

POLYCHAETES (ANNELIDA, POLYCHAETA) ASSOCIATED WITH LITHIC
AND BIOGENIC SUBSTRATA IN MESOPHOTIC CORAL ECOSYSTEMS IN
PUERTO RICO AND THE US VIRGIN ISLANDS

By

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ABSTRACT

There are no studies on the taxonomy and ecology of the polychaetes from the Caribbean Mesophotic Coral Ecosystems (MCE) and this work represents the first effort to identify and catalog the polychaetes of these ecosystems in the Caribbean. To fill this information gap, several substrata samples were collected using technical diving from several mesophotic localities (between 46-91 m) in Puerto Rico and the U.S. Virgin Islands, between 2007 and 2012. The samples were processed on board, washed on sieves with mesh eye of 1.0 mm and 0.125 mm; sediment and organisms retained were fixed in 95% ethanol, for future studies. In the laboratory, samples were analyzed under the stereo-microscope and specimens belonging to 76 genera (distributed among 34 families) were identified. All of them have been previously reported from marine substrata around the Caribbean, but from other ecosystems. Syllidae was the family best represented across all sampled localities, with the largest number of genera (15) and the highest number of individuals (5,755 or 80.85% of the total recorded fauna). *Haplosyllis* was the most abundant and most frequently sampled genus in the sampled sites. Bajo de Sico, an MCE on the west coast of Puerto Rico, was the locality with the highest abundance (1,183 individuals), while the extended MCE off La Parguera Natural Reserve, on the southwest coast of Puerto Rico, was the locality with the highest number of genera (59), which seems related to the greater spatial heterogeneity of substrata and the high variety of microhabitats that it offers. The greatest generic diversity and the highest abundances were found in the upper zone (UM) of the mesophotic range (30-60 m) compared to the lower zone (LM) (60-91m).

RESUMEN

No hay estudios sobre la taxonomía y la ecología de los poliquetos de los ecosistemas coralinos mesofóticos del Caribe (MCE) y este trabajo representa el primer esfuerzo para identificar y catalogar los poliquetos de estos ecosistemas en el Caribe. Para llenar este vacío de información, se recolectaron muestras de sustratos variados utilizando buceo técnico en varias localidades mesofóticas (entre 46 y 91 m) en Puerto Rico y las Islas Vírgenes de los EE. UU., entre 2007 y 2012. Las muestras se procesaron a bordo, se lavaron sobre tamices con malla de ojo de 1,0 mm y 0,125 mm; los sedimentos y los organismos retenidos se fijaron en etanol al 95%, para estudios futuros. En el laboratorio, las muestras se analizaron bajo el estereoscopio y se identificaron especímenes pertenecientes a 76 géneros (distribuidos entre 34 familias). Todos estos géneros han sido registrados previamente en sustratos marinos alrededor del Caribe, pero en otros ecosistemas. Syllidae fue la familia mejor representada en todas las localidades muestreadas, con el mayor número de géneros (15) y el mayor número de individuos (5,755 u 80.85% del total de la fauna registrada). *Haplosyllis* fue el género más abundante y más frecuentemente muestreado en los sitios muestreados. Bajo de Sico, un MCE en la costa oeste de Puerto Rico, fue el lugar con la mayor abundancia (1,183 individuos), mientras que el extenso MCE aguas afuera de la Reserva Natural La Parguera, en la costa suroeste de Puerto Rico, fue el lugar con el mayor número de géneros (59), lo que parece estar relacionado con la mayor heterogeneidad espacial de los sustratos y la alta variedad de microhábitats que ofrece. La mayor diversidad genérica y las mayores abundancias se encontraron en la zona superior (MS) del rango mesofótico (30-60 m) en comparación con la zona inferior (MI) (60-91m).

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DEDICATION

To the memory of my beloved Teresin (my mother) and Blanquis (my maternal grandmother), my female “Double I”. They both are two of those women that Silvio Rodríguez immortalized when he wrote: “*And other unknown giant women, who simply can't fit in a (history) book*”. Mom, you taught me to persevere and not give up until I reach my goals; Grandma, you taught me to observe, ask questions and look for coherent answers, the basis of the scientific method.

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INTRODUCTION

The Mesophotic Coral Ecosystems or Mesophotic Coral Communities (MCE) are light-dependent benthic communities ranging between 30 and 150 m depth (Hinderstein et al. 2010; Baker et al. 2016). In the Caribbean basin, MCEs are usually found in the upper insular and continental slopes (Locker et al. 2010; Sherman et al. 2010, 2013; Appeldoorn et al. 2015). In some areas, MCEs occupy a greater area than that of shallower coral reefs (Pyle et al. 2016).

According to their geomorphology, MCE may be grouped in two broad categories: (1) *low-gradient platforms*, that comprise outer insular shelves that dip gently into mesophotic depths and isolated banks with relatively flat tops that rise towards the surface; and (2) *high gradient slopes*, that include the steeper margins of insular shelves and banks that extend from the platform break to the adjacent basin (Locker et al. 2010). The structural habitat associated with these ecosystems includes two different community types: the “upper mesophotic” (30-60 m) -characterized by high coral cover composed of massive, mostly shallow dweller, scleractinian species, gorgonians, crustose coralline algae (CCA), sponges, octocorals and few black corals-, and the “lower mesophotic” (>60 m) –dominated by black corals, sponges and CCA and some macro algae (*Lobophora* spp.) (Kahng et al. 2010; Bongaerts et al. 2015; Appeldoorn et al. 2015; 2018), although these ranges can fluctuate depending on the geomorphology and sunlight penetration (Sherman et al., 2010).

During the last 20 years, the improvement in marine habitat mapping, in technologies such as Remotely Operated Underwater Vehicles (ROVs) equipped with photographic cameras, video-recorders, sensors and sampling devices, together with safety advances in trimix-rebreather technical diving, has allowed the collection of visual information, and samples in precise, minimally invasive manner (compared to dragging) from MCEs (Singh et al. 2004; Sherman et al. 2009, 2013; Appeldoorn et al. 2015).

The increased motivation to study these ecosystems in recent years has been promoted by its potential key role as a "refuge" of shallow coral reef biota and a possible source of larvae who could replenish the deteriorating shallower reefs (Bongaerts et al. 2010). MCEs are further

removed from anthropogenic disturbances and are presumed to be relatively good states (Pyle et al. 2016), however this assumption may not be met in all MCEs (e.g. Appeldoorn et al. 2015).

Caribbean MCEs had been shown to have a characteristic biota, part of it new to science. Among the studied taxonomic groups in the region so far, the following stand out: macroalgae (Ballantine and Ruiz 2005, 2008, 2010, 2011; Athanasiadis et al. 2013), microcrustaceans (Petrescu et al. 2012; Corgosinho and Schizas 2013; Petrescu et al. 2013; Petrescu et al. 2014 a, b, c; Senna et al. 2014; Guerra-Garcia et al. 2015; Schizas et al. 2015; Corgosinho et al. 2016; Petrescu et al. 2016) and the marine chelicerates (Pesic et al. 2008; Pesic et al. 2012; Pesic et al. 2014). However, no reports exist for one of the most important macrofaunal benthic group in terms of abundance and function, the annelids.

Polychaetes occur in all marine benthic habitats (Fauchald 1977). In soft-sediments, they are often the dominant component of the macrofauna, both in terms of the number of species and abundances (Grassle and Maciolek 1992; Ward and Hutchings 1996). In addition, polychaetes are associated with hard bottoms -rocky and coral substrata-, in some cases as members of the megafauna, i.e., some serpulids, sabellids and amphinomids species; and in most cases in cryptic habitats, where they are part of the macro- and meiofauna (Glasby et al. 2013), as cavity dwellers (coelobites) (Gischler and Ginsburg 1996; Gischler 1997) and macroborers (Perry 1998; Ochoa-Rivera et al 2000; Hutchings and Peyrot-Clausade 2002; Fernández et al. 2012). In these habitats, the polychaete family Syllidae dominates in both numbers of species and individuals (Giangrande, 1988; Bailey-Brock 2003; Gobin 2010). In example, Gobin (2010) recorded 14 syllid genera and 1,646 individuals that colonized, in five months, artificial substrate units deployed in rocky substrata at 12-15 m depth from Trinidad and Tobago, with the genera *Exogone* and *Haplosyllis* as two of the three more abundant in those substrata.

Until now the record of polychaetes in Caribbean MCEs is anecdotal, since only two families have been recorded, in video- or photo-transects that were used to characterize MCE benthic macro- and megafauna. These families were Sabellidae and Serpulidae, recorded for Bajo de Sico, western Puerto Rico, (García-Sais et al. 2007) and Abrir la Sierra (García-Sais et al. 2010).

The objective of this work is to do a first evaluation of the polychaete diversity, abundance and distribution throughout some representative MCEs of Puerto Rico and the US Virgin Islands. This study represents the first systematic characterization of polychaetes from MCEs of the Caribbean region which will significantly improve our knowledge of the hidden-biodiversity associated to these ecosystems, the diversity and abundance of polychaetes and their potential ecological function in MCEs and help promote their integration in coastal conservation programs.

REVIEW OF LITERATURE

The taxonomical study of polychaetes in the Caribbean Sea

The presence of polychaetes in the Caribbean Sea has been recorded since the 18th century, when the amphinomid *Eurythoe complanata* and the serpulid *Spirobranchus giganteus* (as *Serpula gigantea*) were described by Pallas (1766). Later, during the first half of the 19th century several European naturalists carried out samplings in the region, mainly in shallow habitats (Dean 2012). Subsequently, during the second half of that century, the work of McIntosh (1885) stood out, who described the polychaetes collected during the Challenger Expedition. At that time, the first American expeditions to the Caribbean that collected polychaetes were carried out, they were the Albatross described by Benedict (1887) and the Blake described by Ehlers (1887). Later, during the first four decades of the 20th century, new works increased the knowledge of the polychaetes of the Caribbean, they were those of Treadwell (1901, 1917, 1921, 1939), Augener (1906, 1922, 1927), and Monro (1928). Subsequently, during the second half of 20th century several sub-regional studies were conducted, mainly on the Caribbean coasts of South America (Laverde-Castillo and Rodríguez 1987) and Mexico (Salazar-Vallejo 1996), and in Cuba (see a review in Dean 2012).

The taxonomical study of polychaetes in Puerto Rico and US Virgin Islands

The first work on polychaetes from Puerto Rico was that of Treadwell (1901), who registered 38 species from shallow waters. Subsequent work significantly increased the number of recorded species, several of them in deep waters in the north and south sides of the island (Treadwell 1917, 1924, 1929, 1931, 1934, 1939, 1941; Hoagland 1919). Later works increased slightly the number of known species from shallow habitats of the island (Allen 1957, 1964; Erdman 1965; Pettibone 1989; Stoner and Acevedo 1990). Recently, Dean (2012) indicated that up until 2012, 208 species of polychaetes had been registered from Puerto Rico. In the case of the US Virgin Islands, records on polychaetes are scarcer; in St Croix and in St Thomas the first records were in the middle of the 19th century and in St John at the beginning of the 20th

century. According to Dean (2012), up to that 2012, the number of registered polychaete species for these islands was: 85 for St Croix, 47 for St Thomas, and 17 for St John.

MATERIAL AND METHODS

Sampling localities

Between the fall of 2007 and the fall of 2009, scientists from the University of Puerto Rico at Mayagüez (UPRM) Caribbean Coral Reef Institute (CCRI) and Department of Marine Sciences (DMS) run several technical and ROV dives to characterize the MCEs off La Parguera Natural Reserve (LPNR) in the southwest coast of Puerto Rico (Sherman et al. 2009). As part of this study (DeepCres), lithic (sediment, coral fragments, etc.) and biogenic (sponge, algae, scleractinian corals, etc.) substrate samples were collected at several specific sites: Precipicio, El Hoyo, Hole-in-wall, Black Wall, Barranca, Weinberg and SE Slope (Figure 1, see Appendix 1 for the GPS position and depth range of the sampling sites in which polychaetes were collected). In October 2010, additional samples were collected at Ponce Ledge (east of LPNR). From the fall of 2010 to the spring of 2012, UPRM-CCRI-DMS carried out three research cruises to survey other localities and improve the knowledge on MCEs distribution, structure and diversity knowledge over a broader geographic range within the eastern Caribbean. Substrate (lithic and biogenic) samples were collected at Mona Island; Desecheo Island, Bajo de Sico, Abrir La Sierra, Tourmaline, North of Buoy #4 (in the western coast of Puerto Rico); Grappler Bank (off the south-eastern coast of Puerto Rico); Vieques Island; Grammanik Bank (off the southern coast of St Thomas); east St John; Armageddon or Frederiksted Pier (western coast of St Croix); Cane Bay, North Star, Davis Bay and Salt River Canyon (off north-eastern St Croix), and Lang Bank (eastern St Croix) (Figure 1, see Appendix 1 as mentioned above). The cruises took place from 9-23 January 2010, 15 April – 5 May 2011 and 24 April – 10 May 2012 (Sherman et al. 2013). The depth of the sampling sites, where the polychaetes in this study were found, ranged between 46 and 91 m, and they were grouped according to the concepts of “upper mesophotic (UM)” and “lower mesophotic (LM)” ecosystems described above.

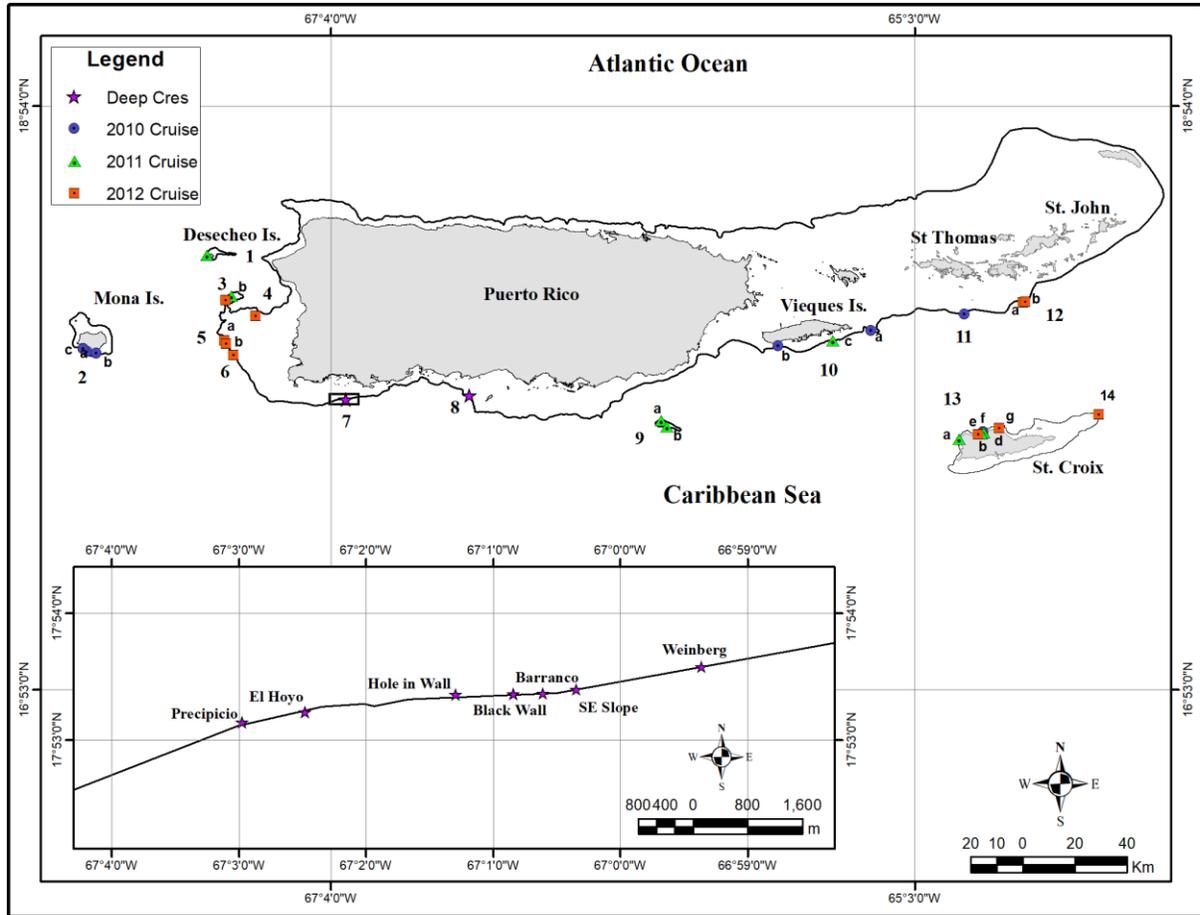


Figure 1. Map of Puerto Rico (PR) and the U.S. Virgin Islands (USVI), showing the location of mesophotic sampling sites. The extended insular shelf (circa 200 m depth) is noted by a black line. Numbers indicate the sampling sites of polychaetes collected from mesophotic coral ecosystems. 1 = West Desecheo Island, PR; 2= Mona Island, PR; 3 = Bajo de Sico, PR; 4 = Tourmaline, PR; 5 = Abrir la Sierra, PR; 6 = North of Buoy 4, PR; 7 = La Parguera, PR; 8 = Ponce Ledge, PR; 9 = Grappler Bank, PR; 10 = Vieques Island, PR; 11 = Grammanik Bank (South St. Thomas), USVI; 12 = East St. John, USVI; 13 = St. Croix, USVI; and 14 = Lang Bank, USVI. Colored figures indicate the exact sampling locations (Appendix 1). Stars represent the designated mesophotic localities of the DeepCres program; circles, triangles and squares indicate samples collected during the 2010-2012 cruises respectively (see Sherman et al. 2013). Prepared from data from NOAA NCCS Biogeography Team and General Bathymetric Chart of the Oceans (GEBCO).

Sampling and preliminary processing

In each sampling site, technical research divers utilizing mixing gas with re-breathers techniques carried out an opportunistic collection of lithic –sand, rubble, live and dead corals colonies and fragments, sponges and sclerosponges, macroalgae, octocorals, etc.- and exposed limestone substrate (cf. Sherman et al. 2009, 2013). In each case, sample size, sample effort, and sampling collecting were not standardized, so the sampling was mostly exploratory and

qualitative. Each substrate sample was placed in a zip-lock bag with *in situ* sea water, with a label recording location, date, and depth data. Samples were sent to the surface with a lift bag to be recovered quickly by the cruise crew, students and/or scientists on the boat for immediate processing (Sherman et al. 2013). Each substrate sample was washed over a 1 mm to retain the macrofauna and the large material and then through a 0.125 mm sieve, for the meiofauna and smaller size rubble and sediments, respectively. All samples were stored separately in medium size plastic vials (10.0 to 100.0 ml) with 95% ethanol. Samples were ultimately stored at the Marine Genomics Laboratory at Magueyes Island, UPRM for future processing and analyses.

Laboratory protocols

In the laboratory, large samples were washed over a 0.5 mm mesh sieve and with the aid of a binocular microscope (Leica MZ16, Polychaete specimens were hand sorted directly from sediments), or after a Ludox AM-30 colloidal silica re-suspension and centrifugation process, and stored in 1.5 mL plastic vials, with 95 % ethanol, at 4°C for future work. Specimens were examined under stereoscope (Leica MZ16) and compound light microscope (Nikon Optiphot), and identified firstly at the family level, and posteriorly at the genus level, following regional, specialized and updated literature, i.e. de León-González et al. (2009), and in the case of the Syllidae according to San Martín and Aguado (2014). Further analysis under a light microscope, were made from specimens and/or detached parapodia in semi-permanently mounted on slides in glycerine jelly. Due to damage caused during sampling and processing, aided by the typical polychaete autotomy, and the use of centrifugation in the initial laboratory processing phase, the most fragile specimens were deteriorated or fragmented. In these cases, to avoid double-counting or sub-counting of specimens, the following criteria for the determination of an individual were applied: the presence of the prostomium and the mouth-parts (most of the Errantia group), the presence of prostomium and at least the first five setigers (most of the Sedentaria group) the presence of tentacle crowns and / or opercula (in Sabellidae and Serpulidae), and the presence of elitrae in good condition (in scale-worms). To get an idea of the body sizes, the total length of organisms, that were complete, was measured to the nearest millimeter; from the tip of the palps/tip of the tentacular crown to the tip of the pygidium, excluding anal cirri/posterior tip. After measuring, polychaetes were divided into three different size groups: <5 mm (small-sized

group), 5-25 mm (medium-sized group), and 25-100 mm (large-sized group). Voucher specimens were deposited in the Invertebrate Collection of the Department of Marine Sciences UPRM at Magueyes Island, all them preserved in 95% ethanol. Taxa were named following the World Register of Marine Species (WoRMS) database (WoRMS 2018).

Characterization of the lithic and biogenic substrata

Taking into account the information collected during the sampling (Sherman et al. 2013) and the qualitative analysis of the substrata at the time of laboratory work, the substrata samples were divided into: sand (coarse, medium, and fine); lithic substrate; algae; algae debris (macroalgae fragments); sponges; live and dead coral.

Data management

Although the samples were obtained qualitatively, and a sampling area was not standardized, in this work "abundance" is understood as the total number of individuals of each taxa counted per sampling site.

RESULTS

Taxonomic composition

A total of 7,118 benthic polychaete specimens from 34 families and 76 genera were collected from lithic and biogenic substrata, in 18 sampling sites in MCEs of Puerto Rico and the U.S. Virgin Islands (Table 1 and Appendix 2 contains the abundance data per site and bathymetric ranges). Fifty two genera in 19 families belonged to the subclass Errantia, whereas the subclass Sedentaria had 24 genera in 15 families. In the case of the Errantia, which contains 35 free-living benthonic families, there were representatives of the three orders in which Read and Fauchald (2018) divided the subclass. The "Amphinomida" were represented by two families, both usually members of the epifauna; the "Eunicida" had four families, which may be inhabiting epifaunal, infaunal and cryptic habitats or may be epiphytic; and the "Phyllodocida" had 13 families, with a wide diversification of the habitats they occupy, being mainly infaunal (living in the sediments) and epifaunal (living on the surface of sediments) (Glasby et al 2000; Rouse and Pleijel 2001). On the other hand, in the case of the "Sedentaria", which as a group with around 27 free-living benthonic families, there were representatives of the two infraclasses in which Read and Fauchald (2018) divided the subclass. On the one hand, the "Scolecida" were represented by four families, usually members of the infauna. On the other hand, the "Canalipalpata" had 11 families, which can be, mostly, epifaunal or epiphytic ("Sabellida"); infaunal or cryptic ("Spionida"); and infaunal ("Terebellida") (Glasby et al 2000; Rouse and Pleijel 2001). All the recorded taxa have been previously reported from benthic habitats of the Caribbean Sea, but in another types of ecosystems (cf. Dean, 2012). Unfortunately, Dean (2012) does not discriminate the information by bathymetric ranges.

Table 1. Taxonomic list of Polychaeta reported in this study*

Subclass/Infraclass						
	Order/Suborder	Family	Genus			
Errantia	Amphinomida	Amphinomidae	<i>Amphinome</i> Bruguière, 1789			
			<i>Chloeia</i> Lamarck, 1818			
			<i>Eurythoe</i> Kinberg, 1857			
	Eunicida	Euphrosinidae	Euphrosinidae	<i>Euphrosine</i> Lamarck, 1818		
				<i>Dorvillea</i> Parfitt, 1866		
		Dorvilleidae	Dorvilleidae	<i>Schistomeringos</i> Jumars, 1974		
				<i>Eunice</i> Cuvier, 1817		
				<i>Leodice</i> Lamarck, 1818		
				<i>Lysidice</i> Lamarck, 1818		
				<i>Marphysa</i> Quatrefages, 1866		
				<i>Lumbrineris</i> Blainville, 1828		
		Oeononidae	Oeononidae	<i>Arabella</i> Grube, 1850		
				<i>Oenone</i> Savigny in Lamarck, 1818		
	Phyllodocida	/ Aphroditiformia	Aphroditidae	<i>Aphrodita</i> Linnaeus, 1758		
			Eulepethidae	<i>Grubeulepis</i> Pettibone, 1969		
			Polynoidae	<i>Harmothoe</i> Kinberg, 1856		
					<i>Lepidonotus</i> Leach, 1816	
					Sigalionidae	<i>Pelogenia</i> Schmarda, 1861
						<i>Sthenelais</i> Kinberg, 1856
		/ Glyceriformia		Glyceridae	<i>Glycera</i> Lamarck, 1818	
<i>Hemipodia</i> Kinberg, 1865						
/ Nereidiformia			Goniadidae	<i>Goniada</i> Audouin and H Milne Edwards, 1833		
			Chrysopetalidae	<i>Bhawania</i> Schmarda, 1861		
		<i>Chrysopetalum</i> Ehlers, 1864				
		<i>Paleanotus</i> Schmarda, 1861				
				Hesionidae	<i>Hesione</i> Lamarck, 1818	
					<i>Gyptis</i> Marion and Bobretzky in Marion, 1874	
					<i>Oxydromus</i> Grube, 1855	
					Nereididae	<i>Ceratonereis</i> Kinberg, 1865
						<i>Nereis</i> Linnaeus, 1758
						<i>Perinereis</i> Kinberg, 1865
	<i>Platynereis</i> Kinberg, 1865					
	<i>Stenoninereis</i> Wesenberg-Lund, 1958					
		Pilargidae	<i>Ancistrosyllis</i> McIntosh, 1878			
		Syllidae	<i>Brania</i> Quatrefages, 1866			
<i>Branchiosyllis</i> Ehlers, 1887						
<i>Erinaceusyllis</i> San Martín, 2003						
<i>Eusyllis</i> Malmgren, 1867						
<i>Exogone</i> Örsted, 1845						
<i>Haplosyllides</i> Augener, 1922						
<i>Haplosyllis</i> Langerhans, 1879						
<i>Myrianida</i> Milne Edwards, 1845						
<i>Odontosyllis</i> Claparède, 1863						

Table 1. Continuation.

			<i>Plakosyllis</i> Hartmann-Schröder, 1956
			<i>Salvatoria</i> McIntosh, 1885
			<i>Sphaerosyllis</i> Claparède, 1863
			<i>Syllides</i> Örsted, 1845
			<i>Syllis</i> Lamarck, 1818
			<i>Trypanosyllis</i> Claparède, 1864
	/ Phyllodocida i.s.	Nephtyidae	<i>Nephtys</i> Cuvier 1817
	/ Phyllodociformia	Phyllodocidae	<i>Nereiphylla</i> Blainville, 1828
			<i>Phyllodoce</i> Lamarck, 1818
Sedentaria			
/ Canalipalpata			
	Sabellida	Oweniidae	<i>Owenia</i> Delle Chiaje, 1844
		Sabellidae	<i>Acromegalomma</i> Gil and Nishi, 2017
			<i>Chone</i> Krøyer, 1856
			<i>Parasabella</i> Bush, 1905
		Serpulidae	<i>Hydroides</i> Gunnerus, 1768
			<i>Protula</i> Risso, 1826
			<i>Pseudovermilia</i> Bush, 1907
			<i>Vermiliopsis</i> Saint-Joseph, 1894
	Spionida/		
	/ Spioniformia	Poecilochaetidae	<i>Poecilochaetus</i> Claparède in Ehlers, 1875
		Spionidae	<i>Paraprionospio</i> Caullery, 1914
			<i>Prionospio</i> Malmgren, 1867
	Terebellida/		
	/ Cirratuliformia	Cirratulidae	<i>Caulleriella</i> Chamberlin, 1919
		Flabelligeridae	<i>Trophoniella</i> Caullery, 1944
	/ Terebellomorpha	Ampharetidae	<i>Amphicteis</i> Grube, 1850
		Pectinariidae	<i>Pectinaria</i> Lamarck, 1818
		Terebellidae	<i>Streblosoma</i> M. Sars in G.O. Sars, 1872
		Trichobranchidae	<i>Terebellides</i> Sars, 1835
/ Scolecida	**Capitellida	Capitellidae	<i>Dasybranchus</i> Grube, 1850
			<i>Mastobbranchus</i> Eisig, 1887
			<i>Mediomastus</i> Hartman, 1944
		Maldanidae	<i>Axiothella</i> Verrill, 1900
			<i>Clymenella</i> Verrill, 1873
		Paraonidae	<i>Aricidea</i> Webster, 1879
	**Opheliida	Opheliidae	<i>Armandia</i> Filippi, 1861

*The taxonomic categories and their authors are listed as they appear in the WorMS database (WORMS 2018)

** Read and Fauchald (2018) considered these orders superfluous (*nomen dubium*).

Number of genera

In the entire studied area, Syllidae was the family with the highest number of genera (15), followed by Nereididae (five), and Serpulidae and Eunicidae (four each). In addition, five

families were represented by three genera each, eight families had two genera each, and 17 families had only one genus each (Figure 2). On the other hand, Syllidae was represented by 15 genera in the UM and by 12 in the LM, whereas Nereididae, Serpulidae, and Eunicidae were represented by five, and four genera in each bathymetric range, respectively. Overall, 32 families were represented in the UM, by at least one genus, while 29 were in the LM (Figure 2). The contribution of the syllids was very important, in the entire area and in the two bathymetric zones (upper and low mesophotic).

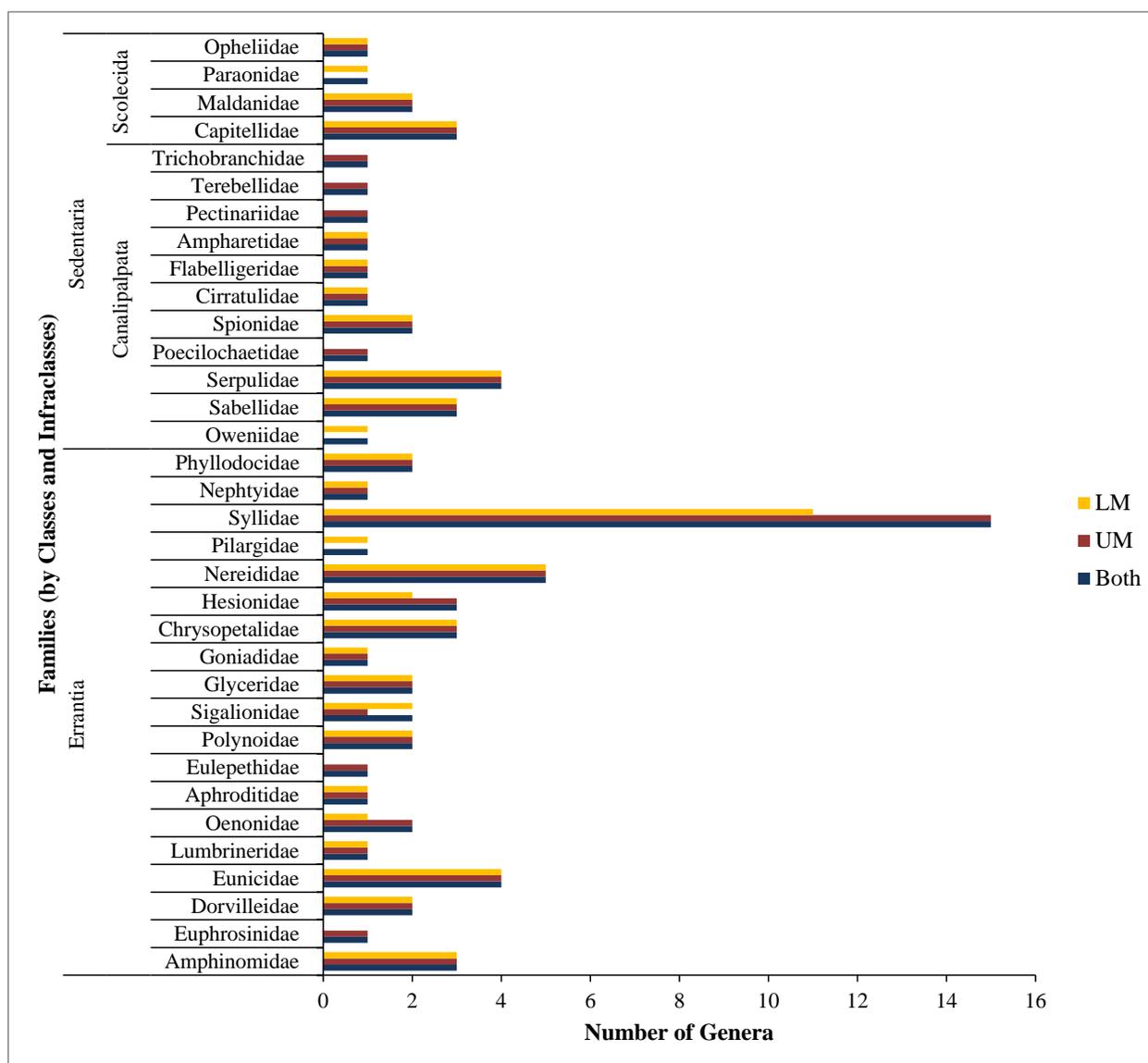


Figure 2. Number of polychaete genera, grouped by families, infraclasses and classes from all mesophotic sampling localities and mesophotic zones (UM and LM).

Abundance

Syllidae was the family with the highest abundance in the entire studied area with 5,755, corresponding to 80.85% of the total of the recorded polychaete fauna (Table 2). It was followed by Sabellidae, (187) Chrysopetalidae (170), Serpulidae (164), Nereidae (143), and Eunicidae (132). In addition, four families (Oweniidae, Poecilochaetidae, Pectinariidae, and Trichobranchidae) were represented by only one specimen each.

Syllidae was the most abundant (3,061 individuals) in the UM, followed by Sabellidae (155), Serpulidae (102), Nereididae (98,) and Eunicidae (92 individuals). In addition, six families (Nephtyidae, Flabelligeridae, Owenidae, Poecilochaetidae, Pectinariidae, and Trichobranchidae) were represented by one specimen each. Syllidae was also the most abundant family in the LM (2,694 individuals), followed by Chrysopetalidae (88), Serpulidae (62), Nereididae (45), and Eunicidae (40 inds.). Three families (Terebellidae, Aphroditidae, and Goniadidae) were represented by one specimen each (Table 2). Syllids were clearly the most abundant by orders of magnitude in all localities and in both depth ranges. *Haplosyllis* and *Syllis*, (3,810 and 1,843 individuals, respectively) were the two genera with the highest abundances.

Analysis by sampling localities

Number of genera.- In the visited localities, the highest number of genera was found in La Parguera, (see Figure 1), which added 59 genera across 7 stations, 43 of them present in Precipicio, the most genera-diverse locality. Most of the sampling sites (twelve) had an intermediate number of genera, which fluctuated between 17 in North Buoy #4 and 35 in Mona Island. This group of localities with intermediate values includes sites along the entire west-east direction, from the west of PR (Desecheo, Bajo de Sico, Abrir La Sierra, etc.), passing through the south-west (La Parguera) and south-center coast (Ponce), the south-eastern coast (Grappler bank); to south of St Thomas, St John, up to St Croix, including most of its locations. Four other localities had a low number of genera, Davis Bay (12), Tourmaline (13), Vieques Island and Cane Bay (15 genera each). The locality with the lowest number of genera was Salt River, at the NE of St Croix, with only six genera (Figure 3). Only nine localities were surveyed at both the

upper mesophotic- and lower mesophotic zones. Of these, a higher generic diversity was observed in the UM in five localities (Desecheo, Bajo de Sico, Abrir La Sierra, La Parguera, Cane Bay). The other four (Mona island, Vieques island, East St John, North Star) had higher generic diversities in the LM zones (Figure 3). Three localities on the west of PR (Desecheo, Bajo de Sico, and Abrir La Sierra, La Parguera) and one at NE St Croix (Cane Bay), the number of genera was higher in the shallower stations; whereas, in places like Mona, Vieques, east of St John and in a site northeast of St Croix (North Star), the opposite was observed.

Abundance.- In the visited localities, the largest abundance was found in Bajo de Sico with 1,183; followed by La Parguera and Abrir La Sierra with 1,021 and 869 individuals, respectively (Figure 4). Other five sites had an intermediate number of individuals, Grappler Bank (365), Desecheo (556), St Thomas (603), Davis Bay (639) and Ponce Ledge (639). Additionally, other nine locations had a low number of individuals, which fluctuated between 57 in North Buoy # 4 and 231 in Tourmaline.

The locality with the lowest number of individuals was Salt River with 15 individuals (Figure 4). a higher abundance was observed on the UM zone in six sites (Desecheo, Bajo de Sico, Abrir La Sierra, La Parguera, East St John, Cane Bay), whereas in the remaining three, such number was higher on the LM zone (Mona, Vieques, North Star) (Figure 4). In the three locations with the higher abundance, the contribution of syllids, mainly *Haplosyllis* and *Syllis*, were important; representing 66% and 26% of the total in Bajo de Sico; 40% and 26% in La Parguera, and 55% and 40% in Abrir La Sierra, respectively. Moreover, it should be noted that in Davis Bay, *Haplosyllis* contributed 77% of the total individuals collected, and *Syllis* contributed another 20%. Furthermore, the localities with the highest number of individuals were mainly located in the west and southwest of Puerto Rico; and the locations with intermediate abundances were along the west-east direction that goes from Mona Channel to St Croix; that the sites with low values were distributed scattered throughout the study area; and that the lowest value was obtained in the NE of St Croix. It should be noted that these results are not a reflection of the diving-collecting effort, but are related to the attributes of the substrates sampled in each place and the heterogeneity of the sampled habitats. Thus, for example, in the case of the extended MCE offshore La Parguera, the site that contributed the greatest abundances (Precipicio) was

only sampled once in each mesophotic zone (UM and LM); whereas other sites that were visited several times had a minimal contribution (Hole-in-Wall, Black Wall, etc.).

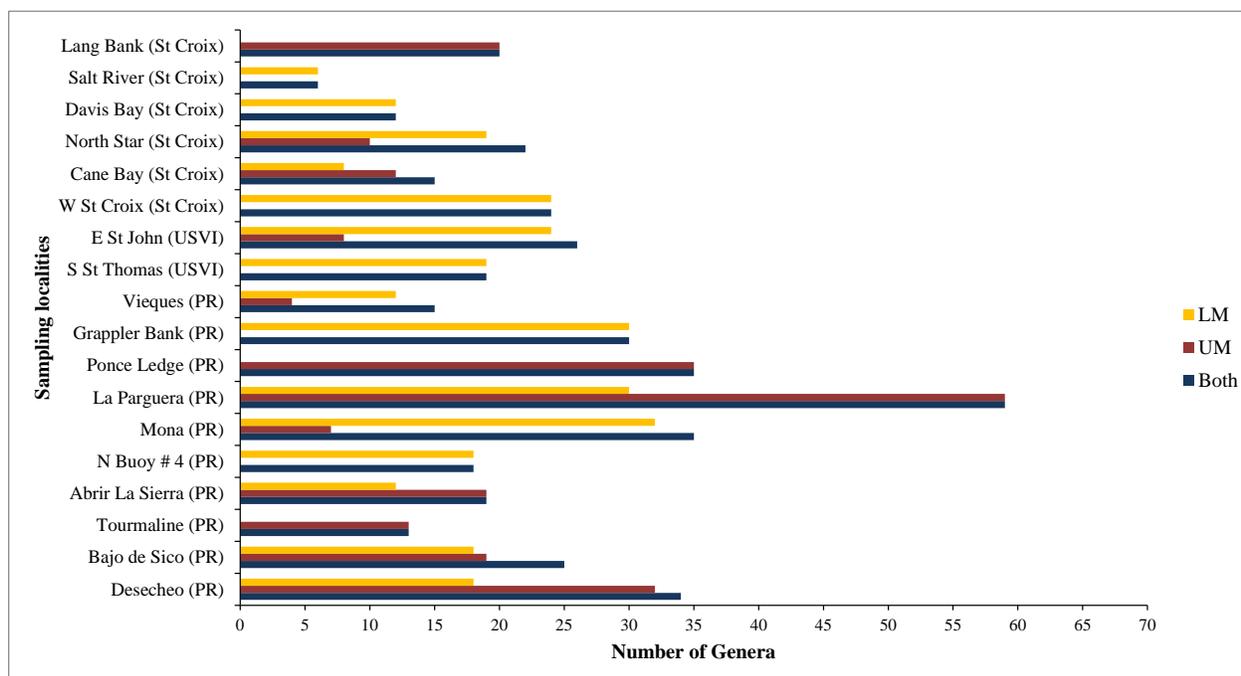


Figure 3. Number of polychaete genera at each mesophotic sampling locality and mesophotic zones (upper and lower).

Specimens size-groups

Appendix 3 summarizes the information on the sizes of the polychaetes found in the surveys of MCEs. The medium size-group (5-25 mm) was the most common, followed by the small size-group (<5 mm), and finally by the large size-group (25 mm-100 mm). In addition, it is emphasized that the most abundant genera (*Haplosyllis* and *Syllis*) have the majority of their specimens in the small size-group. Likewise, genera such as *Eunice* and *Marphysa* (Eunicidae), and *Nereis* and *Ceratonereis* (Nereididae), with representatives in the two major size-categories, were the most abundant. On the other hand, *Syllis* had representatives in all three size categories. Photographs of selected syllid species are provided in Figure 5.

Table 2. Abundance of polychaetes, grouped by families, infraclasses and classes from all mesophotic sampling localities and mesophotic zones.

Subclass	Infraclass	Family	Abundance		
			Both	UM	LM
Errantia		Amphinomidae	54	33	21
		Euphrosinidae	3	3	0
		Dorvilleidae	22	11	11
		Eunicidae	132	92	40
		Lumbrineridae	5	3	2
		Oeonidae	27	19	8
		Aphroditidae	3	2	1
		Eulepethidae	5	0	5
		Polynoidae	33	11	22
		Sigalionidae	14	4	10
		Glyceridae	86	45	41
		Goniadidae	3	2	1
		Chrysopetalidae	170	82	88
		Hesionidae	84	38	46
		Nereididae	143	98	45
		Pilargidae	4	0	4
		Syllidae	5755	3061	2694
		Nephtyidae	4	1	3
		Phyllodocidae	31	22	9
Sedentaria	Canalipalpata	Oweniidae	1	1	0
		Sabellidae	187	155	32
		Serpulidae	164	102	62
		Poecilochaetidae	1	1	0
		Spionidae	22	9	13
		Cirratulidae	4	2	2
		Flabelligeridae	4	1	3
		Ampharetidae	23	19	4
		Pectinariidae	1	1	0
		Terebellidae	9	8	1
		Trichobranchidae	1	1	0
	Scolecida	Capitellidae	32	17	15
		Maldanidae	17	9	8
		Paraonidae	13	0	13
		Opheliidae	61	28	33

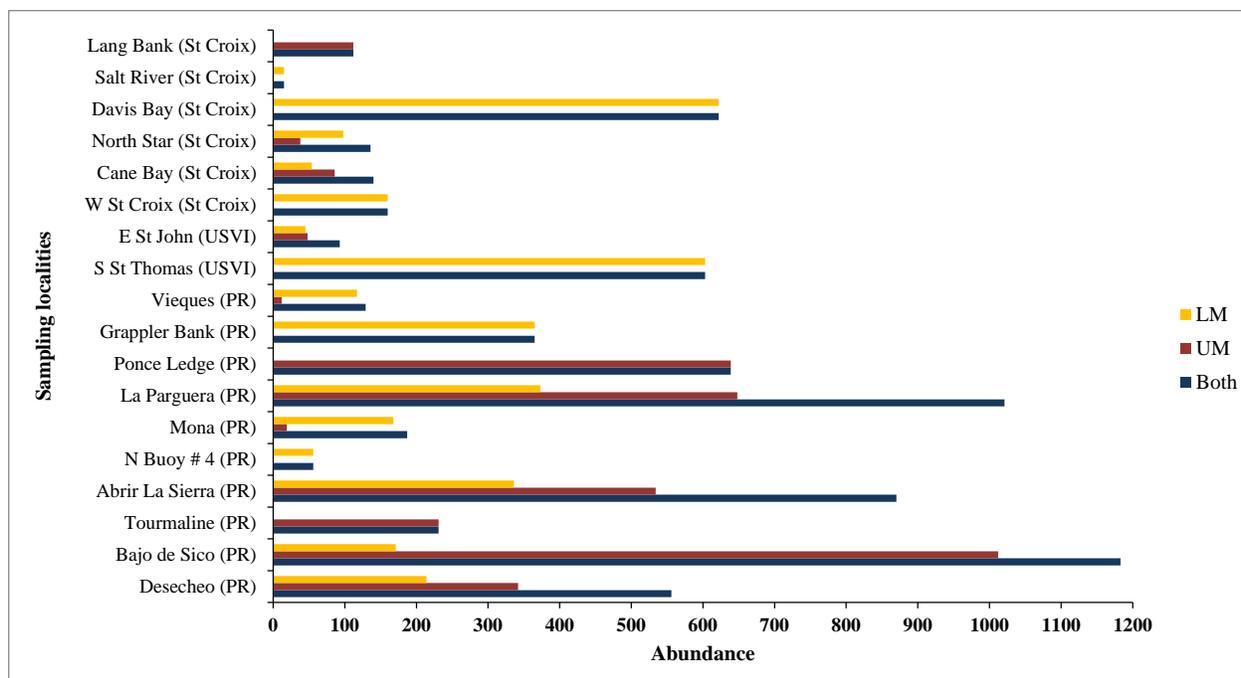


Figure 4. Abundance of polychaetes at each mesophotic sampling locality and mesophotic zones (upper and lower).

Lithic and biogenic substrata

Appendix 4 summarizes the information on the lithic and biogenic substrata collected from the MCE localities. In this context, lithic means substrate of inorganic origin, e.g. : sands, fragments of rocks, etc., and biogenic means substrate of biological origin, e.g., algae, sponge, scleractinian corals, etc. Sand, in three different size ranges, were the most frequent substrate, followed by corals, sponges and algae/algae debris. In turn, the less common substrates were dead coral debris and lithic (rock fragments). Most of these types of substrates were represented in La Parguera; in particular, in "Precipicio", so that this locality has a greater spatial heterogeneity, which generates multiple microhabitats, inhabited by macrofauna. On the other hand, the presence of algae detritus, algae, and, above all, sponges, provides other microhabitats, successfully occupied by some organisms, such as the Syllidae.

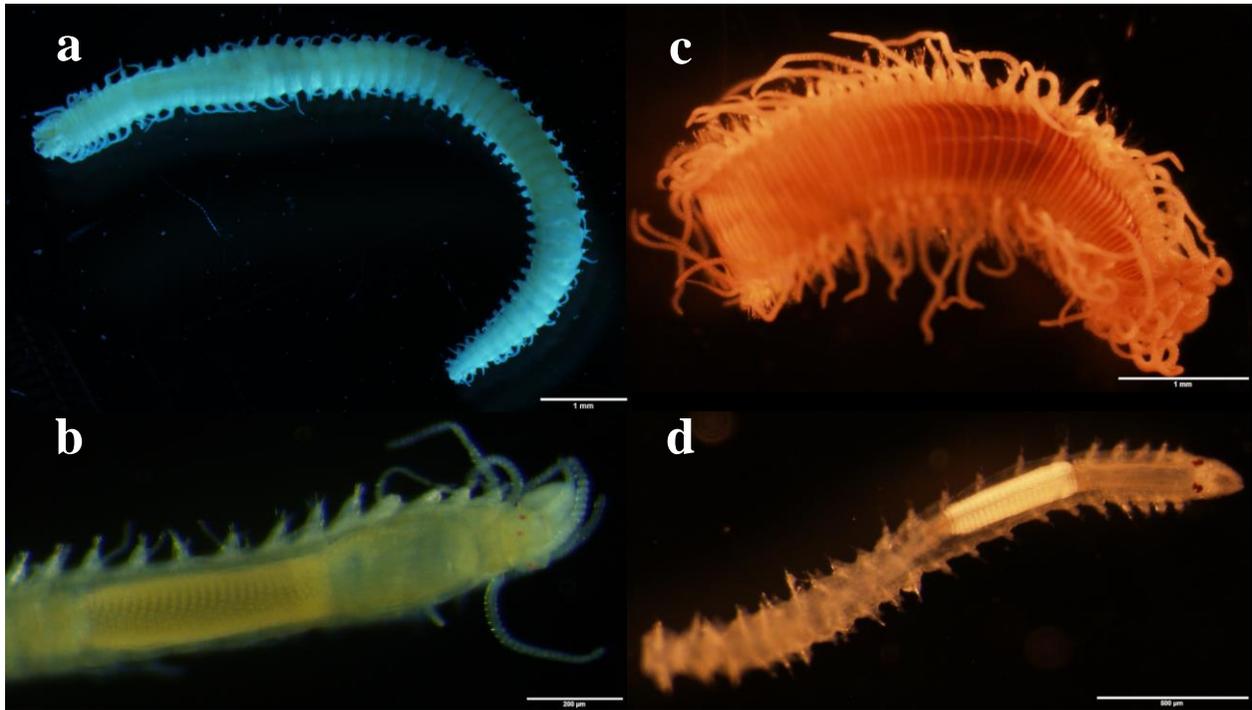


Figure 5. Representative syllids collected from Puerto Rican Mesophotic Coral Ecosystems. a. *Haplosyllis* sp.; b. *Syllis* sp.; c. *Trypanosyllis* sp.; d. *Exogone* sp. Scale-bar in a, c: 1 mm, in b, d 500 µm.

DISCUSSION

Taxonomic composition

Dean's review (2012) of the literature on polychaetes of the Caribbean Sea highlighted the state of current knowledge of the group. A revaluation of this information resulted in total of 50 free-living benthic polychaetes families known for the Caribbean Sea. This number of families resulted by subtracting the four holoplanktonic families, a parasitic family and three families that, according to the classification system followed in the present work, are part of other recognized taxa (ie: Pisionidae is integrated into Sigalionidae, Ctenodrilidae to Cirratulidae, and Spirorbidae to Serpulidae). According to the revaluation, by that date, 33 benthic polychaete families had been registered for all habitats in Puerto Rico, 19 for St Croix, 18 for St Thomas and 11 for St John. This study reports a total of 34 families of benthic polychaetes that are found in MCE environments (33 in Puerto Rico, 24 in St Croix, 12 in St Thomas and 27 in St John), expanding the depth range of distribution of these genera and families and indicating that this type of deep habitats are suitable and harbor a high biodiversity of polychaetes, mainly of small size, comparable to that of shallow water ecosystems.

As part of this hidden biodiversity, polychaete families typical of both, soft bottoms (members of the infauna and/or epifauna) and hard substrata (living on the surface or within them, as cryptic organisms) were part of this deep biodiversity. Thus, representatives of 20 typical infaunal families were found in this study (Opheliidae, Paraonidae, Maldanidae, Capitellidae, Trichobranchidae, Terebellidae, Pectinariidae, Ampharetidae, Flabelligeridae, Cirratulidae, Poecilochaetidae, Oweniidae, Nephtyidae, Pilargiidae, Goniadidae, Glyceridae, Sigalionidae, Eulepethidae, Oeonidae, Lumbrineridae) (Fauchald 1977, Glasby et al. 2000, Rouse and Pleijel 2001). All these organisms take advantage of sediment accumulations in cavities of the matrix that forms the reef structure, or in plate-shaped corals, to settle and colonize them; mostly on top of colony.

Also, representatives of epifaunal families, crawling freely on the sediment, were found, i.e.: Aphroditidae. In addition, typical families of hard bottoms were found: Euprosinidae,

Polynoidae, Serpulidae (Glasby et al. 2000, Rouse and Pleijel 2001). On the other hand, families that inhabit a variety of substrates, both lithic –sediments, rocks, etc.– and biotic –algae, sponges, corals, etc.– were found: Spionidae, Sabellidae, Phyllodocidae, Syllidae, Nereididae, Hesionidae, Chrysopetalidae, Eunicidae, Dorvilleidae, and Amphinomidae (Glasby et al. 2000, Rouse and Pleijel 2001). The representatives of these families are usually cryptic forms, living in crevices of the substrata or within it.

As for the known genera from Puerto Rico and its surroundings, Dean (2012) recorded the presence of 131 genera in Puerto Rico, 36 in St Croix, 40 in St Thomas and 15 in St John. Overall, 75 genera were found in mesophotic communities off Puerto Rico, 45 off St Croix, 18 off St Thomas and 27 off St John. This information extends the depth and habitat range of all these polychaete genera for the region, and indicates the presence of a diverse and abundant polychaete fauna in these environments. Most of these genera are infaunal organisms, living in the substrate rather than on top of it, and, and similar to the polychaete fauna living, in shallow water habitats, mainly, the soft bottoms (Santa-Isabel et al. 2000, Domínguez-Castanedo et al. 2015). Secondly, there are genera represented by organisms associated with hard substrates, occupying cryptic habitats, which also have a typical fauna, as happens in shallow coral ecosystems (Ochoa-Rivera et al. 2000, Fernández et al. 2012, Rivolta et al. 2015). Many of these organisms have the plasticity to indistinctly colonize and live in a variety of substrates, both lytic -sands, etc.- and biotic-corals, algae, sponges, etc.-. Most of the genera associated with MCE sponges are represented by small and abundant species (Carrera-Parra and Vargas 1996).

A comparison was made between the results presented here and the data recorded from mesophotic depths in the Gulf of Mexico (Reuscher and Shirley 2014). Data from the South-West and South-East Gulf localities, those with conditions more comparable (temperature and depth range) was more similar to the mesophotic fauna found in the Caribbean, and a re-analysis of the data was done. Reuscher and Shirley (2014) recorded 55 families and 299 genera of polychaetes, for the Gulf, with 45 families and 215 genera for the SW sector and 39 families and 96 genera for the SE sector. It is appreciated that, although the Gulf of Mexico is a much larger basin than the sector sampled in the MCE of Puerto Rico and US Virgin Islands, the values here presented (34 families and 76 genera) are more than representative, evidencing the high

polychaete diversity associated with MCE in the north-eastern Caribbean. Obviously, this comparison is qualitative, since there is not enough evidence about the quantity and size of the areas sampled in the Gulf of Mexico. Apart from the size of the basin, these differences are due to the fact that in MCEs of Puerto Rico and US Virgin Islands, the recorded fauna of polychaetes is of tropical nature, hence its great similarity with the data provided by Dean (2012) ,and other authors (see Laverde-Castillo and Rodríguez 1987); while the fauna of the Gulf of Mexico has a significant proportion of temperate components, as it is evidenced by the biogeographical analysis conducted by Reuscher and Shirley (2014).

Number of genera and abundance

In the mesophotic studied locations, Syllidae was the family that contributed the highest number of genera in both bathymetric ranges. This is not surprising, since this family has the most genera registered for the Caribbean basin with 38, (Dean 2012) and for the Gulf of Mexico, with 30 and 27 respectively in mesophotic depths (Reuscher and Shirley 2014). Likewise, in particular studies- in coral, cryptic or sponge-associated habitats-, this family is usually the best represented (Carrera-Parra and Vargas 1996, Ochoa-Rivera et al 2000, Granados-Barba et al. 2003). This family is one of the most diverse and widely distributed polychaete family worldwide, both in soft and hard bottoms and especially in shallow waters. The reason for this success lies in its small size, its diversity of reproductive strategies and versatility in its feeding mechanism and diet (San Martín and Aguado 2014). In particular, syllids are very successful in cryptic coralline substrates and coarse sediments of various types, especially coarse sands mixed with coral and shell rubble (Granados-Barba et al. 2003). This is so, because the many interstices present in coarse sands, make this habitat a suitable one for most syllid genera, even if the micro-distribution of species is influenced (Somaschini and Gravina 1994). In addition, the slight decrease in the number of genera that was appreciated in the LM zone, reaffirms what is indicated in the literature, in this family the number of genera decreases with the increase in depth (Cinar 2003).

Other families present in the mesophotic sites, which contribute a moderate number of genera –Nereididae, Serpulidae, Eunicidae and Sabellidae- , usually have a similar presence in

shallower ecosystems (Dean 2012; Rivolta et al. 2015). However, it should be noted that in that other ecosystems, the members of these families tend to have a larger organismal size than sizes recorded from the MCE samples (pers. Obs.). This could be related to the characteristics of the microhabitats, availability of food and the type / depth of sediments available in the MCE.

The fact that Syllidae was the family that contributed the most individuals is not surprising either. This is due to its small size. They usually live associated with biotic substrata, such as algae, sponges, and corals, where they reach abundances of thousands of individuals, i.e., the case of *Haplosyllis* (Carrera-Parra and Vargas 1996, Lattig and Martin 2011). Additionally, the slight decrease in the number of individuals that was appreciated in LM zone, reaffirms what is indicated in the literature, in this family the number of genera decreases with the increase in depth.

Furthermore, other families present in the mesophotic localities, which contribute to a moderate number of individuals - Sabellidae, Chrysopetalidae, Serpulidae, Nereidae, and Eunicidae-, usually have a greater contribution in shallower ecosystems, for example in soft bottoms in the vicinity of coral ecosystems (Domínguez-Castanedo et al. 2015). Likewise, as indicated above, it should be noted that in that other ecosystems, the members of these families tend to have a larger size than that recorded at the MCE.

Results by sampling localities

Number of genera.- The information collected allows to obtain a first approximation of this polychaete biodiversity associated with MCEs regardless of the limitations of the sampling and the qualitative nature of the data. Different effort and different substrates and number of particular samples from each substrate in the different localities introduce high variability and probably obscure the patterns of the results. Increases or decreases in biodiversity and abundances vary across the surveyed localities without a particular, defined pattern and seems to be more related to particularities of each locality, the supply of certain substrates or the incidence of other local factors, such as sedimentation, proximity to local runoff or disturbance factors. For example, the highest generic diversity was found in La Parguera, where factors such as low

sedimentation (see Sherman et al. 2016) and high heterogeneity of the substrates are present, especially in the "Precipicio" station, where the highest number of genera was found. The spatial heterogeneity is emphasized, because in this place, the largest number of lithic and biogenic substrata were sampled, as evidenced by the laboratory analysis. This spatial heterogeneity and substrate variability offered more microhabitats for the polychaetes. In turn, the majority of the other sampling sites, from the Mona channel to St Croix, with notable differences in sedimentation regimes, prevailing surface currents and neighborhood external factors (Hubbard 1989; Hubbard 1992; Hubbard et al. 1985, Hubbard et al. 1981; Hubbard et al. 1986, Hubbard et al. 1990; GMI 2003; Warne et al. 2005; Baums et al. 2006; Nemeth et al. 2007; Smith et al. 2010; García-Sais et al. 2010; Cherubin and Garabelli 2016), but that have in common the types of substrata present, have a similar number of genera.

Furthermore, sites with low substrate heterogeneity, low sedimentation (GMI 2003; Cherubin and Garabelli 2016) and located in different places of the studied area, such as Vieques or Davis Bay (Hubbard 1989; Capella et al. 2003, García-Sais et al. 2011), for example, have a low number of genera, which seems related to the low heterogeneity of the substrate, as it was appreciated during laboratory work. Likewise, it should be noted that in those locations where the biotic substrates had a significant contribution, the tendency was to find a greater number of genera, when compared with the sites where such substrates were less conspicuous. Apparently, this was so, because these biotic substrates offer more opportunities to find shelter and / or habitat, as in shallower assemblages associated with sponges and algae (Carrera-Parra and Vargas 1996, Antoniadou and Chintiroglou 2006). On the other hand, the tendency was to find the highest number of genera in the UM sites (<60 m), where higher heterogeneity of substrates was found, as it was corroborated during laboratory work.

Abundance.- As mentioned above, the fact that the sample collection was qualitative, with differences in sampling effort and in the amount and type of substrates collected, may affect the results. Regarding the number of individuals found, as observed during the laboratory analysis, this was directly related to the type of substrate to which the organisms were associated. Thus, in those places where sponges were present, the numbers of individuals were, in general, higher. Added to this is the fact that the more abundant genera (*Haplosyllis* and *Syllis*), were constituted

by organisms with smaller size (<5 mm). Due to the presence of organisms of these two genera, localities as Bajo de Sico, La Parguera, Abrir La Sierra, Ponce Ledge or Davis Bay showed the highest numbers of individuals. In contrast, those localities with low substrate heterogeneity, such as Salt River (in St Croix), showed the lowest abundances. Furthermore, the highest abundances were found in the UM habitat (<60 m), where substrate heterogeneity was higher.

CONCLUSIONS AND RECOMMENDATIONS

This study was the first one carried out in the Caribbean basin on the distribution and diversity of polychaetes associated with MCEs, and showed the high hidden biodiversity associated with these ecosystems. 76 genera and 34 families of polychaetes were recorded from 28 sampling localities around MCE of Puerto Rico and US Virgin Islands; these organisms represent forms associated with soft bottoms and hard substrata.

Analyses of selected taxa continue, and further results and descriptions of new species will be published in the near future.

It is recommended to carry out quantitative sampling in the future, considering the different microhabitats present in this type of ecosystems to corroborate and extend the results presented here.

LITERATURE CITED

- Allen MJ (1957) The breeding of polychaetous annelids near Parguera, Puerto Rico. *Biological Bulletin* 113: 49–57.
- Allen MJ (1964) Embryological development of the Syllid, *Autolytus fasciatus* (Bosc) (Class Polychaeta). *Biological Bulletin* 127: 187–205.
- Antoniadou C, Chintiroglou C (2006) Trophic relationships of polychaetes associated with different algal growth forms. *Helgol Mar Res* (2006) 60: 39–49
- Appeldoorn R, Ballantine D, Bejarano I, Carlo M, Nemeth M, Otero E, Pagan F, Ruiz H, Schizas N, Sherman C, Weil E (2015) Mesophotic coral ecosystems under anthropogenic stress: a case study at Ponce, Puerto Rico. *Coral Reefs*. DOI 10.1007/s00338-015-1360-5
- Athanasiadis A, Ballantine DL, Ruiz H (2013) *Hydrolithon abyssophila* sp. nov. (Hydrolithoideae, Corallinales), a Bisporic Coralline from the Insular Shelf Edge of Puerto Rico and the Virgin Islands. *Bot. Mar.* 56:495–505. doi:10.1515/bot-2013-0019.
- Augener H (1906) Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea and on the east coast of the United States, 1877 to 1880, by the U.S. Coast Survey steamer "Blake," Lieut. Commander C.D. Sigsbee, U.S.N., and commander J.R. Bartlett, U.S.N., commanding. 42. Westindische Polychaeten. *Bulletin of the Museum of Comparative Zoology* 43: 91–196.
- Augener H (1922) Über Litorale Polychaeten von Westindien. *Gesellschaft der Naturforschender Freunde zu Berlin* 38–63.
- Augener H (1927) Polychaeten von Curaçao. *Bijdragen tot de Dierkunde* 25: 39–82.
- Bailey-Brock JH (2003) Coral reef polychaetes of Guam and Saipan, Mariana Islands. *Micronesica* 35-36: 200-217.
- Baker EK, Puglise KA, Harris PT (Eds) (2016) Mesophotic coral ecosystems — A lifeboat for coral reefs? The United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal, 98 p.
- Ballantine DL, Ruiz H (2005) Two *Peyssonnelia* Species (Peyssonneliaceae, Rhodophyta) from Puerto Rico Including *Peyssonnelia flavescens* sp. nov. *Phycologia* 44: 328–334. doi:10.2216/0031-8884(2005)44[328:TPSPRF]2.0.CO;2.
- Ballantine DL, Ruiz H (2008) *Botryocladia iridescens* sp. nov. (Rhodymeniaceae, Rhodophyta) from Puerto Rico, Caribbean Sea. *Cryptog. Algal.* 29: 293–302.
- Ballantine DL, Ruiz H (2010) Two New Deep-Water *Peyssonnelia* Species, *Peyssonnelia iridescens* and *Peyssonnelia gigaspora* (Peyssonneliaceae, Rhodophyta) from Puerto Rico, Caribbean Sea. *Phycologia* 49: 537–544. doi:10.2216/09-88.1.

- Ballantine DL, Ruiz H (2011) A New Encrusting Deep-Water Coral Reef Alga, *Peyssonnelia incomposita* (Peyssonneliaceae, Rhodophyta), from Puerto Rico, Caribbean Sea. *Cryptog. Algol.* 32: 19–26. doi:10.7872/crya.v32.iss1.2011.016.
- Baums IB, Paris CB, Chérubin LM (2006) A bio-oceanographic filter to larval dispersal in a reef-building coral. *Limnol. Oceanogr.* 51 (5): 1969–1981.
- Benedict JE (1887). Descriptions of ten species and one new genus of annelids from the dredgings of the U. S. Fish Commission steamer Albatross. *Proceedings of the United States National Museum* 9: 547–553.
- Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral Reefs* 29:309–327. DOI 10.1007/s00338-009-0581-x
- Bongaerts P, Frade PR, Hay KB, Englebert N, Latijnhouwers KRW, Bak RPM, Vermeij MJA, Hoegh-Guldberg O (2015) Deep down on a Caribbean reef: lower mesophotic depths harbor a specialized coral-endosymbiont community. *Scientific Reports* 5: 7652. DOI: 10.1038/srep07652
- Capella J, Alston DE, Cabarcas-Núñez A, Quintero-Fonseca H, Cortés-Maldonado R (2003) Oceanographic considerations for offshore aquaculture on the Puerto Rico - U.S. Virgin Islands Platform. pp. 247-262. In: Bridger C (ed.) *Ocean Open Aquaculture IV* June 17-20, 2001, St. Andrews, New Brunswick, Canada. Mississippi-Alabama Sea Grant Consortium, Ocean Springs, Mississippi, USA.
- Carrera-Parra LF, Vargas JL (1996) Comunidad crítica de esponjas del arrecife de Isla de Enmedio, Veracruz, México. *Rev. Biol. Trop.* 44 (3) / 45 (1): 311-321.
- Chérubin LM, Garavelli L (2016) Eastern Caribbean Circulation and Island Mass Effect on St. Croix, US Virgin Islands: A Mechanism for Relatively Consistent Recruitment Patterns. *PLoS ONE* 11(3): e0150409. doi:10.1371/journal.pone.0150409
- Corgosinho PHC, Schizas NV (2012) *Archeolourinia*, a new genus and species of Louriniidae Monard, 1927 (Copepoda, Harpacticoida) from a Caribbean mesophotic zone. *Journal of Marine Biological Association of the UK.* doi:10.1017/S0025315412001336
- Corgosinho PHC, Alfaro M, Schizas NV (2016). A new species of *Atergopedia* (Copepoda: Harpacticoida: Novocriniidae) from a Caribbean mesophotic reef. *Marine Biodiversity* 46 (4): 841-852.
- Dean HK (2012) A literature review of the Polychaeta of the Caribbean Sea. *Zootaxa* 3596: 1–86.
- de León González JA, Bastida-Zavala JR, Carrera-Parra LF, García-Garza ME, Peña-Rivera A, Salazar-Vallejo SI, Solís-Weiss V (Eds.) (2009) *Poliquetos (Annelida: Polychaeta) de México y América tropical*. Univ. Autónoma de Nuevo León, Monterrey, México, 737 p.

Domínguez-Castanedo N, Granados-Barba A, Solís-Weiss V (2015) The soft-bottom macrofauna of Sacrificios reef lagoon, SW Gulf of Mexico. *Hidrobiológica* 25 (1): 107-119

Ehlers E (1887) Report on the annelids of the dredging expedition of the U. S. coast survey steamer "Blake". *Memoires of the Museum of Comparative Zoology at Harvard College* 15: 1-335.

Erdman DS (1965) Lunar periodicity in the swarming of luminescent worms, *Odontosyllis octodentata* Treadwell (Annelida) off La Oarguera, P.R. *Caribbean Journal of Science* 5: 103-107.

Fauchald K (1977) The Polychaete Worms Definitions and Keys to the Orders, Families and Genera. Natural History Museum of Los Angeles County, Science Series 28.

Fernández PV, Bone D, Rodríguez C (2012) Cryptofaunal polychaetes from oceanic and continental reefs in Venezuela. *Bulletin of Marine Science* 88(2):339-352.
doi.org/10.5343/bms.2010.1081

García-Sais JR, Castro R, Sabater-Clavell J, Carlo M, Esteves R (2007) Characterization of benthic habitats and associated reef communities at Bajo de Sico Seamount, Mona Passage, Puerto Rico. Submitted to the: Caribbean Fishery Management Council. San Juan, Puerto Rico. Final Report Coral Grant 2004 NA04NMS4410345. 91 p.

García-Sais JR, Castro-Gomez R, Sabater-Clavell J, Esteves R, Williams S, Carlo M (2010) Mesophotic benthic habitats and associated marine communities at Abrir La Sierra, Puerto Rico. Final Report Coral Grant 2004 FNA07NMF4410117. 115 p.

García-Sais JR, Sabater-Clavell J, Esteves R, Capella J, Carlo M (2011) Characterization of benthic habitats and associated mesophotic coral reef communities at El Seco, southeast Vieques, Puerto Rico. Final Report. Submitted to the: Caribbean Fishery Management Council, San Juan, Puerto Rico. 96 p.

Giangrande A (1988) Polychaete zonation and its relation to algal distribution down a vertical cliff in the western Mediterranean (Italy): a structural analysis. *Journal of Experimental Marine Biology and Ecology* 120 (3): 263-276.

Gischler E (1997) Cavity dwellers (coelobites) beneath coral rubble in the Florida Reef Tract. *Bulletin of Marine Science* 61(2): 467-484.

Gischler E, Ginsburg RN (1996) Cavity dwellers (coelobites) under coral rubble in Southern Belize Barrier and Atoll Reefs. *Bulletin of Marine Science* 58 (2): 570-589.

Glasby CJ, Hutchings PA, Fauchald K, Paxton H, Rouse GW, Watson Russell G, Wilson RS, 2000. Class Polychaeta. In Beesley, P. L., G. J. B. Ross & C. J. Glasby (eds), *Polychaetes and Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publishing, Melbourne, Australia XII: 1-296.

Glasby CJ, Wei N-W, Gibb KS (2013) Cryptic species of Nereididae (Annelida: Polychaeta) on Australian coral reefs. *Invertebrate Systematics* 27: 245–264. doi.org/10.1071/IS12031

GMI (Geo-Marine, Inc.) (2003) Reef ecosystem baseline assessment survey and monitoring, Vieques Island, Naval Station Roosevelt Roads, Puerto Rico. Prepared for Atlantic Division, Naval Facilities Engineering Command, Norfolk, Virginia. 341 p.

Gobin JF (2010) Free-living marine polychaetes (Annelida) inhabiting hard-bottom substrates in Trinidad and Tobago, West Indies. *Rev. Biol. Trop.* 58 (1): 147-157.

Granados-Barba A, Solís-Weiss V, Tovar-Hernández MA, Ochoa-Rivera V (2003) Distribution and diversity of the Syllidae (Annelida: Polychaeta) from the Mexican Gulf of Mexico and Caribbean. *Hydrobiologia* 496: 337–345

Grassle JF, Maciolek NJ (1992) Deep-sea species richness; regional and local diversity estimates from quantitative bottom-sampling. *Am. Nat.* 139: 313–41.

Guerra-García JM, Chatterjee T, Schizas NV (2015) New genus and new species of Caprellidae (Crustacea: Peracarida: Amphipoda) from mesophotic coral ecosystems of Puerto Rico and St. Croix, Caribbean Sea. *Zootaxa* 4018 (1):080-096 <http://dx.doi.org/10.11646/zootaxa.4018.1.4>

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Theme section on ‘‘Mesophotic Coral Ecosystems: Characterization, Ecology, and Management’’. *Coral Reefs* 29: 247–251. DOI 10.1007/s00338-010-0614-5

Hoagland RA (1919) Polychaetous annelids from Puerto Rico, the Florida Keys, and Bermuda. *Bulletin of the American Museum of Natural History* 16: 571–591.

Hubbard DK (1989) The shelf-edge reefs of Davis and Cane Bays, northwestern St. Croix, U.S.V.I. pp. 167-179. In: *Terrestrial and Marine Geology of St. Croix, US Virgin Islands*. West Indies Lab. Special Publ. No. 8.

Hubbard DK (1992) Hurricane-induced sediment transport in open-shelf tropical systems- An example from St. Croix, U.S. Virgin Islands. *Journal of Sedimentary Petrology* 62:946-960.

Hubbard DK, Burke RB, Gill IP (1985) Accretion in deep shelf-edge reefs, St. Croix, U.S.V.I. pp. 491-527. In: Crevello PD, Harris PM (eds). *Deep Water Carbonates, SEPM Core Workshop* 6.

Hubbard DK, Burke RB, Gill IP (1986) Styles of reef accretion along a steep, shelf-edge reef, St. Croix, U.S. Virgin Islands, *J. Sedim. Petrol.* 56: 848-861.

Hubbard DK, Miller AI, Scaturo D (1990) Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): Applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Petrology* 60: 335-360.

Hubbard DK, Sadd JL, Miller AI, Gill IP, Dill RF (1981) The production, transportation and deposition of carbonate sediments on the insular shelf of St. Croix, U.S. Virgin Islands, Tech Rept. No MG-1, West Indies Laboratory, St. Croix, USVI, 145 p.

Hutchings PA, Peyrot-Clausade M (2002) The distribution and abundance of boring species of polychaetes and sipunculans in coral substrates in French Polynesia. *Journal of Experimental Marine Biology and Ecology* 269: 101–121.

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29: 255–275. DOI 10.1007/s00338-010-0593-6

Laverde-Castillo JJA, Rodríguez H (1987) Lista de los poliquetos registrados para el caribe Colombiano, incluyendo comentarios sobre su zoogeografía. *Anales del Instituto de Investigaciones Marinas de Punta de Betín* 17: 95–112.

Lattig P, Martin D (2011) Sponge-associated *Haplosyllis* (Polychaeta: Syllidae: Syllinae) from the Caribbean Sea, with the description of four new species. *Scientia Marina* 75 (4): 733–758

Locker SD, Armstrong RA, Battista TA, Rooney JJ, Sherman C, Zawada DG (2010) Geomorphology of mesophotic coral ecosystems: current perspectives on morphology, distribution, and mapping strategies. *Coral Reefs* 29: 329–345. DOI 10.1007/s00338-010-0613-6

McIntosh WC (1885) On the Annelida Polychaeta collected by H.M.S. CHALLENGER during the years 1873–1876. *Challenger Reports* 12: 1–554.

Monro CCA (1928) Polychaeta of the families Polynoidae and Acoetidae from the vicinity of the Panama Canal, collected by Dr. C. Crossland and Dr. Th. Mortensen. *Journal of the Linnean Society of London (Zoology)* 36: 553–576.

Nemeth RS, Blondeau J, Herzlieb S, Kadison E (2007) Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environmental Biology of Fishes* 78: 365–381.

Ochoa-Rivera V, Granados-Barba A, Solís-Weiss V (2000) The Polychaete cryptofauna from Cozumel Island, Mexican Caribbean. *Bulletin of Marine Science*, 67(1): 137–146.

Pallas PS (1766) *Miscellanea zoologica. Quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur.* Petrum van Cleef, Hagí Comitum, 224 p.

Perry CT (1998) Macroborers within coral framework at Discovery Bay, north Jamaica: species distribution and abundance, and effects on coral preservation. *Coral Reefs* 17: 277–287.

Pettibone MH (1989) Revision of the Aphroditoid Polychaetes of the Family Acoetidae Kinberg (=Polyodontidae Augener) and reestablishment of the *Acoetes* Audouin and Milne-Edwards, 1832, and *Euarche* Ehlers, 1887. *Smithsonian Contributions to Zoology*, 464, 1–138.

- Pesic V, Chatterjee T, Schizas NV (2008) Marine water mites (Acari: Hydrachnidia: Pontarachnidae) from the Caribbean Sea, with description of one new species. *Cahiers de Biologie Marine* 49 (3): 253-259.
- Pesic V, Chatterjee T, Schizas NV (2012) A new species of *Pontarachna* (Acari, Hydrachnidia, Pontarachnidea) from a mesophotic coral ecosystem off Vieques Island, Puerto Rico, Caribbean Sea. *Zootaxa* 3440: 63-67.
- Pesic V, Chatterjee T, Alfaro M, Schizas NV (2014) A new species of *Litarachna* (Acari, Hydrachnidia, Pontarachnidae) from a Caribbean mesophotic coral ecosystem with notes on a littoral *Litarachna* sp. *Zookeys* 425: 89-97.
- Petrescu I, Chatterjee T, Schizas NV (2012) New genus and new species of Cumaceans (Crustacea: Peracarida: Cumacea) from the mesophotic coral ecosystem of SW Puerto Rico, Caribbean Sea. *Zootaxa* 3476: 55-61.
- Petrescu I, Chatterjee T, Schizas NV (2013) Two new species of the genus *Cumella* (Crustacea: Cumacea: Nannastacidae) associated with mesophotic reefs of Puerto Rico and St. Croix, Caribbean Sea. *Cahiers de Biologie Marine* 54: 257-262.
- Petrescu I, Chatterjee T, NV Schizas NV (2014a) Three new Nannastacidae (Crustacea: Cumacea) species from a Caribbean mesophotic ecosystem. *Zootaxa* 3765 (4): 360-370.
- Petrescu I, Chatterjee T, Schizas NV (2014b) New species of *Cumella* (Crustacea: Cumacea: Nannastacidae) from mesophotic habitats of Mona Island, Puerto Rico, Caribbean Sea. *Cahiers de Biologie Marine* 55(2): 183-189.
- Petrescu, I, Chatterjee T, Schizas NV (2014c) New records of Bodotridae (Crustacea: Cumacea) from Puerto Rico with description of three new species. *Zootaxa* 3873 (5): 526-540
- Petrescu I, Chatterjee T, Schizas NV (2016) A new species of the genus *Campylaspis* (Crustacea: Cumacea) from the mesophotic reefs of St. John, US Virgin Islands, Caribbean Sea. *Caribbean Journal of Science* 49 (1): 17-26. <https://doi.org/10.18475/cjos.v49i1.a3>
- Pyle RL, Boland R, Bolick H, Bowen BW, Bradley CJ, Kane C, Kosaki RK, Langston R, Longenecker K, Montgomery A, Parrish FA, Popp BN, Rooney J, Smith CM, Wagner D, Spalding HL (2016) A comprehensive investigation of mesophotic coral ecosystems in the Hawaiian Archipelago. *PeerJ* 4:e2475; DOI 10.7717/peerj.2475
- Read G, Fauchald K (Ed) (2018) World Polychaeta database. Scolecida. Accessed through: World Register of Marine Species at: <http://marinespecies.org/aphia.php?p=taxdetails&id=183607> on 2018-04-21
- Reuscher MG, Shirley TC (2014) Diversity, distribution, and zoogeography of benthic polychaetes in the Gulf of Mexico. *Mar Biodiv* 44: 519–532

Rivolta A, Rodríguez C, Rodríguez J, Molins L (2015) Criptofauna asociada a colonias muertas de *Orbicella annularis* en el Parque Nacional San Esteban, Venezuela. Bol. Inst. Oceanogr. Venezuela 54 (2): 191-200

G. W. Rouse, F. Pleijel (2001) Polychaetes Oxford University Press; 384 p.

Salazar-Vallejo SI (1996) Lista de especies y bibliografía de Poliquetos (Polychaeta) del Gran Caribe. Anales Instituto Biología Universidad Nacional Autónoma de México Serie Zoología 67 (1): 11-50.

San Martín G, Aguado MT (2014) Family Syllidae. Handbook of Zoology Online. Editor-in-Chief: Schmidt-Rhaesa, Andreas. Universität Osnabrück, 52 p.

Santa-Isabel LM, Leão ZM, Peso-Aguiar MC (2000) Polychaetes from the Guarajuba Coral Reefs, Bahia, Brazil. Bulletin of Marine Science 67(1): 645–653

Schizas NV, Dahms H-U, Kangtia P, Corgosinho PHC, Galindo Estronza A (2015). A new species of Longipedia Claus, 1863 (Copepoda: Harpacticoida: Longipediidae) from Caribbean mesophotic reefs with remarks on the phylogenetic affinities of *Polyarthra*. Marine Biology Research DOI: 10.1080/17451000.2015.1013556

Senna AR, R Sorrentino, T Chatterjee, NV Schizas (2014). A new species of Boca Lowry and Stoddart, 1997 (Amphipoda: Lysianassoidea: Aristiidae) from a mesophotic coral ecosystem off Puerto Rico, Caribbean Sea. Zootaxa 3884 (5): 429-436

Sherman C, Appeldoorn R, Carlo M, Nemeth M, Ruíz H, Bejarano I (2009) Use of Technical Diving to Study Deep Reef Environments in Puerto Rico. pp. 58-65. in: Pollock NW, ed. Diving for Science 2009. Proceedings of the American Academy of Underwater Sciences 28th Symposium, Dauphin Island, AL: AAUS; 2009.

Sherman C, Nemeth M, Ruíz H, Bejarano I, Appeldoorn R, Pagán F, Schärer M, Weil E (2010) Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. Coral Reefs 29: 347–360. DOI 10.1007/s00338-010-0607-4

Sherman C, Appeldoorn R, Ballantine D, Bejarano I, Carlo M, Kesling D, Nemeth M, Pagan F, Ruiz H, Schizas N, Weil E (2013) Exploring the Mesophotic Zone: Diving Operations and Scientific highlights of three Research Cruises across Puerto Rico and US Virgin Islands. pp. 297-312. In: Lang MA, Sayer MDJ (eds), 2013. Proceedings of the 2013 AAUS/ESDP Curaçao Joint International Scientific Diving Symposium, October 24-27, 2013, Curaçao. Dauphin Island, AL: American Academy of Underwater Sciences.

Sherman C, Schmidt W, Appeldoorn R, Hutchinson Y, Ruiz H, Nemeth M, Bejarano I, Cruz Motta JJ, Xu H (2016) Sediment dynamics and their potential influence on insular-slope mesophotic coral ecosystems. Continental Shelf Research 129: 1-9.

Smith TB, Blondeau J, Nemeth RS, Pittman SJ, Calnan JM, Kadison E, Gass J (2010) Benthic structure and cryptic mortality in a Caribbean mesophotic coral reef bank system, the Hind Bank

Marine Conservation District, U.S. Virgin Islands. Coral Reefs 29: 289–308. DOI 10.1007/s00338-009-0575-8

Stoner AW, Acevedo C. (1990) The macroinfaunal community of a tropical estuarine lagoon. *Estuaries* 13: 174–181.

Treadwell AL (1901) Polychaetous annelids of Puerto Rico. *Bull. US Fish Comm.* 20 (2): 181–210.

Treadwell AL (1917) Polychaetous annelids from Florida, Porto Rico, Bermuda, and the Bahamas. *Carnegie Institute of Washington Publication* 251: 255–272.

Treadwell AL (1921) Leodicidae of the West Indian region. *Publications of the Carnegie Institution of Washington* 15: 1–131.

Treadwell AL (1924) *Dasychonopsis arenosa*, a new species of polychaetous annelid from Porto Rico. *American Museum Novitates*, 107, 1–2.

Treadwell AL (1929) New species of polychaetous annelids in the collections of the American Museum of Natural History from Porto Rico, Florida, lower California, and British Somaliland. *American Museum Novitates* 392: 1–13.

Treadwell AL (1931) New species of polychaetous annelids from California, Mexico, Porto Rico, and Jamaica. *American Museum Novitates* 482: 1–7.

Treadwell AL (1934) Reports on the collections obtained by the first Johnson– Smithsonian deep–sea expedition to the Puerto Rican deep. New polychaetous annelids. *Smithsonian Miscellaneous Collections* 91(8): 1–9.

Treadwell AL (1939) Polychaetous Annelids of Porto Rico and Vicinity. *Scientific Survey of Porto Rico and the Virgin Islands* 16 (2): 151–319.

Treadwell AL (1941) Polychaetous annelids from the New England region, Porto Rico and Brazil. *American Museum Novitates*: 1138, 1–4.

Ward T, Hutchings PA (1996) Effects of trace metals on infaunal species composition in polluted intertidal and subtidal marine sediments near a lead smelter, Spencer Gulf, South Australia. *Mar. Ecol. Progr. Ser.* 135: 123–35.

Warne AG, Webb RMT, Larsen MC (2005) Water, Sediment, and Nutrient Discharge Characteristics of Rivers in Puerto Rico, and their Potential Influence on Coral Reefs: U.S. Geological Survey Scientific Investigations Report 2005-5206, 58 p.

WoRMS (2018) Polychaeta. Accessed at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=883> on 2018-04-24

APPENDICES

Appendix 1. GPS Coordinates, depth, depth range, date and comments of sampling sites from MCEs of Puerto Rico (PR) and U.S. Virgin Islands (USVI)

Sampling Site Name	ID #	Latitude°	Longitude°	Depth (m)	>60m	<60m	Date	Comments
SE Slope, La Parguera (PR)	7	17.89808	-66.84813	66	yes	-	6 Apr 2008	Wash from substrate
Weinberg, La Parguera (PR)	7	17.90423	-66.59320	58	-	yes	3 Jun 2008	Wash from algae
Precipicio, La Parguera (PR)	7	17.87516	-67.04882	69	yes	-	3 Oct 2008	Wash from substrate; dead coral debris
Barranco, La Parguera (PR)	7	17.89808	-66.94345	70	yes	-	6 Oct 2008	<i>Agaricia</i> sp. substrate
Black Wall, La Parguera (PR)	7	17.88484	-67.01438	61	yes	-	27 Apr 2009	Wash from substrate
El Hoyo, La Parguera (PR)	7	17.87656	-67.04061	52	-	yes	18 Jun 2009	Wash from substrate
Black Wall, La Parguera (PR)	7	17.88484	-67.01438	52	-	yes	8 Sep 2009	<i>Agaricia</i> sp. substrate
El Hoyo, La Parguera (PR)	7	17.87656	-67.04061	101	yes	-	3 Jun 2010	Wash from substrate
Hole in Wall, La Parguera (PR)	7	17.88476	-67.02192	91	yes	-	8 Jun 2010	Substrate rocks
Ponce Ledge (PR)	8	17.924356	-66.544189	52	-	yes	19 Oct 2010	Wash from substrata, algae debris and sponge
Hole-in-wall, La Parguera (PR)	7	17.88476	-67.02192	47	-	yes	10 Feb 2011	Wash from substrate
Precipicio, La Parguera (PR)	7	17.87516	-67.04882	46	-	yes	13 Apr 2011	Wash from substrate; dead coral debris
SW Mona (PR)	2a	18.05148	-67.90917	71	yes	-	10 Jan 2010	Wash from lithic substrata, algae and corals
SE Mona (PR)	2b	18.04553	-67.87821	62	yes	-	12 Jan 2010	Wash from lithic substrate and corals
Carabinero, Mona (PR)	2c	18.06250	-67.92223	68	yes	-	14 Jan 2010	Wash from lithic substrata, algae and corals
Carabinero, Mona (PR)	2c	18.06250	-67.92223	53	-	yes	15 Jan 2010	Wash from lithic substrate and corals
El Seco, Vieques (west) (PR)	10a	18.12357	-65.20160	52	yes	-	17 Jan 2010	Wash from lithic substrata, algae and corals
SW Vieques (PR)	10b	18.07065	-65.52224	67	-	yes	18 Jan 2010	Wash from lithic substrata, algae and corals

Continuat. Appendix 1.

Cane Bay , St. Croix (USVI)	13b	17.77327	-64.81383	70	yes	-	20 Jan 2010	Wash from lithic substrata, algae and corals
Cane Bay , St. Croix (USVI)	13b	17.77327	-64.81383	55	-	yes	20 Jan 2010	Wash from lithic substrata, algae, sponge and corals
Grammanik Bank - South St Thomas (USVI)	11	18.18200	-64.87860	70	yes	-	21 Jan 2010	Wash from lithic substrata, algae, sponge and corals
W Desecheo (PR)	1	18.38588	-67.49560	73	yes	-	18 Apr 2011	Wash from lithic substrata, algae, sponge and corals
W Desecheo (PR)	1	18.38588	-67.49560	57	-	yes	19 Apr 2011	Wash from lithic substrata, algae, sponge and corals
Bajo de Sico (east)	3a	18.24491	-67.41272	70	yes	-	20 Apr 2011	Wash from lithic substrata, algae, sponge and corals
Grapppler Bank (PR)	9a	17.81460	-65.92705	71	yes	-	23 Apr 2011	Wash from lithic substrate and corals
Grapppler Bank (PR)	9b	17.79458	-65.90825	65	yes	-	24 Apr 2011	Wash from lithic substrate and corals
SE Vieques (PR)	10c	18.09117	-65.33367	55	-	yes	26 Apr 2011	Wash from lithic substrate, sponge and corals
W St. Croix (Armageddon) (USVI)	13a	17.75062	-64.8978	52	-	yes	28 Apr 2011	Wash from lithic substrate and corals
Cane Bay , St. Croix (USVI)	13c	17.77398	-64.81403	83	yes	-	30 Apr 2011	Wash from lithic substrate and sclerosponges
Cane Bay , St. Croix (USVI)	13d	17.77398	-64.81403	60	-	yes	30 Apr 2011	Wash from lithic substrate and corals
North Star, St. Croix (USVI)	13f	17.76985	-64.82173	52	-	yes	1 May 2011	Wash from lithic substrate and corals
North Star, St. Croix (USVI)	13f	17.76985	-64.82173	62	yes	-	2 May 2011	Wash from lithic substrate and corals
Abrir la Sierra (PR)	5a	18.09083	-67.43467	52	-	yes	25 Apr 2012	Wash from lithic substrate and corals
Abrir la Sierra (PR)	5b	18.76197	-67.15696	70	yes	-	26 Apr 2012	Wash from lithic substrate and corals
Bajo de Sico (west) (PR)	3b	18.23075	-67.43177	52	-	yes	28 Apr 2012	Wash from lithic substrate and corals
Tourmaline, (PR)	4	18.17530	-67.32730	54	-	yes	29 Apr 2012	Wash from lithic substrate and sponge
N of Buoy 4 (PR)	6	18.03939	-67.40445	70	yes	-	30 Apr 2012	Wash from lithic substrate, sponge and corals

Continuat. Appendix 1.

Salt River Canyon, St. Croix (USVI)	13g	17.78689	-64.75856	70	yes	-	4 May 2012	Wash from lithic substrate and corals
Lang Bank, St. Croix (USVI)	13h	17.83421	-64.47584	55	-	yes	6 May 2012	Wash from lithic substrate and corals
Davis Bay, St. Croix (USVI)	13e	17.76600	-64.83100	92	yes	-	7 May 2012	Wash from lithic substrate and sponge
E St. John (USVI)	12a	18.22186	-64.67596	54	-	yes	8 May 2012	Wash from lithic substrate and corals
E St. John (USVI)	12b	18.22389	-64.66849	71	yes	-	9 May 2012	Wash from lithic substrate and corals

Continuat. Appendix 2.

Paraonidae																															
<i>Aricidea</i>	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	13	0	13
Pectinariidae																															
<i>Pectinaria</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Phyllodocidae																															
<i>Nereyphylla</i>	4	0	0	0	1	1	0	0	0	4	5	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	20	12	8	
<i>Phyllodoce</i>	2	0	0	0	0	0	0	0	0	0	1	0	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11	10	1
Pilargidae																															
<i>Ancistrosyllis</i>	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
Poecilochaetidae																															
<i>Poecilochaetus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Polynoidae																															
<i>Lepidonotus</i>	1	3	1	2	1	2	1	0	0	1	1	5	0	0	0	0	0	1	0	0	0	0	2	0	0	2	23	8	15		
<i>Harmothoe</i>	0	0	0	0	0	0	0	0	0	0	1	2	0	2	1	0	3	0	0	0	1	0	0	0	0	0	0	10	3	7	
Sabellidae																															
<i>Chone</i>	3	4	7	3	3	1	0	0	0	9	1	5	94	2	0	0	1	0	0	0	0	1	0	0	2	0	0	136	109	27	
<i>Acromegalomma</i>	0	0	0	0	0	0	0	0	0	3	2	0	39	0	0	0	0	0	0	0	0	2	2	0	0	0	48	43	5		
<i>Parasabella</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	3	0		
Serpulidae																															
<i>Hydroides</i>	3	1	5	3	0	1	0	0	0	4	12	0	0	0	0	1	0	0	0	0	0	0	2	1	0	1	34	22	12		
<i>Protula</i>	0	0	0	0	0	0	0	1	0	0	1	1	0	6	0	0	0	0	2	1	1	1	0	0	0	0	14	3	11		
<i>Pseudovermilia</i>	0	0	0	4	0	2	2	7	2	8	18	0	0	0	1	0	7	1	1	5	0	0	0	0	0	2	60	31	29		
<i>Vermiliopsis</i>	11	0	0	0	0	4	0	0	2	5	12	3	17	0	0	0	0	0	0	0	0	0	0	2	0	0	56	46	10		
Sigalionidae																															
<i>Pelogenia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	
<i>Sthenelais</i>	1	2	0	1	0	1	0	0	0	5	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	12	4	8	
Spionidae																															
<i>Paraprionospio</i>	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	7	4	3		
<i>Prionospio</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	3	0	0	9	0	0	0	15	5	10	

Continuat. Appendix 2.

Syllidae																															
<i>Branchiosyllis</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	1		
<i>Haplosyllis</i>	195	154	714	70	129	295	184	0	6	6	255	159	259	151	8	68	376	18	8	62	58	40	23	45	483	8	36	3810	2058	1752	
<i>Plakosyllis</i>	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	5	4	1	
<i>Syllis</i>	43	32	252	53	85	192	138	5	5	7	146	125	134	158	0	32	198	21	3	34	9	5	0	8	125	2	31	1843	952	891	
<i>Trypanosyllis</i>	3	2	2	0	1	0	0	1	0	1	1	2	0	2	0	0	3	0	0	0	1	0	0	2	0	1	0	22	8	14	
<i>Brania</i>	2	1	0	0	0	0	0	1	0	0	1	3	0	0	0	2	0	0	0	1	0	1	0	0	0	0	1	13	5	8	
<i>Exogone</i>	4	1	0	2	2	3	0	1	2	0	1	5	0	3	2	0	0	0	2	2	0	0	1	2	2	0	3	38	20	18	
<i>Salvatoria</i>	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5	3	2	
<i>Sphaerosyllis</i>	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	4	2	2	
<i>Odontosyllis</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	1	
<i>Myrianida</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	
<i>Syllides cf.</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	
<i>Eusyllis</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	2	
<i>Eurinceusyllis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	
<i>Haplosyllides</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	
Terebellidae																															
<i>Streblosoma</i>	0	0	0	0	0	0	0	0	0	0	1	0	7	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9	8	1
Trichobranchidae																															
<i>Terebellides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Sum	342	214	1012	171	231	534	336	56	19	168	648	373	639	365	12	117	603	48	45	160	86	54	38	98	622	15	112	7118	3881	3237	

Appendix 3. Size-groups of polychaete genera found in the MCEs of Puerto Rico and the U.S. Virgin Islands

"XX" indicates that this category had the largest number of individuals of that genus

	Size-groups		
	<5 mm Small-size	5 mm-25 mm Medium-size	25 mm-100 mm Large-size
Ampharetidae			
<i>Amphicteis</i>	-	X	-
Amphinomidae			
<i>Chloeia</i>	-	X	-
<i>Eurythöe</i>	-	X	-
<i>Amphinome</i>	-	X	-
Aphroditidae			
<i>Aphrodita</i>	-	X	-
Capitellidae			
<i>Dasybranchus</i>	-	X	-
<i>Mediomastus</i>	-	X	-
<i>Mastobbranchus</i>	-	X	-
Chrysopetalidae			
<i>Bhawania</i>	-	X	-
<i>Chrysopetalum</i>	-	X	-
<i>Paleanotus</i>	-	X	-
Cirratulidae			
<i>Caulleriella</i>	-	X	-
Dorvilleidae			
<i>Dorvillea</i>	-	X	-
<i>Schistomeringos</i>	-	X	-
Eulepethidae			
<i>Grubeulepis</i>	-	X	-
Eunicidae			
<i>Eunice</i>	-	XX	X
<i>Lysidice</i>	-	X	-
<i>Marphysa</i>	-	XX	X
<i>Leodice</i>	-	X	-
Euphrosinidae			
<i>Euphrosine</i>	X	-	-
Flabelligeridae			
<i>Trophoniella</i>	-	X	-
Glyceridae			
<i>Glycera</i>	-	X	-
<i>Hemipodia</i>	-	X	-

Continut. Appendix 3

Goniadidae			
<i>Goniada</i>	-	X	-
Hesionidae			
<i>Hesione</i>	-	X	-
<i>Gyptis</i>	-	X	-
<i>Oxydromus</i>	-	X	-
Lumbrineridae			
<i>Lumbrineris</i>	-	X	-
Maldanidae			
<i>Axiothella</i>	-	X	-
<i>Clymenella</i>	-	X	-
Nephtyidae			
<i>Nephtys</i>	-	X	-
Nereididae			
<i>Ceratonereis</i>	-	XX	X
<i>Nereis</i>	-	XX	X
<i>Perinereis</i>	-	X	-
<i>Platynereis</i>	-	X	-
<i>Stenonereis</i>	-	X	-
Oeononidae			
<i>Arabella</i>	-	X	-
<i>Oenone</i>	-	X	-
Opheliidae			
<i>Armandia</i>	-	X	-
Oweniidae			
<i>Owenia</i>	-	X	-
Paraonidae			
<i>Aricidea</i>	-	X	-
Pectinariidae			
<i>Pectinaria</i>	-	X	-
Phyllodocidae			
<i>Nereyphylla</i>	-	X	-
<i>Phyllodoce</i>	-	X	-
Pilargidae			
<i>Ancistrosyllis</i>	-	X	-
Poecilochaetidae			
<i>Poecilochaetus</i>	-	X	-
Polynoidae			
<i>Lepidonotus</i>	-	X	-
<i>Harmothoe</i>	-	X	-

Continut. Appendix 3

Sabellidae			
<i>Chone</i>	-	X	-
<i>Acromegalomma</i>	-	X	-
<i>Parasabella</i>	-	X	-
Serpulidae			
<i>Hydroides</i>	-	X	-
<i>Protula</i>	-	X	-
<i>Pseudovermilia</i>	-	X	-
<i>Vermiliopsis</i>	-	X	-
Sigalionidae			
<i>Pelogenia</i>	-	X	-
<i>Sthenelais</i>	-	X	-
Spionidae			
<i>Paraprionospio</i>	-	X	-
<i>Prionospio</i>	-	X	-
Syllidae			
<i>Branchiosyllis</i>	-	X	-
<i>Haplosyllis</i>	XX	X	-
<i>Plakosyllis</i>	X	-	-
<i>Syllis</i>	XX	X	X
<i>Trypanosyllis</i>	-	X	-
<i>Brania</i>	X	-	-
<i>Exogone</i>	X	-	-
<i>Salvatoria</i>	X	-	-
<i>Sphaerosyllis</i>	X	-	-
<i>Odontosyllis</i>	-	X	-
<i>Myrianida</i>	X	-	-
<i>Syllides cf.</i>	X	-	-
<i>Eusyllis</i>	X	-	-
<i>Eurinaceusyllis</i>	X	-	-
<i>Haplosyllides</i>	X	-	-
Terebellidae			
<i>Streblosoma</i>	-	X	-
Trichobranchidae			
<i>Terebellides</i>	-	X	-

Appendix 4. Type of substrata found in the MCEs of Puerto Rico and the U.S. Virgin Islands

X indicates this kind of substrata is present in the sampling site; C = coarse sand; M = medium sand; F = fine sand; DD = algae debris, DD indicates that this category was predominant; S = sclerosponge

Sampling Sites	Substrata					
	Sand	Lithic	Dead coral debris	Algae/algae debris	Sponge	Corals
W Desecheo (PR)	C	-	-	X	X	X
Bajo de Sico (PR)	C, M	-	-	X	X	X
Tourmaline (PR)	C, M	-	-	-	X	-
Abrir La Sierra (PR)	C, M	-	-	-	-	X
N Buoy # 4 (PR)	C	-	-	-	X	X
Mona (PR)	C	-	-	X	-	X
La Parguera (PR)	C, M	X	X	X	X	X
Ponce Ledge (PR)	M	-	-	X, DD	X	-
Grapppler Bank (PR)	C	-	-	-	-	X
Vieques (PR)	C	-	-	X	-	X
S St Thomas (USVI)	C	-	-	X	X	X
E St John (USVI)	C	-	-	-	-	X
W St Croix (USVI)	C	-	-	-	X	X
Cane Bay (USVI)	C	-	-	X	S	X
North Star (USVI)	C	-	-	-	S	X
Davis Bay (USVI)	C	-	-	-	X, S	X
Salt River (USVI)	C, M, F	-	-	-	-	X
Lang Bank (USVI)	C	-	-	-	-	X