UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO

CENTRO DE CIÊNCIAS HUMANAS E NATURAIS

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

Macrofauna bentônica profunda em cânions submarinos das Bacias do Espírito Santo e Campos

Rodrigo Novo Gama

Vitória, ES
Abril, 2018

UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO

CENTRO DE CIÊNCIAS HUMANAS E NATURAIS

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

Macrofauna bentônica profunda em cânions submarinos das Bacias do Espírito Santo e Campos

Rodrigo Novo Gama

Orientador (a): Dr. Angelo Fraga Bernardino

Dissertação submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para obtenção do grau de Mestre em Biologia Animal

Vitória, ES
Abril, 2018

AGRADECIMENTOS

"A natureza é a manifestação divina como Mãe,
pródiga em beleza, doçura, bondade e ternura.
As flores perfumadas, o riso das águas que fluem,
a fecundidade da terra, o desenvolvimento das plantas e
dos seres, o amor de toda criatura para com seus filhotes,
o bosque, a montanha, o céu azul, a areia branca, o mar
refulgente; vendo isto, uma profunda ternura surge
em nosso interior."

Paramahansa Yogananda

SUMÁRIO

LISTA DE TABELAS

LISTA DE FIGURAS

RESUMO

Cânions submarinos (cânions) são ecossistemas heterogêneos que criam cenários diferenciados através de margens continentais. Cânions são globalmente reconhecidos por abrigar uma grande diversidade e biomassa de espécies e, portanto, possuem importância ecológica para outros ecossistemas das margens continentais. A dinâmica oceanográfica e o aumento da profundidade naturalmente moldam a composição da biota presente dentro deles, por meio da complexa topografia de cânions, que compõe uma variedade de habitats e ecossistemas com específicas características bióticas e abióticas, agindo como rotas preferenciais para o transporte e assimilação de partículas de origem de ambientes com maior indice energético e de produtividade até o mais estável profundo assoalho oceânico. No presente trabalho, nós amostramos e comparamos a macrofauna bentônica dos cânions Watu Norte e Doce na bacia do Espírito Santo e os cânions Almirante Câmara e Grussaí da bacia de Campos. Testamos diferenças entre densidade, composição e diversidade das comunidades de macrofauna ao longo da batimetria (todos os cânions, de 150 a 1300 metros) e entre cânions (gradiente latitudinal dentro de cada faixa de profundidade), e comparamos os efeitos dos cânions ao longo da margem continental comparado a taludes adjacentes. O "efeito cânion" foi observado como um aumento na densidade e distinta composição de organismos da macrofauna dos cânions Watu Norte, Doce, Almirante Câmara e seus taludes adjacentes. As diferenças foram, em sua maioria, relacionadas à quebra da plataforma continental e ao talude superior (150 – 400m), provavelmente como uma consequência de maior entrada de matéria orgânica e a heterogeneidade de sedimento (e.g. distúrbio) dentro dos cânions nessas profundidades. Os cânions também se diferenciaram entre eles mesmos na quebra da plataforma e talude superior, apresentando diferenças na densidade e estrutura das assembleias de macrofauna. Houve uma clara influência do aumento da profundidade em todos os cânions e taludes adjacentes, negativamente relacionado com a heterogeneidade e abundância da macrofauna bentônica. De forma geral, poliquetas e crustáceos peracáridos dominaram a composição da macrofauna na maioria das estações amostradas, com exceção de uma dominância de moluscos no talude superior (400m) do cânion Almirante Câmara e seu talude adjacente H. Pesquisas futuras são necessárias para o melhor entendimento da heterogeneidade ecológica dos cânions e a relação presente entre os processos biológicos e físicos dos mesmos.

Palavras-chave: Mar profundo; cânions submarinos; macrofauna bentônica; ecologia; Atlântico sudoeste

Deep-sea benthic macrofaunal assemblages of submarine canyons from Espirito Santo and Campos basins, Eastern Brazilian margin

Abstract

Submarine canyons (canyons) are heterogeneous ecosystems that create distinct landscapes across continental margins. Canyons are globally recognized to host a high diversity and biomass of species and therefore have ecological importance to other continental margin ecosystems. The oceanographic dynamics and the increasing depth naturally shape the biota composition present within them, throughout a complex topography of canyons, which compounds a variability of habitats and ecosystems with specific biotic and abiotic features and act as preferential routes for the transportation and assimilation from greater energy and productivity sites particles to the most stable deep oceanic seabed. In the present work, we sampled and compared the benthic macrofauna from the Watu Norte and Doce canyons in the Espirito Santo basin canyons with canyons Almirante Camara and Grussai from Campos basin. We tested differences between density, composition and diversity of macrofaunal communities along the bathymetry (all canyons, 150 to 1300 meters) and between canyons (latitudinal gradient within each depth range), and compared the effects of canyons along the continental margin compared to adjacent slopes. The "canyon effect" was observed as an increase in density and distinct composition of macrofaunal organisms from the canyons Watu Norte, Doce, Almirante Camara and their adjacent slopes. The differences were mostly related to the shelf break and upper slope (150 – 400m), likely as a consequence of higher organic input and sediment heterogeneity (i.e. disturbance) within canyons at those depths. Canyons also differentiate among themselves at the shelf break and upper slope, presenting differences in density and structure of the macrofaunal assemblages. There was a clear influence of the increasing depth for all canyons and adjacent slopes, negatively related to the heterogeneity and abundance of benthic macrofauna. Overall, polychaetes and peracarid crustaceans dominated the macrofaunal composition in most sample stations, with exception of a greater dominance of molluscs at the upper slope (400m) of Almirante Camara canyon and its adjacent slope H. Further research is necessary for better understanding of the canyons ecological heterogeneity and relation between their physical and biological processes.

Keywords: Deep-sea; submarine canyons, benthic macrofauna, ecology, SW Atlantic

1. Introduction

The increasing exploitation and depletion of land resources led to an increasing attention towards the deep-sea ocean (Ramirez-Llodra et al., 2011). The increased anthropogenic exploration led to globally depleted stocks of fisheries, increases in waste discards, crescent interest in mining activities and exploration oil and gas reserves, which have resulted in extensive environmental impacts to coastal and oceanic ecosystems (Davies et al., 2007; Almada and Bernardino, 2017; Gomes et al., 2017; Griffiths et al., 2017). Hence, there is a necessity to study and identify key marine ecosystems with important ecological roles, in terms of their associated biodiversity and their essential ecological services provided, such as climate regulation, food resources, biogenic cycling and pollutant detoxification (Vetter, 1994; Danovaro et al., 2008; Fernandez-Arcaya et al., 2017) .

Deep sea ecosystems represent more than 65% of the earth surface and are the largest Earth's existing biome. Yet, the knowledge of the biodiversity shaping deep-sea processes still remains scarce (E. Ramirez-Llodra et al., 2010; Romano et al., 2017). The deep-sea contributes to ecological processes that have importance to global nutrient cycling, carbon sequestration and storage, biogenesis, and promoting resources for humanity in many forms such as fisheries, oil and gas operation practices (Fernandez-Arcaya et al., 2017). Within the deep-sea, continental margins comprise about 20% of the total area of the oceans and normally are regions with a strong depth gradient, varying from 150 to more than 3000 meters, and are ecosystems of great importance and abundant resources (Levin and Sibuet, 2012). The deep sea and continental margins are known for their vast heterogeneity in terms of topography, including different mega-habitats such as continental slopes, banks, seamounts, as also cold-seeps and hydrothermal vents. Submarine canyons are among those habitats, and retain their particular biotic and abiotic features (Quattrini et al., 2015; Robert et al., 2015; Fernandez-Arcaya et al., 2017). They are major geomorphic seabed structures that cut the continental shelves and slopes (Lastras et al., 2007; Ingels et al., 2009; Harris and Whiteway, 2011). Submarine canyons are recurrent and abundant, with approximately 9000 great submarine canyons cover the world's continental slopes, encompassing about 25.000km of extent dimension (Harris et al., 2014; Huang et al., 2014). Canyons spread also through oceanic islands, and make connection between shallower waters (i.e. continental shelves) and the deep seabed throughout their structure variety (De Leo et al., 2010).

From the beginning, the remarkable curiosity and interest about the development, incidence and distribution of canyons was motivated by a necessity to assist naval submarine operations, by placing pipelines and cables around the seafloor; as well for the understanding of the physical/geological evolution of continental margins and to comprehend the processes that take place in canyons oceanography and ecology (Piper and Morrison, 1999; Harris and Whiteway, 2011). The origin of submarine canyons at continental margins are linked with two key hypotheses: 1) seaward excavation/formation of submarine canyons across the continental shelf and slope through erosion and turbidity flows of rivers and erosion below shallow-water

conditions (e.g. sea-level lowstands); 2) slumps and failures in the continental slope, summed with upward (retrogressive) canyon erosion that happen at the depth gradient by processes such as earthquakes, tectonism and oversteepening (Puga-Bernabéu et al., 2011; Harris and Whiteway, 2011; Puig et al., 2014; de Almeida et al., 2015). Those mechanisms of complex genesis can dictate the topography of the canyons, but to understand the relation between canyons variability and their morphology with their origin is often a tough task (Soh and Tokuyama, 2002; Chiang and Yu, 2006). However, apparently canyons that incise the continental shelf and its linked regions are known to be related to the first hypothesis (river erosion and seaward entrenchment) (Pratson et al., 1994; Kineke et al., 2000; Popescu et al., 2004; Puga-Bernabéu et al., 2011), while canyons that are called "blind" or confined to the continental slope is ought to be related to the second hypotheses (slope failure with upward erosion) (Orange et al., 1997; Green et al., 2007; de Almeida et al., 2015).

Sediment instability is a remarkable feature in canyon ecosystems, caused by factors such as organic matter resuspension of shelf river influxes and marine currents that transport a dense sediment and water mix from canyon heads to deep benthic regions (Xu, 2011). That process moves plant debris and small faunistic fragments, resulting in an organic matter insertion of great organism density, probably bigger compared to other marine habitats of the same depth, like slopes and continental shelves for example (Houston and Haedrich, 1984; Vetter, 1995; Vetter and Dayton, 1999; Duineveld et al., 2001; Escobar Briones et al., 2008). In addition, the narrow and sinuous structures of canyons promote strong up and down reverting currents, and these fluxes combined with a slower deposition of euphotic matter, can entail nutrients and particulates in the water column within the canyons, supporting a higher primary productivity within euphotic zones (Bosley et al., 2004; Fernandez-Arcaya et al., 2017). Therefore, submarine canyons can work as preferential routes for the transportation of organic matter and sediment from the continent to the deep sea, which potentially would produce different ecological parameters in those regions over the resource availability (Gardner, 1989; Durrieu de Madron, 1994: Puig and Palanques, 1998; Schmidt et al., 2001; Palanques et al., 2005; Ingels et al., 2009). Besides their topography and current fluxes, canyons exhibit a high sediment heterogeneity, which strongly contributes for the high diversity of faunistic assemblages within those environments. Among those it is possible to encounter mud, sand, gravel, plaster, boulder and others; that occur in different combinations in a spatial gradient (Baker et al., 2012; De Leo et al., 2014).

The bathymetry is a factor that strongly influences continental slopes and submarine canyons benthic communities (Hessler and Sanders, 1967; Levin et al., 2001; Carney, 2005). With the increasing depth, there is a tendency of less input of organic matter or food resources for the seabed benthos, a process that decreases the abundance and productivity of those assemblages (Dayton and Hessler, 1972; Rowe et al., 1974). The decrease of food resources also entails a lower rate of bioturbation (often stimulated by benthic organisms) and overall faunistic metabolic rates (Gerino et al., 1999; Levin et al., 2001; Smith et al., 2008; Birchenough

et al., 2013). Although, there are some causes that can change this restriction triggered by the increasing depth, like the canyon feature for itself, which can modify the sinking of food resources through the deep-sea, enriching it with organic matter (Gardner, 1989; Vetter and Dayton, 1998; Popescu et al., 2004); other causes would also be enrichment of food resources by sinking of animal carcass (e.g. whale carcasses), wood falls, macroalgae or seasonal fluxes of detrital particulates from pelagic regions to the deep-sea benthos (Wolff, 1979; Billett et al., 1983; Kiel and Goedert, 2006; Smith et al., 2008; Bernardino et al., 2010). This spatial pattern factor of increasing depth linked to sediment patterns is also studied at the eastern Brazilian continental margin (De Léo and Pires-Vanin, 2006; Lavrado et al., 2017). At the Campos basin, Lavrado et al. (2017) found significant bathymetric and latitudinal variation of macrofaunal benthic communities in terms of abundance, biomass, taxonomic composition and species diversity. That variation is evidently correlated to typical patterns of organic matter decrease caused by the increase of water depth, that consequently decrease abundance and secondary productivity of benthic communities (Rowe et al., 1982; Stuart and Rex, 2009; Lavrado et al., 2017). In submarine canyons, besides the bathymetry, patterns of higher or lower disposal of organic matter in benthic communities are also influenced by geomorphology. Shelf-incising canyons, which can extend through the continental shelf even at depths shallower than the shelf-break zone, are more prone to capture and transport allochthonous sediment from the shelf and also from terrestrial draining systems, such as estuary ecosystems (Johnson et al., 2001; Brothers et al., 2013; Puig et al., 2014; Huang et al., 2014; Fernandez-Arcaya et al., 2017). On the other hand, slope confined (*blind*) canyons are more likely to transport autochthonous sediment, from within the canyon and slope system, where the interaction between deeper and shallower waters can be lower, decreasing the organic matter disposal for benthic ecosystems (Pratson et al., 1994; Pratson and Coakley, 1996; Brothers et al., 2013).

Submarine canyons play an important role as providing habitats for biological resources and socioeconomic benefits that can be divided in support, regulating, cultural and supplying services, requiring great attention for the conservation of those habitats. Support services act in an indirect way, unlike the other ones that are based in their physical and temporal effects. An example of the canyons, is their capacity of nutrient cycling that occurs from the continental shelf to the deep sea, water circulation, provision of habitat areas for larval settlement and refuges, among others that affect the biodiversity maintenance and abundance of species (Armstrong et al., 2012). The carbon storage regulation is a vital process and one of the regulation services exerted by submarine canyons, where they contribute to the carbon sequestration and cycling, taking from surface layers, re-depositing and burying it through their particulate transport and hydrodynamic processes (Canals et al., 2006; Masson et al., 2010) . Pollutant detoxification is also a feature of that transport and hydrodynamic regulation, because this conduit can carry contaminants from continental and shelf areas to the deep sea, where they are buried, transformed or assimilated by bioturbation and decomposition (Armstrong et al., 2012; Jobstvogt et al., 2014). Supplying services refer to products acquired straight from ecosystems, such as food resources (Fernandez-Arcaya et al., 2017). Canyons can provide fish

and crustaceans that inhabit within them, and also serve as habitats and nursery areas for commercial species that live in adjacent slopes, where fishing is easier because of its topographic (Sardà et al., 1994; Van Oevelen et al., 2011; Fernandez-Arcaya et al., 2013). Besides that, there is the occurrence of cold water corals cropping by the jewelry industry (Foley et al., 2010) and canyons can also supply genetic resources for medical discovery purposes, because of its specific conditions and specific fauna adaptations (Skropeta and Wei, 2014). The cultural services are those of non-material values, like benefits of artistic, recreational and scientific aspects of the ecosystem. The limited knowledge and mystery involving submarine canyons brings up a lot of scientific/artistic curiosity and fascination by the human imagination, which is proven by the great amount of capital that is invested in surveys to investigate their ecological role and by the increasing consciousness involving their conservation (Armstrong et al., 2012; Thurber et al., 2014; Fernandez-Arcaya et al., 2017). Canyons services are important for climate, waste and gas regulation, food and jewelry industry, scientific and genetic discoveries; which impacts human health and productivity in an economic way, where the monetary value of those different services are not yet evaluated (Costanza et al., 1998; De Groot et al., 2002; Griffiths et al., 2017).

Recently, the technology advance and scientific initiatives of studies that map, sample and investigate benthic environments have greatly contributed to reveal the complexity, diversity and dynamics of the topography and hydrography present in canyons and other deep-sea mega-habitats, which makes it possible to understand different spatio-temporal patterns of oceanographic processes and their ecological effects in a integrative way (Bernardino et al., 2012; De Leo et al., 2014; Baldrighi et al., 2017).

Most submarine canyons have been studied in detail in respect to their benthic macrofauna in temperate and sub-tropical zones such as the Mediterranean Sea, NE and SW pacific (Escobar Briones et al., 2008), but few studies sampled on the SW Atlantic. The present study was made in tropical eastern Brazilian margin, which can bring different insights and information of macrofauna abundance, composition, diversity, dominance and sediment patterns of four submarine canyons and their adjacent slopes in Espirito Santo and Campos basins.

It is expected to encounter spatial differences of the benthic macrofaunal assemblages in the studied canyon regions if compared to nearby slope ecosystems. So we hypothesize that the density and composition of benthic assemblages would be distinct between submarine canyons and continental slopes in response to a higher food availability and disturbance (e.g. sediment heterogeneity) within canyons. We accessed latitudinal and bathymetric patterns of benthic macrofauna of submarine canyons located on the Espirito Santo and Campos basins, in order to evaluate the role of sediment heterogeneity and organic accumulation of submarine canyons in the SW Atlantic.

2. Materials and methods

2.1. *Study site and sampling*

The Southeastern-Eastern Brazil margin is a highly studied and commercially important region for oil and gas reserves. A huge part of that value is concentrated at the Espirito Santo Basin (ESB)(20.19ºS to 19ºS and 37.88ºW to 40.22ºW) and Campos Basin (CB)(22.58ºS to 20.19ºS and 42.1ºW to 40.2ºW) (Carvalho et al., 1995; Viana et al., 1998; Mohriak, 2003; Mohriak, 2014; Bernardino et al., 2016). By the north, ESB borders the Abrolhos Coral Reef Banks, the major and richest coral reef formation in the South Atlantic Ocean (Costa et al., 2003; Melo et al., 2005; Simon et al., 2016), and Campos Basin by the south. CB on the other hand is limited by the Santos Basin to the south. At ESB/CB border region, to the east there is the Vitoria-Trindade Seamount Chain by 21ºS, where eddy formation and upwelling of cold deep water might be increased, between the chain and the slope to the west (Schmid et al., 1995; Calado et al., 2006). There are five main water masses that effect the continental margin of the study area: 1) the Superficial   Tropical Waters (STW), mostly composed of Brazil current and shelf waters, above 250/300m of water depth, with a varying temperature higher than 18ºC; 2) the South Atlantic Central Water (SACW), between 300 and 550m water depth, temperature from 18 to 6ºC; 3) Antarctic Intermediate Water (AAIW), between 550 and 1200m water depth, with temperature from 6 to 2ºC; 4) the North Deep Water (NADW), between 1200 and 3500m water depth, 4 to 2ºC; 5) the Antarctic Bottom Water (AABW), temperature below 2ºC and water depth below 3500m (Durrieu De Madron and Weatherly, 1994; Viana et al., 1998).

In the present study, we sampled four submarine canyons and two adjacent slope transects in each basin along the continental slope. At the ESB, we sampled the canyons Watu Norte (CANWN) and Doce (CAND) along depths (stations) of 150, 400, 1000 and 1300 meters with six replicates per station (Fig 1). Two sampling transects (D and E) were carried on the adjacent continental slope at the same depths (Fig. 1). The Almirante Camara (CANAC) and Grussai (CANG) canyons were sampled on Campos Basin with six replicates from each station at depths of 400, 700, 1000 and 1300 meters (Fig 1). Similarly, two sampling transects on the adjacent continental slope were carried (G and H; Fig 1).
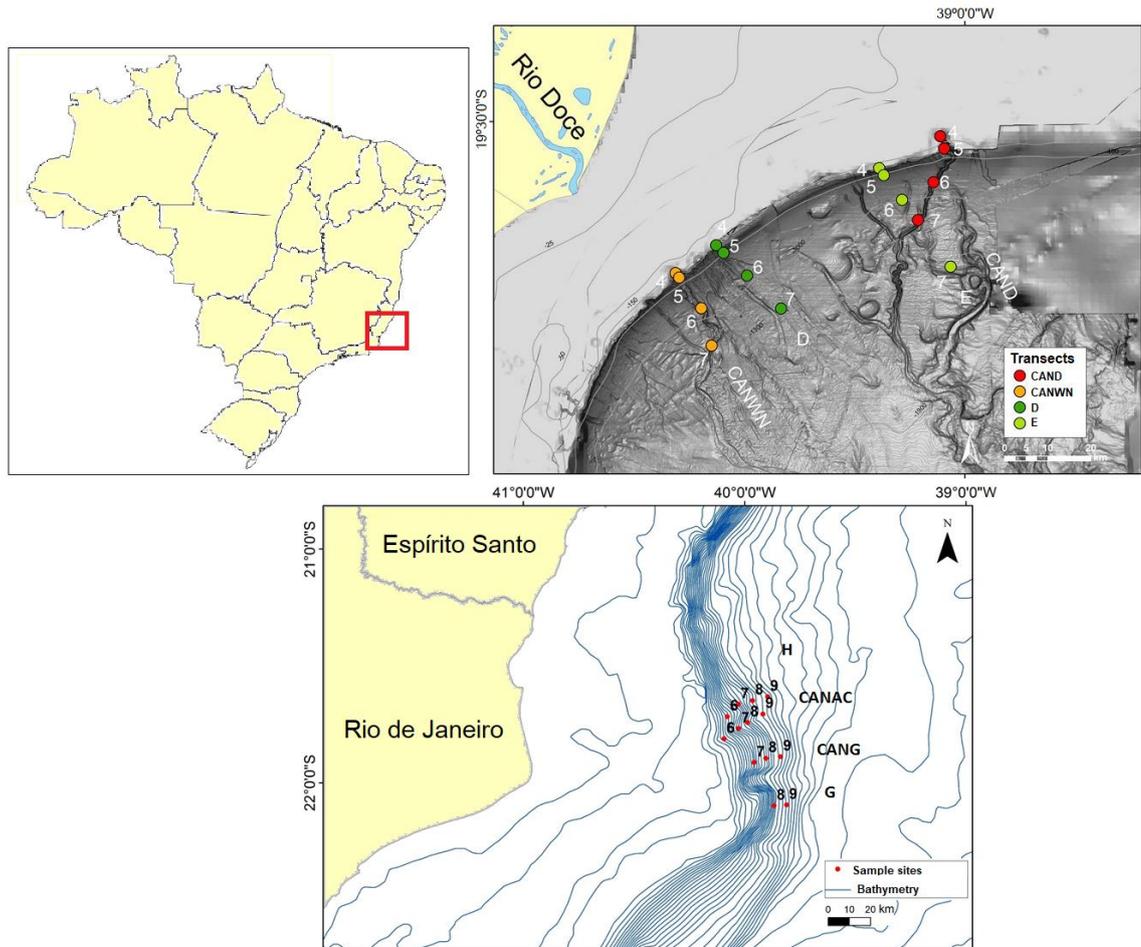
Fig. 1. Map of the sampling stations at Espirito Santo Basin (ESB; above): canyon Doce (CAND), canyon Watu Norte (CANWN), transect E and transect D; and Campos Basin (CB; below): canyon Almirante Camara (CANAC), canyon Grussai (CANG), transect H and transect G. Numbers indicating bathymetry of sampled isobaths for ESB: 4 (150m), 5 (400m), 6 (1000m) and 7 (1300m); and for CB: 6 (400m), 7 (700m), 8 (1000m) and 9 (1300m).

The sampling in ESB was performed during two different oceanographic cruises, at the summer of 2012 and winter of 2013. The replicates were collected with a box corer (top 10 cm over an area of 0.09 m-2 per replicate (Bernardino et al., 2016). Each sample was processed on board and sub-sampled for sediment grain size (*phi*) and organic matter, and macrofauna. Macrofaunal samples were conserved unsieved in 10% formalin with neutral pH buffered with borax, for *posteriori* screening. Likewise, at the CB canyons, sampling occurred on two oceanographic cruises, one in 2008 winter and other in the summer of 2009 (Lavrado et al., 2017).

2.2. *Sample processing and analysis*

At the laboratory, samples were washed with 300μm mesh sieves, and the fauna was preserved (70% alcohol) for later sorting under a stereoscope microscope (Vetter and Dayton, 1998; Gage, 2001). Organisms were identified by taxonomic experts, but given the high number of organisms we used a typical family, order or high taxonomic levels for ecological analysis, which are standard for deep-sea ecological work (Narayanaswamy et al., 2003). For Mollusca phylum, only living specimens were counted with whole shells and soft parts inside. The accounting was made just with individuals of the *stricto sensu* macrofauna, excluding then fauna classified as meiofauna, like the groups Nematoda, Ostracoda and Copepoda (Hughes and Gage, 2004).

Benthic assemblages of canyons and slope were described based on ecological univariate and multivariate indexes, including density (ind.m²), macrofaunal taxonomic composition, species equitability (Pielou J') and assemblage diversity by rarefaction (Es) (Bernardino et al., 2016). Diversity indicators that are sensitive to the sample size change, such as Shannon H' and Simpson d, were not used for their inappropriate description of deep sea community organisms, which present great abundance reduction with depth increase (Magurran, 2004).

Pielou (J') evenness and rarefaction richness was calculated through all replicates of taxon abundance, using the software PRIMER v. 6.0 with the PERMANOVA + add-on package (Clarke and Warwick, 2001; Anderson et al., 2008). According to Hurlbert (1971), the diversity by rarefaction calculates the expected species number in a *n* individual sample, random selected, inside a total group of *N* individuals, *S* species, with *Ni* individuals of the *i* specie. This approach is highly necessary in deep sea studies, where the sample sizes suffer a vast effect of reduction with depth (Magurran, 2004).

Bathymetric and latitudinal diversity variations were compared based on the mean and standard deviation of the rarefaction diversity for a sample of 50 individuals (ES50). Utilizing all samples replicates, rarefaction curves (ESn) were generated to calculate the diversity variation across depth levels. Statistic tests from confidence limits were calculated with a one-tailed 95% confidence interval, designed using values from t distribution (alpha = 0.05). Treatment curves decreasing from the contextual 95% curve were then considered statistically different from other treatments (Zar, 2010; Bernardino et al., 2010; Bernardino et al., 2016).

Multivariate patterns of macrofaunal assemblages were tested by classification and ordination, from Bray-Curtis distance indice, using the abundance data of the individuals, pre-treated with square root transformation (Clarke and Warwick, 2001). SIMPER was used to verify the discriminant taxon grouped and ANOSIM to test the significance of the group discrepancy (software PRIMER v.6.0). An environmental data matrix was designed, including grain size (*phi* – mean grain size), organic matter content (represented by TOC – total organic matter) and

depth. Log [X +1] transformation was operated as a distribution correction pre-treatment and Euclidian Distance indice to test similarities and dissimilarities. Principal component analysis (PCA) also took place for an ordination of the data (Clarke and Warwick, 2001). DistLM (Distance-based linear model) routines were performed (selection procedure = step-wise, selection criterion = adjusted AICc) to correlate the environmental factors (*phi*, COT and depth) across the multivariate patterns of macrofaunal abundance data (Spearman's rank; p between both resemblance matrices). Second-stage MDS, SIMPER, ANOSIM, RELATE, BEST and DistLM analysis were accomplished utilizing the software PRIMER v. 6.0 with the PERMANOVA + add-on package (Clarke et al., 2006; Anderson et al., 2008). Univariate ANOVA was performed, when necessary, using the software BioEstat 5.3 (AYRES et al., 2007).

3. Results

3.1. Grain size and total organic carbon

The sediments from the canyons and adjacent slopes studied were mainly composed of silt particles (mean phi > 4.0). At ESB, there was a significant bathymetric increase in mean grain size (*phi*) from 150m to deeper sites (Table 1) in canyon Doce and the slope transects D and E (ANOVA F = 26.4979, p < 0.01 and ANOVA F = 22.2895, p < 0.01, respectively; Table 1). The sedimentary total organic carbon (TOC) was similar between canyon and the adjacent slope on the ESB (Table 1). In the Campos Basin, a bigger sediment grain size (*phi*) was observed at 400m depth within the Almirante Camara canyon if compared to the nearby slope (ANOVA F = 107.4120, p < 0.01; Table 1). Sedimentary TOC of CANAC was also higher than the adjacent slope H at 400m (ANOVA F = 134.3368, p < 0.01; Table 1).

Table 1. Environmental properties: mean values from sedimentary particle size (*phi*) and total organic carbon (*TOC*) from the canyons and adjacent slopes of Espirito Santo and Campos basins. Tr: transects; --: no samples. Bold values indicate statistical significance; *: between isobaths; *: between canyon and its adjacent slope.

Depth (m)	Tr D		Tr E		CANWN		CAND		Tr G		Tr H		CANG		CANAC	
	Phi	COT	Phi	COT	Phi	COT	Phi	COT	Phi	COT	Phi	COT	Phi	COT	Phi	COT
150	**3.7***	4.4	**2.5***	2.5	4.6	3.2	**2.4***	2.1	--	--	--	--	--	--	--	--
400	6.2*	4.4	6.1*	3.5	6.1	4.4	5.7*	4.5	--	--	**4.8***	**0.9***	--	--	**6.4***	**1.4***
700	--	--	--	--	--	--	--	--	--	--	6.0	1.2	6.1	1.1	6.2	1.2
1000	6.5*	5.4	6.9*	5.4	4.5	1.9	5.3*	4.0	5.7	1.0	6.8	1.3	6.9	1.5	6.9	1.5
1300	6.3*	4.2	7.5*	4.2	5.3	3.7	5.3*	2.8	5.7	0.8	6.7	1.1	6.8	1.2	6.7	1.2

3.2. Macrofaunal assemblages

There was a noticeable difference in macrofaunal abundance between the canyons Watu Norte and Doce. CANWN had higher total macrofaunal density in all bathymetric range – 150 to 1300m – in comparison with CAND (ANOVA, F = 37,4778, p < 0.0001; Fig 2). The organism

abundance in CANWN averaged almost five times higher at 150m (~5,000 to ~25,000 ind.m^{-2}) compared to CAND (ANOVA, F = 31.35, p < 0.01). Comparing the canyons with their adjacent slopes, benthic macrofaunal density did show statistical habitat variance in the upper slope (150 and 400m) between canyon Doce and its adjacent slope E, where the transect E presents a greater macrofaunal density in both isobaths (ANOVA, p < 0.01; Fig 2). In addition, total macrofaunal density showed a significant increase in the canyon Almirante Camara (CANAC) in comparison with its adjacent slope of the transect H, at the bathymetric range of 700 and 1000m (ANOVA, F = 15.6968, p < 0.01; Fig 2).
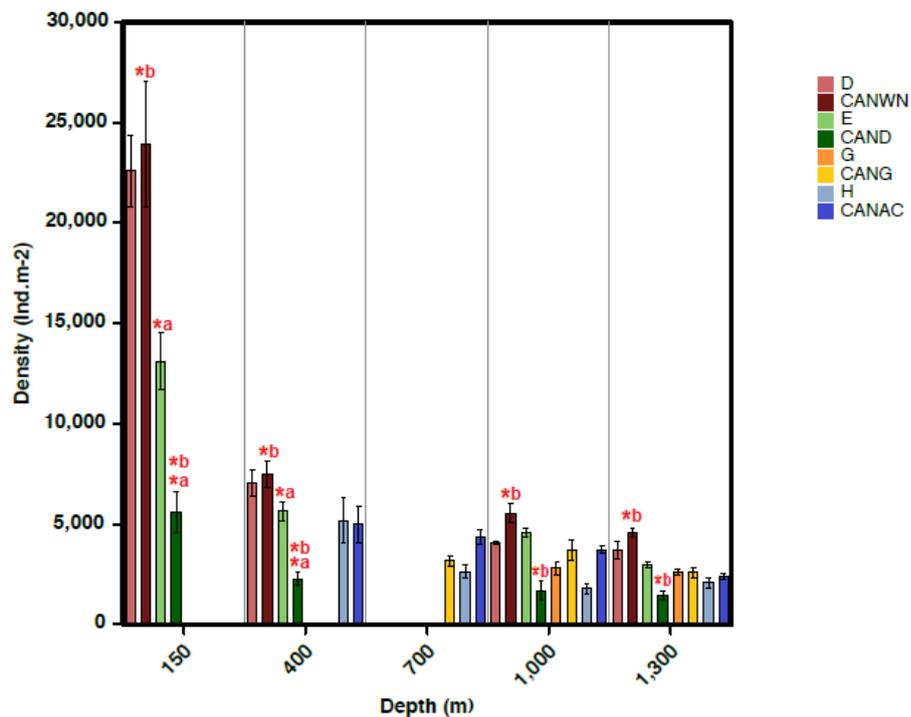
Fig 2. Macrofaunal abundance of canyons Watu Norte, Doce, Grussaí, Almirante Camara and their adjacent slopes D, E, G and H, respectively, in Espirito Santo and Campos basins. Blank spaces indicate non sampled stations. *^{a}: significant variance (p < 0.01) between canyon and slope; *^{b}: significant variance (p < 0.01) between canyon and canyon.

Polychaetes and peracarid crustaceans dominated together with over 50% of macrofaunal abundance in the majority of canyons and slopes (Fig. 3). At CANWN, CAND, and slopes D and E, the polychaete families Spionidae, Paraonidae, Syllidae, Orbiniidae and Sabellidae were the most dominant, followed by Leptochellidae and Agathotanaidae tanaidaceans (table 2). In general, annelids dominated the canyons Watu Norte and Doce assemblages, however in deeper adjacent slope isobaths, such as in 1300m of slope D, it is possible to recognize greater dominance of tanaidaceans (Fig 3; table 2). At the upper slope (400m), molluscs were more abundant at the Almirante Camara canyon, which increased the relative abundance of this taxon compared to other isobaths of CANAC (700 to 1300m) and its

18

adjacent slope H (Fig. 3; table 2). CB, differently from ESB, appeared to present grander organism heterogeneity. In deeper isobaths, at the inferior studied slope (1000 and 1300m) of CB, polychaete families such as Spionidae, Paraonidae, Syllidae, Cirratulidae and Amphinomidae are more dominant overall, for all transects. Still, at the superior slope (400 and 700m), a bigger occurrence of Thyasirids and Rissoids in Almirante Camara canyon and its adjacent slope H is observed (table 2).

Fig 3. Composition of macrofaunal assemblages on the canyons and adjacent slopes of Espirito Santo and Campos basins.

Table 2. Rank of the three main groups of benthic macrofauna with the highest relative abundance (%) for canyons and adjacent slopes in Espirito Santo and Campos basins. (A) – Annelida; (M) – Mollusca; (I) – Isopoda; (T) – Tanaidacea; (Am) – Amphipoda.
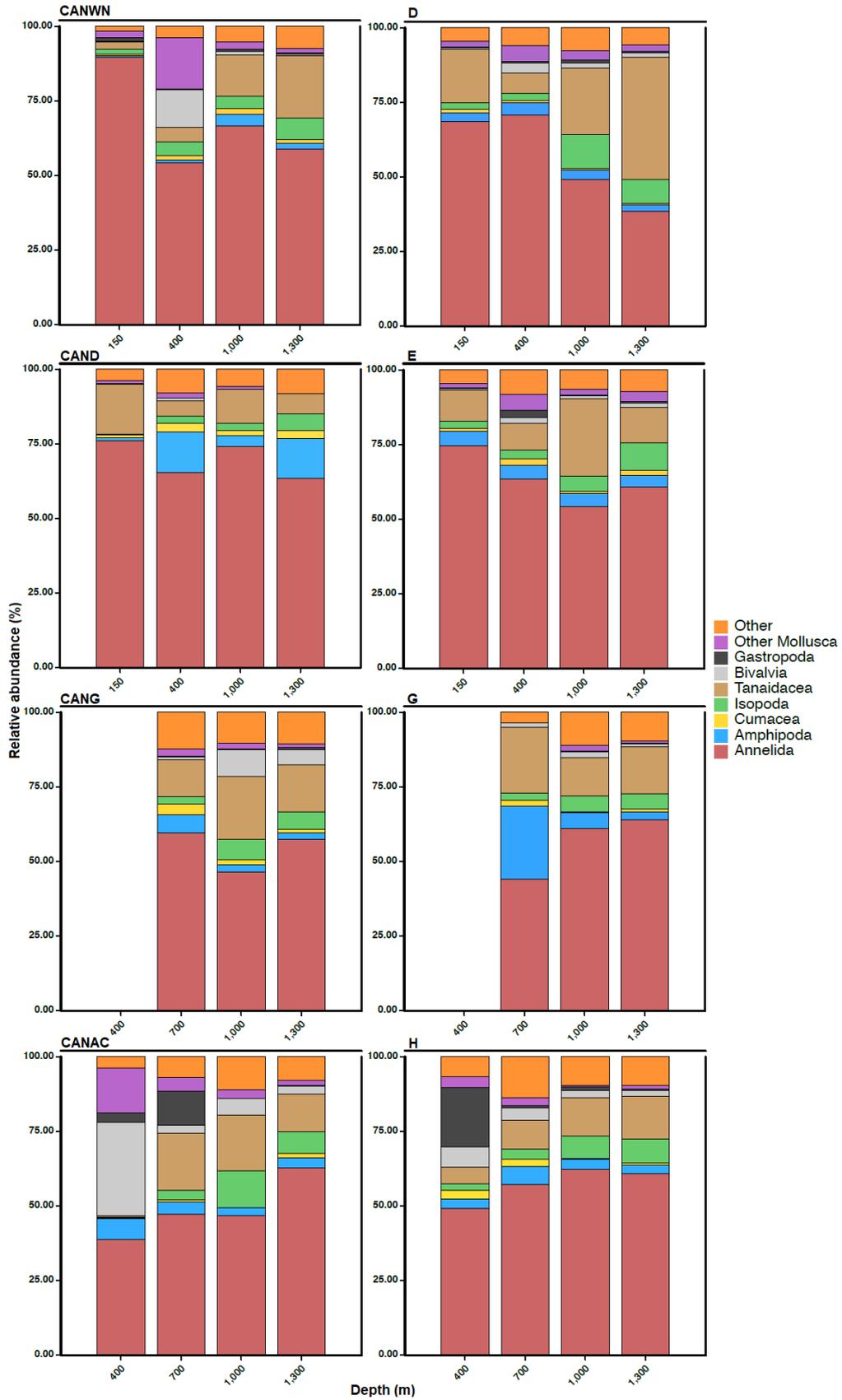
Transect	150 m	400 m	700 m	1000 m	1300 m
CANWN	Paraonidae (A) 46,4%; Spionidae (A) 11,3%; Orbiniidae (A) 5,4%	Paraonidae (A) 17,8%; Yoldiidae (M) 10,7%; Spionidae (A) 6,4%	N.a.	Maldanidae (A) 9,9%; Spionidae (A) 8,4%; Paraonidae (A) 6,1%	Paraonidae (A) 10%; Spionidae (A) 9,3%; Colletteidae (T) 7,2%
CAND	Spionidae (A) 14,7%; Leptochellidae (T) 12,7%; Syllidae (A) 12,5%	Magellonidae (A) 15,7%; Paraonidae (A) 12,7%; Spionidae (A) 9,6%	N.a.	Spionidae (A) 9,1%; Paraonidae (A) 9,1%; Leptocheliidae (T) 9%;	Spionidae (A) 14,4%; Paraonidae (A) 7,1%; Amphinomidae (A) 6,1%
Slope D	Spionidae (A) 19,9%; Syllidae (A) 6,9%; Agathotanaidae (T) 5,9%	Paraonidae (A) 41,6%; Pilargidae (A) 5%; Spionidae (A) 5%	N.a.	Spionidae (A) 10,8%; Desmosomatidae (I) 8,4%; Paraonidae (A) 8,2%	Tanaellidae (T) 15,6%; Anarthruridae (T) 15,1%; Spionidae (A) 7,9%
Slope E	Syllidae (A) 16,1%; Spionidae (A) 11,8%; Sabellidae (A) 5,3%	Spionidae (A) 12,7%; Syllidae (A) 10,4%; Paraonidae (A) 9,2%	N.a.	Spionidae (A) 10%; Tanaellidae (T) 6,7%; Paraonidae (A) 6,5%	Spionidae (A) 12,7%; Paraonidae (A) 10,7%; Amphinomidae (A) 5,5%
CANG	N.a.	N.a.	Syllidae (A) 15,4%; Cirratulidae (A) 11,7%; Spionidae (A) 6,7%	Spionidae (A) 10,1%; Tanaellidae (T) 8,9%; Syllidae (A) 8,3%	Spionidae (A) 11,8%; Paraonidae (A) 11,3%; Amphinomidae (A) 8,3%
CANAC	N.a.	Thyasiridae (M) 17,4%; Spionidae (A) 13,3; Prochaetodermatidae (M) 12,8%	Rissoidae (M) 10,9%; Cirratulidae (A) 8%; Paraonidae (A) 5,7%;	Spionidae (A) 11,9%; Desmosomatidae (I) 10%; Cirratulidae (A) 6,3%	Spionidae (A) 14,5%; Amphinomidae (A) 13,2%; Paraonidae (A) 7,1%
Slope G	N.a.	N.a.	Ampeliscidae (Am) 8,8%; (Cirratulidae (A) 7,3%; Paraonidae (A) 5,9%	Spionidae (A) 11%; Cirratulidae (A) 7,1%; Amphinomidae (A) 6,5%	Spionidae (A) 17,3%; Amphinomidae (A) 11,2%; Sabellidae (A) 6,2%
Slope H	N.a.	Rissoidae (M) 25%; Spionidae (A) 14,7%; Opheliidae (A) 7,5%	Syllidae (A) 8,7%; Spionidae (A) 8,4%; Paraonidae (A) 6,7%	Spionidae (A) 11,7%; Cirratulidae (A) 9,4%; Amphinomidae (A) 8,5%	Spionidae (A) 15,4%; Amphinomidae (A) 11,7%; Cirratulidae (A) 5,4%; Desmosomatidae (I) 5,4%

We identified differences in taxonomic evenness (J) between canyons, slopes and also bathymetric changes in the study area. J was markedly different in a bathymetric scale for the canyon Watu Norte and its adjacent slope D, where at the 150m isobath, we observed a significant inferior evenness of CANWN when compared to CAND and transects D and E (Kruskal-Wallis H = 11.75, p < 0.05; Fig 4). Meanwhile, at the 400m isobath, the adjacent slope

D proffered a significant smaller evenness in comparison with CANWN, CAND and slope E, where the Pielou indice maintained similar (ANOVA F = 17,35, p < 0,01; Fig 4). In addition, at 150m both canyons (Watu Norte and Doce) exhibited lower taxon diversity compared to their adjacent slopes (ANOVA F = 14.08, p < 0.05; Fig 5). At the upper slope (400m), CANAC and its adjacent slope H presented significant inferior evenness (Kruskal-Wallis H = 10.38, p < 0.05; ANOVA, F = 6.35, p < 0.05; Fig 4) when compared to deeper sites. Macrofaunal expected richness (50 individuals sample – Es50) of Hurlbert (1971) shown an isolation of the superior slope (400m) related to the other isobaths (700 to 1300m) at Almirante Camara Canyon (CANAC), evidenced by a lower taxon diversity (ANOVA, F = 14.12, p < 0.01; Fig 5).
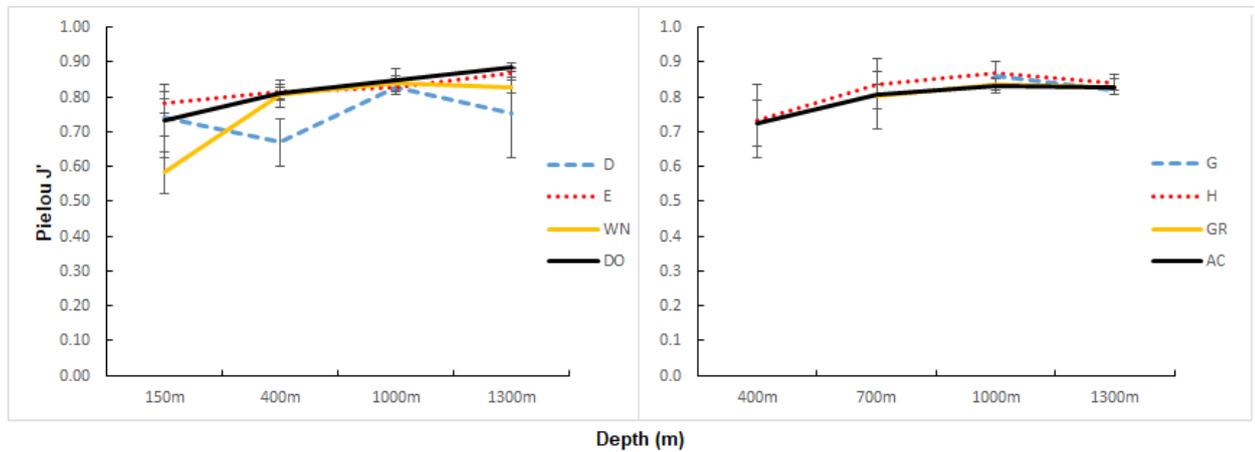

Fig 4. Pielou (J') evenness of benthic macrofaunal assemblages along the canyons and slopes of Espirito Santo (left chart) and Campos (right chart) basins. WN: Watu Norte canyon; DO: Doce canyon; D: adjacent slope D; E: adjacent slope E; GR: Grussai canyon; AC: Almirante Camara canyon; G: adjacent slope G; H: adjacent slope H.

Fig 5. Bathymetric variation of species richness (ES50) across the canyons and slopes of Espirito Santo (left chart) and Campos (right chart) basins. WN: Watu Norte canyon; DO: Doce canyon; D: adjacent slope D; E: adjacent slope E; GR: Grussai canyon; AC: Almirante Camara canyon; G: adjacent slope G; H: adjacent slope H.
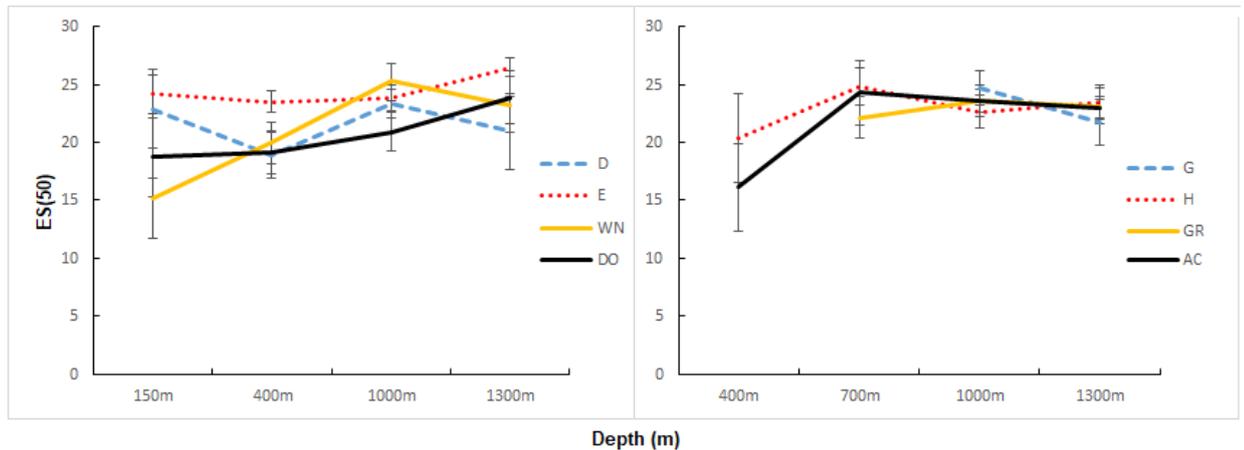
3.3. Multivariate analysis

We found significant differences in macrofaunal assemblages between canyons and slope sediments, and along bathymetric gradients (ANOSIM, R = 0.661, p = 0.001, ANOSIM, R = 0.816, p = 0.001; habitat and bathymetric, respectively). Besides the differences in macrofaunal assemblages between canyons and adjacent slopes, there is marked differences between each canyon, with the highest significance levels (R > 0.82) on pairwise testes (p = 0.001; Table 3). The canyons Watu Norte and Doce were significant distinct between their assemblages (ANOSIM, R = 0.823, p = 0.001; Table 3). Both canyons presented dominance by Paraonids and Spionids in general, but their dissimilarity can be demonstrated by greater abundance of Paraonidae and Yoldiidae members at CANWN in comparison with CAND (SIMPER analysis). In addition, the canyons Grussai and Almirante Camara were also distinct in respect to their macrofaunal assemblages (ANOSIM, R = 0.293, p = 0.001; Table 3), where the former presented more abundance of Syllidae polychaetes and the latter Hesionidae polychaetes. Along the bathymetric gradient in the canyons and adjacent slopes, macrofaunal assemblages were strongly distinct between upper to intermediate slope (150, 400 and 700m, ANOSIM R > 0.87, p = 0.001), if compared to the lower slope of 1000 and 1300m (ANOSIM, R < 0.5; Fig 6). The dissimilarity of the upper and lower slope was correlated with the higher abundance of polychaetes Paraonids, Spionids, Syllids and Cirratulids at the upper slope (> 50% dissimilarity, SIMPER; Fig 6).

Table 3. R values from ANOSIM pairwise tests between transects across all depth groups. Values in bold indicate the highest significance levels (R > 0.82) on pairwise tests (p = 0.001).

Transects	D	E	G	H	CANWN	CAND	CANG	CANAC
E	0.51							
G	0.75	0.75						
H	0.71	0.69	0.25					
CANWN	0.79	0.73	**0.86**	**0.83**				
CAND	0.77	0.74	0.74	0.67	**0.82**			
CANG	0.76	**0.86**	0.53	0.37	**0.92**	**0.86**		
CANAC	**0.82**	**0.84**	0.5	0.5	**0.91**	**0.83**	0.29	

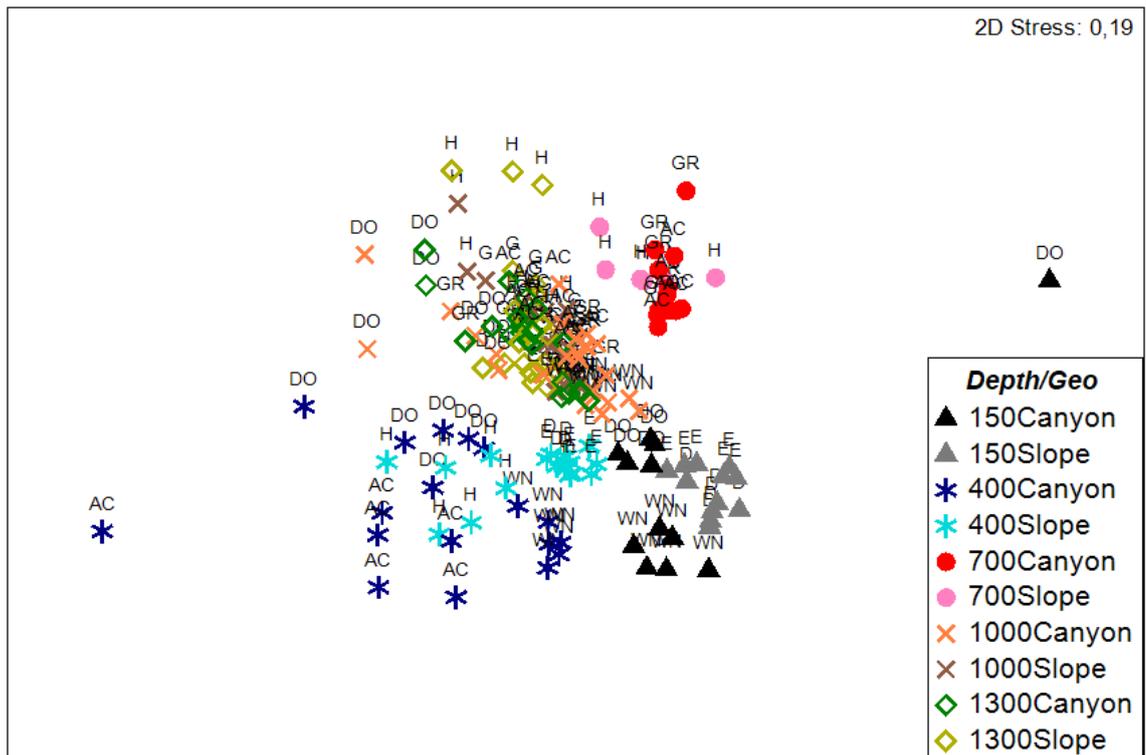**Fig 6.** Non-metric multidimensional scaling (N-MDS) of macrofaunal assemblages along the canyons and adjacent slopes of Espirito Santo and Campos basins. Symbols represent depth, whilst colors distinguish geomorphism type: Canyon or adjacent slope.

Environmental variables including depth, sediment grain size (*phi*) and total organic carbon (*TOC*) were significantly related to the changing patterns of the macrofaunal

24

assemblages of both canyons and adjacent slopes (RELATE, R = 0.394, p = 0.001). The BEST analysis indicated that the depth correlated best with the macrofaunal samples (BEST R = 0.579, p = 0.01; Table 4), followed the sediment grain size and *TOC* plus depth (BEST R > 0.41, p = 0.01; Table 4). Distance-based linear model (DistLM) showed that depth, *TOC* and sediment grain size explained 23% of macrofaunal assemblage total variation, with depth mostly important (DistLM 14.2% of total variation; p = 0.001; Table 5; Fig 7).

Table 4. Best correlations of depth, sediment grain size, total organic carbon and macrofaunal assemblages of the canyons and slopes of Espirito Santo and Campos basins. *Pw* – weighted Spearman coefficients.

No. of variables	*Pw*	Env. Variables
1	0,579	Depth
2	0,477	*phi*, Depth
2	0,410	*TOC*, Depth
3	0,394	*All*
2	0,218	*phi, TOC*
1	0,190	*phi*
1	0,127	*TOC*

Table 5. Distance-based linear model (DistLM) of Bray-Curtis similarities on macrofaunal assemblages, sediment grain size (*phi*) and total organic carbon (*TOC*) of canyons and slopes in Espirito Santo and Campos basins.

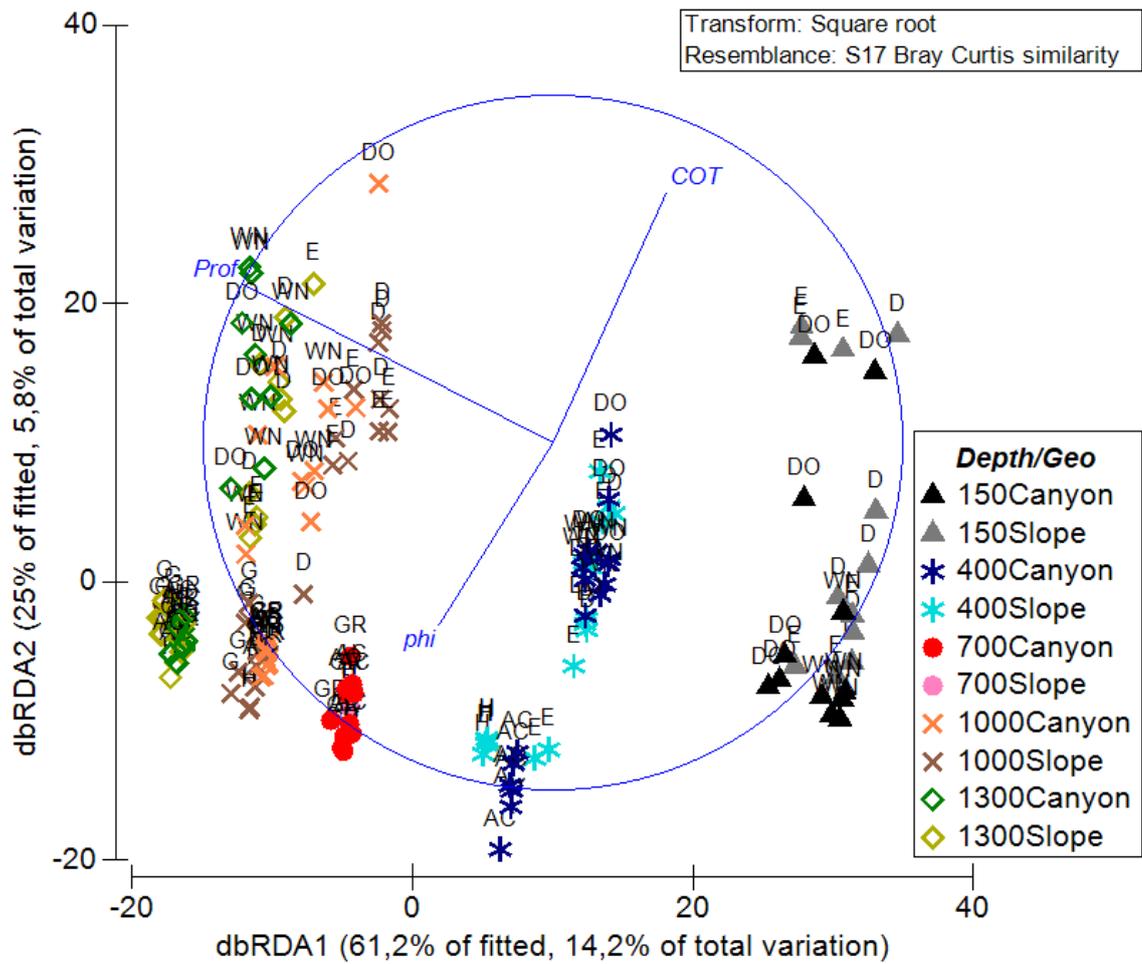| Variables	SS (trace)	Pseudo-F	*p*	Prop.
Depth	38207	26.733	0.001	0,13799
TOC	17516	11.278	0.001	6,3262E-2
Phi	21095	13.772	0.001	7,6185E-2

Fig 7. Distance-based redundancy analysis (dbRDA) plot of the DistLM based on depth, total organic carbon (*TOC*) and sediment grain size (*phi*) that best explained patterns of macrofaunal assemblages of the canyons and adjacent slopes in Espirito Santo and Campos basins. Symbols represent depth, whilst colors distinguish geomorphism type: Canyon or adjacent slope.

4. Discussion

A number of studies suggest that submarine canyons concentrate and facilitate organic matter flux across the slope with a resulting increase of productivity of benthic and demersal fauna (Vetter, 1994; Vetter and Dayton, 1998; De Leo et al., 2010; Rowe et al., 1982; Canals et al., 2006; Lavrado et al., 2017). Truly, great amount of canyon studies provided clear confirmations that canyons act as preferential routes and host differential ecosystems among the deep sea, demonstrating their patterns and processes responsible for that, but many effects that impact communities' assemblages need more robust understandings (Fernandez-Arcaya et al., 2017). All in all, there are also different researches that did not found a correlation of the "canyon effect" with the enhancing of abundance or biomass among submarine canyons, compared to other habitats outside of these (Houston and Haedrich, 1984; Maurer et al., 1994; Maurer et al., 1995; Vetter and Dayton, 1998). Or even with diversity, which is not unusual to encounter more abundance of some benthic fauna inside canyons and lower evenness and species richness compared to non-canyon sites (Gage et al., 1995; Cúrdia et al., 2004; Garcia et al., 2007; Ingels et al., 2009). Similarly, the present study found no significant higher diversity of the macro-benthic fauna of the canyons compared to adjacent slope regions studied, with higher evenness and taxon diversity of the non-canyon slope at specific isobaths.

The Watu Norte, Doce and Almirante Camara canyons did not exhibit sedimentary organic enrichment at depths below 700m, but they likely acted as traps of organic material close to the shelf break and upper slope as observed elsewhere (Escobar Briones et al., 2008; De Leo et al., 2010; Vetter et al., 2010). The Watu Norte canyon exhibited an increase in macrofaunal density at the shelf break (150m). In addition, the macrofaunal abundance of the canyon Watu Norte was also higher if compared to the canyon Doce, which is probably related to the geomorphology and location of the canyons. The Watu Norte canyon is closer to the Rio Doce river mouth and to shore if compared to the Rio Doce canyon, supporting that submarine canyons are highly variable in their geomorphology and in resulting organic accumulation (Williams et al., 2009; Huang et al., 2014). The physical, biological and chemical processes situated in complex topographic canyons can provide variable organic matter resources coming from the continent, resulting on enrichment and increased secondary productivity (Skliris and Djenidi, 2006; Cartes et al., 2010). That process is possibly induced by larger vertical mixing, where there is a flux of both deep rich nutrient waters into the euphotic zone and also a better transportation of organic matter to the deep seabed (Tesi et al., 2010). Truly, the distance that a canyon is located from the source of organic matter flux can decree the amount of nutrient resources that reach this canyon (Vetter and Dayton, 1998; Vetter and Dayton, 1999; Huang et al., 2017). So the closer distance of Watu Norte canyon from the shore and its close proximity to the Rio Doce river mouth are likely to support a higher benthic macrofauna abundance (Hargrave et al., 2004; Mcclain and Barry, 2010; De Leo et al., 2014; Huang et al., 2017).

The origin of a canyon is related to its physical features, such as its size and shape, whether the canyon is of shelf-incising type or slope confined (*blind*) type, and these

characteristics can also influence and help to understand the productivity of the canyon and therefore the benthic macrofaunal density and composition within (Pratson et al., 1994; Puga-Bernabéu et al., 2011; Harris and Whiteway, 2011). Shelf-incising canyons have more potential for providing habitat heterogeneity than slope-confined ones, owed to their bigger size and more complexity in terms of shapes, in different bathymetries (Huang et al., 2014). That can cause the aggregation of more favorable processes, like higher energy flux, due to the interaction between deeper ocean currents and shelf waters that increase the input of organic nutrients from the coast (Greene et al., 1988; Moors-Murphy, 2014; Puig et al., 2014; Fernandez-Arcaya et al., 2017). Watu Norte and Doce canyons were sampled at 150m of depth, which is situated at the shelf break region to the continental slope (Puga-Bernabéu et al., 2011; Harris and Whiteway, 2011; de Almeida et al., 2015), but that data itself does not guarantee that those canyons are indeed of shelf-incised types. The canyons studied here have for sure their particular sizes and types, thus there is a need for surveys that explore the Espirito Santo and Campos basins canyons shapes and types for better geomorphology diagnoses and understanding of the processes that affect the composition, abundance and diversity of the macrofaunal assemblies reported here.

The submarine canyons in general exhibited distinct density and composition of macrofaunal organisms if compared to slopes assemblages, which were mainly significant at the shelf break and upper slope depths (150 – 400m). These observations partially support that submarine canyons hold a distinct set of benthic assemblages, which are likely favored by local resources supporting higher productivity and resistance to disturbance (Krö Ncke et al., 2003; Cartes et al., 2009; Louzao et al., 2010; Currie and Sorokin, 2014; Conlan et al., 2015). However, some canyons did not support distinct assemblages and all canyons had indistinct benthic assemblages from the slope at depths greater than 700m (1000 and 1300m). Given that Almirante Camara canyon acted as a trap of organic matter at the 400m isobath, presenting a higher rate of total organic carbon than its continental slope H, and that the canyon presented heterogeneity of macrofaunal taxon relative abundance at the same isobath, we suggest that CANAC probably work as preferential route for the transportation of organic matter from the continent to deeper waters, which is one of the potential factors that are producing different ecological parameters in those regions over the resource availability, compared to other habitats (Houston and Haedrich, 1984; Gardner, 1989; Durrieu de Madron, 1994; Puig and Palanques, 1998; Vetter and Dayton, 1999; Schmidt et al., 2001; Palanques et al., 2005; Ingels et al., 2009; Fernandez-Arcaya et al., 2017).

The macrofaunal composition on the slope and within canyons was dominated by annelids and peracarid crustaceans, with occasional high abundance of molluscs. In general, slope and canyons had a similar higher taxonomic composition, although species likely differ (Vetter and Dayton, 1998; Escobar Briones et al., 2008; Romano et al., 2017) . However, even at high taxa discrimination, there are clear differences in the structure of macrofaunal benthic assemblages between canyons and slope, with canyons exhibiting a higher heterogeneity if

compared to slope assemblages. The high within canyon heterogeneity is likely a result of variable disturbance levels that create opportunity and niches for colonization of tolerant benthic organisms along continuous community succession (Hess et al., 2005; Danovaro et al., 2009; Paterson et al., 2011; Romano et al., 2013; Gambi and Danovaro, 2016). Spionids and Paraonids were the most dominant families within canyons and slopes, overall. However, the structure heterogeneity of the macrofauna between canyons, and among canyon and slopes, are probably linked to the dominance of some opportunistic lower discriminated taxon inside groups, like for example, of Leptochellids and Magellonids in canyon Doce compared to the dominant Paraonids of Watu Norte canyon, or of bivalvia Thyasirids in Almirante Camara canyon compared to gastropod Rissoids in the adjacent slope H. The canyon topography, connected to disturbance events and sediment instability, decrease in food availability, removed from shallower canyon sites to deep waters, and different erosive flows are possibly creating different conditions, that can be more favorable to some group organisms compared to others (Romano et al., 2013; Pusceddu et al., 2013; Mcclain and Schlacher, 2015; Gambi and Danovaro, 2016).

Macrofaunal diversity was not clearly distinct between canyons and slopes on the Brazil margin, with canyons supporting a lower diversity at depths between 150 and 400m as a result of organic enrichment and disturbance. These patterns suggest that submarine canyons support a subset of species from the slope macrofauna, which are resilient to canyon disturbance (Mcclain and Schlacher, 2015; Gambi and Danovaro, 2016). However, canyons may act locally to increase benthic diversity by excluding dominant species, as suggested by higher species evenness at the shelf break and upper slope of the canyons herein studied. The effects of local physical and organic disturbance effects in the community diversity regulation in canyons have been observed elsewhere (Vetter et al., 2010; De Leo et al., 2010; De Leo et al., 2014). Some observations herein achieved are also important for secondary productivity of the deep sea. The heterogeneity of macro-benthic organisms found at the shelf break zone and upper slope in the canyons, influenced by differential disturbance and organic input, are probably working for exploitation by megafauna such as demersal fishes, creating a propitious environment for ecosystem production (De Leo et al., 2010). Critical ecological areas of reef fishes were also found at the shelf break zone and upper slope of the SW Atlantic margin, decreasing along deeper bathymetry (Haimovici et al., 2009; Olavo et al., 2011). Proper management and inclusion of those areas as hotspots of biodiversity is clearly necessary for conservation, principally considering the increasing anthropic exploitation of the region's deep sea.

Multivariate analysis evidenced that sediments (phi, TOC) and depth are greatly important to explain macrofaunal assemblage variability in canyons and on the slope of Espirito Santo and Campos Basins (Bernardino et al., 2016). Different factors appear to act in the heterogeneity of the abundance, composition and diversity of the Espirito Santo and Campos basins canyons, where possibly organic enrichment effects and physical disturbs are taking

place simultaneously, and these factors can be even more significant in spatial scales smaller than the herein scales studied (Danovaro et al., 2009; Mcclain and Barry, 2010; De Leo et al., 2014). Nonetheless, it was evidenced that the canyons Watu Norte, Doce and Almirante Camara, spite of not induce significant local enrichment of the benthic macrofauna taxon, they harbor distinct assemblage structures and higher punctual densities, contributing for the heterogeneity of the continental margin in a larger spatial scale. There is a great amount of knowledge regarding abiotic and biotic processes of the Espirito Santo and Campos basins canyons necessary for the better understanding, management and conservation of these potential marine hotspot habitats.

This study suggests that the submarine canyons from Espirito Santo and Campos basins support distinct benthic macrofaunal assemblages on the slope as a result of their physical heterogeneity and increased organic input at shelf break and upper slope depths. This suggests that submarine canyons on the SW Atlantic are habitats for a subset of species from the slope, that may exhibit increased biomass and production locally and therefore may be of great ecological importance to other organisms that use canyons as refuge, feeding or reproduction areas (Vetter and Dayton, 1998; Tyler et al., 2009; De Leo et al., 2010; Fernandez-Arcaya et al., 2017) . As a result, over landscape scales on the Brazilian margin, submarine canyons may act as ecologically and biologically relevant areas for conservation (Clark et al., 2014; Dunn et al., 2014) in face of great economic interests on deep-sea living and non-living resources (Cordes et al., 2010; Leduc et al., 2016; Cordes et al., 2016; Almada and Bernardino, 2017).

5. References

Almada, G.V. de M.B., Bernardino, A.F., 2017. Conservation of deep-sea ecosystems within offshore oil fields on the Brazilian margin, SW Atlantic. Biol. Conserv. 206, 92–101. https://doi.org/10.1016/j.biocon.2016.12.026

Anderson, M., Gorley, R.N., Clarke, K., 2008. PERMANOVA+ for primer: Guide to software and statistical methods, 1st ed, Plymouth: Primer-E. Primer-E Ltd, Plymouth.

Armstrong, C.W., Foley, N.S., Tinch, R., van den Hove, S., 2012. Services from the deep: Steps towards valuation of deep sea goods and services. Ecosyst. Serv. 2, 2–13. https://doi.org/10.1016/j.ecoser.2012.07.001

Ayres, M.; Ayres Junior, M; Ayres, D. L.; Santos, A. S. BioEstat 5.0: statistical applications in biological and medical research fields. Belém: MCT; IDSM; CNPq, 2007. 364 p. il. CD-ROM linked.

Baker, K.D., Wareham, V.E., Snelgrove, P.V.R., Haedrich, R.L., Fifield, D.A., Edinger, E.N., Gilkinson, K.D., 2012. Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada. Mar. Ecol. Prog. Ser. 445, 235–249. https://doi.org/10.3354/meps09448

Baldrighi, E., Giovannelli, D., D'Errico, G., Lavaleye, M., Manini, E., 2017. Exploring the Relationship between Macrofaunal Biodiversity and Ecosystem Functioning in the Deep Sea. Front. Mar. Sci. 4. https://doi.org/10.3389/fmars.2017.00198

Bernardino, A.F., Berenguer, V., Ribeiro-Ferreira, V.P., 2016. Bathymetric and regional changes in benthic macrofaunal assemblages on the deep Eastern Brazilian margin, SW Atlantic. Deep. Res. Part I Oceanogr. Res. Pap. 111, 110–120. https://doi.org/10.1016/j.dsr.2016.02.016

Bernardino, A.F., Levin, L.A., Thurber, A.R., Smith, C.R., 2012. Comparative composition, diversity and trophic ecology of sediment macrofauna at vents, seeps and organic falls. PLoS One 7. https://doi.org/10.1371/journal.pone.0033515

Bernardino, A.F., Smith, C.R., Baco, A., Altamira, I., Sumida, P.Y.G., 2010. Macrofaunal succession in sediments around kelp and wood falls in the deep NE Pacific and community overlap with other reducing habitats. Deep. Res. Part I Oceanogr. Res. Pap. 57, 708–723. https://doi.org/10.1016/j.dsr.2010.03.004

Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature. https://doi.org/10.1038/302520a0

Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Queirós, A.M., Romero-ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Colen, C. Van, Hoey, G. Van, Widdicombe, S.,

2013. A bioturbation classification of European marine infaunal invertebrates. Ecol. Evol. 3, 3958–3985. https://doi.org/10.1002/ece3.769

Bosley, K.L., Lavelle, J.W., Brodeur, R.D., Wakefield, W.W., Emmett, R.L., Baker, E.T., Rehmke, K.M., 2004. Biological and physical processes in and around Astoria submarine Canyon, Oregon, USA. J. Mar. Syst. 50, 21–37. https://doi.org/10.1016/j.jmarsys.2003.06.006

Brothers, D.S., ten Brink, U.S., Andrews, B.D., Chaytor, J.D., Twichell, D.C., 2013. Geomorphic process fingerprints in submarine canyons. Mar. Geol. 337, 53–66. https://doi.org/10.1016/j.margeo.2013.01.005

Calado, L., Gangopadhyay, A., da Silveira, I.C.A., 2006. A parametric model for the Brazil Current meanders and eddies off southeastern Brazil. Geophys. Res. Lett. 33, 1–5. https://doi.org/10.1029/2006GL026092

Canals, M., Puig, P., de Madron, X.D., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. Nature 444, 354–357. https://doi.org/10.1038/nature05271

Carney, R., 2005. Zonation of Deep Biota on Continental Margins. Oceanogr. Mar. Biol. An Annu. Rev. 43, 211–278. https://doi.org/10.1201/9781420037449.ch6

Cartes, J.E., Fanelli, E., Papiol, V., Maynou, F., 2010. Trophic relationships at intrannual spatial and temporal scales of macro and megafauna around a submarine canyon off the Catalonian coast (western Mediterranean). J. Sea Res. 63, 180–190. https://doi.org/10.1016/j.seares.2010.01.001

Cartes, J.E., Maynou, F., Fanelli, E., Romano, C., Mamouridis, V., Papiol, V., 2009. The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: Environmental gradients influencing assemblages composition and biomass trends. J. Sea Res. 61, 244–257. https://doi.org/10.1016/j.seares.2009.01.005

Carvalho, M.V.F., De Ros, L.F., Gomes, N.S., 1995. Carbonate cementation patterns and diagenetic reservoir facies in the Campos Basin cretaceous turbidites, offshore eastern Brazil. Mar. Pet. Geol. 12, 741–758. https://doi.org/10.1016/0264-8172(95)93599-Y

Chiang, C.S., Yu, H.S., 2006. Morphotectonics and incision of the Kaoping submarine canyon, SW Taiwan orogenic wedge. Geomorphology 80, 199–213. https://doi.org/10.1016/j.geomorph.2006.02.008

Clark, M.R., Rowden, A.A., Schlacher, T.A., Guinotte, J., Dunstan, P.K., Williams, A., O'Hara, T.D., Watling, L., Niklitschek, E., Tsuchida, S., 2014. Identifying Ecologically or Biologically Significant Areas (EBSA): A systematic method and its application to seamounts in the South Pacific Ocean. Ocean Coast. Manag. 91, 65–79.

https://doi.org/10.1016/j.ocecoaman.2014.01.016

Clarke, K.R., Somerfield, P.J., Airoldi, L., Warwick, R.M., 2006. Exploring interactions by second-stage community analyses. J. Exp. Mar. Bio. Ecol. 338, 179–192. https://doi.org/10.1016/j.jembe.2006.06.019

Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: An approach to statistical analysis and interpretation., 2nd ed, Primer-E Ltd. Primer-E Ltd, Plymouth. https://doi.org/1

Conlan, K.E., Currie, D.R., Dittmann, S., Sorokin, S.J., Hendrycks, E., 2015. Macrofaunal patterns in and around du couedic and bonney submarine canyons, South Australia. PLoS One 10, 1–27. https://doi.org/10.1371/journal.pone.0143921

Cordes, E.E., Cunha, M.R., Galéron, J., Mora, C., Olu-Le Roy, K., Sibuet, M., Van Gaever, S., Vanreusel, A., Levin, L.A., 2010. The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity. Mar. Ecol. 31, 51–65. https://doi.org/10.1111/j.1439-0485.2009.00334.x

Cordes, E.E., Jones, D.O.B., Schlacher, T.A., Amon, D.J., Bernardino, A.F., Brooke, S., Carney, R., DeLeo, D.M., Dunlop, K.M., Escobar-Briones, E.G., Gates, A.R., Génio, L., Gobin, J., Henry, L.-A., Herrera, S., Hoyt, S., Joye, M., Kark, S., Mestre, N.C., Metaxas, A., Pfeifer, S., Sink, K., Sweetman, A.K., Witte, U., 2016. Environmental Impacts of the Deep-Water Oil and Gas Industry: A Review to Guide Management Strategies. Front. Environ. Sci. 4. https://doi.org/10.3389/fenvs.2016.00058

Costa, P. a S., Braga, a C., Rocha, L.O.F., 2003. Reef sheries in Porto Seguro, eastern Brazilian coast. Fish. Res. 60, 577–583.

Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1998. The value of the world's ecosystem services and natural capital. Nature 387, 253–260. https://doi.org/10.1038/387253a0

Cúrdia, J., Carvalho, S., Ravara, A., Gage, J.D., Rodrigues, A.M., 2004. Deep macrobenthic communities from Nazaré Submarine Canyon (NW Portugal). Sci. Mar. 68, 171–180. https://doi.org/10.3989/scimar.2004.68s1171

Currie, D.R., Sorokin, S.J., 2014. Megabenthic biodiversity in two contrasting submarine canyons on Australia's southern continental margin. Mar. Biol. Res. 10, 97–110. https://doi.org/10.1080/17451000.2013.797586

Danovaro, R., Bianchelli, S., Gambi, C., Mea, M., Zeppilli, D., 2009. α-, β-, γ-, δ- and ε-diversity of deep-sea nematodes in canyons and open slopes of northeast Atlantic and Mediterranean margins. Mar. Ecol. Prog. Ser. 396, 197–209. https://doi.org/10.3354/meps08269

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., Gooday, A.J., 2008. Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss. Curr. Biol. 18, 1–8. https://doi.org/10.1016/j.cub.2007.11.056

Davies, A.J., Roberts, J.M., Hall-Spencer, J., 2007. Preserving deep-sea natural heritage: Emerging issues in offshore conservation and management. Biol. Conserv. 138, 299–312. https://doi.org/10.1016/j.biocon.2007.05.011

Dayton, P.K., Hessler, R.R., 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep. Res. Oceanogr. Abstr. 19. https://doi.org/10.1016/0011-7471(72)90031-9

de Almeida, N.M., Vital, H., Gomes, M.P., 2015. Morphology of submarine canyons along the continental margin of the Potiguar Basin, NE Brazil. Mar. Pet. Geol. 68, 307–324. https://doi.org/10.1016/j.marpetgeo.2015.08.035

De Léo, F.C., Pires-Vanin, A.M.S., 2006. Benthic megafauna communities under the influence of the South Atlantic Central Water intrusion onto the Brazilian SE shelf: A comparison between an upwelling and a non-upwelling ecosystem. J. Mar. Syst. 60, 268–284. https://doi.org/10.1016/j.jmarsys.2006.02.002

De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R., 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proc. R. Soc. B Biol. Sci. 277, 2783–2792. https://doi.org/10.1098/rspb.2010.0462

De Leo, F.C., Vetter, E.W., Smith, C.R., Rowden, A.A., McGranaghan, M., 2014. Spatial scale-dependent habitat heterogeneity influences submarine canyon macrofaunal abundance and diversity off the Main and Northwest Hawaiian Islands. Deep. Res. Part II Top. Stud. Oceanogr. 104, 267–290. https://doi.org/10.1016/j.dsr2.2013.06.015

Duineveld, G., Lavaleye, M., Berghuis, E., De Wilde, P., 2001. Activity and composition of the benthic fauna in the Whittard Canyon and the adjacent continental slope (NE Atlantic). Oceanol. Acta 24, 69–83. https://doi.org/10.1016/S0399-1784(00)01129-4

Dunn, D.C., Ardron, J., Bax, N., Bernal, P., Cleary, J., Cresswell, I., Donnelly, B., Dunstan, P., Gjerde, K., Johnson, D., Kaschner, K., Lascelles, B., Rice, J., Von Nordheim, H., Wood, L., Halpin, P.N., 2014. The Convention on Biological Diversity's Ecologically or Biologically Significant Areas: Origins, development, and current status. Mar. Policy 49, 137–145. https://doi.org/10.1016/j.marpol.2013.12.002

Durrieu de Madron, X., 1994. Hydrography and nepheloid structures in the Grand-Rhône canyon. Cont. Shelf Res. 14, 457–477. https://doi.org/10.1016/0278-4343(94)90098-1

Durrieu De Madron, X., Weatherly, G., 1994. Circulation, transport and bottom boundary layers of the deep currents in the Brazil Basin. J. Mar. Res. 52, 583–638. https://doi.org/10.1357/0022240943076975

Escobar Briones, E., Estrada Santillán, E.L., Legendre, P., 2008. Macrofaunal density and biomass in the Campeche Canyon, Southwestern Gulf of Mexico. Deep. Res. Part II Top. Stud. Oceanogr. 55, 2679–2685. https://doi.org/10.1016/j.dsr2.2008.07.017

Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J., Allcock, A.L., Davies, J.S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V.A.I., Macmillan-Lawler, M., Martín, J., Menot, L., Nizinski, M., Puig, P., Rowden, A.A., Sanchez, F., Van den Beld, I.M.J., 2017. Ecological Role of Submarine Canyons and Need for Canyon Conservation: A Review. Front. Mar. Sci. 4, 1–26. https://doi.org/10.3389/fmars.2017.00005

Fernandez-Arcaya, U., Rotllant, G., Ramirez-Llodra, E., Recasens, L., Aguzzi, J., Flexas, M.M., Sanchez-Vidal, A., López-Fernández, P., García, J.A., Company, J.B., 2013. Reproductive biology and recruitment of the deep-sea fish community from the NW Mediterranean continental margin. Prog. Oceanogr. 118, 222–234. https://doi.org/10.1016/j.pocean.2013.07.019

Foley, N.S., van Rensburg, T.M., Armstrong, C.W., 2010. The ecological and economic value of cold-water coral ecosystems. Ocean Coast. Manag. 53, 313–326. https://doi.org/10.1016/j.ocecoaman.2010.04.009

Gage, J.D., 2001. Deep-sea benthic community and environmental impact assessment at the Atlantic Frontier. Cont. Shelf Res. 21, 957–986.

Gage, J.D., Lamont, P. a, Tyler, P. a, 1995. Deep-Sea Macrobenthic Communities at Contrasting Sites Off Portugal, Preliminary-Results .2. Spatial-Dispersion. Int. Rev. Der Gesamten Hydrobiol. 80, 251–265. https://doi.org/10.1002/iroh.19950800211

Gambi, C., Danovaro, R., 2016. Biodiversity and life strategies of deep-sea meiofauna and nematode assemblages in the Whittard Canyon (Celtic margin, NE Atlantic Ocean). Deep. Res. Part I Oceanogr. Res. Pap. 108, 13–22. https://doi.org/10.1016/j.dsr.2015.12.001

Garcia, R., Koho, K.A., De Stigter, H.C., Epping, E., Koning, E., Thomsen, L., 2007. Distribution of meiobenthos in the Nazar?? canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. Mar. Ecol. Prog. Ser. 340, 207–220. https://doi.org/10.3354/meps340207

Gardner, W.D., 1989. Baltimore Canyon as a modern conduit of sediment to the deep sea. Deep Sea Res. Part A, Oceanogr. Res. Pap. 36, 323–358. https://doi.org/10.1016/0198-0149(89)90041-1

Gerino, M., Stora, G., Weber, O., 1999. Evidence of bioturbation in the Cap-Ferret Canyon in the deep northeastern Atlantic. Deep. Res. Part II Top. Stud. Oceanogr. 46, 2289–2307. https://doi.org/10.1016/S0967-0645(99)00063-6

Gomes, L.E. de O., Correa, L.B., Sá, F., Neto, R.R., Bernardino, A.F., 2017. The impacts of the

Samarco mine tailing spill on the Rio Doce estuary, Eastern Brazil. Mar. Pollut. Bull. 0–1. https://doi.org/10.1016/j.marpolbul.2017.04.056

Green, A.N., Goff, J.A., Uken, R., 2007. Geomorphological evidence for upslope canyon-forming processes on the northern KwaZulu-Natal shelf, SW Indian Ocean, South Africa. Geo-Marine Lett. 27, 399–409. https://doi.org/10.1007/s00367-007-0082-2

Greene, C.H., Wiebe, P.H., Burczynski, J., Youngbluth, M.J., 1988. Acoustical Detection of High-Density Krill Demersal Layers in the Submarine Canyons off Georges Bank. Science 241, 359–361. https://doi.org/10.1126/science.241.4863.359

Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S., Winder, M., 2017. The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. Glob. Chang. Biol. 23, 2179–2196. https://doi.org/10.1111/gcb.13642

Haimovici, M., Gomes Fischer, L., Wongtschowski, C.L.D.B.S.R., Avila Bernardes, R., Aguiar dos Santos, R., 2009. Biomass and fishing potential yield of demersal resources from the outer shelf and upper slope of southern Brazil. Lat. Am. J. Aquat. Res. 37, 395–408. https://doi.org/10.3856/vol37-issue3-fulltext-10

Hargrave, B.T., Kostylev, V.E., Hawkins, C.M., 2004. Benthic epifauna assemblages, biomass and respiration in The Gully region on the Scotian Shelf, NW Atlantic Ocean. Mar. Ecol. Prog. Ser. 270, 55–70. https://doi.org/10.3354/meps270055

Harris, P.T., Macmillan-Lawler, M., Rupp, J., Baker, E.K., 2014. Geomorphology of the oceans. Mar. Geol. 352, 4–24. https://doi.org/10.1016/j.margeo.2014.01.011

Harris, P.T., Whiteway, T., 2011. Global distribution of large submarine canyons: Geomorphic differences between active and passive continental margins. Mar. Geol. 285, 69–86. https://doi.org/10.1016/j.margeo.2011.05.008

Hess, S., Jorissen, F.J., Venet, V., Abu-Zied, R., 2005. Benthic Foraminiferal Recovery After Recent Turbidite Deposition in Cap Breton Canyon, Bay of Biscay. J. Foraminifer. Res. 35, 114–129. https://doi.org/10.2113/35.2.114

Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep-sea. Deep. Res. 14, 65–78. https://doi.org/10.1016/0011-7471(67)90029-0

Houston, K.A., Haedrich, R.L., 1984. Abundance and biomass of macrobenthos in the vicinity of Carson Submarine Canyon, northwest Atlantic Ocean. Mar. Biol. 82, 301–305. https://doi.org/10.1007/BF00392410

Huang, Z., Nichol, S.L., Harris, P.T., Caley, M.J., 2014. Classification of submarine canyons of the Australian continental margin. Mar. Geol. 357, 362–383. https://doi.org/10.1016/j.margeo.2014.07.007

Huang, Z., Schlacher, T.A., Nichol, S., Williams, A., Althaus, F., Kloser, R., 2017. A conceptual surrogacy framework to evaluate the habitat potential of submarine canyons. Prog. Oceanogr. https://doi.org/10.1016/j.pocean.2017.11.007

Hughes, D.J., Gage, J.D., 2004. Benthic metazoan biomass, community structure and bioturbation at three contrasting deep-water sites on the northwest European continental margin. Prog. Oceanogr. 63, 29–55. https://doi.org/10.1016/j.pocean.2004.09.002

Hurlbert, S.H., 1971. The Nonconcept of Species Diversity : A Critique and Alternative Parameters. Ecol. Soc. Am. 52, 577–586.

Ingels, J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A., 2009. Nematode diversity and its relation to the quantity and quality of sedimentary organic matter in the deep Nazar?? Canyon, Western Iberian Margin. Deep. Res. Part I Oceanogr. Res. Pap. 56, 1521–1539. https://doi.org/10.1016/j.dsr.2009.04.010

Jobstvogt, N., Townsend, M., Witte, U., Hanley, N., 2014. How can we identify and communicate the ecological value of deep-sea ecosystem services? PLoS One 9, 1–11. https://doi.org/10.1371/journal.pone.0100646

Johnson, K.S., Paull, C.K., Barry, J.P., Chavez, F.P., 2001. A decadal record of underflows from a coastal river into the deep sea. Geology 29, 1019–1022. https://doi.org/10.1130/0091-7613(2001)029<1019:ADROUF>2.0.CO;2

Kiel, S., Goedert, J.L., 2006. a Wood-Fall Association From Late Eocene Deep-Water Sediments of Washington State, Usa. Palaios 21, 548–556. https://doi.org/10.2110/palo.2005.p05-086r

Kineke, G.C., Woolfe, K.J., Kuehl, S.A., Milliman, J.D., Dellapenna, T.M., Purdon, R.G., 2000. Sediment export from the Sepik River, Papua New Guinea: Evidence for a divergent sediment plume. Cont. Shelf Res. 20, 2239–2266. https://doi.org/10.1016/S0278-4343(00)00069-8

Krö Ncke, I., Tü Rkay, M., Fiege, D., 2003. Macrofauna Communities in the Eastern Mediterranean Deep Sea. Mar. Ecol. 24, 193–216. https://doi.org/10.1046/j.0173-9565.2003.00825.x

Lastras, G., Canals, M., Urgeles, R., Amblas, D., Ivanov, M., Droz, L., Dennielou, B., Fabrés, J., Schoolmeester, T., Akhmetzhanov, A., Orange, D., García-García, A., 2007. A walk down the Cap de Creus canyon, Northwestern Mediterranean Sea: Recent processes inferred from morphology and sediment bedforms. Mar. Geol. 246, 176–192.

https://doi.org/10.1016/j.margeo.2007.09.002

Lavrado, H.P., Omena, E.P., Bernardino, A.F., 2017. Macrofauna bentônica do talude continental e cânions da bacia de campos, in: Ambiente Bentônico: Caracterização Ambiental Regional Da Bacia de Campos, Atlântico Sudoeste. Elsevier Ltd., Rio de Janeiro, pp. 259–306. https://doi.org/10.1016/B978-85-352-7263-5.50009-6

Leduc, D., Rowden, A.A., Clark, M.R., Bowden, D.A., Thurber, A.R., 2016. Limited differences among habitats in deep-sea macro-infaunal communities off New Zealand: implications for their vulnerability to anthropogenic disturbance. Mar. Ecol. 37, 845–866. https://doi.org/10.1111/maec.12363

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annu. Rev. Ecol. Evol. Syst. 32, 51–93.

Levin, L.A., Sibuet, M., 2012. Understanding Continental Margin Biodiversity: A New Imperative. Ann. Rev. Mar. Sci. 4, 79–112. https://doi.org/doi:10.1146/annurev-marine-120709-142714

Louzao, M., Anadón, N., Arrontes, J., Álvarez-Claudio, C., Fuente, D.M., Ocharan, F., Anadón, A., Acuña, J.L., 2010. Historical macrobenthic community assemblages in the Avilés Canyon, N Iberian Shelf: Baseline biodiversity information for a marine protected area. J. Mar. Syst. 80, 47–56. https://doi.org/10.1016/j.jmarsys.2009.09.006

Magurran, A.E., 2004. Introduction: measurement of (biological) diversity, in: Measuring Biological Diversity. Blackwell Science Ltd, Oxford, pp. 1–17. https://doi.org/10.2989/16085910409503825

Masson, D.G., Huvenne, V.A.I., de Stigter, H.C., Wolff, G.A., Kiriakoulakis, K., Arzola, R.G., Blackbird, S., 2010. Efficient burial of carbon in a submarine canyon. Geology 38, 831–834. https://doi.org/10.1130/G30895.1

Maurer, D., Robertson, G., Gerlinger, T., 1995. Community Structure of Soft-Bottom Macrobenthos of the Newport Submarine Canyon, California. Mar. Ecol. 16, 57–72. https://doi.org/10.1111/j.1439-0485.1995.tb00394.x

Maurer, D., Robertson, G., Gerlinger, T., 1994. Comparison of community structure of soft-bottom macrobenthos of the Newport Submarine Canyon, California and the adjoining shelf. Int. Rev. Der Gesamten Hydrobiol. 79, 591.

Mcclain, C.R., Barry, J.P., 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. Ecol. Soc. Am. 91, 964–976. https://doi.org/10.1890/09-0087.1

Mcclain, C.R., Schlacher, T.A., 2015. On some hypotheses of diversity of animal life at great

depths on the sea floor. Mar. Ecol. 36, 849–872. https://doi.org/10.1111/maec.12288

Melo, R. de S., Crispim, M.C., Lima, E.R.V. de, 2005. O turismo em ambientes recifais : em busca da transição para a sustentabilidade. Cad. Virtual Tur. 5, 34–42.

Mohriak, W., 2014. Birth and Development of Continental Margin Basins : Analogies from the South Atlantic , North Atlantic , and the Red Sea *. Search Discov. Artic. 41502.

Mohriak, W.U., 2003. Sedimentary basins of the Brazilian continental margin. In: Bizzi, L.A., Schobbenhaus, C., Vidotti, R.M., Gonçalves, J.H. (Eds.), Geologia, Tectônica e Recursos Minerais do Brasil. CPRM, Brasilia, pp. 87–94.

Moors-Murphy, H.B., 2014. Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review. Deep. Res. Part II Top. Stud. Oceanogr. 104, 6–19. https://doi.org/10.1016/j.dsr2.2013.12.016

Narayanaswamy, B.E., Nickell, T.D., Gage, J.D., 2003. Appropriate levels of taxonomic discrimination in deep-sea studies: Species vs family. Mar. Ecol. Prog. Ser. 257, 59–68. https://doi.org/10.3354/meps257059

Olavo, G., Costa, P.A.S., Martins, A.S., Ferreira, B.P., 2011. Shelf-edge reefs as priority areas for conservation of reef fish diversity in the tropical Atlantic. Aquat. Conserv. Mar. Freshw. Ecosyst. 21, 199–209. https://doi.org/10.1002/aqc.1174

Orange, D.L., McAdoo, B.G., Moore, J.C., Tobin, H., Screaton, E., Chezar, H., Lee, H., Reid, M., Vail, R., 1997. Headless submarine canyons and fluid flow on the toe of the Cascadia accretionary complex. Basin Res. 9, 303–312. https://doi.org/10.1046/j.1365-2117.1997.00045.x

Palanques, A., El Khatab, M., Puig, P., Masqué, P., Sánchez-Cabeza, J.A., Isla, E., 2005. Downward particle fluxes in the Guadiaro submarine canyon depositional system (north-western Alboran Sea), a river flood dominated system. Mar. Geol. 220, 23–40. https://doi.org/10.1016/j.margeo.2005.07.004

Paterson, G.L.J., Glover, A.G., Cunha, M.R., Neal, L., de Stigter, H.C., Kiriakoulakis, K., Billett, D.S.M., Wolff, G.A., Tiago, A., Ravara, A., Lamont, P., Tyler, P., 2011. Disturbance, productivity and diversity in deep-sea canyons: A worm's eye view. Deep. Res. Part II Top. Stud. Oceanogr. 58, 2448–2460. https://doi.org/10.1016/j.dsr2.2011.04.008

Piper, D.J.W., Morrison, M.L., 1999. The sequence of events around the epicentre of the 1929 GrandBanks earthquake: initiation of debris ⁻ows and turbiditycurrent inferred from sidescan sonar. Sedimentology 46, 79–97.

Popescu, I., Lericolais, G., Panin, N., Normand, A., Dinu, C., Le Drezen, E., 2004. The Danube submarine canyon (Black Sea): Morphology and sedimentary processes. Mar. Geol. 206,

249–265. https://doi.org/10.1016/j.margeo.2004.03.003

Pratson, L.F., Coakley, B.J., 1996. A model for the headward erosion of submarine canyons induced by downslope-eroding sediment flows. Bull. Geol. Soc. Am. 108, 225–234. https://doi.org/10.1130/0016-7606(1996)108<0225:AMFTHE>2.3.CO;2

Pratson, L.F., Ryan, W.B.F., Mountain, G.S., Twichell, D.C., 1994. Submarine canyon initiation by downslope-eroding sediment flows: evidence in late Cenozoic strata on the New Jersey continental slope. Geol. Soc. Am. Bull. 106, 395–412. https://doi.org/10.1130/0016-7606(1994)106<0395:SCIBDE>2.3.CO;2

Puga-Bernabéu, Á., Webster, J.M., Beaman, R.J., Guilbaud, V., 2011. Morphology and controls on the evolution of a mixed carbonate-siliciclastic submarine canyon system, Great Barrier Reef margin, north-eastern Australia. Mar. Geol. 289, 100–116. https://doi.org/10.1016/j.margeo.2011.09.013

Puig, P., Palanques, A., 1998. Nepheloid structure and hydrographic control on the Barcelona continental margin, northwestern Mediterranean. Mar. Geol. 149, 39–54. https://doi.org/10.1016/S0025-3227(98)00037-1

Puig, P., Palanques, A., Martín, J., 2014. Contemporary Sediment-Transport Processes in Submarine Canyons. Ann. Rev. Mar. Sci. 6, 53–77. https://doi.org/10.1146/annurev-marine-010213-135037

Pusceddu, A., Mea, M., Canals, M., Heussner, S., Durrieu De Madron, X., Sanchez-Vidal, A., Bianchelli, S., Corinaldesi, C., Dell'Anno, A., Thomsen, L., Danovaro, R., 2013. Major consequences of an intense dense shelf water cascading event on deep-sea benthic trophic conditions and meiofaunal biodiversity. Biogeosciences 10, 2659–2670. https://doi.org/10.5194/bg-10-2659-2013

Quattrini, A.M., Nizinski, M.S., Chaytor, J.D., Demopoulos, A.W.J., Roark, E.B., France, S.C., Moore, J.A., Heyl, T., Auster, P.J., Kinlan, B., Ruppel, C., Elliott, K.P., Kennedy, B.R.C., Lobecker, E., Skarke, A., Shank, T.M., 2015. Exploration of the canyon-incised continental margin of the northeastern United States reveals dynamic habitats and diverse communities. PLoS One 10, 1–32. https://doi.org/10.1371/journal.pone.0139904

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B.E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010. Deep, diverse and definitely different: Unique attributes of the world's largest ecosystem. Biogeosciences 7, 2851–2899. https://doi.org/10.5194/bg-7-2851-2010

Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., van Dover, C.L., 2011. Man and the last great

wilderness: Human impact on the deep sea. PLoS One 6.
https://doi.org/10.1371/journal.pone.0022588

Robert, K., Jones, D.O.B., Tyler, P.A., Van Rooij, D., Huvenne, V.A.I., 2015. Finding the
hotspots within a biodiversity hotspot: Fine-scale biological predictions within a submarine
canyon using high-resolution acoustic mapping techniques. Mar. Ecol. 36, 1256–1276.
https://doi.org/10.1111/maec.12228

Romano, C., Coenjaerts, J., Flexas, M.M., Zúñiga, D., Vanreusel, A., Company, J.B., Martin, D.,
2013. Spatial and temporal variability of meiobenthic density in the Blanes submarine
canyon (NW Mediterranean). Prog. Oceanogr. 118, 144–158.
https://doi.org/10.1016/j.pocean.2013.07.026

Romano, C., Flexas, M.M., Segura, M., Román, S., Bahamon, N., Gili, J.M., Sanchez-Vidal, A.,
Martin, D., 2017. Canyon effect and seasonal variability of deep-sea organisms in the NW
Mediterranean: Synchronous, year-long captures of "swimmers" from near-bottom
sediment traps in a submarine canyon and its adjacent open slope. Deep. Res. Part I
Oceanogr. Res. Pap. 129, 99–115. https://doi.org/10.1016/j.dsr.2017.10.002

Rowe, G.F., Polloni, P.T., Horner, S.G., 1974. Benthic biomass estimates from the northwestern
Atlantic Ocean and the northern Gulf of Mexico. Deep Sea Res. Oceanogr. Abstr. 21,
641–650.

Rowe, G.T., Polloni, P.T., Haedrich, R.L., 1982. The deep-sea macrobenthos on the continental
margin of the northwest Atlantic Ocean. Deep Sea Res. Part A, Oceanogr. Res. Pap. 29,
257–278. https://doi.org/10.1016/0198-0149(82)90113-3

Sardà, F., Cartes, J.E., Company, J.B., 1994. Spatio-temporal variations in megabenthos
abundance in three different habitats of the Catalan deep-sea (Western Mediterranean).
Mar. Biol. 120, 211–219. https://doi.org/10.1007/BF00349681

Schmid, C., Schäfer, H., Zenk, W., Podestá, G., 1995. The Vitória Eddy and Its Relation to the
Brazil Current. J. Phys. Oceanogr. https://doi.org/10.1175/1520-
0485(1995)025<2532:TVEAIR>2.0.CO;2

Schmidt, S., de Stigter, H.C., van Weering, T.C.E., 2001. Enhanced short-term sediment
deposition within the Nazare Canyon, North-East Atlantic. Mar. Geol. 173, 55–67.
https://doi.org/10.1016/S0025-3227(00)00163-8

Simon, T., Pinheiro, H.T., Moura, R.L., Carvalho-Filho, A., Rocha, L.A., Martins, A.S., Mazzei,
E., Francini-Filho, R.B., Amado-Filho, G.M., Joyeux, J.C., 2016. Mesophotic fishes of the
Abrolhos Shelf, the largest reef ecosystem in the South Atlantic. J. Fish Biol. 89, 990–
1001. https://doi.org/10.1111/jfb.12967

Skliris, N., Djenidi, S., 2006. Plankton dynamics controlled by hydrodynamic processes near a

submarine canyon off NW corsican coast: A numerical modelling study. Cont. Shelf Res. 26, 1336–1358. https://doi.org/10.1016/j.csr.2006.05.004

Skropeta, D., Wei, L., 2014. Recent advances in deep-sea natural products. Nat. Prod. Rep. 31, 999–1025. https://doi.org/10.1039/C3NP70118B

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 Ecol. Evol. 23, 518–528. https://doi.org/10.1016/j.tree.2008.05.002

Soh, W., Tokuyama, H., 2002. Rejuvenation of submarine canyon associated with ridge subduction, Tenryu Canyon, off Tokai, central Japan. Mar. Geol. 187, 203–220. https://doi.org/10.1016/S0025-3227(02)00267-0

Stuart, C.T., Rex, M.A., 2009. Bathymetric patterns of deep-sea gastropod species diversity in 10 basins of the Atlantic Ocean and Norwegian Sea. Mar. Ecol. 30, 164–180. https://doi.org/10.1111/j.1439-0485.2008.00269.x

Tesi, T., Puig, P., Palanques, A., Goñi, M.A., 2010. Lateral advection of organic matter in cascading-dominated submarine canyons. Prog. Oceanogr. 84, 185–203. https://doi.org/10.1016/j.pocean.2009.10.004

Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J., Hansman, R.L., 2014. Ecosystem function and services provided by the deep sea. Biogeosciences 11, 3941–3963. https://doi.org/10.5194/bg-11-3941-2014

Tyler, P., Amaro, T., Arzola, R., Cunha, M., De Stigter, H., Gooday, A., Huvenne, V., Ingels, J., 2009. Europe' s Grand Canyon: Nazaré Submarine. Oceanography 22, 52–63. https://doi.org/10.5670/oceanog.2009.05

Van Oevelen, D., Soetaert, K., Garcia, R., de Stigter, H.C., Cunha, M.R., Pusceddu, A., Danovaro, R., 2011. Canyon conditions impact carbon flows in food webs of three sections of the Nazaré canyon. Deep. Res. Part II Top. Stud. Oceanogr. 58, 2461–2476. https://doi.org/10.1016/j.dsr2.2011.04.009

Vetter, E.W., 1995. Detritus-based patches of high secondary production in the nearshore benthos. Mar. Ecol. Prog. Ser. 120, 251–262. https://doi.org/10.3354/meps120251

Vetter, E.W., 1994. Hotspots of benthic production. Nature 372, 47–47. https://doi.org/10.1038/372047a0

Vetter, E.W., Dayton, P.K., 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. Mar. Ecol. Prog. Ser. 186, 137–148. https://doi.org/10.3354/meps186137

Vetter, E.W., Dayton, P.K., 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep. Res. Part II Top. Stud. Oceanogr. 45, 25–54. https://doi.org/10.1016/S0967-0645(97)00048-9

Vetter, E.W., Smith, C.R., De Leo, F.C., 2010. Hawaiian hotspots: Enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. Mar. Ecol. 31, 183–199. https://doi.org/10.1111/j.1439-0485.2009.00351.x

Viana, A.R., Faugeres, J.C., Kowsmann, R.O., Lima, J.A.M., Caddah, L.F.G., Rizzo, J.G., 1998. Hydrology, morphology and sedimentology of the Campos continental margin, offshore Brazil. Sediment. Geol. 115, 133–157. https://doi.org/10.1016/S0037-0738(97)00090-0

Williams, A., Bax, N.J., Kloser, R.J., Althaus, F., Barker, B., Keith, G., 2009. Australia's deep-water reserve network: Implications of false homogeneity for classifying abiotic surrogates of biodiversity. ICES J. Mar. Sci. 66, 214–224. https://doi.org/10.1093/icesjms/fsn189

Wolff, T., 1979. Macrofaunal utilization of plant remains in the deep sea. Sarsia 64, 117–136. https://doi.org/10.1080/00364827.1979.10411373

Xu, J.P., 2011. Measuring currents in submarine canyons: Technological and scientific progress in the past 30 years. Geosphere 7, 868–876. https://doi.org/10.1130/GES00640.1

Zar, J.H., 2010. Biostatistical Analysis. Prentica Hall, New Jersey.