	*Divalinga perparvula* (Dall, 1901)	1	0.03		x		x
				Lucinisca	*Lucinisca centrifuga* (Dall, 1901)	1	0.03		x		x
					Lucinidae indet.	1	0.03			x	
			Galeommatidae	*Solecardia*	*Solecardia* sp.	85	2.51			x	
		Nuculida	Nuculidae	*Linucula*	*Linucula declivis* (Hinds, 1843)	1	0.03			x	x
				Nucula	*Nucula schencki* Hertlein & A. M. Strong, 1940	52	1.53	x	x	x	x
		Venerida	Veneridae		*Veneridae* indet.	33	0.97				x
				Paphonotia	*Paphonotia elliptica* (G. B. Sowerby I, 1834)	1	0.03				x
				Pitar	*Pitar* cf. *berryi* Keen, 1971	3	0.09			x	
				Tivela	*Tivela lineata* (G. B. Sowerby II, 1851)	2	0.06				x
					Tivela sp.	1	0.03				x
		Carditida	Condylocardiidae	*Condylocardia*	*Condylocardia* sp.	1	0.03				x
			Crassatellidae	*Crassinella*	*Crassinella coxa* Olsson, 1964	4	0.12	x			x
					Crassinella cf. *ecuadoriana* Olsson, 1961	4	0.12				x
Sipuncula	Phascolosomatidea	Phascolosomatida	Phascolosomatidae	*Apionsoma* (*Apionsoma*)	*Apionsoma* (*Apionsoma*) *trichocephalus* Sluiter, 1902	9	0.27			x	
Annelida	Polychaeta	Amphinomida	Amphinomidae	*Linopherus*	*Linopherus* cf. *kristiani* Salazar-Vallejo, 1987	7	0.21				x
					Linopherus cf. *paucibranchiata* (Fauvel, 1932)	1	0.03			x	
			Euphrosinidae	*Euphrosine*	*Euphrosine* sp.	2	0.06				x
		Eunicida	Dorvilleidae	*Dorvillea*	*Dorvillea* sp.	1	0.03				x
				Protodorvillea	*Protodorvillea* sp.	3	0.09			x	x
			Lumbrineridae	*Lysarete*	*Lysarete* sp.	3	0.09				x
				Ninoe	*Ninoe* cf. *vargasi* Carrera-Parra, 2001	1	0.03			x	
				Scoletoma	*Scoletoma* sp.	92	2.71				x
			Onuphidae	*Onuphis*	*Onuphis eremita* Audouin &	6	0.18		x		x

			Milne Edwards, 1833						
		Diopatra	*Diopatra splendidissima* Kinberg, 1865	1	0.03		*		*
	Capitellidae	*Mediomastus*	*Mediomastus californiensis* Hartman, 1944	71	2.09			*	*
			Capitellidae indet.	1	0.03				*
		Notomastus	*Notomastus tenuis* Moore, 1909	58	1.71			*	*
	Cirratulidae	*Cirriformia*	*Cirriformia violacea* Westheide, 1981	2	0.06	*	*	*	
		Protocirrineris	*Protocirrineris socialis* Blake, 1996	2	0.06	*	*		*
		Kirkegaardia	*Kirkegaardia carrikeri* (Dean & Blake, 2009)	5	0.15			*	*
	Cossuridae	*Cossura*	*Cossura laeviseta* Hartmann-Schröder, 1962	22	0.65				*
	Magelonidae	*Magelona*	*Magelona riojai* Jones, 1963	138	4.07			*	*
	Opheliidae	*Armandia*	*Armandia* cf. *salvadoriana* Hartmann-Schröder, 1956	131	3.86			*	*
	Orbiniidae	*Leitoscoloplos*	*Leitoscoloplos panamensis* (Monro, 1933)	1	0.03				*
			Leitoscoloplos pugettensis (Pettibone, 1957)	27	0.8		*	*	*
	Paraonidae	*Aricidea* (*Aricidea*)	*Aricidea* (*Aricidea*) *catherinae* Laubier, 1967	18	0.53			*	*
			Aricidea (*Aricidea*) *sanmartini* Aguado & López, 2003	14	0.41	*		*	
Phyllodocida	Glyceridae	*Glycera*	*Glycera brevicirris* Grube, 1870	3	0.09			*	
			Glycera prosobranchia Böggemann & Fiege, 2001	3	0.09			*	*
		Hemipodia	*Hemipodia armata* (Hartman, 1950)	47	1.39			*	*
	Goniadidae	*Glycinde*	*Glycinde armigera* Moore, 1911	10	0.29			*	*
	Hesionidae	*Oxydromus*	*Oxydromus pugettensis* (Johnson, 1901)	3	0.09		*	*	
	Nephtyidae	*Aglaophamus*	*Aglaophamus paucilamellata* Fauchald, 1972	2	0.06	*			*
		Nephtys	*Nephtys oculata* Hartmann-Schröder, 1959	123	3.63			*	*
			Nephtys singularis Hartman, 1950	20	0.59			*	*
	Nereididae	*Alitta*	Alitta succinea (Leuckart, 1847)	7	0.21			*	*
		Leptonereis	*Leptonereis laevis* Kinberg, 1866	140	4.13			*	
		Neanthes	*Neanthes* sp.	36	1.06			*	*

				Nereis (Neanthes)	*Nereis (Neanthes) micromma* Harper, 1979	2	0.06			*	
			Phyllodocidae	*Eteone*	*Eteone pacifica* Hartman, 1936	4	0.12	*	*	*	*
				Phyllodoce	*Phyllodoce multiseriata* Rioja, 1941	1	0.03		*	*	
					Phyllodoce sp.	2	0.06			*	
			Pilargidae	*Ancistrosyllis*	*Ancistrosyllis hartmanae* Pettibone, 1966	1	0.03				*
				Cabira	*Cabira incerta* Webster, 1879	1	0.03			*	
				Hermundura	*Hermundura riojai* (Salazar-Vallejo, 1986)	5	0.15			*	*
					Hermundura tricuspis Müller, 1858	56	1.65			*	*
				Sigambra	*Sigambra tentaculata* (Treadwell, 1941)	37	1.09			*	*
				Synelmis	*Synelmis* cf. *albini* (Langerhans, 1881)	3	0.09			*	*
			Pisionidae	*Pisione*	*Pisione remota* (Southern, 1914)	6	0.18		*	*	
			Polynoidae	*Chaetacanthus*	*Chaetacanthus pilosus* (Treadwell, 1937)	5	0.15	*		*	*
			Sigalionidae	*Sigalion*	*Sigalion* sp.	12	0.35			*	*
				Sthenelais	*Sthenelais fusca* Johnson, 1897	10	0.29		*	*	*
			Syllidae	*Odontosyllis*	*Odontosyllis dugesiana* Claparède, 1864	3	0.09		*	*	*
				Westheidesyllis	*Westheidesyllis heterocirrata* (Hartmann-Schröder, 1959)	1	0.03			*	
		Sabellida	Oweniidae	*Owenia*	*Owenia johnsoni* Blake, 2000	7	0.21	*	*	*	*
					Owenia sp.	1	0.03				*
			Sabellidae	*Fabrisabella*	*Fabrisabella similis* Fauchald, 1972	3	0.09	*	*	*	*
		Spionida	Spionidae	*Dispio*	*Dispio glabrilamellata* Blake & Kudenov, 1978	3	0.09			*	
				Malacoceros	*Malacoceros indicus* (Fauvel, 1928)	173	5.1			*	*
					Malacoceros sp.	1	0.03			*	
					Spionidae indet.	1	0.03			*	
				Paraprionospio	*Paraprionospio pinnata* (Ehlers, 1901)	216	6.37			*	*
				Scolelepis (Scolelepis)	*Scolelepis (Scolelepis) acuta* (Treadwell, 1914)	434	12.8	*	*	*	
		Terebellida	Trichobranchidae	*Terebellides*	*Terebellides* sp.	2	0.06				*
Arthropoda	Arachnida				Acari indet.	3	0.09			*	*
	Hexanauplia				Copepoda indet.	33	0.97			*	*
	Insecta	Diptera	Chironomidae		Chironomidae indet.	1	0.03			*	

		Coleoptera	Elmidae		Elmidae indet.	1	0.03			×	
	Malacostraca	Amphipoda	Corophiidae		Corophiidae indet.	315	9.29			×	×
			Talitridae		Talidridae indet.	33	0.97			×	×
		Cumacea			Cumacea indet.	115	3.39			×	×
		Isopoda	Ancinidae		Ancinidae indet.	22	0.65			×	×
			Anthuridae		Anthuridae indet.	10	0.29			×	×
			Idoteidae		Idoteidae indet.	3	0.09			×	
		Mysida			Mysida indet.	29	0.86			×	×
		Decapoda	Albuneidae	*Albunea*	*Albunea lucasia* de Saussure, 1853	2	0.06			×	
			Alpheidae	*Alpheus*	*Alpheus* sp.	2	0.06			×	
			Diogenidae	*Clibanarius*	*Clibanarius* cf. *lineatus* (H. Milne Edwards, 1848)	2	0.06				×
					Diogenidae indet.	3	0.09			×	×
			Hippolytidae		Hippolytidae indet.	1	0.03				×
					Megalopa	3	0.09			×	×
					Zoea	10	0.29			×	×
			Ogyridae	*Ogyrides*	*Ogyrides alphaerostris* (Kingsley, 1880)	5	0.15	***	×	×	×
			Palaemonidae		Palaemonidae indet.	1	0.03				×
			Xanthidae		Xanthidae indet.	2	0.06			×	
			Penaeidae	*Rimapenaeus*	*Rimapenaeus faoe* (Obarrio, 1954)	1	0.03				×
		Stomatopoda	Squillidae	*Meiosquilla*	*Meiosquilla dawsoni* Manning, 1970	1	0.03				×
	Ostracoda				Ostracoda indet.	28	0.83			×	×
	Pycnogonida				Pycnogonida indet.	1	0.03				×
Brachiopoda	Lingulata		Lingulidae	*Glottidia*	*Glottidia* cf. *albida* (Hinds, 1844)	2	0.06			×	
Chaetognatha	Sagittoidea	Phragmophora	Spadellidae	*Spadella*	*Spadella* sp.	8	0.24	**	×	×	×
Echinodermata	Asteroidea				Asteroidea indet.	3	0.09				×
	Echinoidea				Echinoidea indet.	4	0.12				×
	Holothuroidea				Holothuroidea indet.	1	0.03				×
	Ophiuroidea				Ophiuroidea indet.	17	0.5				×
		Amphilepidida	Amphiuridae	*Amphiura (Ophionema)*	*Amphiura* (*Ophionema*) cf. *hexacantha* Nielsen, 1932	1	0.03		×		×
				Microphiopholis	*Microphiopholis* cf. *platydisca* vr. *microplax* (Nielsen, 1932)	1	0.03		×		×
					Microphiopholis platydisca (Nielsen, 1932)	2	0.06		×	×	
					Amphiuridae indet.	2	0.06				×
Chordata	Leptocardii		Branchiostomatidae	*Branchiostoma*	*Branchiostoma californiense* Andrews, 1893	38	1.12			×	×
	Pisci	Perciformes	Gobiidae	*Bollmannia*	*Bollmania* sp.	1	0.03			×	
				Evermannia	*Evermannia* sp.	4	0.12			×	×

New record for: * = Costa Rica (CR), ** Mainland Costa Rica (MA), *** Central America (CA).

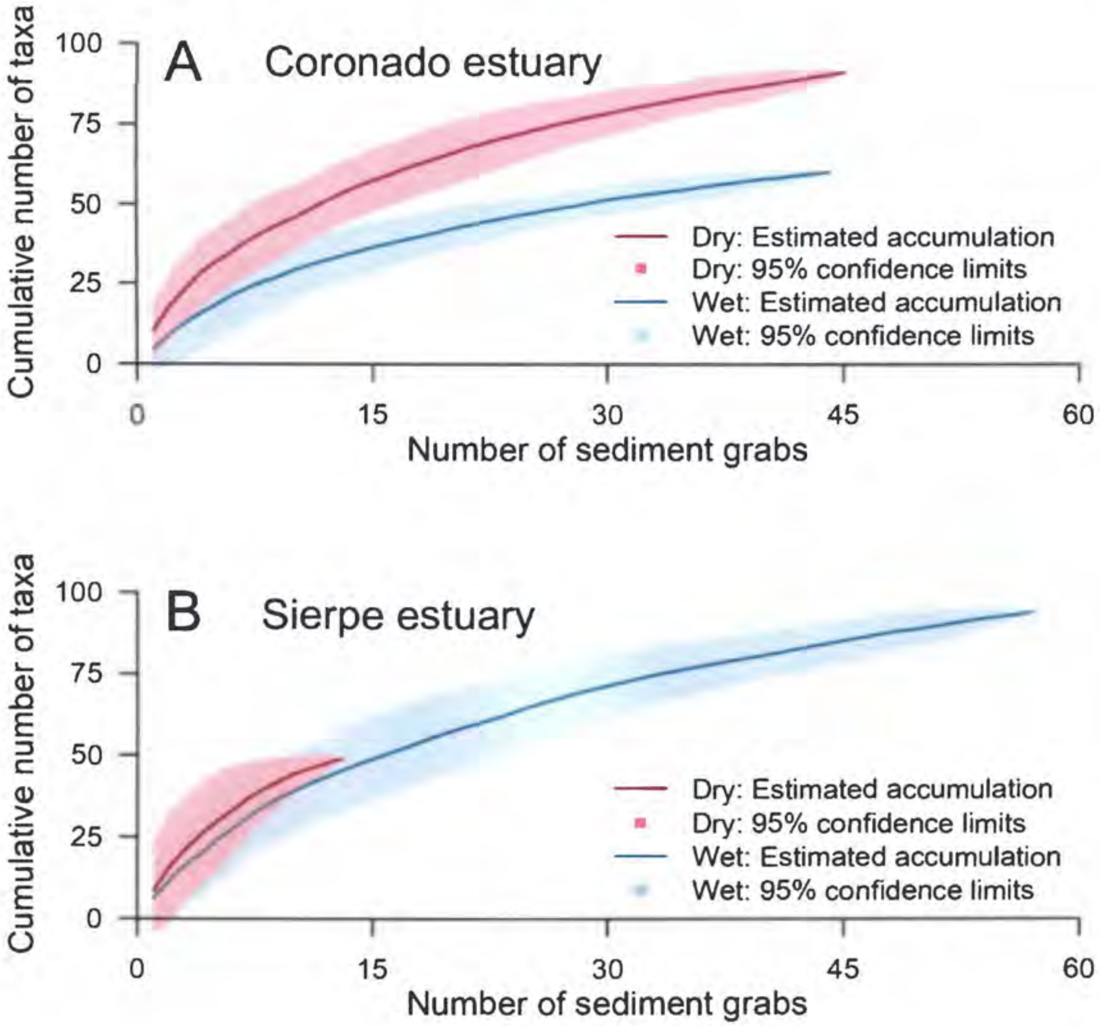

Figure 2S1. *Taxa accumulation curves estimated using the "random" technique and showing 95% confidence limits by sediment grabs of the subtidal benthic macrofauna from A) Coronado and B) Sierpe estuaries, Costa Rica.*

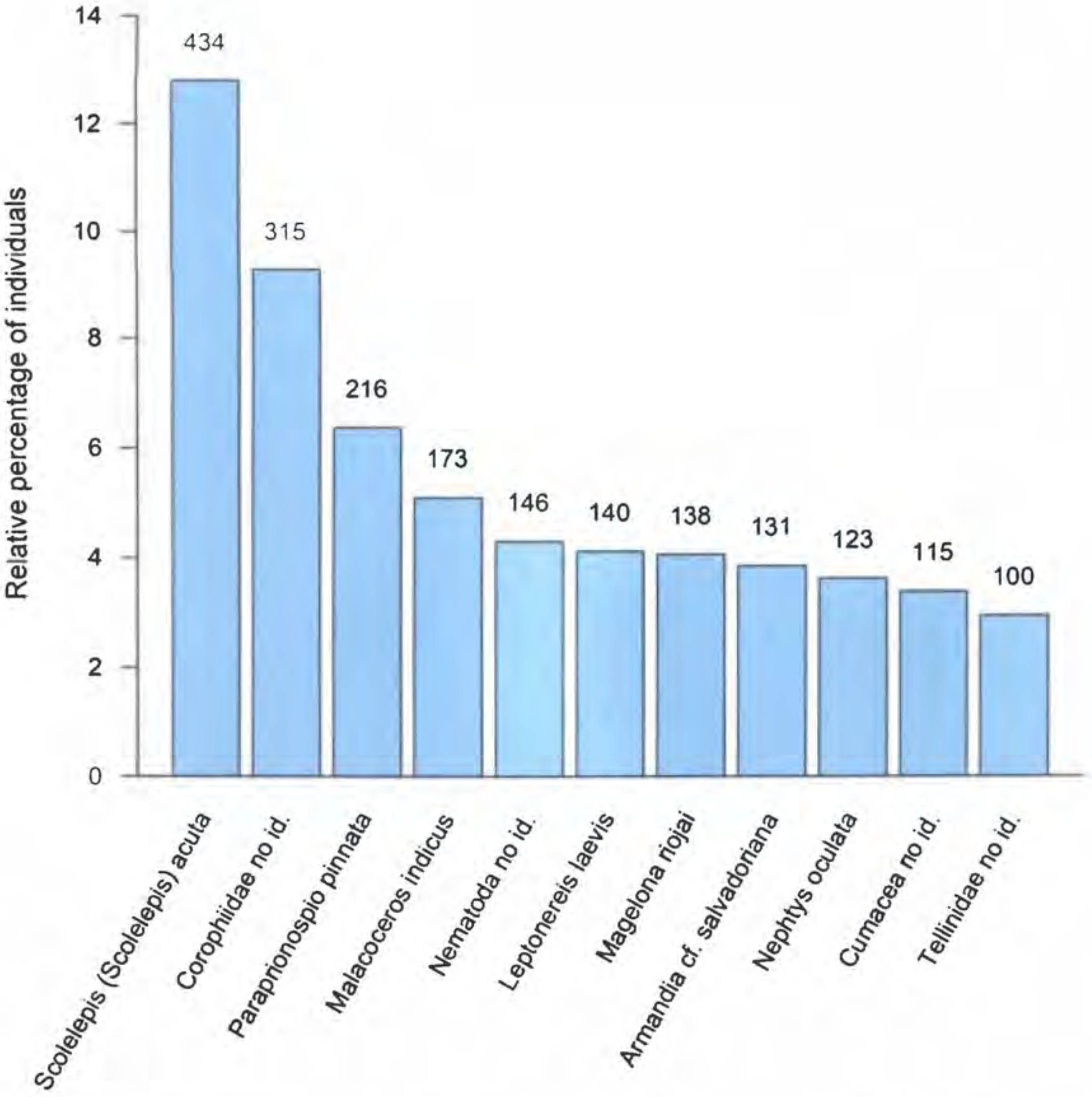

Figure 2S2. *Relative percentage of total individuals (bars) and absolute abundance of individuals (numbers above the bars) by phyla from the subtidal sediments of two tropical mesotidal estuaries, Costa Rica.*

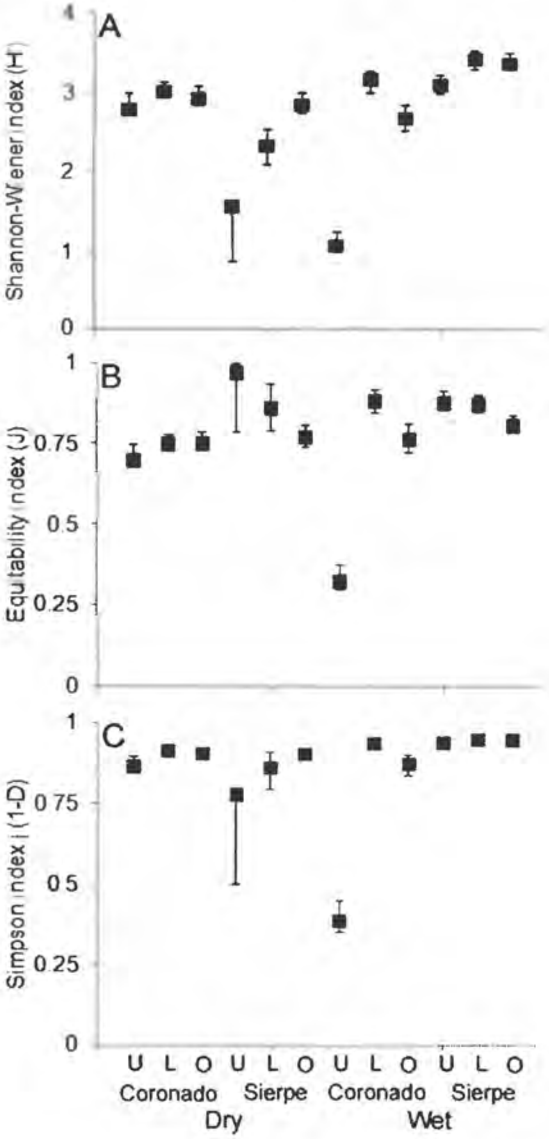

Figure 2S3. *Mean (± 95% confidence limit) of Shannon-Wiener index (H'), Equitability index (J), and Simpson index of dominance (1-D) regarding the estuarine zonation (U: Upper, L: Lower, O: Outer), estuary (Coronado, Sierpe), and season (dry, wet) for the subtidal benthic macrofauna of two tropical mesotidal estuaries, Costa Rica.*

ANEXO 3

Table 3S1. *Sea bottom temperature (ºC), salinity (psu) and dissolved oxygen (mg·L^{-1}) from two tropical mesotidal estuaries, Costa Rica. Measurements were recorded 2 m before reaching the bottom.*

Estuary	Month	Station	Depth (m)	Temperature (°C)	Salinity (psu)	Dissolved oxygen (mg·L^{-1})
Coronado	Jan	Upper	3.18	30.4	23.2	4.63
		Lower	5.25	30.8	30.8	4.41
		Outer	6.70	29.8	30.1	4.48
	Apr	Upper	3.61	29.1	18.6	4.86
		Lower	8.70	30.0	30.9	4.46
		Outer	8.76	29.5	33.4	4.44
	Jun	Upper	4.20	28.4	13.0	5.06
		Lower	3.40	28.6	14.6	5.00
		Outer	7.00	28.9	31.5	4.53
	Aug	Upper	3.99	27.8	21.0	4.90
		Lower	2.99	27.8	13.7	5.12
		Outer	7.15	28.7	26.9	4.67
	Oct	Upper	6.85	28.1	23.2	4.83
		Lower	13.07	26.7	12.8	5.25
		Outer	8.05	28.5	30.0	4.60
	Dec	Upper	5.51	29.2	22.7	6.11
		Lower	8.00	29.3	27.1	4.61
		Outer	8.46	28.9	30.0	4.57
Sierpe	Mar	Upper	10.40	31.0	32.7	4.35
		Lower	9.05	31.0	33.5	4.33
		Outer	8.03	30.0	33.8	4.39
	May	Upper	12.63	28.6	31.3	4.55
		Lower	13.41	28.7	27.6	4.65
		Outer	8.08	29.0	32.9	4.48
	Jul	Upper	5.41	28.7	27.3	4.65
		Lower	8.82	28.8	26.8	4.66
		Outer	8.50	28.7	30.8	4.57
	Sep	Upper	4.60	28.7	26.2	4.68
		Lower	3.60	28.6	26.0	4.69
		Outer	13.66	26.8	31.7	4.68
	Nov	Upper	5.01	28.4	12.7	5.07
		Lower	3.72	28.2	20.5	4.88
		Outer	7.64	28.6	27.5	4.65

Table 3S2. *Taxa, absolute abundance and relative abundance (%) of the subtidal benthic macrofauna from two tropical mesotidal estuaries, Costa Rica.*

Phylum	Class	Order	Family	Genus	**Taxon**	Abundance	Relative abundance	Record at	
								Coronado	Sierpe
Porifera					Porifera indet.	3	0.09	×	
Cnidaria	Anthozoa				Anthozoa indet.	5	0.15		×
	Hydrozoa	Leptothecata	Sertulariidae	*Diphasia*	*Diphasia* sp.	2	0.06		×
			Campanulariidae	*Clytia*	*Clytia* sp.	1	0.03		×
Nematoda					Nematoda indet.	146	4.31	×	×
Nemertea					Nemertea indet.	38	1.12	×	×
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae		Cerithiidae indet.	3	0.09	×	
		Littorinimorpha	Caecidae	*Caecum (Fartulum)*	*Caecum (Fartulum)* sp.	11	0.323	×	×
			Calyptraeidae	*Crepidula*	*Crepidula* cf. *excavata* (Broderip, 1834)	4	0.12	×	×
			Naticidae	*Natica*	*Natica scethra* Dall, 1908	44	1.3		×
		Neogastropoda	Columbellidae	*Anachis*	*Anachis* sp.	1	0.03		×
				Bifurcium	*Bifurcium bicanaliferum* (G. B. Sowerby I, 1832)	1	0.03		×
			Muricidae	*Acanthotrophon*	*Acanthotrophon sorenseni* (Hertlein & A. M. Strong, 1951)	2	0.06		×
			Olividae	*Olivella*	*Olivella aureocincta* Carpenter, 1857	9	0.27	×	×
					Olivella semistriata (Gray, 1839)	34	1	×	×
					Olivella sp.	27	0.8	×	×
			Terebridae	*Terebra*	*Terebra* cf. *crenifera* Deshayes, 1859	2	0.06		×
			Nassariidae	*Phrontis*	*Phrontis* cf. *complanata* (Powys, 1835)	3	0.09	×	
			Pyramidellidae	*Strioturbonilla*	*Strioturbonilla* sp.	6	0.18		×
			Ringiculidae	*Microglyphis*	*Microglyphis estuarina* (Dall, 1908)	1	0.03	×	
	Scaphopoda	Dentaliida	Dentaliidae	*Antalis*	*Antalis* cf. *pretiosa* (Sowerby, 1860)	1	0.03		×
				Graptacme	*Graptacme* cf. *semistriata* (W. Turton, 1819)	2	0.06		×
	Bivalvia	Cardiida	Donacidae	*Donax*	*Donax culter* Hanley, 1845	2	0.06	×	
					Donax gracilis Hanley, 1845	9	0.27	×	
					Donax rothi Coan, 1983	1	0.03	×	
			Semelidae	*Semelina*	*Semelina* cf. *subquadrata* (Carpenter, 1857)	21	0.62	×	×
			Tellinidae	*Ameritella*	*Ameritella* cf. *carpenteri* (Dall, 1900)	5	0.15	×	

				Macoploma	*Macoploma hesperus* (Dall, 1908)	1	0.03		×
					Tellinidae indet.	100	2.95	×	×
				Strigilla	*Strigilla* cf. *ervilia* (Philippi, 1846)	3	0.09	×	×
				Tellinella	*Tellinella zacae* (Hertlein & A. M. Strong, 1949)	2	0.06	×	
		Lucinida	Lucinidae	*Divalinga*	*Divalinga perparvula* (Dall, 1901)	1	0.03		×
				Lucinisca	*Lucinisca centrifuga* (Dall, 1901)	1	0.03		×
					Lucinidae indet.	1	0.03	×	
			Galeommatidae	*Solecardia*	*Solecardia* sp.	85	2.51	×	
		Nuculida	Nuculidae	*Linucula*	*Linucula declivis* (Hinds, 1843)	1	0.03	×	×
				Nucula	*Nucula schencki* Hertlein & A. M. Strong, 1940	52	1.53	×	×
		Venerida	Veneridae		*Veneridae* indet.	33	0.97		×
				Paphonotia	*Paphonotia elliptica* (G. B. Sowerby I, 1834)	1	0.03		×
				Pitar	*Pitar* cf. *berryi* Keen, 1971	3	0.09	×	
				Tivela	*Tivela lineata* (G. B. Sowerby II, 1851)	2	0.06		×
					Tivela sp.	1	0.03		×
		Carditida	Condylocardiidae	*Condylocardia*	*Condylocardia* sp.	1	0.03		×
			Crassatellidae	*Crassinella*	*Crassinella coxa* Olsson, 1964	4	0.12		×
					Crassinella cf. *ecuadoriana* Olsson, 1961	4	0.12		×
Sipuncula	Phascolosomatidea	Phascolosomatida	Phascolosomatidae	*Apionsoma* (*Apionsoma*)	*Apionsoma* (*Apionsoma*) *trichocephalus* Sluiter, 1902	9	0.27	×	
Annelida	Polychaeta	Amphinomida	Amphinomidae	*Linopherus*	*Linopherus* cf. *kristiani* Salazar-Vallejo, 1987	7	0.21		×
					Linopherus cf. *paucibranchiata* (Fauvel, 1932)	1	0.03	×	
			Euphrosinidae	*Euphrosine*	*Euphrosine* sp.	2	0.06		×
		Eunicida	Dorvilleidae	*Dorvillea*	*Dorvillea* sp.	1	0.03		×
				Protodorvillea	*Protodorvillea* sp.	3	0.09	×	×
			Lumbrineridae	*Lysarete*	*Lysarete* sp.	3	0.09		×
				Ninoe	*Ninoe cf. vargasi* Carrera-Parra, 2001	1	0.03	×	
				Scoletoma	*Scoletoma* sp.	92	2.71		×
			Onuphidae	*Onuphis*	*Onuphis eremita* Audouin & Milne Edwards, 1833	6	0.18		×
				Diopatra	*Diopatra splendidissima* Kinberg, 1865	1	0.03		×
			Capitellidae	*Mediomastus*	*Mediomastus californiensis* Hartman, 1944	71	2.09	×	×
					Capitellidae indet.	1	0.03		×

		Notomastus	*Notomastus tenuis* Moore, 1909	58	1.71	×	×
	Cirratulidae	*Cirriformia*	*Cirriformia violacea* Westheide, 1981	2	0.06	×	
		Protocirrineris	*Protocirrineris socialis* Blake, 1996	2	0.06		×
		Kirkegaardia	*Kirkegaardia carrikeri* (Dean & Blake, 2009)	5	0.15	×	×
	Cossuridae	*Cossura*	*Cossura laeviseta* Hartmann-Schröder, 1962	22	0.65		×
	Magelonidae	*Magelona*	*Magelona riojai* Jones, 1963	138	4.07	×	×
	Opheliidae	*Armandia*	*Armandia cf. salvadoriana* Hartmann-Schröder, 1956	131	3.86	×	×
	Orbiniidae	*Leitoscoloplos*	*Leitoscoloplos panamensis* (Monro, 1933)	1	0.03		×
			Leitoscoloplos pugettensis (Pettibone, 1957)	27	0.8	×	×
	Paraonidae	*Aricidea (Aricidea)*	*Aricidea (Aricidea) catherinae* Laubier, 1967	18	0.53	×	×
			Aricidea (Aricidea) sanmartini Aguado & López, 2003	14	0.41	×	
Phyllodocida	Glyceridae	*Glycera*	*Glycera brevicirris* Grube, 1870	3	0.09	×	
			Glycera prosobranchia Böggemann & Fiege, 2001	3	0.09	×	×
		Hemipodia	*Hemipodia armata* (Hartman, 1950)	47	1.39	×	×
	Goniadidae	*Glycinde*	*Glycinde armigera* Moore, 1911	10	0.29	×	×
	Hesionidae	*Oxydromus*	*Oxydromus pugettensis* (Johnson, 1901)	3	0.09	×	
	Nephtyidae	*Aglaophamus*	*Aglaophamus paucilamellata* Fauchald, 1972	2	0.06		×
		Nephtys	*Nephtys oculata* Hartmann-Schröder, 1959	123	3.63	×	×
			Nephtys singularis Hartman, 1950	20	0.59	×	×
	Nereididae	*Alitta*	Alitta succinea (Leuckart, 1847)	7	0.21	×	×
		Leptonereis	*Leptonereis laevis* Kinberg, 1866	140	4.13	×	
		Neanthes	*Neanthes* sp.	36	1.06	×	×
		Nereis (Neanthes)	*Nereis (Neanthes) micromma* Harper, 1979	2	0.06	×	
	Phyllodocidae	*Eteone*	*Eteone pacifica* Hartman, 1936	4	0.12	×	×
		Phyllodoce	*Phyllodoce multiseriata* Rioja, 1941	1	0.03	×	

					Phyllodoce sp.	2	0.06	×	
			Pilargidae	*Ancistrosyllis*	*Ancistrosyllis hartmanae* Pettibone, 1966	1	0.03		×
				Cabira	*Cabira incerta* Webster, 1879	1	0.03	×	
				Hermundura	*Hermundura riojai* (Salazar-Vallejo, 1986)	5	0.15	×	×
					Hermundura tricuspis Müller, 1858	56	1.65	×	×
				Sigambra	*Sigambra tentaculata* (Treadwell, 1941)	37	1.09	×	×
				Synelmis	*Synelmis cf. albini* (Langerhans, 1881)	3	0.09	×	×
			Pisionidae	*Pisione*	*Pisione remota* (Southern, 1914)	6	0.18	×	
			Polynoidae	*Chaetacanthus*	*Chaetacanthus pilosus* (Treadwell, 1937)	5	0.15	×	×
			Sigalionidae	*Sigalion*	*Sigalion* sp.	12	0.35	×	×
				Sthenelais	*Sthenelais fusca* Johnson, 1897	10	0.29	×	×
			Syllidae	*Odontosyllis*	*Odontosyllis dugesiana* Claparède, 1864	3	0.09	×	×
				Westheidesyllis	*Westheidesyllis heterocirrata* (Hartmann-Schröder, 1959)	1	0.03	×	
		Sabellida	Oweniidae	*Owenia*	*Owenia johnsoni* Blake, 2000	7	0.21	×	×
					Owenia sp.	1	0.03		×
			Sabellidae	*Fabrisabella*	*Fabrisabella similis* Fauchald, 1972	3	0.09	×	×
		Spionida	Spionidae	*Dispio*	*Dispio glabrilamellata* Blake & Kudenov, 1978	3	0.09	×	
				Malacoceros	*Malacoceros indicus* (Fauvel, 1928)	173	5.1	×	×
					Malacoceros sp.	1	0.03	×	
					Spionidae indet.	1	0.03	×	
				Paraprionospio	*Paraprionospio pinnata* (Ehlers, 1901)	216	6.37	×	×
				Scolelepis (Scolelepis)	*Scolelepis (Scolelepis) acuta* (Treadwell, 1914)	434	12.8	×	
		Terebellida	Trichobranchidae	*Terebellides*	*Terebellides* sp.	2	0.06		×
Arthropoda	Arachnida				Acari indet.	3	0.09	×	×
	Hexanauplia				Copepoda indet.	33	0.97	×	×
	Insecta	Diptera	Chironomidae		Chironomidae indet.	1	0.03	×	
		Coleoptera	Elmidae		Elmidae indet.	1	0.03	×	
	Malacostraca	Amphipoda	Corophiidae		Corophiidae indet.	315	9.29	×	×
			Talitridae		Talidridae indet.	33	0.97	×	×
		Cumacea			Cumacea indet.	115	3.39	×	×
		Isopoda	Ancinidae		Ancinidae indet.	22	0.65	×	×
			Anthuridae		Anthuridae indet.	10	0.29	×	×

			Idoteidae		Idoteidae indet.	3	0.09	×	
		Mysida			Mysida indet.	29	0.86	×	×
		Decapoda	Albuneidae	*Albunea*	*Albunea lucasia* de Saussure, 1853	2	0.06	×	
			Alpheidae	*Alpheus*	*Alpheus* sp.	2	0.06	×	
			Diogenidae	*Clibanarius*	*Clibanarius* cf. *lineatus* (H. Milne Edwards, 1848)	2	0.06		×
					Diogenidae indet.	3	0.09	×	×
			Hippolytidae		Hippolytidae indet.	1	0.03		×
					Megalopa	3	0.09	×	×
					Zoea	10	0.29	×	×
			Ogyridae	*Ogyrides*	*Ogyrides alphaerostris* (Kingsley, 1880)	5	0.15	×	×
			Palaemonidae		Palaemonidae indet.	1	0.03		×
			Xanthidae		Xanthidae indet.	2	0.06	×	
			Penaeidae	*Rimapenaeus*	*Rimapenaeus faoe* (Obarrio, 1954)	1	0.03		×
		Stomatopoda	Squillidae	*Meiosquilla*	*Meiosquilla dawsoni* Manning, 1970	1	0.03		×
	Ostracoda				Ostracoda indet.	28	0.83	×	×
	Pycnogonida				Pycnogonida indet.	1	0.03		×
Brachiopoda	Lingulata		Lingulidae	*Glottidia*	*Glottidia* cf. *albida* (Hinds, 1844)	2	0.06	×	
Chaetognatha	Sagittoidea	Phragmophora	Spadellidae	*Spadella*	*Spadella* sp.	8	0.24	×	×
Echinodermata	Asteroidea				Asteroidea indet.	3	0.09		×
	Echinoidea				Echinoidea indet.	4	0.12		×
	Holothuroidea				Holothuroidea indet.	1	0.03		×
	Ophiuroidea				Ophiuroidea indet.	17	0.5		×
		Amphilepidida	Amphiuridae	*Amphiura (Ophionema)*	*Amphiura* (*Ophionema*) cf. *hexacantha* Nielsen, 1932	1	0.03		×
				Microphiopholis	*Microphiopholis* cf. *platydisca* vr. *microplax* (Nielsen, 1932)	1	0.03		×
					Microphiopholis platydisca (Nielsen, 1932)	2	0.06	×	
					Amphiuridae indet.	2	0.06		×
Chordata	Leptocardii		Branchiostomatidae	*Branchiostoma*	*Branchiostoma californiense* Andrews, 1893	38	1.12	×	×
	Pisci	Perciformes	Gobiidae	*Bollmannia*	*Bollmania* sp.	1	0.03	×	
				Evermannia	*Evermannia* sp.	4	0.12	×	×

ANEXO 4

Table 4S1. *Functional entities for the 146 taxa of subtidal benthic macrofauna of the Térraba-Sierpe, estuarine system, Costa Rica, based on four life-history traits (habitat, activity, motility, and feeding guild).*

Functional entities	**Taxa**	**Biomass ($g \cdot m^{-2}$)**
Infaunal sedentary burrowing/tube dwelling suspension feeder	Corophiidae indet.	44.22
Infaunal free-living tube-dwelling surface deposit/suspension feeder	*Dispio glabrilamellata*	0.10
	Malacoceros indicus	5.21
	Malacoceros sp.	0.04
	Paraprionospio pinnata	4.00
	Scolelepis (*Scolelepis*) *acuta*	4.19
	Spionidae indet.	>0.01
Epifaunal free-living crawling suspension feeder	*Amphiura* (*Ophionema*) cf. *hexacantha*	10.03
	Amphiuridae indet.	0.50
	Microphiopholis cf. platydisca vr. microplax	10.03
	Microphiopholis platydisca	1.09
	Ophiuroidea indet.	7.84
Infaunal free-living burrowing suspension feeder	*Ameritella carpenteri*	6.93
	Condylocardia sp.	0.05
	Crassinella coxa	0.19
	Crassinella ecuadoriana	0.16
	Donax culter	0.46
	Donax gracilis	11.36
	Donax rothi	1.72
	Linucula declivis	1.53
	Macoploma hesperus	0.09
	Nucula schencki	4.02
	Paphonotia elliptica	0.18
	Pitar berryi	0.79
	Semelina subquadrata	3.10
	Solecardia sp.	1.92
	Strigilla ervilia	1.59
	Tellinella zacae	0.49
	Tellinidae indet.	8.10
	Tivela lineata	0.43
	Tivela sp.	0.32

	Veneridae indet.	3.80
Infaunal/interstitial free-living swimming suspension feeder	Ostracoda indet.	1.18
Epifaunal/infaunal free-living crawling carnivore	Ancinidae indet.	4.28
	Anthuridae indet.	0.16
Infaunal free-living burrowing subsurface deposit feeder	*Aricidea* (*Aricidea*) *catherinae*	0.37
	Aricidea (*Aricidea*) *sanmartini*	0.65
	Armandia cf. *salvadoriana*	3.41
	Capitellidae indet.	0.04
	Cossura laeviseta	0.15
	Holothuroidea indet.	0.04
	Leitoscoloplos panamensis	0.61
	Leitoscoloplos pugettensis	8.89
	Magelona riojai	3.17
	Mediomastus californiensis	1.95
	Notomastus tenuis	5.31
Infaunal free-living burrowing carnivore	*Ancistrosyllis hartmanae*	0.01
	Cabira incerta	>0.01
	Glycera brevicirris	0.66
	Glycera prosobranchia	0.26
	Hemipodia armata	3.08
	Hermundura riojai	0.38
	Hermundura tricuspis	3.03
	Sigalion sp.	2.19
	Sigambra tentaculata	1.43
	Sthenelais fusca	1.04
	Synelmis cf. *albini*	0.04
Epifaunal/infaunal free-living burrowing/crawling carnivore/scavenger	*Eteone pacifica*	0.28
	Phyllodoce multiseriata	0.04
	Phyllodoce sp.	0.10
Infaunal free-living burrowing/crawling/swimming omnivore	*Alitta succinea*	0.40
	Leptonereis laevis	3.11
	Neanthes sp.	3.22
	Nereis (*Neanthes*) *micromma*	0.49
Infaunal sedentary burrowing detritivore/omnivore	Cumacea indet.	1.39
Interstitial free-living swimming carnivore/detritivore/grazzer	Copepoda indet.	0.09
Epifaunal free-living crawling/swimming algaevore/omnivore	Megalopa	0.01
	Zoea	0.04
Infaunal free-living burrowing surface deposit feeder	*Apionsoma* (*Apionsoma*) *trichocephalus*	0.48
Epifaunal/infaunal free-living burrowing carnivore	*Glycinde armigera*	0.81
	Lysarete sp.	0.03

	Ninoe cf. *vargasi*	0.42
	Scoletoma sp.	1.86
Infaunal free-living burrowing/crawling/swimming carnivore	*Aglaophamus paucilamellata*	0.50
	Nephtys oculata	16.04
	Nephtys singularis	12.71
Interstitial free-living crawling carnivore/scavenger	*Dorvillea* sp.	>0.01
	Protodorvillea sp.	0.03
Epifaunal free-living swimming omnivore	Mysida indet.	1.89
Epifaunal free-living crawling carnivore/detritivore/omnivore	*Alpheus* sp.	0.07
	Clibanarius lineatus	15.04
	Diogenidae indet.	0.03
	Hippolytidae indet.	0.02
	Ogyrides alphaerostris	1.85
	Palaemonidae indet.	0.52
	Rimapenaeus faoe	0.36
	Xanthidae indet.	43.62
Epifaunal sessile burrowing suspension feeder	*Glottidia* cf. *albida*	0.04
	Porifera indet.	1.99
Epifaunal/infaunal free-living crawling carnivore/scavenger	*Acanthotrophon sorenseni*	0.95
	Anachis sp.	1.62
	Bifurcium bicanaliferum	6.53
	Linopherus cf. *kristiani*	0.68
	Linopherus cf. *paucibranchiata*	0.40
	Olivella aureocincta	18.48
	Olivella semistriata	36.07
	Olivella sp.	2.78
	Phrontis cf. *complanata*	3.21
	Terebra cf. *crenifera*	0.02
Epifaunal/infaunal free-living crawling surface/sub-surface deposit feeder	*Caecum* (*Fartulum*) sp.	>0.01
	Cerithiidae indet.	0.35
	Crepidula cf. *excavata*	2.59
	Fartulum sp.	1.23
	Microglyphis estuarina	>0.01
	Natica scethra	68.28
Infaunal free-living burrowing detritivore/subsurface deposit feeder	Nematoda indet.	0.24
Infaunal sessile tube-dwelling suspension feeder	*Owenia johnsoni*	0.01
	Owenia sp.	0.05
Epifaunal free-living swimming suspension feeder	Chironomidae indet.	0.02
Epifaunal free-living swimming carnivore	*Bollmania* sp.	1.04
	Evermannia sp.	1.19

	Spadella sp.	0.32
Epizoic free-living crawling parasite	*Strioturbonilla* sp.	1.80
Epifaunal/infaunal free-living/sessile burrowing surface deposit feeder	*Cirriformia violacea*	0.21
	Kirkegaardia carrikeri	0.15
	Protocirrineris socialis	0.01
Infaunal free-living crawling carnivore	Nemertea indet.	2.19
	Pisione remota	0.02
Infaunal free-living crawling carnivore/detritivore	Talidridae indet.	0.96
Epifaunal sessile tube-dwelling suspension feeder	Anthozoa indet.	1.35
	Clytia sp.	>0.01
	Diphasia sp.	0.01
Epifaunal/infaunal sessile tube-dwelling suspension feeder	*Fabrisabella similis*	0.11
Epifaunal/infaunal free-living tube-dwelling detritivore	*Diopatra splendidissima*	1.23
	Onuphis eremita	1.37
Interstitial free-living burrowing carnivore/scavenger/detritivore	Acari indet.	0.01
Epifaunal free-living crawling carnivore/scavenger	Asteroidea indet.	0.08
Epifaunal/infaunal free-living crawling/swimming algaevore/omnivore	Idoteidae indet.	1.10
Epifaunal/infaunal free-living burrowing/crawling carnivore	*Oxydromus pugettensis*	0.06
Infaunal free-living burrowing/swimming suspension feeder	*Branchiostoma californiense*	5.49
Epifaunal/infaunal free-living burrowing/crawling omnivore	*Odontosyllis dugesiana*	0.10
	Westheidesyllis heterocirrata	>0.01
Infaunal free-living crawling chemosynthetic symbionts/suspension feeder	*Divalinga perparvula*	0.03
	Lucinidae indet.	0.15
	Lucinisca centrifuga	0.22
Epifaunal free-living swimming algaevore	Elmidae indet.	0.01
Infaunal sedentary burrowing omnivore	*Albunea lucasia*	0.95
Epifaunal free-living crawling carnivore	*Chaetacanthus pilosus*	0.07
	Euphrosine sp.	0.21
Infaunal free-living tube-dwelling subsurface deposit feeder	*Terebellides* sp.	4.64
Infaunal free-living crawling subsurface deposit feeder	*Antalis* cf. *pretiosa*	1.87
	Graptacme semistriata	2.38
Epifaunal free-living crawling carnivore/detritivore	Pycnogonida indet.	0.01
Epifaunal free-living crawling algaevore	Echinoidea indet.	0.03
Epifaunal free-living crawling/swimming carnivore	*Meiosquilla dawsoni*	6.09

Table 4S2. *General Lineal Models for spatial and temporal variation of the multidimensional functional diversity indices: A) functional richness, B) functional divergence, C) functional evenness, D) functional dispersion, E) functional specialization, and F) functional originality, of the subtidal benthic macrofauna at Térraba-Sierpe estuarine system, Costa Rica.*

A) Functional richness: FRic ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	6.82	2.31	2.95	0.006
Estuary (Sierpe)	-4.05	2.34	-1.73	0.095
Station (Lower)	-0.41	2.97	-0.14	0.892
Station (Outer)	-1.12	1.54	-0.73	0.475
Season (Wet)	4.42	1.86	2.37	0.025*

B) Functional divergence: FDiv ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	1.18	0.06	20.07	>0.001
Estuary (Sierpe)	-0.05	0.06	-0.77	0.451
Station (Lower)	0.09	0.07	1.37	0.181
Station (Outer)	-0.05	0.06	-0.83	0.413
Season (Wet)	0.01	0.06	0.09	0.931

C) Functional evenness: FEve ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	3.32	0.47	7.04	>0.001
Estuary (Sierpe)	-0.59	0.48	-1.24	0.225
Station (Lower)	0.03	0.54	0.06	0.956
Station (Outer)	-0.03	0.42	-0.07	0.946
Season (Wet)	-0.10	0.44	-0.24	0.816

D) Functional dispersion: FDis ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	1.87	0.27	6.85	>0.001
Estuary (Sierpe)	0.26	0.30	0.85	0.402
Station (Lower)	0.58	0.34	1.72	0.097
Station (Outer)	-0.38	0.28	-1.39	0.177
Season (Wet)	0.25	0.28	0.89	0.380

E) Functional specialization: FSpe ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	2.100	0.09	23.60	>0.001
Estuary (Sierpe)	-0.167	0.09	-1.80	0.083
Station (Lower)	0.064	0.10	0.64	0.527
Station (Outer)	0.002	0.08	0.02	0.981
Season (Wet)	-1.046	0.09	-0.53	0.598

F) Functional originality: FOri ~ Estuary + Station + Season

Coefficients	Estimate	Standard error	t value	p
Intercept	68.27	28.11	2.43	0.022
Estuary (Sierpe)	-39.88	24.438	-1.63	0.114
Station (Lower)	18.15	42.48	0.43	0.673
Station (Outer)	-8.09	9.17	-0.88	0.386
Season (Wet)	-17.99	19.21	-0.94	0.357

*: factors are significantly different.