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New reports of echinoderms on the Caribbean continental slope of central America

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Abstract

The Caribbean is considered a unique biogeographic region that represents an important hotspot of marine diversity in the Atlantic Ocean. The Caribbean Continental Slope of Central America (CCCA) is a largely unexplored area that exhibits a variety of habitats. Among this unstudied biodiversity, special importance has been given to the benthic communities associated with deep bottoms, a diverse group that plays a major role in the ocean carbon cycling and nutrient flux. Echinoderms are one of the main benthic deep sea taxa, in which Holothuroidea is the globally dominant class. We present the results from the first exploratory fishing survey campaign on the CCCA, done under the regional coordination of OSPESCA (Central America Fisheries and Aquaculture Organization) on board of the R/V Miguel Oliver in January 2011. Data was collected from a total of 96 trawls arranged in 25 transects that started in Panama and finished in Belize. A Lofoten bottom trawling net was dragged for 30 min between 0 to 1500m depth. The major component of the total invertebrate catch was Holothuroidea with a biomass of 593 kg (16.49% of the total) and represented by seven species. The following are new reports for the Caribbean: Bathyplotes natans in Honduras and Guatemala, Bentothuria funebris in Panama, Benthodytes sanguinolenta in Panama, Costa Rica, Nicaragua and Belize; Hansenothuria sp. in Panama, Costa Rica and Honduras. Paroriza pallens extends its distribution to Panama, Costa Rica, Nicaragua and Honduras, Zygothuria *lactea* its reported in Panama. We also present the first records of the crinoid *Neocomatella pulchella* in Honduras, theasteroid Cheiraster (Cheiraster) planusin Panama, and, for Costa Rica (Asteroidea: Doraster constellatus and Echinoidea: *Clypeaster euclastus*). Holothurians are the predominant invertebrate fauna in terms of biomass in the entire region of the CCCA. These findings suggest that CCCA presents a high echinoderm biodiversity and also supports the ecoregional variation theory. We report higher echinoderm biomass (75%) in the Southwestern Caribbean compared to Western Caribbean ecoregion. The information presented in this paper establishes the baseline information of echinoderms depth fauna in the Caribbean of Central America, and opens new opportunities for future research.

Introduction

The Caribbean is considered a unique biogeographic region that represents an important hotspot of marine diversity in the Atlantic Ocean (Tittensor et al. 2010). Remarkable biodiversity thrives on the Caribbean thanks to its complex geological history, starting 130 million years ago and determined specifically by the emergence of the Isthmus of Panama in the Pliocene (3.0–2.8 Ma) (Rivera-Monroy et al. 2004). This process resulted in increased evolutionary divergence and radiation of species living today in variety of ecosystems ranging from shallow coral reefs to deep-shelf habitats and partially isolated basins and trenches (Miloslavich & Klein 2005, Miloslavich *et al.* 2010) which are characterized by its limited documentation and ecological knowledge, especially on the Central American region (Benavides *et al.* 2014).

The Caribbean region is divided into six ecoregions (Spalding *et al.* 2007, p. 580) from which the Caribbean Coast of Central America contains two (Western Caribbean and Southwestern Caribbean). This is a mostly unexplored area that exhibits a total coastline extension of 3800 km and its continental shelf accounts for an area of 125 000 km² (OSPESCA, 2009). The size of the continental shelf is very narrow on the coasts of Belize, Costa Rica and Panama, while broader off the coast of Honduras and Nicaragua. The remarkable variety of habitats along the extent of the coastline makes this area an utterly understudied site, especially on the deep sea biota research (Alvarado *et al.* 2008; Alvarado 2010). According to Hernández-Ávila *et al.* (2018) the diversity of deep-water megafauna such as corals and echinoderms tends to be higher in this area than in other Atlantic regions.

The Echinodermata constitute a major carbonate-producing marine phylum (1969) that dominates many soft and hard bottom ocean ecosystems at all depths (Lebrato *et al.* 2010). In the deep sea environment, echinoderms dominate the benthic community assemblages, with the Holothuroidea class being the most dominant as common dwellers of soft sediments (Billet *et al.* 2001; Lauerman *et al.* 1996; Williams *et al.* 2018). Caribbean echinoderm fauna is composed of 433 species, of which 253 species are recorded for Central America (Alvarado *et al.* 2008, 2013; Coppard & Alvarado 2013). Most of the species that have been reported come from 20 and 200 m deep, with less than 10% of species from waters deeper than 1000 m (Pérez-Ruzafa *et al.* 2013, Solís-Marín *et al.* 2003). Previous studies in this region focused on shallow waters environments with few reports of deep water echinoderms, making the deep waters of this area of particular interest for biodiversity assessments (Alvarado 2011).

According to Shipley *et al.* (2017), the deep sea remains the most data-deficient biome on the planet and despite this fact, is becoming increasingly exposed to extrinsic ecosystem pressures such as commercial fishing (Norse *et al.* 2012) and deep-sea mining (Van Dover 2011). New technologies provide the opportunity to assess the state of knowledge about these unknown ecosystems and to understand their ecology and dynamics with the purpose of setting future sustainable management actions. In order to contribute to the knowledge of echinoderms in the Caribbean Sea, the main objective of this study was to analyze the echinoderm catch of a fishing survey campaign focused on the continental shelf and slope of the CCCA.

Materials and methods

The oceanographic fishing survey campaign was made on board of the R/V Miguel Oliver in 2011, from January 3rd to February 3rd and coordinated by the Central America Fisheries and Aquaculture Organization (OSPESCA). Sampling was done using a Lofoten bottom trawl equipped with a pair of 850 kg oval steel doors (POLY-ICE) each attached to a 48.7m long polyethylene net by a 100 m long warp. The horizontal mouth opening was 31 m wide and 3.5 m of vertical opening when deployed at the bottom, with a cod end of 14.3 m long and a 35mm polyamide mesh size; trawl net was deployed with 27 steel balls of approximately 1000kg and 20 floaters at its mouth opening. The ship's side-scan sonar (EM 302) was used to locate a suitable area of relatively level, unobstructed bottom prior to each trawl.

Ninety-sixbottom diurnal trawls of 30 minutes were made at speeds of \sim 3–3.5 knots. Trawling time was monitored using ITI-SCANMAR net sensors. A total of 25 transects were done perpendicular to coastline and sampling depth range varied from 0 to 1500 m, and it was made over the continental shelf and slope of Central America's Caribbean Coast, off south Panamá through the north of Belize (Figure 1). Transects were grouped in four main sampling sections; 1) transects 1–6 (Panama), 2) 7–13 (Costa Rica and Nicaragua), 3) 14–18 (Honduras) and 4) transects 19 to 25 (Honduras, Guatemala, Belize). Echinoderms were analyzed by total count of specimens, total weight per taxonomic classification and photographs of best specimens were taken with digital camera and a scale.

Taxonomic identification of the specimens was based on Clark and Downey (1992), Hansen (1975) and Solís-Marín (2003). Total Biomass was calculated for each sampling section and was compared to Total Echinoderm Biomass. Also we calculated the Total Catch Biomass separating between Fishes, Echinoderms and other taxa and we calculated the Total Echinoderm Biomass Catch (whole weight, including viscera and

gonads) discerning between taxonomic classes. Geographical and distribution reports were made for each country based on the extensive echinoderm review for Latin America by Alvarado and Solís-Marín (2013) in conjuction with online consultation of the World Register of Marine Species website (WoRMS) (Boxshall *et al.* 2014).



FIGURE 1. Study area showing the location of the 25 sampling transects divided in four major sections. Total biomass per section and detailed echinoderm biomass is shown on the upper right panel.



FIGURE 2. Echinoderm specimens aboard the R/V Miguel Oliver in 2011. Dorsal (1) and ventral (2) view are shown except for E,H and J. The scale is set individually for each panel. The species names are indicated in Table 1. *Neocomatella pulchella* picture is not displayed because of low quality documentation.

Results

A total of 3599 kg of biomass were collected in the four sampling sections (Fig. 1). Section 1 and 2 showed the highest echinoderm biomass values (277 kg and 172 kg, respectively). Section 1 and 3 had the highest echinoderm relative biomass (27% and 18%) of the total catch. Section 4 showed the lowest biomass values of echinoderm catch with 23 kg in eight transects. In a total of 96 effective trawls, we identified 11 echinoderm species grouped in nine families. All taxonomic information and depth range are detailed on Figure 2 and Table 1. We report new species records for Central American countries: one for Belize and Guatemala, two for Nicaragua, five for Honduras and six for Costa Rica and Panama each. The whole catch of echinoderms was of 596 kg comprising the five echinoderm classes (Asteroidea, Crinoidea, Echinoidea, Holothuroidea and Ophiuroidea) although the ophiuroids were practically absent in the whole sampling range except for just one specimen found at sampling section 1 (transect 2-station number 6) in Panama that could not be identified because of its damaged condition. We found one specimen that was identified as member of family Brisingidae in sampling station six however it could not be identified because of deteriorated condition. The southernmost part (section 1 and 2) showed 75% of the echinoderm biomass, being notably higher compared to northern region. Holothuroids accounted the 99% percent of the total echinoderm biomass and echinoderms were more abundant at south (section 1) and decreased towards north direction.

TABLE 1. New reports of echinoderms in six Central American Caribbean coast countries, BEL: Belize, GUA: Guatemala, HON: Honduras, NIC: Nicaragua, CRC: Costa Rica, PAN: Panama. *: Depth range extension. Species name in bold: new report on the Caribbean. X: new report in country. P: past report in the Caribbean.

Species	Depth (m)	Country						Figure
		BEL	GUA	HON	NIC	CRC	PAN	-
Class Crinoidea								
Family Comasteridae								
Neocomatella pulchella (Pourtalès,1878)	1095*			Х	Р		Р	
Class Asteroidea								
Family Benthopectinidae								
Cheiraster (Cheiraster) planus Verrill, 1915	485-596			Р			Х	А
Family Zorasteridae								
Doraster constellatus Downey, 1970	579-761			Р		Х	Р	В
Class Echinoidea								
Family Clypeasteridae								
Clypeaster euclastus (Clark, 1941)	1050*			Р		Х		С
Class Holothuroidea								
Family Deimatidae								
Deima validum validum Théel, 1879	1017, 1300			Х		Х		D
Family Gephyrothuriidae								
Paroriza pallens (Koehler, 1896)	385-1481			Х	Х	Х	Х	Е
Family Mesothuriidae								
Zygothuria lactea (Théel, 1886)	704, 1292						Х	F
Family Psychropotidae								
Benthodytes sanguinolenta Théel, 1882	385-1481	Х		Р	Х	Х	Х	G
Family Synallactidae								
Bathyplotes natans (M. Sars, 1868)	520, 1308, 496		Х	Х				Н
Benthothuria funebris Perrier, 1898	1225						Х	Ι
Hansenothuria Miller & Pawson, 1989	742-1481			Х		Х	Х	J

Discussion

Since the middle of past century, ocean bottom became the main frontier in the scientific agenda of exploration of the planet (Heezen 1956). This study contributes to deep sea exploration in terms of increasing the knowledge of echinoderms distribution in the relatively unknown deep sea waters of the Caribbean. Most recently, ecoregional variation on the Caribbean was proved from data collected from 1966 to 1971 (Hernández-Avila *et al.* 2018); although only asteroids and echinoids were accounted and holothuroids were excluded. the results of this novel study match our findings and support the hypothesis of variation of deepwater Caribbean benthic assemblages according to ecoregions (Spalding *et al.* 2007). Regarding this, our study area includes two of them Western Caribbean and Southwestern Caribbean and we demonstrate worth standing differences; sixty percent of the new reports are for the southernmost region of the sampling range (six reports for PAN and CRC, each) indicating that the deep waters of the Southwestern Caribbean ecoregion are sub-explored and possibly the most rich in echinoderm biodiversity, as previously reported for the upper depth levels by Alvarado (2011).

Ninety nine percent of echinoderm catch (590 kg) belonged to the Holothuroidea class, in contrast to ophiuroids with only one deteriorated specimen collected. We note the possibility that mesh size and body fragility were the reason for the absence of ophiuroids in the sampling. On the other hand, holothuroids are characterized by having a long gut and heavy gonads (Vergara & Rodriguez, 2015), which could explain the weight values obtained, in conjunction with the number of individuals collected. Out of these samples, the species *Benthodytes sanguinolenta* represented 61% (361 kg); a species within the Elasipodid group.

Our results agree with those of Tyler *et al.* (1988) where they concluded that deep-sea echinoderms, especially elasipodid holothurians, dominate the deep-sea invertebrate megafaunal biomass in the North Atlantic and many other areas of the world's oceans. Most elasipodids have epibenthic habits and feed on superficial sediment as they roam across the seabed. Because of the high biomass found in our sampling at section 1 and 2, we suggest that these regions, continental rise and even deeper associated plains such as Clark Basin and Colombian Abyssal Plain may be rich in organic matter as per Sibuet *et al.* (1982) have suggested that epibenthic holothurians are selective deposit feeders taking the detrital particles richest in bioavailable compounds.

One of the most remarkable results obtained was greater echinoderm biomass at the south of the sampling region decreasing towards north with holothuroids accounting for the higher biomass. We propose that these results could be explained by the bathymetry and composition of the seafloor at these regions, mainly determined by the width size of the continental shelf which is narrower at south and wider at north (Jackson & Budd, 1996). This feature of the continental margin causes that terrigenous inputs such as sediments and vegetable material can reach the deep seafloor more easily in the form of turbidity currents. This type of deep sea influx was addressed by Heezen *et al.*(1955) who indicated that near shore estuarine or terrestrial material can be easily distributed through turbidity currents from near shore to the deep seafloor, especially at the mouths of rivers. Sediment distribution is driven by gravity flows that sometimes form submarine landslides, these types of events transfer massive quantities of sediment and Particulate Organic Carbon (POC) down to the deep seafloor (Meiburg & Kneller 2010)

Heezen (1956) mentioned that turbidity currents are associated with the origin of deep sea submarine canyons where the density flows erode the seafloor and form these scars along the ocean bottom. When a river is linked directly to a submarine canyon, transport of riverine sediment down to the abyss is particularly rapid (Sen *et al.* 2017). Both previous facts are particularly true in our sampling sections 1 and 2, categorized as a runoff region that is influenced by the presence of Magdalena and Sixaola rivers (Chollett *et al.* 2012), and where we detected several submarine canyons and gullies trough the sampling transects. At the north of sampling study site (section 3 and 4) there is one of the largest watershed networks of the Caribbean, with numerous rivers carrying terrigenous inputs out to the coastal ocean region (Sheng *et al.* 2007). In contrast to the southernmost region, a major feature that stands out is the Mesoamerican Barrier Reef, over this system the sediments and vegetable inputs from mainland are attenuated before reaching to the continental slope, so terrigenous influx to open sea is not as strong as in south region (Chérubin *et al.* 2008).Based on the previous facts, we conclude that higher echinoderm biomass is associated to regions influenced by turbidity currents and submarine canyons. This can be explained by the fact that terrigenous inputs represent a major food source for these bottom dwelling organisms (Sen *et al.* 2017).

It is important to consider feeding habitats of echinoderms and its association with the environmental

conditions, particularly the contribution of mainland generated organic matter to its nutrition and diet. Many of these echinoderms feed on the top few mm of the seabed, ingesting freshly deposited phytodetritus and organic matter (OM) that is deposited mainly by turbidity currents (Massin 1982); because of this, echinoderms play a major role in the benthic compartment of the global carbon cycle (McClintock 1994), holothurians in particular could represent the major contribution of organic carbon fixation among the group. Based on these facts and the results obtained, we hypothesize that the CCCA deep sea fauna plays a major role in the regional carbon cycle. We highlight the importance of studying these unexplored sites not only for its bio-diversity but also for the importance to understand underlying deep sea biochemical processes (Lebrato *et al.* 2010; Smith *et al.* 2008).

The present work contributes to knowledge about echinoderm diversity and distribution in the Caribbean by reporting five new species on this region and expanding the distribution range of six species. Moreover, we contribute to the deep sea assessment by reporting high biomass values of holothurians associated to deep waters in the Southwestern Caribbean, one of the most unexplored ecoregions in terms of deep sea diversity. We propose that abundance of echinoderm biomass is related to the organic matter influx and bottom ocean topography, and relate our results with those reported in the Northeastern Atlantic (Billet *et al.* 2010). As we expected, the new species reported for the Caribbean were already reported for the Gulf of Mexico (Pawson *et al.* 2009), reinforcing deep ocean connectivity between these two regions (Young *et al.* 2012). Future molecular taxonomy studies are necessary to be carried in this region to verify for connectivity patterns and genetic structure, in order to assess the underlying diversity of deep sea organisms in the CCCA.

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References

Alvarado, J.J. & Solís-Marín, F.A. (2013) Echinoderm research and diversity in Latin America. In: Alvarado, J.J. & Solís-Marín, F.A. (Eds.), Echinoderm Research and Diversity in Latin America. Springer, Berlin, Heidelberg, NY, pp. 1–9. https://doi.org/10.1007/978-3-642-20051-9

Alvarado, J.J. (2011) Echinoderm Diversity in the Caribbean Sea. *Marine Biodiversity*, 41, 261–285. https://doi.org/10.1007/s12526-010-0053-0

Alvarado, J.J., Baraza, E. & Sancho-Mejía, T. (2013) Central America Echinoderms: diversity, ecology and future perspectives. *In:* Alvarado, J.J. & Solís-Marín, F.A. (Eds.), *Echinoderm Research and Diversity in Latin America*. Springer Berlin Heidelberg, NY, pp. 67–106.

https://doi.org/10.1007/978-3-642-20051-9_3

- Alvarado, J.J., Solis-Marin, F.A. & Ahearn, C. (2008) Equinodermos (Echinodermata) del Caribe Centroamericano. *Revista de Biología Tropical*, 56 (3), 37–55.
- Benavides, R., Brenes, C.L. & Márquez, A. (2014) Population analysis of demersal and deep water chondrichthyes (Vertebrata: Chondrichthyes) along the Caribbean coast of Central America based on a fishery survey using bottom trawling. *Revista Ciencias Marinas y Costeras*, 6, 9–27. https://doi.org/10.15359/revmar.6.1
- Boxshall, G.A., Mees, J., Costello, M.J., Hernandez, F., Gofas, S., Hoeksema, B.W. & Read, G.B. (2014) World register of marine species. Available from: http://www.marinespecies.org (accessed 20 September 2018)
- Chérubin, L.M., Kuchinke, C.P. & Paris, C.B. (2008) Ocean circulation and terrestrial runoff dynamics in the Mesoamerican region from spectral optimization of SeaWiFS data and a high resolution simulation. *Coral Reefs*, 27 (3), 503–519. https://doi.org/10.1007/s00338-007-0348-1
- Chollett, I., Mumby, P.J., Müller-Karger, F.E. & Hu, C. (2012) Physical environments of the Caribbean Sea. *Limnology and Oceanography*, 57 (4), 1233–1244.

https://doi.org/10.4319/lo.2012.57.4.1233

Clark, A.M. & Downey, M.E. (1992) Starfishes of the Atlantic. Natural History Museum Publications. Identification Guide 3.

Chapman and Hall, London, U.K, 779 pp.

- Coppard, S. & Alvarado, J.J. (2013) Echinoderm diversity in Panama: 144 years of research across the isthmus. *In:* Alvarado, J.J. & Solís-Marín, F.A. (Eds.), *Echinoderm Research and Diversity in Latin America. Echinoderm Research and Diversity in Latin America.* Springer Berlin Heidelberg, NY, USA, pp. 107–144. https://doi.org/10.1007/978-3-642-20051-9 4
- Hansen, B. (1975) Systematics and biology of the deep-sea holothurians. Part. 1. Elasipoda. Scientific Results of the Danish Deep-Sea Expedition Round the World 1950–52. *Galathea Report*, 13, 1–262.
- Heezen, B.C. (1956) The origin of submarine canyons. *Scientific American*, 195 (2), 36–41. https://doi.org/10.1038/scientificamerican0856-36
- Heezen, B.C., Ewing, M. & Menzies, R.J. (1955) The influence of submarine turbidity currents on abyssal productivity. *Oikos*, 6 (2), 170–182.

https://doi.org/10.2307/3564853

- Hernández-Ávila, I., Guerra-Castro, E., Bracho, C., Rada, M., Ocaña, F.A. & Pech, D. (2018) Variation in species diversity of deep-water megafauna assemblages in the Caribbean across depth and ecoregions. *PloS one*, 13 (8), e0201269. https://doi.org/10.1371/journal.pone.0201269
- Jackson, J.B.C. & Budd, A.F. (1996) Evolution and Environment: Introduction and Overview. *In:* Jackson, J.B., Budd, A.F. & Coates, A.G. (Eds.), *Evolution and environment in tropical America*. University of Chicago Press, Chicago, 26 pp.
- Lauerman, L.M.L., Kaufmann, R.S. & Smith Jr, K.L. (1996) Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. *Deep Sea Research Part I: Oceanographic Research Papers*, 43 (7), 1075–1103.

https://doi.org/10.1016/0967-0637(96)00045-3

Lebrato, M., Iglesias-Rodríguez, D., Feely, R.A., Greeley, D., Jones, D.O., Suarez-Bosche, N. & Alker, B. (2010) Global contribution of echinoderms to the marine carbon cycle: CaCO3 budget and benthic compartments. *Ecological Monographs*, 80 (3), 441–467.

https://doi.org/10.1890/09-0553.1

Massin, C. (1982) Food and feeding mechanisms: Holothuroidea. Echinoderm nutrition, 43-55.

McClintock, J.B. (1994) Trophic biology of Antarctic shallow water echinoderms. *Marine Ecology Progress Series*, 111, 191–202.

https://doi.org/10.3354/meps111191

- Meiburg, Ev. & Kneller, B. (2010) Turbidity currents and their deposits. *Annual Review of Fluid Mechanics*, 42, 135–156. https://doi.org/10.1146/annurev-fluid-121108–145618
- Miloslavich, P. & Klein, E. (2005) Linking marine biodiversity research and Conservation in the Caribbean. *In:* Miloslavich, P.
 & Klein, E. (Eds.), *Caribbean Marine Biodiversity: The Known and the Unknow*. DEStech Publ, Lancaster, Pennsylvannia, pp. 1–25.
- Miloslavich, P., Díaz, J.M., Klein, E., Alvarado, J.J., Díaz, C., Gobin, J., Escobar-Briones, E., Cruz-Motta, J.J., Weil, E., Cortés, J., Bastidas, A.C., Robertson, R., Zapata, F., Martín, A., Castillo, J., Kazandjian, A. & Ortiz, M. (2010) Marine biodiversity in the Caribbean: regional estimates and distribution patterns. *PloS one*, 5 (8), e11916. https://doi.org/10.1371/journal.pone.0011916
- Norse, E.A., Brooke, S., Cheung, W.W., Clark, M.R., Ekeland, I. & Froese, R. (2012) Sustainability of deep-sea fisheries. *Marine Policy*, 36, 307–320.

https://doi.org/10.1016/j.marpol.2011.06.008

- OSPESCA, Organización del sector pesquero y acuícola de Centroamérica (2009) Propuesta de investigaciones pesqueras de aguas profundas en ambas costas de Centroamérica. *Unidad Regional de Pesca y Acuicultura*. OSPESCA San Salvador, El Salvador: OSPESCA.
- Pawson, D.L., Vance, D.J., Messing, C.G., Solís-Marin, F.A. & Mah, C.L. (2009) Echinodermata of the Gulf of Mexico. Gulf of Mexico: origin, waters, and biota, 1, 1177–1204.
- Pérez-Ruzafa, A., Alvarado, J.J., Solis-Marín, F.A., Hernández, J.C., Morata, A., Marcos, C. & Abreu-Pérez, M. (2013) Latin America echinoderm biodiversity and biogeography: patterns and affinities. *In*: Alvarado, J.J. & Solís-Marín, F.A. (Eds.), *Echinoderm Research and Diversity in Latin America. Springer Berlin Heidelberg*. NY, USA, pp. 511–542.
- Rivera-Monroy, V.H., Twilley, R.R., Bone, D., Childers, D.L., Coronado-Molina, R.C., Feller, I.C., Herrera-Silveira, J., Jaffe, R., Mancera, E., Rejmankova, E., Salisbury, J.E. & Weil, E. (2004) A conceptual framework to develop long-term ecological research and management objectives in the wider Caribbean region. *BioScience*, 54, 843–856. https://doi.org/10.1641/0006-3568(2004)054[0843:ACFTDL]2.0.CO;2
- Sen, A., Dennielou, B., Tourolle, J., Arnaubec, A., Rabouille, C. & Olu, K. (2017) Fauna and habitat types driven by turbidity currents in the lobe complex of the Congo deep-sea fan. *Deep Sea Research Part II: Topical Studies in Oceanography*, 142, 167–179.

https://doi.org/10.1016/j.dsr2.2017.05.009

- Sheng, J., Wang, L., Andréfouët, S., Hu. C., Hatcher, B.G., Muller-Karger, F.E., Kjerfe, B., Heymans, W.D. & Yang, B. (2007) Upper ocean response of the Mesoamerican barrier reef system to hurricane Mitch and coastal freshwater inputs: a study using SeaWiFS ocean color data and a nested-grid ocean circulation model. *Journal Geophysiscs Research*, 112, C07016. https://doi.org/10.1029/2006JC003900
- Shipley, O.N., Brooks, E.J., Madigan, D.J., Sweeting, C.J. & Grubbs, R.D. (2017) Stable isotope analysis in deep-sea chondrichthyans: recent challenges, ecological insights, and future directions. *Reviews in Fish Biology and Fisheries*, 27 (3), 481–497.

https://doi.org/10.1007/s11160-017-9466-1

- Sibuet, M., Khripounoff, A., Deming, J., Colwell, R. & Dinet, A. (1982) Modification of the gut contents in the digestive tract of abyssal holothurians. *In*: Lawrence, J.M. (Ed.), *Echinoderms:Proceedings of the International Echinoderm Conference*. *Tampa Bay.* Rotterdam, Balkema, pp. 421–428.
- Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K. & Arbizu, P.M. (2008) Abyssal food limitation, ecosystem structure and climate change. *Trends in Ecology & Evolution*, 23 (9), 518–528. https://doi.org/10.1016/j.tree.2008.05.002
- Solís-Marín, F.A. (2003) *Phylogeny, Systematics and Biology of the Holothurian Family Synallactidae*. PhD thesis, University of Southampton, National Oceanography Centre (NOC), 361 pp.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 5 (7), 573–583. https://doi.org/10.1641/B570707
- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466 (7310), 1098. https://doi.org/10.1038/nature09329
- Tyler, P.A. & Billett, D.S.M. (1988) The reproductive ecology of elasipodid holothurians from the NE Atlantic. *Biological Oceanography*, 5 (4), 273–296.
- Van Dover, C.L. (2011) Tighten regulations on deep-sea mining. *Nature*, 470, 31–33. https://doi.org/10.1038/470031a
- Vergara, W. & Rodríguez, A. (2015) Histología del tubo digestivo de tres especies de pepino de mar. *Revista Biología Tropical*, 63 (4), 1021–1033.

https://doi.org/10.15517/rbt.v63i4.16887

Williams, A., Althaus, F., MacIntosh, H., Loo, M., Gowlett-Holmes, K., Tanner, J.E., Shirley J.S. & Green, M. (2018) Characterizing the invertebrate megafaunal assemblages of a deep-sea (200–3000 m) frontier region for oil and gas exploration: the Great Australian Bight, Australia. *Deep Sea ResearchPart II: Topical Studies in Oceanography*, 157–158, 78–91.

https://doi.org/10.1016/j.dsr2.2018.07.015

Young, C.M., He, R., Emlet, R.B., Li, Y., Qian, H., Arellano, S.M., Gaest, A.V., Bennett, K.C., Wolf, M., Smart, T.I. & Rice, M.E. (2012) Dispersal of Deep-Sea Larvae from the Intra-American Seas: Simulations of Trajectories using Ocean Models, *Integrative and Comparative Biology*, 52 (4), 483–496. https://doi.org/10.1093/icb/ics090